Assessment of the Impacts Associated with the Harvesting of Marine Benthic Invertebrates for Use as Bait by Recreational Anglers

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Objectives

1. Assess the ecological impacts associated with commercial and recreational harvesting of yabbies and bloodworms on other components of the ecosystem
2. Assess the impacts of bait-harvesting activities on the sustainability of populations of yabbies (*Trypaea australiensis*) and bloodworms (*Marphysa* sp.);
3. Develop a population assessment technique for yabbies and bloodworms;
4. Determine levels of recruitment of these species and assess whether harvesting affects recruitment;
5. Obtain estimates of the recreational harvest of these species

Non Technical Summary:

The harvesting of invertebrate animals for use as bait for fishing is a common practice in Australia but there is little information on whether this activity causes damage to, or loss of, the intertidal habitats in which it occurs. Areas of seagrass and mudflat are regularly dug over by recreational and commercial harvesters in search of worms, crabs, yabbies (ghost shrimp) and other animals, but these same habitats are widely recognised as being important for supporting and sustaining coastal fisheries resources. This project focussed on assessing the damage to intertidal habitats caused by bait-harvesting but the results are more generally applicable to understanding the implications of other sources of damage that may occur (e.g. development of nearshore areas, dredging, tourism). An understanding of the cause-and-effect relationships between damage to key intertidal habitats and effects on the sustainability of fisheries resources is needed if the effects of developmental degradation are to be managed to minimise the adverse impacts on Australia's fisheries resources. The first step in any such assessment is to identify how damage to these habitats affects the plants and animals that live there.

The magnitude of the recreational and commercial catch of yabbies (*Trypaea australiensis* (also known as ghost shrimp or nippers) and bloodworms (*Marphysa* sp.) was assessed through a combination of creel and observational surveys (recreational catch) and analysis of log-book data (commercial catch) for the SE

Queensland region. Although recreational harvesting of these bait species occurs throughout most of the state, commercial activities tend to be centered in the Moreton and Hervey Bay regions. Since the establishment of a catch reporting system in 1997, the commercial catch of yabbies in SE Queensland has remained above one million individuals per annum, with the areas around the Southport Broadwater and Jumpinpin accounting for the largest proportion of the catch. Many areas used by commercial harvesters were only harvested occasionally or returned small numbers of animals. The diffuse nature of the recreational fishery for yabbies made it difficult to obtain detailed information on catch in this sector. Yabbies can be harvested from many areas on the foreshore where there is intertidal sand or mud. Even areas known to be popular spots for collecting bait were often only visited irregularly and it proved too expensive to have teams attempting to monitor these sites over any length of time. Recreational fishers participating in "commercialised" fishing competitions (such as the Stradbroke Island Classic) removed considerable numbers of yabbies in relatively short periods of time, often from a restricted area on the shore, close to the base for launching the boats used in the competition. Other animals, including crabs, shrimp and prawns were incidentally caught during the collection of yabbies.

The Moreton Bay Zoning Plan restricts commercial harvesting of worms to four plots on Fisherman Islands. The commercial catch of bloodworms has been greater than one million worms per annum from these commercial plots since about 1993, with no indication of any decline in catch over this period, although CPUE tended to be greater in winter and spring than summer and autumn, probably related to the extent of the low tides available during the day. Recreational harvesting of bloodworms tended to be restricted to areas of the foreshore with easy access to intertidal seagrass where the worms are found. A focussed study in one of the more popular areas, Wynnum-Manly, indicated that nearly 62,000 worms were taken from this one area in about 10 months, suggesting that the total recreational catch within Moreton Bay could be substantial. Importantly, it was found that few recreational harvesters adhered to relevant regulations, with more than 50% of groups exceeding the bag-limit, failing to replace dug seagrass and removing prohibited species from the area.

Harvesting of yabbies caused significant impacts on the abundance and diversity of several groups of animals (e.g. crabs and worms) living in the sediments, although these effects tended to be less widespread than have been reported from studies overseas. The main impact of harvesting of yabbies was to cause a change in the levels of patchiness in the distribution of animals which has implications for the capacity of these assemblages to cope with other forms of disturbance that may simultaneously impact on them (e.g. pollution, sedimentation). The populations of yabbies were, however, remarkably resilient to harvesting, with no detectable impact on populations under sustained harvesting at levels similar to those resulting from recreational and commercial operations. The decline in the abundance of crabs and worms did, however, have flow-on effects on the foraging of migratory shorebirds that share the same intertidal areas as humans harvesting bait. The feeding behaviour and abundance of bar-tailed godwits, annual visitors to Moreton bay from their Arctic breeding grounds, was significantly reduced in areas where harvesting was occurring. At present, the affected birds simply relocated to other areas but in the future, if the total available habitat declined through other human activities, impacts from bait-harvesting could contribute to a decline in the overall value of the region as an internationally recognised wetland for migratory birds. In contrast, foraging of

Far-eastern curlews, a threatened species of migratory bird, was not affected by harvesting of yabbies. In fact, the birds remove a far greater proportion of yabbies from an area than occurs under current levels of harvesting. Estimates of stock size of yabbies based on counts of their burrow holes proved to be unreliable. A method for assessing stock sizes, based around standardised pumping of a set number of burrows, was developed and tested and proved reliable and repeatable.

The effects of commercial harvesting of bloodworms in the intertidal seagrass beds on Fisherman Islands was examined by (i) monitoring the recovery of damage to the habitats and (ii) the populations of animals living in and on the sediments. Commercial harvesters work in small teams and dig a plot of about 70-90 m^2 in the intertidal seagrass beds. Surrounding the plot, the harvesters construct a raised wall which prevents rapid inundation of the pit by the rising tide. These commercial operations cause marked and immediate changes to the seagrass habitat: sediments become more compacted as gravel and shell is brought to the surface, raised walls lead to changes in water flow and sedimentation and seagrass is removed and/or buried as the mud is dug over. Many of the changes were still evident after 18-20 months after a pit was dug. Despite these effects, the area remained dominated by the same species of seagrass and seagrass biomass was not significantly changed over this time period. Commercial operations resulted in immediate reductions in the abundance and diversity of animals living in the sediments in and around the pits and these were still evident after 4 months. After 12 months, there were no apparent differences in the abundance of animals in the areas dug over and nearby reference areas, but a large proportion of the Fisherman Islands area was affected by a bloom of toxic fireweed (*Lyngbya majuscula*). This caused widespread mortality of animals in and on the surface of the sediment, reducing the overall abundance of animals by nearly 50% and making any specific impacts from bait-harvesting difficult to detect. Very few juvenile (recruits) bloodworms were ever found in the samples from commercial pits and reference areas, or in other intertidal seagrass beds around the Bay. It has previously been suggested that the worms may recruit to subtidal seagrass beds, then move into the intertidal areas as they grow, but this was not assessed due to logistical difficulties sampling in the subtidal areas. This also precluded obtaining information on the effects of harvesting on recruitment of bloodworms, but impacts seem unlikely if the animals are recruiting to entirely different areas from those being harvested.

Experimental disturbance to intertidal seagrass beds simulated the effects of small-scale harvesting operations such as those associated with recreational worm harvesting. These experiments were designed to distinguish between effects due primarily to removal of the seagrass (loss of habitat) or indirect effects from disturbance to the sediments. The results indicated there were widespread impacts on the animals living in the sediments, one month after disturbance, of a similar nature to those associated with commercial pits that were one month old. Importantly, most of the effects were associated with the loss of the seagrass itself, rather than the associated changes to the sediments, suggesting that the replacement of seagrass after commercial and recreational harvesting (a requirement of the Fisheries Act and the Moreton Bay Zoning Plan) would facilitate greatly the recovery of areas that had been dug over and, therefore, the long-term sustainability of harvesting in the region. As noted above though, few recreational fishers bother replacing seagrass after digging worms and it was also apparent that at least some commercial operators also ignored this requirement. Furthermore, the responses of the animals to impacts on the seagrass were variable and could not easily be predicted from a simple knowledge that the vegetation had been affected, or had recovered. Monitoring of seagrass does not provide a detailed understanding of how human activities affect important aspects of ecosystems, such as biodiversity and links to fisheries resources, despite such monitoring being widely accepted by community groups and government agencies.

OUTCOMES ACHIEVED

The outputs of this project are most likely to lead to improved outcomes in natural resource management benefiting natural resource managers, recreational and commercial harvesters and the general public.

Outputs from this project were used by the Queensland State Government to modify the area where recreational bloodworm harvesting was legally able to occur along the Wynnum-Manly foreshore.

There is a statutory review of the Moreton Bay Zoning Plan in 2004 and the outputs of this project are timely and will be valuable for reviewing the regulatory provisions in this Plan that pertain to bait harvesting. In particular, the information on the current low levels of compliance by recreational bloodworm harvesters with existing regulations should be used to review these regulations and make changes to educational material that is distributed to support the new Plan, and more effective enforcement of regulations.

The outputs of the project will allow commercial bloodworm harvesters to use objective and independent information to support the continuation of their activity in an area of high conservation value.

The outputs of this project also have a substantial public good benefit in that they directly provide information on the ecological functioning of intertidal habitats, including the use of these habitats by migratory shorebirds of national and international conservation significance.

KEYWORDS: **bait harvesting, recreational fishing, environmental impacts, disturbance, SE Queensland, Moreton Bay**

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Background

Recreational Fishing and Bait-Harvesting: Compared with the situation for commercial fisheries, little is known about impacts arising from the recreational fishing sector. Work that has been done has focussed largely on the magnitude of the harvest of target or retained species (e.g. McGlennon, 1992; West & Gordon, 1994; Steffe et al., 1996). There have been few studies which have estimated the size of the recreational bait-harvest, but these suggest the magnitude of this harvest is considerable. Steffe et al. (1997) estimated that recreational anglers spent 36,967 hours per annum in collecting bait in northern NSW.

Over 300,000 recreational fishers utilise the Moreton Bay region annually, with expectations that this number will continue to increase in line with increasing population growth and tourism. Additionally, at least 70 fishing clubs, with a membership of >6000 persons, regularly fish within the Bay. Most of these anglers rely on bait, live or processed, during their outings, leading to substantial recreational and commercial harvesting of invertebrates within the Moreton Bay region (QFMA, 1997a). Several organisms, including bloodworms (*Marphysa* sp.) shellfish, soldier crabs (*Mictyris* sp.) and yabbies (*Trypaea australiensis*) are harvested by recreational anglers in the Moreton Bay region (Quinn, 1992).

There are approximately 40 commercial operators in the bait-harvesting fishery for bloodworms in the Moreton Bay region, and a smaller fishery in Hervey Bay. This fishery has recently been extended to interstate and overseas markets (QFMA, 1997a), suggesting the potential for increased pressure on the resource. The commercial catch for 1996/97 was 1,181,497 bloodworms from

Moreton Bay and 49,323 from Hervey Bay (QFMA logbook returns). There are no estimates of the size of the recreational harvest of bloodworms available.

There is also a substantial commercial and recreational fishery for yabbies in Moreton Bay. Commercial operators harvested 314,940 yabbies in 1993/94 but this had increased to 1,210,828 in 1996/97 (QFMA logbook returns). Again, there are no published estimates of the magnitude of the recreational catch. Pilot studies by one of my students have shown, however, that small-group harvesting events (~12 recreational fishers) can result in catches >1000 yabbies over a few hours (Sturkie, 1996). In a survey of 2141 recreational fishers, 84% of respondents used bait on the day surveyed, with up to 60% of people using yabbies having collected their own (Constable, 1995). No estimates of the size of individuals catches were provided in that study. Conservative extrapolations from these data would, however, indicate a substantial resource is being accessed within the SE Queensland region, and elsewhere in Australia. Reliable estimates of the magnitude of commercial nor recreational catches of yabbies or bloodworms are not readily available for most other parts of the Queensland coast (QFMA, 1996a).

Whereas the impacts associated with the commercial fishing sector are increasingly being considered in terms of the effects on target organisms, the by-catch, and other components of the ecosystem, there has been a tendency only to consider the impacts of recreational fishing in terms of the magnitude of the harvest. Impacts arising from other activities, in particular, the collection of bait by commercial and recreational operators to support the recreational fishing sector, have not been considered in any systematic manner.

Various direct and indirect effects can arise from bait-harvesting activities in intertidal areas: (i) direct effects on the populations of the species being exploited (ii) indirect effects on other species which interact with the exploited species (e.g. use them as prey); (iii) direct effects on other species in the habitats which are incidentally killed or injured during harvesting (i.e. by-catch); and (iv) direct and indirect effects due to habitat damage arising from harvesting.

Nursery Habitats: Direct damage to estuarine habitats caused by bait-harvesting has implications for the sustainability of not only the exploited species, but for commercially and recreationally important finfish and crustaceans which are dependent on these areas as feeding and nursery grounds. Extensive research has demonstrated the close relationship between the distribution of many commercially important groups such as prawns and fish and the distribution of specific features of the environment such as mangroves and seagrass habitats. Crabs, prawns and finfish use these habitats as feeding and nursery areas and these "fisheries habitats" are considered critical to sustaining the species that support inshore finfish and trawl fisheries (e.g. QFMA, 1996a, b). Although these habitats have been permanently closed to the trawl fishery, damage to habitats caused by bait-harvesting has not been managed in any systematic manner. Digging for bloodworms occurs primarily in areas with seagrass and involves disturbance and removal of extensive areas of vegetation, some of which is later replaced (WBM Oceanics, 1993). Recovery of the seagrasses can take up to 24 months (Hopper, 1994), but there is no information available on recovery of associated benthic faunal assemblages. Harvesting of yabbies involves pumping, or use of hydraulic suction equipment, both of which cause substantial damage to the substratum. Recruitment of many benthic invertebrates and finfish is influenced by changes to the structure and stability of the substratum, so damage caused by bait-harvesting may affect the utilisation of the intertidal nursery habitats by a wide range of species.

Need

There is currently no detailed information available on the specific effects of loss and/or damage to intertidal estuarine habitats on the faunal assemblages that utilise such habitats, despite the recognised importance of such habitats and this fauna to fisheries resources. Results from studies examining the effects of damage to subtidal habitats and links to fisheries utilising these habitats (e.g. Sainsbury et al., 1993) indicate that similar studies should be a priority for critical intertidal estuarine habitats. Although this project focuses on damage to intertidal habitats caused by bait-harvesting, the results of this work will be applicable to other sources of damage to these habitats, providing an important database establishing causal relationships between effects on the physical structure of the habitat and impacts on the faunal assemblages.

Coastal areas of Australia, especially those in close proximity to urban areas, are coming under increasing pressure from industrial and tourism developments, and all the associated infrastructure to support such activities. These shallow-water coastal and estuarine areas will also continue to be the focus of attention by the recreational and commercial fishing sectors. An understanding of the cause-and-effect relationships between damage to key intertidal habitats and effects on the sustainability of fisheries resources is needed if the effects of developmental degradation are to be managed to minimise the adverse impacts on Australia's fisheries resources.

Objectives

1. Assess the ecological impacts associated with commercial and recreational harvesting of yabbies and bloodworms on other components of the ecosystem

2. Assess the impacts of bait-harvesting activities on the sustainability of populations of yabbies (*Trypaea australiensis*) and bloodworms (*Marphysa* sp.);

3. Develop a population assessment technique for yabbies and bloodworms;

4. Determine levels of recruitment of these species and assess whether harvesting affects recruitment;

5. Obtain estimates of the recreational harvest of these species

Section 1: Assessment of the Magnitude of the Harvest of Yabbies and Bloodworms

1.1. Introduction

Recreational fishing is a ubiquitous activity throughout most of the developed world and is generally "open access" (i.e. there is no restriction on the number of anglers participating). Effort is generally considered to be increasing in most of these fisheries around the world (e.g. van der Elst, 1989; Schramm Jr. & Edwards, 1994; Anon., 2000) and catch often exceeds that of commercial fisheries operating in the same geographic area (e.g. McGlennon, 1992; West and Gordon, 1994; Young et al., 1999). In recent years, the focus of assessment and monitoring of commercial fisheries has broadened considerably from principally examining sustainability of target species to include the impacts of fishing on habitats and the magnitude, fate and impacts on by-catch (e.g. Andrew & Pepperell, 1992; Poiner et al., 1998; Engel & Kvitek, 1998; Watling & Norse, 1998). In contrast, studies on the impacts associated with recreational fishing are still primarily aimed at quantifying the harvest of key species rather than the broader ecological impacts from the activity.

Assessing and monitoring catch and effort is an important requirement for the management of recreational and commercial fisheries. Catch and effort in most Australian commercial fisheries is assessed and monitored through compulsory logbook programmes, although independent observer programmes are also used for some fisheries (e.g. Gulf of Carpentaria Offshore Net fishery). Use of logbook programmes is not, however, practical for assessing the catch and effort for most recreational fisheries and a range of other methods must be used in order to obtain data on the levels of harvesting. These methods can be divided into off-site (e.g. mail surveys, diary programs and phone surveys) and on-site (e.g. creel surveys) methods. The most appropriate method to be used is dependent on the specific objectives of each particular study. Off-site methods can be cost effective when used to obtain general information (including socio-economic information) over a large geographic scale (e.g. statewide). These methods may, however, suffer from several types of biases, including recall bias (not accurately remembering what was caught), prestige bias (exaggerating catch size or number), or intentional deception in an attempt to influence fishery regulations to an individual's benefit (Pollock et al., 1994).

On-site methods such as creel surveys can potentially avoid the sampling biases associated with off-site surveys since anglers are contacted in person during or just after fishing and catches can usually be inspected. Creel surveys can be further divided into access point creel surveys and roving creel surveys. Access point creel surveys involve interviewing fishers at a small number of known access points (e.g. boat ramps) whereas roving creel surveys involve moving from angler to angler and are used where fishers can access the water at many points (e.g. along a stretch of beach or a lake shoreline). Creel surveys are, however, generally costly to implement effectively because of the need for large numbers of staff to administer the surveys if information is to be obtained over large spatial and temporal scales.

Another potential on-site method for estimating catch is to conduct an observational survey, that is, observing anglers' catches during their fishing or harvesting. This method allows estimates to be made of the catch of anglers who refuse to participate in a creel surveys. To be practical, however, the number and types of organisms which are caught or harvested need to be clearly discernible by an observer and, ideally, the period spent fishing or harvesting needs to be short and the number of participants in an area reasonably low.

The harvesting of a variety of organisms for bait is an important component of the ecological impacts associated with recreational fishing. Anglers may harvest bait themselves or rely on the harvesting of bait organisms by licensed commercial harvesters. In this chapter, current knowledge of the magnitude of bait harvesting in Australia and overseas is reviewed and catch and effort information for the commercial harvest of bloodworms (*Marphysa* spp.) and yabbies (*Trypea australiensis*) is examined. The focus here is only on those studies which deal specifically with harvesting for bait. Other studies which examine the impacts and effects of harvesting of invertebrates by humans for food are reviewed in other chapters. A combination of creel surveys and observational surveys was used to quantify catch and effort of harvesting for bloodworms and yabbies used as bait by recreational anglers in south-east Queensland, including anglers participating in a large scale commercialised fishing competition.

1.1.1. Recreational Bait Harvesting - Global

Overall, the harvest of bait by recreational anglers has not been well documented but there is sufficient information to demonstrate that a wide variety of organisms are harvested from several different types of habitats. Along rock intertidal shores in New South Wales (Australia), the taking of cunjevoi (*Pyura stolonifera*), crabs, gastropods and algae (*Enteromorpha* and *Ulva*) for use as bait has been shown to be substantial, with even relatively small numbers of people able to collected large numbers of organisms (Underwood and Kennelly, 1990; Fairweather, 1991; Kingsford et al., 1991).

From sandy ocean beach habitats, bivalves of the genus *Donax* (pipis and surf clams) are frequently harvested for use as bait (Schoeman, 1996; Murray-Jones and Steffe, 2000). Along Stockton Beach (NSW), an estimated 3.4 tonnes of pipis per annum were harvested for use as bait, but this harvest was only a small component (2%) of the total harvest of pipis from the area (Murray-Jones and Steffe, 2000). The majority of pipis were taken by commercial harvesters. In contrast, in the coastal region of Port Elizabeth (South Africa), Schoeman (1996) recorded that most of the 600 tonnes of the annual pipis harvest were for use as bait by recreational fishers. This harvest was estimated to represent between 3 and 7% of the maximal sustainable yield for this population.

In estuarine soft sediment habitats, various types of invertebrates are harvested by recreational fishers for use as bait, including polychaetes (Klawe and Dickie, 1957; Blake, 1979; McLusky et al., 1983; Creaser and Clifford, 1986), bivalves (Jackson and James, 1979) and thalassinidean shrimps (Wynberg and Branch, 1994). The magnitude of the recreational harvest from these habitats has generally not been quantified, although Wynberg & Branch (1991) have estimated that over 1,222,500 thalassinidean shrimp (*Callianassa kraussi*), were removed annually from a single lagoon in South Africa. Concerns over the sustainability of these fisheries and their broader ecological effects are common (e.g. Brown, 1993; Hall and Harding, 1997).

1.1.2. Recreational Harvesting - Moreton Bay

Approximately 300,000 recreational fishers utilise the Moreton Bay region (south east Queensland, Australia) annually, with expectations that this number will continue to increase in line with increasing population growth and tourism (Skinner et al., 1998). A variety of invertebrates are harvested for use as bait by recreational fishers, including polychaetes (Families Nereididae and Eunicidae), soldier crabs (*Mictyris longicarpus*: Family Mictyridae), bivalves and yabbies (*Trypea australiensis*: Family Callianassidae) in the Moreton Bay region (Quinn, 1992; O'Neill, 2000).

Yabbies are harvested from many intertidal areas of Moreton Bay using a locally developed implement, the yabby pump (Hailstone and Stephenson, 1961). In Pumicestone Passage alone (northern Moreton Bay), 29% of fishing groups harvested their own bait, with yabbies and polychaete worms being the baits most commonly harvested (O'Neill, 2000). Various types of polychaetes are harvested with the use of garden forks from intertidal seagrass and rubble areas, with the bloodworm (*Marphysa* sp.) considered the most popular harvested species (Forbes, 1984). For the recreational harvesting of bloodworms, commercial style "bail and dyke" pits may be dug (described more fully in Section 1.1.5.), but more usually the less time-consuming and physically easier method of digging "trenches" or "pot holes" with a standard garden fork is used. The harvesting of bait organisms such as worms and yabbies has not been previously comprehensively quantified in the Moreton Bay region.

1.1.3. Fishing Competitions

A consistent trend in recreational fisheries is the heterogenous nature of the participants and the large variation between the motivations and aspirations of individual anglers (e.g. Wilde et al., 1998; Vigliano et al., 2000). Many anglers may fish only once a year with their primary motivation being non-catch related (e.g. to be outdoors) while others may fish at least once a week and be motivated by a desire to catch large fish or a large number of fish to win angling tournaments.

Recreational angling competitions and tournaments are a growing component of total recreational fishing effort in the United States and in Australia (e.g. Schramm et al., 1991a, b). Fishing competitions are highly variable in the number of participants and, therefore, the potential ecological impacts which may arise. Schramm et al. (1991a, b) have raised concerns about the lack of information on the impacts on fish stocks from the elevated and highly concentrated fishing effort during fishing tournaments in the USA. The growth of competitive angling in Queensland (and Australia) is relatively recent but similar concerns regarding the impacts from such competitions have also been expressed by management agencies. The impacts of fishing tournaments potentially extend beyond impacts on the targeted species, including impacts from large numbers of 4WD vehicles transporting recreational anglers along beaches, impacts on terrestrial systems from large numbers of campers in a relatively restricted area (Hockings & Twyford, 1997) and impacts from recreational anglers harvesting large numbers of organisms for bait over a short period of time.

Many fishing competitions are held in the Moreton Bay region. The most prevalent are those competitions conducted by recreational fishing clubs that are restricted to club members and generally held on a weekend with participants numbering less than thirty. There is also a growing number of so-called "commercialised fishing competitions", which are open to the general public, where anglers compete to catch the heaviest fish of various species. Up to 1,500 anglers may participate in these competitions which can last for a week. Often, the bait for use in such competitions is harvested from localised areas over a relatively short period of time.

Commercialised fishing competitions are competitions where anglers compete for large prizes typically by catching the heaviest fish of various species. The two biggest and best known competitions are the Toyota Fraser Island Classic and the 'Straddie' Classic. There is an increasing community focus on the impacts of these competitions and the Queensland Fishing Management Authority (QFMA) has enacting a policy to regulate the number and size of these competitions. The focus of research on these competitions to date has been principally limited to estimating the species composition and number of fish captured by anglers. There has been little attention paid to the effects from the collection of bait to support the anglers during the competitions.

Previous work showed that anglers in the Straddie Classic collected yabbies extensively for use as bait in the fishing competition (Sturkie, 1996), but detailed information on the number of people harvesting and their specific activities while collecting bait was not obtained. In order to quantify the spatial extent and intensity of bait-harvesting associated with a commercialised fishing competition, creel and observational surveys of recreational bait harvesters during the 1998 Straddie Classic were done. The specific objectives of the surveys of were to:

1. Estimate the minimal number of yabbies harvested in the Straddie Classic;

2. Estimate the size-distribution and size-selectivity of the yabby harvest in the Straddie Classic;

3. Calculate the average number of people in a "yabby harvesting team" and for how many anglers a "yabby harvesting team" is collecting yabbies;

4. Provide information on the species of fish subsequently targeted by anglers harvesting yabbies in the Straddie Classic;

5. Provide information on areas other than those surveyed from which yabbies are harvested in south-east Queensland;

6. Provide information on animals other than yabbies retained for bait by harvesters in the Straddie Classic;

7. Develop a method to estimate the number of yabbies harvested without interviewing harvesters; and,

8. Estimate catch per unit effort of yabby harvesting in terms of time and the number of pumps per yabby in the Straddie Classic.

1.1.4. Commercial Bait Harvesting - Global

Commercial harvesting of two polychaete species- *Glycera dibranchiata* (bloodworm) and *Nereis* (*Neanthes*) *virens* (sandworm or clamworm) has occurred in the eastern U.S.A. since the 1920s (Creaser et al., 1983). Both species spawn in March, April, and May and harvesters avoid taking the spawning worms because they are fragile (and also possibly for reasons of resource sustainability). The annual harvest in the State of Maine of each species between 1946 and 1980, although variable, was generally in the order of 10s of millions (Creaser et al., 1983). Market demand is thought to be the major source of the variance in annual landings (Brown, 1993). The fishery is an open access fishery and it only requires payment of a small annual license fee to enter the fishery. The annual harvest is believed to be close to the maximal sustainable yield for these species or perhaps even beyond it (Brown, 1993).

Brown (1993) outlined concerns regarding the sustainability of bait worm harvesting in Maine. Bloodworm landings peaked in the 1970s and have not returned to these levels since that time. Warm water from a nuclear power plant adjacent to one of the most important areas (Sheepscot Estuary) for harvesting bloodworms is thought to have led to the worms reproducing at a smaller size than previously which, in turn, is thought to have causes an overall decrease in productivity. Any decrease in productivity from animals reaching maturity at a smaller size may be balanced by an increased growth rate but no data exist to support or refute this. Brown (1993) also concluded that harvested flats appeared to be self-recruiting (i.e. adults from the intertidal flats were producing the juveniles recruiting to these areas). Genetic analysis indicated that recruits to intertidal populations of bloodworms were not produced by animals from subtidal populations and heterozygosity of common alleles had been reduced in intertidal areas (Bristow and Vadas, 1991). The implications for such localised patterns of recruitment and population isolation for management of bloodworm stocks are serious because migration of larvae or post-larval individuals from other estuaries cannot be relied upon to renew depleted stocks in areas subjected to unsustainable harvesting.

1.1.5. Commercial Harvesting - Moreton Bay

The harvesting of bloodworms (*Marphysa* spp.) and yabbies occurs commercially in Moreton Bay, SE Queensland. Yabbies are collected using a yabby pump, the same method used by recreational anglers. *Marphysa* sp. is harvested commercially by digging “plots” in the designated areas at Fisherman Islands (Figure 1.1). In the past, *Marphysa* sp. was also harvested commercially in Moreton Bay in other areas such as Deception Bay (Figure 1.1; Forbes, 1984), but this is no longer permitted under the Moreton Bay Marine Park Zoning Plan 1998. Currently, under the provisions of Plan, worms may only be commercially harvested in Moreton Bay within four designated worm banks in the Fishermen’s Island area. The Morton Bay Zoning Plan also requires that seagrass which is disturbed during harvesting is replanted. The commercial harvest is monitored through a compulsory (but unvalidated) logbook program administered by the Queensland Fisheries Service. Commercial plots on Fisherman Islands consist primarily of a raised wall (dyke) surrounding an area of variable size from which the animals are dug with a pitchfork. Water is bailed from inside the dyke with either buckets, or in some cases, using petrol-driven hydraulic pumps. Digging continues within the plot until the incoming tide breaks the dyke and floods the area.

Bait harvesters in Queensland are regulated by means of an annually renewed permit rather than a secure license. Returns to the harvesters for worms in 1980 varied from between $1.10 and $1.40 per packet of four worms (Forbes, 1984), but prices in 1999 ranged from between $4.00 and $4.50 for a similar quantity of animals. The magnitude of the price rise may reflect the continued high demand for live worms in bait shops. Forbes (1984) noted that commercial worm diggers generally did not stockpile worms because of the difficulty of maintaining them (particularly in summer), but tended to adjust their levels of harvesting to meet increased demand over short time periods. It has been suggested (Forbes, 1984) that if stockpiling of bloodworms were to become more commonplace it may lead to an increase in effort and catch, particularly during the spring low tides when time available for digging is greater. Several commercial worm diggers do, however, currently stockpile bloodworms and maintain them in aquaria for sale during periods of high demand (e.g. public holidays) (M. Cowling pers. comm.).

Forbes (1984) and Hopper (1994) presented estimates of catch-rate by commercial bloodworm harvesters. Estimates of catch per metre^2 at Fisherman Islands ranged from 5.5 to 20 worms per metre^2 and there was no obvious change in bloodworm catch evident over the time period the two studies were done. The impact of changes in technology on catch rates of bloodworms is probably minor, given the restriction to use of hand implements (i.e. garden forks) for digging, although there may have been a limited increase in the use of hovercraft vehicles that have improved access to and within the harvest areas. Hopper (1994) presented more detailed seasonal analysis of catch per metre^2 than Forbes (1984) and concluded that catch rates at Fisherman Islands were significantly greater in summer than other times of the year. Anecdotal evidence from commercial worm harvesters suggests that worms are, however, “easier” to dig during winter. This apparent discrepancy may be because the time available to harvest during winter is increased because of the lower, low tides that occur during this period, compared with summer, thus increasing the area from which animals can be harvested and allowing harvesters to access areas which are not dug over so regularly, but the increased demand over summer leads to an increase in total effort compared with winter.

Commercial yabby harvesting also occurs in Moreton Bay and, similar to bloodworm harvesting, participation in this fishery is by an annually renewable permit rather than a secure license. From 1997 onwards, monitoring of both the commercial bloodworm and yabby catch has been via compulsory daily logbook returns. Between 1993 and 1996 harvesters were only required to submit logbook returns on a quarterly basis. There have been no previous studies that have examined the commercial yabby fishery in the Moreton Bay region and little is know of the scale and scope of this fishery to date.

In this chapter the catch and effort data for commercial bloodworm and yabby harvesting in southern Queensland are analysed and reviewed.

1.2. Methods

1.2.1. Analysis of Logbook Data from Commercial Yabby and Bloodworm Harvesters

Catch and effort data for the commercial yabby and bloodworm fishery were obtained from the compulsory logbook programme administered by the Queensland Fisheries Service. Total annual catch (number of yabbies or bloodworms), effort (number of active participants and days fished), and catch per unit effort (yabbies or bloodworms/harvesters/day) were calculated for the 1993 to 2000 period. Catch and catch per unit effort (yabbies or bloodworms/harvesters/day) were also calculated on a monthly basis for the period of 1997 to 2000, reflecting the increased frequency of logbook returns for that period. The geographic location used for yabby and bloodworm harvesting was identified from the information provided in the logbooks.

1.2.2. Harvesting of Yabbies

1.2.2.1. Recreational Harvesting of Yabbies.

Creel (Table 1.1) and observational surveys were administered by trained volunteers between April and October 1999 at Toorbul, Point Halloran, One Mile, Lota and Golden Beach. Surveyors arrived at the study sites approximately three hours before low tide or at dawn and left three hours after low tide or at dusk. Arrival and departure times of all harvesters were recorded. Surveyors recorded the number of people in each yabby harvesting team and categorised these people as either 'harvesters' (operating the yabby pump) or 'helpers' (sorting the disturbed sediment and/or carrying a container to hold yabbies).

At the end of their harvesting activities, fishers who volunteered to have their catch examined had their harvest counted. Where possible, all individuals or a sub-sample of the catch was measured with vernier calipers (mm carapace length (CL)). During the creel survey, harvesters were shown three different sized (7, 8 and 9 mm CL) yabbies and asked which size would be discarded as being too small for use as bait. These sizes were based on initial observations and anecdotal reports of the size-distribution of yabbies in the study area and the size at which anglers appeared to retain yabbies.

<u>Observational Surveys:</u> Yabbies are usually collected with a yabby pump (Hailstone & Stephenson, 1961) which is pushed into an area of sand or mud with yabby holes, the plunger withdrawn, and the core of sand or mud is ejected by pushing down the handle. The yabby pump is then reinserted into the hole a number of times and further cores of sediment and water are removed. Yabbies extracted and deposited on the surface of the substratum are then collected by hand. Yabby pumping, therefore, consists of a number of sets of 'pulls' of the yabby pump followed by a collection of the exposed animals. This process forms an easily defined and observable set of behaviours which was used to estimate the catch of the harvesting teams and to determine the correlation between the estimated catch and the actual catch, from counts from teams which allowed their catch to be quantified with the creel survey (McPhee & Skilleter, 2002).

An observational survey team of two people recorded: (1) the general spatial pattern of harvesting (e.g. haphazard, transect perpendicular to the water, transect parallel to the water); (2) the number of steps and their direction (left or right relative to the shore, or up or downshore) taken by the harvesters between a set of pulls; (3) the number of pulls per set; and (4) the number of times a helper appeared to pick up an object from the substratum (hereafter called a 'peck'). Observations were made from the top of the shore, at a distance of approximately 100-150 metres from where teams of harvesters were operating. Patterns of movement during harvesting was recorded for use in later studies where the impacts of recreational harvesting were to be experimentally simulated but also to provide estimates of the area of substratum which was disturbed during harvesting events.

Additional information on the harvesting effort directed at yabbies in the Wynnum area was obtained during the observational surveys directed at obtaining catch and effort estimates from bloodworm harvesting (described in Section 1.2.3.1.).

1.2.2.2. Commercialised Fishing Competitions

Surveys of Bait-Harvesters: Creel surveys (Table 1.1) and observational surveys were administered at two locations on North Stradbroke Island (One Mile near Dunwich and Amity Point: Figure 1.1) during the Straddie Classic (8th-15th August 1998). The yabby beds at these sites are the easiest to access on the island and prior observations indicated that the majority of fishers would harvest bait from these sites. Yabbies are available elsewhere in Moreton Bay, but the fishing competition requires that anglers are based on North Stradbroke Island, greatly reducing the likelihood of anglers travelling to other locations to collect yabbies. The observational surveys, and the administering of the creel surveys were identical to those used to assess recreational yabby catch and effort in Moreton Bay.

1.2.3. Harvesting of Bloodworms.

1.2.3.1. Recreational Harvest of Bloodworms

Creel surveys (Table 1.2) were administered monthly between September 1999 and April 2001 and observational surveys were done between July 2000 and April 2001 in the Wynnum area of western Moreton Bay (Figure 1.1). Days on which creel and observational surveys could potentially be done within each month were selected based on the timing of the high tide. Initial observations and discussions with recreational fishers suggested that very little bloodworm harvesting occurred when the high tide fell between 10:00 AM and 2:00 PM as the intertidal flat was not generally exposed for long enough in daylight hours to allow digging. Potential sampling days within a month consisted of all days other than those where the high tide occurred between 10:00 AM and 2:00 PM. The potential sampling days were then stratified *a priori* into "high harvesting effort" and "low harvesting effort". The former consisted of Fridays, Saturdays and Sundays, whereas, the latter was Mondays through to Thursdays. Friday was included as a day with high harvesting effort as initial observations and discussions with recreational fishers suggested that considerable levels of harvesting of worms occur on Fridays in order to obtain bait for use over the weekend. Three days per month from each stratum were surveyed from July 2000 to February 2001, but this was reduced to two days per month for March and April 2001 (Table 1.3).

Three zones were defined along the Wynnum foreshore (Figure 1.2) and the zone in which harvesters dug was recorded. These zones were delineated by the presence of distinct boundaries (creeks, jetties, etc.) between them. These boundaries are also used to define management zones by the Queensland Fisheries Management Authority (now Queensland Fisheries Service). From north to south, the zones were: (i) from Alex's Gutter to the Wynnum Creek rock groyne; (ii) from the Wynnum Creek groyne to Wynnum Jetty; and (iii) from Wynnum Jetty to Darling Point.

Observers were stationed in a vehicle in the car park adjacent to the foreshore and they used a pair of binoculars for observations. Observational surveys to assess bloodworm harvest were similar to those used to estimate yabby harvest (described in Section 1.2.2.1.). The time of arrival and departure of the harvesters, and harvest based on how many times a worm digger picked up a bloodworm and placed it in the bucket was recorded. Two clear digging methods were differentiated and recorded. The first was the "bail and dyke" method which is the method used to harvest bloodworms commercially and the second was the "pothole" or simple pit method.

On some survey days, it was not always possible to observe the activities of all worm harvesters over the entire duration of their harvesting. When this was the case, only a part of their harvesting activities were observed to obtain a catch per unit effort (worms per hour) for those harvesters. This estimate of catch per unit effort was then multiplied by the entire time they spent harvesting to obtain an estimate of total catch.

1.3. Results.

1.3.1. Harvesting of Yabbies

1.3.1.1. Commercial Yabby Logbook Data

The annual commercial harvest of yabbies ranged from 188,470 (1993) to a maximum of 1,402,103 individuals (1997) with a trend of increasing catch from 1993 to 1997 followed by a slight decline although catch remained above 1,102,505 individuals per annum from 1997 to 2000 (Figure 1.3A). Commercial activities were based primarily at ten different sites in SE Queensland (Figure 1.4), although a number of records failed to indicate the precise position of the sites used, or provided ambiguous information and had to be combined under the category of unknown (Figure 1.3B). Most of the yabby harvest was taken from the Southport Broadwater and Jumpinpin areas with a clear increase in harvest at Jumpinpin from 1997 onwards (Figure 1.3B). None of the other major sites used by commercial harvesters exceeded a catch of 200,000 yabbies per annum and some appeared to be only used occasionally, or only returned small numbers of animals.

The number of commercial yabby harvesters on record as having harvested yabbies in any year was initially small (7) in 1993 before peaking in 1995 at 20 and remaining between 12 and 15 fishers during the 1997 to 2000 period (Figure 1.5A). The total commercial effort, based on the days spent harvesting yabbies, showed a general increase over the 1993 to 2000 period (Figure 1.5B). Based on the more detailed monthly log-book data, there was no monthly trend in catch between 1997 and 2000 (Figure 1.6A), nor was there any monthly trend in CPUE (the number of yabbies harvested per person per day) (Figure 1.6B).

1.3.1.2. Commercialised Fishing Competitions

Surveyors spent a total of 44 hours and 16 minutes at One Mile and 21 hours and 8 minutes at Amity Point during the course of the Straddie Classic. The catch of yabbies by harvesters that allowed their catch to be counted was 2,604 (n=32 teams) at One Mile and 1,342 (n=23 teams) at Amity Point. Fewer than 50% of teams allowed their harvest to be counted, so that the total harvest from these sites during the competition was considerably greater. Significantly more time was spent harvesting at Amity Point than One Mile, but harvest rates were not significantly different between the sites using either yabbies/minute/harvester or yabbies/set/harvester as a measure of effort. This may be due to greater variability in the measures of harvest rate compared with time spent harvesting (Table 1.3). There was a trend towards a greater harvest rate at One Mile than Amity Point.

Most yabby harvesters worked alone or with one helper, very few worked as large teams (Figure 1.7A). Few teams collected fewer than 25 or more than 200 yabbies on each harvesting event (Figure 1.7B). At One Mile, nine harvesters (28%) also retained animals other than yabbies for bait (soldier crabs, echiurans and penaeid prawns). Soldier crabs (*Mictyris longicarpus*) were the most common animals other than yabbies retained for bait but only in small numbers (mean ± SE = 7.9± 2.8; range: 1 to 25). At Amity Point the incidence of retention of animals other than yabbies for bait was less with only three harvesters (13%) retaining other species.

The majority of yabby harvesting teams collecting yabbies was participating in the Straddie Classic (Table 1.4). The proportion of Straddie Classic competitors versus general recreational harvesters was not significantly different ($X_1^2= 2.27$, $P > 0.05$) between the two locations, nor was there a significant difference between the average number of yabbies harvested by competitors (mean ± SE = 60.92 ± 54.8) and non-competitors (mean ± SE = 54.4 ± 96.2) in the Straddie Classic ($t_{31}= 0.42$, $P > 0.05$) (locations combined). Generally, yabby harvesters surveyed at One Mile reported that they fished more frequently (33% fishing weekly) than those harvesting at Amity Point (16% fishing weekly) although similar proportions from each location reported that they fished either weekly or fortnightly (approximately 40%, Table 1.4). The majority of yabby harvesting teams interviewed were planning to target whiting (*Sillago* spp.) and yellowfin bream (*Acanthopagrus australis*) (Figure 1.8A).

From observational surveys, the number of pecks was linearly related to the number of yabbies harvested at both One Mile (n= 20) and Amity Point (n= 11 teams) suggesting that harvest of yabbies could be estimated from an observational survey. At Amity Point, 98% of the variability in total catch could be estimated from counts of the number of pecks. At One Mile, 94% of the variability in total catch could be estimated from counts of the number of pecks. The average number of steps between sets was 4.9 (± 15.7) at Amity Point and 4.1 (± 4.0) at One Mile. The average number of steps between sets at the two locations was not significantly different ($t_{27}= 2.05$, $P> 0.05$) but the number of steps between sets at Amity Point was more variable than the number at One Mile ($F_{19,23}= 3.92$,

$P < 0.05$). This suggests that the average distance between patches of substratum which are harvested is on the order of 3-5 metres.

Sixty-four percent of harvesters estimated the number of yabbies they had harvested within 25% of their actual harvest (Table 1.5). Under-estimating harvest was more common than over-estimation. Most yabby harvesters nominated that they were selective with respect to the yabbies they retained for bait. Eighty-nine percent of harvesters nominated that they released yabbies if they considered them too small for bait, while 50% of harvesters nominated that they released yabbies if they had sustained damage during harvesting or were soft. Although, not specifically asked, some harvesters also indicated that they released gravid female yabbies. Of those harvesters who indicated they only retained yabbies above a particular size, the majority considered yabbies smaller than 7 mm CL as too small and 9 mm CL as being the size above which they retained them (Table 1.6). It was evident, however, that harvesters were not very good at estimating the size of yabbies they retained for bait. Thirty-two percent (n= 25) of harvesters had retained yabbies below the size at which they claimed to release them. The size frequency distribution of the yabby harvest was unimodal with a peak around 11 and 12 mm CL and did not differ significantly between the two locations (Figure 1.8B).

1.3.1.3. Recreational Harvesting of Yabbies

Thirty-nine yabby harvesters were present during 21 survey periods encompassing a total of 37 hours of surveying. A further 50 yabby harvesters were observed at Wynnum during the period when bloodworm surveys were being administered. On many occasions, no yabby harvesters were operating in the areas under observation and no data were obtained for these periods. There is a large number of potential sites in Moreton Bay from which yabbies could be harvested and it was not logistically possible to cover all these sites at any time. The relatively low rate of return of information on recreational harvesting of yabbies from the creel surveys meant it was not cost-effective to continue this activity. As noted above, information on yabby harvesting was still obtained as part of observations on recreational bloodworm harvesting.

Thirty four yabby harvesters agreed to answer the creel survey, with the most frequent level of fishing activity from those surveyed being weekly (Figure 1.9A). Yellowfin bream and summer whiting were the two most frequent fish species subsequently targeted by yabby harvesters (Figure 1.9B). On average, yabby harvesters spent only 31 minutes harvesting yabbies (S.D.= 18 minutes) collecting bait on each occasion. The size frequency of yabbies harvested was unimodal with the with a mode at 10 mm CL (Figure 1.10A). Harvesters were generally selective regarding the yabbies they harvested with size being the most frequent reason to release yabbies, although being “too soft”, gravid or damaged were also important (Figure 1.10B). Of the 29 harvesters who nominated that they released yabbies below a certain size, 23 nominated that they released yabbies below 7 mm CL, 14 nominated that they released yabbies below 8 mm CL, but only one nominated that they released yabbies below 9 mm CL.

1.3.2. Harvesting of Bloodworms

1.3.2.1. Commercial Bloodworm Logbook Data

The annual commercial catch of bloodworms from Moreton and Hervey Bays between 1993 and 2000 ranged from 710,672 to 1,127,307 with no clear increasing or decreasing trend apart from an initial increase after 1993 (Figure 1.11A). The number of commercial bloodworm harvesters who reported harvesting bloodworms in any given year showed a small decrease over time (Figure 1.11B). There was no clear trends in monthly bloodworm harvest (Figure 1.12A) or monthly effort (number of person days per month on which fishing occurred (Figure 12B), however catch per unit effort (worms per digger per day) tended to be greater in winter and spring and lower in summer and autumn (Figure 13).

1.3.2.2. Recreational Harvest of Bloodworms

Creel surveys.

A total of sixty-three creel surveys on recreational fishers harvesting bloodworms in the Wynnum area were completed. A further 128 harvesters were contacted during the period when creel surveys were being done but these had already been interviewed previously and were not questioned again. The majority of bloodworm harvesters fished at least once a month (Figure 1.14A) and relied heavily or exclusively on bloodworms for bait (Figure 1.14B). Recreational bloodworm harvesters also identified that they harvested a range of other invertebrates from intertidal areas for use as bait: yabbies were the groups most frequently identified other than bloodworms (Figure 1.15A). "Summer" whiting (*Sillago ciliata* and *Sillago analis*) and diver whiting (*Sillago maculata*) were the most common fish species subsequently targeted with harvested bloodworms (Figure 1.15B).

Bloodworm harvesters generally had little knowledge of the details of regulations pertaining to bloodworm harvesting. While 73% of harvesters interviewed were aware of the in-possession bag limit (50 worms per person) applying to the harvesting of bloodworms only 30% of harvesters were aware that bloodworm harvesting was prohibited within 100 metres of the foreshore and only 6% were aware of the requirement for replanting any seagrass disturbed during harvesting.

Observational surveys

Two-hundred and seventy five bloodworm harvesters were present during 159 survey hours and from these estimates of catch and catch per unit (worms per hour) were obtained for 197 groups. Most harvesting of bloodworms (65.9%) was conducted in Zone 1 (Alex's Gutter to Wynnum Creek groyne), with 32.1% occurring in Zone 2 (Wynnum Creek groyne to Wynnum Jetty) and only 1.9% in Zone 3 (Wynnum Jetty o Darling Point). The number of harvesters collecting bloodworms did not show any seasonal trend over the study period, but there were clearly more harvesters operating on weekends (including Friday) than during the week except for one period in March 2001 (Figure 1.16A).

Overall, the most commonly used digging method was using simple pits which were used by 127 (64.5%) harvesters. Harvesters using the bail and dyke method spent significantly longer periods of time collecting bait than those digging simple pits (mean ± SE: $\overline{X}_{Bail\&\ Dyke} = 98.8 \pm 3.4$ minutes; $\overline{X}_{Pits}=69.1 \pm 2.4$; $t_{195}= 8.22$; $p < 0.01$) but harvesters using bail and dyke method were able to achieve significantly greater total CPUE than those using the pit method (mean ± SE: $\overline{X}_{Bail\&\ Dyke}=0.79\pm 0.05$ worms per minute; $\overline{X}_{Pits} = 0.61 \pm 0.03$; ($t_{195}= 7.26$; $p < 0.01$). Most harvesters worked alone (Figure 1.16B), but where there were multiple people in a team, there was a slightly greater proportion of teams using the bail and dyke method than digging simple pits.

An estimated total of 61,757 bloodworms (25,991 from "weekdays" and 35,766 from "weekends") were harvested during the 10 months observations were made for the Wynnum foreshore area (Figure 1.17). A large proportion of harvesters exceeded the bag limit of 50 worms per person, with the maximal number of worms collected during any one session as many as 353. A significantly larger proportion (X_1^2 test – $p<0.05$) of harvesters using the bail and dyke method (0.48) exceeded the bloodworm bag limit, compared with those using the pit method (0.25). Most harvesters exceeding the bag limit while using the pit method were usually only just over this limit (Table 1.8). Thirteen instances of bivalve molluscs being harvested from the foreshore at Wynnum were also observed during bloodworm surveys, despite the presence of numerous signs on the foreshore stating that this was a prohibited activity.

1.4. Discussion.

1.4.1. Harvesting of Yabbies

1.4.1.1. Commercial Harvesting of Yabbies

The annual commercial catch of yabbies increased between 1993 and 1997 before becoming relatively consistent from 1997 to 2000. There are two possible explanations for this pattern although they are not mutually exclusive: (i) there was a real increase in catch over the period for which data were available; and/or (ii) there was an increase in compliance with the compulsory logbook program over this period.

An increase in catch during this period may have been associated with the increase in the number of harvesters registering their activity. In 1993 only seven commercial yabby harvesters reported catching yabbies but this increased in subsequent years (Figure 1.5A). An initial period of poor compliance with the log book programme may also account for the change in total harvest. Logbooks were only introduced to the fishery in 1993 and there was likely to have been an initial period with incomplete reporting (Sian Breen, Queensland Fisheries Service, personal communication). Additionally, during the period between 1993 and 1996, commercial operators were only required to submit logbook returns on a quarterly basis. This may have meant that unless the fishers were keeping daily records, recall bias (e.g. Pollock et al., 1994) may have influenced the accuracy of the catch and effort data recorded in the quarterly returns. Furthermore, there are several instances of catch being recorded prior to 1997 without a corresponding record of effort (i.e. the number of days on which harvesting occurred). This again suggests recall bias in the data – the commercial harvesters may have been unable to remember how many days they spent harvesting during any specific period.

The commercial yabby harvest was dominated by harvest from the Southport Broadwater and Jumpinpin areas. The commercial harvest at Jumpinpin increased markedly during 1997 which corresponded to the introduction of daily logbook reporting. Again, it is unclear if this increase in catch at Jumpinpin represents a real increase in catch or reflects greater compliance with the logbook program. Renewal of annual permits prior to 1997 was not dependent on the return of logbook data, but after 1997 a condition for the renewal of permits was compliance with the requirement for daily logbook returns and this may have encouraged the accurate return of logbook data. There are no independent estimates of the catch of yabbies during this period, so it is not possible to distinguish between the two alternatives, although it seems likely that some component of the increase in recorded catch was related to the issue of changes in the level of compliance with the logbook programme.

It is important to consider the temporal pattern of harvesting in order to estimate the magnitude of any impacts from harvesting and the likelihood of recovery of affected benthic communities. There were no clear monthly trends in the commercial yabby harvest between 1997 and 2000, with yabbies being harvesting during all months of the year (Figure 1.6A). This is not surprising given previous reports of yabbies being harvested throughout the year (Hailstone and Stephenson, 1961), but it does indicate that demand for commercially caught yabbies occurs throughout the year, despite the relative ease with which an individual fisher could capture their own bait.

1.4.1.2. Commercialised Fishing Competitions

The present study provided estimates of the number of yabbies harvested during the Straddie Classic fishing competition. This estimate should only be considered as a minimum because observations were not obtained at Amity Point on all days of the fishing tournament, and it is possible that yabby banks other than those at One Mile and Amity Point were also utilised. Yabbies are known to be harvested from a large number of areas within Moreton Bay (e.g. Lota, Victoria Point, Pumicestone Passage, Jumpinpin, and Southport) and elsewhere along the east coast of Australia (Hailstone & Stephenson, 1961). Nonetheless, based on the number of harvesters from whom data were obtained, the catch of yabbies from a single fishing competition was in the order of thousands of animals. Combined with estimates of catch from small-group fishing trips (Skilleter, unpublished data), it is evident that large numbers of animals are being harvested annually by recreational fishers to support the recreational fishing sector.

The substantial harvest recorded during the 1998 Straddie Classic was despite the observed number of yabby harvesters being fewer than anticipated. Approximately 1500 fishers were registered to participate in the Straddie Classic in 1998, but only a small proportion of these appeared to be collecting yabbies for bait. Most fishers who were collecting yabbies for bait were using them to target estuarine and inshore species such as yellowfin bream (*Acanthopagrus australis*) and whiting (*Sillago* spp.), the species that numerically dominate the catch of recreational anglers in Queensland (Higgs, 1999). One possible explanation for the smaller than anticipated number of competitors collecting their own bait was that the calm weather (generally less than 10 knots) which occurred during the tournament in 1998 was more suited to offshore fishing than in other years (McPhee personal observation) and many boat fishers may have ventured offshore and targeted species such as snapper (*Pagrus auratus*) and pearl perch (*Glaucosoma scapulare*), species not usually fished for with yabbies (QFMA, 1998). Weather has been found to influence strongly recreational fishing effort and the distribution of this effort between offshore and inshore waters elsewhere (Steffe et al, 1996). In other years, or for other competitions, when more fishing effort is conducted in inshore and estuarine areas because of weather conditions, the magnitude of the harvest of yabbies would be expected to be much greater.

The proportion of harvesters that identified themselves as fishers active on a weekly basis (26% for both sites combined) was considerably greater than the percentage (7.7%) estimated overall in south east Queensland (QFMA, 1999). Anglers that fish in the Straddie Classic may represent a disproportionate number of 'keen' anglers, a fact that has been established for fishing club members and competition anglers elsewhere (Clarke & Buxton, 1989; McGlennon, 1992; Thwaites & Williams, 1994; Wilde et al., 1998). Many of those harvesters surveyed who were not participating in the Straddie Classic also, however, identified themselves as being active on a weekly basis so this explanation alone is probably insufficient to account for the results. A caveat to this conclusion is that there were relatively few harvesters interviewed who were not participating in the Straddie Classic, so more detailed surveys of other recreational (i.e. non-competition) anglers may provide a different result.

Discrepancies were evident between the magnitude of the harvest claimed by fishers and the actual number of animals taken, despite the response categories being relatively broad. Furthermore, a small proportion of harvesters was unwilling to be interviewed and only 50% allowed their catch to be counted. It is therefore unclear how representative those harvesters who submitted their catch for examination were of the whole population of harvesters, a problem common to many creel surveys (reviewed by Pollock et al., 1994). Clearly, estimates of the total harvest of bait-species should not be based only on the results of interviews with harvesters. The observational surveys trialed here provided a method for estimating the harvest of yabbies without the need to conduct an interview, thus ensuring that the harvest could be estimated for those people who did not want to be interviewed or who would not submit their harvest for counting. The observational study, however, does have the disadvantage of not providing size-frequency data. Alternatives to creel surveys for estimating the magnitude of recreational harvests are often not possible, but in this case, where harvesting occurs in easily accessible areas which can be externally monitored, alternative approaches may reduce biases introduced through a dependence on human responses to questions.

Although yabbies clearly comprised the majority of the harvest, the results show that other invertebrates were also retained for use as bait. The retention of soldier crabs (*Mictyris longicarpus*) was not surprising as they are abundant and generally considered good bait (Quinn, 1992). The retention of the echiuran, *Ochetostoma australiense*, for bait was surprising and appears not to have been documented previously for this region, although the harvesting of another echiuran, *Urechis caupo*, for bait has been recorded from California (Suer, 1984). Although the life history and ecology of *O. australiense* are unknown, echiurans are generally long lived and their deposit feeding activities can be important determinants of benthic community composition (Suer, 1984; Hughes et al., 1994, 1996a, b). The potential impacts of yabby harvesting on *O. australiense* are unknown but warranted further investigation (see Chapter 2).

Callianassid shrimp are efficient bioturbators (Roberts et al., 1981; Suchanek, 1983) and levels of bioturbation are often important in determining the composition of the surrounding benthic communities in soft-sediments (Brenchley, 1981; Murphy, 1985; Posey, 1986). Furthermore, callianassid shrimp also have an important regulatory role in many sedimentary biogeochemical processes (e.g. Koike & Mukai, 1983; Waslenchuk et al., 1983; Murphy & Kremer, 1992; Schlacher & Wooldridge, 1996) which directly influence the structure of meio- and macrofaunal communities (Branch & Pringle, 1987; Dobbs & Guckert, 1988; Wynberg and Branch, 1994; Dittman, 1996). Finally, some callianassids, including *Trypea australiensis*, are active deposit-feeders (Boon et al., 1997) and the influence of deposit-feeders on surrounding community structure is well-known (e.g. Rhoads & Young, 1970; Brenchley, 1981; Hunt et al., 1987). Clearly, the removal of large numbers of callianassid shrimp over relatively short periods of time for use in commercial fishing competitions therefore has the potential to cause marked changes in the benthic community through a sizable disturbance (*sensu* Bender et al., 1984) (Chapter 2).

The observational survey described here provided a method for identifying, in general terms, the spatial scale of the potential impacts from yabby harvesting. The patterns of movement of teams of harvesters indicated that disturbance of the sediment is intensive in the patch where pumping occurs, but these patches are interspersed within areas of relatively undisturbed sediment. Based on estimates of the number of steps between sets, any impacts from yabby harvesting on benthic infauna, for instance, are likely to result in patchiness at the scale of metres. This assertion is based on the average number of steps between sets being four to five and assuming a step is equivalent to approximately 50-75 cm. This information is important for the design of future manipulative experiments to examine the ecological impacts of yabby harvesting (including impacts from trampling) and in distinguishing the impacts from yabby harvesting from other impacts that may operate at different spatial scales (Chapter 2).

Individual recreational anglers are typically considered to have minimal impacts on target species because most harvest no or few fish on any outing (e.g. Hilborn, 1985) and habitat damage while fishing is considered to be negligible or absent. In contrast, all yabby harvesters in the Straddie Classic fishing competition successfully removed (caught) relatively large numbers of animals and all contributed to habitat damage through trampling and turning over sediment. There were also potentially indirect impacts on other species which interact with the exploited species (e.g. use them as prey), and direct effects on other species which are damaged or killed during harvesting (Wynberg & Branch, 1991, 1994). This difference further suggests that any consideration of the influence of recreational anglers on the ecosystems in which they are fishing must incorporate information on the effects of collection of bait to be used on the fishing trips, in addition to assessment of the catch and by-catch.

1.4.1.3. Recreational Harvesting of Yabbies

There was insufficient information obtained from the general creel surveys to estimate the recreational harvest of yabbies in Moreton Bay. This was because of the low frequency of recreational yabby harvesting (approximately one per hour) at any particular site, the large number of possible areas from which yabbies could be harvested in Moreton Bay and the short duration of each harvesting event (approximately 1/2 an hour) increasing the likelihood of missing an individual event. These factors were also noted by O'Neill (2000) in a broad scale assessment of fisheries resources in Pumicestone Passage. These results should not, however, be taken to imply that yabby harvesting is not of a sufficient magnitude that it should be ignored by management, as indicated by the focussed study of fishing competitions and the large number of persons engaged in recreational fishing within the region. Any future surveys of yabby harvesting in Moreton Bay will need take these factors into consideration and develop an alternative method of obtaining data on the magnitude of the catch.

Although robust estimates of recreational yabby harvesting were not acquired, information relevant to the management of yabby harvesting was still obtained. Much of the information obtained from the creel surveys of yabby harvesting in Moreton Bay was consistent with that obtained during the Straddie Classic suggesting that several of the results from the Straddie Classic are applicable generally to yabby harvesting in Moreton Bay. Consistent with the results from the bloodworm surveys (see Section 1.4.2.2) and yabby harvesting during the Straddie Classic, yabby harvesters in Moreton Bay (not associated with a fishing competition) were generally avid anglers. Yabby harvesters were also principally targeting yellowfin bream (*Acanthopagrus australis*) and whiting (*Sillago* spp.) with the proportion of harvesters not subsequently planning to target a specific species less than that of anglers overall in Queensland (Higgs, 1999). Like yabby harvesters operating during the Straddie Classic, harvesters in Moreton Bay were generally size selective with regards to the yabbies they retained and generally considered yabbies below 7 mm CL to be too small for use as bait.

1.4.2. Harvesting of Bloodworms

1.4.2.1. Commercial Harvesting of Bloodworms

The number of commercial bloodworm harvesters recording catch in a given year has generally shown a slight decreasing trend (Figure 1.11B). A likely explanation for this is because renewal of the annual permit requires demonstration of participation in the bloodworm fishery in the previous year or a reason why participation in the fishery did not occur (e.g. health reasons). Such a management approach helps reduce latent or unused effort in the fishery and in this case may have been successful in reducing participation in the fishery.

Overall, the commercial harvest of bloodworms was of a considerable magnitude and has remained relatively constant over the last 7 years, after an initial increase in 1994 (Figure 1.11A). Like the annual commercial yabby harvest, the lower recorded catch of bloodworms in 1993 is likely to have been influenced by the introduction of logbooks for commercial bloodworm harvesters in that year.

Bloodworms were harvested during all months of the year. From direct observations, Hopper (1994) found that catch rates of bloodworms at Fisherman Islands were significantly greater during summer than winter, but analysis of the commercial logbook data suggested the opposite with a slight increase in catch rates (worms/harvester/day) during winter and spring compared with the summer months. The results from analysis of the logbooks supports anecdotal reports from commercial bloodworm harvesters that it is easier to dig for worms during winter. During winter, a greater area of shoreline is exposed during low tide because the low tides are lower than during summer. The increased area of shoreline from which bloodworms can be harvested may provide increased access to the areas that are dug over less regularly. The difference in the catch rates between summer and winter from Hopper (1994) and detailed analysis of the log books may simply be a result of the latter being based on more extensive and detailed records from the entire commercial fishery in Moreton Bay over several years whereas Hooper's results were based on direct observations of the catch of fishers working a single bank on Fisherman Islands during the full or new moon period over ~12 months.

1.4.2.2. Recreational Harvesting of Bloodworms

A combination of creel and observational surveys were used to obtain information on the recreational harvest of bloodworms at Wynnum in Moreton Bay. This area of Moreton Bay was chosen for the detailed study of the recreational bloodworm fishery because it had been the focus of numerous complaints from the general public about habitat destruction and over-harvesting (QFMA, Baitworm harvesting advisory group meetings). The use of the observational surveys was necessary in order to obtain an estimate of the catch of groups harvesting worms. Anecdotal information suggested that the level of non-compliance with regulations such as bag limits tended to be large. This study obtained important information for the future management of the recreational bloodworm fishery including the avidity of recreational harvesters, level of recreational harvest and the level of compliance with management measures.

The harvest of bloodworms from the Wynnum foreshore was considerable with 61,575 bloodworms estimated to have been harvested in a ten month period from approximately < 4 kilometres of shoreline. The Wynnum area is believed to be the most popular area for harvesting bloodworms in Moreton Bay, although digging by recreational harvesters is known to occur in several other areas of Moreton Bay including Lota, Point Halloran and Godwin's Beach. Observations suggest that the spatial extent of the intertidal area at these other sites is considerably less than that in the Wynnum area and it is therefore likely that these other parts of the bay experience less harvesting.

Community concerns have arisen regarding the impacts of worm harvesting by recreational harvesters on the ecology and visual amenity of the Wynnum area. An area closure was proposed by Queensland Fisheries Management Authority in response to these concerns, corresponding to Zone 3 here (Wynnum Jetty to Darling Point), to address ecological and visual amenity issues. If this closure were to be implemented it would have little impact on the magnitude of recreational harvesting of bloodworms and probably little ecological benefit since only 1.9% of the harvesting effort occurred in this zone. The closure may, however, have benefits from the perspective of public perception and visual amenity but this was not assessed in the current study.

In addition to documenting the magnitude of recreational harvesting, there is a need to understand the motivation and patterns of harvesting for effective fisheries management, but this is often overlooked (Novinger, 1984; Reynard and Hilborn, 1986; Chipman and Helfrich, 1988). The concept of "recreational specialisation" is a useful tool, frequently used in the U.S., for understanding recreational fisheries and guiding fisheries management (Loomis and Ditton, 1987; Chipman and Helfrich, 1988; Wilde et al., 1998). The concept recognises that anglers are not an homogenous group, but rather an heterogenous collection of people with differing objectives, preferences and expectations (Bryan, 1977; Chipman and Helfrich, 1988). However within a population of anglers, sub-groups are able to be identified, ranging from the least specialised "novice" to the highly specialised angler for whom angling is a central life interest (Chipman and Helfrich, 1988). As the level of specialisation of an angler increases, it is expected that there would be: (i) a greater acceptance and support for rules; (ii) an increase in the cost of individual participation (greater "willingness to pay" in economic evaluation terms); (iii) an increase in the targeting of specific species; (iv) more years of previous experience; (v) greater attention to the equipment used and the use of improving technology; (vi) a greater appreciation for both catch and non-catch related motivations; and (vii) a greater frequency of participation in the fishery (Ditton et al., 1992). Not all of these variables are relevant to the present study, but four are important here (greater acceptance and support for rules; greater appreciation for both catch and non-catch related motivations; increased targeting of specific species; and a greater frequency of participation in the fishery).

Harvesting bloodworms requires considerably physical exertion - both from digging and walking through soft mud and seagrass to reach sites suitable for harvesting. In the case of recreational bloodworm harvesters, their principal motivation is catch related (obtaining sufficient bait to allow angling) which contrasts to recreational angling itself where non-catch related motivations are frequently identified as being very important (e.g. Fedler and Ditton, 1994). Recreational bloodworm harvesters were more avid anglers than the majority of anglers in Queensland. Approximately 30% of bloodworm harvesters surveyed at Wynnum fished weekly or more regularly, compared with only 7.7% of Queensland anglers generally. This was also the case for yabby harvesters participating in the "Straddie Classic" fishing competition and those collecting yabbies for personal fishing trips (discussed in Sections 1.4.1.1 and 1.4.1.3). Combined, these findings suggest that anglers who harvest their own bait from soft sediment environments, are generally more avid anglers than the broader recreational fishing sector which would include the many anglers who purchase bait from commercial suppliers.

A frequent feature of recreational fishing effort is that a considerable proportion of it is not directed at catching any specific species. For instance, when asked to identify which species was being targeted, anglers frequently respond with comments such as "anything" or "whatever's biting" (e.g. O'Neill, 2000). In contrast, more specialised anglers tend to target specific species (e.g. Kitner and Maiolo, 1988). All bloodworm harvesters interviewed were specifically targeting bloodworms and were generally targeting one or more specific fish species with the bloodworms they had harvested. For instance, only 4% of bloodworm harvesters stated that they were subsequently planning on targeting "anything" with their harvested bloodworms which is a considerably smaller percentage than that of anglers in Queensland overall (63.4% - Higgs, 1999). Clearly, whiting (*Sillago* spp.) were the fish species most frequently targeted by bloodworm harvesters. Management of the recreational fishery for whiting should take into consideration that the "ecological footprint" (*sensu* Wackernagel and Rees, 1996) of this fishery also includes the harvesting of bloodworms and the subsequent impacts on the habitat (seagrass) and associated fauna.

Non-compliance with regulations is also a frequent feature of recreational fisheries (e.g. Gigliotti and Taylor, 1990; Schramm Jr. and Dennis, 1993; West and Gordon, 1994; Schill and Kline, 1995). The findings here suggested that harvesters were generally unaware of regulations pertaining to bloodworm harvesting and of those that were aware of such regulations many did not obey them. The bag limit of 50 worms per person was the regulation most frequently cited as being known, but there was considerable non-compliance with this regulation. Nearly 50% of the harvesters who used the bail and dyke method and 25% of the harvesters who dug simple pits exceeded the limit of 50 worms per person. During the creel surveys, several harvesters indicated that although they were aware of the bag limit they would not comply with it because they disagreed with the limit and/or believed they had little chance of being caught by enforcement officers.

In this study, only 30% of harvesters were aware that they could not harvest bloodworms within 100 metres of the foreshore and only 6% of harvesters were aware that they were required to replant seagrass after their digging activities. These low levels of awareness of regulations were despite Government agencies embarking on an extensive education and awareness campaign involving television advertisements and numerous published articles in angling publications. Generally, there appears to be little effort from Government agencies in Australia to determine if such awareness and education campaigns directed at recreational anglers are effective (McPhee et al., 2002). This study strongly suggests that the education and awareness campaigns aimed at limiting recreational bloodworm harvests and minimising habitat damage have not been effective to date. In addition to non-compliance with bloodworm harvesting regulations, non-compliance with the prohibition on the taking of molluscs from the foreshore was observed while conducting bloodworm surveys, despite the presence of multi-lingual signs prohibiting this activity (see also Keough et al., 1993). It was unclear whether the molluscs which were harvested were for consumption or for use as bait.

In terms of the concept of recreational specialisation, bloodworm harvesters can be considered highly specialised given that their motivations are catch related and they are generally avid anglers and subsequently target specific species with their harvested bloodworms. However, highly specialised anglers generally have greater awareness and compliance with regulations which was not the case in this study. One possible reason to explain the large proportion of harvests greater than the limit of 50 worms per person was that some of the bloodworm harvesters may have been illegally selling all or part of their harvest. Enforcement officers have reported that this has occurred.

1.5. Conclusions

After an initial increase in the first year after compulsory logbooks were introduced, the commercial harvest of bloodworms has been relatively constant. The number of operators registering activity within the fishery has, however, shown a decreasing trend between 1993 and 2000 suggesting that the limited entry arrangements have been successful in capping and slowly reducing participation in this fishery. Commercial bloodworm harvesting in Moreton Bay is restricted to four banks on the Fisherman Islands. Commercial yabby harvesting, in contrast, occurs in many areas within Moreton Bay although the majority of the registered harvest is from the southern section of the Bay, at Jumpinpin and the Southport Broadwater. The number of yabbies harvested commercially showed an increasing trend between 1993 and 1997, followed by a slight decline from 1998 to 2000.

Observational surveys were trialed to obtain estimates of the catch for recreational bloodworm harvesters and the method proved successful. Recreational harvesting of bloodworms from a single site in Moreton Bay, the Wynnum area, south of Fisherman Islands, was considerable with an estimated 61,575 worms caught during a ten month period. Bloodworms are harvested from a number of other areas within Moreton Bay, so the total recreational catch is from the region is likely to be large. Recreational bloodworm harvesters were generally avid and specialised anglers who were generally targeting whiting (*Sillago* spp.). Their knowledge of, or compliance with, regulations relating to harvesting bait from intertidal seagrass beds was, however, generally poor. Nearly 50% of the harvesters using the bail and dyke method and nearly 25% of those using the simple pit method for collecting bait exceeded the bag-limit of 50 worms and few bothered to replace seagrass plugs disturbed during their digging. Many of the complaints lodged by local residents and concerned citizens arose from the noticeable damage and disturbance to the seagrass beds in the area.

Estimating the recreational harvest of yabbies throughout Moreton Bay proved problematic because of the diffuse nature of this fishery. The large number of potential sites available for collecting yabbies and the low frequency of harvesting at any particular site meant it was not cost-effective to administer on-site creel surveys at any particular site. The harvest of yabbies associated with a large-scale commercialised fishing competition was estimated using a combination of creel surveys and an observational survey. The estimate of the yabby harvest from this one event was nearly 4,000 animals in a single week, again suggesting the overall catch of bait in the recreational component of the fishery is likely to be considerable. Yabby harvesters did not quantify their catch accurately for the creel surveys and the observational survey provided more accurate estimates of total catch.

Table 1.1: Creel survey administered to recreational bait harvesters observed collecting yabbies in the intertidal area around Moreton Bay. The same survey was used for individuals and small groups collecting bait for personal use and for groups participating in the Straddie Classic Fishing Tournament.

CREEL SURVEY OF YABBY HARVESTING.

Date:.............. Location:.. Arrival Time:..............

Departure Time:.............. Interviewers:.........................Internal Code: ....

Number of pumpers/helpers:..

Distinguishing features of fishers:...

...

Q1a. Have you been interviewed previously about your yabby harvesting activities.

○ Yes ○ No

Q1b. If so when and where?..

....

Q2. Approximately how often have you been fishing in the past twelve months?

○ Weekly or more often ○ Fortnightly ○ Once a month

○ Less often or on holidays ○ Unsure

Q3a. Are you a member of an amateur fishing club?

○ Yes ○ No

Q3b. Are the yabbies you are harvesting today to be used in a fishing club competition?

○ Yes ○ No

Q4. Approximately what percentage of fishing trips do you dig yabbies for?

....

Q5. How many fishers are you harvesting yabbies for?................................

Q6. Approximately how many yabbies are you intending to harvest during this bait harvesting session?

○ 0-50 ○ 51-100 ○ 101-200 ○ 201-300 ○300-400

○ 400-500 ○ >500 (please specify)..

Q7. Approximately when are you planning to use the yabbies?

○ Within 6hrs ○ Within 12hrs ○ Within 24hrs

○ Within 48hrs ○ Other (please specify)..

Q8. Which species of fish are you targeting with the yabbies you have harvested?

○ Bream ○ Whiting ○ Flathead

○ Dart ○ Other (please specify) ○ Anything

....

Q9. Do you let some yabbies go because they are:

a) Too small? ○ Yes ○ No (*if no go to Q9.*)

b) Too soft? ○ Yes ○ No

c) Carrying eggs? ○ Yes ○ No

d) Too damaged? ○ Yes ○ No (if yes please specify what kind of damage)

....

Q8b. Which if any of these yabbies do you consider to be too small?

a) Size A (7mm CL) ○ Yes ○ No

b) Size B (8mm TL) ○ Yes ○ No

c) Size C (9mm TL) ○ Yes ○ No

d) None e) All

Q9. While pumping yabbies do you retain for bait any other animals encountered?

○ Yes (please specify) ○ No

....

Q10. What other locations apart from the present one do you harvest yabbies at?

....
....

Q11. When you are finished would we be able to count and measure the yabbies you have harvested?

○ Yes ○ No

Table 1.2: Creel survey administered to recreational bait harvesters observed collecting bloodworms in the intertidal area around Moreton Bay.

CREEL SURVEY OF BLOODWORM HARVESTING IN MORETON BAY

Date: .... **Location:** ....

Arrival Time .... **Departure Time**..

Interviewers...................................... **Internal Code:** ....

GPS Coordinates:............................ ....

Number of diggers/helpers ....

....

Car/boat registration number..

Method of digging (trenches, pits, bail and dyke)...

Q1a. Have you been interviewed previously about your bloodworm digging activities.

o Yes o No (go to Q2.)

Q1b. If so when and where?..

....

Q2. Approximately how often have you been fishing in the past twelve months?

o Weekly or more often o Fortnightly o Once a month

o Less often or on holidays o Unsure

Q3a. Are you a member of an amateur fishing club?

o Yes o No (go to Q4.)

Q3b. Are the blood worms you are digging today to be used in a fishing club competition?

o Yes o No

Q4. Approximately what percentage of fishing trips do you dig bloodworms for?

....

Q5. How many fishers are you harvesting bloodworms for?.................

Q6. Approximately how many bloodworms are you intending to harvest during this bait harvesting session?

o 0-10 o 11-20 o 21-30 o 31-40 o41-50

o >51 (please specify)...

Q7. Approximately when are you planning to use the bloodworms?

o Within 6hrs o Within 12hrs o Within 24hrs

o Within 48hrs o Other (please specify)...

Q8. Which species of fish are you targeting with the bloodworms you have harvested?

o Bream o Summer Whiting o Winter Whiting

o Dart o Other (please specify) o Anything

....

Q9. What other locations apart from the present one do you harvest bloodworms from?

....

....

Q10. Do you harvest any of the following for bait. If you do approximately in what locations:

Rock worms	o Yes	o No	o NR
Wriggler worms	o Yes	o No	o NR
Surf worms	o Yes	o No	o NR
Bloodworms from mangrove areas	o Yes	o No	o NR
Yabbies	o Yes	o No	o NR
Pippies	o Yes	o No	o NR
Soldier crabs	o Yes	o No	o NR
Other	o Yes	o No	o NR

Locations

....

....

....

....

Q11a. Are you aware of the restrictions on worm digging in Moreton Bay that have resulted because of the Moreton Bay Marine Park Zoning Plan?

o Yes o No (if yes go to Q11b)

Q11b. What restrictions in the Moreton Bay Zoning Plan are you aware of?

....

....

Table 1.3: Summary information from observational surveys on recreational harvesters collected bloodworms (*Marphysa* sp.) from the Wynnum area of western Moreton Bay during (1) weekdays and (2) weekends. The number of harvesters that could be observed in any session was dependent on how long each one spent collecting worms and the total time available in that session. For groups where detailed harvesting information could not be gathered, the total time spent on the mudflat collecting bait was recorded and it was assumed that their CPUE was equal to the mean for the other groups.

(1) Weekdays

Month	Survey Days	Total Days in Stratum	Total Hours for Survey per mo	Number of Harvesters Present	Harvesters per hour	Number of harvesters observed	Estimated CPUE of observed harvesters (worms per hour)	Estimated catch of observed harvesters (per day) [1]	Estimate of total harvest on survey days [2]	Scaling factor	Estimate of monthly catch [3]
Jul-00	3	11	8	11	1.38	8	51.13	409	562	3.66	2062
Aug	3	14	6	9	1.50	6	59.00	354	531	4.67	2478
Sep	3	15	7	12	1.71	11	64.18	706	770	5.00	3851
Oct	3	12	10	12	1.20	9	78.11	703	937	4.00	3749
Nov	3	8	10	10	1.00	7	56.43	395	564	2.66	1505
Dec	3	10	8	10	1.25	6	118.00	708	1180	3.33	3933
Jan-01	3	10	10	20	2.00	14	56.29	788	1126	3.33	3752
Feb	3	9	8	7	0.88	5	83.80	419	587	3.00	1760
Mar	2	8	1.5	4	2.67	3	70.00	210	280	8.00	2240
Apr	2	11	3.5	2	0.57	2	30.00	60	60	11.00	660
TOTAL	28	108	72	97	-	71	-	4752	6597		25990

1: estimated total catch for observed harvesters = CPUE (worms per hour) x total number of hours for which observations were done
2: estimated total harvest for survey days = estimated catch per day x number of harvesters present / number of harvesters observed
3: estimate of monthly catch = estimated total catch for survey days x scaling factor (total days in stratum / number of survey days)

(2) Weekends

Month	Survey Days	Total Days in Stratum	Total Hours for Survey per mo	Number of Harvesters Present	Harvesters per hour	Number of harvesters observed	Estimated CPUE of observed harvesters (worms per hour)	Estimated catch of observed harvesters (per day)[1]	Estimate of total harvest on survey days[2]	Scaling factor	Estimate of monthly catch[3]
Jul-00	3	13	8	14	1.75	8	65.88	527	922	4.33	3996
Aug	3	8	9.5	16	1.68	12	70.33	844	1125	2.67	3001
Sep	3	8	7	15	2.14	11	154.55	1700	2318	2.67	6182
Oct	3	12	9	18	2.00	17	78.24	1330	1408	4.00	5633
Nov	3	10	10	19	1.90	13	67.31	875	1279	3.33	4263
Dec	3	8	11	25	2.27	14	62.93	881	1573	2.67	4195
Jan-01	3	6	9	21	2.33	14	38.64	541	812	2.00	1623
Feb	3	7	10	17	1.70	13	66.77	868	1135	2.33	2649
Mar	2	9	6	15	2.50	12	41.42	497	497	9.00	2237
Apr	2	8	7.5	16	2.13	12	45.25	543	497	8.00	1988
TOTAL	28	89	87	176	-	126	-	8606	11566	-	35767

1: estimated total catch for observed harvesters = CPUE (worms per hour) x total number of hours for which observations were done
2: estimated total harvest for survey days = estimated catch per day x number of harvesters present / number of harvesters observed
3: estimate of monthly catch = estimated total catch for survey days x scaling factor (total days in stratum / number of survey days)

Table 1.4: Summary of the results from the creel survey questionnaire and the observational surveys on fishers collecting bait for use in the 1998 Straddie Classic Fishing Tournament. Surveys were administered at the two locations previous work had indicated would be most likely used by participants in the tournament. *=P < 0.05.

	Location		**Statistical Comparison**
	One Mile	**Amity Point**	
Total no. of harvesters observed to be present	63	52	-
Mean time spent harvesting (min)	27.4± 2.1 (n=56)	37.6± 2.6 (n=31)	$t_{df=85,\ p<0.005}$= -3.66*
No. of interviews	45	31	-
Provided counts of yabbies	32	23	-
Yabbies/minute/harvester	2.6± 0.3 (n= 30)	2.0± 0.4 (n= 18)	$t_{df=46,\ p>0.005}$= -1.15
Yabbies/set/harvester	1.2± 0.1 (n= 20)	1.0± 0.2 (n=11)	$t_{df=29,\ p>0.005}$= 1.10

Table 1.5: Frequency with which yabby harvesters interviewed during the 1998 Straddie Classic Fishing Tournament went fishing. Non-Straddie Classic indicates teams of harvesters which were collecting bait but were not participants in the Straddie Classic.

Study site	**Weekly**	**Fortnightly**	**Monthly**	**Holidays**
One Mile (Straddie Classic)	9	4	13	8
One Mile (non Straddie Classic)	6	0	3	2
TOTAL	15	4	16	10
Amity Point (Straddie Classic)	2	3	4	11
Amity Point (non Straddie Classic)	3	4	1	3
TOTAL	5	7	5	14

Table 1.6: Comparison of the stated and actual harvest of yabbies by individual teams collecting bait for use in the 1998 Straddie Classic Fishing Tournament. Only teams which allowed detailed examination of their catch after the creel survey were included.

Nominated harvest category	Harvest within nominated category	Harvest differed from nominated category by <25%		Harvest differed from nominated category by >26% but <50%		Harvest differed from nominated category by >50%	
		Catch > Estimate	Catch < Estimate	Catch > Estimate	Catch < Estimate	Catch > Estimate	Catch < Estimate
1-50	16	5	N/A	2	N/A	6	N/A
51-100	3	3	-	2	2	2	-
101-200	2	-	1	1	1	1	-
TOTAL	21	8	1	5	3	9	0

Table 1.7: Percentage of harvesters who claim to release yabbies below three different sizes. Teams of harvesters were presented with a tray containing animals which were 35, 40 and 45 mm carapace width and asked to choose the size closest to that which they would discard animals collected during a harvesting event.

Yabby size (mm CL)	Amity Point (n=42)	One Mile (n=25)
7	92.5%	88.0%
8	47.6%	64.0%
9	21.4%	24.0%

Table 1.8: Frequency of different sized harvests by recreational harvesters at Wynnum. The red figures refer to harvests greater than 50 worms per person which is the in-possession limit.

Harvest Method	P	B&D	P	B&D	P	B&D	P	B&D
No. of people	1D	1D	1D, 1H	1D, 1H	2D	2D	>2P	>2P
1-50 worms	36	7	17	3	7	4	10	2
51-100 worms	29	9	9	8	11	5	5	3
101-150 worms	0	7	0	5	1	4	0	4
151-200 worms	0	2	0	3	2	3	0	0
> 201 worms	0	0	0	0	0	1	0	0

P= using pits as the harvesting method, B&D= using the "bail and dyke" as the harvesting method, D= digger, and H= helper.

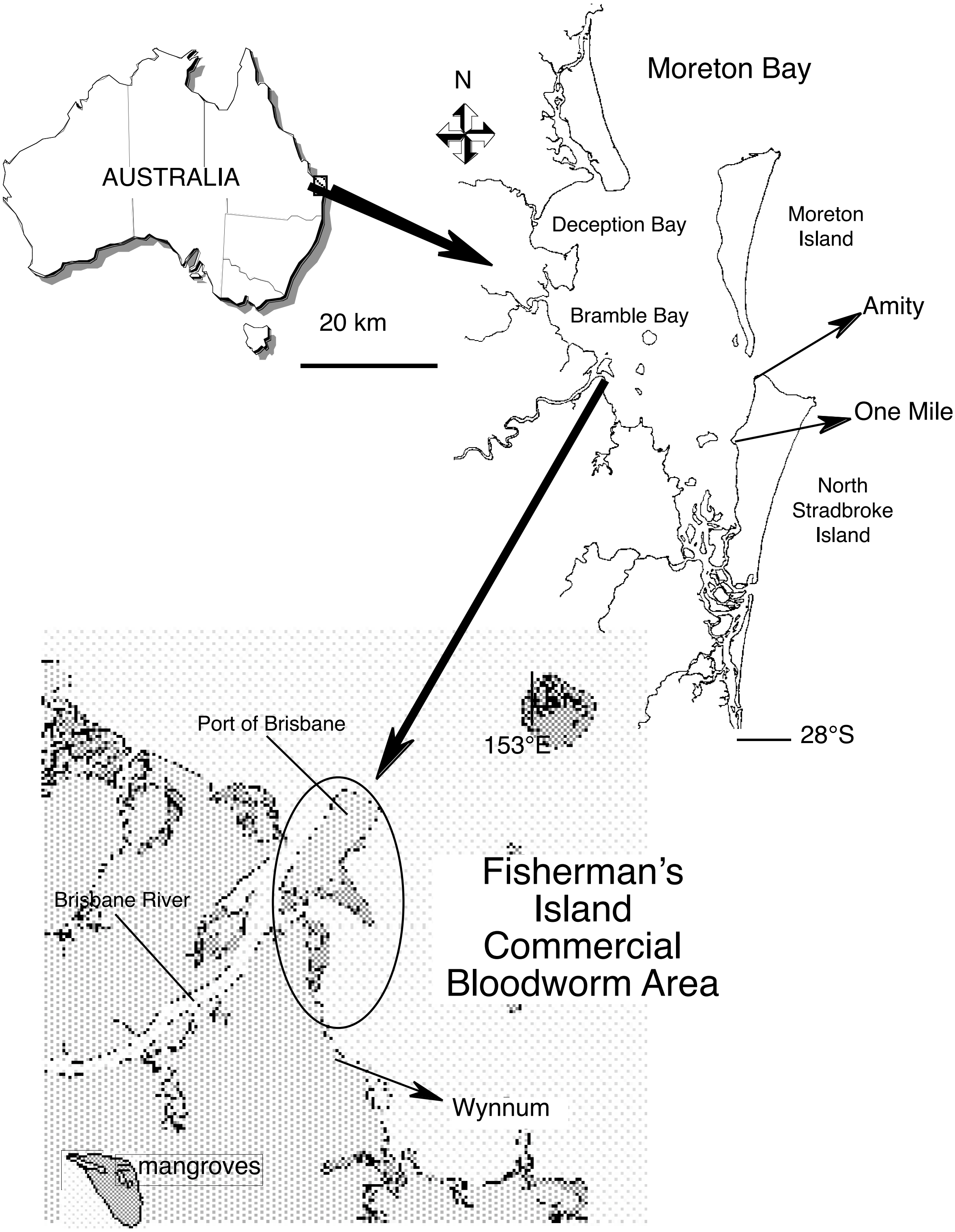
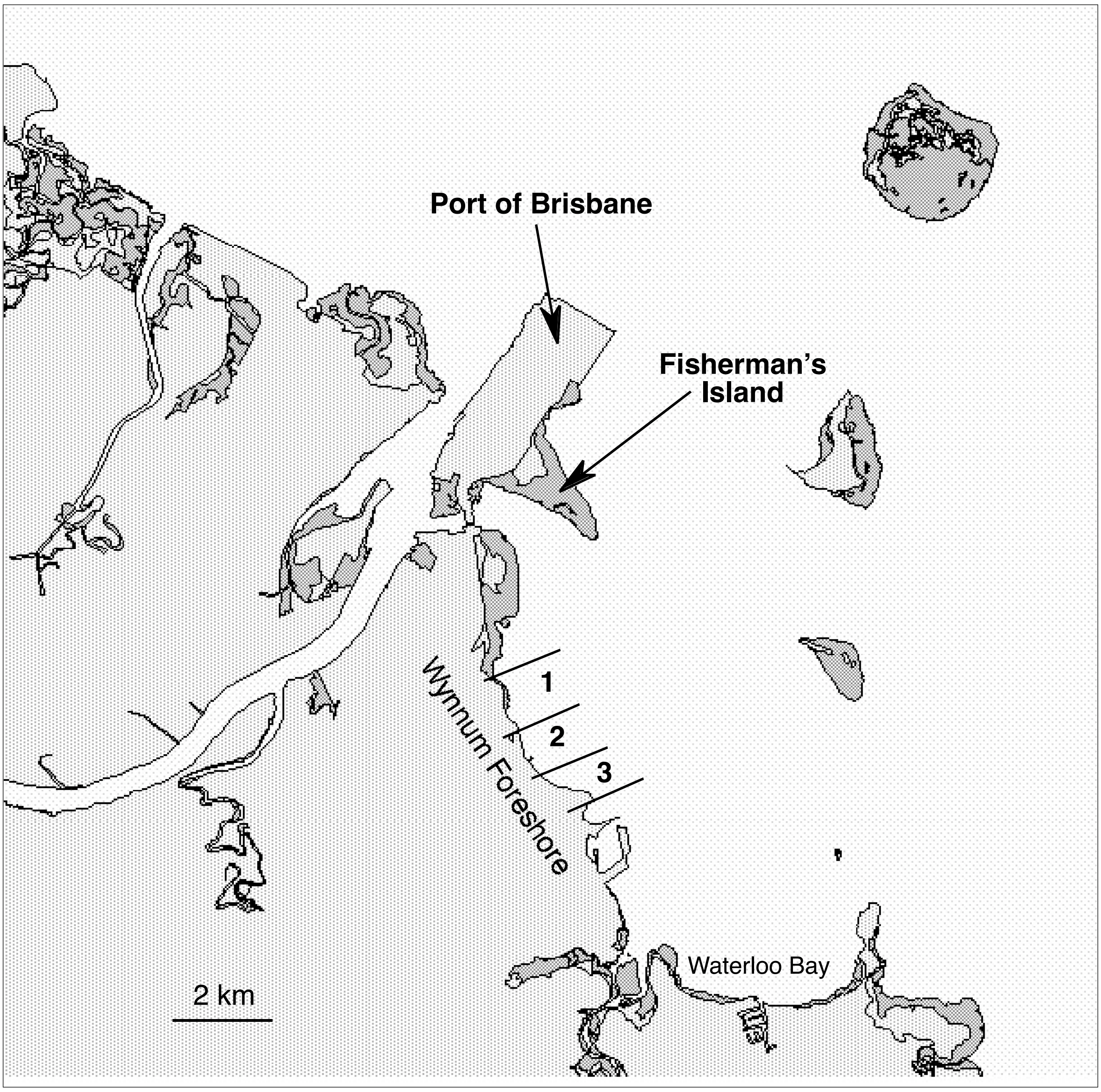


Figure 1.1: Map of Australia and the Moreton Bay region of SE Queensland showing the position of the Fishermen's Island Commercial Bloodworm harvesting areas and the sites used for examination of the harvesting of yabbies for a commercialised fishing competition and recreational harvesting of bloodworms. Harvesting of bloodworms occurs in intertidal seagrass, downshore from mangrove areas.



1 = Alex's Gutter to Wynnum Ck. groyne
2 = Wynnum Ck. groyne to Wynnum Jetty
3 = Wynnum Jetty to Darling Pt.

Figure 1.2: Map of the Moreton Bay region and the area around Wynnum where creel and observational surveys were don on fishers harvesting bloodworms from intertidal seagrass beds. The Wynnum foreshore was divided into three distinct zones based on the presence of distinct boundaries between the zones, used to define management zones by the Queensland Fisheries Management Authority.

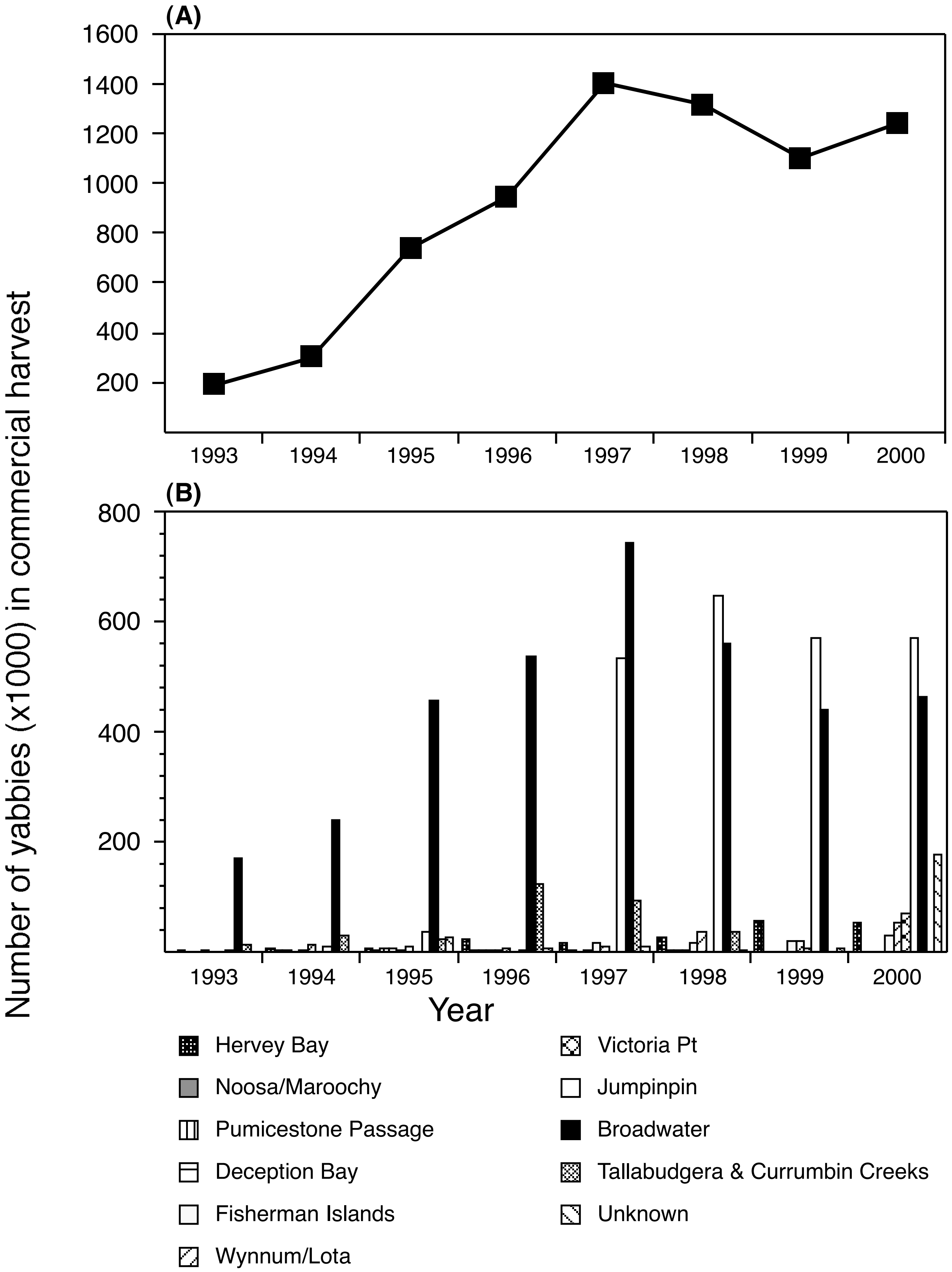


Figure 1.3: (A) Total annual catch (numbers x 1000) of yabbies harvested by commercial fishers and (B) annual catch at each of 10 major sites in SE Queensland from 1993 to 2000 based on commercial log-book returns. An additional category of unknown indicates that specific information on location was not available from log-book entries. See Figure 1.4 for position of each of the sites in SE Queensland.

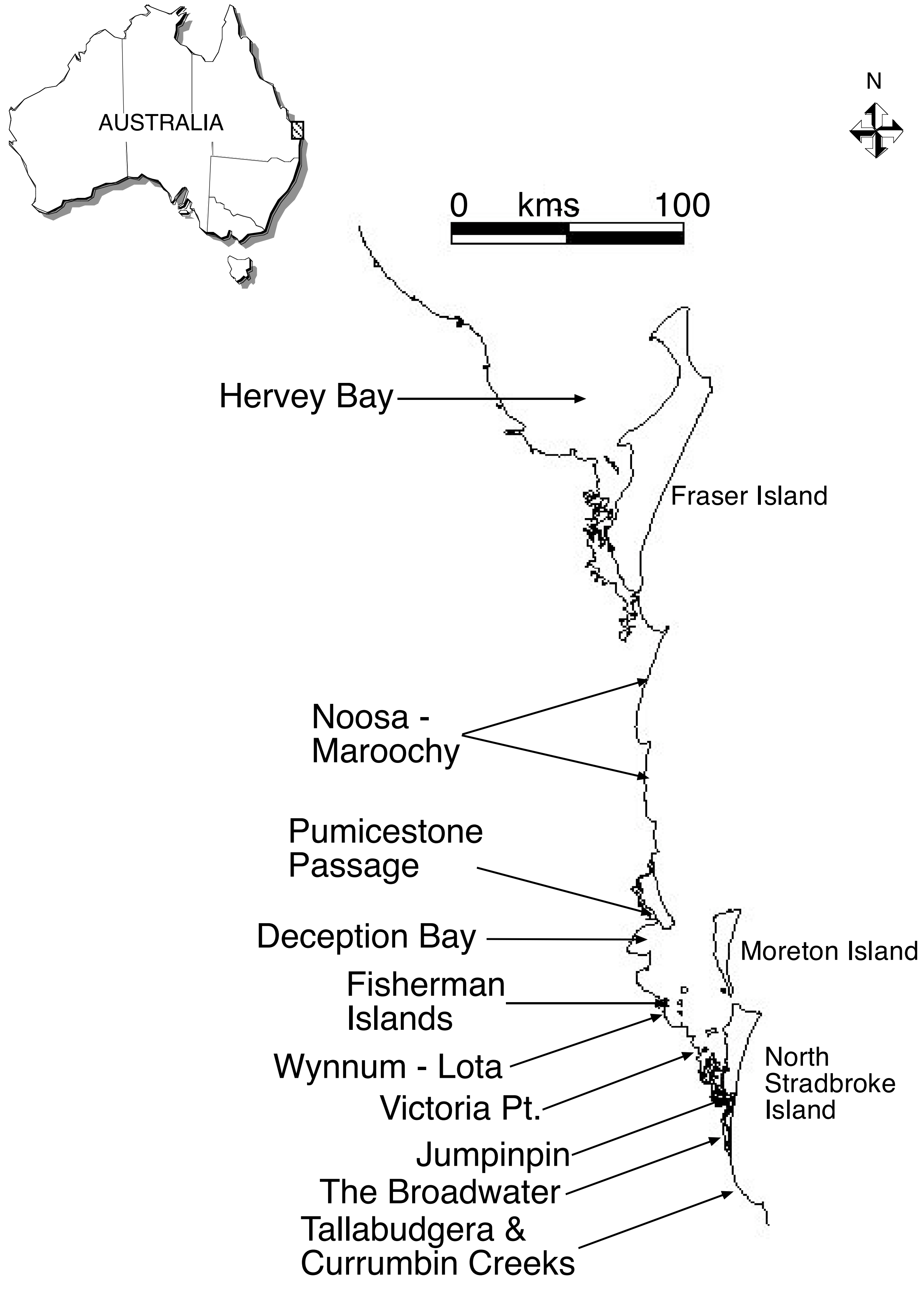


Figure 1.4: Map of SE Queensland showing the position of the major sites used by commercial yabby harvesters from 1993-2000, based on information in the commercial log-book returns. Some returns did not record the precise position of the sites in which harvesting was done and these were recorded as unknown (see Figure 1.3).

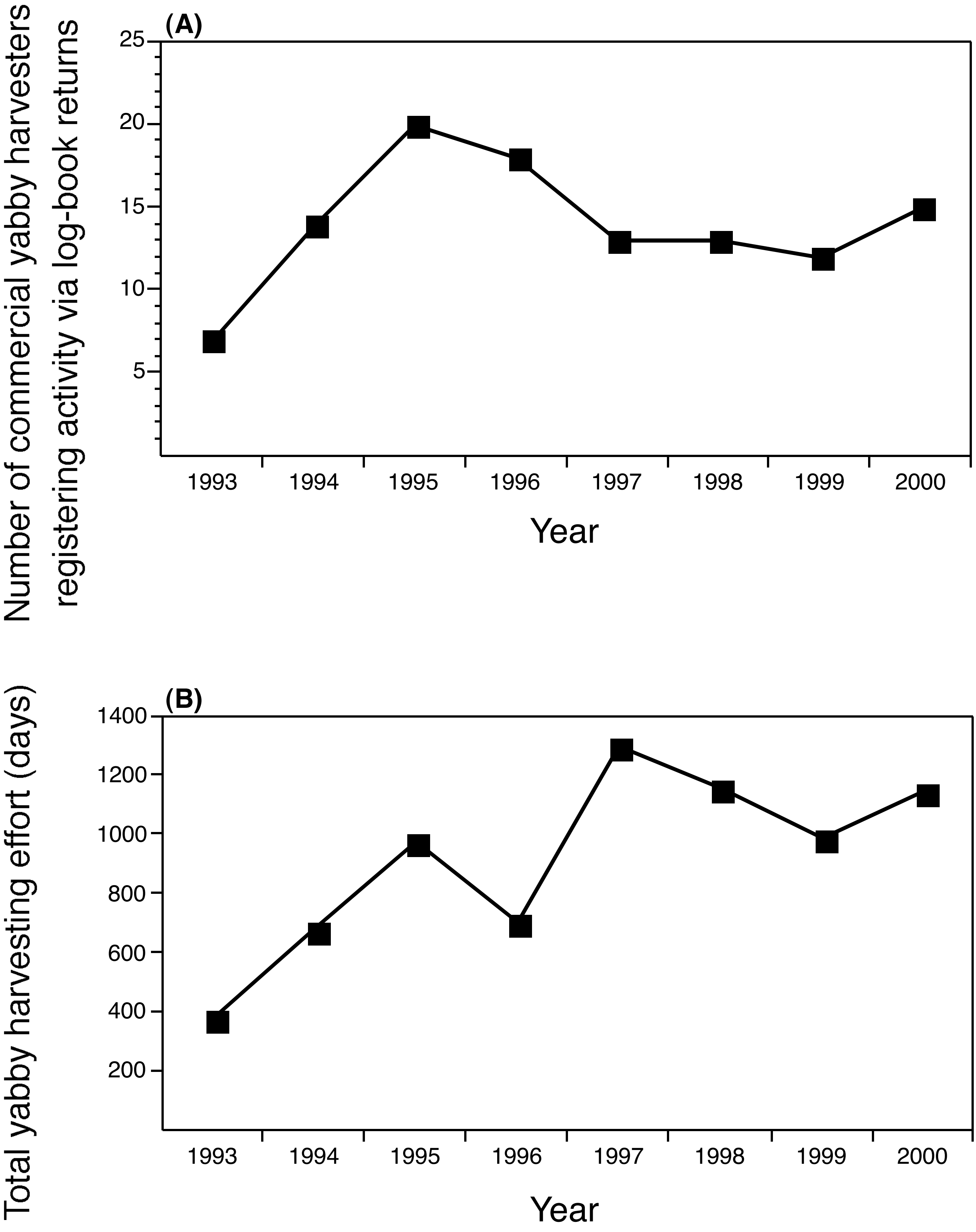


Figure 1.5: (A) Number of commercial yabby harvesters registering activity through log-book returns from 1993 to 2000. (B) Total annual number of days (effort) directed by commercial fishers towards harvesting of yabbies in SE Queensland between 1993 and 2000.

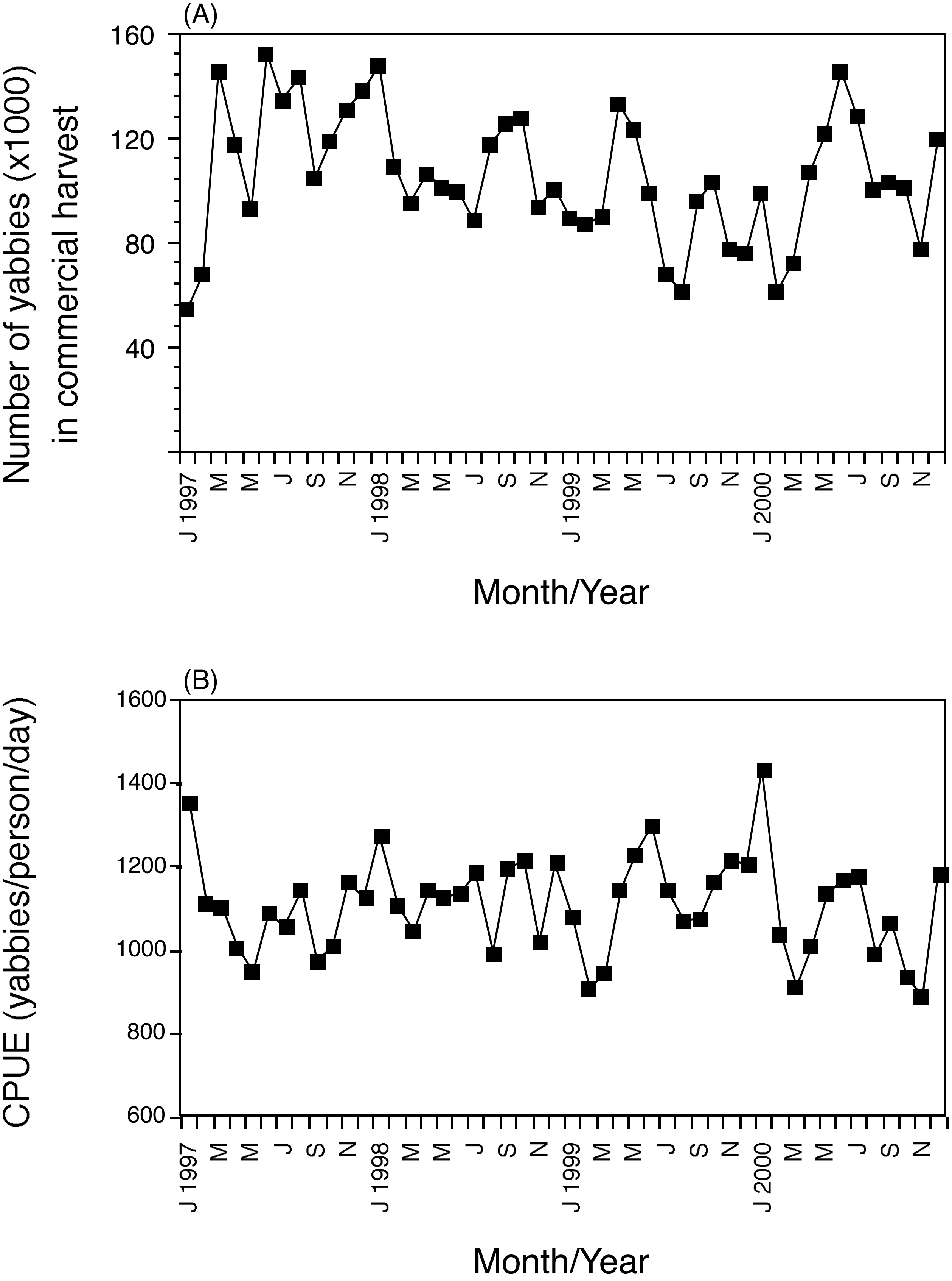


Figure 1.6: (A) Number of yabbies (x1000) harvested by commercial fishers on a monthly basis from January 1997 to December 2000 based on commercial log-book returns. (B) Monthly catch per unit effort (CPUE: yabbies per harvester per day) fro commercial harvesters working in SE Queensland. Monthly log-book returns were introduced in January 1997.

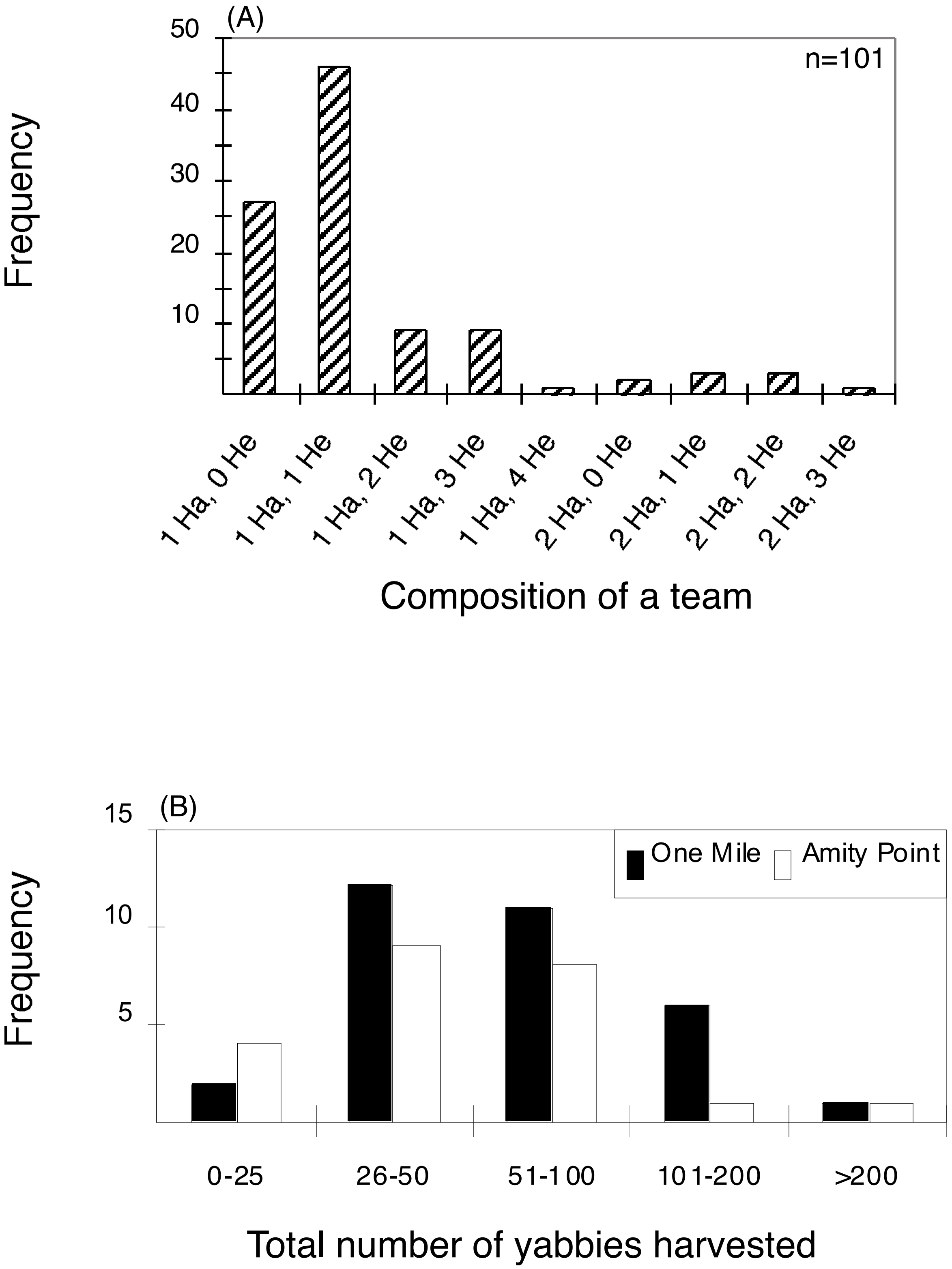
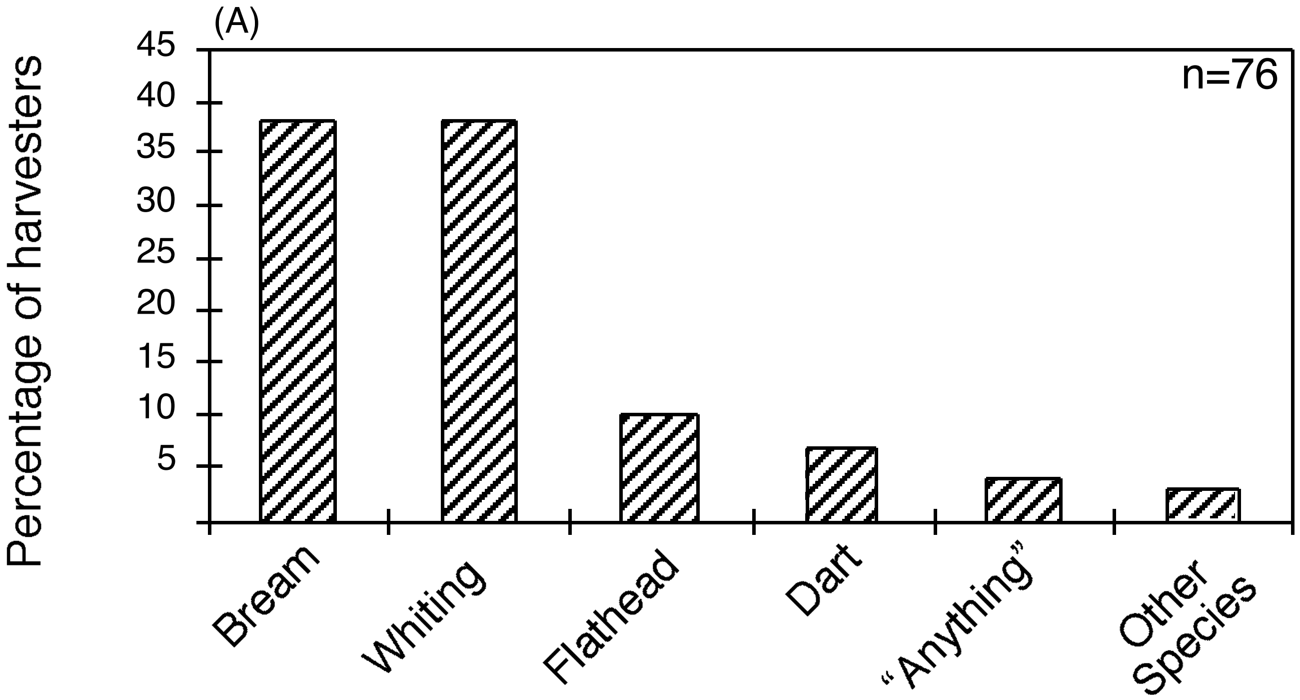


Figure 1.7: (A) Frequency histogram showing the size and composition of yabby harvesting teams participating in the 1998 Stradie Classic Fishing Tournament (Ha=harvester, He=helper. (B) Frequency histogram showing the magnitude of the harvest of yabbies for teams participating in the 1998 Straddie Classic Fishing Tournament at the two sites used by most groups.



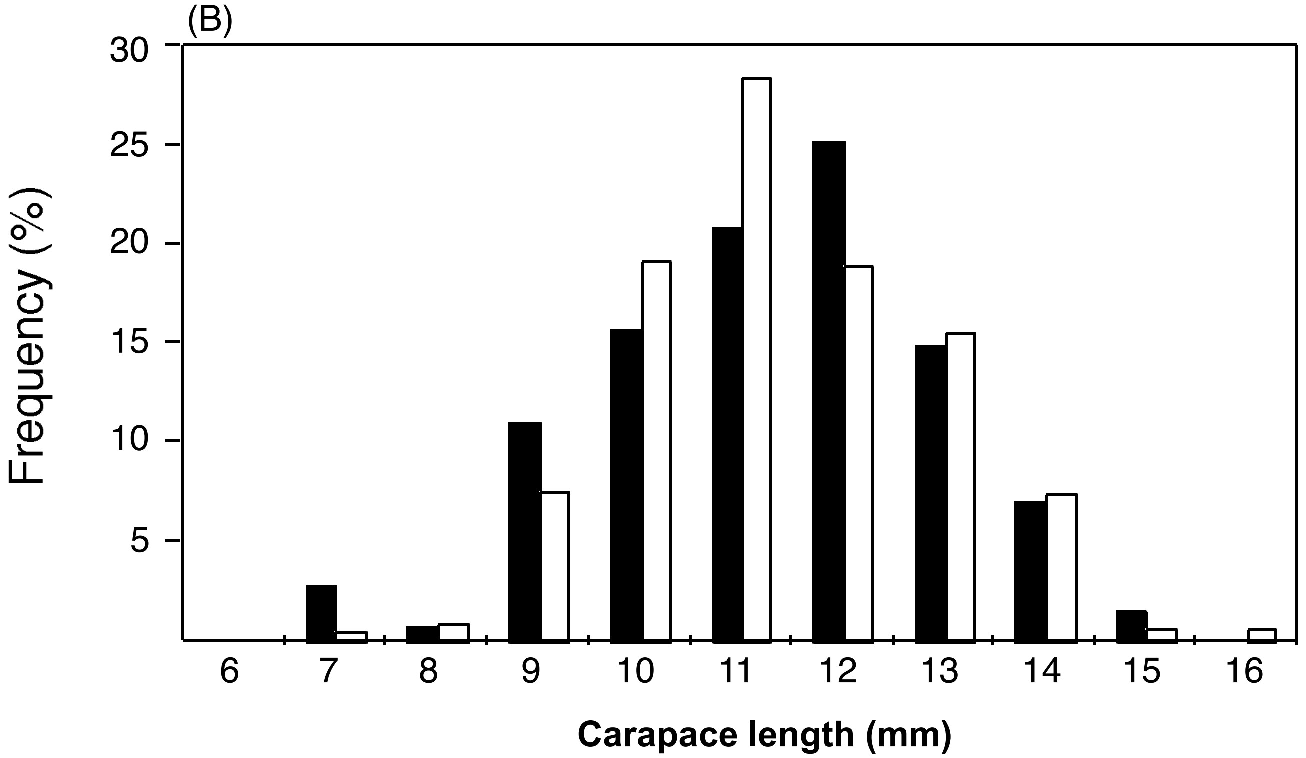


Figure 1.8: (A) Proportion of teams targeting different species of fish using yabbies harvested as bait during the 1998 Straddie Classic Fishing Tournament. (B) Size-frequency distribution of yabbies from Amity and One Mile harvested by tteams collecting bait for use in the 1998 Straddie Classic Fishing Tournament.

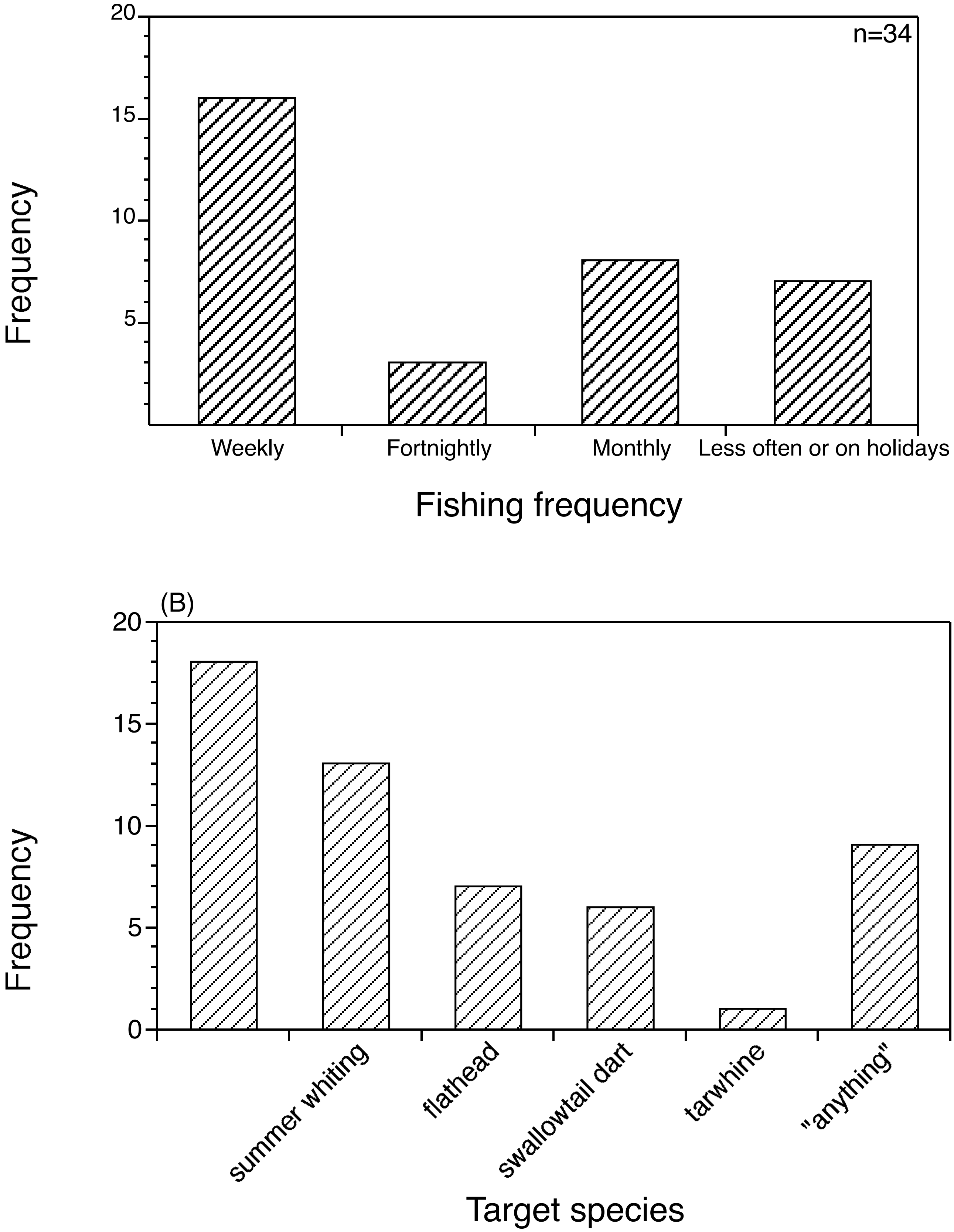
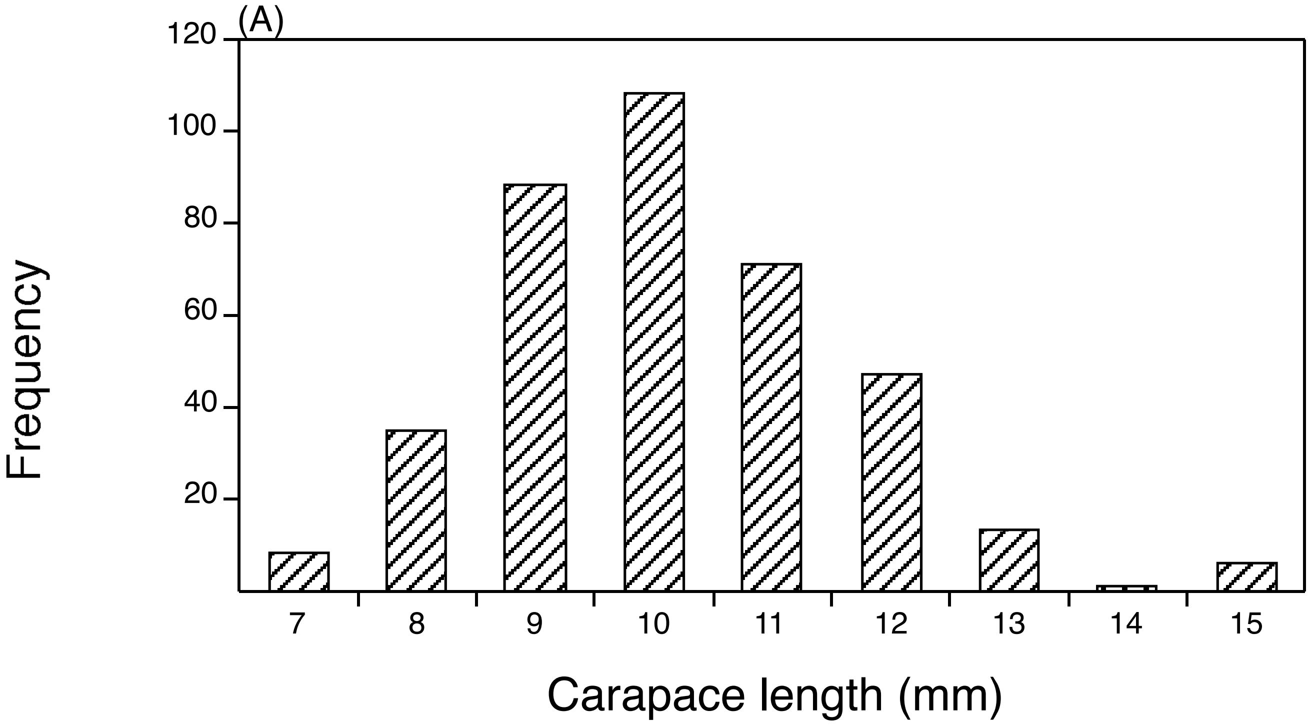


Figure 1.9: (A) Frequency histogram showing how often yabby harvesters participated in recreaetional fishing in Moreton Bay in 1999. (B) Proportion of teams targeting different species of fish using yabbies harvested for bait in Moreton Bay in 1999.



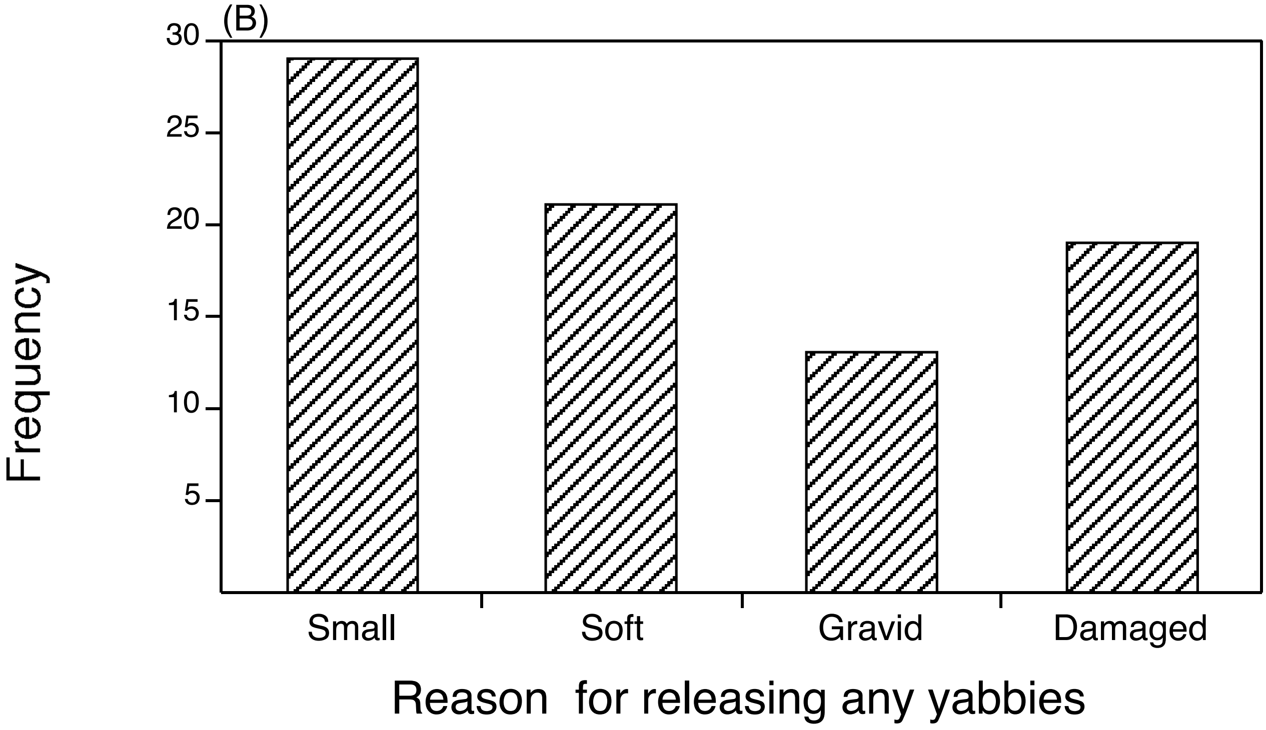


Figure 1.10: (A) Size-frequency histogram showing the size of yabbies harvested by recreational fishers in Moreton Bay during 1999. (B) Frequency histogram showing the relative importance of various reasons for why recreational harvesters released yabbies they had caught.

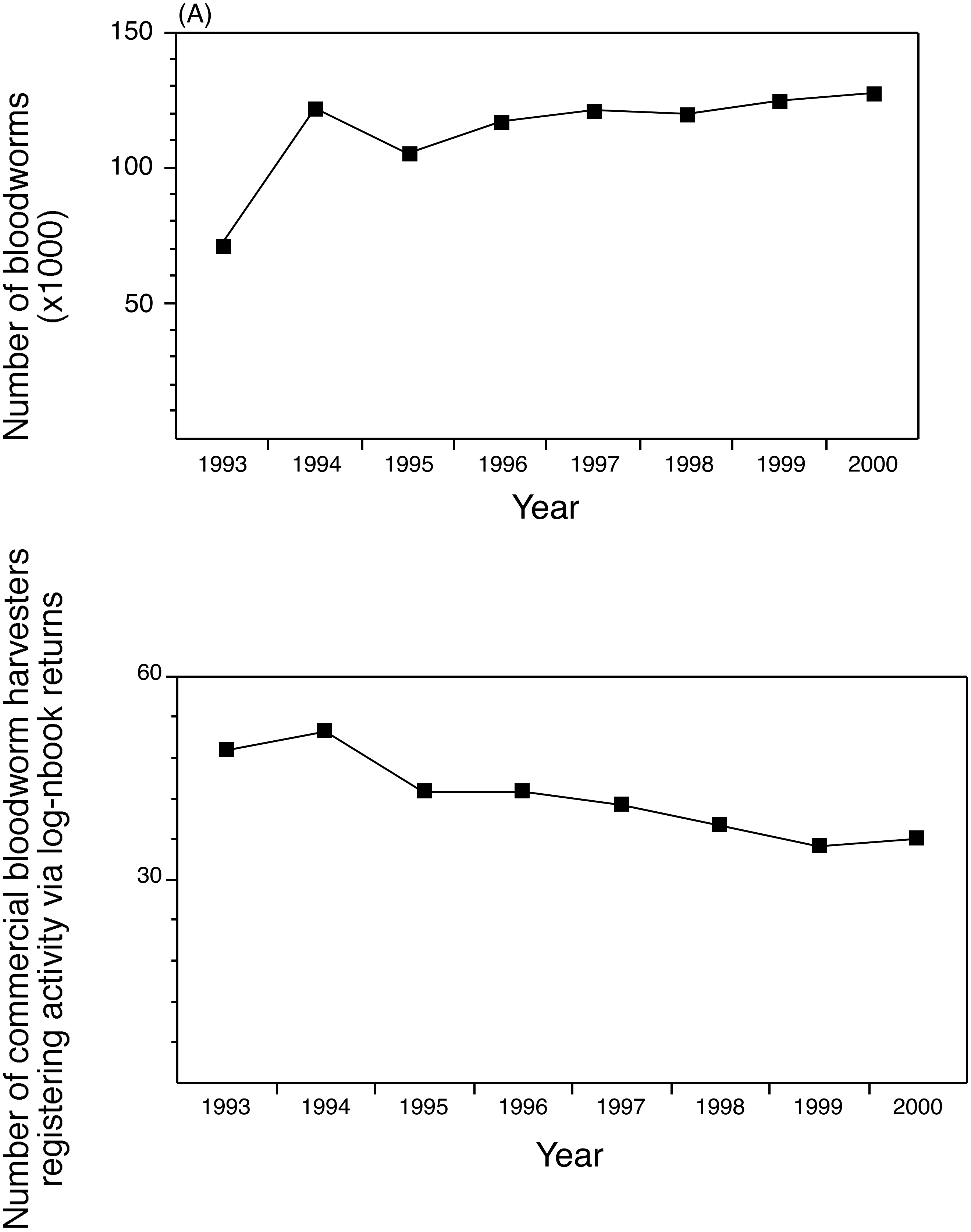
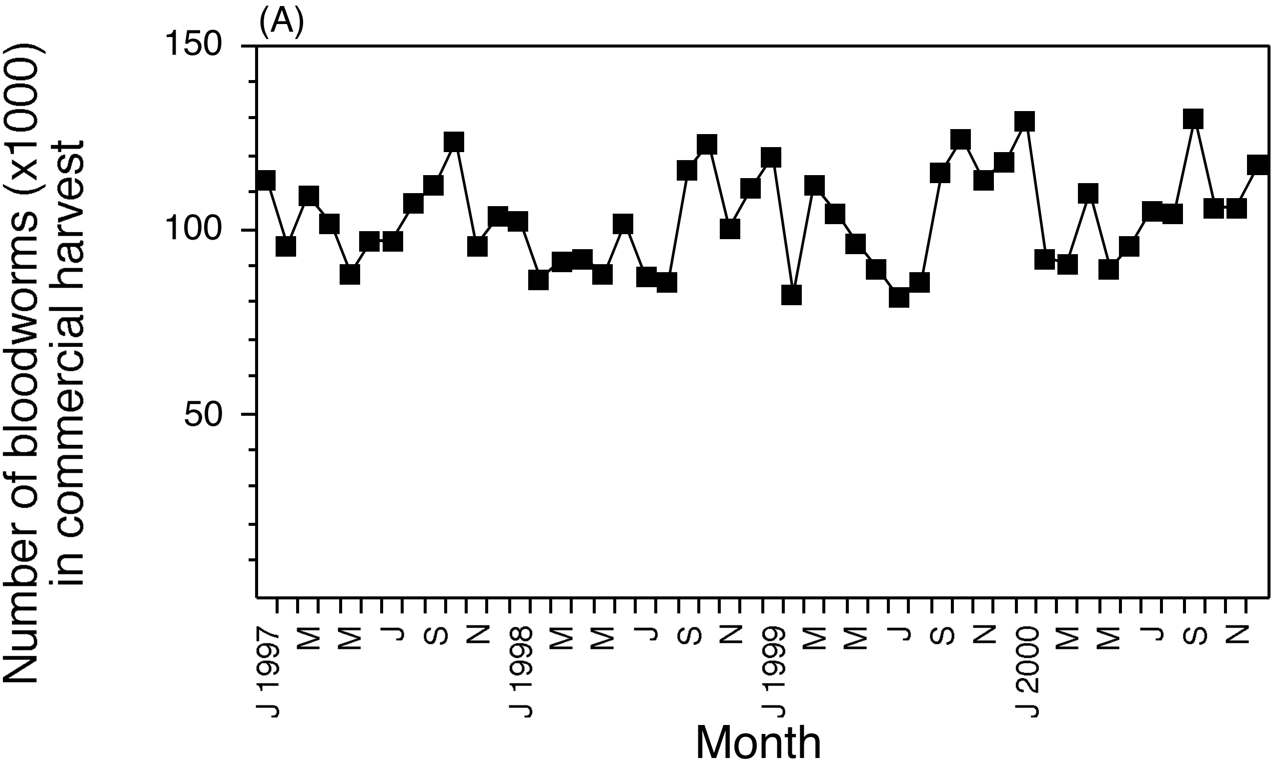


Figure 1.11: (A) Annual number (x1000)of bloodworms (*Marphysa* sp.) harvested by commercial fishers from 1993 to 2000 in Moreton and Hervey Bays based on commercial log-book returns. (B) Number of commercial bloodworm harvesters registering activity through log-book returns from 1993 to 2000.



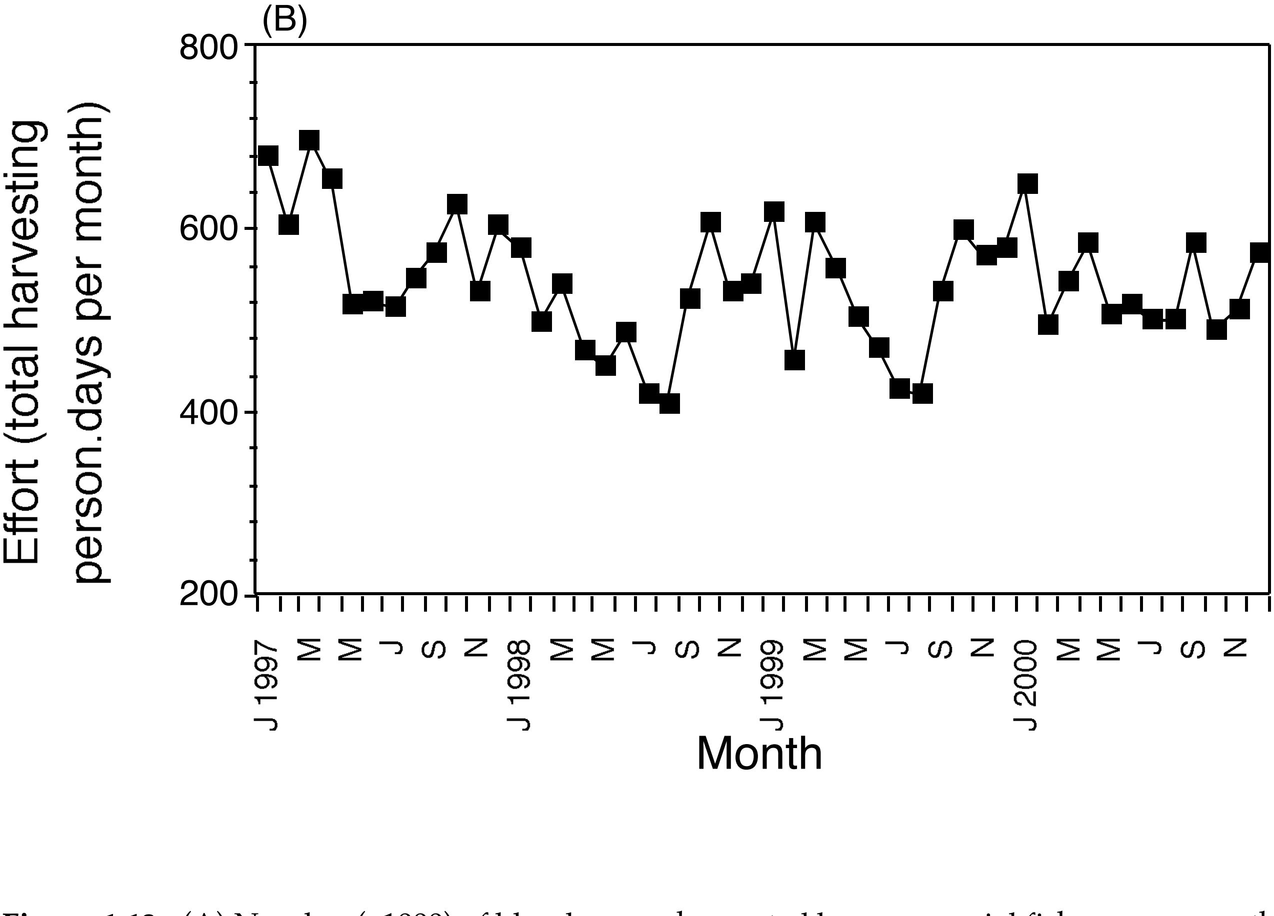


Figure 1.12: (A) Number (x1000) of bloodworms harvested by commercial fishers on a monthly basis from January 1997 to December 2000 based on commercial log-book returns. Monthly returns were introduced in January 1997. (B) Monthly effort (person.days per month fished) for commercial harvesters working at Fishermen's Island from 1997 to 2000.

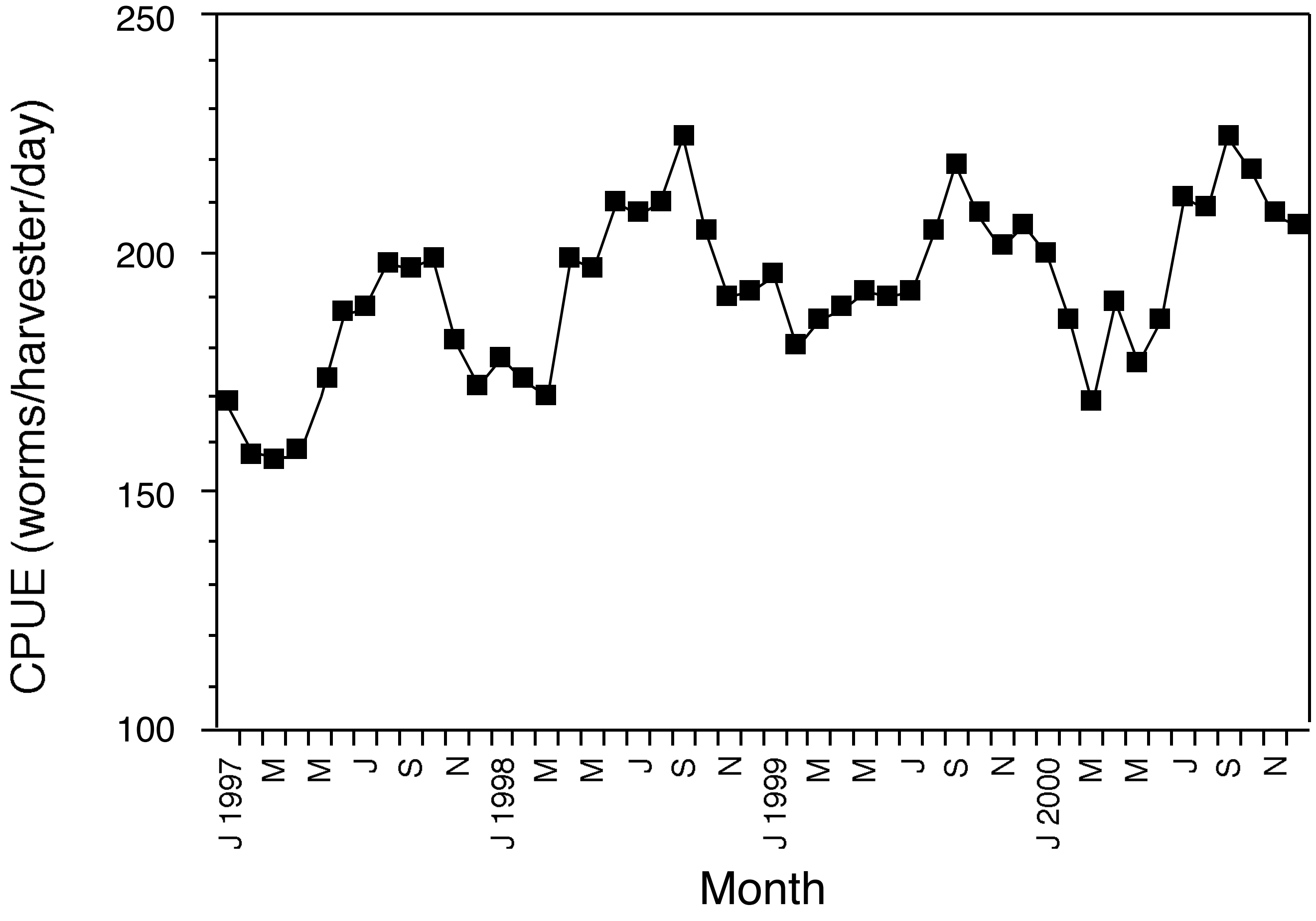


Figure 1.13: Monthly catch per unit effort (CPUE: worms per harvester per day) for commercial harvesters working at Fishermen's Island from 1997 to 2000.

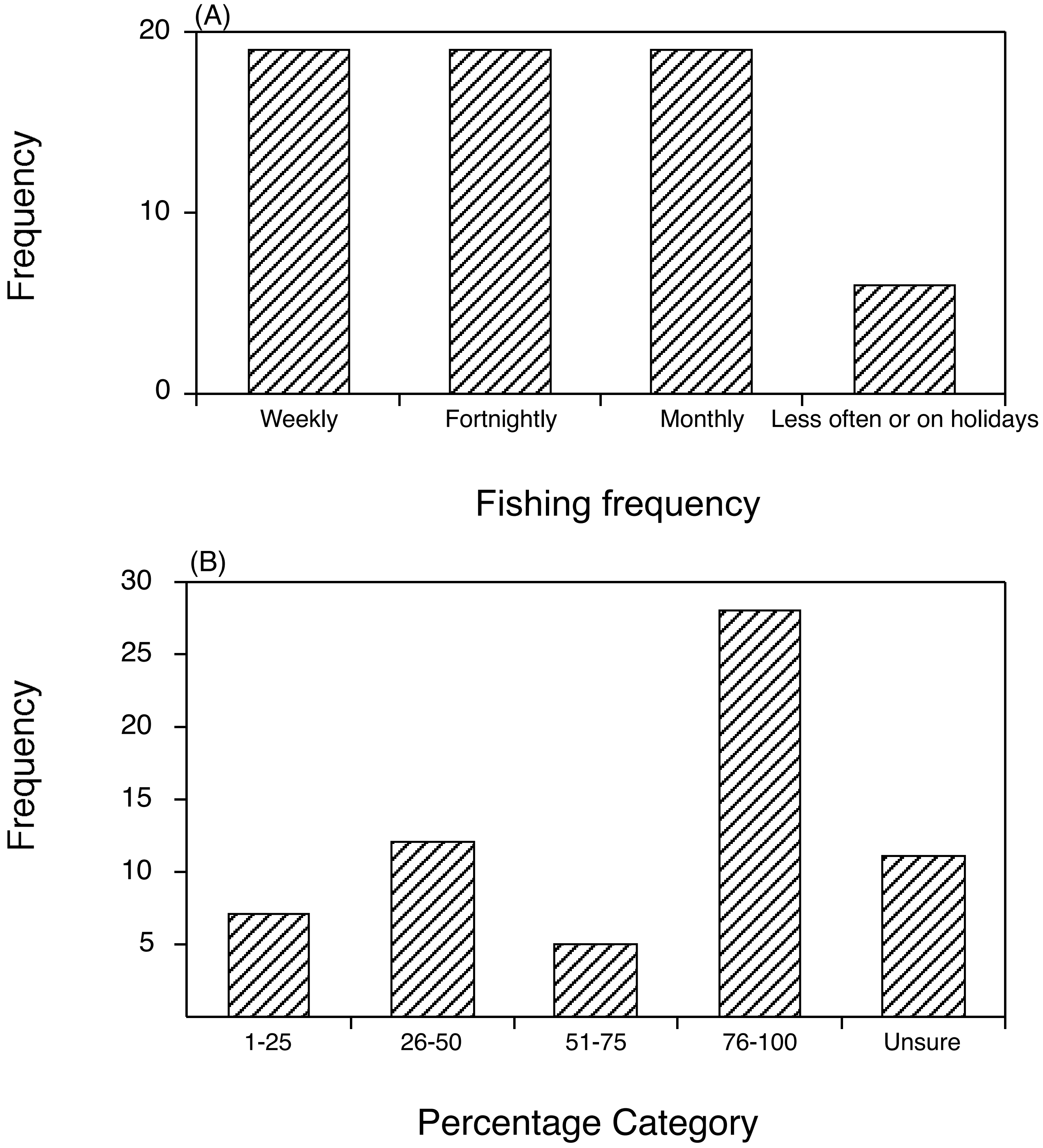


Figure 1.14: (A) Frequency histogram showing the frequency with which bloodworm harvesters collecting bait from Wynnum in 2000 and 2001 participate in recreational fishing. (B) The percentage of fishing trips for which bloodworms are harvested for use as bait by fishers working at Wynnum in 2000 and 2001.

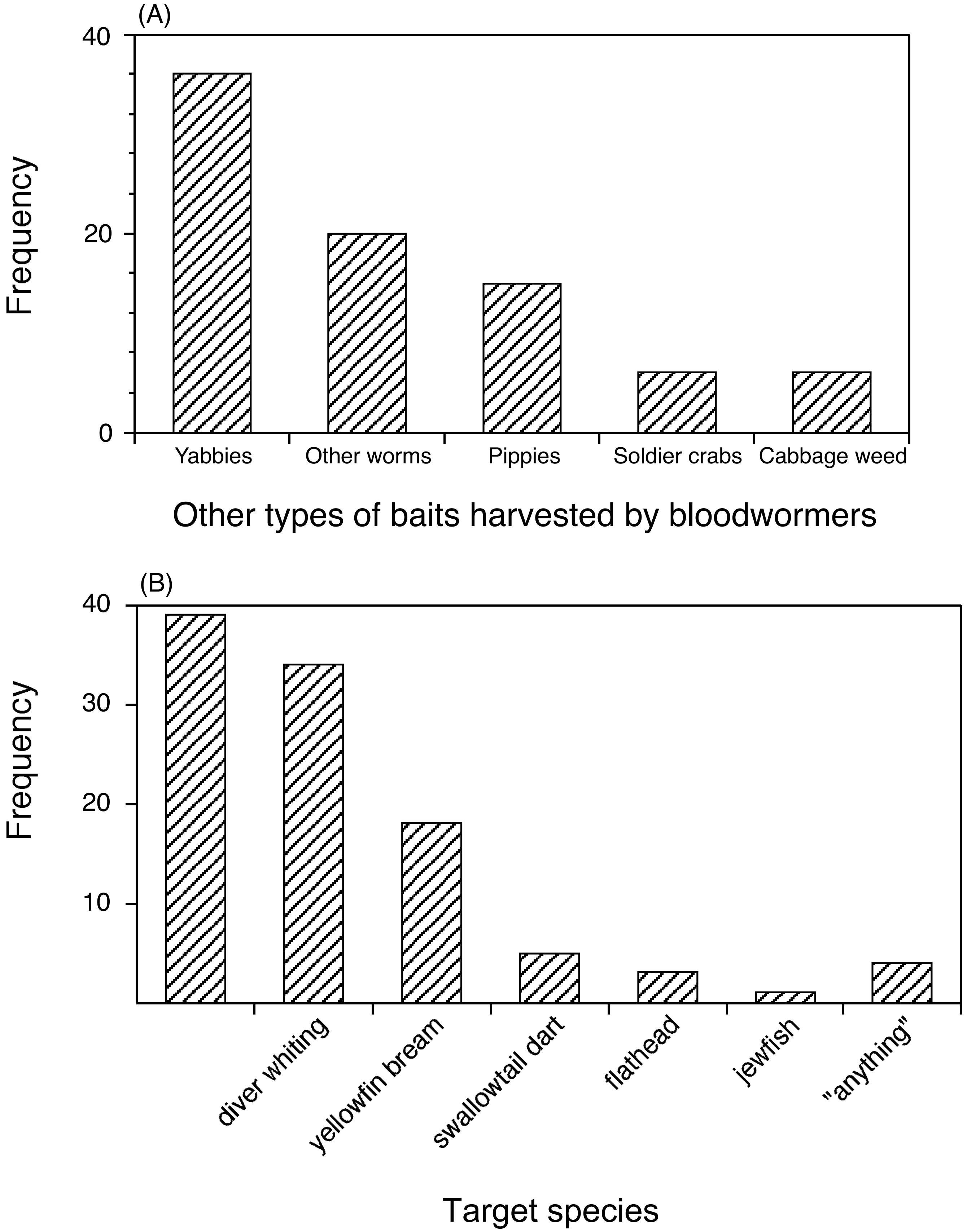


Figure 1.15: (A) Frequency histogram showing the frequency with which bloodworm harvesters collecting various groups of animals for use as biat from Wynnum in 2000 and 2001. (B) Proportion of bloodworm harvesters collecting bait from Wynnum in 2000 and 2001 targeting different species of fish using bloodworms as bait.

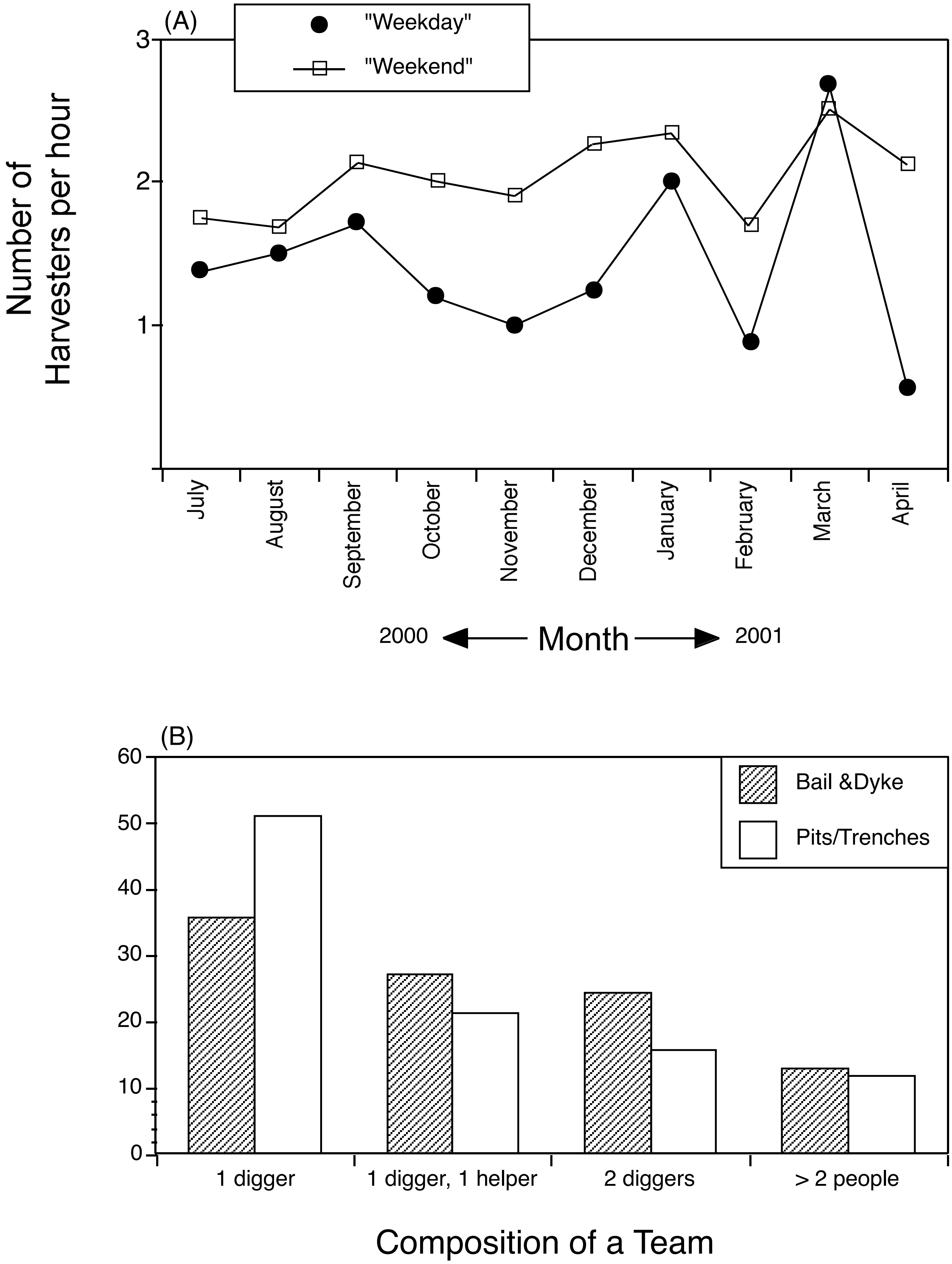


Figure 1.16: (A) Number of recreational harvesters per hour (summed over 3 day period divided by total number of hours of observation per month for each stratum: see Table xx) collecting bloodworms from the Wynnum foreshore (pooled across the three zones). (B) Histogram showing the size and composition of bloodworm harvesting teams collecting bait from the Wynnum foreshore between July 2000 and April 2001.

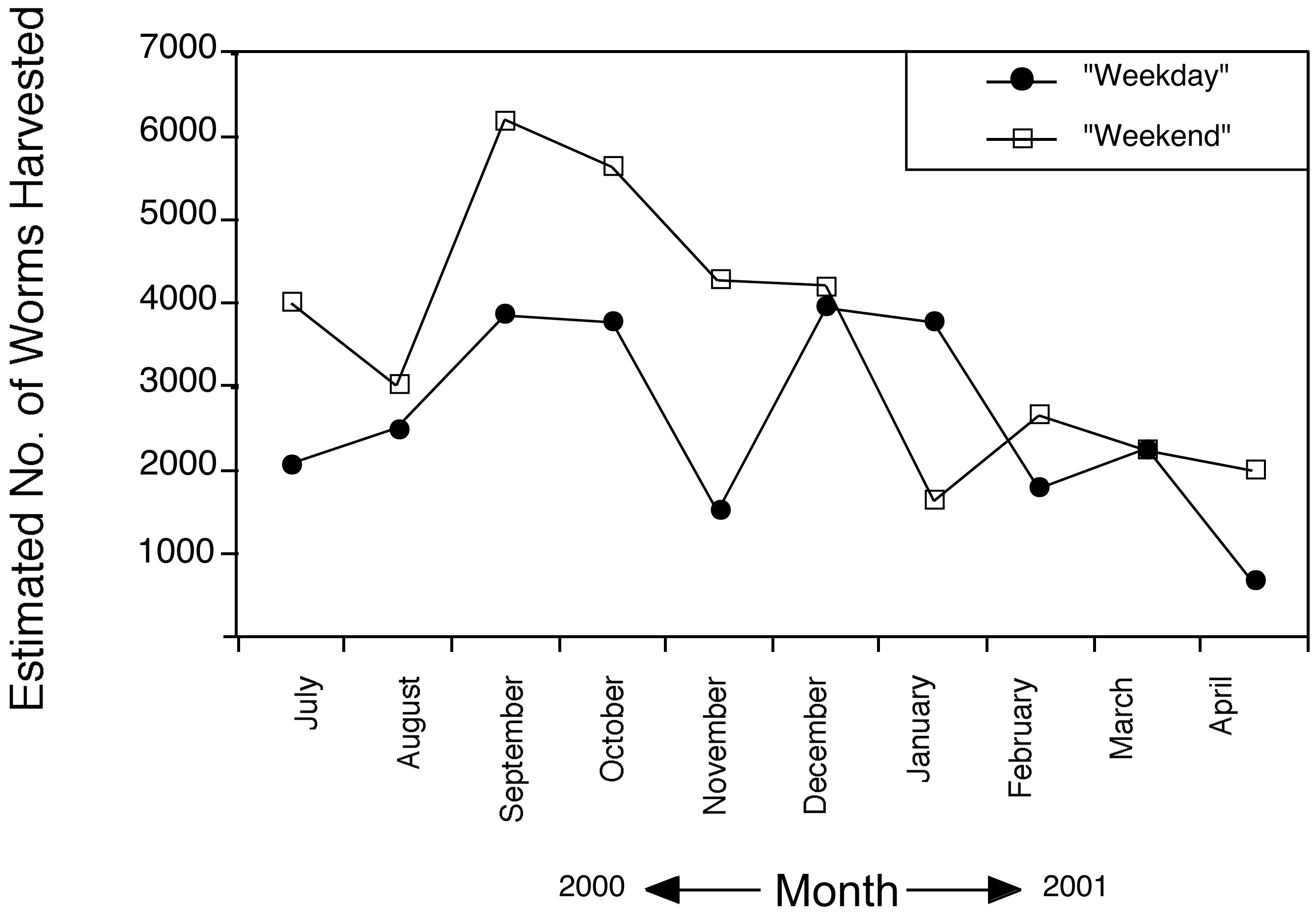


Figure 1.17: Total number of bloodworms harvested from the Wynnum foreshore based on observational surveys done on each of 3 days per month (July 2000 to February 2001) or 2 days per month (March-April 2001).

Section 2: Impacts Associated with the Harvesting of Yabbies

2.1. Introduction

The harvesting of invertebrates for use by recreational fishers is a widespread phenomenon around the world (e.g. Klawe and Dickie, 1957; Hailstone and Stephenson, 1961; Blake, 1979a, b; McLusky et al., 1983; Creaser et al, 1983; Forbes, 1984; Kingsford et al., 1991; Fairweather, 1991; Wynberg and Branch, 1991; Olive, 1993; Underwood, 1993; Van den Heiligenberg, 1987; Ambrose et al., 1998; McPhee and Skilleter, 2002) and has been associated with a broad range of different direct and indirect impacts on target species and other components of the ecosystem. These can be briefly categorised as: (i) direct effects on the populations of the species being exploited; (ii) indirect effects on other species which interact with the exploited species (e.g. use them as food); (iii) direct effects on other species in the habitats which are incidentally killed or injured during harvesting (i.e. by-catch) and (iv) direct and indirect effects due to habitat damage arising from harvesting (Underwood, 1993).

In Moreton Bay, SE Queensland and in other parts of Australia, large areas of seagrass and other intertidal habitat are dug over to collect yabbies (Callianassidae: *Trypaea australiensis*), bloodworms (Eunicidae: *Marphysa* sp.) and other invertebrates. This comprises a fishery, the products of which are sold to recreational fishers for bait. Large numbers of recreational fishers also dig their own bait, increasing the area of habitat that may be damaged or destroyed. Many of the habitats from which the bait is collected are important nursery areas for commercial species of finfish and decapods (Blaber & Blaber, 1980; Morton et al., 1987; Warburton & Blaber, 1992; Laegdsgaard & Johnson, 1995). Additionally, many of the other invertebrates that also live in these habitats and which may be affected by bait-digging, are important food items for these fish and crustaceans (Quinn, 1992; Shaw & Jenkins, 1992; Warburton & Blaber, 1992; Coull et al., 1995).

Whereas the impacts of commercial fishing on target organisms, the by-catch and other components of the ecosystem are now examined in an integrated manner, the impacts of recreational fishing have generally been related only to the size of the catch (see McPhee et al., 2002 and references therein). Impacts from other activities, in particular, bait-collection by commercial and recreational operators, have not been considered systematically in Australia, although there have been several detailed studies from elsewhere in the world that provide a basis for predicting that intensive harvesting of animals from such habitats is likely to cause significant impacts on the associated biota (e.g. Wynberg & Branch, 1991, 1994).

The impacts on benthic communities arising from harvesting related disturbances are likely to vary considerably depending on the nature of the habitat being disturbed, with fundamental differences apparent between hard and soft-substrata (Lake, 1990). Any disturbance in soft-sediments, whether caused by natural or human processes, has the capacity to cause marked modification of the habitat (Dayton & Oliver, 1980; Peterson, 1982; Skilleter, 1996) with direct effects on other taxa in the area. Jackson & James (1979) showed that digging for lugworms, *Arenicola marina*, in unvegetated sediments led to increased mortality of another commercially and recreationally important species, the cockle *Cerastoderma edule*, due to smothering and exposure on the surface during low tide. Similar effects on small bivalves were noted by Peterson (1976) in relation to harvesting of callianassid shrimp, *Callianassa californiensis*, in Californian coastal lagoons. Importantly, the effects of smothering after sediment resuspension have the capacity to affect juvenile and adult bivalves differentially with the former being more susceptible (Peterson, 1985). Removal of lugworms has also been shown to affect population fluctuations for some small species of infauna (Reise, 1983). A large proportion (~53%) of infauna exposed as a result of bait collection using a yabby pump may also fall prey to foraging gulls (Wynberg & Branch, 1991; see also Peterson, 1977 and Blake, 1979) suggesting the potential for indirect impacts to be widespread.

In this chapter, the effects of the harvesting of yabbies (*Trypaea australiensis*) on the abundance and composition of the benthic community of unvegetated sediments in subtropical Moreton Bay, SE Queensland were examined at multiple spatial scales, using a combination of mensurative and manipulative experiments. First, detailed sampling was done in an area that is used regularly for the harvesting of yabbies by fishers visiting North Stradbroke Island, near One Mile in the township of Dunwich. The abundance and composition of the benthic fauna in the harvested area was compared with that in two references areas, only accessed by bait fishers irregularly. Second, a focussed Before/After-Control/Impact study was done based around the annual, commercialised fishing competition, the Straddie Classic, also held on North Stradbroke Island. These competitions are open to the general public and anglers compete to catch the heaviest fish of various species. Up to 1,500 anglers may participate in these competitions which can last for a week. Bait for use in the Straddie Classic is often sourced from a few sites on North Stradbroke Island, including the One Mile area (McPhee & Skilleter, 2002) over a relatively short period of time. Third, information collected during the first two components of this study and from creel and observational surveys of the harvesting activities of fishers (McPhee & Skilleter, 2002) was used to design a large-scale, controlled manipulative experiment where yabbies were harvested from 1 hectare plots to examine the impacts on the benthic fauna.

2.2. Methods

2.2.1. Spatial Scales

A number of different spatial scales (Figure 2.1) was examined in this component of the work. These were selected based on other studies in the region demonstrating a large amount of variation in the abundance of benthic infauna at scales ranging from metres to hundreds of metres (Skilleter, unpublished data; see also Morrisey et al., 1992) and the distances over which harvesters moved when collecting bait (McPhee & Skilleter, 2002). These scales were incorporated explicitly in this study in order to test hypotheses about whether disturbance from harvesting led to increased or decreased spatial patchiness (e.g. Warwick & Clarke, 1993). Harvesters targeting yabbies and other infauna often search on the basis of visible cues, such as the density of burrow openings (personal observation). In this case, the expectation would be that one effect of harvesting would be to reduce spatial patchiness as harvesters would reduce large-density patches and ignore small-density patches. Alternatively, if the spatial distribution of burrow openings and animals is more uniform, then harvesters may cause an increase in patchiness by removing animals from some patches but not others (McPhee & Skilleter, 2002). The primary spatial scales included in each of the components of the study were: Locations (scale of kilometres), among Sites (within Locations; scale of 100's metres) and Plots (within sites; scale of 10's of metres).

2.2.2. Impacts Associated with Recreational Harvesting

In 1996, samples of sediment were collected to determine whether the abundance and composition of benthic infauna differed between an area regularly used for harvesting of yabbies compared with nearby areas where harvesting was infrequent or did not occur. One Mile (Figure 2.2) was chosen as the putatively impacted area because it was adjacent to the main boat ramp in the township of Dunwich on North Stradbroke Island. The area is readily accessible for bait collection by fishers using boating facilities and many visitors collected bait from this sandflat before traveling to other parts of the island for fishing. It was also the major area for collection of yabbies for use in the annual Straddie Classic Fishing Tournament (McPhee & Skilleter, 2002). Two other locations, Adam's Beach and Myora Springs (Figure 2.2) served as references areas because they contained a similar range of habitats to One Mile but little bait collection was done at either location (Curley, 1996; personal observations).

Samples were collected from two different heights on the shore, representing two distinct habitats. The mid-intertidal habitat was primarily an unvegetated area, in which most harvesting of yabbies occurred. The low intertidal area was dominated by *Zostera capricorni* intermixed with small amounts of *Halophila ovalis*. Observations of the activities of recreational fishers harvesting bait at One Mile (Sturkie, 1996), indicated that few harvesters ventured far into the seagrass beds to pump for yabbies, although yabbies do occur in these habitats (personal observation and see Results).

By sampling in the low-shore seagrass beds where little or no harvesting of yabbies occurs, the aim was to obtain an independent measure against which to assess whether any significant differences in the composition of the intertidal benthic assemblages at One Mile compared with the reference locations were likely to be due to bait-harvesting, or caused by other, larger-scale environmental effects. Any effects caused by, say, the presence of the boat-mooring area and associated jetty facilities at One Mile would likely affect organisms in the seagrass beds in addition to affecting the animals in the unvegetated sediments. In contrast, because harvesting of bait primarily occurs in the unvegetated areas, bait-harvesting is less likely to have a direct impact on the organisms in the vegetated areas compared with the unvegetated mudflats (Table 2.1). Samples from the seagrass beds would also provide information on whether juvenile yabbies were recruiting to vegetated areas lower on the shore, where harvesting rarely occurs.

The sampling programme incorporated four different spatial scales: among Locations (scale of kilometres), between Sites (within Locations; scale of 100's of metres), between Plots (within Sites; scale of 10's of metres) and among replicate cores (scale of metres) (Table 2.1). Four replicate cores (15 cm diameter x 10 cm deep) were collected from each of two plots in the sites in the seagrass and unvegetated habitats. Samples were fixed in 7% formalin/seawater containing the stain Rose Bengal. The sediments were then sieved across a 500 μm mesh sieve and the contents retained in the sieve were preserved in 70% ethanol until sorting.

2.2.2.1. Statistical Analyses

Data on the total number of individuals and the number of different taxa were analysed using three-factor asymmetrical analyses of variance to compare the abundance in the harvested location (One Mile) with the average of the two control locations (Myora and Adam's Beach). Two nested scales of sampling were incorporated into the design: sites within each location and plots within each site. Where possible, nested levels were pooled to increase the power of the test for specific differences among the locations (Winer et al., 1991). Additionally, 2-tailed F-tests were used to compare the amounts of variation at different spatial scales to determine whether there were differences in the patchiness of the fauna in the harvested location compared with the control locations (see Underwood, 1992).

Differences in community composition in the three locations were examined using NPMANOVA, a non-parametric multivariate analysis of variance (Anderson, 2001), based on the Bray-Curtis similarity measure on fourth-root transformed data and also for untransformed data. The patterns of dispersion (variability) of samples within the three locations were examined using NPDISP, a non-parametric test for multivariate dispersion (Anderson, in preparation), also based on the Bray-Curtis similarity measure on fourth-root transformed data. At present, these programs can only analyse data for a 2-factor design, so a two-stage process was used. First, variation between sites within each location was examined using a 2-factor analysis (Sites and Plots within Sites). None of these analyses showed significant variation at the scale of Sites ($P > 0.25$: but there was significant variation at the small scale of plots), so the final analysis examined variation among the three Locations with a single nested term of Plots, with 4 levels (pooled from the two sites). Differences in community composition were also examined graphically using non-metric multidimensional scaling (ordination) using the Bray-Curtis similarity measure on fourth-root transformed data (Clarke, 1993).

2.2.3. Impacts from Commercialised Fishing Competitions

Potential impacts on the benthic assemblages from bait-harvesting for the 1998 Straddie Classic Fishing Tournament were examined using a Before-After/Multiple Control – Impact experimental design (e.g. Underwood, 1993). The sampling design used was along the lines of the Beyond-BACI asymmetrical analyses described in Underwood (1993), except that additional spatial scales were included (plots nested within sites), because of the small-scale spatial variability known to occur in these estuarine soft-sediment assemblages (Skilleter, unpublished data). The specific aim of this component of the study was to determine whether the intensive bait-harvesting associated with the Straddie Classic Fishing Tournament (McPhee & Skilleter, 2002) caused significant changes in the abundance and composition of the benthic infaunal assemblage.

The design for this experiment incorporated the same spatial scales as in the general sampling described above (Section 2.2.2). Based on preliminary analysis of the data from the first part of the study, the number of plots per site was increased from two to four to account for the small-scale (10's of metres) spatial variability in the abundance of the dominant fauna. Samples were collected approximately one week before the start of the Straddie Classic and, again, one month after completion of the competition.

Within each of the three locations (One Mile, Adams Beach & South Myora), two sites were selected haphazardly, but ensuring they were at least 100-150 metres apart. Four replicate samples were collected from each of four Plots per Site in each Location. Plots were selected haphazardly, with the only criterion being that they were at least 2 metres from the nearest patch of seagrass (primarily *Zostera capricorni*).

From within each of the plots, the four cores of sediment for examination of the macro-infauna were collected using hand-held PVC corers pushed into the substratum. Samples were transferred to plastic containers and preserved within five hours of collection in a 7% formalin solution containing the red stain Rose Bengal for at least 10 days, then sieved across a 500 μm sieve, the fraction retained on the sieve examined under a dissecting microscope and all animals were removed, identified and counted.

2.2.3.1. Statistical Analyses

Data on the total number of individuals and the number of different taxa were analysed using four-factor asymmetrical analyses of variance (Beyond-BACI) to compare the pattern of change from Before to After (Period) the Straddie Classic Tournament in the harvested location (One Mile) to the average pattern of change in the reference locations (Underwood, 1992). Two nested scales of sampling were incorporated into the design: sites within each location and plots within each site. Where possible, nested levels were pooled to increase the power of the test for specific differences among the locations (Winer et al., 1991). Additionally, 2-tailed F-tests were used to compare the amounts of variation at different spatial scales to determine whether there were differences in the patchiness of the fauna in the harvested location compared with the control locations (see Underwood, 1992).

Detection of asymmetrical changes in the composition of the community using multivariate analyses is problematic because of current limitations in the complexity of designs which can be handled in available software. Ideally, analysis of the multivariate dataset would make use of the same logical approach used for single variables (e.g. abundances), but this was not possible. As an alternative, several different approaches were used to examine the nature of the changes in the community composition from Before to After the fishing tournament and whether these temporal fluctuations varied between the harvested location and the reference locations.

(1) For each location, data were analysed to determine if there were small scale (between sites and among plots) variation in community composition before and after the fishing tournament. In all cases, there was significant variation among the plots within each site, but there were no significant differences between the sites. The term for sites was therefore removed from subsequent analyses, and a single nested term for Plots was analysed (with 8 levels). Differences in community composition in the three locations after the Straddie Classic were examined using a 2 factor NPMANOVA, comparing the three locations, with a nested factor of plots within locations.

(2) The patterns of dispersion (variability) of samples within the three locations after the fishing tournament were examined using NPDISP, based on the Bray-Curtis similarity measure on fourth-root transformed data. Again, variation between sites within each location was examined using a 2-factor analysis (Sites and Plots within Sites). None of these analyses showed significant variation at the scale of Sites (but there was significant variation at the small scale of plots), so the final analysis examined variation among the three Locations with a single nested term of Plots, with 8 levels (pooled from the two sites). Differences in community composition were also examined graphically using non-metric multidimensional scaling (ordination) using the Bray-Curtis similarity measure on fourth-root transformed data.

2.2.4. Impacts from Bait-Harvesting – Controlled Experimental Harvesting

A controlled field experiment was done to determine the specific effects of harvesting of yabbies on benthic macrofauna and to allow comparisons with the results obtained from the sampling programmes detailed in Sections 2.2.2 and 2.2.3 above. One component of this experiment examined the impacts of bait-harvesting on large macrofauna (> 1mm in size) used as food by migratory shorebirds. These results are examined in detail in Section 6, later in the report. Here, impacts on the general benthic macrofaunal community (animals > 500 μm in size) are examined. Some results are repeated in both sections, for continuity of discussion and to avoid having to refer to other parts of the report.

The experiment was done at Chigill Chigill on the western shore of North Stradbroke Island, Moreton Bay between October 1998 and February 2000. Six 100 x 100 m (1 hectare) sites were permanently marked with 40 cm long wooden stakes pushed half-length into the substratum at the corners and half-distance in between. The sites were located at the same tidal height along a visually uniform stretch of the mudflat without any natural barriers (creeks, sloughs, etc). Adjacent plots were separated by 75-100 m. Three of the sites were designated at random for experimental manipulations and the remaining three sites served as controls that were undisturbed apart from sampling to determine the abundance of the benthic fauna (see below). The sites were sufficiently isolated from the nearest access point (> 2 km on either side of the study area) onto the mudflat to prevent any uncontrolled bait-harvesting within any of the plots.

Yabbies, *Trypaea australiensis*, were harvested from the experimental sites using a yabby pump, a device widely employed in the region by bait collectors (Hailstone & Stephenson, 1961). The usual procedure for collecting yabbies with a yabby pump is to push the unit into the substratum and extract the sediment, which is then dumped onto the substratum to collect suitable sized animals. Typically, the pump is pushed into the substratum at the same point a number of times. The harvester then moves to a new point and begins the process again.

Teams of two people, a pumper and a collector, worked through the experimental sites pumping in areas with visible yabby holes. The effort was roughly uniform among the three experimental sites and equaled ca. 4-5 pumper-hours per plot per harvesting event. All yabbies with a carapace length (CL) of 7+ mm were removed (98.2% of the total) from the sites and subsequently counted. Harvesting of the sites was done on eight occasions: November 1998, January, March, May, June, July, and December 1999, and February 2000.

Abundance of Yabbies and Soldier Crabs: To determine the abundance of yabbies in each of the six sites, exhaustive, controlled pumping was done using a yabby pump (McPhee and Skilleter, 2003). The number of pumps needed to extract all the yabbies from a single point was determined in a previous study in the same region (Skilleter, unpublished data). The pumps at a single point were considered as a set. The number of sets needed to harvest all the yabbies in a 2 x 2 metre (4 m^2) quadrat was determined from a pilot experiment where the cumulative percentage of yabbies harvested from a quadrat was plotted against the number of sets completed. These data indicated that complete harvesting of a 4 m^2 quadrat required 18 sets of 7 pumps per point.

The density and size-structure of yabbies were estimated in each of the six sites at the beginning of the experiment in October 1998 and on five other occasions: March, July, August and December 1999 and February 2000. Estimates were obtained in each of ten 4 m^2 quadrats per plot on the first five occasions and in fifteen 4 m^2 quadrats on the final occasion. Sediment collected from each of the quadrats was passed through a 2.0 mm sieve and the retained yabbies were stored. In the laboratory, yabbies were counted and their carapace length (from the tip of the rostrum to the end of the carapace) measured with calipers to the nearest millimetre. Densities of the Indo-Pacific soldier crab, *Mictyris longicarpus* (Latrielle) were also estimated using this method. The method of sampling used here captured *T. australiensis* and *M. longicarpus* with the carapace length of ≥ 2 mm and ≥ 5 mm respectively.

Abundance of Infauna: The abundance of small benthic infauna in each of the six sites was determined on three subsequent occasions, October 1999, January and May 1999 (Times 1-3). On each occasion, 5 replicate cores were collected to a depth of 15 cm into the substratum, at three haphazardly selected plots within each site, using a 15 cm diameter PVC core. Each plot was at least 10 metres apart. All cores were preserved in 4% Rose Bengal-stained formaldehyde solution, then sieved across a 1000 μm and 500 μm mesh sieve and the retained organisms identified to various taxonomic levels. The data from the 1000 μm sieve were examined in detail in relation to shorebird foraging (see Section 6 below). The data from the material retained on the 500 μm mesh sieve (including those animals retained on the 1000 μm sieve) were analysed in relation to more general impacts associated with bait-harvesting.

Abundance of Deep-Burrowing and Mobile Fauna: Sampling using small hand-held cores, taken to a depth of 15 cm, does not adequately estimate the abundance of those animals that are able to burrow deep into the substratum, nor those that are more patchily distributed and more mobile than the relatively sedentary small infauna. Estimates of the abundance of these taxa were obtained at the end of the experiment, using the method developed for yabbies. All the material collected using exhaustive pumping (described above) from 15, 4 m^2 quadrats per plot, was sieved across a 2 mm mesh sieve, fixed in formalin and sorted in the laboratory.

2.2.4.1. Statistical Analyses

Data on the abundance of yabbies, estimated from the stock assessments, were analysed with a three factor, hierarchical mixed model ANOVA, with factors Time (fixed; a=6 levels), Treatment (fixed; b=2 levels), Site (random, nested in Treatment; c=3 levels) with n=10 quadrats sampled per site on each occasion. On the final date, where 15 quadrats were sampled, a random subset of these data was chosen for the analysis to maintain a balanced design. For this, and all subsequent analyses, post-hoc pooling of mean square estimates was used to increase the power for specific terms in the ANOVAs following the principles detailed in Winer et al. (1991). Comparisons of the size-frequency distributions of yabbies in the control and harvested plots were done with two-sample Kolmogorov-Smirnov tests, on the pooled data from the animals harvested from the three plots per treatment on each of the eight harvesting events.

Data on the abundance of infauna were analysed with four factor, hierarchical mixed model ANOVAs, with factors Time (fixed; a=3 levels), Treatment (fixed; b=2 levels), Sites (random, nested in Treatment; c=3 levels) and Plot (random, nested in Time x Plot(Treatment); d=3 levels) with n=4 cores sampled per site on each occasion. Additionally, 2-tailed F-tests were used to compare the amounts of variation at different spatial scales (1 hectare Sites within each treatment and Plots within each Site) to determine whether there were differences in the patchiness of the fauna under harvesting compared with the control sites (see Underwood, 1992).

Data on the composition of the benthic assemblage in the control and harvest sites were analysed separately on each of the three occasions (October 1998, January and May 1999) using two-factor, non-parametric multivariate analyses of variance (NPMANOVA, Anderson, 2001) on fourth-root transformed data. The factors were Treatment (fixed) and Plots (nested within treatment, random). The patterns of dispersion of samples within the two treatments were examined with NPDISP on fourth-root transformed data. Again, data were analysed separately for each of the sampling periods. A two stage process was used because of the current limitations in the complexity of the designs that can be analysed. First, variation among Treatments and Sites within each Treatment was examined using a 2-factor analysis. None of these analyses showed significant variation at the scale of Sites, so the final analysis examined variation between the two Treatments with a nested term of Plots, with 9 levels (3 plots from each of 3 sites per treatment).

2.3. Results

2.3.1. Impacts Associated with Recreational Harvesting-Mudflat

2.3.1.1. Distribution of juvenile yabbies:

Of the 214 juvenile yabbies sampled from the mudflat and seagrass habitats in the three locations in 1996, 91% (195 juveniles) were from the mudflat habitat. Although based only on a single time of sampling, this observation suggests that recruitment of the common yabby, *Trypaea australiensis*, is primarily in unvegetated habitats, where the adults are most abundant. Harvesting effort by recreational fishers is generally focussed away from vegetated areas, partly because of the increased difficulty in extracting yabbies from among the vegetation due to interference by the roots and rhizomes, but also because of the reduced numbers of animals that are found there.

2.3.1.2. Effects on abundance and diversity

Despite the sustained and regular harvesting of yabbies from the mudflats around One Mile, North Stradbroke Island, there was no indication that this was associated with significant differences in the abundance or diversity of macrofaunal animals in the sediments there compared with similar habitats in places rarely used for bait-harvesting. There was considerable variation in the abundance of animals between the two reference locations. Eight of the 13 variables analysed showed significant differences in abundance between the two reference locations (Table 2.2; Figure 2.3 and 2.4). The magnitude of the differences between the two reference locations often exceeded those between the reference locations and the harvested location (One Mile) (e.g. numbers of gastropods – Figure 2.3D; numbers of *Tellina diluta* – Figure 2.3E; numbers of capitellid polychaetes – Figure 2.3G). In some cases, there was a trend towards more animals in the harvested location than either of the control locations (e.g. number of individuals – Figure 2.3A; number of gammarid amphipods – Figure 2.3B; number of polychaetes – Figure 2.3F; number of oligochaetes – Figure 2.3H), but these differences were not significant (Table 2.2). As an example, the total number of individuals at One Mile (harvested location) was 21-45% greater than at either of the two reference locations, but these varied by 30%. The significant variation in the abundance of animals between the controls would reduce the power to detect any significant impact, given the variance associated with the reference locations forms the denominator for the appropriate F-test (Underwood & Chapman, 2003).

The numbers of species of bivalves (Figure 2.4A) and gastropods (Figure 2.4B) and the number of families of polychaetes (Figure 2.4C) at One Mile (harvested) were intermediate between the levels observed at the two control locations and no significant difference in these measures of richness were detected between the harvested location and the average of the reference locations (Table 2.2). The number of species of bivalves and gastropods varied significantly between the two reference locations.

For six different groups (numbers of gammarid crustaceans, bivalves, *Tellina diluta*, polychaetes, capitellid polychaetes and numbers of bivalve species), there was significantly more variation evident among the plots (10's of metres) in the harvested location compared with the reference locations. That is, the abundance of these groups was significantly more variable (patchy) at this small scale in the harvested location than elsewhere. In one case, the number of bivalve species (Table 2.2), there also a significant difference in the spatial variation at the scale of sites (100 metres apart), again with the harvested location being more patchy than the reference locations.

2.3.1.3. Effects on community composition

The composition of the benthic community varied significantly among each of the three locations (NPMANOVA, $P < 0.001$, Figure 2.5A) but there was no indication that the harvested location (One Mile=OM) was any more distinct than the two reference locations (Adam's Beach=AB; Myora Spring=MS) were from each other (AB vs OM, $P<0.035$, MS vs OM, $P<0.03$, AB vs MS, $P<0.01$). There was also significant variation at the smaller spatial scales within each of these locations (NPMANOVA, $P < 0.001$). The most discrete grouping of samples was for Myora, one of the reference locations (Figure 2.5A), with some overlap in the ordination for samples from Adam's Beach (reference location) and One Mile (harvested location: Figure 2.5A).

There were no differences in the patterns of dispersion among the three locations at any of the spatial scales examined: among samples within locations, among samples within plots, nor among the plots within a location. Generally speaking, this indicates that the variability within and among plots in each of the three locations was similar (Figure 2.5B), with no indication that community composition was more patchy in the harvested location than in the reference locations, despite the findings for individual taxa described above.

2.3.1.4. Comparisons with Seagrass

The results from the analysis of the data from the mudflat (Section 2.3.1.2) indicated that the distribution of some taxa was significantly more patchy at the spatial scale of plots in the harvested location (One Mile) than in the reference locations. If this increased patchiness on the mudflat was linked to the harvesting activities rather than larger-scale environmental disturbances (e.g. boat-mooring area, jetties, etc.) which occur in the vicinity of One Mile, then the prediction was that these taxa would show different patterns of distribution in the seagrass habitat, where little or no harvesting occurs. That is, the distribution of these taxa would not be significantly more patchy at the scale of plots in the seagrass habitat at One Mile compared with the reference locations.

Of the six taxa that were more patchily distribution in the harvested location than the reference locations for the mudflat habitat (Table 2.3A), only two of these showed similar patterns of increased patchiness for the seagrass habitat: the number of polychaetes and the number of bivalve species (Table 2.3B). This suggests that the increased patchiness in the abundance of polychaetes and the species richness of bivalves in the harvested location (One Mile), occurs over a larger spatial scale than that associated with bait-harvesting and is, therefore, unlikely to be linked to these activities. Conversely, for capitellid polychaetes, gammarid amphipods, bivalves and, specifically, *Tellina diluta*, increased patchiness in the harvested location was only evident in the mudflat habitat (Table 2.3) suggesting a possible link with the bait-harvesting activities.

2.3.2. Commercialised Fishing Competitions

2.3.2.1. Effects on abundance

Two taxa, bivalves and polychaetes, showed patterns of temporal change in abundance from Before to After the Straddie Classic Fishing tournament that were different in the harvested location (One Mile) than in the reference locations (Table 2.4). The abundance of bivalves in sediments at One Mile increased at a significantly greater rate than occurred in either of the reference locations (Figure 2.6A). The abundance of polychaetes also show a marked increase in abundance at One Mile, in contrast to the slight decrease in abundance evident in the two reference locations (Figure 2.6B).

For the other taxa, the changes in abundance from Before to After the fishing tournament varied considerably between the harvested location and the reference locations, but also between the two reference locations. There was also considerable variation at small spatial scales (between sites and among plots). The test for a significant interaction between Period (Before vs After) and Harvest vs Between Controls was dominated by the considerable variation that existed in the temporal trajectories in the reference locations. For example, the total number of individuals (Figure 2.7A) showed a marked increase in all three locations, but the pattern in the Harvest location was similar to one of the reference locations (Adam's Beach) and not the other (Myora). A similar pattern was observed for the change in the number of gammarid amphipods (Figure 2.7B), but in this case, the temporal change in the Harvest location was more similar to Myora than Adam's Beach. In other cases, for example the number of crabs (primarily *Mictyris longicarpus*: Figure 2.7C) and the number of yabbies (Figure 2.7D), the temporal trajectories in the reference locations were in the opposite direction, indicating the considerable temporal variation against which any effects of bait harvesting must be assessed. Despite the obvious differences in the temporal patterns between the two reference locations, the spatial-temporal interaction was rarely significant (Table 2.4), reflecting the significant variation present at the smaller spatial scales.

There was strong evidence for greater patchiness in the abundance of animals, at the scales of Sites and Plots, in the harvested location compared with the reference locations (Table 2.4). If a pattern of greater patchiness in the harvest location was correlated with the Straddie Classic Fishing tournament, the expectation was that there would be a significant result for comparisons of variation among samples collected After the fishing tournament, but not Before or vice versa (if harvesting reduced spatial patchiness). This pattern was observed for two taxa, the number of gammarids at the scales of Sites and Plots and the number of polychaetes at the scale of Plots. Additionally, the total number of individuals, the number of yabbies and the number of polychaetes (Table 2.4) each showed significantly greater patchiness in the Harvest location than the reference locations at the scale of Sites, but this patchiness was evident independent of when the samples were collected (i.e. Before or After). Finally, the number of yabbies was significantly more patchy at the scale of Plots Before the Straddie Classic but this pattern was not detected After (Table 2.4).

2.3.2.2. Effects on community composition

The composition of the benthic community varied significantly among the three locations Before and After the Straddie Classic Fishing tournament (Figure 2.8). Analysis of the data collected after the tournament indicated that the difference between the two reference locations (Myora and Adam's Beach: average dissimilarity = 37.6%) was as great as the difference between the harvested location (One Mile) and either of the reference locations (average dissimilarity: Myora vs One Mile = 33.4%; Adams' Beach vs One Mile = 38.2%). There was also significant small-scale variability in community composition among the Plots within each location (NPMANOVA: $P < 0.0002$).

The patterns of dispersion of individual samples were similar among the three locations Before the Straddie Classic (Table 2.5), as were the levels of heterogeneity of replicates within the plots in the different locations. The dispersion of the individual plots was also similar in the three locations (i.e. the magnitude of the differences among the plots were similar in each location) before the start of the fishing tournament. After the Straddie Classic though, there were significant differences in the dispersion of the replicate samples among the three locations, with the samples from One Mile (harvested location) being significantly less dispersed than the samples from either of the reference locations, which were not different from each other (Table 2.5: average dispersion – One Mile = 0.82, Myora = 1.03, Adam's Beach = 1.15). The dispersion of the replicate samples within the plots was similar in all three locations and there was no significant difference in the dispersion of the plots among the three locations.

2.3.3. Experimental Impacts

Abundance of yabbies: A total of 8,338 yabbies was removed from the three harvested plots over the course of 15 months (October 1998-December 1999). Despite the large number of yabbies that were removed, there was no significant impact on the abundance of yabbies in the harvested plots compared with the control plots (Table 2.6). On most dates, there was a trend towards more yabbies to be present in the control plots (Figure 2.9A), but this was masked by significant variation among the three plots within each treatment. When the abundance of large (> 7 mm CL) yabbies (i.e. the size range removed during harvesting – see below) was analysed separately there was still no indication of a significant decline in the abundance of yabbies as a result of the harvesting (Table 2.6), although the magnitude of the difference between the control and harvested plots was larger on most dates than when all sizes were considered, with more yabbies being present in the control plots (Figure 2.9B).

Size structure of yabby populations: Only animals that were considered to be of a size suitable for use as bait were removed from the harvested plots on each occasion. The target size for removal was animals larger than approximately 7 mm carapace length although some animals that were smaller than this were occasionally retained. At the start of the experiment, in October/November 1998, the population was mostly comprised of small animals in the control and harvested plots (Figure 2.10A & 2.10B), so some of these smaller animals were retained during the experimental harvesting (Figure 2.10C) on this occasion. At the other times of experimental harvesting, the proportion of smaller animals that were retained was much less than in November (Figure 2.11) because there were fewer smaller animals in the population being harvested. On all occasions, the size of animal that was retained was subjectively determined by the person harvesting the yabbies, reflecting the situation that occurs during recreational bait-collection.

Before the first harvesting event, the mean size of yabbies in the harvest plots was larger than in the control plots and the size-frequency distributions of yabbies in the two treatments were significantly different from each other (Figure 2.12A). By March 1999, however, the mean size of yabbies in the control plots was greater than in the harvest plots (Figure 2.12B), after the removal of 1,888 animals during the first two harvesting events (November 98 & January 99). Between July and December 1999, there were no significant differences in the size structure of the yabby populations in the control and harvested plots (Figure 2.12C-E), but in February 2000, the mean size of yabbies was again larger in the harvested plots than the controls (Figure 2.12E).

Total abundance of individuals: At the start of the experiment (October 1998), there was significantly more benthic animals present in the harvested than control plots (Figure 2.13A), despite these plots being allocated to a treatment at random. The number of animals in the two treatments had converged by January 1999 and remained similar for the duration of the experiment. Despite the marked change in the relative numbers of animals in the two treatments, there was no significant difference between the harvested and control plots (Table 2.7). There was considerable small-scale variation at the scale of the three replicate plots and among the three sites within each plot, suggesting that the power to detect a significant interaction or main effect of treatment may have been relatively poor.

Abundance of solider crabs: The abundance of *Mictyris longicarpus*, the Indo-Pacific soldier crab, was also initially greater in the harvested than the control plots (Figure 2.13B), but had converged by January 1999. There was a significant effect of harvesting on the abundance of soldier crabs (Table 2.7) seen as an initial decline in abundance between October 1998 and January 1999 that much greater in the harvested plots than the control plots (Figure 2.13B).

Abundance of gammarid amphipods: The abundance of gammarid amphipods did not change through time in the same way in each of the three plots in the harvested and/or control treatments (Table 2.7: P x Plot(Treat) interaction). In each of the three harvested plots, there was an overall decrease in abundance of gammarids during the course of the experiment (Figure 2.13C-Harvested), whereas there was an increase in abundance in two of the control plots but a decrease in one (Figure 2.13C - Controls). This is suggestive of a potential impact on the abundance of gammarid amphipods although caution needs to be exercised. The latter plot (Plot 1-Controls) started with a significantly greater density of gammarids than the other control plots, then declined in abundance to similar levels to the three harvested plots, so the change in abundance that was observed could be related to a factor other than harvesting.

Abundance of juvenile yabbies (*Trypaea australiensis*): There was no indication of any impact of the harvesting on the abundance of the juvenile yabbies. The abundance of juvenile yabbies varied through time in different ways in the three plots from the harvested and/or control treatments (Table 2.7: P x Plot(Treat) interaction). The overall pattern was similar in all cases though, only the relative magnitude of the change between each time varied (Figure 2.13D).

Abundance of bivalves: The abundance of bivalves varied significantly among the plots within each of the treatments and also among the sites within each plot (Table 2.7), reducing the power to detect a significant treatment effect. There was some suggestion of a Period x Treatment interaction (Table 2.7, $P<0.10$), seen as marked fluctuations in the abundance of bivalves in the control plots but not in the harvested plots (Figure 2.13E). After the first period of harvesting (in November 1998), the abundance of bivalves increased in the control plots but not in the harvested plots. The number of bivalves subsequently declined in the control plots but not in the harvested plots, so it was difficult to interpret these patterns in relation to any simple effects from harvesting.

Abundance of polychaetes: There were clear indications of an impact of harvesting on the abundance of polychaete worms (Figure 2.13F), with a significant interaction (Table 2.7) highlighting the suppression of the numbers of worms in the harvested plots. There was no significant variability among the plots within the treatments, but there was significant small scale variability at the scale of the sites within the plots.

Abundance of gastropods: The abundance of snails varied through time in different ways in the three plots from the harvested and/or control treatments (Table 2.7: P x Plot(Treat) interaction). The overall pattern of change was similar in all cases with a general increase in numbers through time except in a single harvested plots that showed an initial increase followed by a decline in abundance (Figure 2.13G).

Spatial Patchiness: The only taxon that showed a significant effect of experimental harvesting on spatial patchiness was the polychaetes. The abundance of polychaetes was significantly more patchy at the scale of 1 hectare Plots and Sites (within Plots) under harvesting compared with the control treatment.

Composition of the benthic assemblage: There was no indication that the harvesting affected the composition of the infaunal assemblage on any of the three occasions (NPMANOVA: October 1998 – $P > 0.19$; January 1999 – $P > 0.83$; May 1999 – $P > 0.82$). In all cases, there was significant variation in the composition of the infaunal assemblage at the smaller scale of Plots within each of the treatments. Similarly, there was no indication that harvesting affected the spatial dispersion (patchiness) of the samples, at the scale of Plots within the Treatments, or Sites within the Plots.

Abundance of Deep-Burrowing and Mobile Fauna: A total of 8,930 individuals was collected from the samples taken at the end of the experiment using the exhaustive pumping method in 4 m^2 plots, including yabbies and soldier crabs. Most of these individuals were species that only occurred infrequently in the smaller, 15 cm diameter cores, collected to 15 cm depth. Two species of bivalves, *Mysella vitrea* and *Gari crassula*, comprised ca. 36% of these individuals, while two species of gastropods, *Nassarius burchardi* and an unidentified juvenile, comprised another ca. 27% of individuals. The largest animals, yabbies, soldier crabs and the echiuran, *Ochetostoma australiense*, comprised another 27% of the total individuals. No other taxon was sufficiently abundant to analyse individually.

The abundance of *Gari crassula* (Figure 2.14A) was significantly greater and *Mictyris longicarpus* (Figure 2.14B) was significantly smaller in the control than the harvested plots (Table 2.8) at end of the experiment in February 2000, although the magnitude of these differences were quite small. None of the other abundant taxa showed any significant effect of the 15 months of harvesting and, in most cases, the final abundance was very similar in both treatments (Figure 2.14C-F). There was no significant effect of harvesting on the composition of the deep-dwelling benthic assemblage (NPMANOVA, $P > 0.17$), with no clear pattern of separation of samples collecting from plots in the two treatments (Figure 2.15A-B). The composition of the benthic assemblage did vary significantly among the three plots in the harvested and control treatments though (NPMANOVA, $P < 0.002$).

2.4. Discussion

2.4.1. Impacts from Recreational Bait Harvesting

The approach used here to examine the effects of bait harvesting is an improvement over previous studies. A combination of approaches was used, including general sampling of areas regularly exposed to harvesting compared with suitable reference areas, a focussed Before-After/Control-Impact study based around a competitive fishing tournament and a controlled, manipulative experiment. Each of these components incorporated measures of variability at several spatial scales (Morrisey et al., 1992). Previous studies have only examined or manipulated relatively small areas (e.g. < 20m^2 - Jackson & James, 1979; Wynberg & Branch, 1994, 1997) although McLusky et al. (1983) manipulated areas of 100-500 m^2. Keough et al. (1993) caution against the interpretation of studies on bait-harvesting based around the examination of relatively small areas and/or where the reference (control) areas were adjacent to harvested areas because of the potential for confounding with other factors causing change in the dynamics of the bait populations. One hectare plots (10,000 m^2 in area) were manipulated in the controlled experiment, an area determined to be of an appropriate size to take into account the patterns of 'foraging' of bait-harvesters (McPhee & Skilleter, 2002) and shorebirds (Zharikov & Skilleter, 2003). The reference areas for the general sampling and the focussed examination of the Straddie Classic Fishing Tournament were located >1km from the putatively impacted location.

Previous studies on the impacts of bait-harvesting in soft-sediments done elsewhere (e.g. Blake 1979a, b; Jackson & James, 1979; McLusky et al., 1983; Wynberg & Branch, 1991, 1994) have shown widespread effects on the abundance and diversity of a broad range of taxa. This is in marked contrast to the results here where only a few taxa showed a significant decline in abundance. Importantly though, there was evidence of more subtle effects from harvesting with changes detected in the degree of spatial variation (patchiness) of several taxa.

Three lines of evidence suggest that the disturbance associated with the recreational harvest of yabbies causes significant impacts on benthic assemblages in subtropical Moreton Bay. First, the distribution of some taxa at One Mile was significantly more patchy than at nearby references areas. The nearshore zone of One Mile is subjected to a range of human activities, including boating (launching ramp, fuel distribution and periodic dredging of the boating channel) and regular harvesting of yabbies. The reference areas were not exposed to these activities. Capitellid polychaetes, gammarid amphipods, total numbers of all bivalves and the tellinid, *Tellina diluta*, were all relatively abundant at each of the three locations, but were significantly more patchy in their distribution on the mudflat at One Mile than the other areas. These differences were evident only in the intertidal unvegetated habitat used for the collection of yabbies. These same taxa were not more patchily distributed in the adjacent, vegetated (seagrass) habitats at One Mile compared with the reference areas. This suggests that the factors causing the increased spatial patchiness on the mudflat are specific to that habitat and are not operating more generally in the area, otherwise these taxa would have been likewise affected in the seagrass. Recreational bait harvesting, specifically for yabbies, is common at One Mile because of its proximity to the boat ramp, used as a primary launching site for fishing expeditions from the island (McPhee & Skilleter, 2002). Harvesting of yabbies occurs almost exclusively in unvegetated sediments (McPhee & Skilleter, 2003; Rotherham and West, 2003). Additionally, several taxa tended to be more abundant at the harvested location than either of the reference locations, but the significant variation between the latter areas reduced the power to detect a significant effect. Any increase in power for these specific analyses would have required additional reference locations to be sampled (Underwood & Chapman, 2003), with all the requisite sub-sampling and this was beyond the logistics of the study.

Second, the abundance of gammarid amphipods and polychaetes was also more variable (patchy) as a result of the short-term, intense harvesting associated with the Straddie Classic Fishing Tournament. Both these taxa showed increased patchiness in the harvested locations at the scale of sites (100's metres) and plots (10's metres) after the completion of the Classic. Additionally, at the scale of Sites (100's metres) the patchiness in the abundance of yabbies decreased significantly from before to after the fishing tournament, suggesting that intense harvesting produced a more even distribution of these animal across the mudflat. The latter result is perhaps not surprising, given that experienced harvesters, such as those participating in the Straddie Classic (McPhee & Skilleter, 2002), move to patches on the mudflat where there are apparently greater densities of animals, based on the number of holes visible on the surface (see also Beal & Vencile, 2001). Removal of the yabbies through such harvesting would lead to a more even distribution of the animals.

Third, the controlled, experimental harvesting of yabbies caused significant declines in the abundance of soldier crabs (*Mictyris longicarpus*) and polychaete worms and a significant increase in the patchiness of the polychaetes, at scales commensurate with the activities of recreational and commercial operators (see below). In addition, there was clear evidence of a decline in the abundance of gammarid amphipods in each of the three harvested plots, although this was not detected as being significant because of a simultaneous decline in the abundance of the amphipods on one of the three control plots. In combination, these outcomes indicate that bait-harvesting of yabbies has the potential to cause significant impacts, but only on a limited range of taxa in intertidal sediments.

Capitellid polychaetes are often considered to be opportunist species, able to colonise rapidly areas that have been disturbed. Such species are thought to be adapted for life in a rapidly changing and temporally unpredictable habitat. They are widely recognised for their occurrence in disturbed sediments. Studies of benthic succession following environmental disturbances, including an oil spill (Grassle & Grassle, 1974), dredging for a boating channel (Reish, 1961), organic enrichment and pollution (Pearson & Rosenberg, 1979) and dredge spoil disposal (Oliver et al., 1977), have shown capitellids to be amongst the first arrivals into an area following the disturbance. Similarly, gammarid amphipods have been reported as early colonisers of disturbed sediments (Oliver et a., 1977), primarily via immigration from surrounding patches (e.g. Saila et al., 1972; Wildish & Thomas, 1985). While capitellid polychaetes are mostly characterised as burrowing, deposit-feeders (Fauchald & Jumars, 1979), it is less easy to generalise about a large taxonomic grouping such as the gammarids. Dittman (1996) found that the experimental exclusion of *Trypaea australiensis* (*Callianassa australiensis* in that study) from patches of sediment led to a reduction in the abundance of amphipods within those areas because of the loss of the burrows. She contended that the burrows provided a “promotive effect” (sensu Reise, 1983). The small tellinid bivalve, *Tellina diluta*, was also more patchily distributed in the sediments at One Mile than elsewhere. *T. diluta* is primarily a deposit-feeder that responds to a range of other impacts, including dredging (Skilleter, unpublished data from Noosa River estuary).

The significant impacts on the abundance of amphipods, polychaetes and soldier crabs observed in the large-scale experiment were not consistent with the lack of such effects on these groups observed from the sampling done in the area regularly used by recreational harvesters (i.e One Mile). The area used for the experimental study (Chigill Chigill) was selected because of its remote location and general inaccessibility from the nearest access points. This area is rarely, if at all, visited by recreational harvesters and, due to zoning regulations in the Moreton Bay Marine Park, is not used by commercial operators. From the perspective of the harvesting of yabbies, this site could be considered relatively pristine and undisturbed. In contrast, the area around One Mile has experienced sustained bait-harvesting for decades. Studies done elsewhere (e.g. Jackson & James, 1979; McLusky et al., 1983; Wynberg & Branch, 1991, 1994) have also been primarily focussed in areas subjected to extensive and sustained bait-harvesting. In effect, the manipulative experiment at Chigill Chigill formed a 'pulse' stress on previously undisturbed populations whereas the sustained harvesting at One Mile represents a 'press' perturbation (Underwood, 1989). Potentially, the differences in the type of disturbance the benthic assemblages were exposed to may account for why these groups of animals responded differently to the effects of harvesting. Press and pulse stresses are likely to cause different types of responses, over different time periods (Bender et al., 1984), but more focussed work is required to understand better the way in which press and pulse disturbances specifically affect natural populations.

Bait-harvesting is an activity that involves considerable disturbance to the sediments (e.g. Reise, 1983; Wynberg and Branch, 1994, 1997), in addition to the removal of the target species. Sediments are turned over and animals, including under-sized or undetected yabbies, are left exposed on the surface (Jackson & James, 1979; Ambrose et al., 1998; Beal & Vencile, 2001; personal observation), where they often fall prey to gulls (Ambrose, 1986; Wynberg & Branch, 1991) and scavengers such as crabs and worms (Beal & Vencile, 2001; personal observation). The patches that are disturbed are typically about 4m^2 in area: the animals in that patch are removed, before the harvester moves to another patch (McPhee & Skilleter, 2002; Skilleter unpublished data). Interspersed with these disturbed patches are areas of sediment that are left untouched, forming a complex mosaic (Johnson, 1970), similar in appearance to an area subjected to intense ray predation (e.g. Van Blaricom, 1982; Grant, 1983; Thrush et al., 1991; Valentine et., 1994; personal observation) during a high tide. Impacts from ray predation on the abundance of bivalves, polychaetes and amphipods have been reported in these studies, although specific effects on spatial patchiness have not been examined in detail (but see Thrush et al., 1991 who report increased heterogeneity for the bivalve *Tellina liliana* in New Zealand).

Warwick & Clarke (1993) suggested that increased spatial variability among samples may be a general symptom of the effects of environmental disturbances, based on their analyses on a range of taxa and systems, including sedimentary meio- and macrofauna , corals and fish (but see Chapman et al., 1995 for a counter-example). The increased patchiness of various sedimentary infauna, at several spatial scales, as a result of bait-harvesting is consistent with Warwick & Clarke (1993) hypothesis, even if this result was restricted to a few specific taxa. Rather than an environmental disturbance, harvesting of bait could also be viewed as predation (by humans) (e.g. Castilla & Durán, 1985; Oliva & Castilla, 1986; Duran & Castilla, 1989) and predation has been shown to increase or decrease the patchiness of prey populations (Schneider, 1992). Which of these alternative models (i.e. disturbance versus predation) is most appropriate to understand the implications of bait-harvesting depends on whether the primary effect arises from the physical aspect of harvesting or the removal of the prey. This study was not designed to distinguish between these two (see below), but such a distinction would be of interest from an ecological perspective.

The design of the harvesting experiment was intended to mimic the spatial scales and intensity of harvesting of yabbies by recreational and commercial harvesters operating in SE Queensland and therefore provide a realistic indication of whether such harvesting causes impacts on benthic assemblages. Several lines of evidence indicate that the design of the harvesting experiment was appropriate and the intensity of harvesting applied to the experimental plots was of the correct order of magnitude.

First, on average, ca. 350 yabbies (SE: ±40; range: 115-834 individuals) were removed from each of the one hectare experimental plots on each harvesting event or episode. The pattern of our experimental harvesting was modelled on the patterns exhibited by recreational harvesters collecting bait for the 1998 Straddie Classic Fishing Tournament (McPhee & Skilleter, 2002). The information used to determine the patterns of experimental harvesting including the number of steps taken between each point where pumping was done and the number of times each point was pumped by a recreational harvester. Recreational bait collectors harvested ca. 84 yabbies per episode (SE: ± 12; range: 30-300 individuals), covering an average distance of ca. 700 metres (SE:± 39) in doing so. Each patch that is pumped is approximately 4 m^2 in area (McPhee and Skilleter, 2003), so the harvest of yabbies by recreational fishers participating in the Straddie Classic equates to ca. 84 yabbies per 2,800 m^2 or ca. 300 yabbies per hectare per episode.

Second, based on the total number of harvesters collecting yabbies during the Straddie Classic (Table 1, McPhee & Skilleter, 2002), ca. 4,500 yabbies were removed from One Mile and ca. 3,900 yabbies from Amity Point over 7 days. The area at One Mile and Amity available for harvesting was ca. 4 ha and 1.6 ha respectively, equating to a total harvest from a commercialised fishing competition of between 160 (One Mile) and 350 (Amity) yabbies per hectare per episode (day). Although data are limited, these levels of harvesting recorded during the Straddie Classic were also similar to those recorded elsewhere in Moreton Bay for recreational harvesters not involved in competitions. The average harvest per episode in northern Moreton Bay (Toorbul) was, for example, ca. 160 yabbies (SE: ±39; range 20-460 individuals; n=12 creel surveys) per episode. Again, these figures are close to the intensity used for the harvesting experiment.

Third, between 1997 and 2000, daily log-book returns from commercial yabby harvesters (see Section 1), indicated that the average harvest per day was ca. 1100 (SE: ± 11) yabbies, but 42% of operators harvested less than 800 yabbies per day and 12% harvested less than 400 yabbies per day. Although the area from which these animals were taken during each episode is not recorded in the log-book records, it seems a reasonable assumption that this area would be of the same order of magnitude as for recreational harvesters, simply on the basis of the logistical constraints associated with the tidal range and walking across the soft mudflats. While this indicates that commercial operators are, on average, harvesting yabbies more intensively than the levels employed in the experiment, a proportion of these operators are working at similar intensities. Overall, these calculations suggest that the intensity of employed in the experiments was well within the range exerted by recreational and commercial harvesters operating in the region, with recreational harvesters at one end of the scale and commercial operators at the other. The experiment was designed to fall in between these two extremes, given logistical constraints prevented the experiment incorporating different harvesting intensities in the design.

An important component of impacts associated with harvesting of intertidal animals arises from the disturbance to the habitat during the collection of animals (e.g. Underwood, 1993). In the case of the harvesting of animals from rocky shores, considerable damage to the habitat may arise depending on the methods used for locating and extracting the targeted animals. Use of crowbars, sledge-hammers and other implements may aid in exposing the animals, although this may not always be a necessary component of the harvesting routine and would likely depend on the species being harvested (e.g. cryptic versus exposed). In sedimentary environments, trampling and digging are two side-effects from harvesting that may cause significant impacts on the fauna, even as much as that caused by removal of the animals themselves (e.g. Peterson, 1977; Wynberg & Branch, 1997).

No attempt was made to partition the effects of physical disturbance from the removal of the prey in the experiment examining the effects of harvesting of yabbies. The disturbance to the substratum from use of a yabby pump or other extractive device is an inherent element of the bait collection process: yabbies are rarely if ever found on the surface of the substratum naturally, so harvesting requires digging and turn-over of the sediments. This disturbance occurs irrespective of whether the pumping is successful or not (i.e. whether yabbies are caught from each patch of sediment). The design of the experiment focussed on duplicating the patterns of pumping employed by recreational and commercial operators, rather than removal of a specific number of animals per se. Similar levels of pumping were done on each occasion, although very different numbers of yabbies were removed, thus the results reflect the total effects of harvesting. As highlighted by Wynberg & Branch (1997), knowledge of the number of animals removed from an area alone does not provide a thorough understanding of the impacts from harvesting. The approach taken here avoided this problem, by duplicating the harvesting intensity from recreational and commercial efforts, not their success at capturing the animals.

The populations of yabbies on the mudflats of eastern Moreton Bay proved to be resilient to the levels of harvesting imposed on them in the experiment, levels that were intermediate between those caused by recreational and commercial harvesters (see above). The density of yabbies remained relatively constant throughout the study, with few significant differences observed between the harvested and control plots. Stable adult population densities with occasional pulses of recruitment are common among thalassinideans (e.g. Buchanan, 1963; Dumbauld et al., 1996; Tamaki et al., 1997; Berkenbusch & Rowden, 1998). Tunberg (1986), drawing on earlier work by Buchanan (1963), suggested thalassinideans emigrate from surrounding areas (see also Blake, 1979a for another harvested benthic invertebrate, the lugworm) or recruit from the plankton replacing dead individuals very rapidly and called this *neighborhood* stability. In the context of the harvesting of yabbies, this would mean that for *Trypaea australiensis* (and perhaps for thalassinideans in general), removal of animals would reduce populations from initially large post-recruitment levels. The large abundances of juveniles recruiting to areas already occupied by adults (McPhee & Skilleter, 2003) may be related to the apparent gregarious behaviour of larval thalassinideans (Tamaki & Ingole, 1993), but these juveniles then redistribute themselves to areas that have been recently harvested. The combination of decreasing population levels in areas with large densities after recruitment and rising population densities via immigration in areas that have been harvested ,ay lead to the relatively consistent and apparently stable populations observed in this and other studies on thalassinideans.

In conclusion, harvesting of yabbies for bait by recreational and commercial fishers is likely to cause significant but localised impacts on the benthic fauna of intertidal mudflats. Harvesting was related to increased patchiness in the distribution and abundance of several taxa and reduced abundance for several other groups. The changes in the availability of benthic organisms has the potential to influence the foraging activities and behaviour of higher trophic levels, such as migratory shorebirds (see Section 6).

Table 2.1: Details of the sampling design used in the pilot study to examine the impacts of bait-harvesting on the intertidal mudflat at One Mile, North Stradbroke Island.

Spatial ➡ Scale	**Locations**	**Habitat**	**Sites**	**Plots**	**Cores**
	One Mile	Mudflat	One, Two	1-2, 3-4	16
		Seagrass	Three, Four	5-6, 7-8	16
	Adam's Beach	Mudflat	Five, Six	9-10, 11-12	16
		Seagrass	Seven, Eight	13-14, 15-16	16
	South Myora	Mudflat	Nine, Ten	17-18, 19-20	16
		Seagrass	Eleven, Twelve	21-22, 23-24	16
	Total		12 sites	24 plots	96 cores

Comparison: The composition of macrofaunal assemblages One Mile differs from the average at Adam's Beach and South Myora suggesting some activity or condition at One Mile has led to differences at this location compared with similar places on the western side of North Stradbroke Island.

Potential Causes of Differences:

- Natural variability – this location is different due to natural variability in the assemblages found in the sediments on the western side of the Bay;
- Intensive bait-harvesting at One Mile has caused a significant change to the structure of the assemblages in this area compared with similar habitats north and south of One Mile. Prediction that effects should be evident for assemblage of animals in unvegetated sediments because bait-harvesting only occasionally extends into the low-shore seagrass beds;
- Larger-scale environmental impacts associated with all the recreational activities in the One Mile area have caused changes to the structure of the assemblages found there compared with similar habitats north and south of One Mile. These activities include presence of a boat-mooring area, the water-taxi terminal, boat-launching ramp and yacht-club all at One Mile Jetty. Prediction that effects from these activities would not be restricted to the unvegetated sediments, but would also impact on the assemblages found in the low-shore seagrass beds adjacent to the unvegetated areas utilised for harvesting of bait.

Table 2.2: Summaries of asymmetrical analyses of variance on the abundance of different taxa in the mudflat habitat from three different locations in eastern Moreton Bay. One Mile is exposed to recreational yabby harvesting and is shown as the 'Harvest' location. Myora and Adams Beach were designated as 'Controls'. N=4 replicates from each of two plots within two sites per location. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of heteroscedasticity after Cochran's test. Results are shown for the asymmetrical comparison of One Mile with the average of the two Controls (Impact vs Controls) and the measure of variation between the Control locations. *** = P<0.001, ** = P<0.01, * = P<0.05, ns = P>0.05.

Results for F-test Sites and F-test Plots are based on 2-tailed F-tests for significant differences in levels of variation between the Harvested and Control locations at these two spatial scales. For 2-tailed tests, ns denotes not significant, P>0.10, * = P<0.10, ** = P<0.05, *** = P<0.01 (after Underwood, 1992).

Variable	**Harvested vs Controls**	**Between Controls**	**F-test Sites**	**F-test Plots**	**> Spatial Variation**
Total No. Individuals	ns	*	ns	ns	
Gammarids	ns	***	ns	***	Harvested
Mictyris longicarpus	ns	ns	ns	ns	
Molluscs	ns	**	ns	ns	
Gastropods	ns	***	ns	ns	
Bivalves	ns	***	ns	*	Harvested
Tellina diluta	ns	***	ns	**	Harvested
Polychaetes	ns	ns	ns	***	Harvested
Capitellids	ns	ns	ns	**	Harvested
Oligochaetes	ns	ns	ns	ns	
Polychaete families	ns	ns	ns	ns	
Gastropod species	ns	***	ns	ns	
Bivalve species	ns	***	*	*	Harvested

Table 2.3: Summaries of asymmetrical analyses of variance on the abundance of different taxa in the (A) mudflat and (B) seagrass habitats from three different locations in eastern Moreton Bay. Only results for taxa showing a significant difference between the harvested location (One Mile) and the average of the control locations in the mudflat habitat (see Table 2.2) are shown for comparison. *Tellina diluta* could not be analysed in the seagrass habitat because of very small abundances. Other details as in Table 2.2.

(A) Mudflat

Variable	Impact vs Controls	Between Controls	F-test Sites	F-test Plots	> Spatial Variation
Gammarids	ns	***	ns	***	Harvested
Bivalves	ns	***	ns	*	Harvested
Tellina diluta	ns	***	ns	**	Harvested
Polychaetes	ns	ns	ns	***	Harvested
Capitellids	ns	ns	ns	**	Harvested
Bivalve species	ns	***	*	*	Harvested

(B) Seagrass

Variable	Impact vs Controls	Between Controls	F-test Sites	F-test Plots	> Spatial Variation
Gammarids	ns	***	ns	ns	
Bivalves	ns	***	ns	ns	
Tellina diluta	-	-	-	-	-
Polychaetes	ns	ns	ns	***	Harvested
Capitellids	ns	ns	ns	**	
Bivalve species	ns	***	*	ns	Harvested

Table 2.4: Summaries of asymmetrical analyses of variance on the abundance of different taxa in the mudflat habitat from three different locations in eastern Moreton Bay. One Mile is exposed to recreational yabby harvesting and was designated as the 'Harvest' location. Myora and Adams Beach were designated as 'Controls'. Data were collected from each location on one occasion Before the beginning of the Straddie Classic Fishing Tournament and on one occasion After. N=4 replicates from each of two plots within two sites per location. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of heteroscedasticity after Cochran's test. Results are shown for the asymmetrical comparison of the interactions between the temporal change (Before to After = Period) and the comparison of Harvested vs Controls or Between Controls. *** = P<0.001, ** = P<0.01, * = P<0.05, ns = P>0.05.

Results for F-test Sites and F-test Plots are based on 2-tailed F-tests for significant differences in levels of variation between the Impact and Control locations at these two spatial scales. For 2-tailed tests, ns denotes not significant, P>0.10, * = P<0.10, ** = P<0.05, *** = P<0.01 (after Underwood, 1992).

Variable	**Period x Harvested vs Controls**	**Period x Between Controls**	**F-test Sites**	**> Spatial Variation**	**F-test Plots**	**> Spatial Variation**
Total No. Individuals	ns	ns	***	Harvest [1]	ns	-
Gammarids	ns	ns	*	Harvest [3]	*	Harvest [3]
Crabs	ns	ns	ns	-	ns	-
Yabbies	ns	***	**	Harvest [1]	*	Harvest [2]
Gastropods	ns	ns	ns	-	ns	-
Bivalves	***	ns	ns	-	ns	-
Polychaetes	*	ns	**	Harvest [1]	**	Harvest [3]

1 = significant patchiness exists in either the Harvested location or Control locations averaged across both times;
2 = significant patchiness exists in either the Harvested location or Control locations BEFORE the Straddie Classic;
3 = significant patchiness exists in either the Harvested location or Control locations AFTER the Straddie Classic

Table 2.5: Non-parametric multivariate analyses of variance (NPMANOVA) based on Bray-Curtis distance measure for the community composition of macrofauna from cores collected in the mudflat habitat in each of three locations (Myora and Adam's Beach = reference locations; One Mile = harvested location). Data were unstandardised and fourth root transformed; n=4 cores in each of 8 plots per location (pooled across 2 sites). NPMANOVA was done using permutations of residuals (Anderson, 2001 for full details).

(A) Comparisons Before Straddie Classic – dispersion among replicates
(B) Comparisons Before Straddie Classic – dispersion among Plots
(C) Comparisons After Straddie Classic – dispersion among replicates
(D) Comparisons After Straddie Classic – dispersion among Plots

(A) Before - Replicates

Source	df	MS	F	P
Location	2	189.74	2.46	0.109
Plots (Location)	21	77.27	1.54	0.093
Residual	72	50.21		
Total	95			
(B) Before - Plots				
Location	2	182.76	3.28	0.060
Plots (Location)	21	55.64		
Total	23			

(C) After - Replicates

Source	df	MS	F	P
Location	2	354.54	19.20	0.0002
Plots (Location)	21	18.46	0.62	0.878
Residual	72	29.70		
Total	95			
(D) After - Plots				
Location	2	11.40	0.90	0.417
Plots (Location)	21	12.73		
Total	23			

Table 2.6: Summaries of analyses of variance on the abundance of (A) all yabbies and (B) large yabbies (>7 mm carapace length) in 4 m^2 quadrats from 1 hectare harvested and control plots sampled on six occasions between October 1998 and February 2000. N=10 replicate quadrats from each of three plots per treatment on each occasion. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of homoscedasticity after Cochran's test.

Source Variation	df	All Yabbies		Large Yabbies	
		F	P <	F	P <
Time	5	16.85	0.001	5.13	0.003
Treatment	1	3.72	0.126	1.04	0.367
Time * Treatment	5	0.85	0.534	2.14	0.102
Plot (Treatment)	4	1.44	0.222	1.07	0.372
Time * Plot (Treatment)	20	1.58	0.056	0.96	0.506
Residual	324				

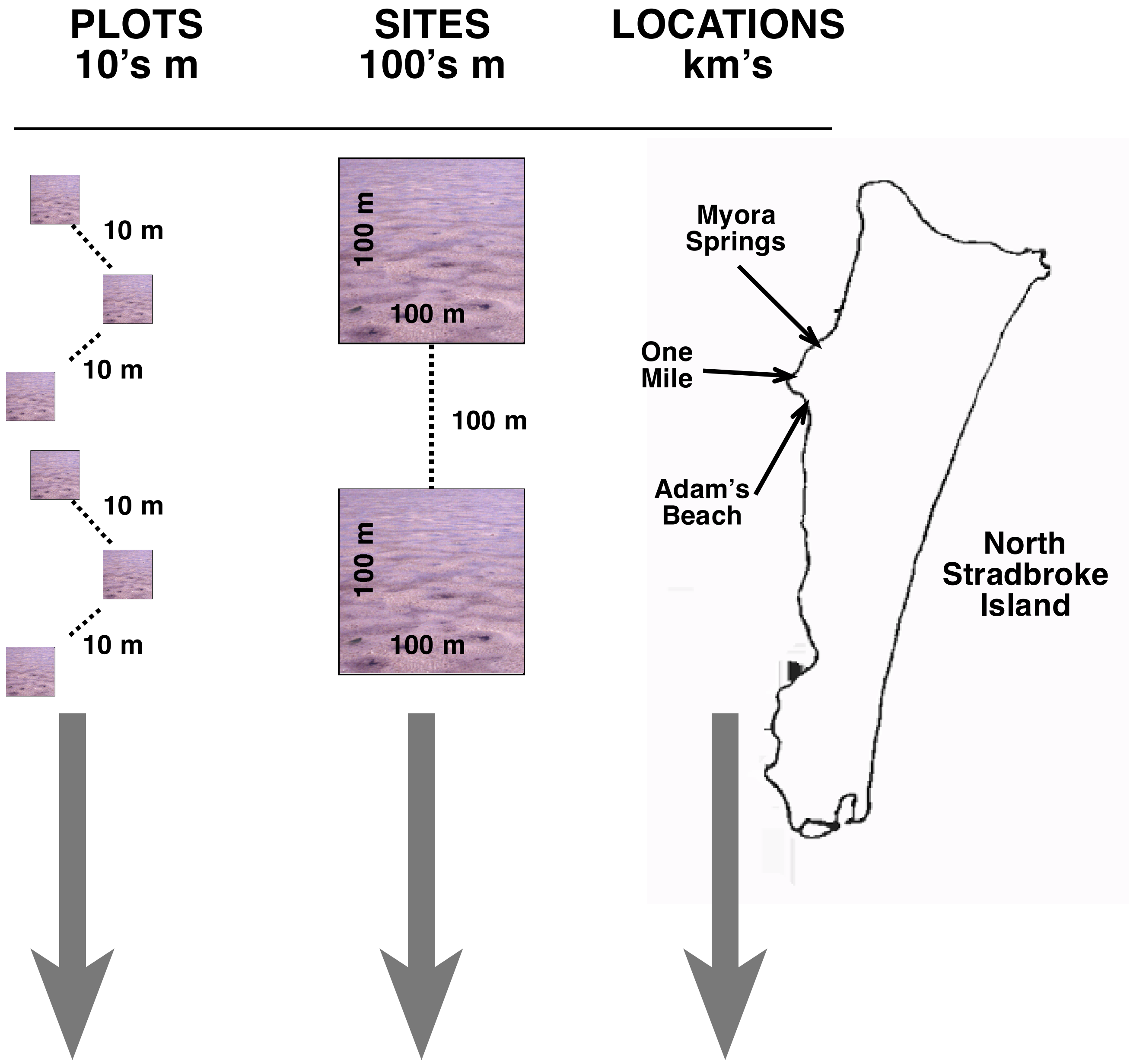
Table 2.7: Summaries of analyses of variance on the total number of individuals and the abundance of individual taxa in 15 cm deep x 15 cm diameter cores processed across a 0.5 mm sieve from each of 3 sites in 1 hectare harvested and control plots sampled on three occasions between October 1998 and May 1999. N=5 replicate cores from each of three sites from 3 plots per treatment on each occasion. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of homoscedasticity after Cochran's test. *** = P<0.001, ** = P<0.01, * = P<0.05, ns = P>0.05.

Variable	**Period**	**Treatment**	**P x T**	**Plot (Treat)**	**P x Plot (Treat)**	**Sites (P x P(T))**
Total No. Individuals	ns	ns	ns	***	ns	***
Mictyris longicarpus	***	ns	* [1]	ns	ns	ns
Gammarids	ns	ns	ns	***	*	***
Yabbies (juveniles)	*	ns	ns	ns	*	***
Bivalves	*	ns	ns [2]	***	ns	***
Gastropods	*	ns	ns	ns	*	**
Polychaetes	**	ns	* [3]	ns	ns	*

1 = Period x Treatment tested over pooled Residual + Sites(PxP(T)) + PxP(T)
2 = not significant, but P<0.10
3 = Period x Treatment tested over pooled Sites(PxP(T)) + PxP(T)

Table 2.8: Summaries of analyses of variance on the abundance of different taxa in 1 hectare plots which were either experimentally harvested for yabbies over a 15 month period and in control plots. Data are from 15 replicate 4 m^2 quadrats within each plot sampled using the exhaustive pumping method (see text for details) at the end of the experiment in February 2000. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of homoscedasticity after Cochran's test.

Variable	**Treatment: T**	**Plots (T)**
Gari crassula	**P < 0.052**	P > 0.583
Mictyris longicarpus	**P < 0.027**	P > 0.963
Individuals	P > 0.674	P > 0.219
Bivalves	P > 0.983	**P < 0.047**
Mysella vitrea	P > 0.676	**P < 0.006**
Gastropods	P > 0.418	P > 0.305
Gastropod Sp. A	P > 0.221	P > 0.758
Nassarius burchardi	P > 0.790	**P < 0.002**
Trypaea australiensis	P > 0.372	P > 0.059
Ochetostoma australiense	P > 0.316	P > 0.793



Plots: within each site, replicate samples were collected from plots (10 x 10m) each ~10 m apart.

Sites: 2 sites (100 x 100m), each ~100 m apart sampled in each reference location & location subjected to harvesting. Sites also represent the unit that was experimentally harvested.

Locations: two reference locations compared with location subjected to harvesting of yabbies

Figure 2.1: Schematic showing the spatial scales incorporated into the studies on the impacts associated with harvesting of yabbies (*Trypaea australiensis*).

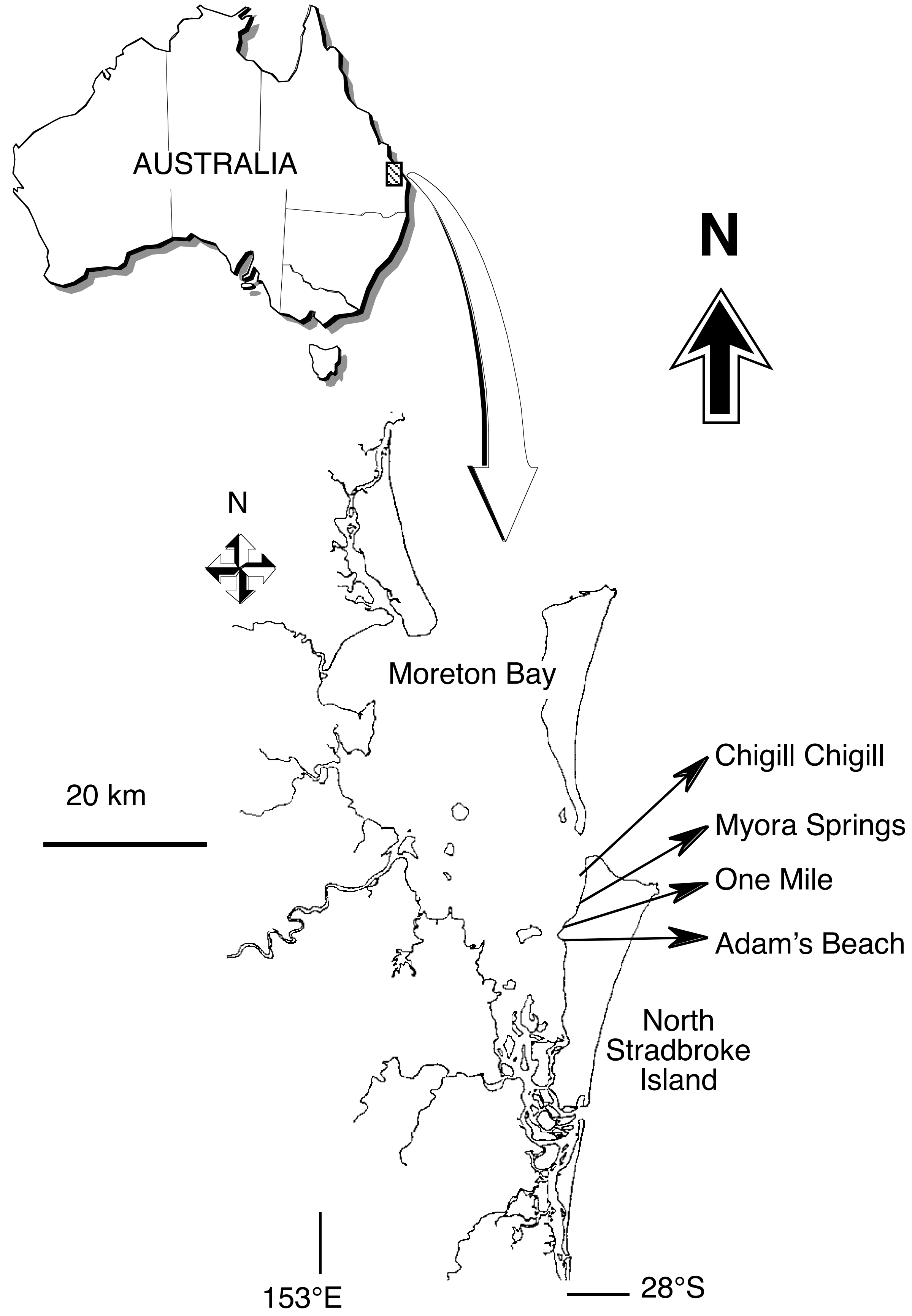


Figure 2.2: Map of Australia and the Moreton Bay region of SE Queensland showing the position of the three locations in eastern Moreton Bay used for the study on the effects of recreational bait-harvesting on benthic macrofauna.

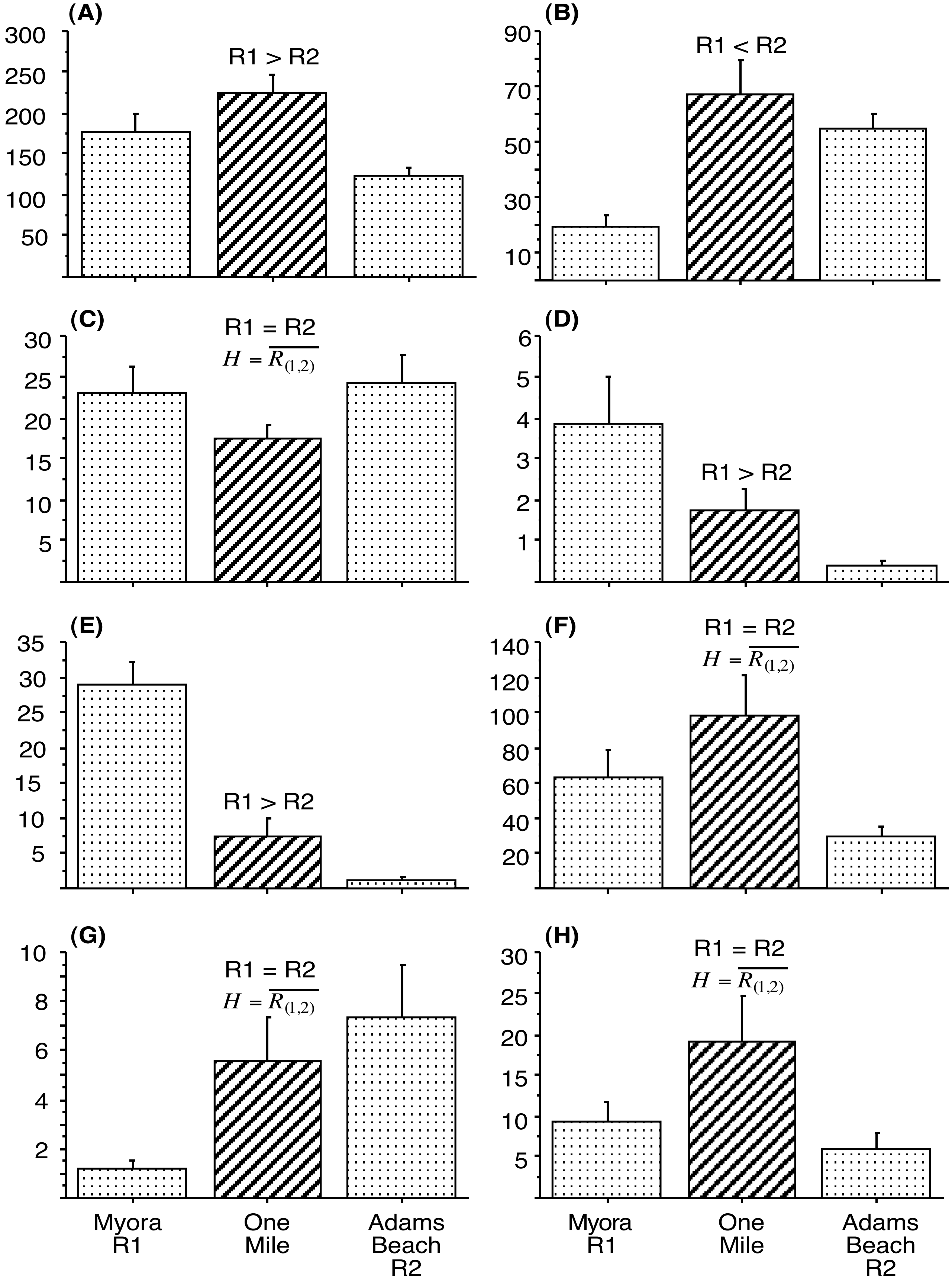


Figure 2.3: Mean (+SE) number of animals in different taxa from the mudflat habitat at three locations in eastern Moreton Bay. One Mile is exposed to recreational yabby harvesting (H), Myora and Adams Beach are reference locations (R1 & R2). (A) number of individuals; (B) gammarid amphipods; (C) *Mictyris longicarpus*; (D) gastropods; (E) *Tellina diluta*; (F) polychaetes; (G) capitellid polychaetes; (H) oligochaetes. N=16 cores for each location (4 replicates from each of two plots in two sites per location).
$\overline{R_{(1,2)}}$= average of two reference locations.

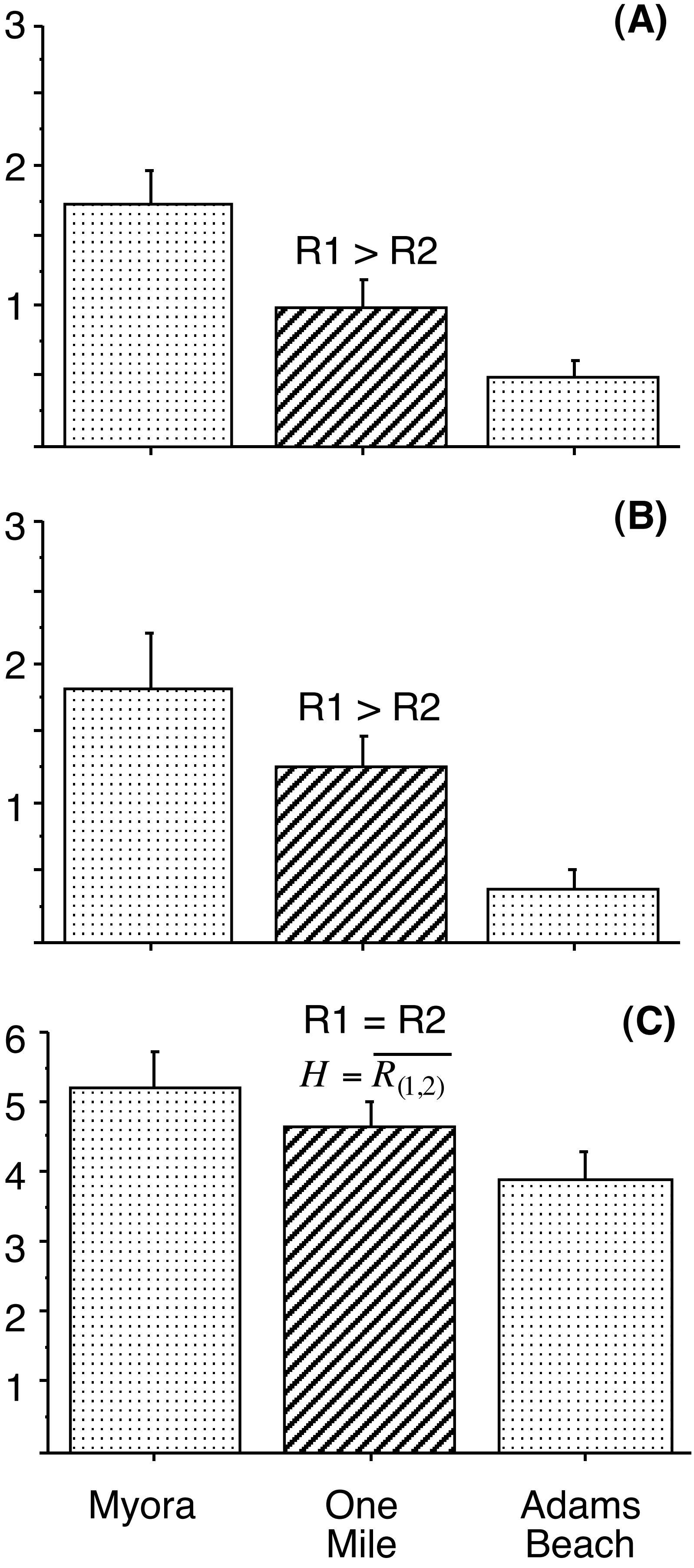


Figure 2.4: Mean (+SE) number of taxa from the mudflat habitat at three locations in eastern Moreton Bay. One Mile is exposed to recreational yabby harvesting, Myora and Adams Beach are reference locations. (A) number of species of bivalves; (B) number of species of gastropods; (C) number of families of polychaetes. N=16 cores for each location (4 replicates from each of two plots in two sites per location). Other details as in Figure 2.2.

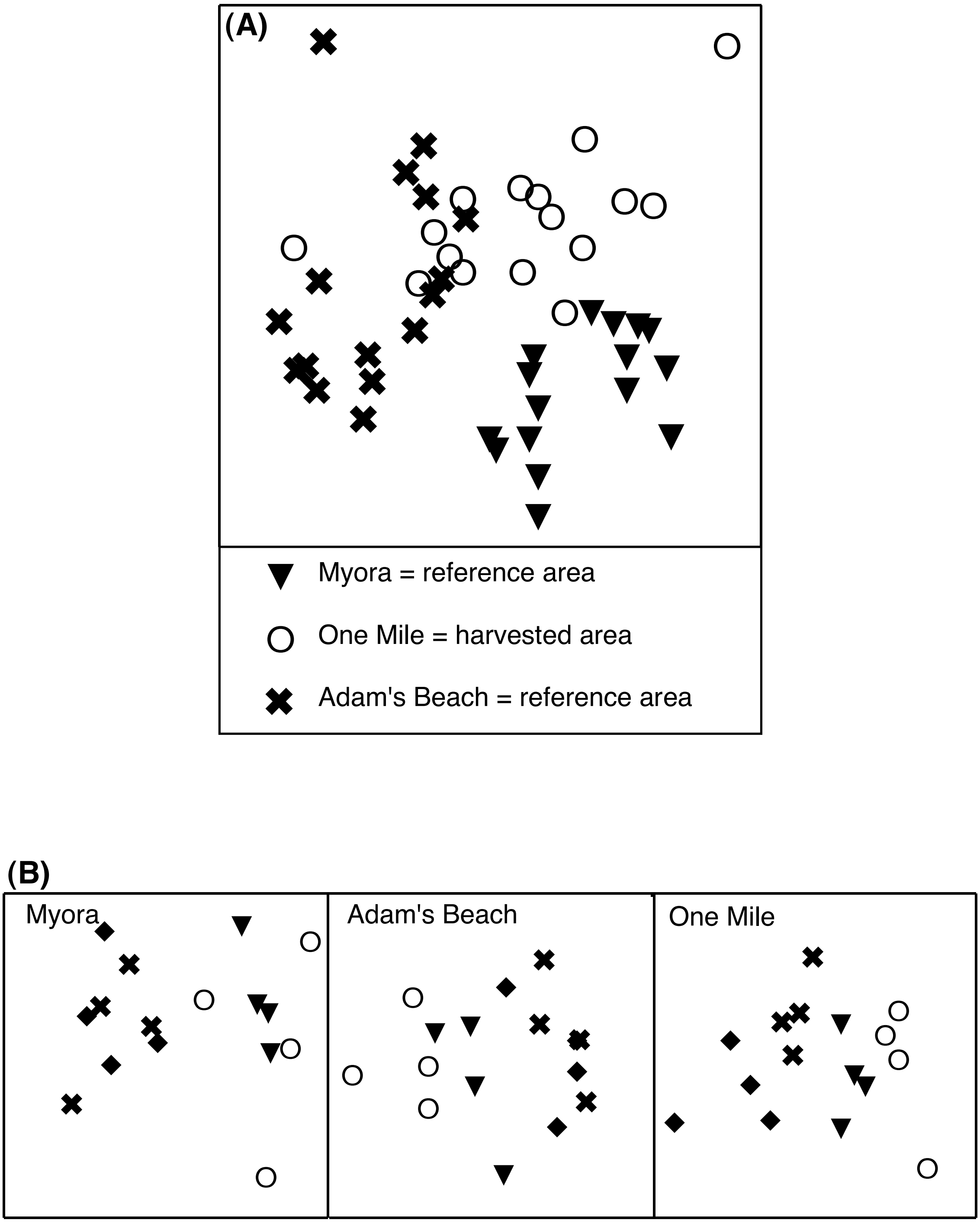


Figure 2.5: nMDS ordinations on fourth root transformed data for the abundance of macrofauna in the mudflat habitat from three different locations in eastern Moreton Bay (One Mile = harvested; Myora and Adam's Beach = reference locations. (A) All data, comparing community composition among locations (stress=0.18); (B) Data for each individual location to highlight patterns of community composition among sites within each location (stress=0.12 for each). Data are for 4 replicates from each of 2 plots per site in each location.

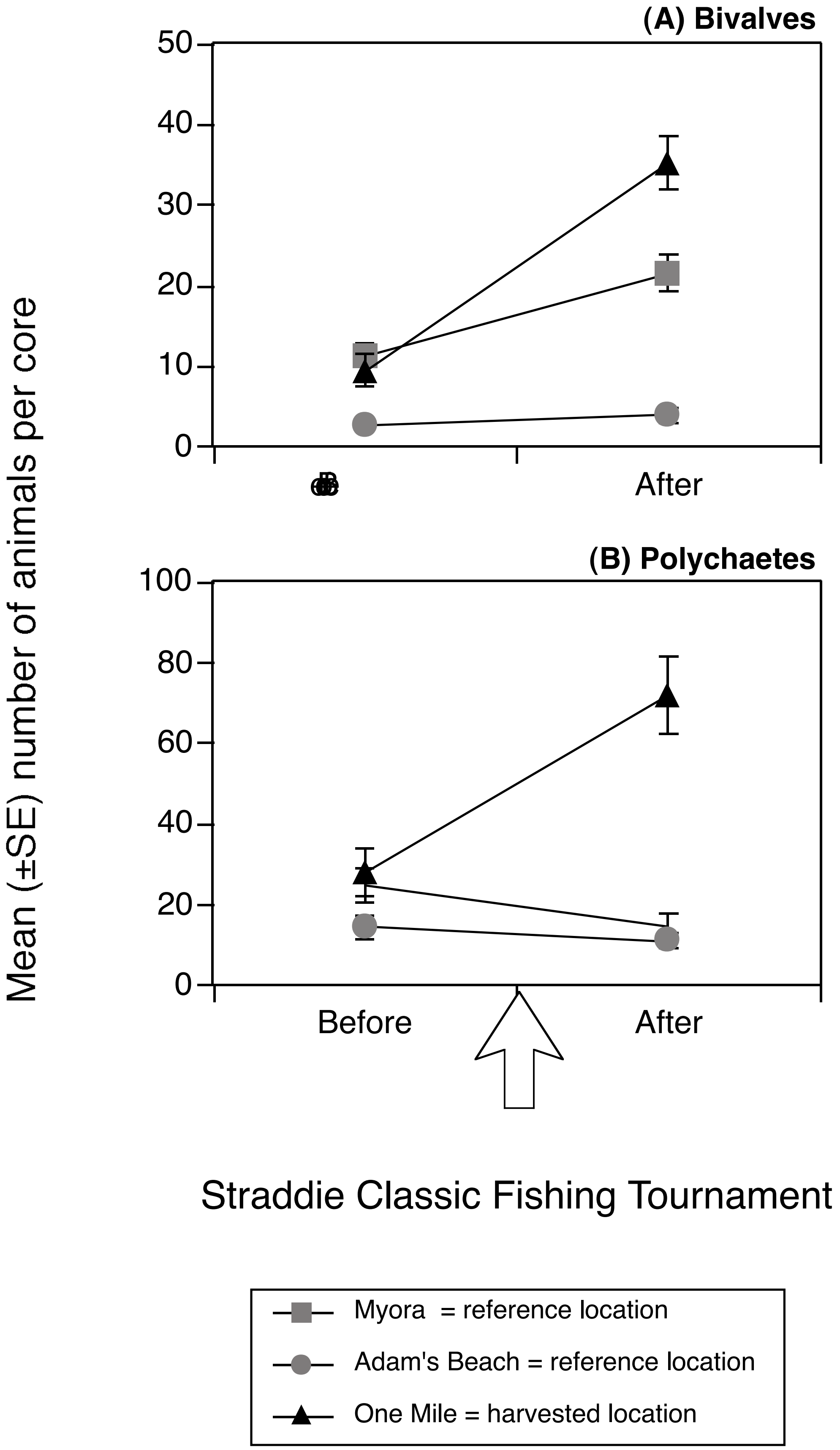


Figure 2.6: Mean (±SE) number of (A) bivalves and (B) polychaetes from the mudflat habitat at three locations in eastern Moreton Bay. One Mile is exposed to recreational yabby harvesting, Myora and Adam's beach are reference locations. N = 32 cores for each location (4 replicates from each of 4 plots in each of 2 sites per location).

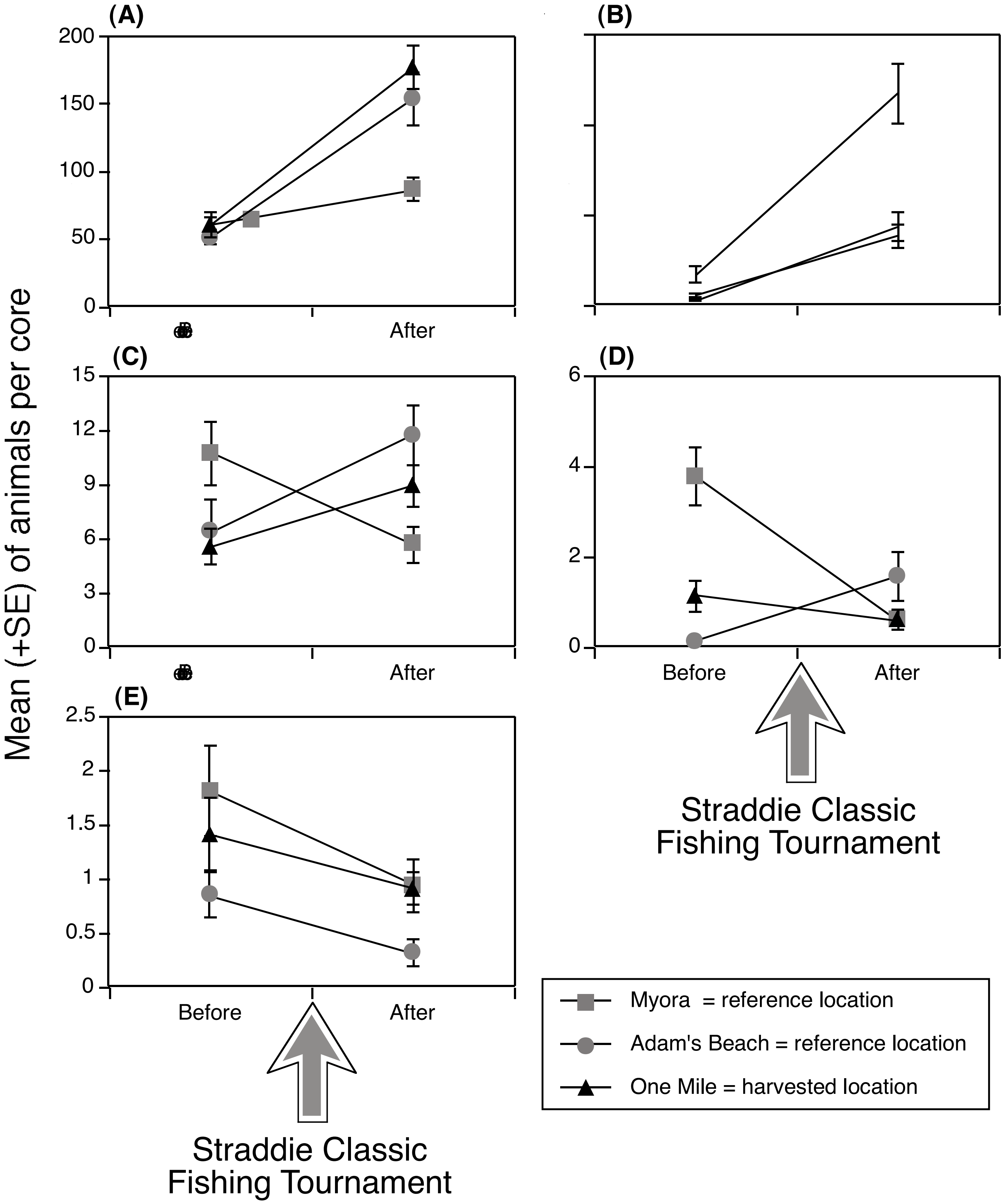


Figure 2.7: Mean (±SE) number of (A) individuals, (B) gammarid amphipods, (C) crabs, (D) yabbies and (E) gastropods from the mudflat habitat at three locations in eastern Moreton Bay. Other details as in Figure 2.6.

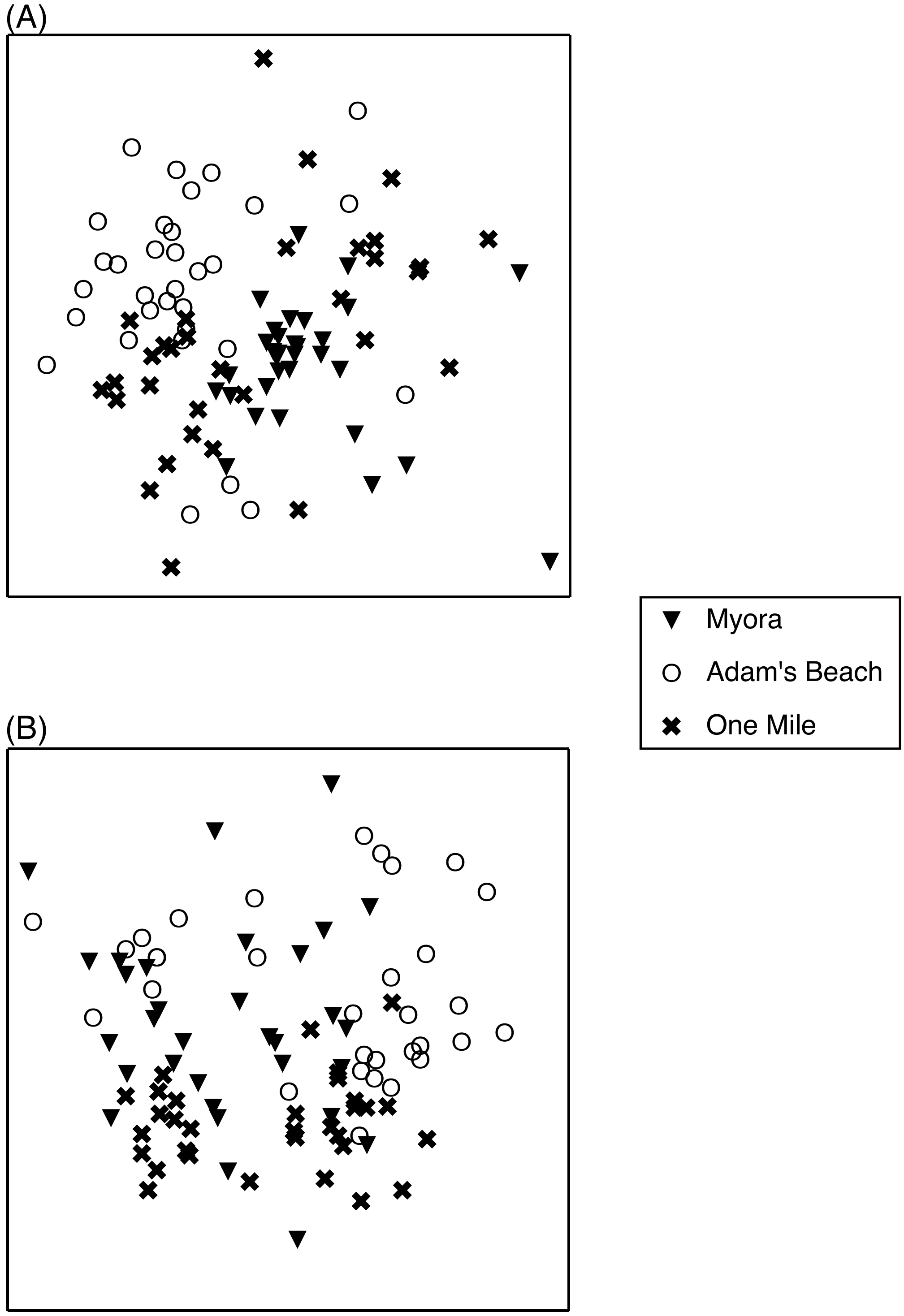


Figure 2.8: nMDS ordinations on fourth root transformed data for the abundance of macrofauna in the mudflat habitat from three different locations in eastern Moreton Bay (One Mile = harvested; Myora and Adam's Beach = reference locations. (A) Before data (stress=0.22); (B) After data (stress=0.21). Data are for 4 replicates from each of 4 plots in 2 sites in each location.

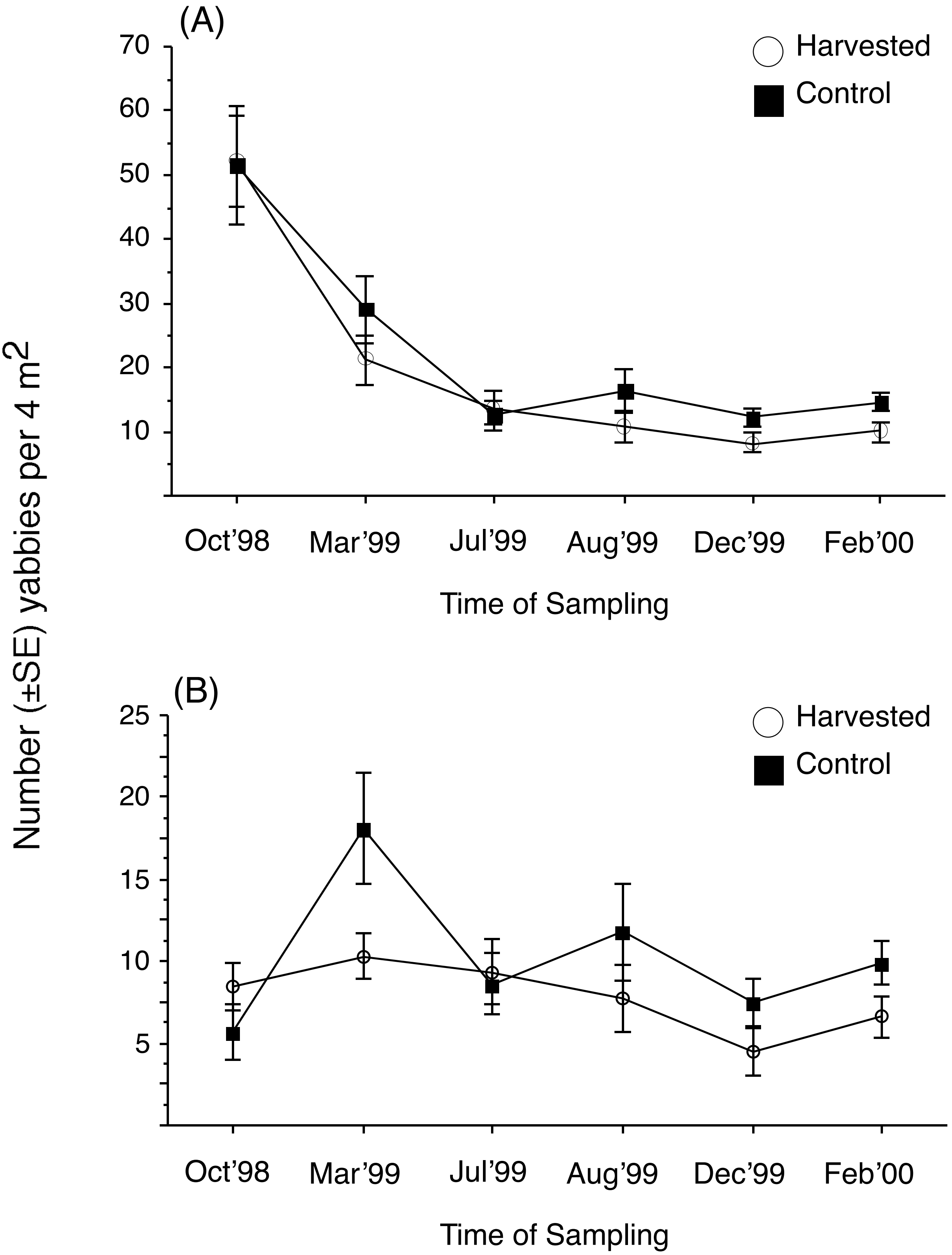


Figure 2.9: Mean (±SE) density of yabbies, *Trypaea australiensis,* in 1 hectare control or harvested plots sampled on six occasions after the start of experimental bait harvesting. N=10 replicate 4 m2 quadrats on each occasion for each treatment. (A) Total number of all yabbies; (B) Number of large (> 7 mm CL) yabbies.

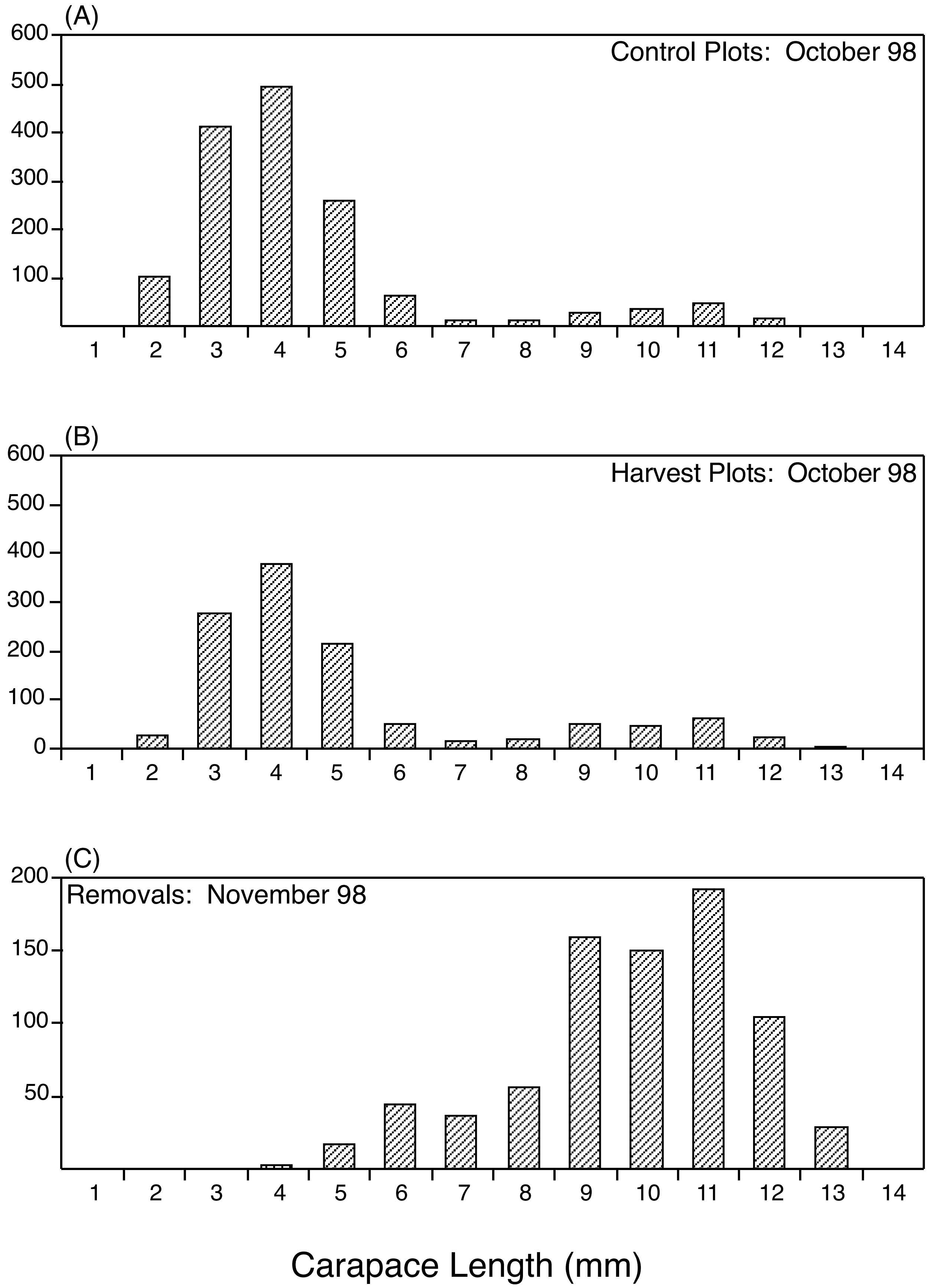


Figure 2.10: Size frequency distributions of yabbies in (A) Control plots and (B) Harvest plots in October 1998 (stock assessment data) and (C) the size frequency distribution of yabbies removed from the Harvest plots in November 1998. Only animals considered to be of a size suitable for use as bait were removed from the plots (smaller animals were left on the surface of the mud).

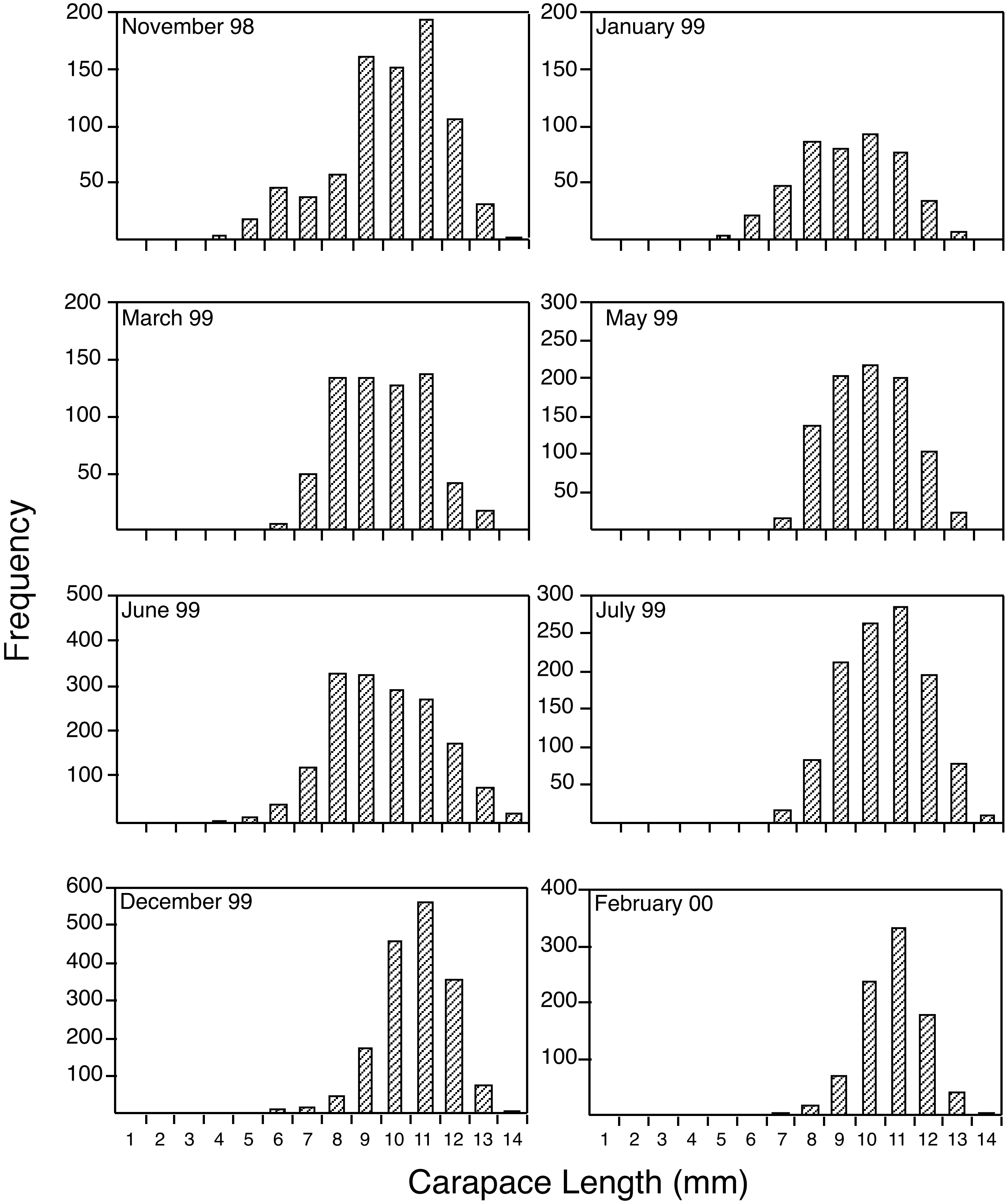


Figure 2.11: Size frequency distributions of yabbies removed from the Harvest plots on each of the eight occasions experimental harvesting was done. Only animals considered to be of a size suitable for use as bait were removed from the plots (smaller animals were left on the surface of the mud).

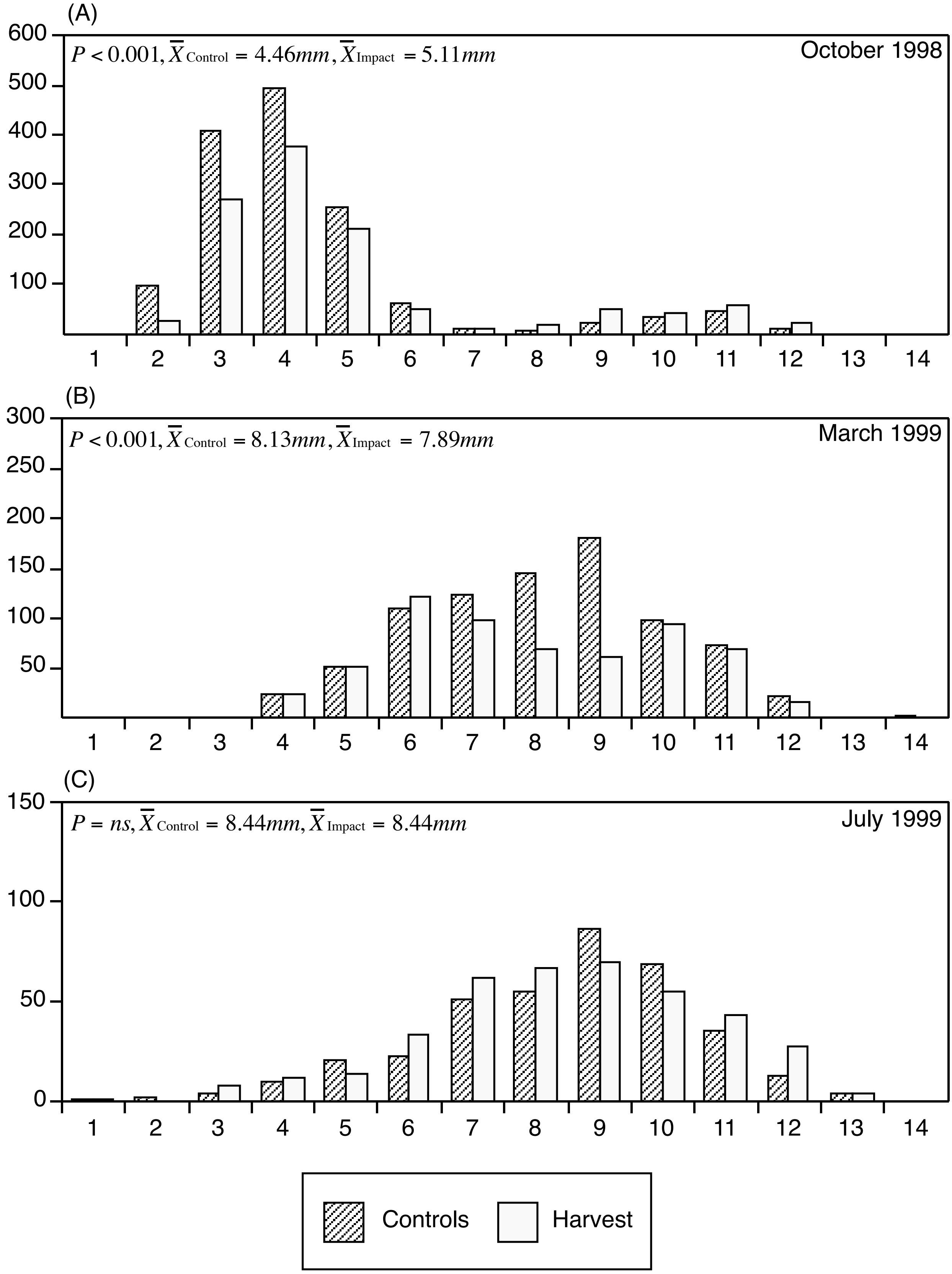


Figure 2.12: Size frequency distributions for yabbies sampled from 1 hectare plots in the mid-intertidal at North Stradbroke Island. Control plots were not subjected to experimental bait harvesting; Harvest plots were harvested on eight occasions during the course of the experiment (see Methods for details). Total counts for each treatment are pooled from 3 replicate plots on each occasion. Probability values are from Kolmogorov-Smirnov two sample tests for unequal sample sizes.

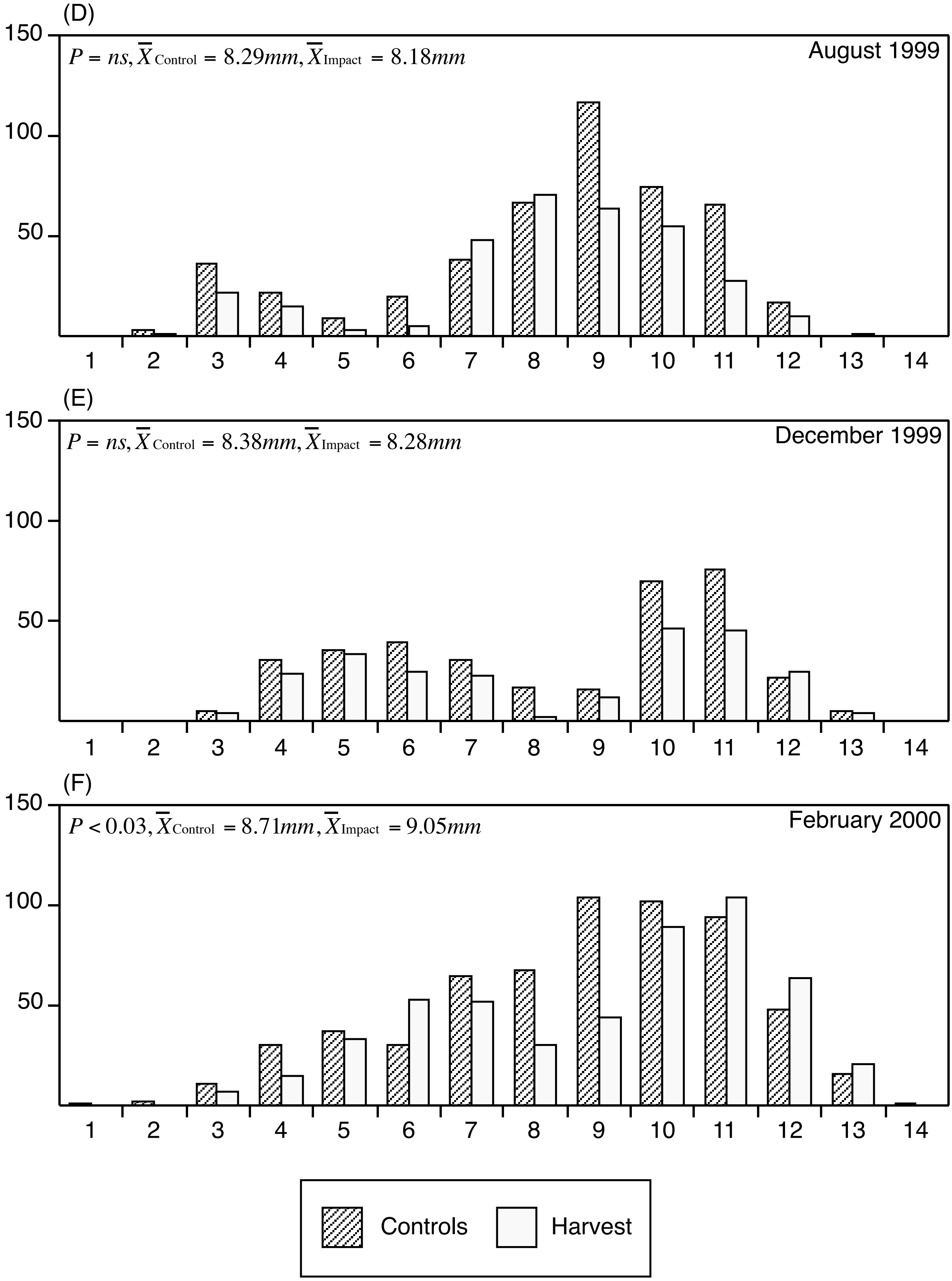


Figure 2.12 continued: Size frequency distributions for yabbies sampled from 1 hectare plots in the mid-intertidal at North Stradbroke Island.

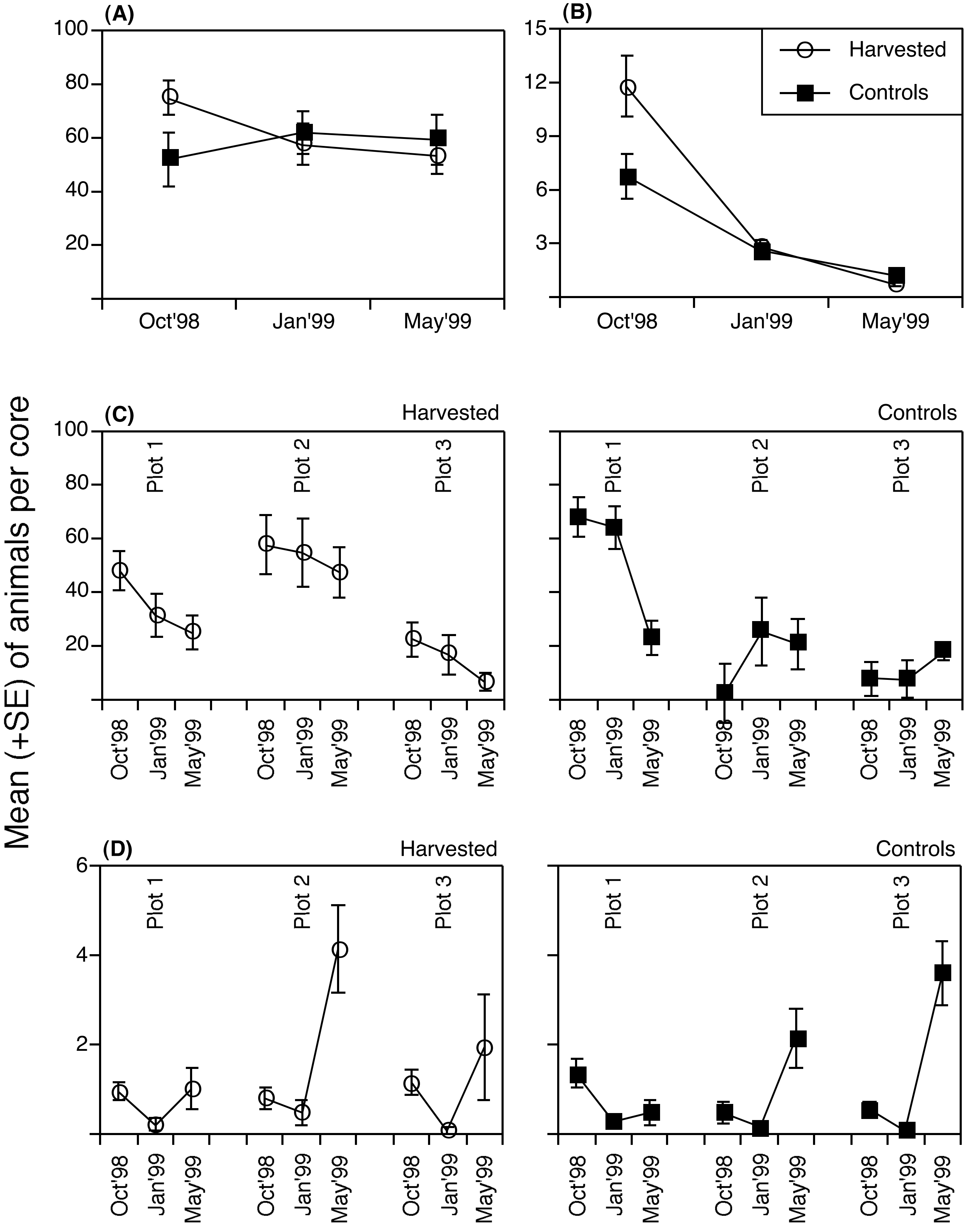


Figure 2.13: Mean (+SE) number of animals in 1 hectare control or harvested plots sampled on three occasions after the start of experimental bait harvesting. (A) number of individuals; (B) *Mictyris longicarpus*; (C) gammarid amphipods; (D) juvenile *Trypaea australiensis*; (E) Bivalves; (F) Gastropods. N=15 cores for each location (5 replicates from each of three sites in each plot on each occasion).

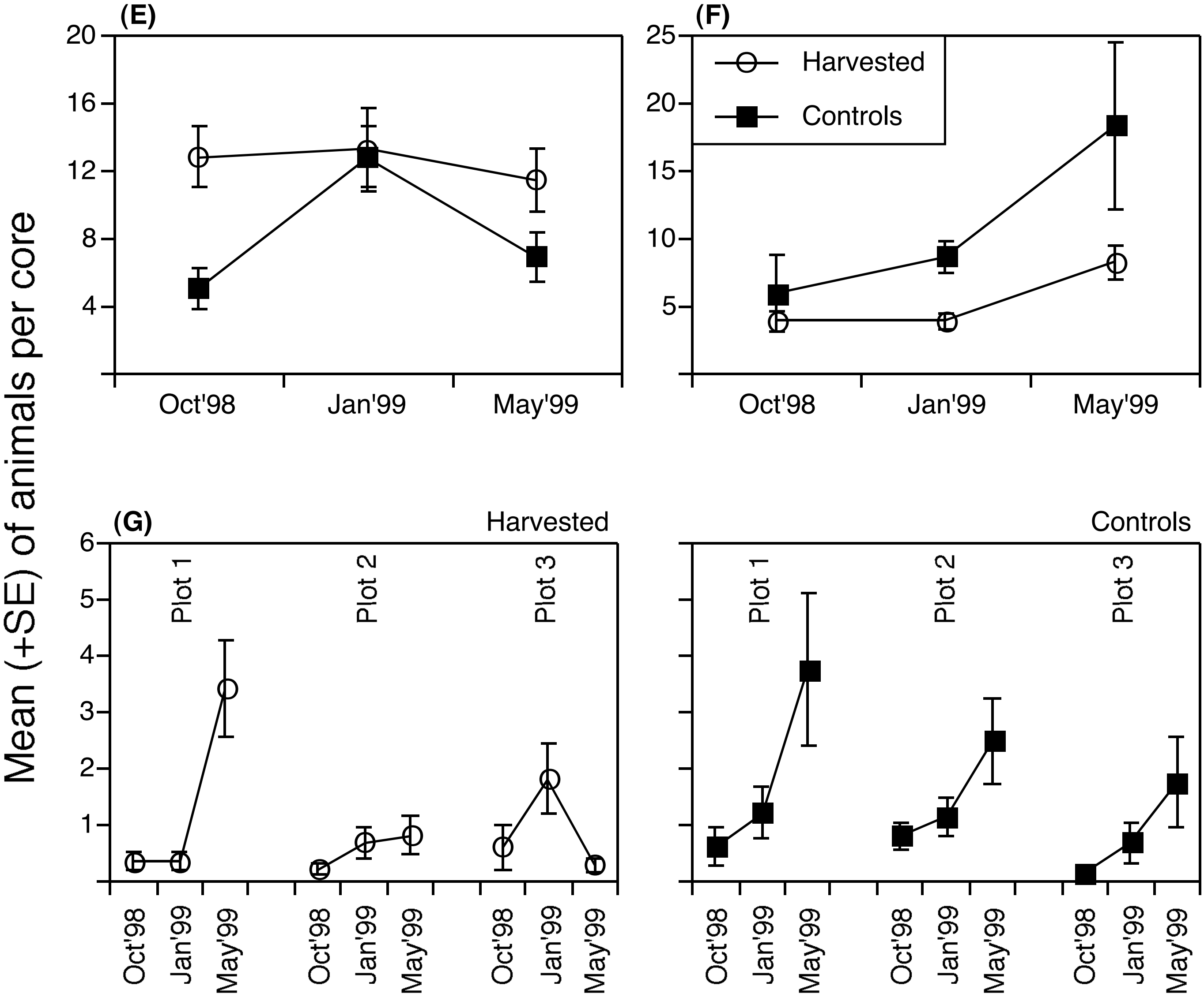


Figure 2.13 continued: Mean (+SE) number of animals in 1 hectare control or harvested plots sampled on three occasions after the start of experimental bait harvesting. (E) number of bivalves; (F) polychaetes; (G) gastropods.

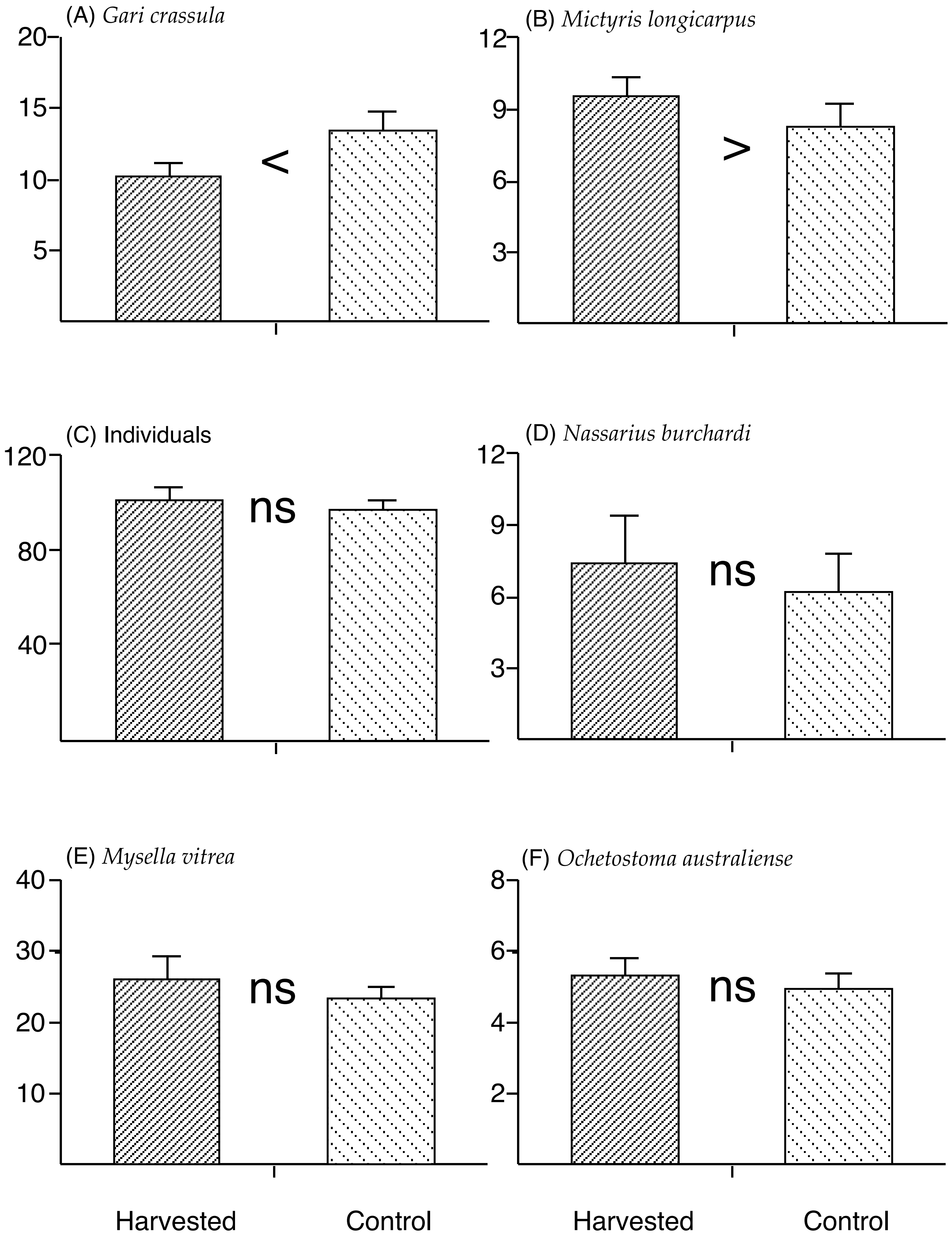


Figure 2.14: Mean number of animals sampled from 1 hectare plots (100 x 100 m) in the mid-intertidal area of North Stradbroke Island. Harvested plots has yabbies removed irregularly over a 15 month period, using standard harvesting methods. Control plots were unmanipulated. N=15 quadrats per plot, sampled at the end of the experiment in February 2000.

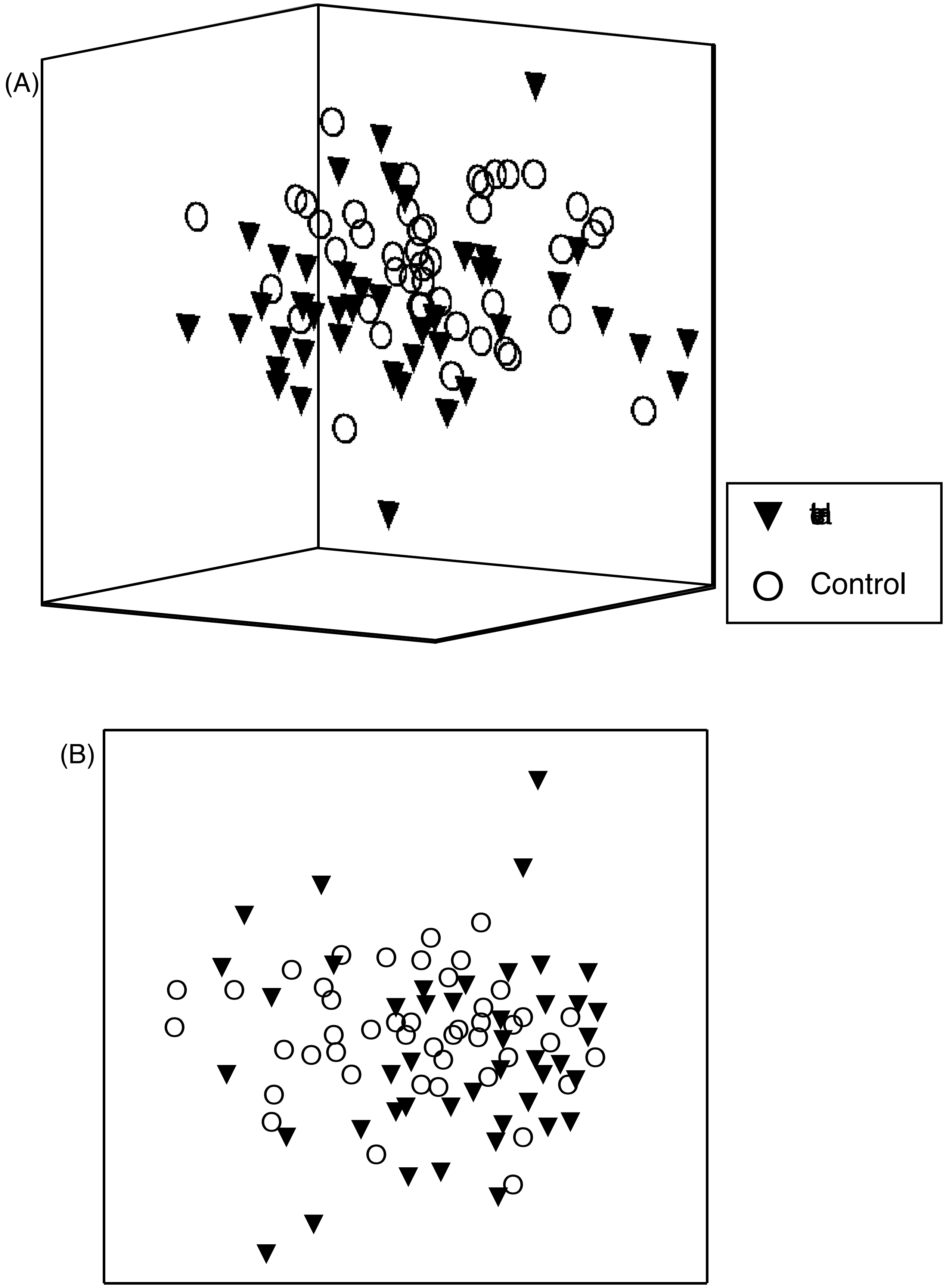


Figure 2.15: nMDS ordinations on fourth root transformed data for the abundance of macrofauna in 1 hectare plots from two different treatments (harvested and control). (A) 3 dimension plot (stress=0.18); (B) 2 dimenion plot (stress=0.24). Data are for 15 replicates from each of 3 plots per treatment.

Section 3: Development of Stock Assessment Methods for Yabbies

3.1. Introduction

The rapid and non-intrusive method of estimating the abundance of thalassinids from counting surface openings has been used in several previous studies (e.g. Hailstone and Stephenson, 1961; Branch and Day, 1983; Posey et al., 1991; Wynberg and Branch, 1992, 1994; Constable, 1995; Ziebis et al., 1996). Some of these studies (e.g. Wynberg and Branch, 1992, 1994) have directly validated the relationship between the number of surface openings and the abundance of thalassinids, but most have relied on 'rules of thumb' based on a standard number of openings per shrimp. This is useful where there is such a predictable relationship between the number of openings and the abundance of the animals, but is of little use for species where such a consistent and predictable relationship does not exist. For example, it is known that the burrows of *Upogebia africana* are typically U-shaped giving a ratio of two surface openings to one each animal (Fielding et al., 1994) and allowing counts of surface openings to be used as an indirect assessment of the abundance of the animals. The burrow structure of many other thalassinids is, however, more complex and often highly variable (Griffis and Suchanek, 1991) and no simple relationship exists between the number of burrow openings an individual creates.

Despite the uncertainty in this relationship, counts of surface openings have been used in the past to estimate the abundance of *Trypaea australiensis* with little or no validation in the field (e.g. Hailstone and Stephenson, 1961; Constable, 1995). The primary aim of this component of the project was to examine the validity of using counts of surface openings to estimate the abundance of *T. australiensis*. This was done by comparing the counts of surface openings with estimates of abundance of yabbies obtained using a yabby pump.

In order to compare the abundance of yabbies within the substratum with counts of surface openings, it was necessary to develop a method that could provide accurate estimates of the true density of yabbies, was easy to implement and could be standardised among different people obtaining the data in the future This component of the study has been published in the journal Hydrobiologia (Volume 485: pp. 133-141: Appendix 1).

3.2. Methods

Study Site and Sampling: The population biology of yabbies was examined at three 100 x 100 m sites, each separated by 50-75 metres, in the mid-intertidal zone of the western shore of North Stradbroke Island (Queensland, Australia) (Figure 3.1). This zone forms a 10 km long continuous stretch of course sand/mud with occasional patches of seagrass and bounded upshore by mangroves (*Avicennia marina*, (Forsk.) Vierh.)) and downshore by seagrass (*Zostera capricorni* Ascherson, *Halodule uninervis* (Forsk.) Ascherson, *Halophila ovalis* Hook. F. and *Syringodium isoetifolium* (Ascherson).

To determine the abundance of yabbies in each of the three sites, exhaustive, controlled pumping was done using a yabby pump. The usual procedure for collecting yabbies with a yabby pump is to push the unit into the substratum and extract the sediment, which is then dumped onto the substratum to collect suitable sized animals. Usually, the pump is pushed into the substratum to a depth of approximately one metre at the same point a number of times. The harvester then moves to a new point and begins the process again. The number of pumps needed to extract all the yabbies from a single point was determined in a previous study in the same region (Skilleter, unpublished data). The pumps at a single point were considered as a set. The number of sets needed to harvest all the yabbies in a 2 x 2 metre (4 m^2) quadrat was determined from a pilot experiment where the cumulative percentage of yabbies harvested from a quadrat was plotted against the number of sets completed. These data indicated that complete harvesting of a 4 m^2 metre quadrat required 18 sets each of 7 pumps per point.

The density and size-structure of yabbies were estimated in each of the three sites on six occasions between October 1998 and February 2000. Estimates were obtained in each of ten 4 m^2 quadrats per site on the first five occasions and in fifteen 4 m^2 quadrats on the final occasion. Before the sediment in the quadrat was pumped, estimates were obtained of the number of surface openings in the quadrat, using 3 x 0.1 m^2 quadrats haphazardly positioned within the larger unit. It was not logistically feasible to count all the burrow openings in the 4 m^2 area because of the abundance of the holes, but the sub-sampling provided reasonable estimates of the total abundance of surface openings within the plots. Yabbies were then harvested from each of the sites using yabby pumps and the sediment collected from each of the quadrats was passed through a 2.0 mm sieve and the retained yabbies were stored. As part of an associated study in the same sites, samples collected to determine the abundance of benthic macrofauna were processed across a 0.5 mm sieve (see Section 2.2.3). Very few yabbies smaller than 2 mm were detected in these samples, so we assume our stock assessment method sampled the entire yabby population. In the laboratory, yabbies were counted and their carapace length (from the tip of the rostrum to the end of the carapace) measured with calipers to the nearest millimetre. Ovigerous females were identified by examination under a dissecting microscope.

Data Analysis: Changes in the abundance of yabbies were examined with a two factor ANOVA with sample period (random) and site (fixed) as main effects. The relationship between the number of surface openings (independent variable) and the abundance of yabbies (dependent variable) was examined using linear regressions. A one-factor ANCOVA, with sample period as the main effect, yabby abundance as the dependent variable and the number of surface openings as the covariate, was used to determine whether the relationship between the number of surface openings and the abundance of yabbies changed through time.

3.3. Results

Yabby abundance varied considerably among the three sites, despite their relatively proximity to each other (Figure 3.2), but no site consistently had greater abundances of yabbies than the other sites through time (ANOVA interaction; $P<0.01$). Overall, the abundance of yabbies was significantly greater in October 1998 than at other sampling times (ANOVA; $P<0.05$ and Tukey’s post hoc test; $P<0.05$).

The size frequency (%) distribution of yabbies during October 1998 was dominated by a cohort centered at 4 mm CL, probably indicating a recruitment event just prior to that sampling period (Figure 3.3). This cohort could be followed through subsequent sampling periods. Another (smaller) recruitment event may have occurred between August 1999 and December 1999 represented by a second cohort in the population with a mean size of 5 mm CL in the December 1999 sample.

Predicting yabby abundance from counts of burrow openings was unreliable. The proportion of the variation in the numbers of yabbies accounted for by counts of burrow openings (R^2 values) varied considerably among sampling periods and was generally small, explaining less than 20% of the variation in four of the six sampling periods (Figure 3.4). The specific relationship between the number of burrow openings and yabby density varied significantly through time (ANCOVA; $p< 0.05$).

Ovigerous female yabbies were present in all sampling periods, although the number present at any time was generally small, only reaching a maximum of 5.1% of all females present at that time (Table 1). The majority of ovigerous females recorded were below 6 mm CL with only six of the 38 ovigerous females being 8 mm CL or larger (Figure 3.5).

3.4. Discussion

3.4.1. Burrow Opening Counts as an Indirect Measure of Yabby Population Density

In this study, counts of burrow openings proved an unreliable measure of yabby population density casting doubt over previous unvalidated estimates of population sizes using this method (Hailstone & Stephenson, 1961). These findings highlight the importance of validating indirect assessment methods in the field (e.g. Warren, 1990). Where appropriate validation has been done, burrow counts have proved unreliable for estimating the population density of the grapsid crab, *Helograpsus haswellianus* (McKillup & Butler, 1979) and seasonally unreliable for the ocypodid crab, *Heloecius cordiformis*, which tends to plug its burrow openings during winter (Warren, 1990).

In contrast, burrow counts as an indirect measure of abundance of benthic invertebrates have been validated and used in several other studies (e.g. Hanekom et al., 1988; Warren, 1990; Wynberg & Branch, 1991; Dumbauld et al., 1996; Tuck et al., 1997). Species for which burrow counts are a reliable measure of population density generally have simple burrow structures and have been solitary. For instance, *Callianassa kraussi* (Hanekom et al., 1988), some ocypodid crabs (Warren, 1990) and Norwegian lobsters (Tuck et al, 1997) all construct relatively simple burrows that generally only have one opening and one animal per burrow. Similarly, thalassinideans of the genus *Upogebia* construct ‘Y’ shaped burrows leading to a predictable relationship of two burrow openings to one individual (Griffis & Suchanek, 1991). However, even in species that build simple burrows, there can be intra-specific differences in burrow architecture (and hence the number of burrow openings) due to the sex of the inhabitant (Rowden & Jones, 1995), the time of the year (Warren, 1990; Dumbauld et al., 1996), variation in sediment grain size (Griffis & Chavez, 1988; Griffis & Suchanek, 1991; Rowden &

Jones, 1995), or the organic content of the sediment (Stamhuis et al., 1997). These factors need to be taken into account when designing studies which intend to use indirect measures of abundance, such as hole counts, for population assessment.

Like many thalassinidean species, *Trypaea australiensis* constructs complex burrows with a variable number of openings and individuals per burrow and the burrows may be interconnected to form galleries (Hailstone & Stephenson, 1961; Griffis & Suchanek, 1991; Rowden & Jones, 1995). Thalassinideans are not unique in constructing such complex burrows, with some species of grapsid crabs also constructing burrows with multiple and variable numbers of entrances (Seiple & Salmon, 1982). Various species of grapsid and ocypodid crabs may also usurp another species burrow or co-occur in a communal system of burrows (Warner, 1969). Given the structure of the burrows formed by *Trypaea australiensis* and other thalassinideans it is not surprising that counts of the number of burrow openings are unreliable as an estimate of the abundance of the animals. The marked changes in the nature of the relationship through time was, however, surprising

The presence and activities of benthic macrofauna other than yabbies may have been a factor contributing towards the large variation in the relationship between the number of yabbies and the number of burrow openings. Occasionally, it was apparent that an echiuran (*Ochetostoma australiensis*) rather than a yabby occupied a burrow, based on the presence of a proboscis or characteristic stellate feeding scars (Hughes et al., 1996). It was not possible though to distinguish the presence of echiurans reliably or consistently because not all these animals were feeding at the time the surveys were done and because disturbance to the surface of the sediment from the foraging activities of soldier crabs (*Mictyris longicarpus* (Latrielle)) obscured the presence of these feeding marks.

Soldier crabs rework the sediment surface during their foraging, creating large quantities of pseudofaeces (Dittmann, 1996) and may also burrow into the sediment if disturbed by predators (e.g. shorebirds) or humans. The activities of soldier crabs obscure the fine scale morphological details of the burrow openings necessary to identify unequivocally the inhabitant (Zoutendyk & Bickerton, 1988). In some instances, the activity of soldier crabs almost completely obscured burrow openings over large areas (> 1 hectare) of the intertidal flat.

Saiz-Salinas and Gonzalez-Oreja (1999) have suggested that burrow counts can be used to assess and monitor the impacts of disturbance on inshore marine systems but our findings indicate that caution needs to be exercised in the application of burrow counts as an indirect method of population assessment unless burrows are clearly distinguishable and the relationship between the number of burrow openings and the number of individuals is consistent. The latter is unlikely to be the case in animals such as the yabby that build complex burrows with a variable number of entrances and individuals per burrow.

Recently, Rotherham & West (2003) compared coring and pumping methods for estimating the abundance of yabbies on New South Wales mudflats and determined that standardised pumping was more efficient and cost-effective. They determined that an effort of 12 pumps (four pumps from each of 3 burrows) per $0.1m^2$ quadrat was the optimal level for the areas in which they worked. This translates to an effort of 480 pumps per $4m^2$ (120 burrows) compared with 126 pumps (7 pumps from each of 18 burrows). The abundance of yabbies in their study was 3-4 times greater than recorded for North Stradbroke Island, so it is not surprising that it required a greater effort to extract fully all the animals from a patch of sediment. The important result here is that both these studies indicate that a relatively cost-effective method of assessing stock sizes for *Trypaea australiensis* could be implemented as part of the management of stocks, especially if commercial and/or recreational harvesting were to increase in the future.

3.4.2. Population Density and Stability

Except for an initial peak in abundance, the population density of yabbies remained relatively constant throughout the study. The initial peak in abundance was a function of the large numbers of small individuals in the population, likely to be recent recruits. It is possible that the subsequent decline in numbers after October 1998 was a result of the disturbance caused by the sampling (e.g. Skilleter, 1996) but this is unlikely for several reasons. First, there was no equivalent decline in numbers observed after sampling on any of the other occasions, even when population assessments were separated by only one month. Furthermore, the large decline in numbers was only observed at one of the three sites, yet each was sampled in an identical manner. Second, experimental removal of yabbies from replicate hectare plots between October 98 and February 2000, at levels commensurate with recreational harvesting (see Section 2 above), did not cause any significant decline in their abundance compared with control plots suggesting that the smaller-scale disturbance from stock assessment would not cause any significant changes in abundance.

Stable adult population densities with occasional recruitment pulses of juveniles are common among thalassinideans (Buchanan, 1963; Dumbauld et al., 1996; Tamaki et al.,1997; Berkenbusch & Rowden, 1998). Tunberg (1986), drawing on earlier work by Buchanan (1963, suggested thalassinideans emigrating from surrounding areas or recruiting from the plankton replace dead ones very quickly and called this neighbourhood stability. This would mean that for *Trypaea australiensis* (and possibly thalassinideans in general), death through aggressive interactions or emigration of growing juveniles would likely reduce population densities from initially large post-settlement levels. The large abundances of juveniles recruiting to areas already occupied by adults may be related to the apparent gregarious behaviour of larval thalassinideans (Tamaki & Ingole, 1993), but these juveniles then redistribute themselves to areas with relatively smaller densities. The combination of decreasing population levels in areas with large densities after recruitment, and rising population densities in other areas may lead to the relatively consistent and apparently stable population densities observed in this and other studies of thalassinideans.

The population densities recorded for the yabby in this study are at the lower end of the range for thalassinideans but of a similar magnitude to those recorded (by direct assessment methods) for *Callianassa filholi* (Berkenbusch & Rowden, 1998), *Callianassa japonica* (Koike & Mukai, 1983), *Upogebia deltaura* (Tunberg, 1986), *Callianassa macandreae* (Buchanan, 1963), *Callianassa arenosa*, *Trypea* (as *Callianassa*) *australiensis* and *Callianassa limosa* (Coleman & Poore, 1980). From the studies of Posey (1986), Cockcroft & Tomalin (1987), Hanekom et al. (1988), Witbaard & Duineveld (1989), Wynberg & Branch (1991) and Dumbauld et al. (1996) it is clear that thalassinideans can reach densities in excess of 100 per m^{-2} and up to 500 per m^{-2}, but these densities are perhaps the exception rather than the rule. The possibility that the sampling regime employed in the present study substantially under-estimated the abundance of yabbies is unlikely. Examination of quadrats up to three days after sampling showed no signs of the presence of yabbies or new burrow openings suggesting all animals had been removed by the stock assessment procedure.

3.4.3. Reproductive Period and Size at Maturity for Females

There is a consistent trend amongst thalassinideans for the smallest ovigerous females to be encountered at 7 mm CL but more usually at 8 mm CL or greater (Hailstone & Stephenson, 1961; Hanekom & Erasmus, 1988; Felder & Lovett, 1989; Rowden & Jones, 1994; Dumbauld et al., 1996; Dworschak, 1998; Berkenbusch & Rowden, 1998). One exception was recorded by Berkenbusch & Rowden (2000) for a population of *Callianassa filholi* where size at maturity was 4.8 mm CL, however, the average size of this population was relatively small (5.6 mm CL). Here, we recorded ovigerous female yabbies as small as 3 mm CL, considerably smaller than the 8 mm CL reported by Hailstone & Stephenson (1961) for the same species in an adjacent area. This discrepancy may have arisen because Hailstone & Stephenson (1961) attempted to identify ovigerous females macroscopically in the field rather than undertaking more careful observations in the laboratory with the aid of a binocular microscope. Small ovigerous females frequently only carried a few eggs, easily missed by casual observation in the field.

The size at maturity for female thalassinideans with an average maximal size similar to *Trypaea australiensis* is still larger than we found (Forbes, 1977; Tamaki et al., 1997; Berkenbusch & Rowden 2000). While, the overall number of ovigerous females recorded were low, principally due to not sampling during the peak of reproductive activity (April-May; Hailstone & Stephenson, 1961), small ovigerous females (below 6 mm CL) were found on all sampling dates. It is unclear if the small ovigerous females are 'precocious' or slow growing and this is a potential area of further research.

Hailstone & Stephenson (1961) recorded no reproductive activity for this species during November to March (austral summer). Again, this may have been because of their approach of identifying reproductive activity macroscopically in the field, but several other studies of intertidal thalassinideans have also indicated a reduction in spawning activity during summer months (Forbes, 1977; Tamaki et al., 1997; Berkenbusch & Rowden, 1998). However, reproduction in subtidal populations of some thalassinideans species does occur in summer (e.g. Buchanan, 1963; Tunberg, 1986; Rowden & Jones, 1994; Dumbauld et al., 1996). For *Callianassa japonica* in the intertidal zone, Tamaki et al. (1997) hypothesised that reproductive activity did not occur during the hottest parts of the year due to metabolic restrictions and anoxic conditions caused by high temperatures. Paterson & Thorne (1995) found experimentally that under anoxic conditions, *Trypaea australiensis* reduced its metabolic rate and given that the respiration rate of yabbies is positively correlated with body mass (Patterson & Thorne, 1995), it is possible that there is a critical size above which metabolic restrictions prevent the yabby from reproducing during the hottest parts of the year. The small ovigerous individuals we recorded during December, February and March are possibly below this critical size and are thus unaffected by these metabolic restrictions.

Given the positive correlation between egg clutch size and body size in thalassinideans (Dumbauld et al., 1996; Thessalou-Legaki & Kiortsis, 1997) the clutch size for the small ovigerous individuals recorded in this study would be small. However, the presence of reproductively active animals throughout the year provides a potential year round source of recruits which may further add to the ability of *Trypaea australiensis* to maintain relatively stable populations throughout the year.

Table 3.1. The total number of females and the number and percentage of ovigerous females collected during six sampling periods at North Stradbroke Island.

Sample Date	Total Number of Females	Number of Ovigerous Females	% of Ovigerous Females
October 1998	645	13	2.0
March 1999	382	1	0.3
July 1999	217	5	2.3
August 1999	238	2	0.8
December 1999	177	9	5.1
February 2000	290	9	3.1

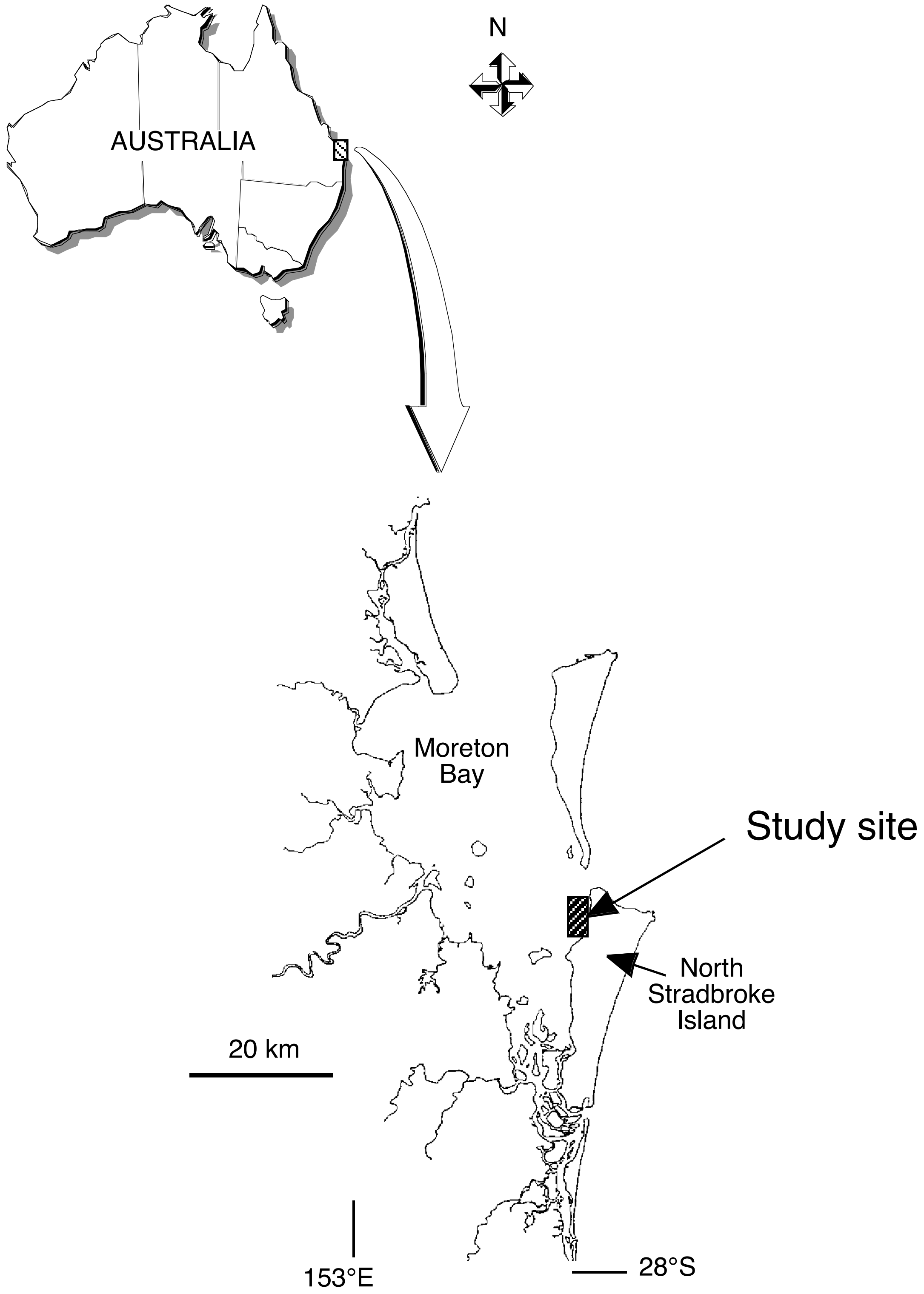


Figure 3.1: Map of Australia and the Moreton Bay region of SE Queensland showing the position of the study site.

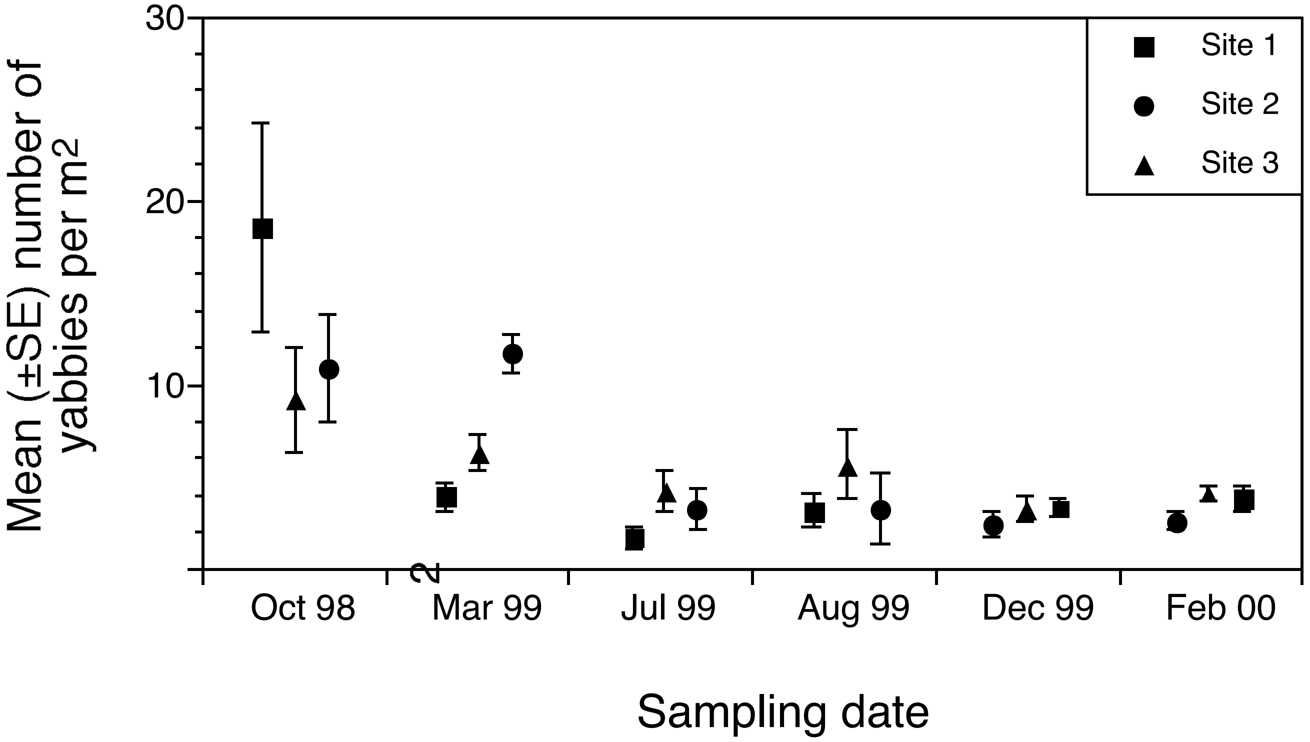


Figure 3.2: Mean (±SE) abundance of yabbies, *Trypaea australiensis*, in each of three 1 hectare control or sites on North Stradbroke Island sampled on six occasions. Data are numbers of yabbies per m2 calculated from 10 x 4m^2 quadrats on the first five occasions and 15 x 4m^2 quadrats on the final occasion.

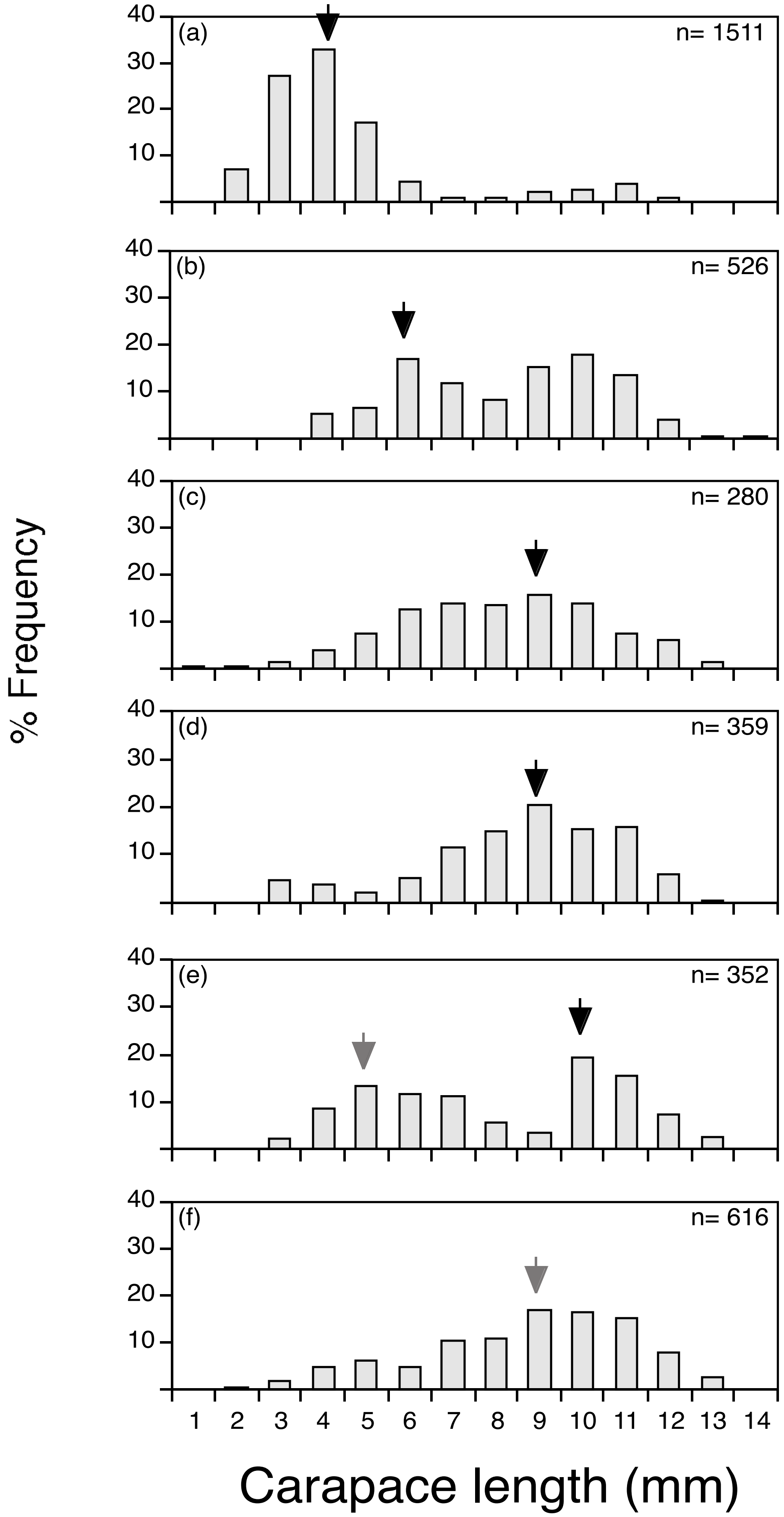


Figure 3.3: Size (mm carapace length) frequency histograms for yabbies sampled from three x 1 hectare sites at North Stradbroke Island during six consecutive sampling periods: (a) October 1998, (b) March 1999, (c) July 1999, (d) August 1999, (e) December 1999, (f) February 2000. Samples are pooled from all animals collected from the 3 sites on each occasion. Arrows indicate the mean size of the population, or mean size of each cohort in December 1999.

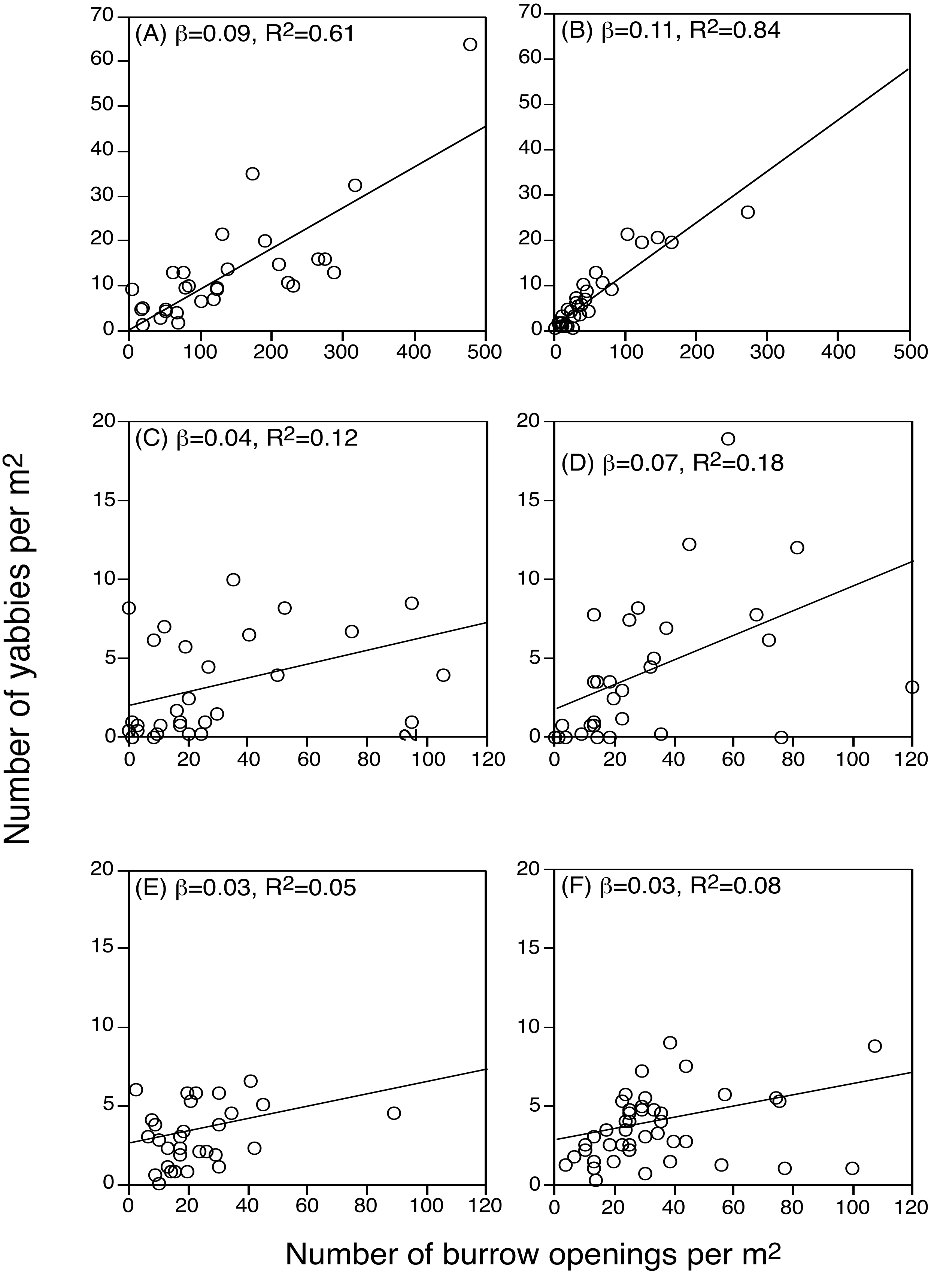


Figure 3.4: Regression plots showing the relationship between the abundance of yabbies and the number of burrow openings per m^{-2}, from three 1-hectare sites at North Stradbroke Island during six sampling periods (see text for details). N=30 quadrats (pooled across 10 quadrats from each of 3 sites) from October 1998-December 1999 and N=45 quadrats (pooled from 15 quadrats from each of 3 sites) in February 2000. Values for slope of the regression line and proportion of total variance in number of yabbies explained by the number of holes (R^2) are shown.

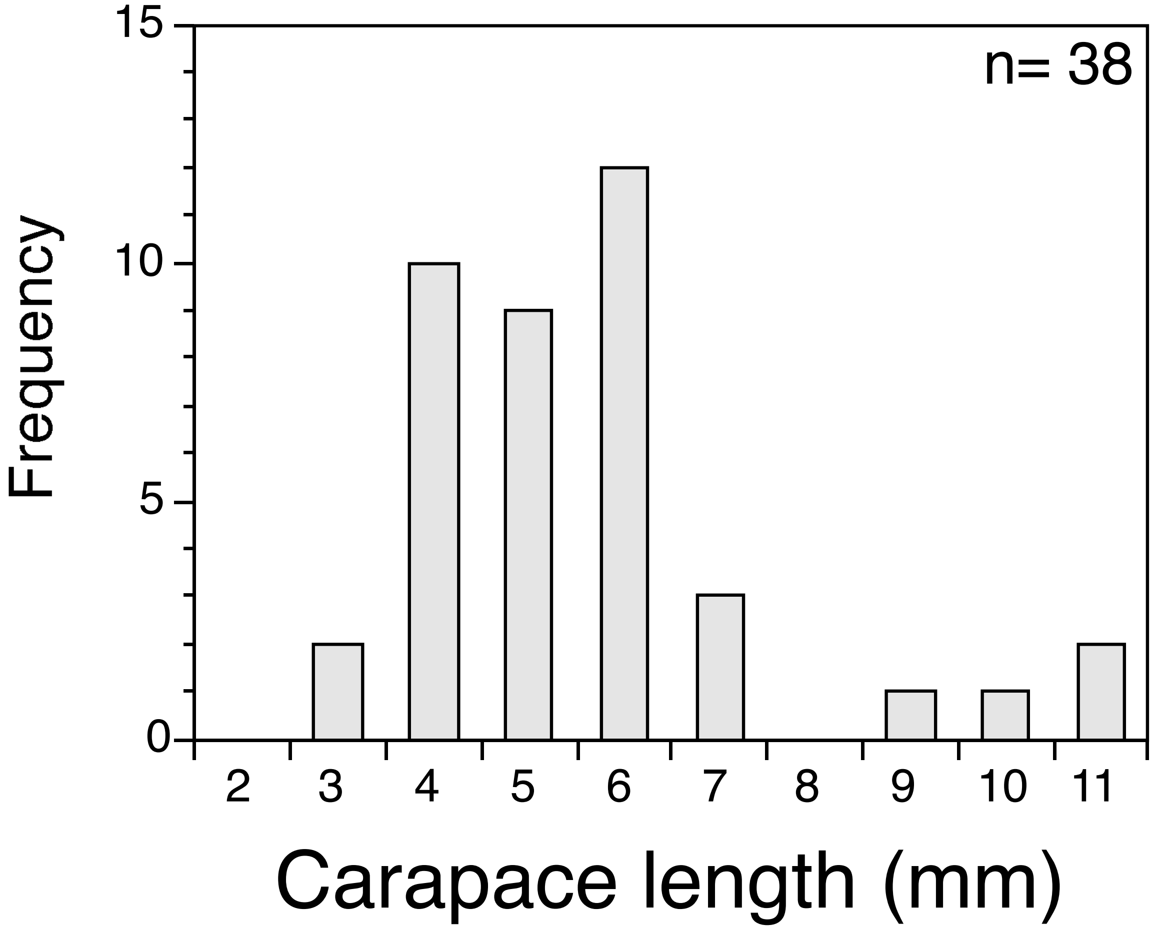


Figure 3.5: Size (mm carapace length) frequency histogram for ovigerous yabbies sampled from three sites at North Stradbroke Island. N=38 females pooled from all three sites on all six occasions.

Section 4: Impacts Associated with the Commercial Harvesting of Bloodworms

4.1. Introduction

Harvesting of bloodworms (*Marphysa* sp.) occurs almost exclusively in *Zostera* seagrass beds because this is the habitat where the worms are commonly found (Day, 1967; Fauchald, 1977). Catching the worms is an activity that damages the seagrass because the animals are infaunal, burrowing deep into the muddy sediments and the seagrass must be dug over in order to harvest the worms. As such, the bait fishery attracts attention from government departments and agencies and environmental/conservation groups concerned about this damage and the implications for the plants and animals utilising the seagrass beds. In recent years, focus has perhaps become even more intense because of the world-wide decline in the distribution and health of seagrass beds (e.g. Shepherd et al., 1989; Walker & McComb, 1992; Short & Wyllie-Echeverria, 1996).

While there has been a number of studies examining the ecological impacts of bait-harvesting in different parts of the world (e.g. Klawe and Dickie, 1957; Hailstone and Stephenson, 1961; Blake, 1979a, b; McLusky et al., 1983; Creaser et al, 1983; de Boer & Prins, 2002) , most of these have focussed on areas of unvegetated intertidal habitat. There is little detailed information on how bait-harvesting affects vegetated habitats such as seagrass beds. The effects of other sources of physical disturbance, such as wave action, recreational boating, trampling and storms, on seagrass beds have, however, been examined (e.g. Posey et al., 1996; Dawes et al., 1997; Creed & Amado Filho, 1999; Eckrich & Holmquist, 2000) and these results suggest that disturbance from activities associated with bait-harvesting are likely to impact significantly on seagrass systems.

There are four components to the work described in this section. First, the temporal changes in the physical structure of the seagrass habitat in and around areas that have been dug for bait was examined. Changes to attributes such as structural complexity provided by the seagrass have implications for other components of the ecosystem because many animals obtain a partial refuge from predation in the spatially heterogeneous habitat (e.g. Coen et al., 1981; Heck & Thoman, 1981; Stoner, 1982; Summerson & Peterson, 1984; Leber, 1985; Irlandi & Peterson, 1991; Levin et al., 1997). Changes to the sediments as a result of digging (e.g. granulometry, compaction) may also influence the organisms that are found in these habitats because of the often close association between soft-sediment infauna and sediment parameters (e.g. Sanders, 1958, 1960; McNulty et al., 1962). As the tide inundates the intertidal habitats, finer particles, including organic particles and detritus, will be redistributed. This organic material is an important food source for deposit-feeding animals (Levinton, 1979, 1989), so one effect of any changes to sediment grain size may be a decrease in the abundance of deposit-feeders, with subsequent cascading effects on other components of the system (reviewed by Levinton, 1979, 1989).

Second, the abundance of infauna in the sediments in and around the commercial pits of known age was examined to determine rates of recovery of the benthic assemblage in areas where the seagrass was disturbed through commercial harvesting. The nature of bloodworm harvesting operations is similar to a small-scale dredging operation in that the sediment is excavated and placed elsewhere, leaving large holes and pits in the surface of the substratum. The habitat is modified because gravel and rubble previously buried deep into the substratum is brought to the surface: topographic and structural complexity is changed through this and the loss of the seagrass. Rates of recolonisation of soft-sediment systems after physical disturbances such as dredging vary considerably, ranging from 2-3 months to several years depending on the system and the intensity and frequency of the dredging operations (e.g. May, 1973). Kenny & Rees (1994) examined rates of recolonisation after gravel extraction off the coast of England and found that even after 7 months some taxa had not "fully recovered". They suggested that changes to the substratum after disturbance affected recolonisation, making the area less suitable for colonising larvae (see also Saila et al., 1972; Oliver et al., 1977; Wildish & Thomas, 1985). Previous studies of recolonisation and recovery of the intertidal habitats used for commercial harvesting in Moreton Bay have only examined the vegetated components (i.e. the seagrasses) of the system (e.g. WBM Oceanics, 1993; Hopper, 1994). There is no information available on the recovery of the fauna found in the affected seagrass beds.

Third, the abundance of larger (> 1mm size) epibenthic animals was determined in the harvested areas, immediately adjacent to commercial pits and in undisturbed, reference areas. The habitat examined was the area of intertidal seagrass that surrounded the commercial pits and was subjected to the indirect effects of disturbance primarily associated with the movement of the harvesters in and out of the pits rather than complete removal of the seagrass. The epibenthic component of the benthic assemblage is often not well represented in cores of sediment taken for examining the infauna, but these animals often have a close association with structures such as seagrass (Fonseca et al., 1990; Edgar, 1992; Connolly, 1994, 1997) and rubble (Dumbauld et al., 1993; Skilleter, 1994) and so may be affected by changes to these components of the system. Additionally, the time taken to process samples of sediment to quantify the abundance and diversity of the infauna is often prohibitive (James et al., 1995). Use of the infaunal component of the intertidal, benthic assemblage for regular monitoring of the sustainability of commercial harvesting of bloodworms would be difficult because of the associated costs and need for expert taxonomic help for many of the key infaunal groups. The epibenthos is a taxonomically less diverse assemblage compared with the infauna and processing of samples takes less time because sediment does not need to be processed to remove the animals.

Fourth, the effects of small-scale physical disturbance of the intertidal seagrass beds were examined experimentally to determine whether the epibenthic assemblage was affected. These experimental manipulations were intended to mimic the disturbances associated with the movement of harvesters in and out of the commercial pits, rather than the direct removal of the seagrass through digging, complementing the general sampling of the epibenthic fauna (see above). These experiments were done on Fisherman Islands, in the area used for commercial harvesting, and on North Stradbroke Island, in an isolated area that was not used for commercial or recreational harvesting.

4.2. Methods

4.2.1. Habitat Composition

The distribution of different substrata in and around commercial pits on Fisherman Islands was estimated along each of five transects that extended for 200 metres from the top of the shore, across an area previously dug by commercial bait-harvesters. At the time the initial characterisation of the benthic habitats was done (August 1999), the majority of harvesters were working approximately 500-600 metre east of the area selected for this component of the study. Discussions with several groups of harvesters suggested that they would be unlikely to return to that part of the intertidal flats for some time, given it had been worked within the last 2-3 months. Commercial harvesters voluntarily leave areas for approximately 18-24 months before re-harvesting, to allow recovery of the seagrass (Bunger Johnson-professional bloodworm fisher, personal communication).

Transects were approximately 100 metres apart (Table 4.1). Nine categories of substratum were defined on the basis of initial observations (Table 4.2). Some categories, such as 'seagrass-*Zostera*' were relatively broad in terms of the range of substrata that fell within the category: the broad category did not make distinctions between dense and sparse seagrass for example. Variation in characteristics of the substrata within these categories were quantified in more detail through examination of the biomass of vegetation within the patch (see Section 4.2.1.2 below). The extent of each category of substratum crossed by a transect was measured to the nearest centimeter. Transects were sampled initially in August-September, 1999 and then again in April-May, 2001, 20 months later. This interval was chosen on the basis of the time period commercial harvesters claimed to leave an area fallow before re-harvesting it for worms.

4.2.1.1. Sediment Compaction

The compaction of the sediment in different substrata along each transect was determined using a penetrometer constructed from a 50 cm long rod of stainless steel, weighing approximately 280 grams. The rod was dropped from a constant height of 1.3 m above the substratum, inside a narrow PVC tube to ensure it struck the surface perpendicularly, and the depth to which it penetrated the sediment was used as an index of the relative compaction of the sediment. Five to ten measurements were made within a 1m^2 quadrat located along the transect whenever there was a transition from one substratum category to another.

The five transects crossed areas of intertidal habitat that were visibly different in general characteristics (height above sea level, gradient, degree of previous harvesting, etc.), from each other. Analysis of the data on compaction was done separately for each transect, focusing specifically on the comparisons among the different habitat categories traversed by the transects. Data were analysed with one-factor analyses of variance for each transect and time. These analyses were unbalanced because of the different number of readings taken depending on the overall length of the habitat along the transect. Post-hoc Student-Neuman-Keuls (SNK tests) were done comparing among means where ANOVA indicated significant differences in compaction among habitat types.

4.2.2.2.. Seagrass Characteristics

Cores of sediment were collected to determine the above- and below-ground biomass of seagrass in each of the patches of the different substratum categories along the transect. That is, where the transect crossed one of the substratum categories that included seagrass (seagrass, seagrass-mixed and seagrass-algae: see Table 4.2), samples were collected to characterise the vegetation along that section of the transect. Within pits (i.e. areas that had been dug to harvest bloodworms), cores were only collected from the sections that were undug. The section of the pit that had been dug was usually 1-1.5 metres deeper than the surrounding area and filled with soft mud. The cores that were collected in the undug section therefore represent the seagrass in the pit prior to it being harvested, or after recolonisation had begun. Sections of the pits were often left undug in order to facilitate this recolonisation (personal communications from commercial harvesters), although it was clear that not all harvesters did this (see Section 4.3.4. below). Cores were 15 cm in diameter and taken to a depth of 15 cm, below which there was rarely any below-ground seagrass root material.

Variable numbers of replicate cores were collected dependent on the extent of the patch of habitat. At least one sample was collected from each metre of the substratum for that patch (e.g. 10 replicate samples from a 10 metre length), with a minimum of 3 samples collected from each patch. The cores of sediment were placed into labelled plastic bags and frozen for later processing in the laboratory. Each species of seagrass was separated into above- and below-ground components which were dried (approximately 72 hours at 70°C) and weighed separately. Macroalgae were also separated into species and dried and weighed.

4.2.3.3. Commercial Pits

For each of the commercial pits encountered along the transects, additional information was collected to describe the size, depth, height of all walls and the presence and size of any gaps in the walls. The latter was determined because discussions with commercial harvesters early in the project indicated that many of them felt it was important that fishers breach the walls that are formed around a pit, once the pit has been dug over, because it facilitated more rapid recovery of the seagrass. It was evident during initial visits to the commercial areas that not all commercial harvesters were doing this. The height of each of the walls was measured on the inside and outside edges at five equally-spaced points along the walls.

4.2.2. Infauna and Commercial Pits

4.2.2.1. Tagging and Sampling of Commercial Pits

Pits being dug by commercial operators were tagged on the day the pit was first opened. Multiple tags were located, one in each corner of the pit and the harvesters were requested to not move or bury the tags. Tag recovery was almost 100% and in some cases commercial operators indicated they had replaced tags that were partly buried.

The abundance of infauna in and around commercial pits and in reference areas away from the area used by commercial operators was determined from cores of sediment associated with pits of different ages. Five replicate cores of sediment, each 15cm diameter x 15cm deep, were collected from five different habitat types: (i) inside a commercial pit of known age; (ii) from the surrounding walls (dyke) of the pit; (iii) outside the pit but within 10-15 cm of the wall; (iv) undug areas (primarily seagrass) at least 10 metres from the nearest pit, but still within the area available to commercial operators (internal reference area); and (v) undug areas outside the area available to commercial operators (external reference area). Thus, 25 samples were collected for each of the pits of known age that were sampled.

Sampling caused considerable disturbance to the habitats in and immediately around the commercial pits. The substratum was soft and easily churned when walked on and it was impossible to collect samples without sinking into the mud. Replicate samples were separated by at least 1 metre to avoid collecting sediment from an area that had been disturbed while collecting the previous replicate. To avoid artifacts associated with repeated sampling of the same pits (see Skilleter, 1996), pits were only sampled on one occasion. Sufficient pits were tagged to allow a new set of pits to be sampled on each occasion, although the number that were available was determined by the number of commercial teams working on any particular day and the specific areas they were working. On some occasions, commercial teams were only working in areas distant from where the study was being done and these pits could not be tagged. Pits that were 1 month, 2 months, 4 months and 12 months old were sampled.

The choice of these five habitat types was based on the physical structure and composition of the habitat (e.g. sediment compaction, seagrass biomass, rubble content of sediment) determined from the detailed mapping (see above) of the commercial digging area. Samples collected from the internal reference area were collected to determine if there were small-scale indirect effects on abundance and community composition of the infauna from the commercial operations. These samples were collected from patches of seagrass where there were no obvious signs of recent digging (e.g. rubble on the surface, walls or small pits).

At the time the 12 month old pits were sampled there was extensive coverage of fireweed (*Lyngbya majuscula* (Gomont)) over Fisherman Islands. This cyanobacterium is known to cause severe skin, eye and respiratory irritation in humans (Osborne et al., 2001), and several members of the research team were exposed to its effects. *L. majuscula* is also thought to affect a range of different marine organisms that come in contact with or consume it (Dennison et al., 1999). There were noticeably fewer animals than previously on the surface of the substratum (see also Section 4.3.2.-Results) and inspection of several sediment cores indicated there were also fewer infaunal animals present. On this occasion, an additional two pits were sampled, but only four replicate cores were taken from each of the habitat types, samples were not collected from the internal reference area (habitat type (iv)) and samples were collected from eight external reference areas (habitat type (v)) rather than four. This increase in sampling intensity was intended to determine how widespread the apparent effects of the *L. majuscula* bloom was. The continued presence of the *Lyngbya majuscula* bloom in Moreton Bay, including across Fisherman Islands, and the associated human health concerns meant that further sampling was abandoned.

Samples were placed into sealed jars and returned to the laboratory where they were fixed in a 7% formalin solution containing the vital stain Bengal Red and left for at least 72 hours. The samples were then washed in freshwater to remove the formalin and the sample was stored in 70% ethanol until processing. Samples were sieved across a 1mm sieve and the animals retained on the sieve were identified and counted.

4.2.3. Epibenthos and Commercial Pits

Samples of the epibenthos were collected in three different regions used for the harvesting of bloodworms (Figure 4.1). Commercial Plot 1, at the southern end of Fisherman Islands, and Commercial Plot 4, at the northern end of Fisherman Islands, are the two most important commercial harvesting plots in Moreton Bay, accounting for over 75% of total commercial harvest of bloodworms in the region (Section 1). Wynnum-Manly is the area in Moreton Bay most heavily accessed by recreational harvesters (see Section 1).

Samples were collected from the area of seagrass immediately surrounding the commercial pits rather than inside the pits because initial sampling indicated that the trampling and digging in the pits resulted in all epibenthos either being buried or leaving the pits and not recolonising until the surrounding walls had collapsed and the pit had almost completely merged with the surrounding substratum (see Section 4.3.1.). Examination of the area around the pits examined whether there were impacts from harvesting on the epibenthos in the seagrasses close to the commercial operations. Only pits with fully intact walls were selected.

At each of the harvested sites examined (Table 4.3), five replicate samples were collected from around the commercial pit, between 10-50cm from the edge of the pit wall. Five, haphazardly positioned, replicate samples were also collected from each of an equal number of reference sites. Reference sites were positioned in the area of Fisherman Islands that was not available to commercial operators for digging. Each sample comprised all the material to a depth of approximately 5 mm into the substratum from within a 1m^2 quadrat. Data were analysed with two-factor, mixed model analyses of variance, with factors Habitat (fixed: Pits versus Reference) and Sites (nested within Habitat). Data were examined separately for each of the three regions examined. The composition of the epibenthic assemblage was compared between the commercial or recreational pits and reference sites using two-factor ANOSIMs on untransformed and fourth root transformed data and plotted using nMDS.

4.2.4. Experimental Manipulations of Disturbance and Epibenthos

4.2.4.1. Study Sites

The effects of physical disturbance on epibenthos in intertidal seagrass beds were examined in manipulative experiments done on the intertidal mudflats at Fisherman Islands (western Moreton Bay) and on North Stradbroke Island (eastern Moreton Bay). Two sites, approximately 1 km apart, were used on Fisherman Islands, close to Commercial Plot 1 (Figure 4.1), in an area that had extensive coverage of *Zostera capricorni* but was at least 100-150 metres from the nearest commercial pit. Commercial fishers were notified of the experiments and their position on the Islands so they could avoid disturbing these areas. Two sites, hereafter NS-Site 1 and 2 (Figure 4.1), approximately 2 km apart were used on North Stradbroke Island. These sites were distant from areas generally accessed by the public and the experiments were therefore unlikely to be disturbed.

4.2.4.2. Experimental Design and Methods

To determine the effects of physical disturbance on the epibenthic assemblage, patches of intertidal seagrass and sediment, each $1m^2$ in area, were experimentally manipulated. Three levels of disturbance were used at the sites on North Stradbroke Island. High disturbance plots were disturbed using a pitchfork of the same sort employed by bait harvesters, with the tines pushed approximately 20 cm into the sediment, loosening the sediment and the associated roots and rhizomes of the seagrass, although no seagrass was removed. The sediment and seagrass in these patches were trampled and disturbed during this process in a manner consistent with harvesters moving around an area. This treatment was intended to simulate the disturbance associated with preliminary digging of commercial pits, when commercial operators trialed areas of the intertidal prior to determining the location of the pit. Low disturbance plots had the surficial sediments moved around with the tines of the pitchfork, but the seagrass was left intact. This treatment was intended to determine whether any effects of disturbance in the High disturbance plots was a specific result of the damage to the seagrass. Control plots were left untouched. Only two levels of disturbance (High disturbance and Controls) were used on Fisherman Islands. Four replicate $1m^2$ patches for each treatment were established at each site. The three different treatments on North Stradbroke Island were sampled after 8 and 21 weeks (total of 48 patches - 2 times x 2 sites x 3 treatments x 4 replicates). The treatments on Fisherman Islands were only sampled after 8 weeks.

Epibenthic macrofauna were collected from a $0.25m^2$ quadrat positioned in the centre of the $1m^2$ experimental patch. Only the smaller central area of each patch was sampled to reduce the likelihood of edge effects (Bowden et al., 2001). First, all large and easily visible animals such as *Pyrazus ebeninus*, *Macrophthalmus* sp. and *Clibanarius taeniatus* were collected by hand. Next, the above ground seagrass was removed (without uprooting the plants) by cutting shoots flush with the sediment to expose the sediment surface. Smaller animals were then collected by lightly brushing the surface of the mud into a small dustpan. This material was then added to the plucked seagrass and washed across a 1mm sieve before being preserved in a 5% formalin/seawater solution containing the red stain, Rose Bengal.

Two 10cm diameter cores of seagrass were collected with a PVC corer pushed to a depth of 20cm from the area outside the central quadrat to determine the biomass of seagrass in each experimental patch. The seagrass was washed across a 1mm sieve, separated into above ground (shoots) and below ground (roots and rhizomes) components which were then dried separately for 72 hours at 70°C, before being weighed.

4.3. Results

4.3.1. Habitat Composition

4.3.1.1. Qualitative Changes to Habitat Composition

During the 18 months the transects were monitored, no additional pits were dug along the transects. The area had been dug over just prior to the first survey (August 1999) and many of the pits along the transects were of a known age (1-2 months old) having been tagged on the day there were created. The characteristics of the habitats along the transects in August 1999 therefore reflect the condition in an area recently dug by commercial harvesters, with only a few months recovery. At the end of the study, all the pits along the transects were at least 18 months old, providing a broad baseline against which to assess recovery of the habitats.

There were marked qualitative changes to the types of substratum along the transects over the course of 18 months. On four of the five transects, there was a shift from patches dominated by *Zostera capricorni*, to substratum dominated by either a mixture of different seagrass species (Seagrass-mxd: Figure 4.1) or seagrass with abundant macroalgae (Seagrass-algae: Figure 4.1). The extent of area covered by commercial pits along the transects either changed very little (e.g. Transect 1, Figure 4.1A and Transect 5, Figure 4.1E) or the pits became indistinguishable from the surrounding substratum (Transect 3, Figure 4.1C) over the course of the 18 months.

4.3.1.2. Sediment Compaction

In August 1999, there were consistent, significant differences in the degree of compaction and hardness of the substratum among the different habitat categories along the transects, although the magnitude of these differences varied from transect to transect. Substrata surrounding the commercial pits (i.e. walls, wall-grass, rubble and trenches) were significantly more compacted and impenetrable than areas away from the pits (i.e. *Zostera*, seagrass-mixed and seagrass-algae) (Figure 4.2). There were large quantities of shell material in the walls and associated habitat, exposed and dumped as the pits were dug. This shell material consolidated the substratum and formed a dense layer, often extending 5-10 cm deep.

The seagrass habitat, including primarily *Zostera*, areas with mixed seagrass (*Zostera*, *Halophila* and *Halodule*) and seagrass-algae, was significantly less compacted than the wall areas. There were generally few significant differences among these three habitat types, with the exception that the seagrass-algal habitat was sometimes slightly more compacted (e.g. Figure 4.2C(A) and 4.2D(A)). Sediment compaction for the undug areas of the pits was generally similar to the areas of seagrass that had not been harvested (i.e. outside the pits).

These differences in compaction among the habitat types still persisted after 18-20 months (April 2001), with the walls surrounding pits still dominated by shell material restricting penetration of the sediment. Only on a single transect (Figure 4.2C(B)) did levels of compaction become similar across each of the habitat types, but this was associated mostly with an increase in compaction of the seagrass habitats than a decrease in compaction of the walls (cf. Figure 4.2C (A) and (B)).

4.3.1.3. Seagrass Biomass

The biomass of seagrass was generally less in the areas associated with the commercial pits compared with the nearby undug areas, although the extent of these differences varied considerably among the five transects across Fisherman Islands. Areas with rubble and the walls surrounding the pits often supported a smaller total biomass of seagrass than other areas of habitat, although in some cases (e.g. Figure 4.3A-B), the difference was not significant for one or other of these habitat types. Despite the 20 month period separating the times when the transects were sampled, there was little change in the biomass of seagrass present in the rubble and on the wall habitats: these areas continued to support significantly less seagrass than the other habitats on all the transects (Figure 4.3A-E). On four of the five transects (Figure 4.3B-E), the total biomass of seagrass in the pits was also less than in the surrounding undug habitats, despite the fact that the cores from within pits were collected from that portion that had not been harvested.

Between August 1999 and April 2001, one of the most marked changes in the overall composition of the habitat along the transects was associated with the shift from *Zostera* dominated areas to areas with a mix of different species of seagrass (Seagrass-mixed) and/or seagrass with macroalgae (Seagrass-algae) (Section 4.3.1. above). Despite this qualitative change in the composition of the habitat, it did not translate to marked changes in the biomass of seagrass present in these areas. On two of the transects (Figure 4.3A and 4.3E), there was a significantly smaller biomass of seagrass in the mixed habitat than in the *Zostera* dominated areas, but along the other transects there was no significant differences among the different areas dominated by seagrass. In those areas along the transect where the change was to seagrass-algae dominated areas, the additional plant material would provide an increase in overall plant biomass above-ground, given there was no significant difference in the biomass of the seagrass component.

4.3.1.4. Changes to Commercial Pits

The average area of the pits along the transects was 85.1 m^2 in August 1999 and 74.4 m^2 in April 2001. There was no significant difference in the size of the pits in different parts of Fisherman Islands (i.e. along different transects) nor was the difference in the area of the pits between the periods significant (ANOVA, $P>0.05$).

The height of the walls around the commercial pits was similar across the five transects, except for along Transect 1 where the walls were slightly smaller (Figure 4.4). There was also a small difference in the height of the outside and inside margins of the walls but although this difference was often significant, it only represented a few millimetres. There was a considerable decrease in the height of the walls along all the transects between August 1999 and April 2001, as the walls collapsed and merged with the surrounding substratum. Data are not shown for Transect 3 (Figure 4.4) because no walls were evident along this transect in April 2001 (i.e. had completely merged with the surrounding area - see also Figure 4.1C).

The number of breaches in the pits ranged from 0-5, with the greatest proportion (39%) having two holes present. Eighteen percent of the pits along the transects were not breached at all, effectively forming heated pools during low tide, trapping water and not flooding until the tidal height was greater than the height of the walls.

4.3.2. Infauna and Commercial Pits

One Month Old Pits: The abundance of infauna in and around the commercial pits was generally less than in undug areas inside and outside the commercial plot (internal and external reference area respectively) although the magnitude of any differences varied considerably among the different taxa but also between the two commercial pits that were examined. For example, the number of animals inside the commercial pits was 39-71% less, on the walls 23-57% less and outside the pit 16-42% less than in the external reference areas (Figure 4.6A). The abundance of gammarid amphipods (Figure 4.6B) and polychaetes (Figure 4.6E) mirrored the patterns for the total abundance of infauna with significantly fewer animals present in and around the commercial pits than in undug areas. In contrast, the abundance of gastropods (Figure 4.6C), bivalves (Figure 4.6D) and ophiuroids (Figure 4.6F) in and around the commercial pits was not different from the reference areas. There were no significant differences in the abundance of any of the taxa between the internal and external reference areas.

Multivariate analysis of the composition of the benthic infaunal assemblage showed that there were significant differences among the five habitat types (ANOSIM), although the specifics of which of the habitat types were different from each other were not clear (Figure 4.7). Generally though, the assemblage in the area inside the pit and on the wall was significantly different from the undug areas, whereas the area outside the pit was less obviously different from these reference areas.

Two Month Old Pits: The differences in the abundance of infauna in the habitats in and around the commercial pits and the undug area after two months were remarkably similar to those for one month old pits. The total number of infauna was 78-81% less inside the pits, 60-82% less on the walls and 63-78% less outside the pits compared with the external reference areas (Figure 4.8A). The differences between the two commercial pits were less at two months than at one month after construction (cf. Figure 4.6 with Figure 4.8). Again, there were significantly fewer (53-100%) gammarid amphipods (Figure 4.8B) and polychaetes (Figure 4.8E) in and around the pits than the undug areas. The differences for bivalves (Figure 4.8C) and gastropods (Figure 4.8D) were now more clearly defined, with significantly fewer animals present in at least some of the habitats associated with the pits than the undug areas. Again, there was little indication of any differences in the abundance of infauna between the internal and external reference areas.

The composition of the infaunal assemblage was significantly different among the five habitats for both commercial pits (ANOSIM), but again it was difficult to distinguish between the specific combinations of habitats (Figure 4.9). The assemblage inside the pit was significantly different from that found outside the pit and in the undug reference areas. The assemblage on the walls and outside the pit was different from the undug areas for one of the commercial pits but not the other. Notably though, the assemblage in the internal and external reference areas was significantly different from each other.

Four Month Old Pits: There were few indications of significant recovery of infauna within the commercial pits and on the walls four months after the pits had been dug, although there were now fewer significant differences in the abundance of animals in the area outside the pits compared with the undug reference areas. The total abundance of infauna was 70-72% less inside the pits, 46-72% less on the walls and 35-45% less outside the pits compared with the external reference areas (Figure 4.10A).

There were 83-97% fewer gammarid amphipods (Figure 4.10B), 70-86% fewer bivalves (Figure 4.10D) and 69-94% fewer nereidid polychaetes (Figure 4.10G) in dug areas of the commercial pits (inside, walls and outside) than the external reference areas, but there were no significant differences present among the various types of dug habitat. In contrast, for groups such as tanaid crustaceans (Figure 4.10C), gastropods (Figure 4.10E), spionid polychaetes (Figure 4.10H) and syllid polychaetes (Figure 4.10I), only some habitat types (usually the inside and the wall) had fewer animals than in the external reference areas and there were large differences between the two commercial pits.

The composition of the benthic assemblage after 4 months recovery fell into three distinct groupings, each significantly different from each other (ANOSIM; Figure 4.11). The three dug habitat types (inside, walls and outside) were not different from each other, but were all significantly different from the undug reference areas, and the internal and external reference areas were both different from each other.

Twelve Month Old Pits: A total of 862 animals was recovered from 80 samples (48 in and around pits, 32 from external reference areas), compared with 1417 animals from 50 samples collected after 2 months recovery. More importantly, the data collected in and around the commercial pits after 12 months recovery was characterised by substantial variation, with many samples having no or few animals present and many taxa only occurring at a few of the eight external reference areas. This was most noticeable for groups such as the bivalves (Figure 4.12C) and polychaetes (Figure 4.12E) which had been relatively abundant and widely distributed during previous periods of sampling.

No significant differences in the abundance of any taxa were detected among any of the habitats in and around the commercial pits and the external reference areas (Figure 4.12A-F). There were no significant differences in the composition of the benthic assemblage in and around any of the four commercial pits and the external references areas (Figure 4.13).

4.3.3. Epibenthos and Commercial Pits

Commercial Plot 1: There was no indication that the abundance of epibenthic animals was affected by the presence of the commercial pits in the main commercial area on Fisherman Islands. There was considerable variation in the abundance of all fauna among the different pits but also among the different reference sites that were sampled (Figure 4.14) resulting in a significant site effect in all analyses (ANOVA, Site(Habitat)), but no significant effect of habitat. For some taxa, on average there were more animals present in the pits than the reference areas (e.g. hermit crabs-Figure 4.14B, mud whelks, *Pyrazus ebeninus*-Figure 4.14D) but this was usually the result of one or a few pits having very large numbers present. The converse was also true, with more of some taxa (e.g. oyster drills, *Bedeva paivae*-Figure 4.14C, *Nassarius burchardi*-Figure 4.14F) on average in the reference sites than around the commercial pits.

Commercial Plot 4: A similar pattern was evident around the commercial pits at the other end of Fisherman Islands (Figure 4.15), with the exception that there were significantly more hermit crabs (primarily *Clibanarius taeniatus*) around the commercial pits than in the reference sites (Figure 4.15B). This result was primarily a function of the very large numbers present at a single commercial pit though. Again, there was usually significant variation in the abundance of the taxa among the different commercial pits and/or reference sites.

Manly-Wynnum (Recreational Harvest Area): The abundance of epibenthos in the area used heavily by recreational harvesters was not significantly different between the habitat around the recreational pits and the reference sites (Figure 4.16), but again there was significant variation among the sites within these habitats for all taxa.

There were no significant differences in the composition of the epibenthic assemblages between the area around the pits and the reference sites at either of the commercial plots, or in the Manly-Wynnum recreational harvest area (ANOSIM and nMDS: Figure 4.17). As was evident from analyses on the individual taxa, there was significant variation in the composition of the epibenthic assemblage among the different sites examined (ANOSIM).

4.3.4. Effects of Experimental Disturbance on Epibenthos

North Stradbroke Island: There was no consistent, significant effect of physical disturbance on the above-ground biomass of seagrass at the sites on North Stradbroke Island (Figure 4.18A). There was a significant Site x Time interaction ($P<0.02$), a result of the greater decrease in average biomass between 8 and 21 weeks at Site 2 compared with Site 1. None of the terms involving the Disturbance treatments was significant. There was a trend towards less seagrass in the High Disturbance treatment than in the other treatment after 8 weeks ($\overline{X_{HD}}\pm SE = 0.46\pm0.06$g; $\overline{X_{LD}}\pm SE = 0.68\pm0.04$g; $\overline{X_{CTL}}\pm SE = 0.61\pm0.06$; 28.7% decrease) but not at 21 weeks ($\overline{X_{HD}}\pm SE = 0.58\pm0.04$g; $\overline{X_{LD}}\pm SE = 0.57\pm0.08$g; $\overline{X_{CTL}}\pm SE = 0.56\pm0.04$) but the Time x Disturbance interaction was not significant (ANOVA, $P>0.08$) suggesting low power in the test for that term.

The biomass of below ground seagrass (roots and rhizomes) varied significantly between sites (ANOVA, $P < 0.001$; Figure 4.18Bi) and among disturbance levels ($P < 0.006$; Figure 4.18Bii), but there was no significant interaction between disturbance and site. There was a 17% decline in below ground seagrass in the High disturbance treatment compared with the other two over the course of the experiment. None of the interactions were significant.

Despite the loss of seagrass in the High disturbance patches, there was no significant effect of disturbance on any of the epibenthic taxa, at 8 or 21 weeks after the start of the experiment (Figure 4.19). Numbers of individuals of the different taxa were generally very consistent among treatments and between the two sites although there were occasionally significant differences between the two times (e.g. *Clanculus* sp.; Time - $P<0.05$; Figure 4.19B; nereid polychaetes; Time – $P<0.05$; Figure 4.19E; amphipods; Time – $P<0.05$; Figure 4.19F). There was no significant effect of disturbance as an interaction (with Time or Site) or main effect for any taxon examined.

Fisherman Islands: Physical disturbance had no detectable influence on the biomass of seagrass on Fisherman Islands (ANOVAs: Figure 4.20A-B) after 8 weeks. There were no significant effects on the abundance of any of the epibenthic animals in the seagrass at Fisherman Islands with the exception of brittle stars. Where there was a difference in abundance between the High disturbance and Control patches at one site, the other site usually showed the opposite pattern (e.g. *Batillaria australis* – Figure 4.21C; *Smaradgia souverbiana* – Figure 4.21D; *Ilyograpsus paludicola* – Figure 4.21F). The abundance of brittle stars was significantly greater in the High disturbance than Control patches at one site but the opposite pattern occurred at the second site (Disturbance x Site interaction, $P<0.01$; Figure 4.21G).

4.4. Discussion

The substratum in areas immediately adjacent to commercial pits was markedly different from those areas further away. There was significantly less seagrass (above- and below-ground), the sediment was more compacted and there were extended areas where the substratum was elevated compared with the surrounding undug areas of habitat. All these differences were associated with the harvesting of bloodworms by commercial operators on Fisherman Islands.

The primary technique used by commercial operators on Fisherman Islands is the bail-and-dyke technique (see Section 1.1.5 and Forbes, 1984; WBM Oceanics, 1993). A raised wall (the dyke) is built from the substratum, surrounding an area of seagrass from which the bloodworms will be dug. Water is bailed from inside the dyke with either buckets, or in some cases, using petrol-driven hydraulic pumps. During this process, buried shell material and rubble is brought to the surface and piled onto the walls of the dyke. This shell and rubble often forms an almost impenetrable layer on or just below the substratum, significantly increasing the overall compaction of these areas. Even after 18-20 months, the walls and areas of rubble surrounding the pits were still significantly more compacted that other habitats along the transects, presumably because the large fragments of shell and rubble remain close to the surface and are only slowly buried in the relatively benign physical environment.

The presence of the layer of shell material on and just below the surface of the substratum may create a substantial hindrance to burrowing animals, preventing them from obtaining an important refuge from predation through burial (Hines & Comtois, 1985; Barshaw & Able, 1990). This would account for the relatively low abundances of infauna in the wall habitat, even after 4 months recovery of the pit area. At the same time, large epibenthic predators, such as shorebirds (Charadrii) tend to avoid heavily compacted substrata (Yates et al., 1993), although the area affected at any one time may be too small to have a strong effect on shorebird distribution (Cummings et al., 1997). The only animals that were significantly more abundant in the wall area were hermit crabs (primarily *Clibanarius taeniatus*) which were presumably responding to the increased availability of shells available for occupation (e.g. Abrams, 1980; Abrams et al., 1986; Hazlett, 1996; Garcia & Mantelatto, 2001).

Although the commercial pits are dug during low tide, there is considerable suspended fine sediment that remains in the pit during this process. Additionally, the water that is continually bailed from the pit to facilitate digging is usually heavy in suspended sediments. This material is initially deposited on the substratum during low tide but is resuspended as the tide rises (personal observation). Fine-grained sediments which are resuspended in the water column as the tide rises will eventually be deposited back onto the substratum at locations dependent on the flow regime in across the mudflats, potentially burying animals left in the pits, or ones attempting to colonise. Direct burial of organisms due to sedimentation is a potential impact arising from the digging of the pits, especially when there is inadequate attention paid to restricting the extent of transport of the resuspended material (e.g. Morton, 1977; Maurer et al., 1981a, b, 1982). In the case of the commercial operations, there are no mechanisms in place to restrict this and, indeed, this would be extremely difficult to do given the nature of the fishery. Organisms that are attached to hard substrata (e.g. oysters, mussels and barnacles) are likely to be killed outright when they are smothered by fine sediments because of their inability to burrow above the deposited material (e.g. Carriker, 1967, 1986; Saila et al., 1972; Moran, 1991). This may also include the numerous animals that live on seagrass blades (Keough, 1986; Ward, 1989; Dirnberger, 1994). In a series of laboratory experiments, Maurer et al. (1981a, b, 1982) examined the ability of polychaetes, crustaceans and molluscs to migrate vertically after being buried in natural (i.e. locally occurring) sediments. They found that survival decreased as the depth of burial and the length of time the animals were buried increased. Depth of burial may not be an issue outside of the pit because the layer of fine sediments settling back onto the substratum after resuspension accumulates slowly, allowing animals time to adjust their vertical position in the sediment. Burial may be a more significant problem for animals inside the pits though, some of which are greater than 1 metre deep and animals are buried beneath substantial amounts of fine sediment.

Most of the field-based experimental studies that have dealt with the effects of sediment disturbance on soft-sediment communities have been done on relatively small scales, e.g. patches of defaunated sediments (Zajac & Whitlatch, 1982) and have been primarily interested in rates of recovery and the successional sequence involved in recolonisation (reviewed by Thistle, 1981), but there have been some which have dealt with the effects of smothering on infauna (Rhoads, 1974; Thistle, 1981; Wilson, 1981). Brenchley (1981), for example, found that the impact of burial on infauna depended on the mobility of the animals (tube-dwellers vs. mobile burrowers) and their feeding type (suspension-feeders vs, deposit-feeders). Similarly, Peterson (1985) found that suspension-feeding clams were more susceptible to mortality from burial than deposit-feeding clams. None of these studies specifically examined the effects of smothering from continuously deposited sediments on the survival of new recruits.

The potential effect of the rubble and shell material in hindering the burial of infauna and reducing diversity and abundance may be counteracted by the enhanced stability of the sediments provided by the additional structure. Animal tubes (Buchanan, 1963; Rhoads & Young, 1971; Woodin, 1979) and seagrass (e.g. Ginsburg and Lowenstam, 1958; den Hartog, 1970; Fonseca et al., 1983; Fonseca, 1989) have been observed to stabilise sediments with an associated increase in species richness and abundance. It is likely that material such as rubble may have a similar stabilizing effect. Rubble has also been shown to enhance the settlement and recruitment of some crabs (e.g. Arnold, 1984; Armstrong et al., 1992; Dumbauld et al., 1993) and bivalves (Skilleter, 1994) through the provision of enhanced refuges from predation. It is important to note though that the total area of wall and rubble associated with commercial pits along any of the transects was very small, so any such effects may be quite restricted in the overall importance.

The shift from an intertidal area dominated by *Zostera capricorni* to one with a mixture of Z. *capricorni*, *Halophila* sp. and *Halodule uninervis* in response to physical disturbance is not surprising given past work on the factors determining species diversity in seagrass meadows (e.g. den Hartog, 1971; Fonseca & Kenworthy, 1987; Clarke & Kirkman, 1989; Duarte et al., 1997). Genera such as *Halophila* and *Halodule* maintain a small total biomass but are often able to recover rapidly after disturbances, especially those associated with sedimentation (Fonseca et al., 1987;

Poiner et al., 1989; Duarte et al., 1997). *Halophila ovalis* in particular has been shown to recover from being buried within a few months (Brouns, 1987; Clarke & Kirkman, 1989; Supanwanid, 1996; Duarte et al., 1997).

Despite the qualitative change in the composition of the seagrass community, *Zostera capricorni* was still the dominant species of seagrass along the transects, and the biomass of the other species (primarily *Halodule uninervis* and *Halophila ovalis*) was always relatively small. The maintenance of the biomass of *Zostera capricorni* (and the total biomass of seagrass), especially the below-ground component, along the majority of the transects suggests that any indirect changes from commercial bait-harvesting on the benthic fauna may be relatively minor. This dense mat of roots and rhizomes helps to stabilise the sediments (e.g. Fonseca et al., 1983; Fonseca, 1989) and is important in the development of infaunal communities (Orth, 1977).

The presence of the intact root and rhizome mat is likely also to be important in subsequent recolonisation and recovery of the dug areas. Recolonisation of seagrass is often via clonal growth into gaps created by a disturbance (Sand-Jensen, 1975; Vermmat et al.,1997; Creed & Amado Filho, 1999; Rasheed, 1999). The walls and rubble banks around the pits had a relatively small biomass of seagrass present, even after 18-20 months of recovery, suggesting the compacted sediment, with the large proportion of shell material, may hinder lateral growth of the seagrass from the surrounding undug areas. If this is the case, then recolonisation of the dug sections of each pit may be heavily dependent upon the remaining undug portion, or the creation of sufficient gaps in the walls after the pit has been harvested. Commercial harvesters indicated that they left a portion of each pit undug in order to facilitate recolonisation of the dug areas: the seagrass in these sections had a similar above- and below-ground biomass to other parts of the transect and would likely provide good opportunities for subsequent recolonisation of the dug areas once the sediment had stabilised. Similarly, many operators deliberately opened gaps into the walls because of the belief that it enhanced recovery of seagrass into the pits.

The walls of the pit and associated areas of rubble were the main habitats along the transects that showed little change over the course of the 18-20 months. The biomass of seagrass in the walls remained significantly less than in other habitats. The height of the walls decreased markedly over the time course of the monitoring as the walls collapsed and merged with the surrounding substratum, but on four of the five transects the walls were still prominent. It is very important to note though that despite these prolonged effects and changes on this component of the intertidal area, the walls and rubble banks only represent a very small component of the area along the transects and, therefore, across the mudflat. The greater proportion of the habitats in the areas being commercially harvested showed few prolonged (i.e. after 18-20 months) effects from the digging of the bloodworms.

There were clear and distinct impacts on the abundance of benthic infauna in and around the commercial pits and these effects were still detectable after 4 months recovery. The affected groups included gammarid amphipods, a range of different families of polychaetes, gastropods (primarily *Velacumantus australis* and *Nassarius burchardi*) and bivalves. These results are consistent with previous detailed studies on the effects of bait-harvesting on macrofauna, albeit in unvegetated sediments (McLusky et al., 1983; Van den Heiligenberg, 1987;

Zharikov & Skilleter, 2003a). The most marked effects were observed for the habitat inside the commercial pits and on the walls raised during the digging process. This is not surprising, given the extent of the physical changes that occur in the seagrass habitat during harvesting. The area inside the pit is almost completely dug over, often to a depth >1m, leaving unconsolidated almost fluid mud, except in the patches of undisturbed seagrass. Rubble and shell material is used to create the raised dykes (walls) allowing the harvesters to then bail out any retained water in the pit and search for worms as the seagrass is dug.

After 12 months, there were no detectable differences in the abundance of infauna between the dug areas of a pit (inside, walls and outside) and the reference areas suggesting recovery of the commercially dug areas, but this result should be treated with caution because of the potential effects arising from the outbreak of *Lyngbya majuscula* in western Moreton Bay. There were noticeable changes in the areas affected by the cyanobacterial mats, with fewer epibenthic animals present and extremely patchy distributions for many of the infauna. This resulted in 16% of the samples not containing any animals and 40% containing less than 5 animals (mostly the snail *Batillaria australis* remained). This pattern was not restricted to the area around the commercial pits, but extended across much of the southern end of Fisherman Islands (personal observation). There have been few detailed ecological studies of the effects of *Lyngbya majuscula* on the communities in seagrass, although the toxicity of the cyanobacterium on a range of other biota has been well reported (e.g. Dennison et al., 1999; reviewed by Osborne et al., 2001) and links have been made in the popular press between *Lyngbya* blooms and impacts on fisheries in Moreton Bay (and see Nagle & Paul, 1998 for other examples of impacts on fish). The implications of the extensive coverage of *Lyngbya* across Fisherman Islands on the diverse community of plants and animals that are found in the habitats there are unclear, but need to be taken into account when considering the apparent recovery of fauna in and around the commercial pits.

Very few bloodworm (*Marphysa* sp.) recruits or juveniles were detected in any of the samples in and around the commercial pits or in the reference areas during the study, consistent with the findings of Hopper (1994) who suggested that worms recruit subtidally, then migrate into the intertidal. If this is the case, then the subtidal may provide an important refuge for the populations of worms because these habitats are not harvested due to current restrictions on allowable harvesting methods (hand harvesting with pitchforks would not be feasible in the subtidal). Blake (1979) found that recolonisation by *Nereis virens* also occurred from neighboring, unharvested areas. Vadas & Bristow (1985) and Bristow & Vadas (1991) studied gene flow and genetic changes in a heavily harvested population of Atlantic bloodworm (*Glycera dibranchiata*) and found, however, that there was restricted migration and colonisation from populations between and within estuaries and suggested that colonisation of intertidal areas was unlikely to occur from subtidal refuge populations, countering previous suggestions by Klawe & Dickie (1957), Creaser (1973) and Creaser & Clifford (1986). The presence of refuge populations of *Marphysa* sp. in the subtidal region of Fisherman Islands may be an important issue for the long-term viability of the fishery, if over-harvesting of the intertidal areas were to occur (but see below). Detailed genetic studies of sub-populations around Moreton Bay, in both intertidal and subtidal areas, would be needed to determine this.

Despite the significant impacts detected on both the habitat (seagrass and sediments) and infaunal community from the digging of commercial pits, the total area of Fisherman Islands that is affected at any time is relatively small. The total area of the four commercial plots on Fisherman Islands are: Plot 1 = 918,142.5 m^2, Plot 2 = 438, 531.4 m^2, Plot 3 = 1,083,212.9 m^2 and Plot 4 = 1,288,544.2 m^2. At the time this study was being done, most commercial activity was based on Plot 1, yet the total area within that plot that showed any signs of having been dug (i.e. modified habitat) was only 360,931.2 m2, approximately 39%. This represents the area contained within an outer perimeter bounding the overall section that had been dug over but there was a great deal of the habitat within that perimeter that was intact (usually >50%: see Section 4.3.1.1.). If the data from Commercial Plot 1 are also representative of the pattern of digging in the other commercial plots, then only approximately 20% of the available intertidal habitat within the commercial plots is being harvested at any time. As long as harvesters do not revisit a previously dug area for 18-24 months, the time it takes for the habitat to recover significantly, then the long-term sustainability of the commercial industry should be maintained.

Table 4.1: GPS coordinates for the five transects monitored over 12 months to examine changes of the habitat characteristics found in areas subjected to commercial bloodworm harvesting.

Transect Number	Coordinates	
	Start	End
One	153°11.640' E 27°24.290' S	153°11.573' E 27°24.288' S
Two	153°11.655' E 27°24.216' S	153°11.555' E 27°24.232' S
Three	153°11.684' E 27°24.177' S	153°11.549' E 27°24.205' S
Four	153°11.680' E 27°24.164' S	153°11.543' E 27°24.189' S
Five	153°11.679' E 27°24.105' S	153°11.563' E 27°24.132' S

Table 4.2: Major categories of substratum along 200 metre transects perpendicular to the shoreline at Fisherman Islands, and crossing the main areas used by commercial bait-harvesters.

Substratum Category	Criteria for category
Seagrass - *Zostera*	Habitat is primarily *Zostera capricorni*, with less than 5% coverage of other seagrass species and/or algae.
Seagrass - mixed	Habitat is a mixture of *Zostera capricorni*, *Halodule uninervis*, *Halophila ovalis* and *Halophila decipiens*.
Seagrass - algae	Habitat is a mixture of *Zostera capricorni* and macroalgae, mostly *Gracilaria*, *Laurencia*, *Colpomenia sinuosa*, *Hydroclathrus clatharatus* and *Padina fraseri*.
Wall	Habitat consists of a raised wall or dyke created when harvesters start to dig using the bail-and-dyke method. A wall is raised around an area (pit) from which worms will be harvested and then water is bailed from the area within the walls before the seagrass is dug over. Walls consist primarily of coarse rubble and shell fragments when the intermixed sediment washes away on the rising tide.
Wall - seagrass	An area of wall where *Zostera capricorni* has re-grown.
Pit	An area of habitat, surrounded by walls, from which seagrass has been dug over for worms. Characterised by the presence of the surrounding walls and deep holes.
Trench	A narrow channel immediately outside the walls surrounded a pit, formed when the walls are being dug for the bail-and-dyke method of harvesting.
Rubble	Patches of habitat characterised by piles of shell material lying on the surface of the mud. These areas were in close proximity to pits and may have represented areas where shell material from several pits had accumulated.
Bare sediment	Areas without coverage of vegetation (seagrass or algae) or obvious amounts of shell rubble on the surface.

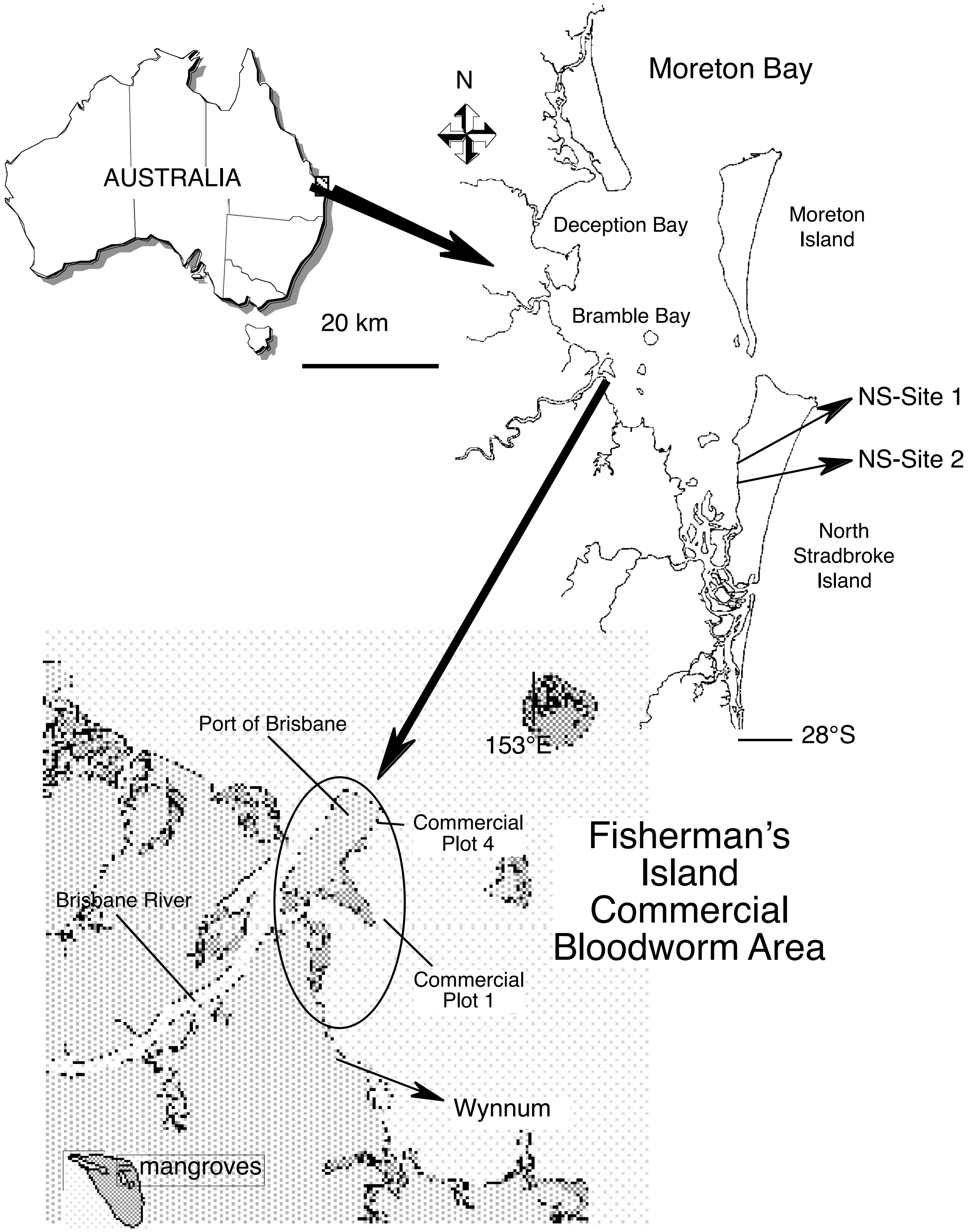


Figure 4.1: Map of Australia and the Moreton Bay region of SE Queensland showing the position of the Fishermen's Island Commercial Bloodworm harvesting areas, the Wynnum-Manly foreshore used by recreational harvesters and the sites on North Stradbroke Island used for the experimental examination of the effects of disturbance on epibenthos.

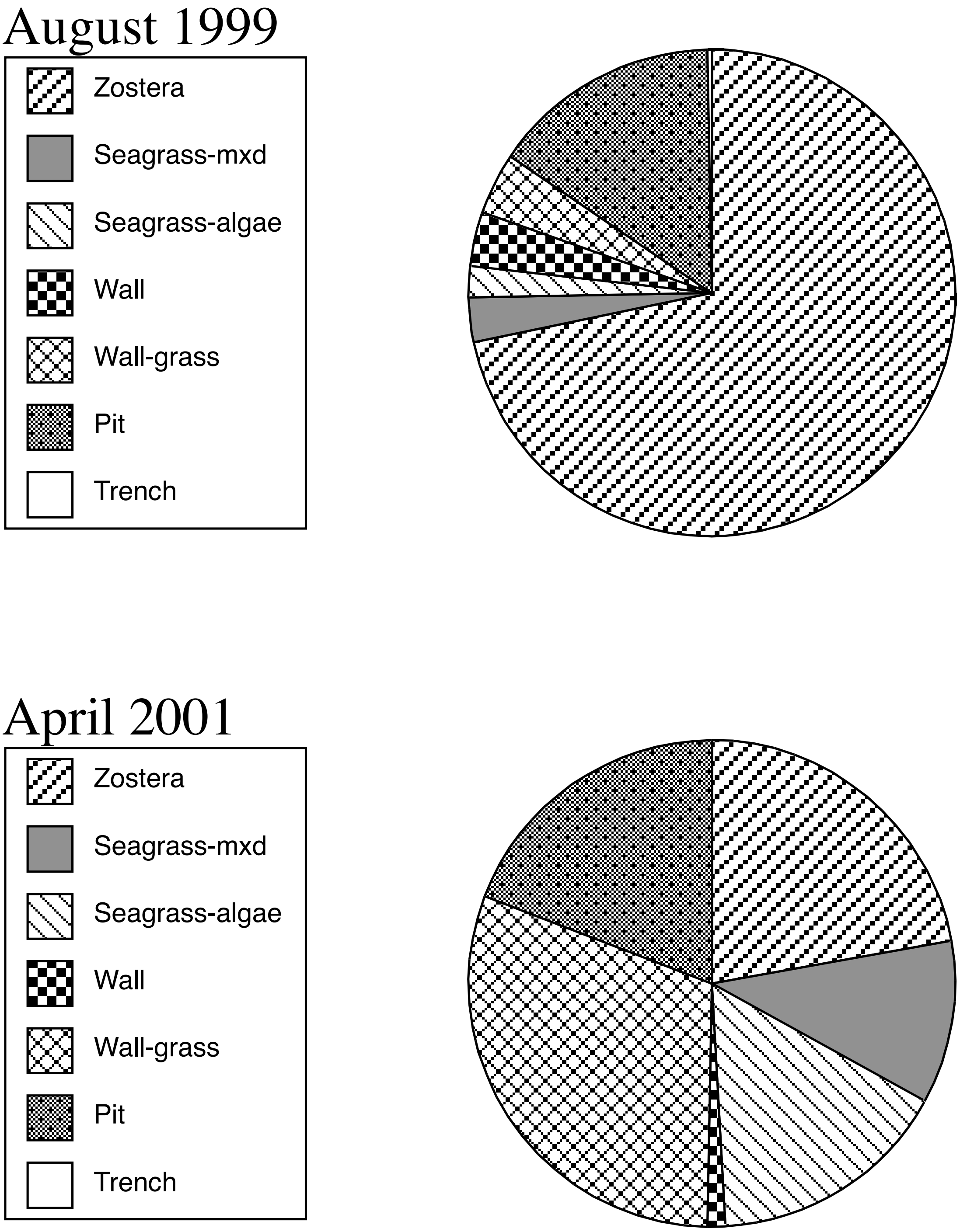


Figure 4.2A: Broad changes in the proportion of each of the different types of substratum along Transect 1 (Fisherman Islands) after an 18 month (August 1999-April 2001) period. Each transect was 200 metres long and the length of each substratum type was measured to the nearest centimeter (see Section 4.2.1. for other details of methods).

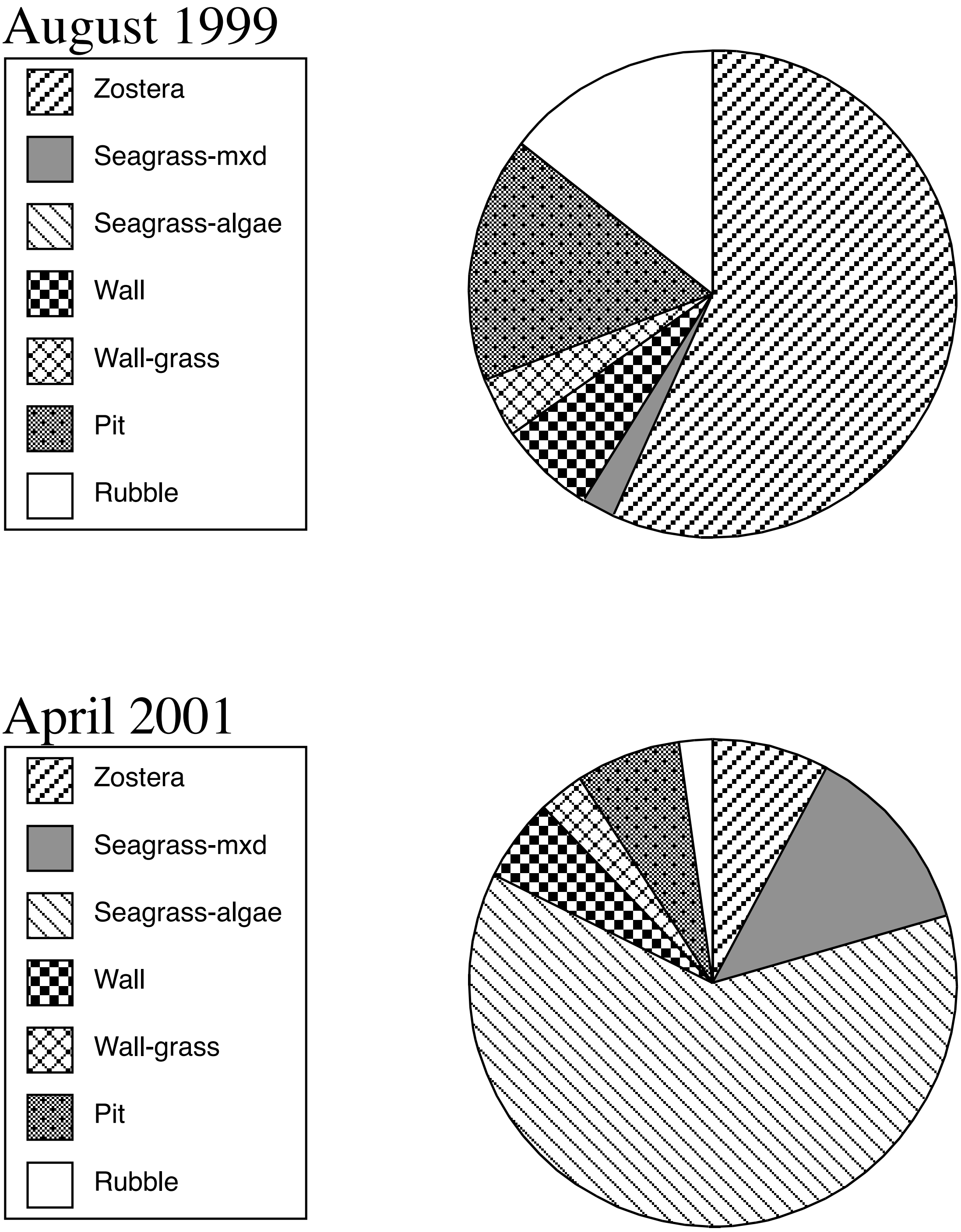


Figure 4.2B: Broad changes in the proportion of each of the different types of substratum along Transect 2 (Fisherman Islands) after an 18 month (August 1999-April 2001) period. Each transect was 200 metres long and the length of each substratum type was measured to the nearest centimeter (see Section 4.2.1. for other details of methods).

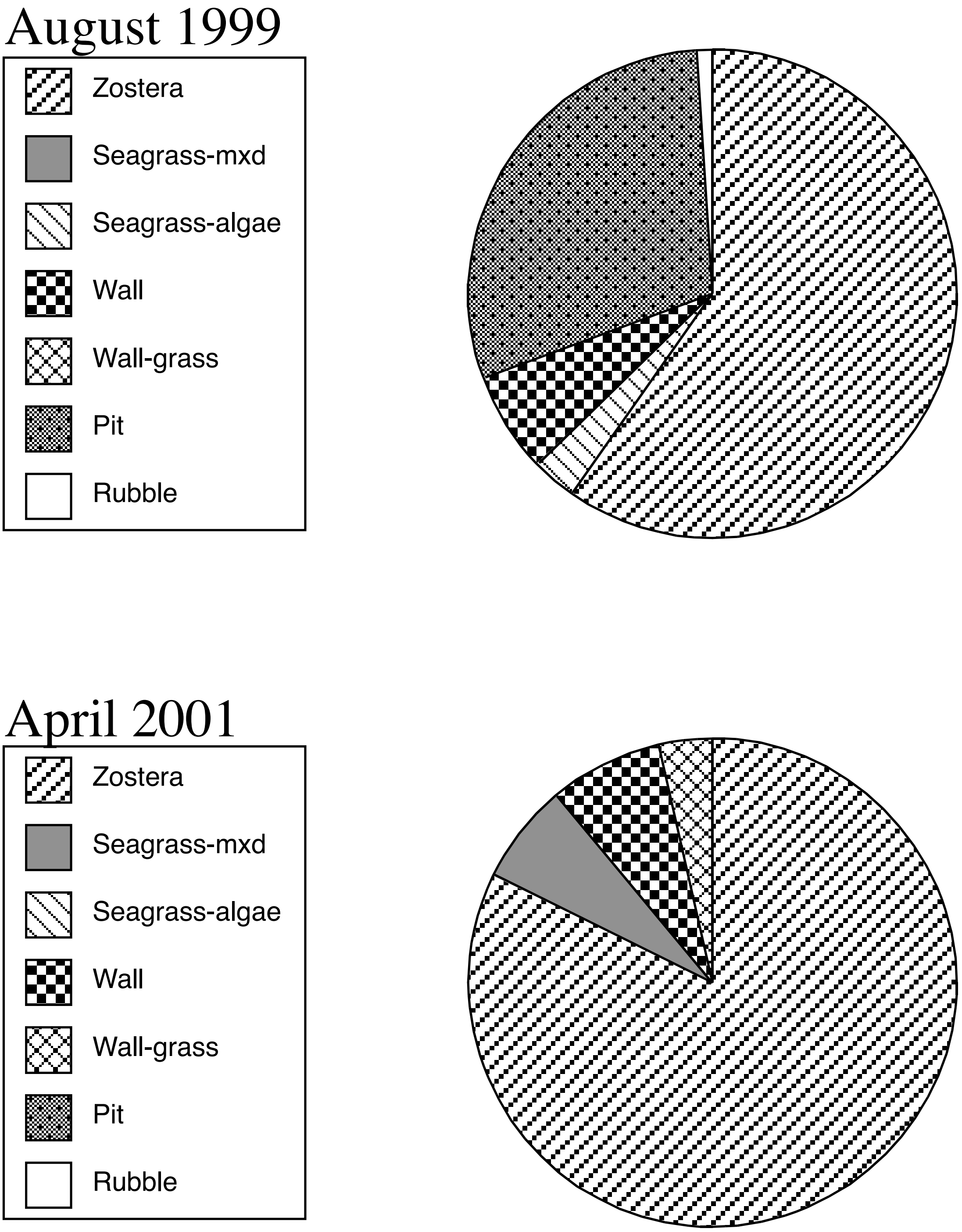
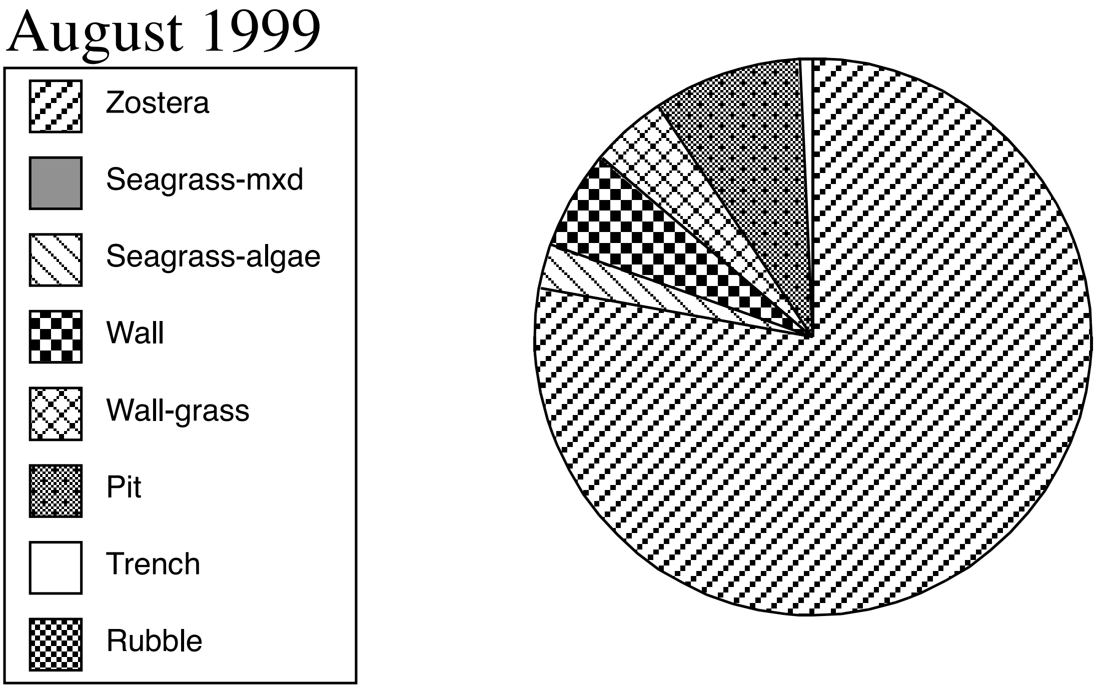


Figure 4.2C: Broad changes in the proportion of each of the different types of substratum along Transect 3 (Fisherman Islands) after an 18 month (August 1999-April 2001) period. Each transect was 200 metres long and the length of each substratum type was measured to the nearest centimeter (see Section 4.2.1. for other details of methods).



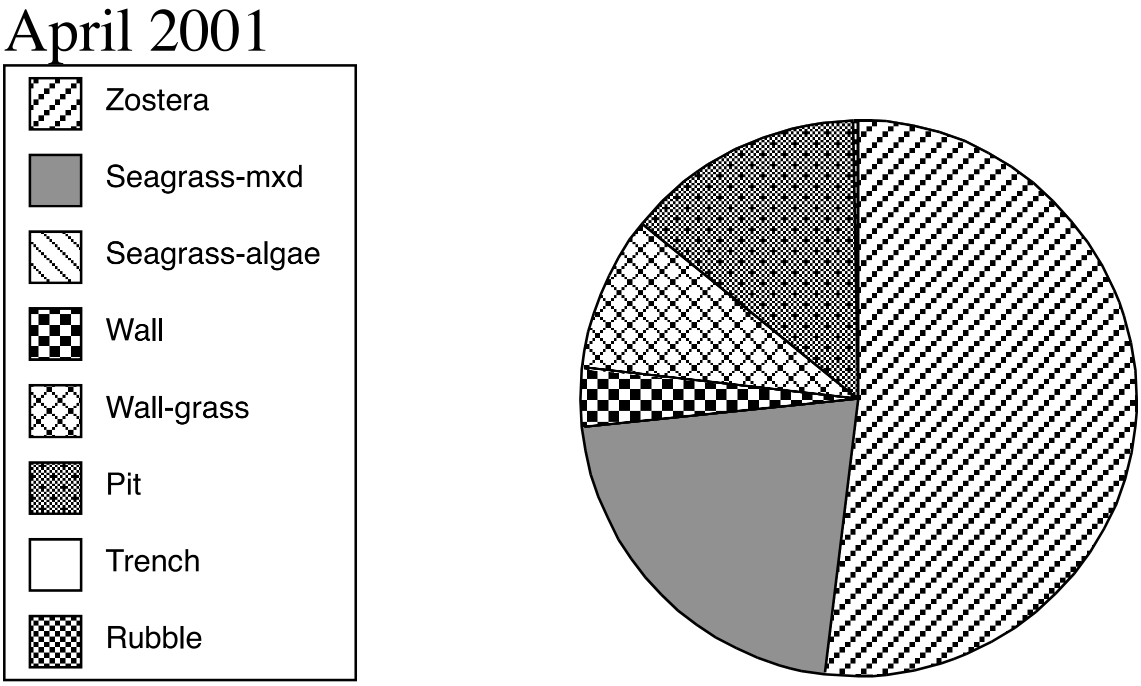


Figure 4.2D: Broad changes in the proportion of each of the different types of substratum along Transect 4 (Fisherman Islands) after an 18 month (August 1999-April 2001) period. Each transect was 200 metres long and the length of each substratum type was measured to the nearest centimeter (see Section 4.2.1. for other details of methods).

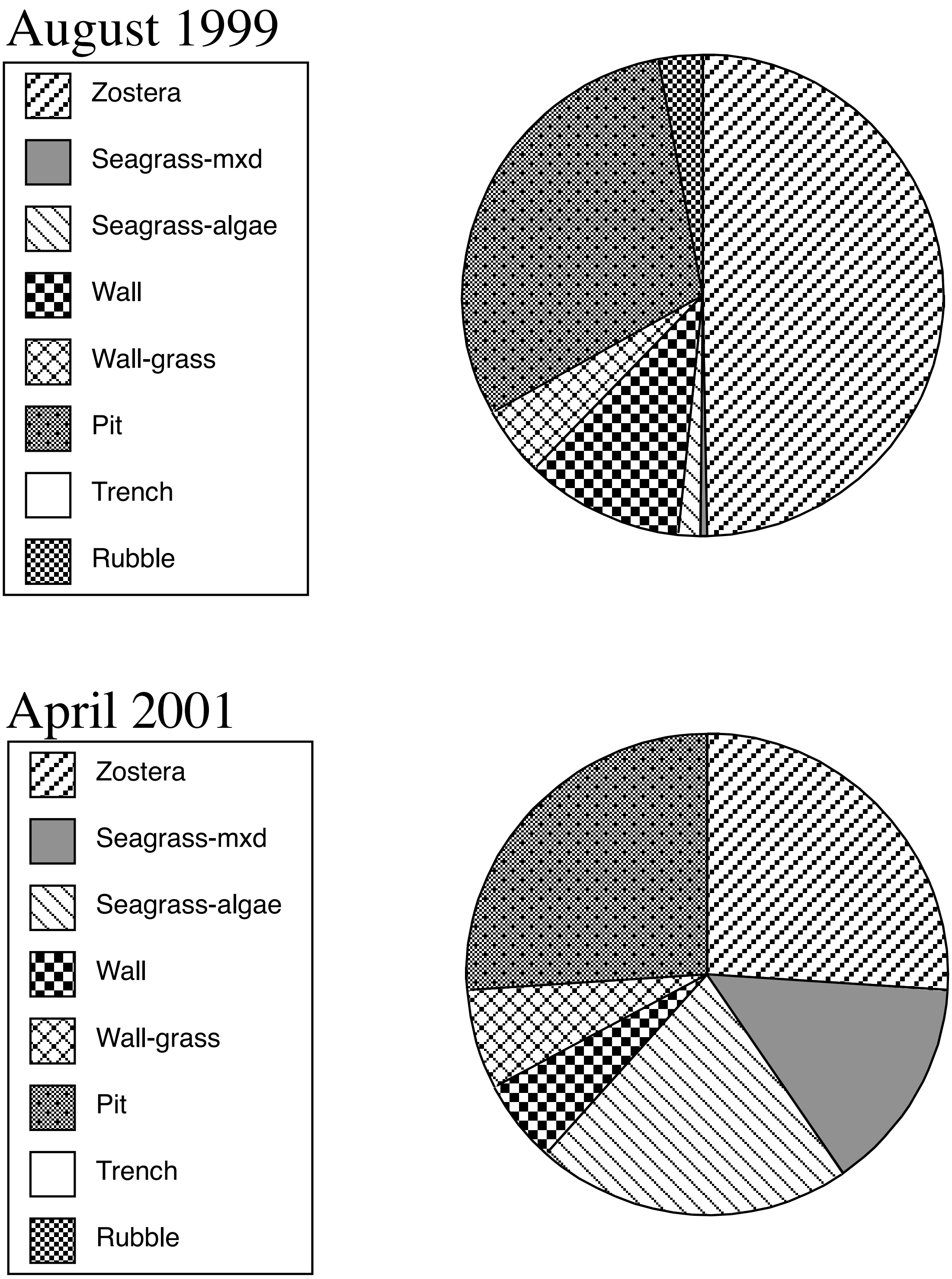


Figure 4.2E: Broad changes in the proportion of each of the different types of substratum along Transect 5 (Fisherman Islands) after an 18 month (August 1999-April 2001) period. Each transect was 200 metres long an5 the length of each substratum type was measured to the nearest centimeter (see Section 4.2.1. for other details of methods).

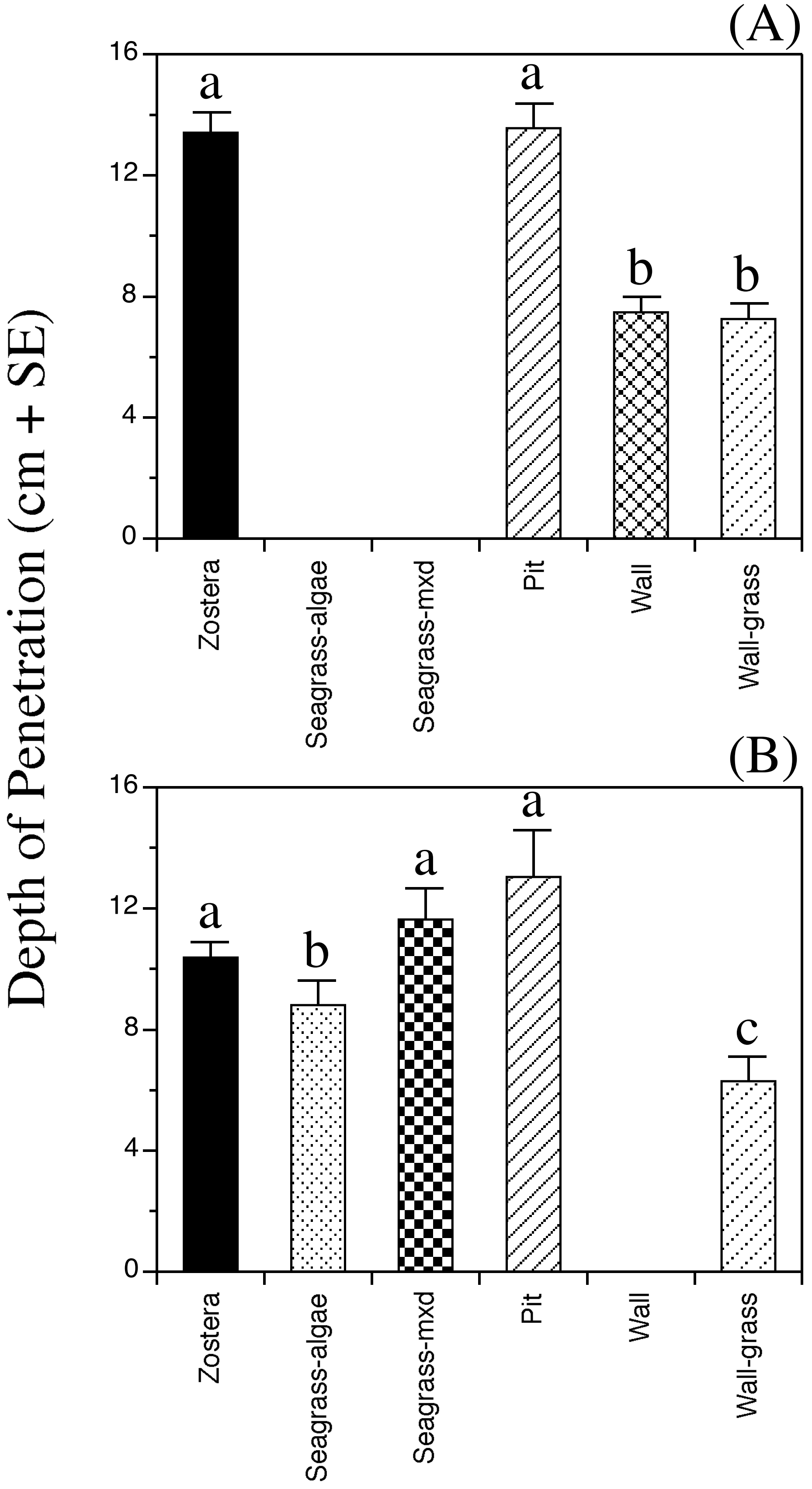


Figure 4.3A: Depth of penetration (cm +SE) into the substratum for different habitats along Transect 1 (Fisherman Islands) in (A) August 1999 and (B) April 2001, after an 18 month period. Details of methods are given in Section 4.2.1.1. Lack of a value for a habitat-type indicates that habitat was only present in a small proportion of the total transect, so measurements of compaction were not recorded (see Figure 4.1 for details of the habitats present along the transects). The letters above the bars show the results of SNK post-hoc contrasts: means topped by the same letter were not significantly different (P>0.05).

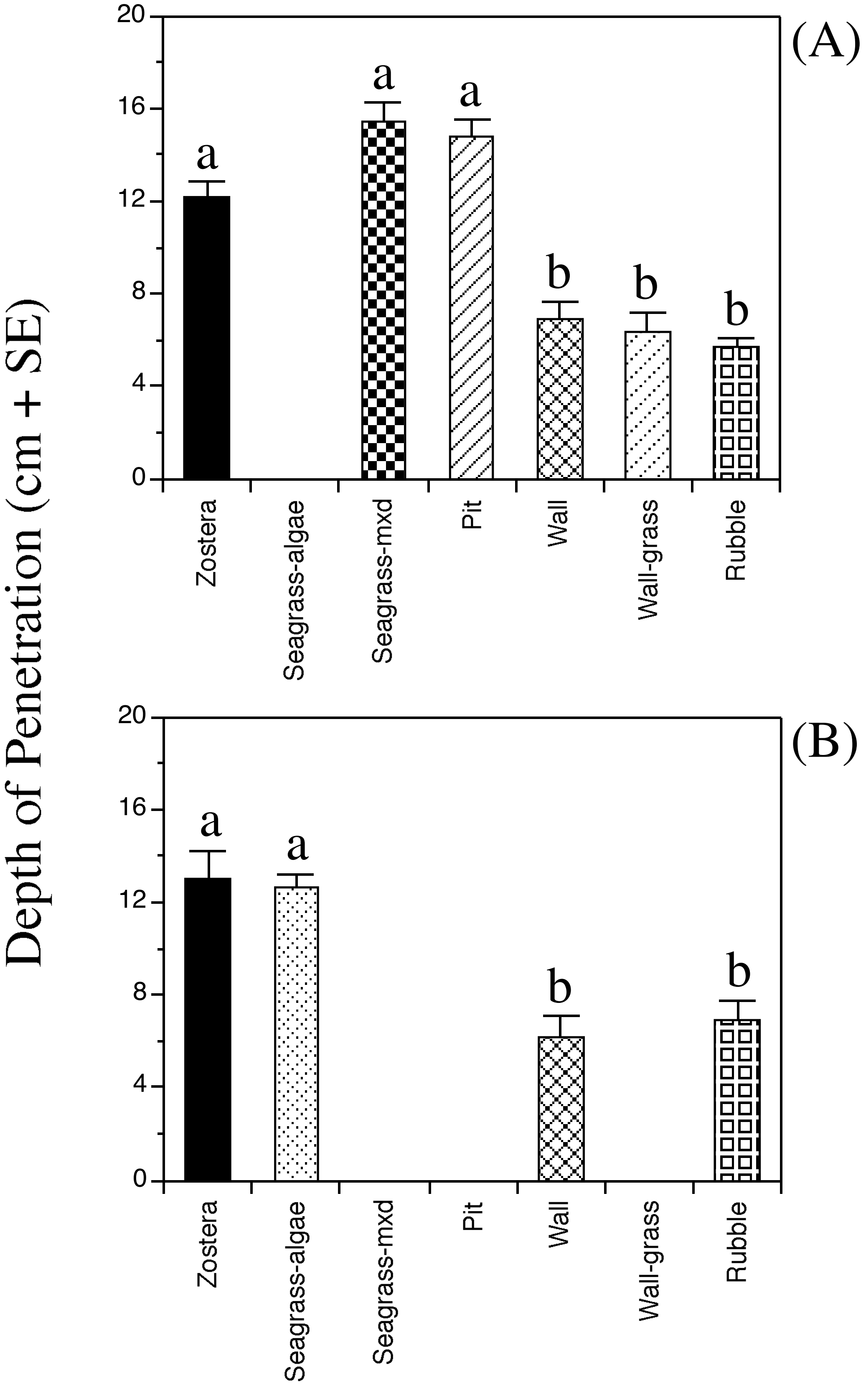


Figure 4.3B: Depth of penetration (cm+SE) into the substratum for different habitat types along Transect 2 (Fisherman Islands) in (A) August 1999 and (B) April 2001 after an 18 month period. Details of methods are given in Section 4.2.1.1. Oher details as in Figure 4.3A.

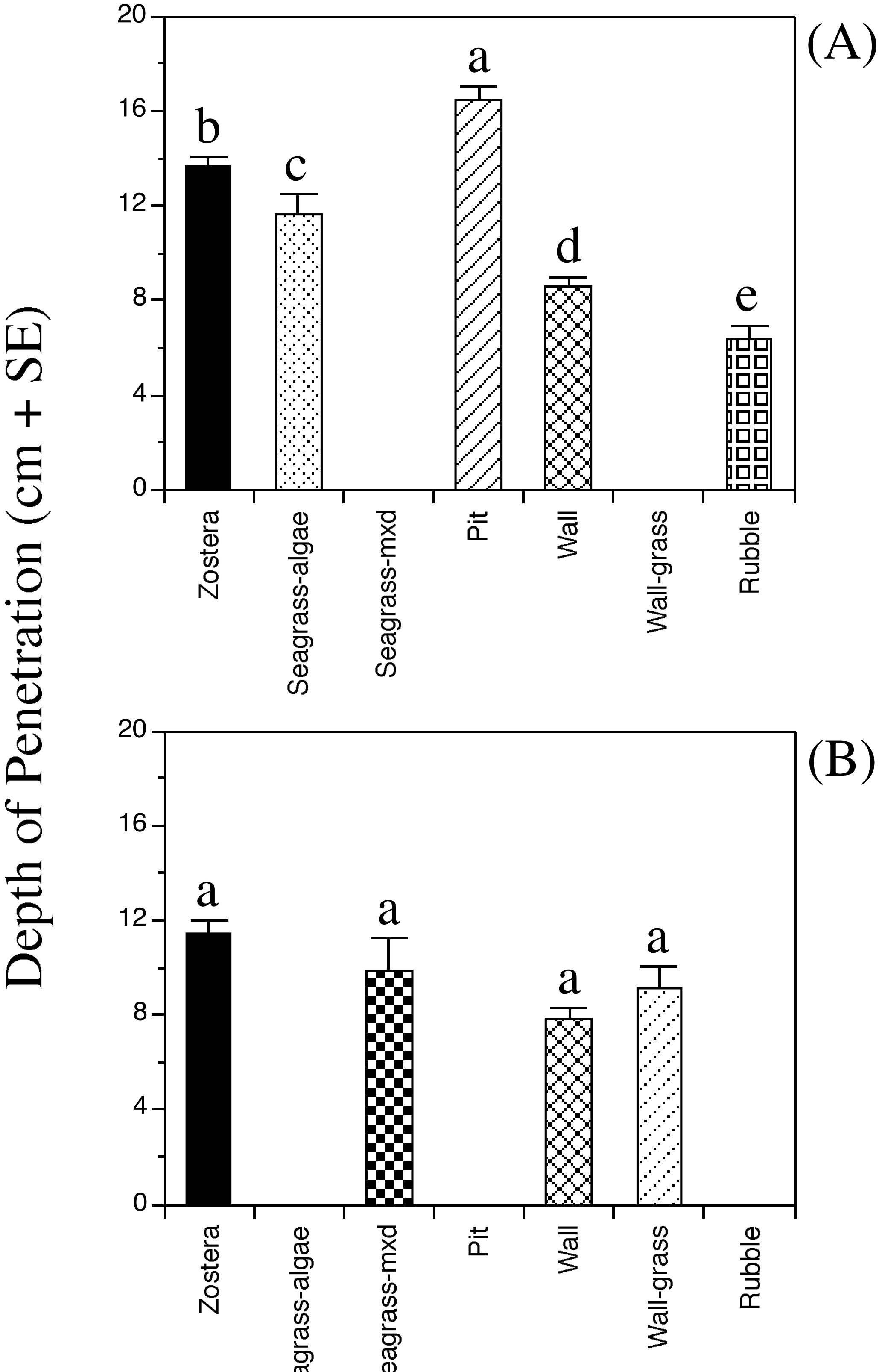


Figure 4.3C: Depth of penetration (cm+SE) into the substratum for different habitat types along Transect 3 (Fisherman Islands) in (A) August 1999 and (B) April 2001 after an 18 month period. Details of methods are given in Section 4.2.1.1. Oher details as in Figure 4.3A.

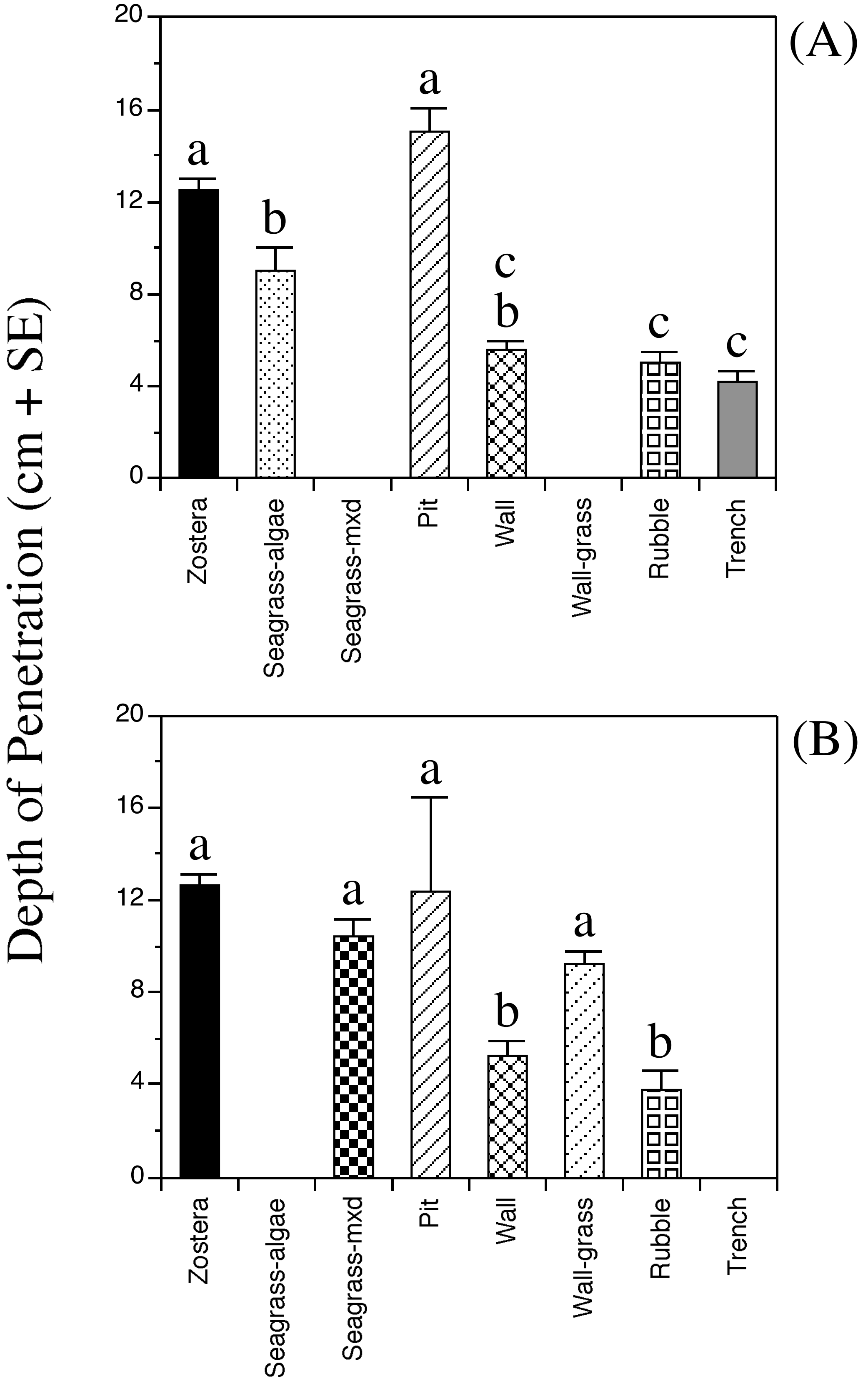


Figure 4.3D: Depth of penetration (cm+SE) into the substratum for different habitat types along Transect 4 (Fisherman Islands) in (A) August 1999 and (B) April 2001 after an 18 month period. Details of methods are given in Section 4.2.1.1. Oher details as in Figure 4.2A.

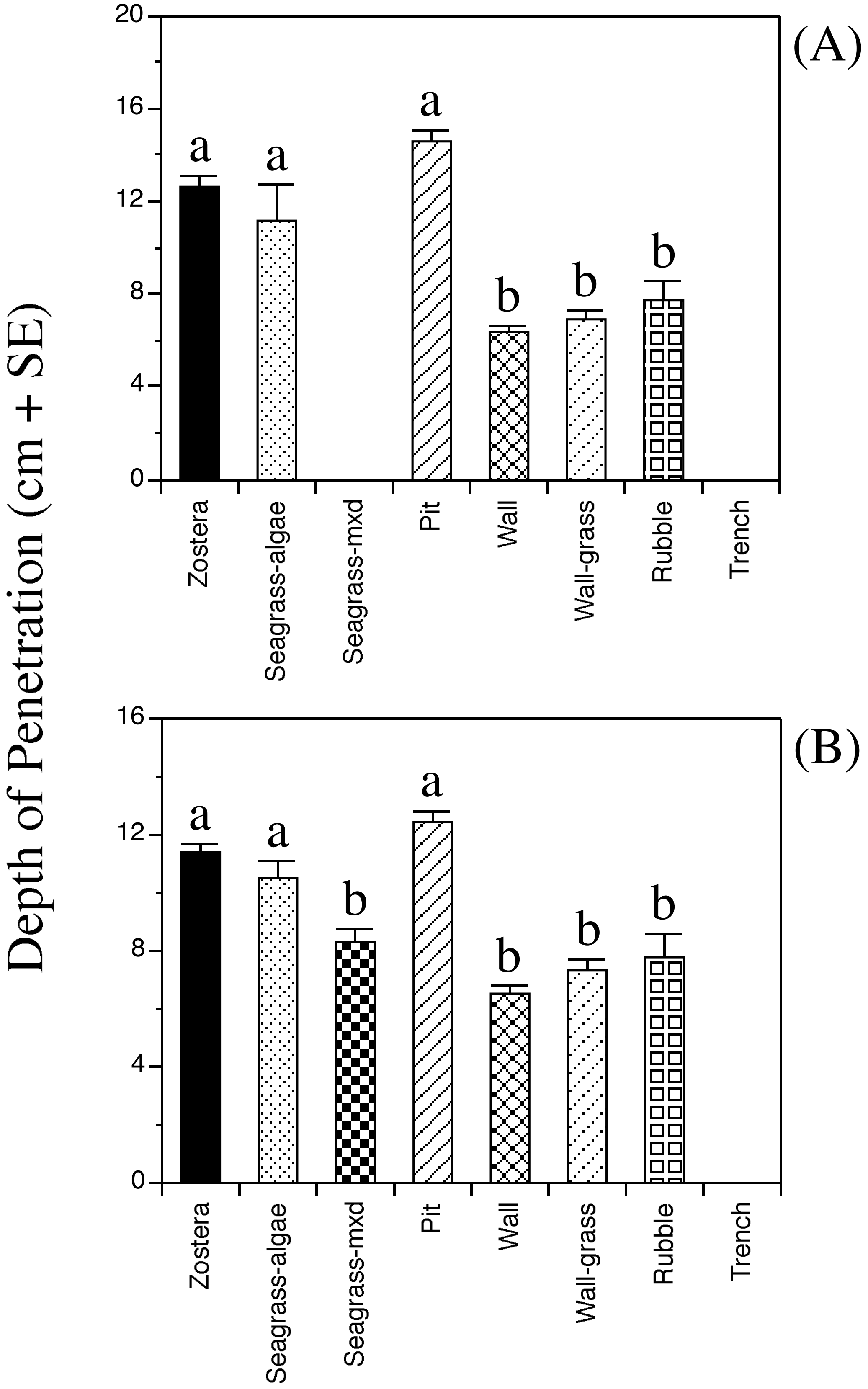


Figure 4.3E: Depth of penetration (cm+SE) into the substratum for different habitat types along Transect 5 (Fisherman Islands) in (A) August 1999 and (B) April 2001 after an 18 month period. Details of methods are given in Section 4.2.1.1. Oher details as in Figure 4.2A.

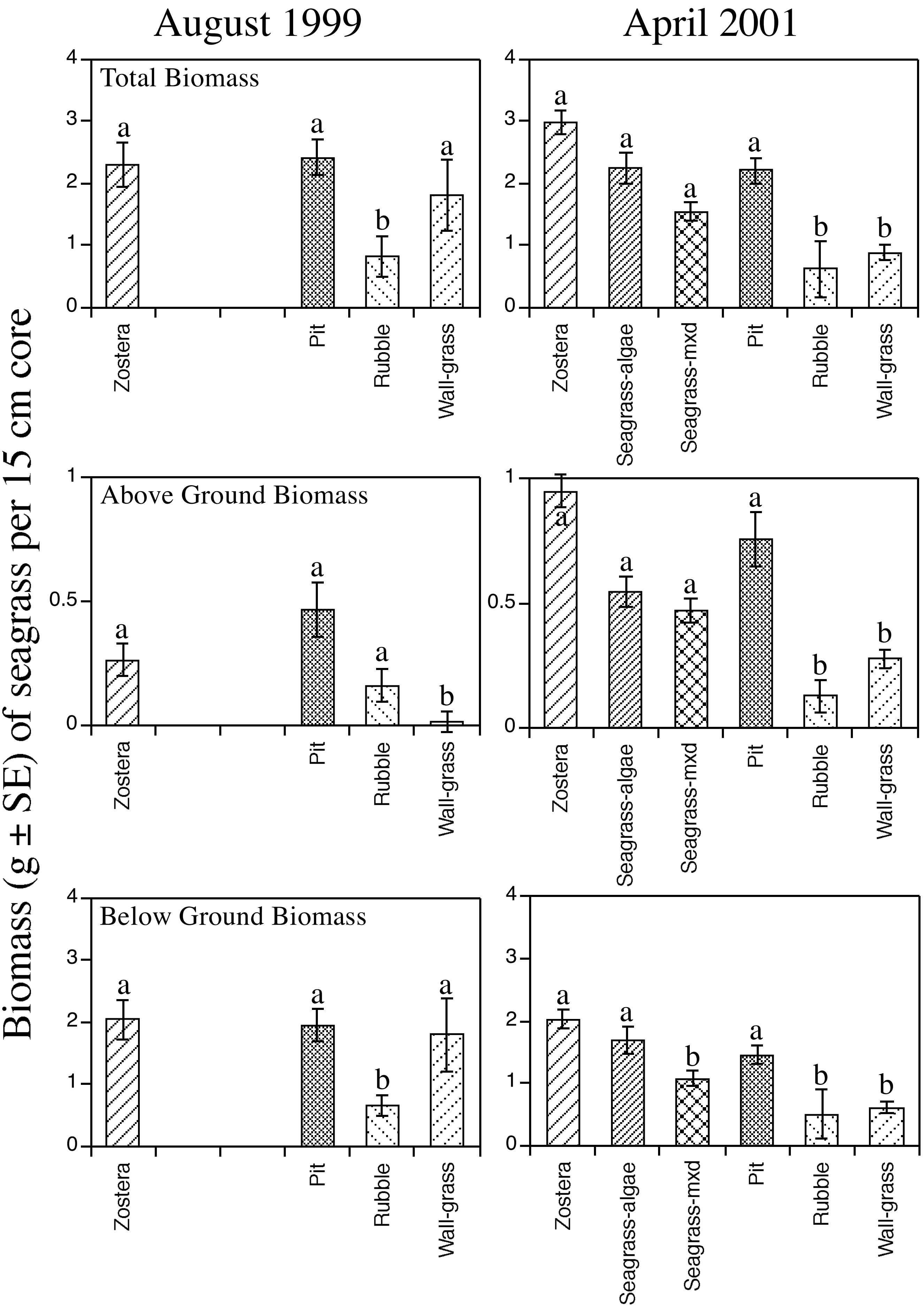


Figure 4.4A: Total biomass, above ground biomass and below ground biomass of seagrass (*Zostera*, *Halophila* and *Halodule*) for different habitats along Transect 1 (Fisherman Islands) in August 1999 and April 2001. Details are given in Section 4.2.1.2. Other details as in Figure 4.2.

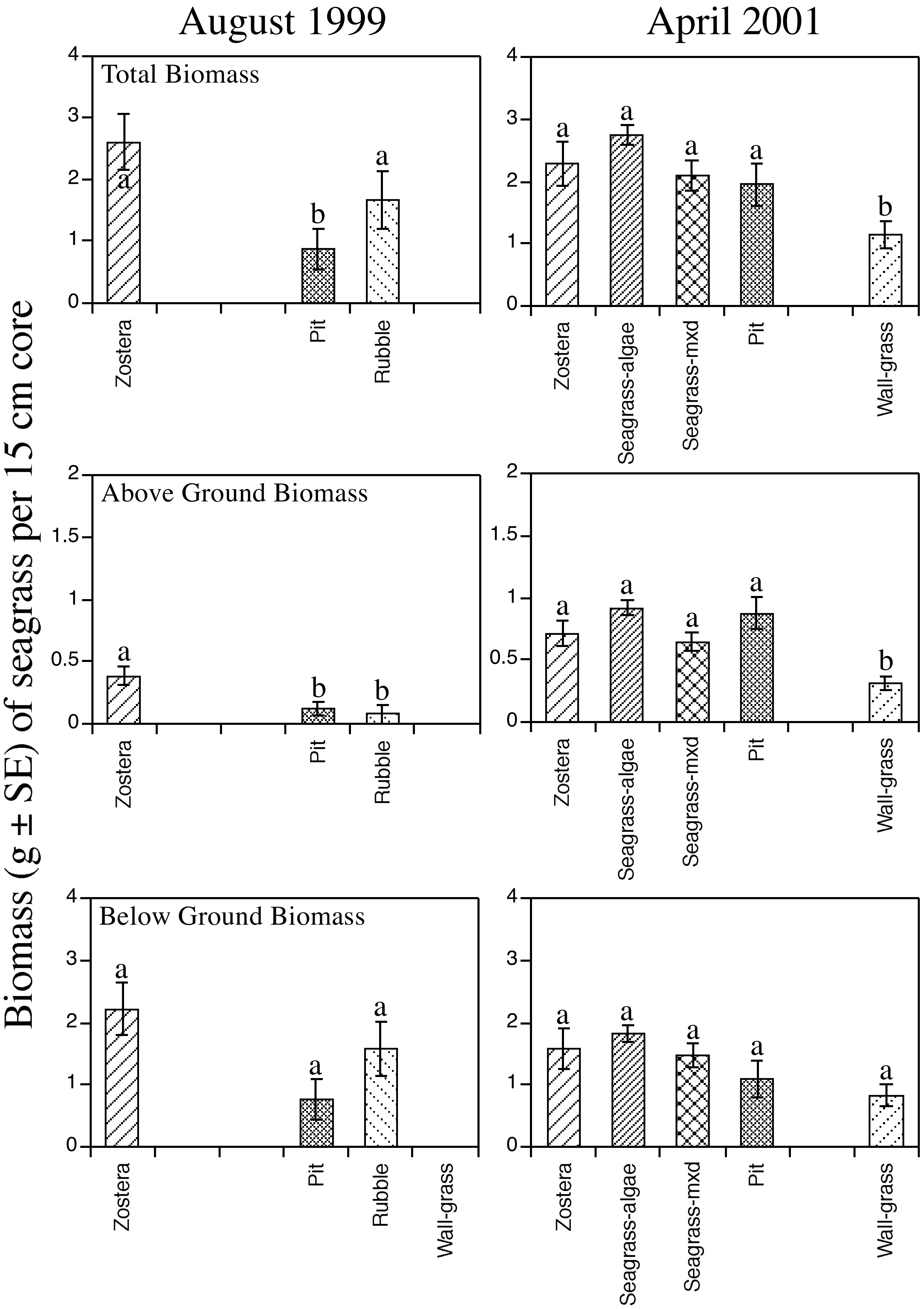


Figure 4.4B: Total biomass, above ground biomass and below ground biomass of seagrass (*Zostera*, *Halophila* and *Halodule*) for different habitats along Transect 2 (Fisherman Islands) in August 1999 and April 2001. Details are given in Section 4.2.1.2. Other details as in Figure 4.2.

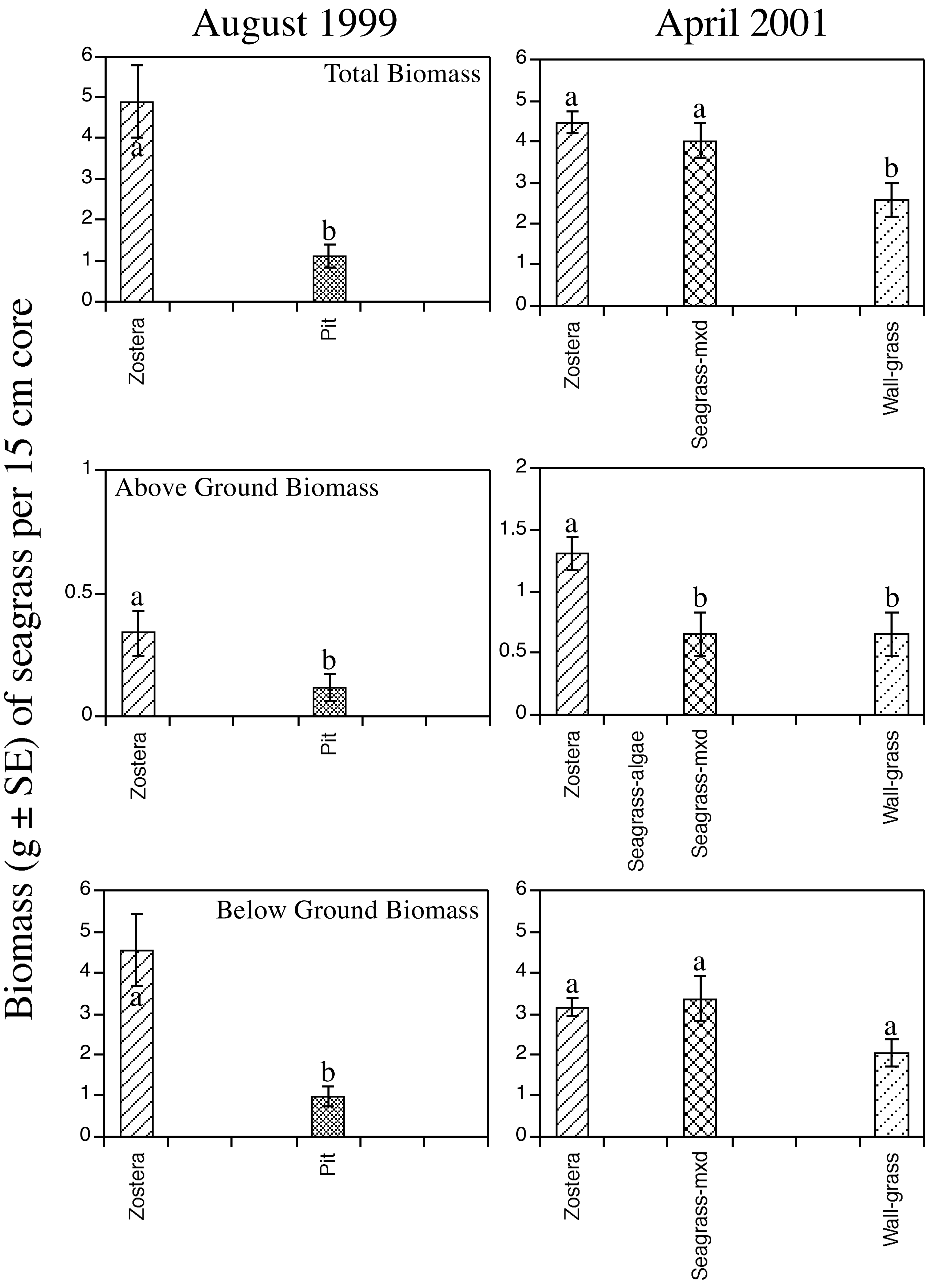


Figure 4.4C: Total biomass, above ground biomass and below ground biomass of seagrass (*Zostera*, *Halophila* and *Halodule*) for different habitats along Transect 3 (Fisherman Islands) in August 1999 and April 2001. Details are given in Section 4.2.1.2. Other details as in Figure 4.2.

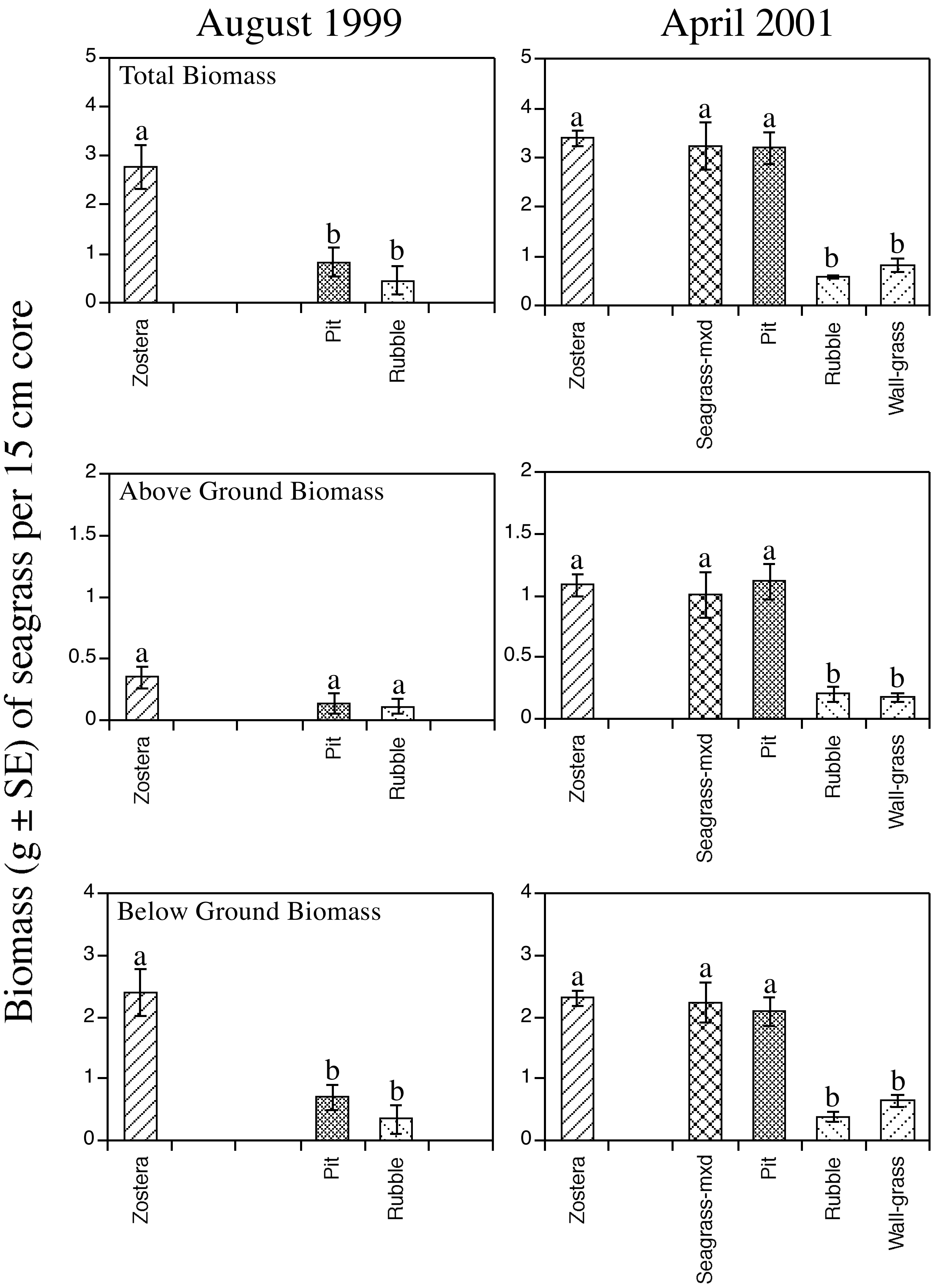


Figure 4.3D: Total biomass, above ground biomass and below ground biomass of seagrass (*Zostera*, *Halophila* and *Halodule*) for different habitats along Transect 4 (Fisherman Islands) in August 1999 and April 2001. Details are given in Section 4.2.1.2. Other details as in Figure 4.2.

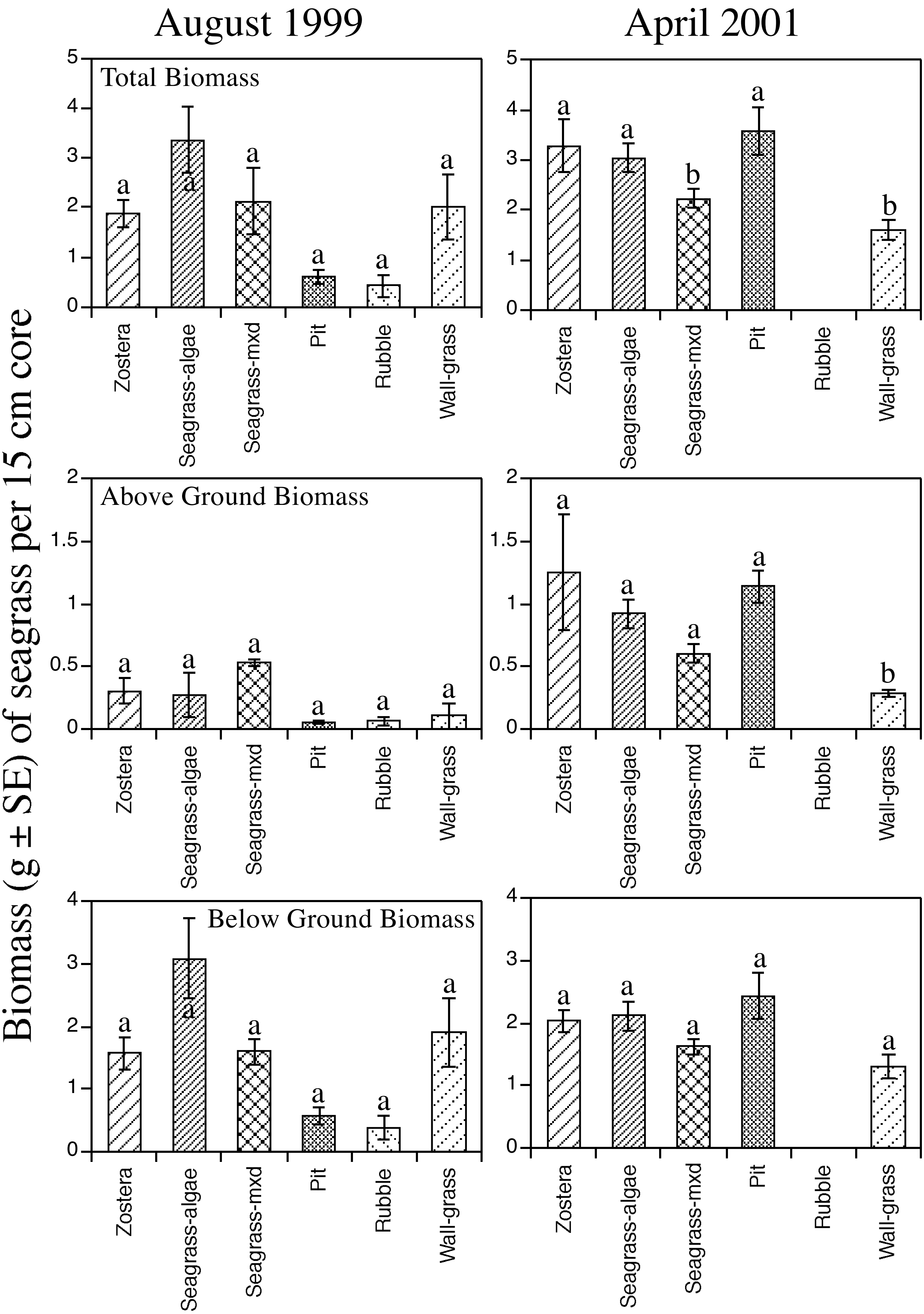


Figure 4.4E: Total biomass, above ground biomass and below ground biomass of seagrass (*Zostera*, *Halophila* and *Halodule*) for different habitats along Transect 5 (Fisherman Islands) in August 1999 and April 2001. Details are given in Section 4.2.1.2. Other details as in Figure 4.2.

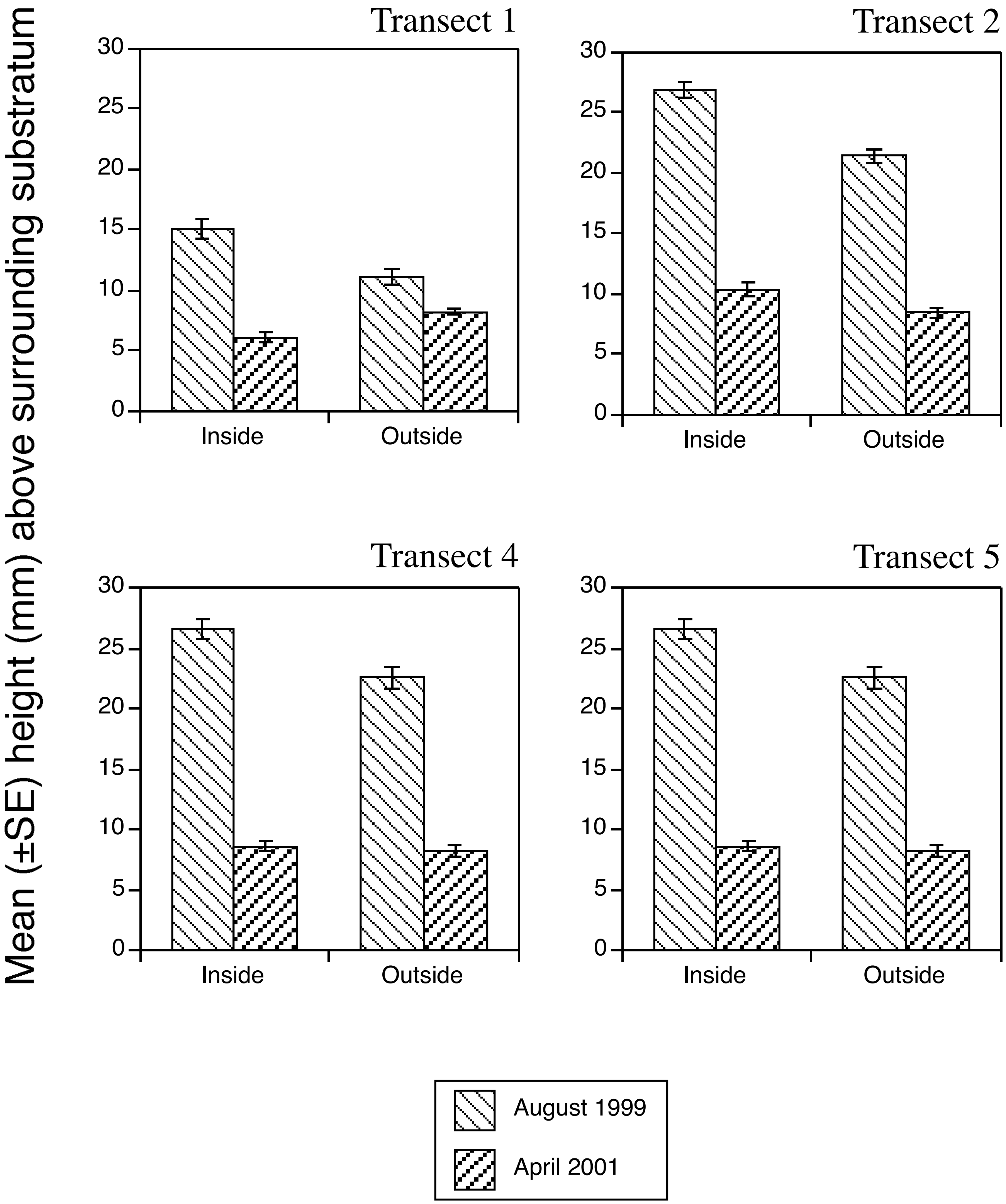


Figure 4.5: Height of the walls surrounding commercial pits along the transects across Fisherman Islands. Data are the means of five readings along each of the four walls per pit in August 1999 and April 2001. Transect 3 is not shown because no pits were evident along this transect in April 2001. Details are given in Section 4.2.1.3.

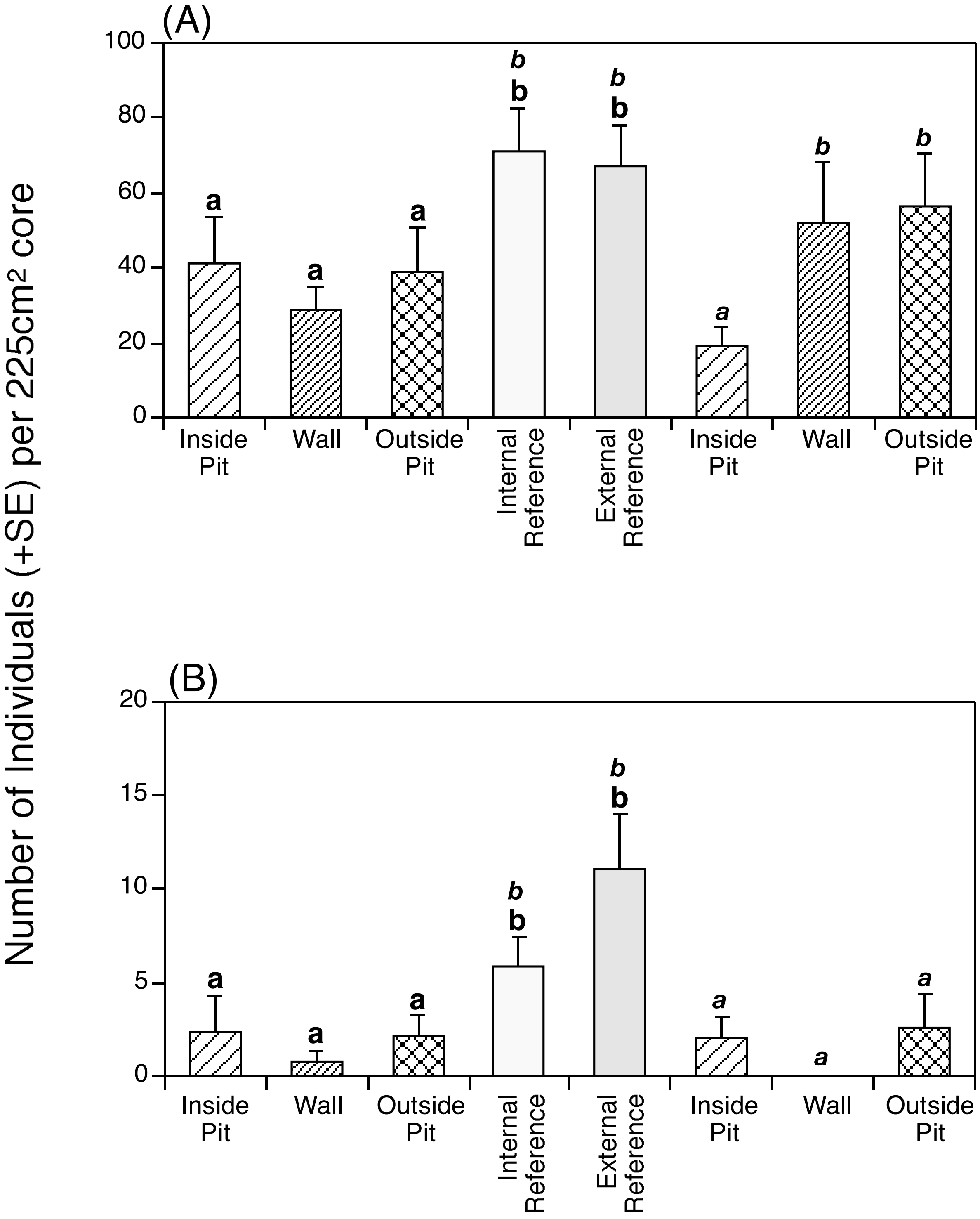


Figure 4.6: Mean (±SE) abundance of (A) individuals and (B) gammarid amphipods in 225cm^2 cores collected from in and around commercial bloodworm pits dug 1 month earlier. Five habitat types were sampled: (i) inside the commercial pit; (ii) the walls (dyke) surrounding the pit; (iii) the area immediately (10-15cm) from the external wall; (iv) an undug area within the commercial plot=Internal Reference; (v) undug area away from commercial plot=External Reference. N=5 replicates for habitats (i)-(iii), but N=10 replicates (pooled from 2 patches) for habitats (iv)-(v) (see text for further details). The letters above the bars show the results of SNK post-hoc contrasts: means topped by the same letter were not significantly different (P>0.05). Italicised letters indicate a separate set of contrasts (see text for further details).
Note the difference in scale on the Y-axes.

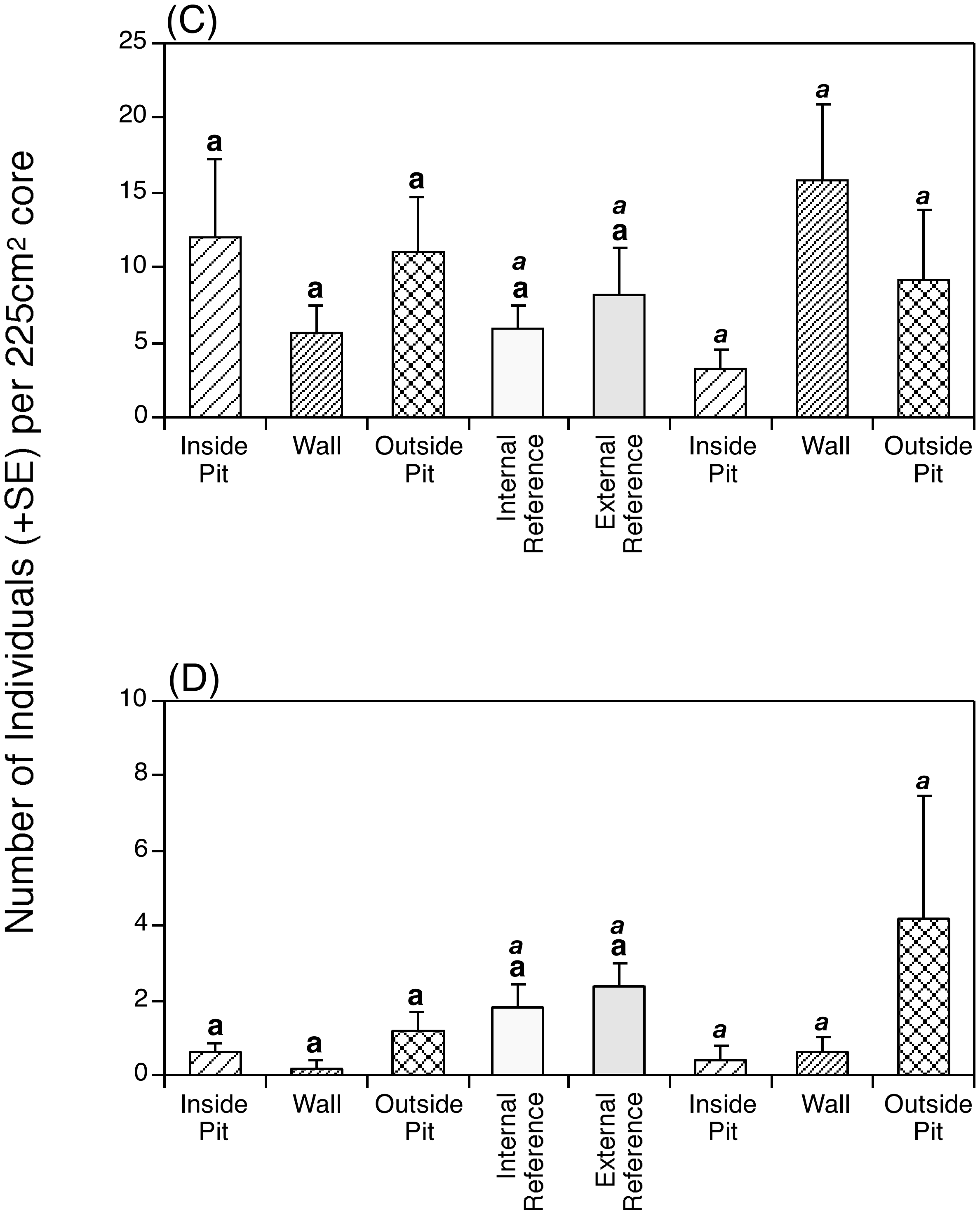


Figure 4.6 continued: Mean (±SE) abundance of (C) gastropods and (D) bivalves in 225cm^2 cores collected from in and around commercial bloodworm pits dug 1 month earlier. Note the difference in scale on the Y-axes. Other details as in Figure 4.6A-B.

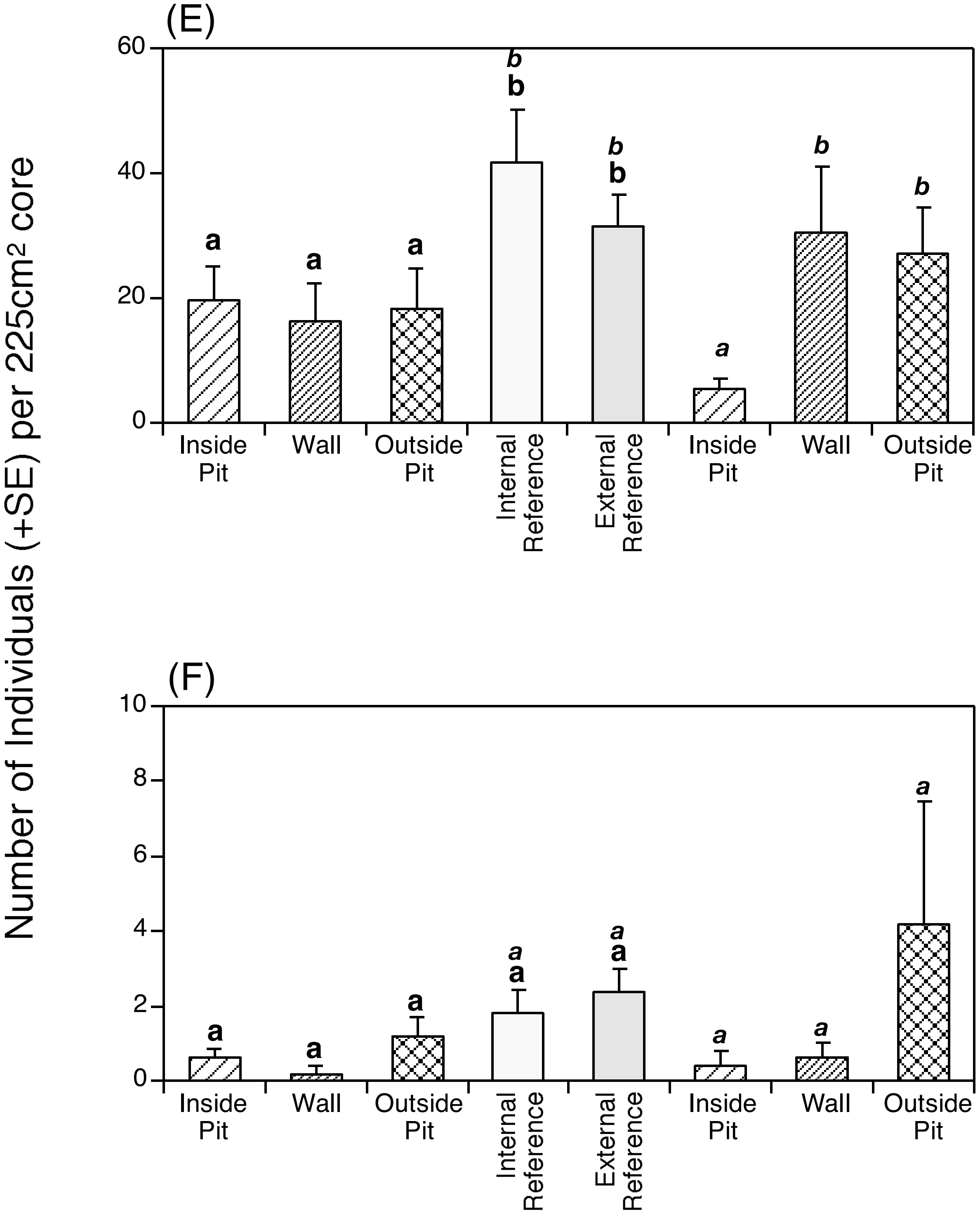
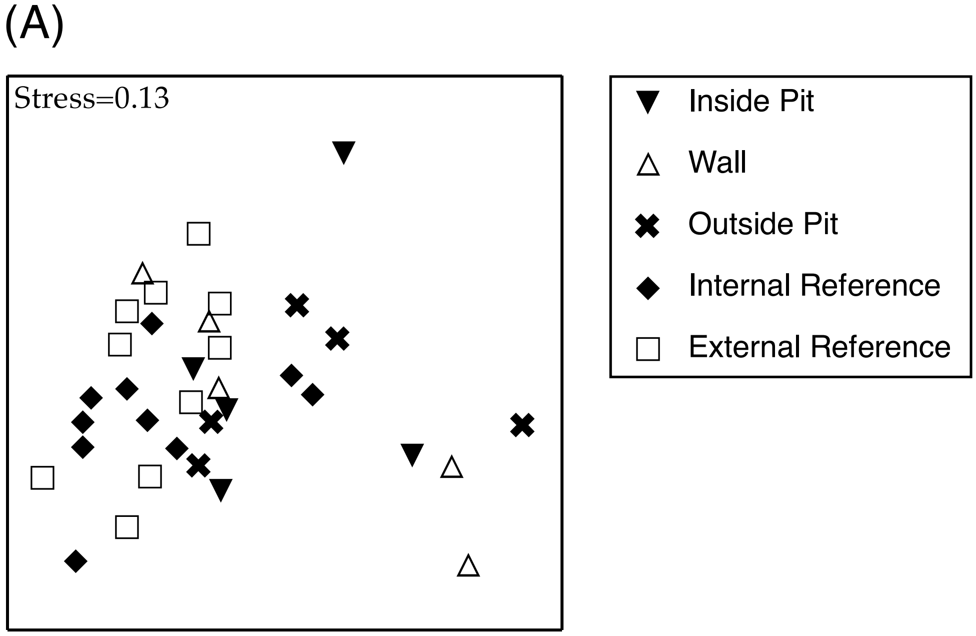


Figure 4.6 continued: Mean (±SE) abundance of (E) polychaetes and (F) ophiuroids in 225 cm^2 cores collected from in and around commercial bloodworm pits dug 1 month earlier. Note the difference in scale on the Y-axes. Other details as in Figure 4.6A-B.



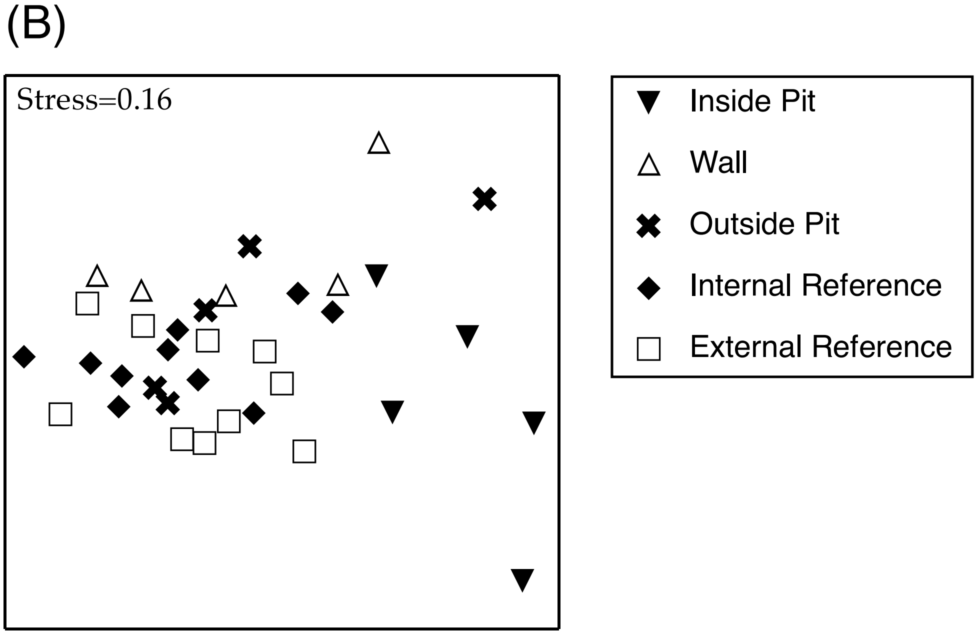


Figure 4.7: nMDS ordination of untransformed data on the abundance of macrofauna from cores collected in and around commercial bloodowrm pits dug 1 month earlier. Five habitat types were sampled: (i) inside the commercial pit; (ii) the walls (dyke) surrounding the pit; (iii) the area outside (10-15 cm) the external wall; (iv) an undug area within the commercial plot=Internal Reference; (v) undug area away from commercial plot=External Reference. (A) Pit 1 and (B) Pit 2. Data are for 5 replicates for each of habitat types (i)-(iii) and for 10 replicates (5replicates pooled from each of two patches) for habitats (iv)-(v).

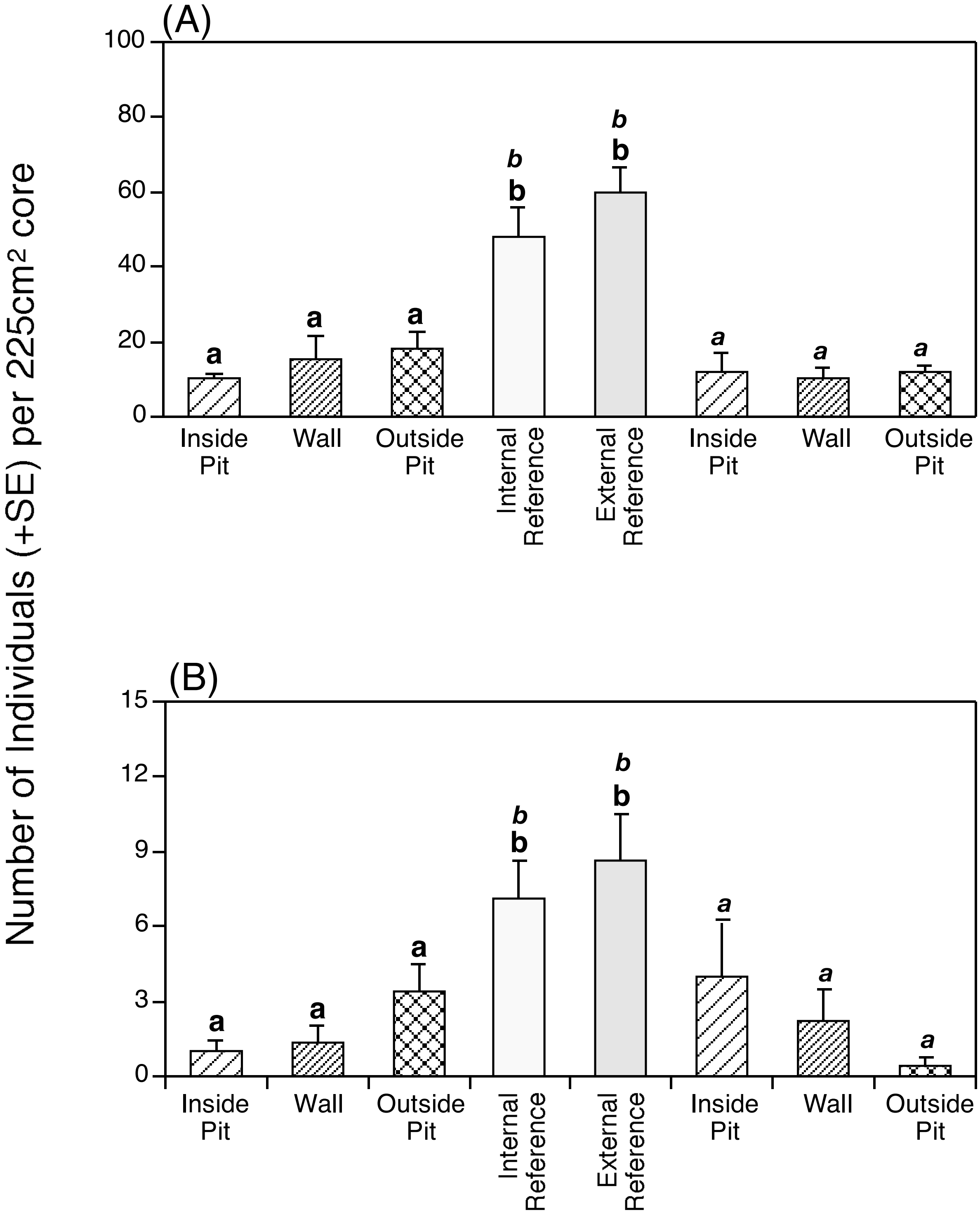


Figure 4.8: Mean (±SE) abundance of (A) individuals and (B) gammarid amphipods in 225cm^2 cores collected from in and around commercial bloodworm pits dug 2 months earlier. Other details as in Figure 4.6A-B.

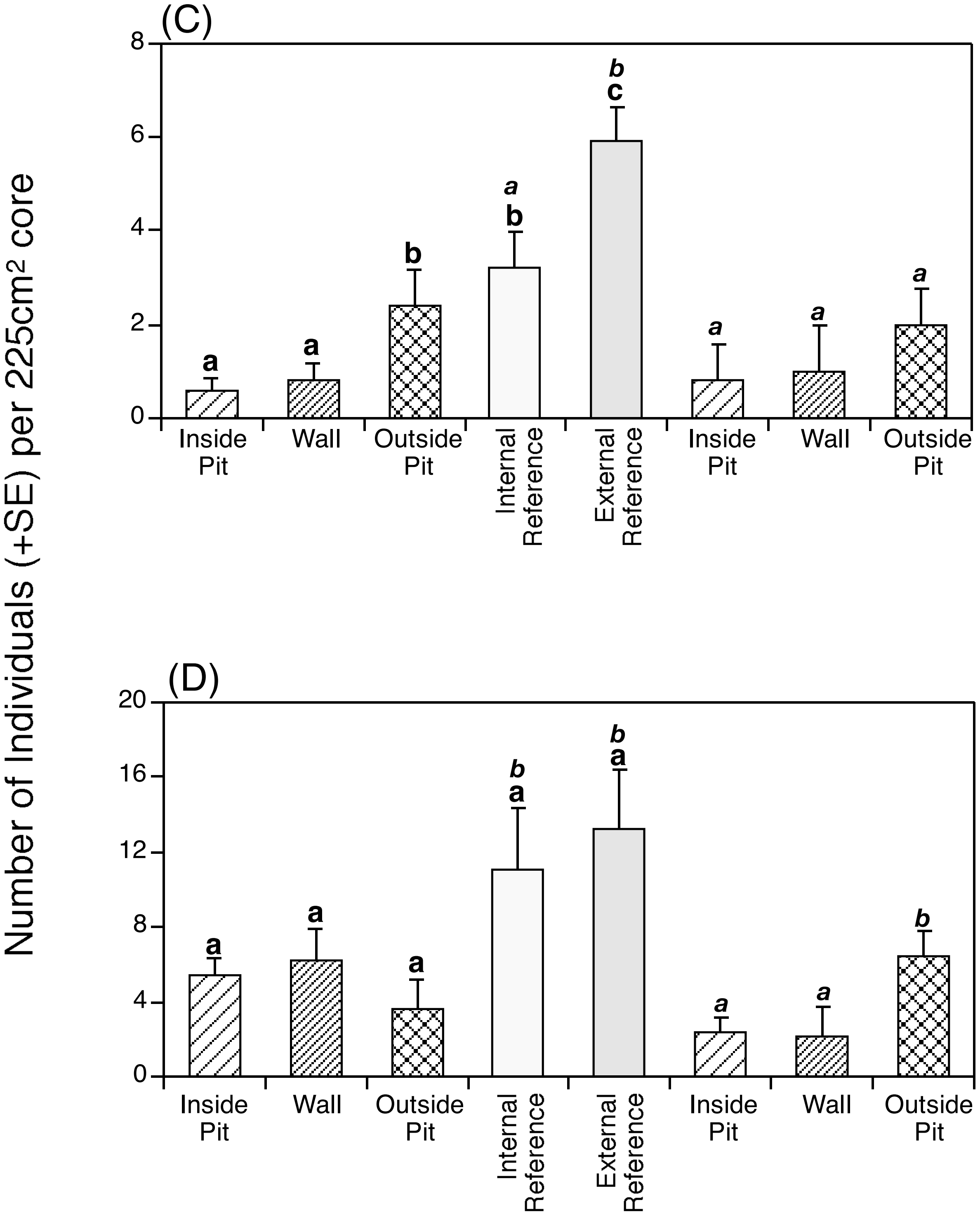


Figure 4.8 continued: Mean (±SE) abundance of (C) bivalves and (D) gastropods in 225cm^2 cores collected from in and around commercial bloodworm pits dug 2 months earlier. Other details as in Figure 4.6A-B.

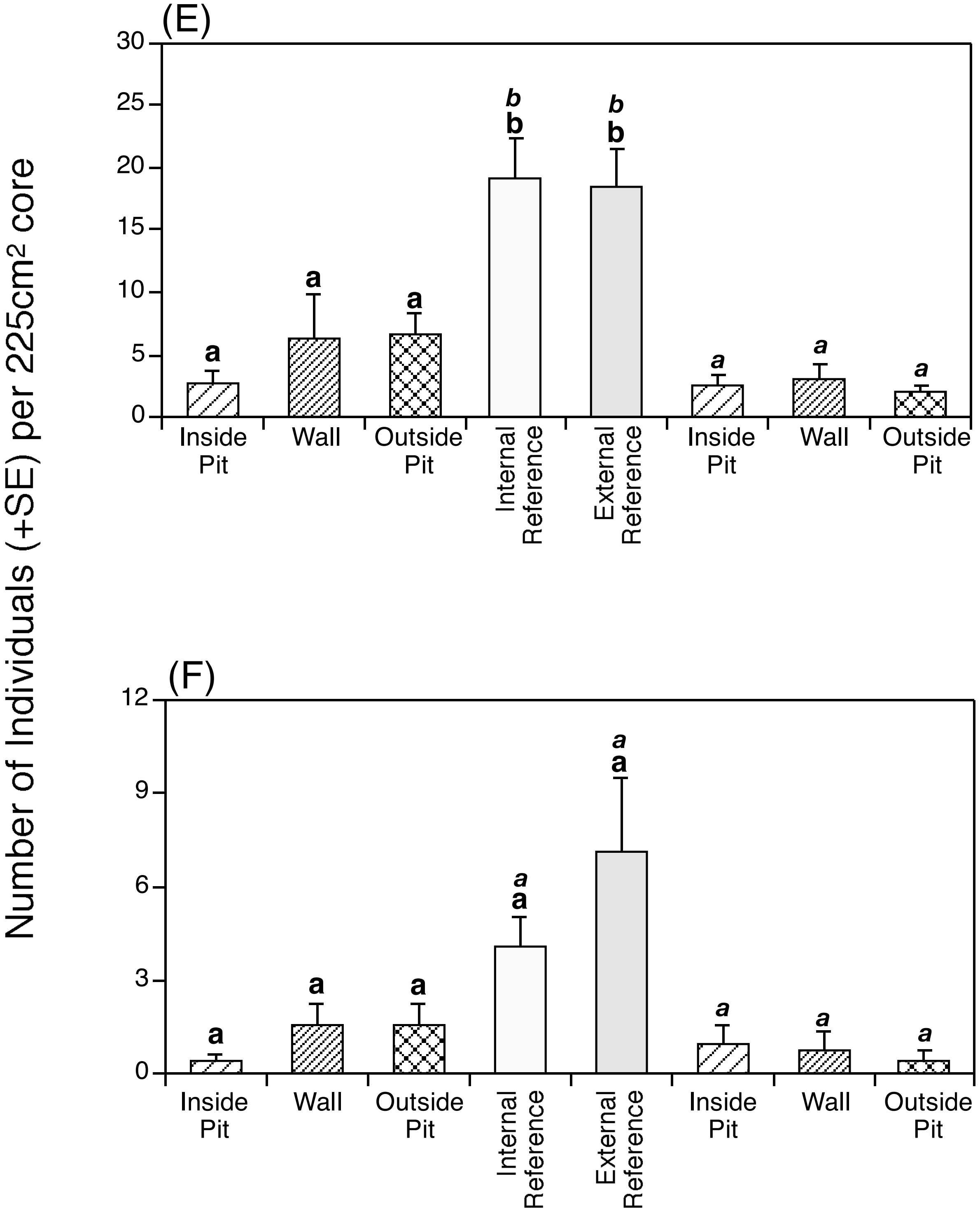


Figure 4.8 continued: Mean (±SE) abundance of (E) polychaetes and (F) capitellids in 225cm^2 cores collected from in and around commercial bloodworm pits dug 2 months earlier. Other details as in Figure 4.6A-B.

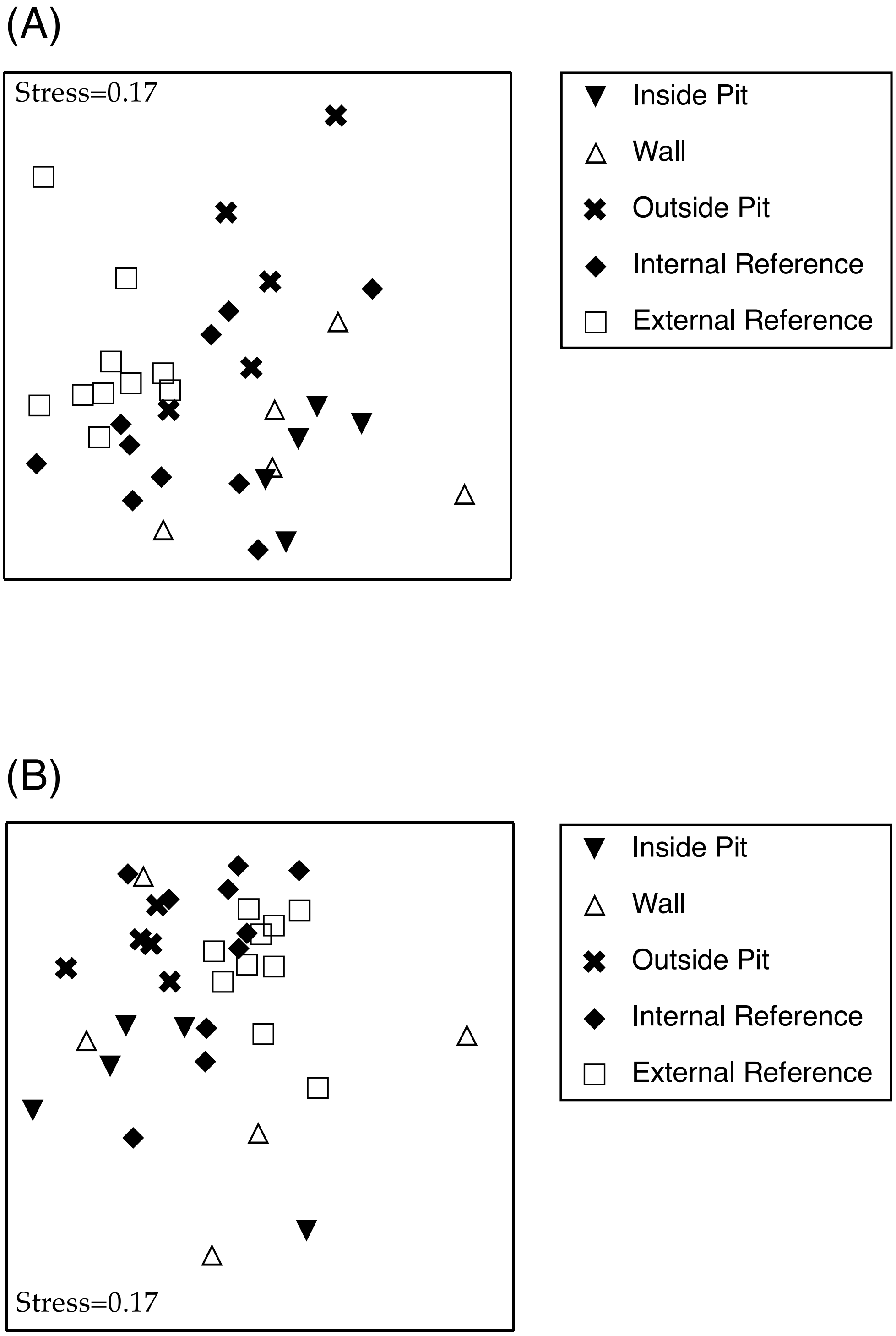


Figure 4.9: nMDS ordination of untransformed data on the abundance of macrofauna from cores collected in and around commercial bloodowrm pits dug 2 months earlier. Five habitat types were sampled: (i) inside the commercial pit; (ii) the walls (dyke) surrounding the pit; (iii) the area outside (10-15 cm) the external wall; (iv) an undug area within the commercial plot=Internal Reference; (v) undug area away from commercial plot=External Reference. (A) Pit 1 and (B) Pit 2. Data are for 5 replicates for each of habitat types (i)-(iii) and for 10 replicates (5replicates pooled from each of two patches) for habitats (iv)-(v).

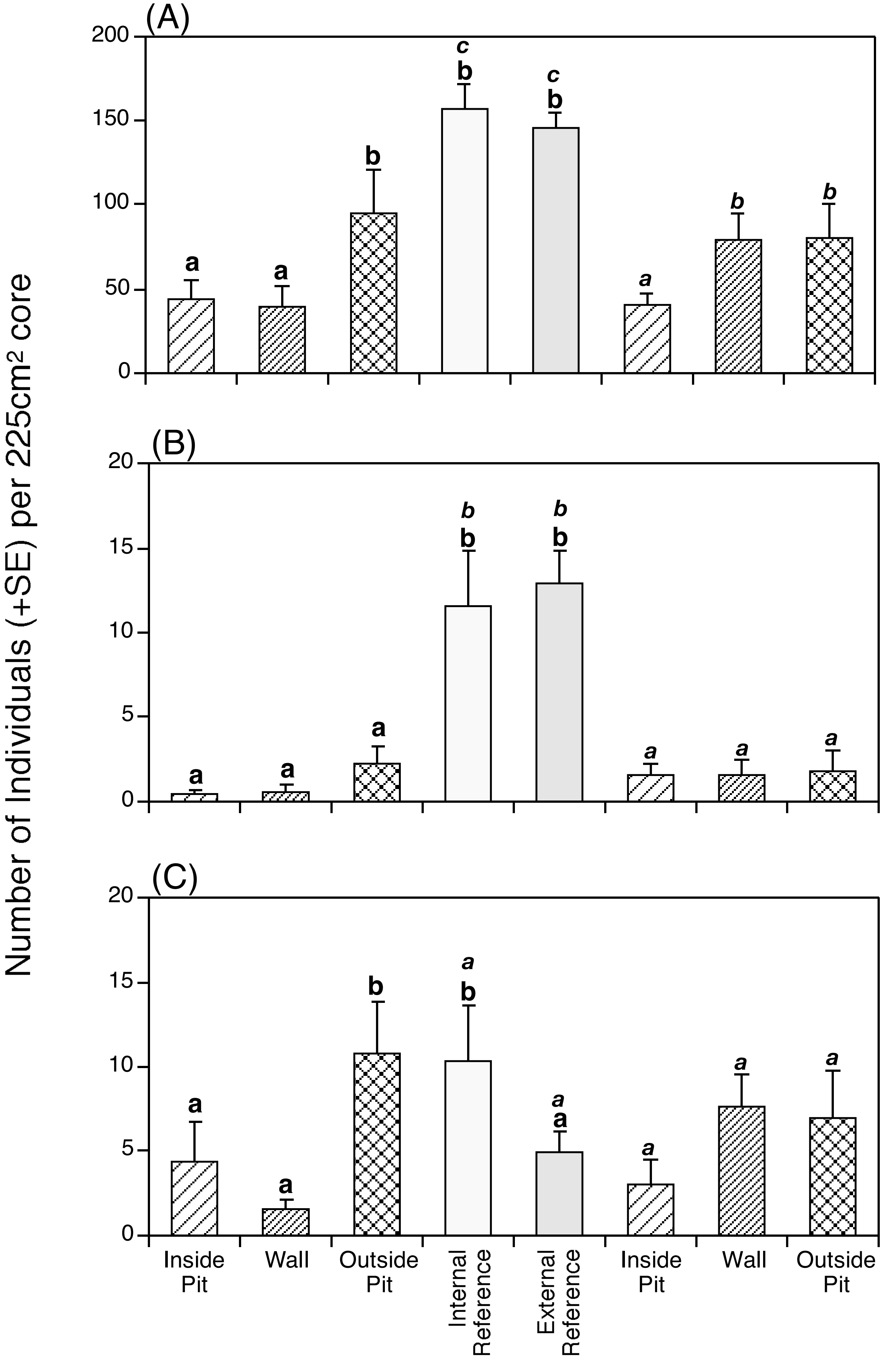


Figure 4.10: Mean (±SE) abundance of (A) individuals, (B) gammarid amphipods and (C) tanaids in 225cm^2 cores collected from in and around commercial bloodworm pits dug 4 months earlier. Other details as in Figure 4.6A-B.

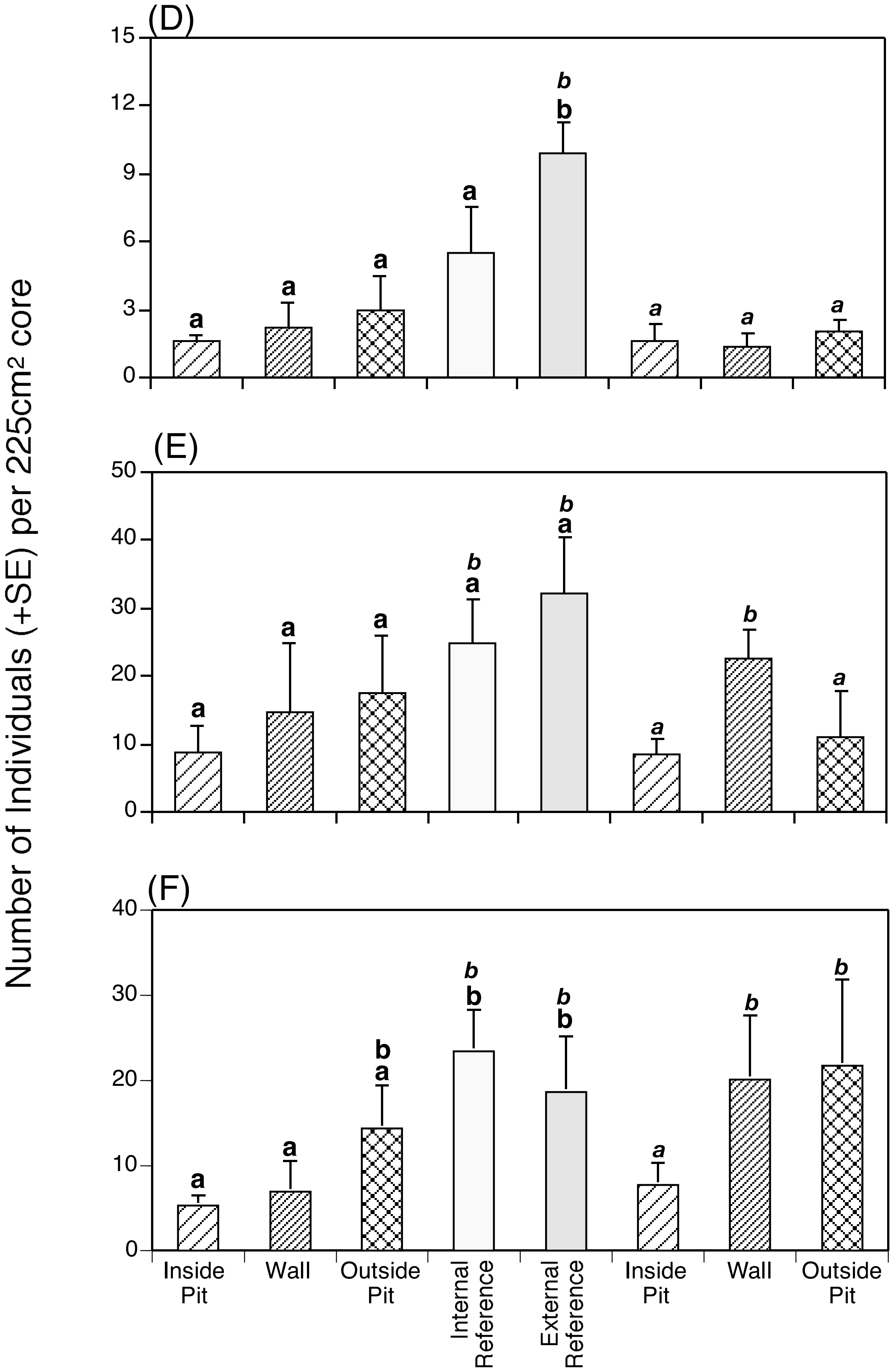


Figure 4.10 continued: Mean (±SE) abundance of (D) bivalves, (E) gastropods and (F) capitellid polychaetes in $225cm^2$ cores collected from in and around commercial bloodworm pits dug 4 months earlier. Other details as in Figure 4.6A-B.

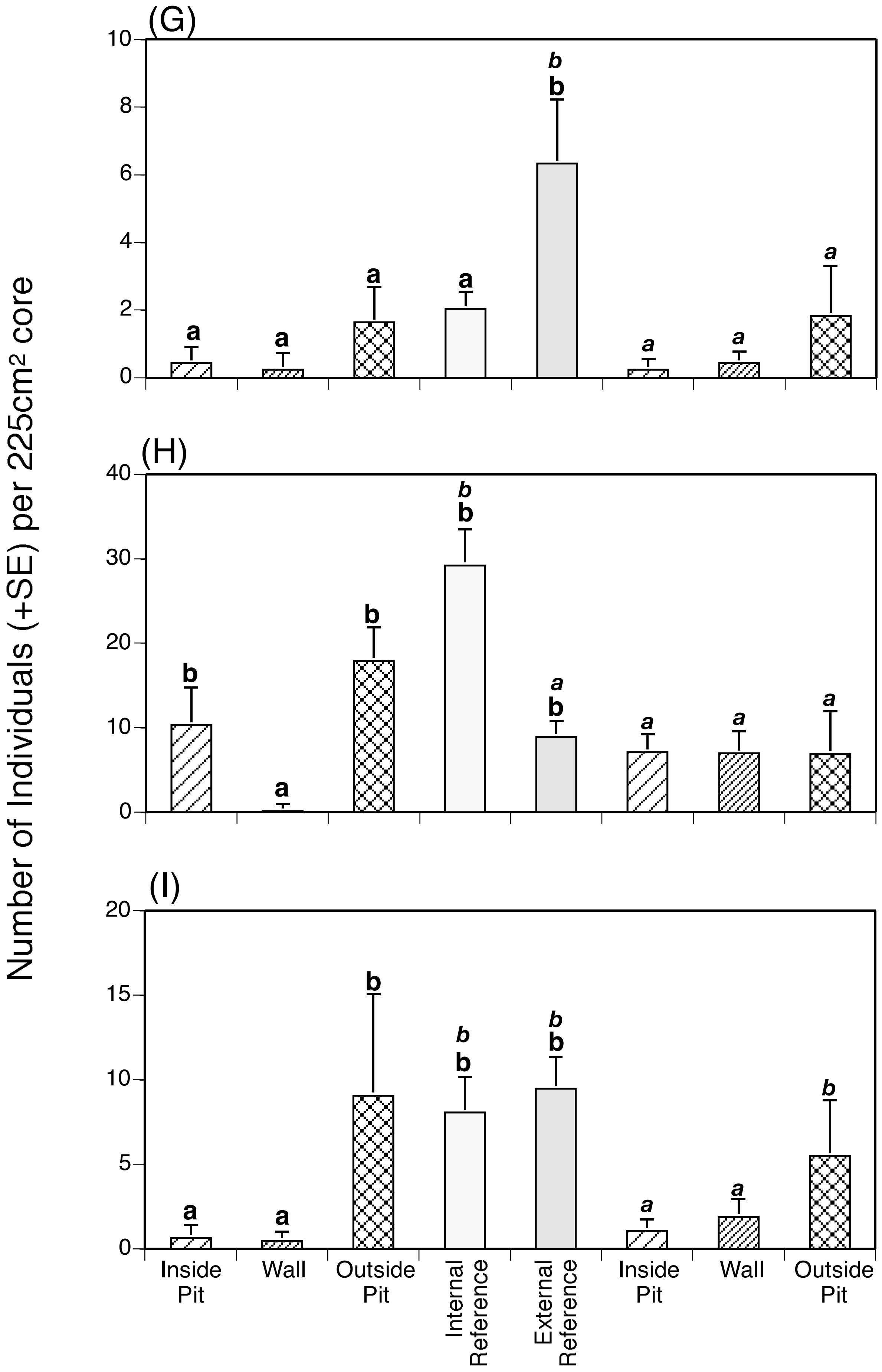


Figure 4.10 continued: Mean (±SE) abundance of (G) nereidid polychaetes, (H) spionid polychaetes and (I) syllid polychaetes in 225cm^2 cores collected from in and around commercial bloodworm pits dug 4 month earlier. Other details as in Figure 4.6A-B.

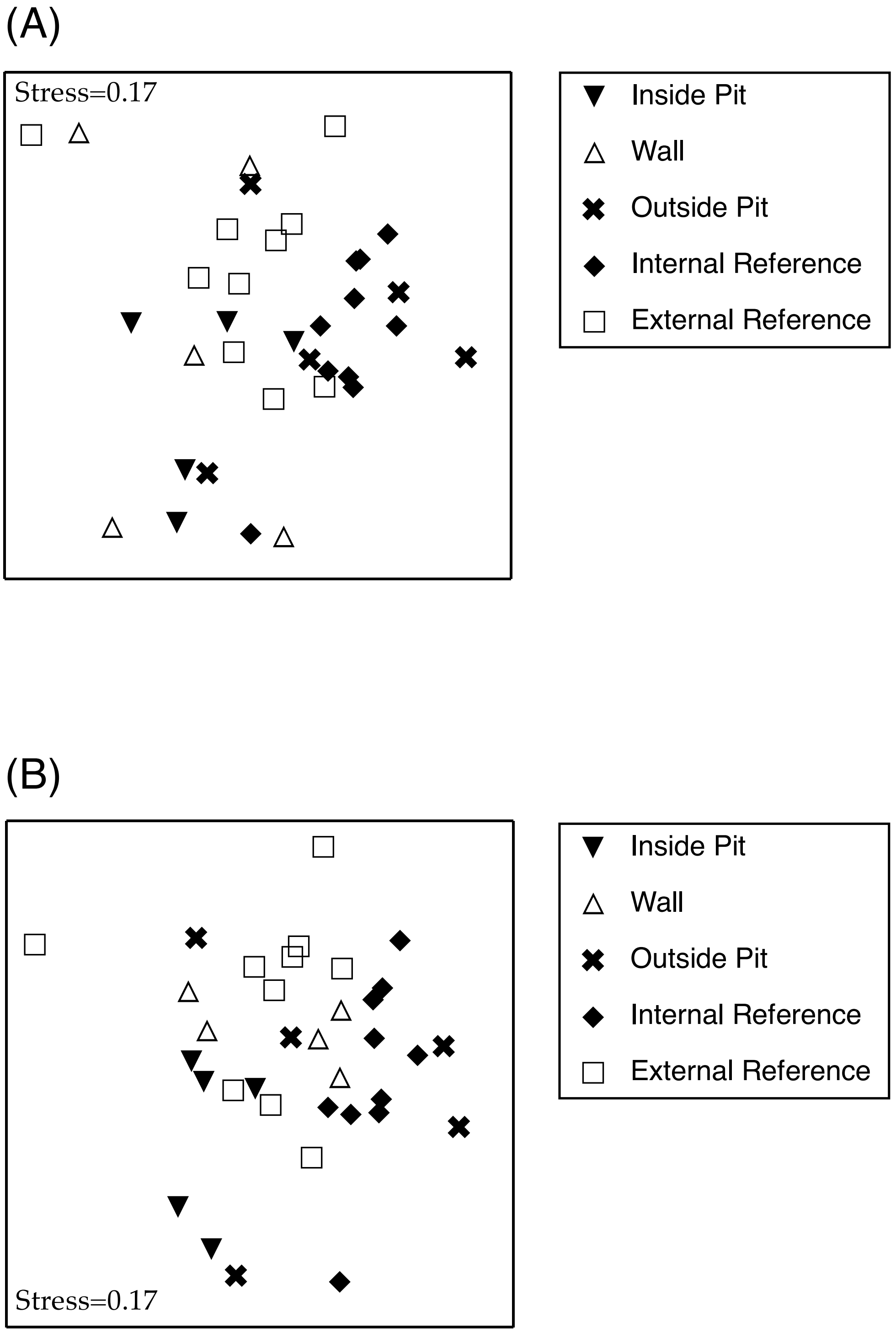


Figure 4.11: nMDS ordination of untransformed dataon the abundance of macrofauna from cores collected in and around commercial bloodowrm pits dug 4 months earlier. Five habitat types were sampled: (i) inside the commercial pit; (ii) the walls (dyke) surrounding the pit; (iii) the area outside (10-15 cm) the external wall; (iv) an undug area within the commercial plot=Internal Reference; (v) undug area away from commercial plot=External Reference. (A) Pit 1 and (B) Pit 2. Data are for 5 replicates for each of habitat types (i)-(iii) and for 10 replicates (5replicates pooled from each of two patches) for habitats (iv)-(v).

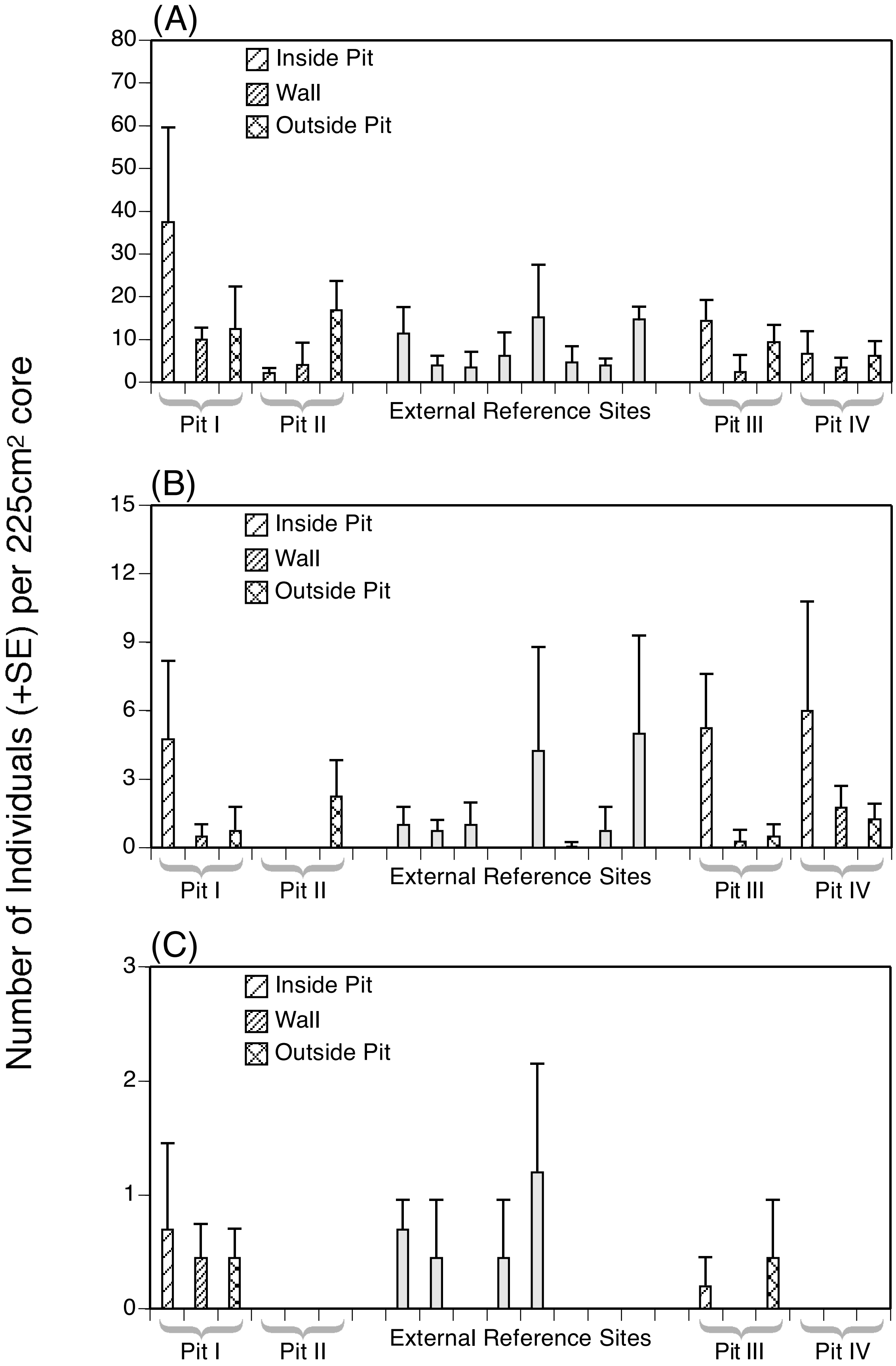


Figure 4.12: Mean (±SE) abundance of (A) individuals, (B) crustaceans and (C) bivalves in $225cm^2$ cores collected from in and around commercial bloodworm pits dug 12 months earlier. Four habitat types were sampled: (i) inside the commercial pit; (ii) the walls (dyke) surrounding the pit; (iii) the area immediately (10-15cm) from the external wall; (iv) undug area away from commercial plots=external reference sites. N=4 replicates for all habitats (see text for further details). Other details as in Figure 4.6A-B.

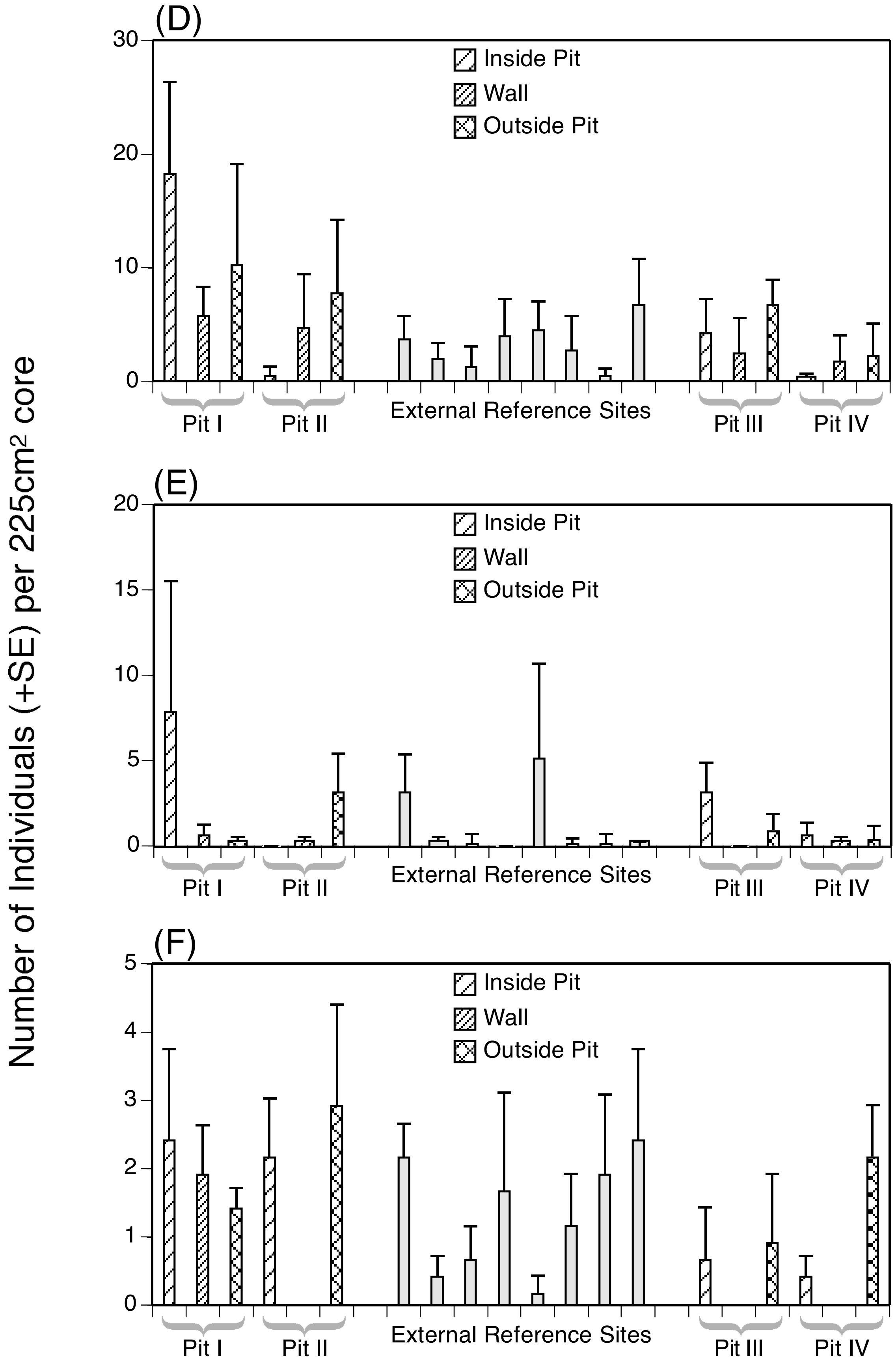


Figure 4.12 continued: Mean (±SE) abundance of (D) gastropods, (E) polychaetes and (F) brittle stars in $225cm^2$ cores collected from in and around commercial bloodworm pits dug 12 months earlier. Other details as in Figure 4.6A-B.

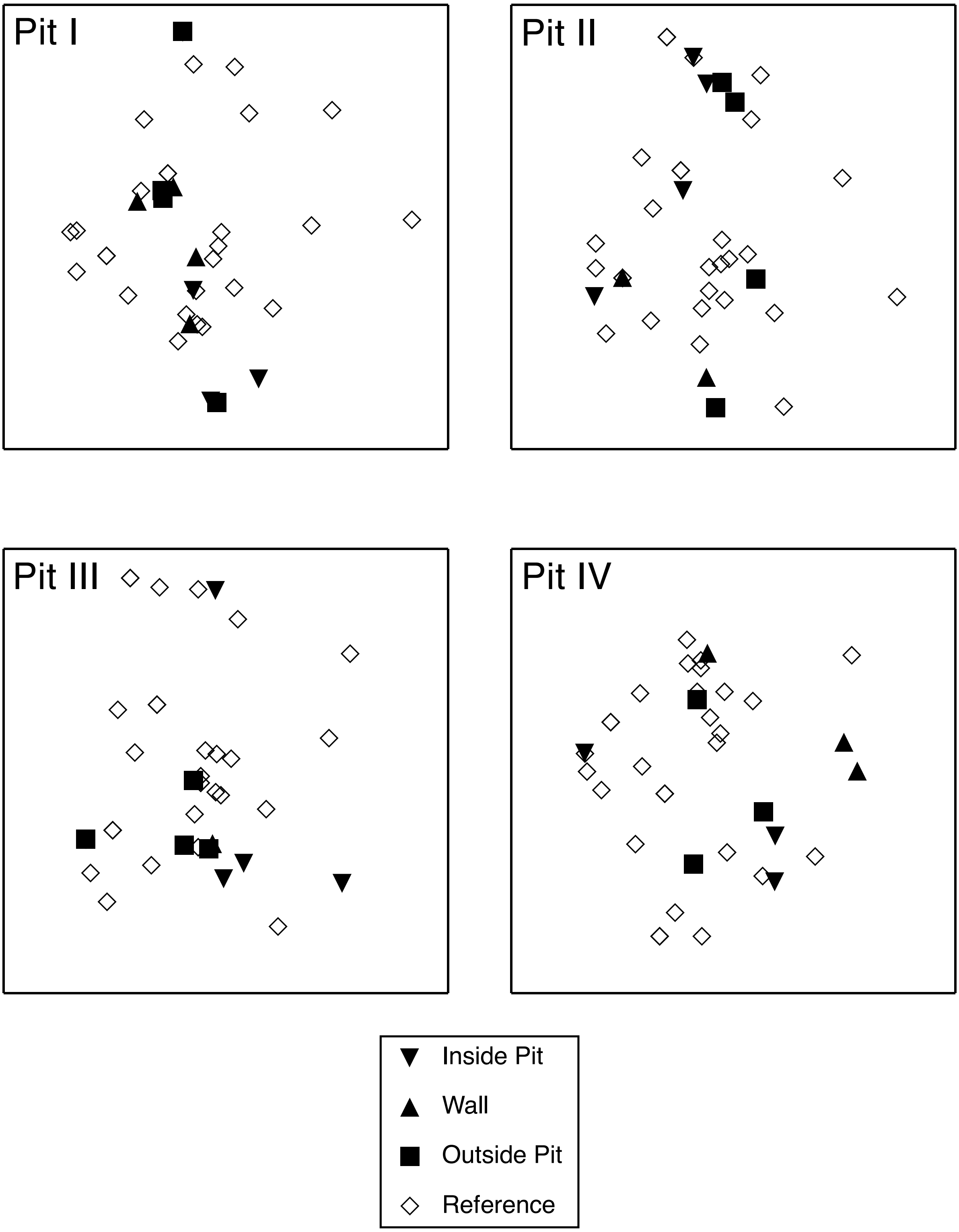


Figure 4.13: nMDS ordination of untransformed dataon the abundance of macrofauna from cores collected in and around commercial bloodowrm pits dug 12 months earlier. Four habitat types were sampled: (i) inside the commercial pit; (ii) the walls (dyke) surrounding the pit; (iii) the area outside (10-15 cm) the external wall; (iv) undug areas away from commercial plot=Reference. Four different pits were sampled (Pits I-IV) and eight reference areas. Different numbers of samples were available for different treatments because a large number of samples did not contain any animals and were excluded from the nMDS analyses (see text for further details). Stress = 0.14 for all plots.

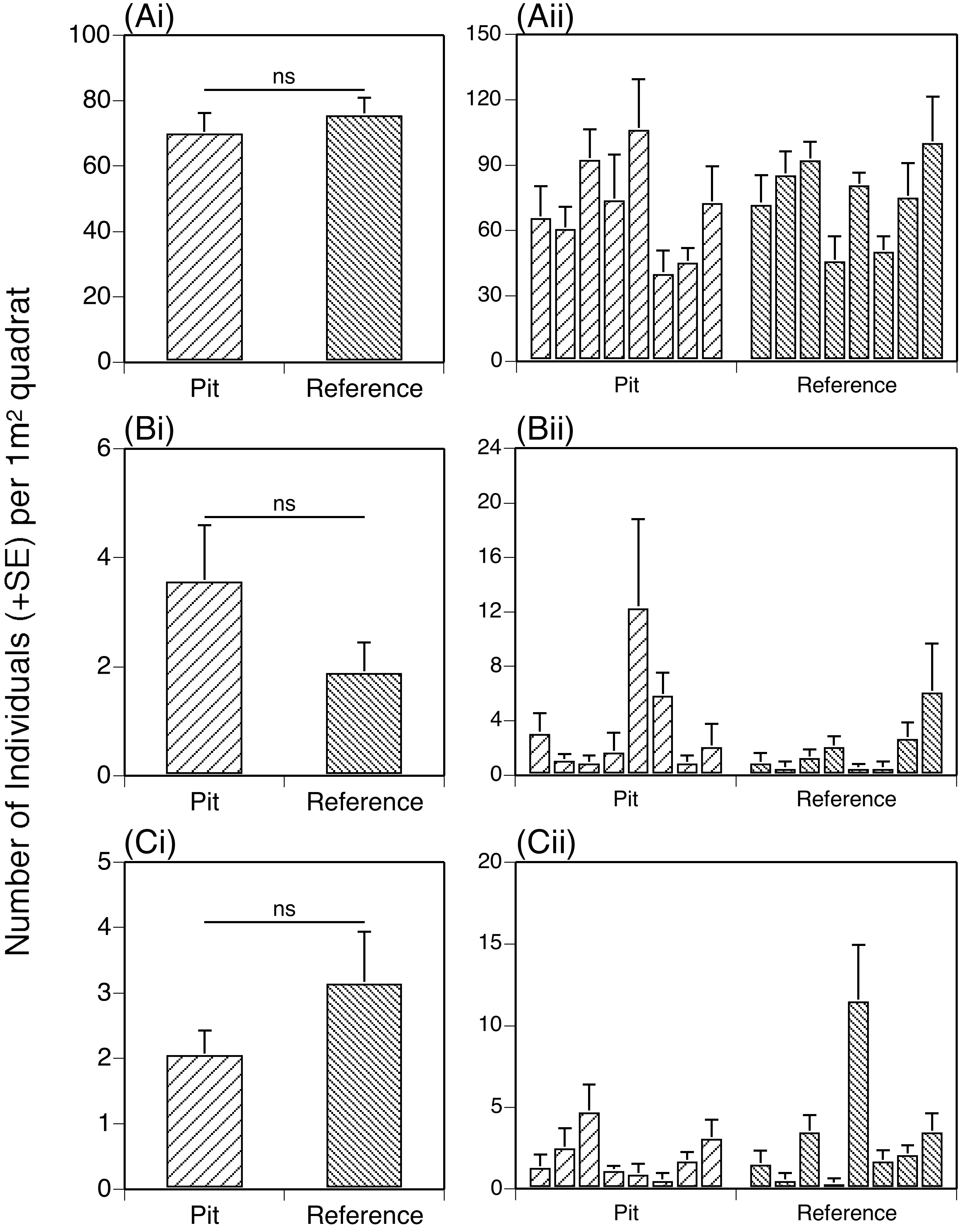


Figure 4.14: Mean (±SE) abundance of (A) individuals, (B) hermit crabs and (C) *Bedeva paivae* in 1.0m^2 quadrats collected from the seagrass adjacent to commercial pits and in reference sites near Commercial Plot 1. (i) N=40 quadrats, 5 replicates pooled from each of 8 pits or 8 reference sites. (ii) Variability among the 8 pit and reference sites - N=5 quadrats. ns indicates no significant (P>0.05) difference between treatments (Pit vs. Reference) in 2-factor analysis of variance: see text for further details.

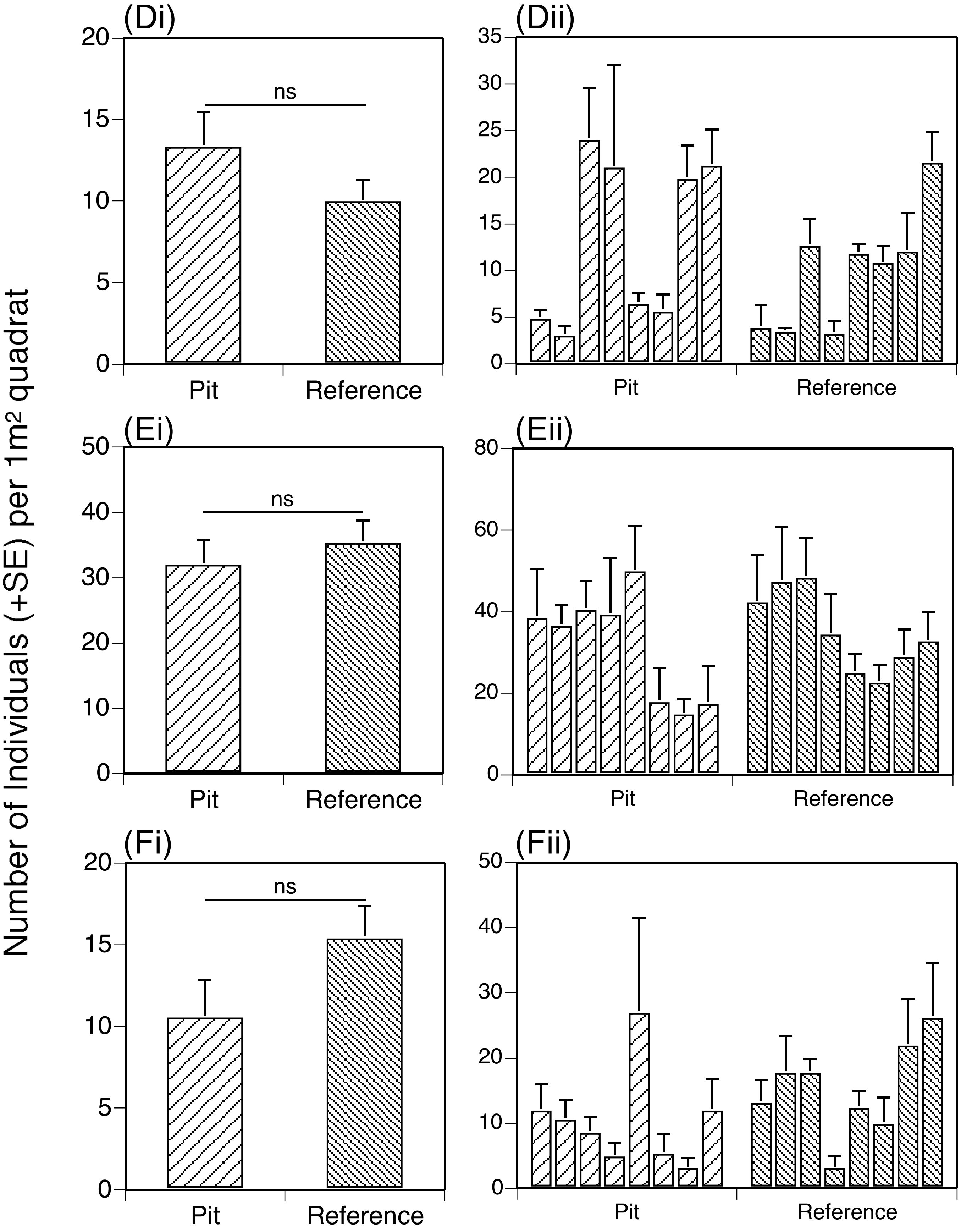


Figure 4.14 continued: Mean (±SE) abundance of (D) *Pyrazus ebeninus*, (E) *Thalotia marginatain* and (F) *Nassarius burchardi* in 1.0m^2 quadrats collected from the seagrass adjacent to commercial pits and in reference sites near Commercial Plot 1. Other details as in Figure 4.14A-C.

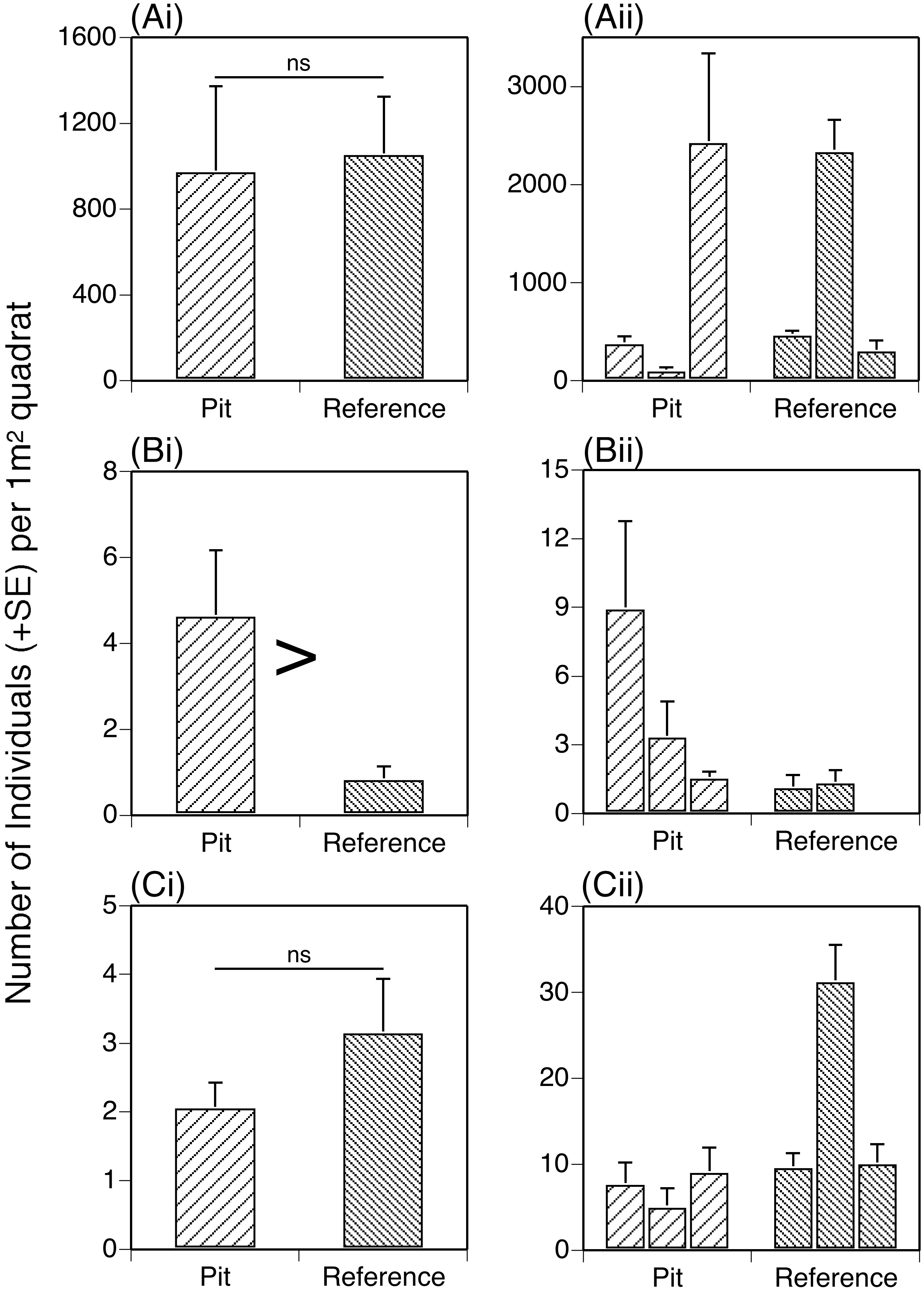


Figure 4.15: Mean (±SE) abundance of (A) individuals, (B) hermit crabs and (C) *Bedeva paivae* in 1.0m^2 quadrats collected from the seagrass adjacent to commercial pits and in reference sites near Commercial Plot 4. ns indicates no significant ($P>0.05$) difference between treatments (Pit vs. Reference) in 2-factor analysis of variance. > indicates significant difference ($P<0.05$) between treatments. Other details as in Figure 4.14.

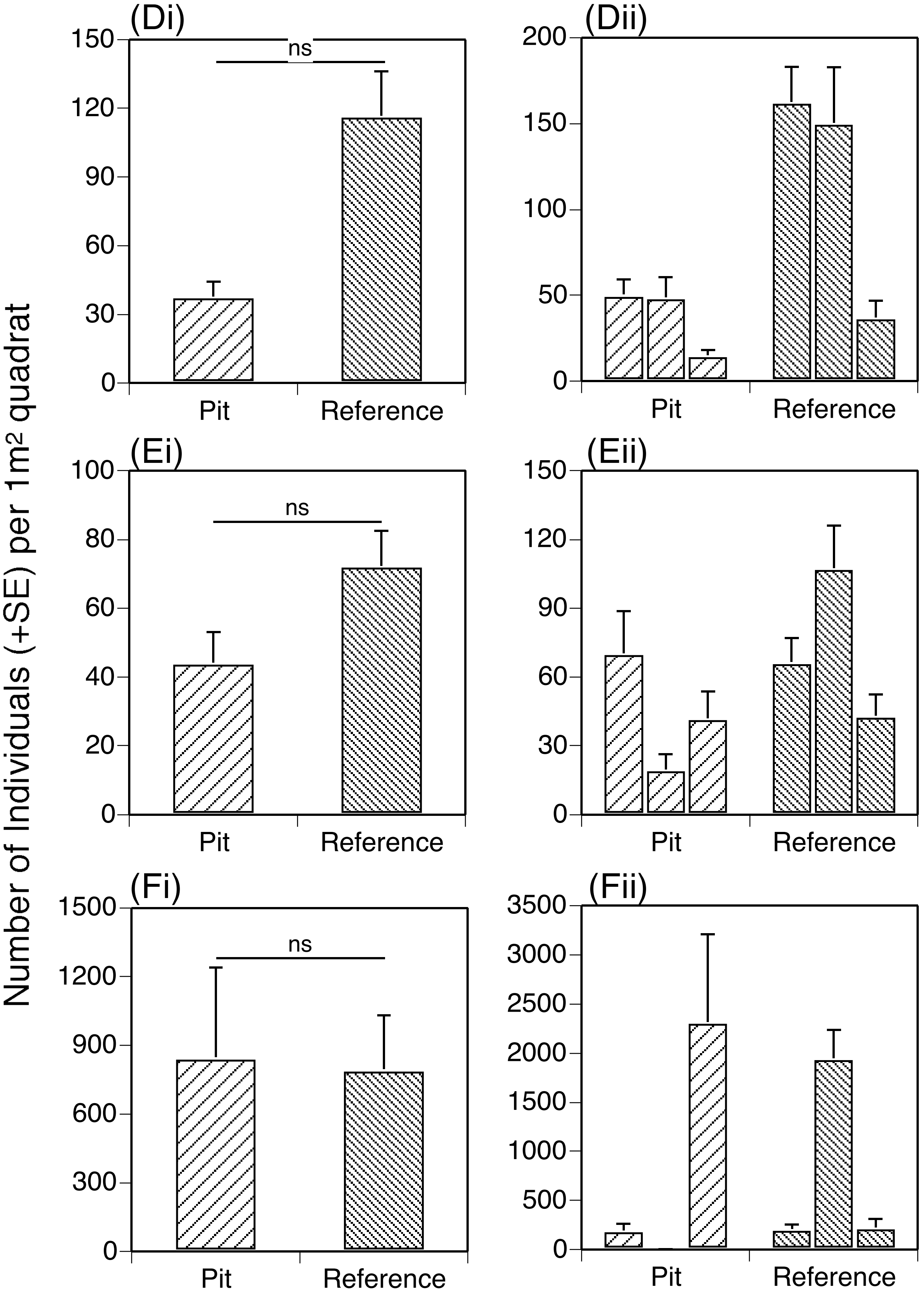


Figure 4.15 continued: Mean (±SE) abundance of (D) *Thalotia marginatain* and (E) *Nassarius burchardi* and (F) *Batillaria australis* in 1.0m^2 quadrats collected from the seagrass adjacent to commercial pits and in reference sites near Commercial Plot 4. Other details as in Figure 4.14.

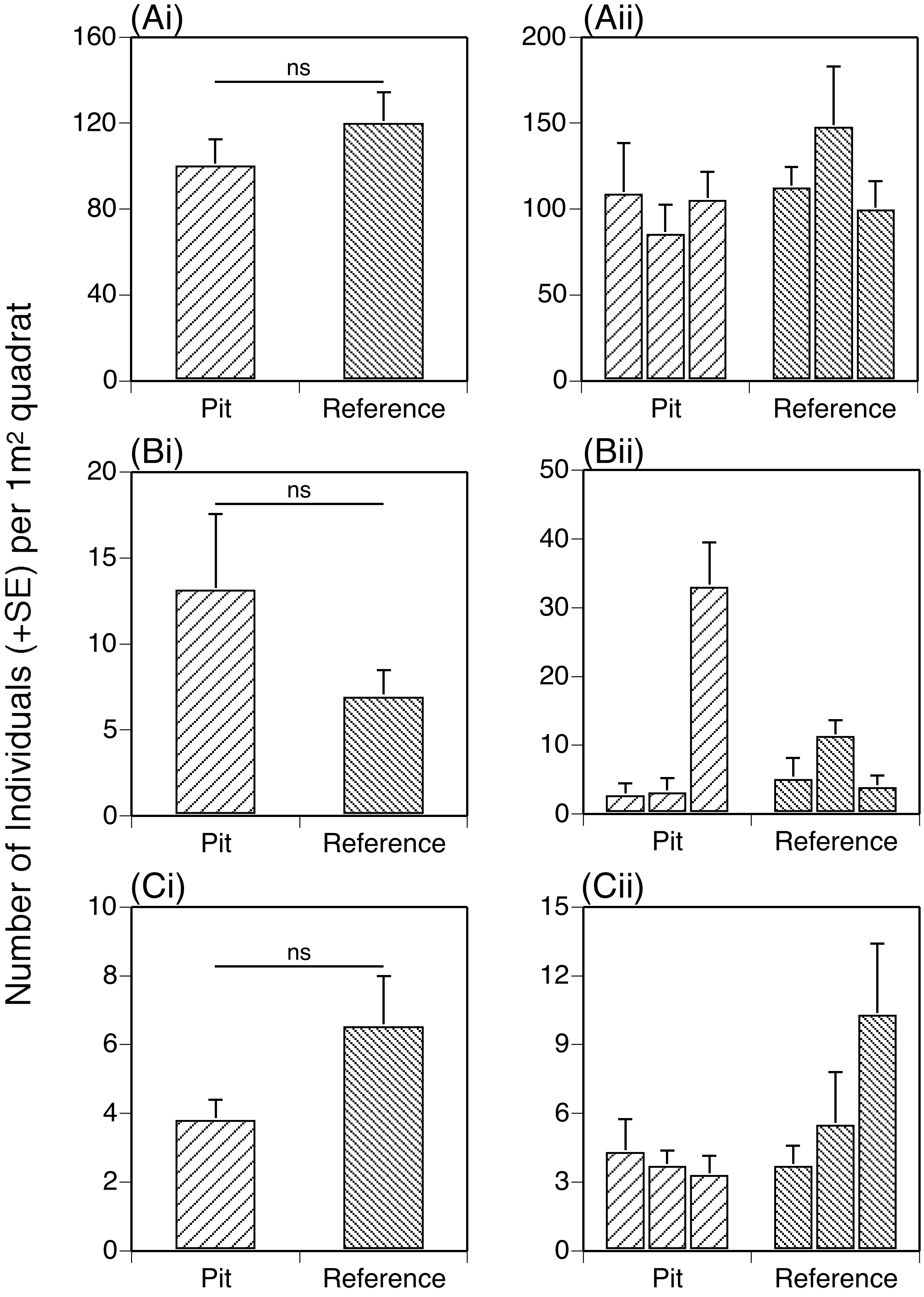


Figure 4.16: Mean (±SE) abundance of (A) individuals, (B) hermit crabs and (C) *Bedeva paivae* in 1.0m^2 quadrats collected from the seagrass adjacent to recreational pits and in reference sites near the Manly-Wynnum recreational digging area. ns indicates no significant ($P>0.05$) difference between treatments (Pit vs. Reference) in 2-factor analysis of variance. Other details as in Figure 4.14.

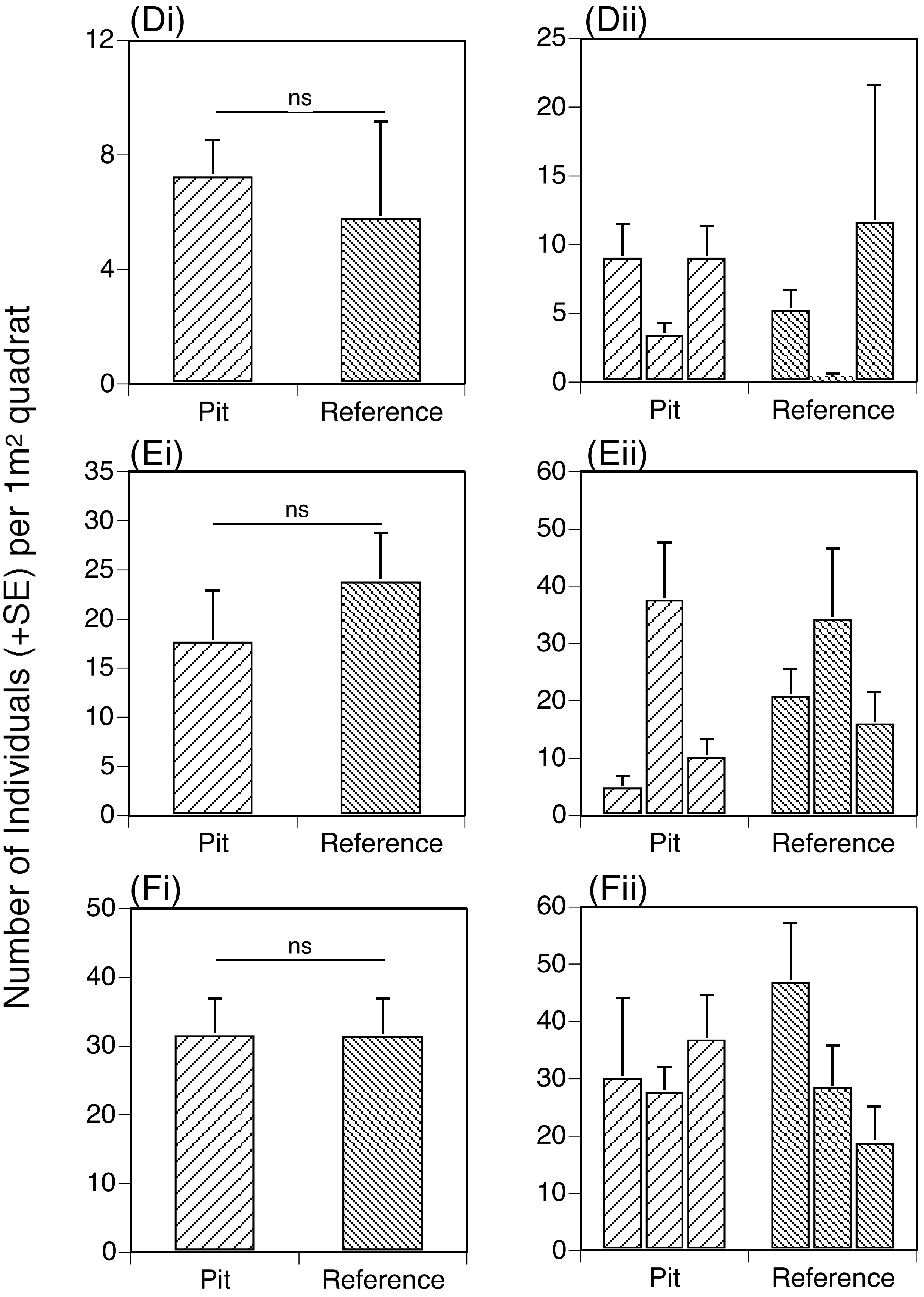


Figure 4.16 continued: Mean (±SE) abundance of (D) *Pyrazus ebeninus* (E) *Thalotia marginata* and (E) *Nassarius burchardi* in 1.0m^2 quadrats collected from the seagrass adjacent to recreational pits and in reference sites near the Manly-Wynnum recreational digging area. Other details as in Figure 4.14.

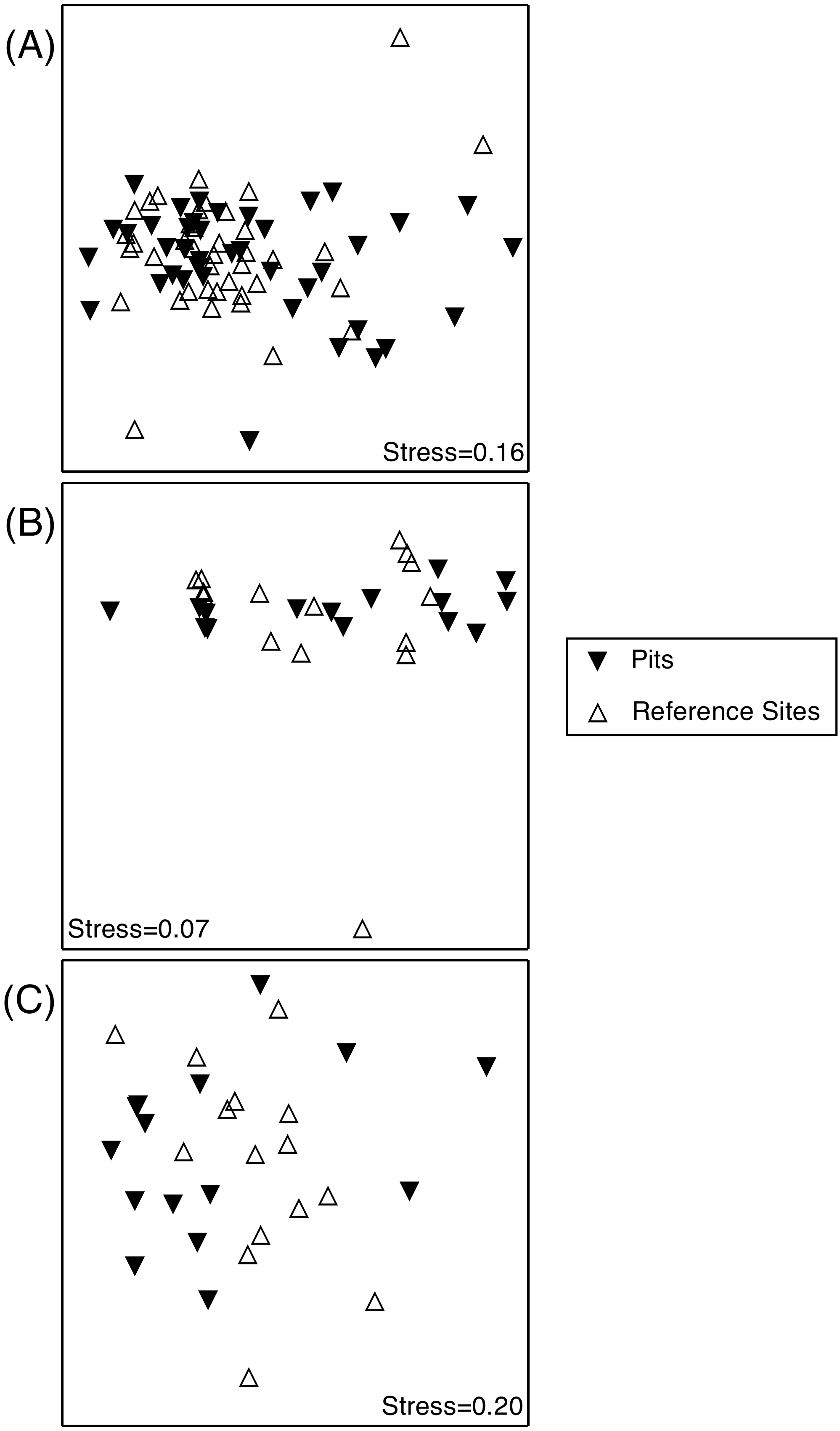


Figure 4.17: nMDS ordination of untransformed dataon the abundance of macrofauna from the seagrass adjacent to commercial and recreational pits and in reference sites near (A) Commercial Plot 1, (B) Commercial Plot 4 and (C) Manly-Wynnum recreational digging area. N=5 replicate $1m^2$ quadrats for each site (pit or reference area) sampled.

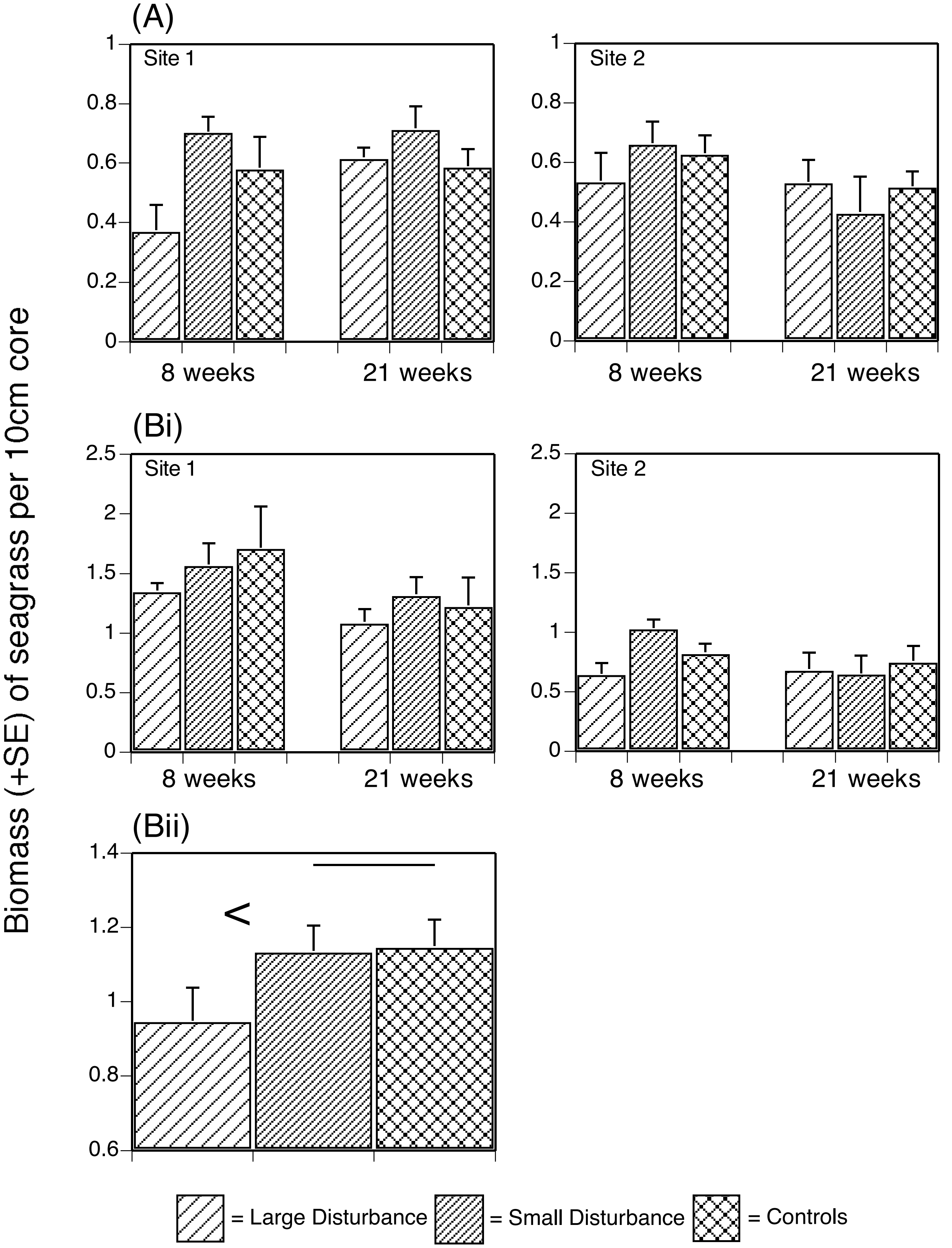


Figure 4.18: Mean (±SE) biomass of (A) above ground and (B) below ground seagrass in 1m^2 patches of intertidal *Zostera capricorni* habitat at three different levels of disturbance (High, Low and Control-see text for details) sampled 8 and 21 weeks after start of the experiment at two different sites on North Stradbroke Island. (Bi) shows differences between the two sites at each time and (Bii) shows the differences among the three treatments. N=4 replicates for each treatment. < = significant difference among treatments (P<0.05) from SNK tests after ANOVA.

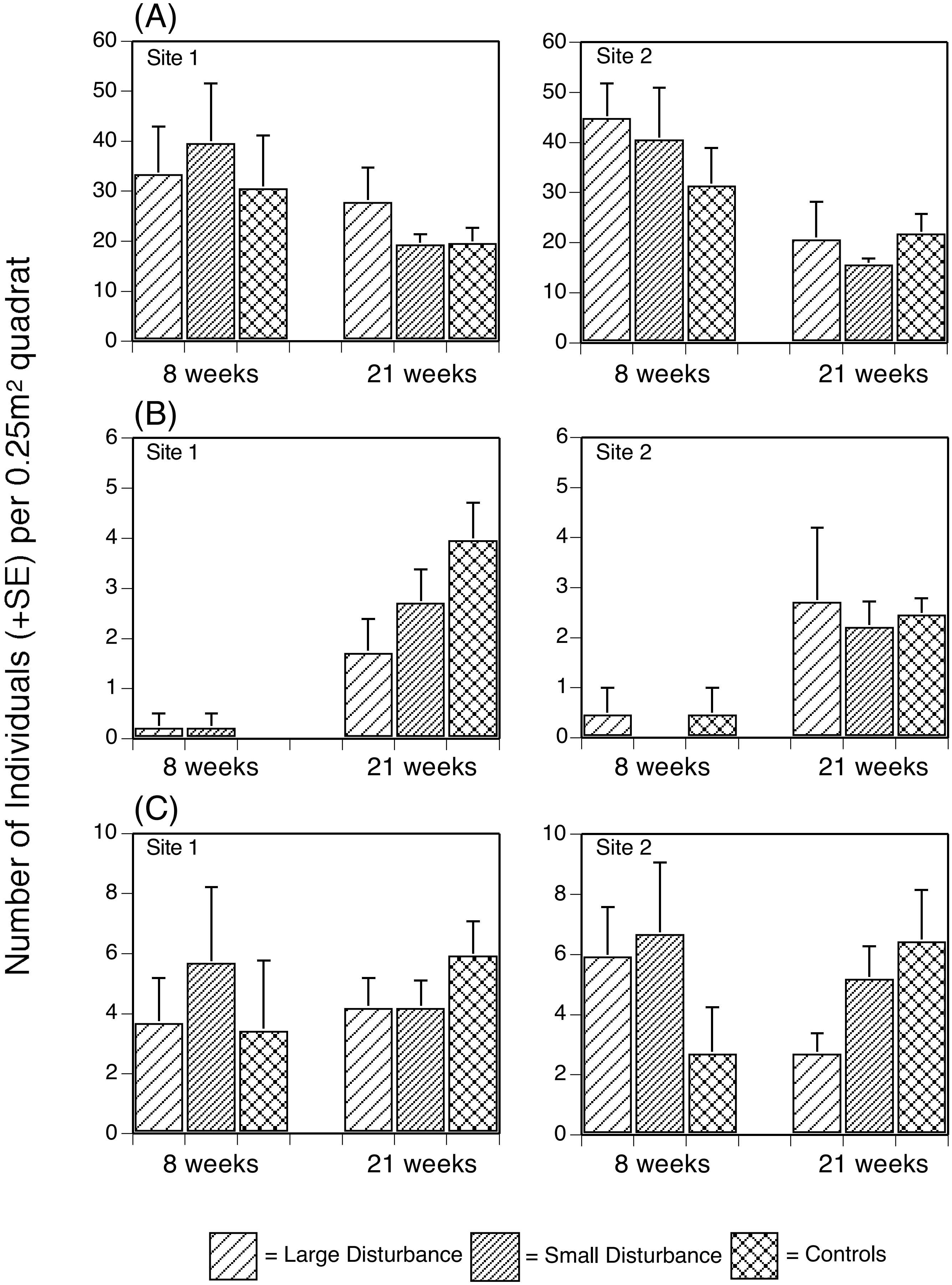


Figure 4.19: Mean (±SE) number of (A) individuals, (B) *Clanculus* sp. and (C) *Nassarius burchardi* in 1m^2 patches of intertidal *Zostera capricorni* habitat at three different levels of disturbance (High, Low and Control-see text for details) sampled 8 and 21 weeks after start of the experiment at two different sites on North Stradbroke Island. N=4 replicates for each treatment.
< = significant difference among treatments ($P<0.05$) from SNK tests after ANOVA. Note the differences in scale on Y-axis.

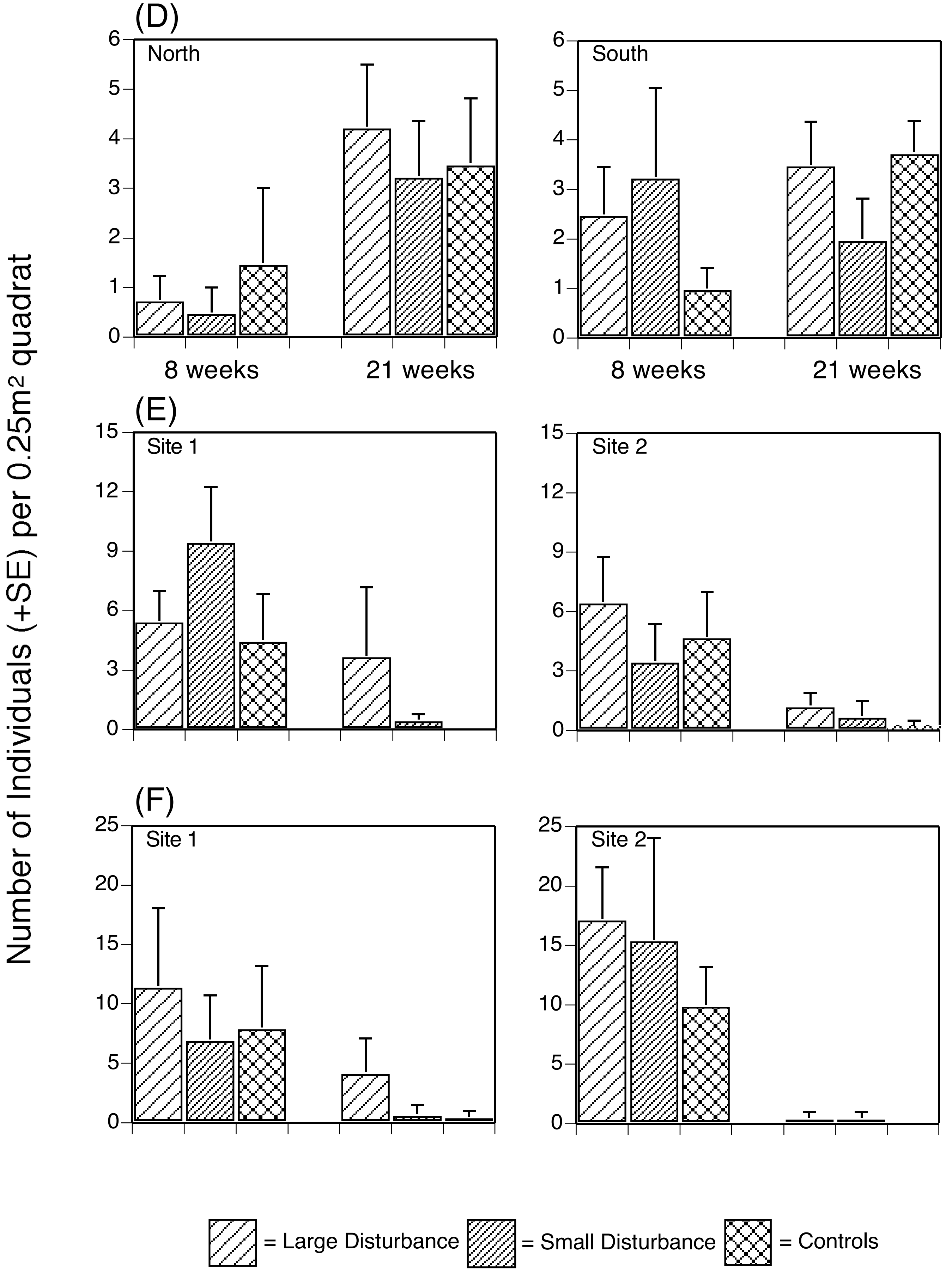


Figure 4.19 continued: Mean (±SE) number of (D) *Thalotia marginata,* (E) nereid polychaetes and (F) gammarid amphipods in 1m^2 patches of intertidal *Zostera capricorni* habitat at three different levels of disturbance (High, Low and Control-see text for details) sampled 8 and 21 weeks after start of the experiment at two different sites on North Stradbroke Island. Other details as in Figure 4.19A-C.

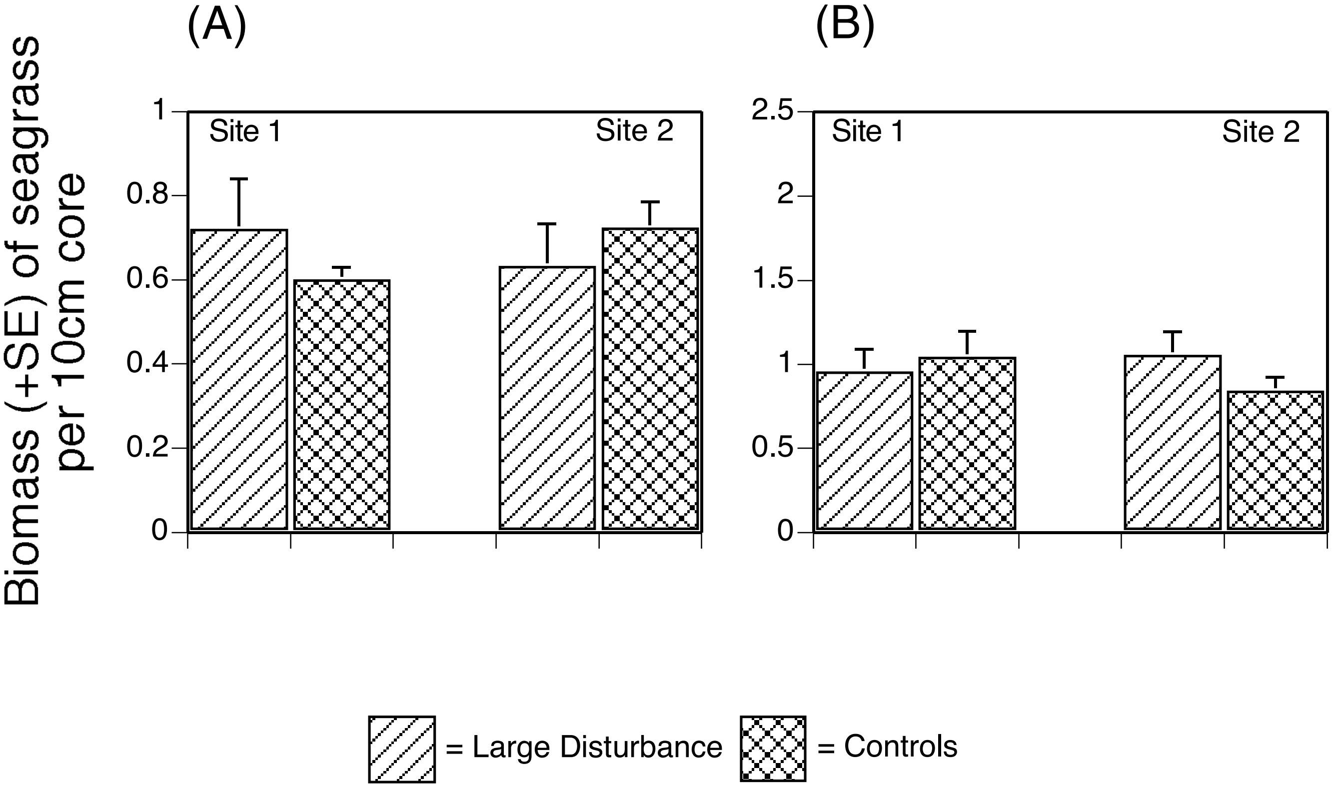


Figure 4.20: Mean (±SE) biomass of (A) above ground and (B) below ground seagrass in 1m^2 patches of intertidal *Zostera capricorni* habitat at three different levels of disturbance (High, Low and Control-see text for details) sampled 8 weeks after start of the experiment at two different sites on Fisherman Islands. N=4 replicates for each treatment. < = significant difference among treatments (P<0.05) from SNK tests after ANOVA.

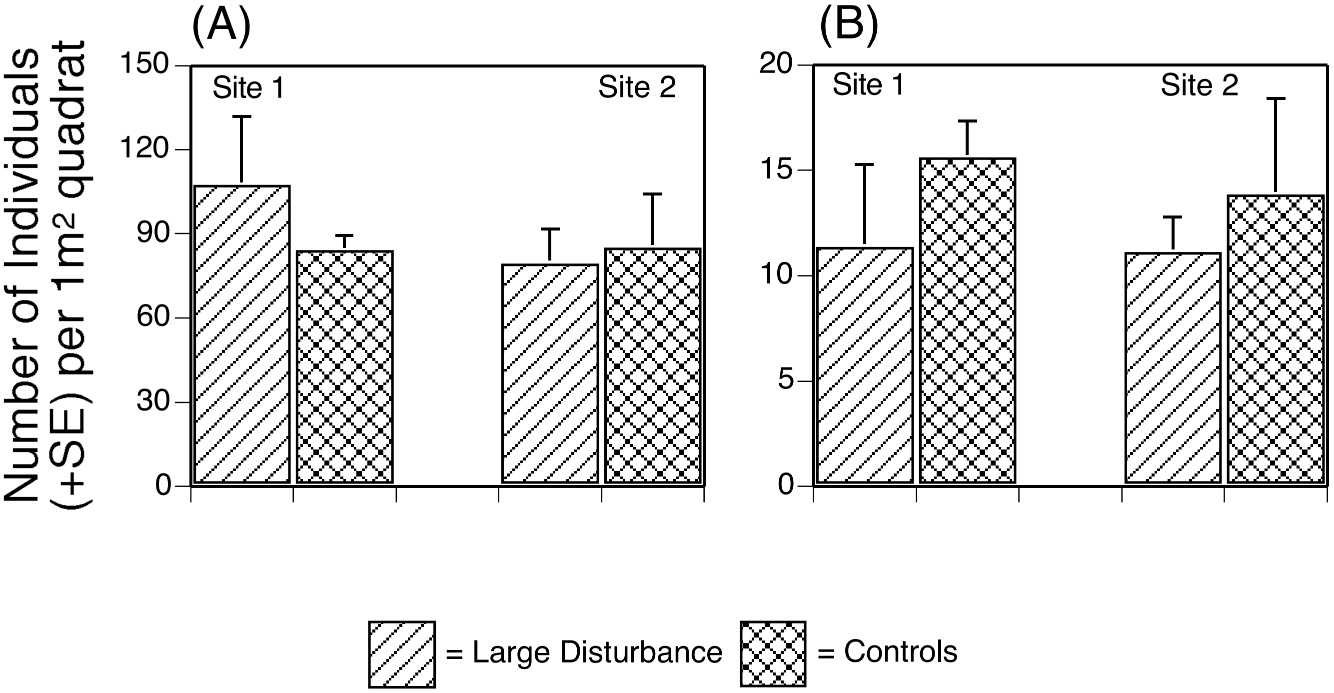


Figure 4.21: Mean (±SE) number of (A) individuals and (B) *Nassarius burchardi* in 1m^2 patches of intertidal *Zostera capricorni* habitat at two different levels of disturbance (High and Control-see text for details) sampled 8 weeks after the start of the experiment at two different sites on North Stradbroke Island. Other details as in Figure 4.19

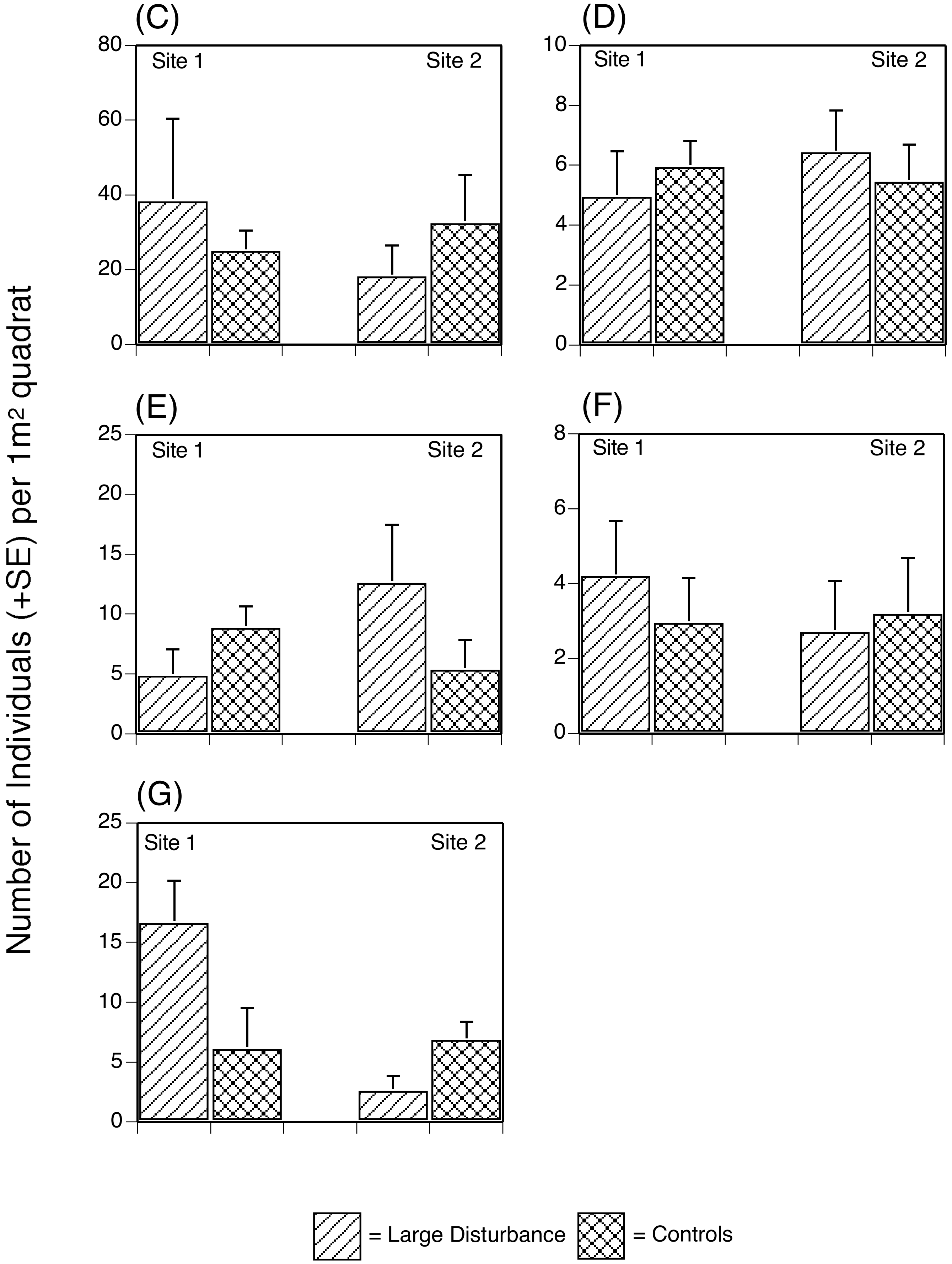


Figure 4.21 continued: Mean (±SE) number of (C) *Batillaria australis*, (D) *Smaragdia souverbiana*, (E) gammarid amphipods, (F) *Ilyograpsus paludicola* and (G) brittle stars in $1m^2$ patches of intertidal *Zostera capricorni* habitat at two different levels of disturbance. Other details as in Figure 4.21A-B.

Section 5: Effects of Disturbance on Macrofauna in Seagrass Beds

5.1. Preamble

The results reported in the previous section (Section 4), indicated that the commercial harvesting of bloodworms resulted in significant changes to the intertidal seagrass habitat (primarily *Zostera capricorni*) and the associated benthic infaunal assemblages. In contrast, there was little or no indication that the physical changes to the habitat led to any impacts on the epibenthic (surface dwelling) assemblages in these same areas. Environmental impacts on the plants and animals in estuarine benthic habitats have potentially important implications for higher trophic levels (e.g. fishes and shorebirds) that are dependent on the macrobenthic organisms as food and on the habitat for protection and breeding sites. For example, if the abundance or availability of food organisms decreased to a point where sites could no longer support foraging species, then these species would be forced to move elsewhere to feed, potentially placing them in competition with animals already using the new areas, or exposing them to predators during the search for suitable habitat (see Section 6).

During the course of the current study, the opportunity arose to examine the dynamics of macrobenthic and epibenthic communities simultaneously in seagrass beds subjected to different levels of disturbance, albeit from a natural source, grazing by a mega-herbivore, the dugong. This work used a combination of sampling and experimental manipulation to determine the effect of grazing by dugongs on the macro-infaunal and epibenthic communities. Grazing by dugongs results in both the removal of the seagrass and physical disturbance to the substratum with displacement of sediments and the potential for smothering of infaunal and epifaunal animals. Grazing by dugongs in intertidal seagrass beds leads to changes in the structure of the habitat, with different species of seagrass recolonising the disturbed areas compared with those in undisturbed beds (Preen, 1995). There is little information available, however, on whether these changes in the composition of the species of seagrass and changes to the density and height of the seagrass within an area, have any effects on the macrobenthic community living in the sediments or the epibenthic community living among the seagrass blades and shoots. The scales at which this form of physical disturbance takes place are similar to those caused by small-scale harvesting operations associated with recreational bait digging.

Specifically, the results from this study on the effects of grazing by dugongs on the faunal communities in intertidal seagrass beds provide the following information that is relevant when considering the more general implications of recreational and commercial bait-harvesting in seagrass systems:

(i). A broader understanding of the effects of habitat (seagrass) modification and removal on benthic communities. Dugongs are effective at removing a large proportion of the seagrass by grazing and in doing so they create a patchy environment, where grazed areas are surrounded by ungrazed seagrass. This patchy environment is similar to that created by bait harvesters working in intertidal seagrass systems.

(ii). Greater generality in our understanding of how modifications to seagrass systems affect the animals using them, through examination of the impacts of seagrass removal and disturbance at a larger number of sites that was examined in the previous section.

The Effect of Dugong Grazing on Community Composition in Intertidal Seagrass Beds

5.2. Introduction

Seagrass meadows are highly productive and dynamic coastal ecosystems that are involved in a range of different processes within estuaries (e.g. den Hartog, 1977; papers in Larkum et al., 1989). They provide food, shelter and breeding and nursery grounds for numerous animals, with many of these being important to commercial and recreational fisheries (Thayer et al. 1984a, b; Bell & Pollard, 1989; Butler & Jernakoff, 1999). Seagrass communities may also act to trap sediments and organic nutrients (Ginsburg & Lowenstam, 1958; Eckman, 1983), providing an increased supply of detritus that is the staple food for numerous animals within the seagrass beds. Direct grazing of seagrasses is often considered to be a relatively insignificant component of the utilisation of organic matter in seagrass beds with few herbivores feeding on the seagrass material itself (Thayer et al. 1984a; Klumpp et al., 1993). In tropical and sub-tropical regions, however, large marine herbivores, including dugongs, sea turtles and sea urchins, consume considerable amounts of seagrass material and may have a significant impact on seagrass communities (Best, 1981; Kirkman & Young, 1981; Valentine & Heck, 1991; de Iongh et al., 1995; Greenway, 1995; Preen 1995; Aragones, 1996).

Grazing by macro- and mega-herbivores has been shown to alter rates of plant growth and species diversity, primary production, nutrient cycling, energy flow and age distribution in terrestrial plant communities (e.g. McNaughton, 1979; Brown & Ewel, 1987; Cyr & Pace, 1993; Olff & Ritchie, 1998). These and other studies on terrestrial plant-herbivore interactions have demonstrated that not only does grazing have a significant and lasting impact on plant communities, but there is also the potential for cascading effects through the ecosystem, resulting in changes to associated animal communities (e.g. Baines et al., 1994; Landsberg et al., 1997; Bromham et al., 1999). The role of large herbivores in aquatic systems has not been studied as extensively as in terrestrial systems, yet the data that are available suggest that aquatic mega-herbivores may exert as much, if not more, influence on plant communities as their terrestrial counterparts (Preen, 1992; Cyr & Pace, 1993; Cebrian & Duarte, 1994; Aragones, 1996; Aragones & Marsh, 2000). Grazers such as fish, sea urchins, turtles and dugongs have the capacity to modify the species composition, nutrient and fibre content, productivity, biomass, growth rate and regeneration of seagrasses (Preen, 1992; Aragones, 1996; Rose et al., 1999; Aragones & Marsh, 2000; Macia, 2000).

The dugong, *Dugong dugon* (Muller, 1776) is the only strictly marine herbivorous mammal (Marsh, 1988; Marsh et al., 1995) feeding almost exclusively on seagrasses (Lanyon et al., 1989; Preen, 1992) and consuming up to 10-15% of their body weight in seagrass daily (Best, 1981). Dugongs are highly selective foragers, primarily consuming seagrasses of the genera *Halophila* and *Halodule* which have greater digestibility and nutritional value compared with other species of seagrass (Preen, 1992; Aragones, 1996). Dugongs are also known to eat some algae, especially when seagrass is sparse (Heinsohn & Spain, 1974; Preen & Marsh, 1995)

Dugongs are widely distributed in the Indo-Pacific region, between the longitudes of 30°E and 170°E and latitudes of 27°N and 27°S (Nishiwaki et al., 1979; Marsh & Lefebvre, 1994), inhabiting tropical and subtropical warm, shallow coastal and inland waters (Marsh & Lefebvre, 1994). Australia appears to be a stronghold of the Indo-Pacific dugong populations (Marsh, 1988) and dugongs are widespread throughout the northern waters of Australia and down the east and west coasts to approximately 27°S (Marsh et al., 1995; Aragones, 1996). In the northern populations, dugongs are often solitary (Marsh & Saafeld, 1989) or occur in small herds (Preen, 1992; Aragones, 1996) but in Moreton Bay, the southern limit of the dugong's range, they often move in large herds of 100-300 animals (Preen, 1992). Moreton Bay has a population of between 800-1000 dugongs (Lanyon, 2003) with the majority of this population found in the eastern parts of the Bay over shallow sandbanks inshore from Moreton and North Stradbroke Islands. The dugongs in Moreton Bay feed predominantly on *Halophila ovalis* and *Halodule uninervis* dominated seagrass beds, with herds sometimes grazing in a single location for up to 35 days (Preen, 1992). This intensity of grazing has been shown to result in changes to the composition of species of seagrass present on the banks and the nutrient availability, fibre content, age distribution and biomass of the seagrasses (Preen, 1992).

Grazing by dugongs may also cause considerable short-term disturbance to the seagrass community. When feeding on their preferred seagrasses, dugongs dig up the entire plant, removing between 63-86% of the available biomass and leaving distinct feeding trails (19-25 cm wide, 3-5 cm deep and 1-5 metres long) through the seagrass bed (Wake, 1975; Preen, 1992). Their feeding also causes substantial disturbance to the sediment as the plant material is removed. While it is known that the intensive grazing can cause changes to the plant communities it is not known whether there are any direct or indirect effects on the animal communities that are associated with the seagrasses.

The main objective of this study was to investigate the effects of dugong grazing on the abundance and composition of animal communities in seagrass beds in Moreton Bay. The study was also designed to determine whether any effects of grazing were due primarily to the removal of plants from the system (direct effects of grazing) or a result of the disturbance to the sediments which occurs during feeding (i.e. indirect effects from grazing).

5.3. Methods

5.3.1. Study Sites

This work was done in the seagrass beds located on the eastern side of Moreton Bay, south-east Queensland, Australia (27°S; 153°E; Figure 5.1). This region of Moreton Bay is characterised by expanses of shallow sand banks, Moreton, Amity and Wanga Wallen Banks, which support extensive seagrass meadows. Diurnal intrusion of oceanic water through the South Passage maintains high water quality and clarity throughout this region, providing ideal conditions for the growth of seagrasses (Gabric et. al 1998). A variety of seagrass species are found throughout the region including *Zostera capricorni*, *Halophila ovalis*, *H. spinulosa* and *Halodule uninervis* as the most common species, and *Cymodocea serrulata*, *Syringodium isoetifolium* and *Halophila decipiens* being considerably less abundant (Preen 1992). These seagrass meadows are the principal feeding grounds for dugongs and green turtles in Moreton Bay (Preen, 1992) and they also provide food and shelter for a variety of commercially targeted fish and crustaceans (Young, 1978; Coles et al., 1987, 1993).

5.3.2. Small-Scale Disturbance in Seagrass

During feeding, dugongs leave distinct trails through the sediment from which they have removed most (60-85%) of the seagrass. To determine whether the removal of the vegetation and/or the associated effects changed the composition of the epifaunal and infaunal communities in the seagrass, benthic cores were collected from a series of recently created trails and from surrounding ungrazed seagrass. An aerial survey was done on the 18th of April, 2000 to record positions of dugong herds in the eastern region of Moreton Bay. Five herds of 40 or more dugongs were sighted during the survey. The locations of the herds sighted from the air were later inspected by boat and the intertidal area of Amity Banks that had the most easily distinguishable fresh feeding trails was selected as the study site. The site had a relatively sparse seagrass cover (~55.2 grams dry weight biomass of seagrass per m^2) and was dominated by *Halophila ovalis* and *H. spinulosa*. Three feeding trails were randomly selected from the within the seagrass bed. From each trail, three replicate sediment samples were collected using a hand-held corer (15cm diameter and 15cm deep, volume~2650mls). Replicates were taken at least 30cm apart along the length of the trail. From within the same seagrass bed, sediment samples were also taken from outside of the feeding trails. Three patches of seagrass outside of the trails were randomly selected and sampled in the same manner as the trails. These patches of ungrazed seagrass were at least 2 metres from the nearest trail.

The sediment samples were fixed using formalin (5%), stained with Rose Bengal, which targets biological material, then sieved across stacked 1mm and 500um sieves and preserved in 70% methylated spirits until they were sorted. The seagrass in each sample was removed for determination of biomass and the epifauna and infauna were sorted into the lowest possible taxonomic unit. The seagrass removed from the samples was dried at 70°C for 72 hours then weighed to determine the combined above- and below-ground seagrass biomass.

5.3.3. Experimental Manipulations of Seagrass Density

A manipulative experiment in the field was done in order to determine whether patterns identified in previous section could be attributed to the effects of dugong grazing, or were more likely due to natural environmental variation among the grazed and ungrazed sites (i.e. confounding). Simulated dugong grazing was done in a seagrass bed on Amity banks known to be grazed regularly by dugongs (see Figure 5.2). To avoid the possibility that the dugongs would interfere with the experiment or influence the results, the experiment was done in early August, after the large herds had dispersed from the Bay for the winter (Janet Lanyon, personal communication). The experiment was done at two separate sites approximately one kilometre apart.

There were three different treatments used in the experiment: grazed plots, disturbance control plots and ungrazed control plots (Figure 5.2). The grazing treatment involved removing 80% of the seagrass in the plot in a manner meant to simulate dugong grazing. A garden rake was modified to correspond with the width of a dugong's muzzle (20cm wide; 5 cm long tines) and was used to simulate the grazing. The rake was pulled six times across the length and six times across the width of the plot in a grid-like fashion. Seagrass, roots and rhizomes were removed to a depth of 5 cm below the surface of the sediment (similar to dugong grazing). A similar approach was used in the disturbance control plots, however the back of the rake was rubbed over the surface of the seagrass and sediment without removing any seagrass. This treatment was necessary to distinguish between the effects caused by the removal of the seagrass material during dugong feeding versus any effect related to the physical disturbance of the sediment associated with the feeding. The ungrazed control plots were left undisturbed. At each site, 24, 2x2 metre plots were marked with wooden stakes and coloured flagging tape. Eight replicate plots for each treatment were randomly assigned among the 24 marked plots at each site. The intention was to sample four replicate plots after one week, and the other four remaining plots after 4 weeks to allow examination of any temporal patterns in the effect of the simulated grazing on the benthic communities. At the appropriate times, five replicate sediment samples (15cm diameter and 15cm deep, volume~2650ml) were randomly collected from within each of the four replicate plots per treatment. These samples were processed and sorted in the same manner as previously described (Section 5.3.3). The seagrass in each samples was separated from the sediment during sorting, dried at 75°C to constant weight and then weighed to determine total (above and below-ground) biomass.

5.3.4. Large-Scale Disturbance in Seagrass

Epibenthic fish and crustacean communities were examined on intertidal seagrass beds on banks in eastern Moreton Bay, near Amity on North Stradbroke Island (Figure 5.3). Recently grazed and ungrazed areas on these banks were identified from the air during aerial surveys of the dugong herds (Lanyon, unpublished data). Within the grazed and ungrazed areas, three sites were selected, each approximately 500-750 metres apart, and at each site, four replicate 50 metre trawls were done using a beam trawl (1 metre wide x 0.5 metre high, 1 mm cod-end, 2 mm body mesh). The trawl was towed behind a small outboard powered vessel at a speed of approximately 1.5 knots. Replicate trawls were sufficiently far apart to avoid resampling an already disturbed area, thus maintaining independence of samples. All material retained in the cod-end at the end of the trawl was fixed in ethanol and returned to the laboratory for identification and enumeration.

5.3.5. Statistical Analyses

5.3.5.1. Small-Scale Disturbance in Seagrass

Nested two factor ANOVAs were done to determine whether there were any significant differences between the abundance of animals in trails and non-trails. The data were log transformed ($\log_e(x+1)$) to satisfy the assumption of homoscedastic error variances (Underwood, 1981). Separate ANOVAs were done on the component of the fauna retained on the 1 mm sieves and the total number of animals retained on the 500 μm sieve. This was done to determine whether the interpretation of the effects of seagrass removal (via dugong grazing) changed as a result of analysis of the samples across difference sieve sizes. It is less expensive and faster to process samples across the larger sieve size than the finer mesh (e.g. James et al., 1995) and such information would be useful in making decisions about future monitoring programmes aimed at detecting significant impacts on seagrass-related fauna.

The total number of individuals and the abundance of any taxa that comprised greater than 10% of this total were analysed using univariate ANOVA. For the larger fraction (> 1 mm size) analyses were done for numbers of gammarid amphipods, ostracods, bivalves, polychaetes and nematodes. For the total number of animals retained on the 500 μm sieve (which includes those retained on the 1 mm sieve), analyses were done for numbers of gammarid amphipods, ostracods, bivalves, polychaetes, nematodes, cumaceans, tanaids and gastropods.

Differences in the community composition of the fauna between trails and non-trails were examined with non-metric multidimensional scaling on fourth-root transformed data, using the Bray-Curtis similarity measure. The data were transformed to the fourth-root to reduce the dominance in the analysis of a few particularly abundance taxa (Clarke, 1993). The statistical significance of any differences in the composition of the fauna between trails and non-trails was tested using a non-parametric multivariate ANOVA (NPMANOVA; Anderson, 2001). Separate analyses were done on the data from the animals larger than 1 mm (retained in a 1 mm sieve) and those larger than 500 μm (retained on a 500 μm sieve). Correlation coefficients were calculated between the biomass of seagrass and the total abundance of animals and the abundance of individual taxa in cores collected from areas with trails and those without (non-trails).

5.3.5.2. Experimental Manipulations of Seagrass Density

Although the experiment was established at two sites, not all samples from one of these sites were processed due to logistical constraints, so two separate sets of analyses were done. All samples were available from the first site (hereafter Site A), allowing a balanced design to be used to examine the effects of seagrass removal (simulated grazing) on the macrofaunal community after one and four weeks post-disturbance. At the second site (hereafter Site B), data were analysed to examine whether the composition of the macrofaunal community after 4 weeks post-disturbance were similar to those observed at the Site A. Analyses were again done separately on the animals larger than 1 mm size and the entire macrobenthic community (> 500 μm size) to determine whether sampling methodology (sieve size) affected interpretation of the results in this experiment.

5.3.5.3. Large-Scale Disturbance in Seagrass

Data on the abundance of individual species and higher order taxa and the total number of individuals were analysed with nested analyses of variance with factors Treatment (grazed versus ungrazed: fixed) and Sites nested within Treatment (3 random sites within each treatment). Data were transformed to loge(x) to remove heterogeneity of variances after Cochran's tests.

5.4. Results

5.4.1. Small-scale Disturbance in Seagrass

There was a clear pattern in the abundance of fauna in the areas which had been recently grazed compared with nearby areas of seagrass untouched by the dugong herds. For the larger (>1 mm) specimens, generally there were more animals present in the Non-trail areas than the Trails, with the exception of the number of bivalves (Table 5.1A; Figures 5.4 A - F). The abundance of animals in the ungrazed areas was between 23.5% (nematodes) and 65.6% (ostracods) greater than in the grazed areas, although there was no statistical difference detected between the treatments for nematodes (Table 5.1A). There were more bivalves (9.5%) in the Trail areas than Non-trail areas but this difference was not significant.

The pattern was similar for the fraction of the fauna greater than 500 μm in size (Table 5.1B; Figures 5.5 A –I). There was no significant difference in the abundance of bivalves (Figure 5.5 D), nematodes (Figure 5.5 F) or cumaceans (Figure 5.5 G) between the grazed (Trails) and ungrazed (Non-trails) areas but for other taxa there were significantly more animals in the ungrazed than grazed areas. For cumaceans, the magnitude of the difference between the treatments was 64%, but this was not detected as being significant suggesting low power in the ANOVA. The abundance of animals in the ungrazed areas was up to 85.5% greater than the grazed areas (e.g. tanaids, Figure 5.5 H); Table 5.1B).

There was no significant difference in the composition of the community between the grazed and ungrazed areas nor among the multiple plots within each Treatment (Table 5.2A). If a precautionary approach is taken (e.g. Underwood, 1993) to detecting the impacts associated with the removal of seagrass and the term for Plots (within Treatments) is removed from the analysis, a significant difference in community composition between Treatments is evident (Table 5.2B; Figure 5.6 A). This conclusion should only be considered tentative though because the probability associated with detecting differences among the Plots was only $P>0.09$, rather than the customary $P>0.25$ (e.g. Winer et al., 1991). There was a clear difference between the grazed and ungrazed areas in the composition of the entire macrofaunal community (> 500 μm) (Table 5.2 B; Figure 5.6 B). This difference was detected despite the large variation at the scale of plots within each treatment (Table 5.2 B; $P<0.06$) and suggests that the similar result obtained for the larger animals (> 1 mm) was related to the effects of grazing.

The abundance of animals in the area was positively correlated with the biomass of seagrass present, although the strength of the correlation varied considerable among taxa (Figure 5.7). The total number of animals showed the strongest positive correlation with seagrass biomass ($r=0.78$, $P<0.0001$), but other groups including tanaids ($r=0.74$, $P<0.0003$), bivalves ($r=0.71$, $P<0.0007$), ostracods ($r=0.75$, $P<0.0002$) and polychaetes ($r=0.70$, $P<0.0009$) were also more abundant in patches with a greater biomass of seagrass. The abundance of other groups such as gammarid amphipods ($r=0.42$) and copepods ($r=0.39$) were not correlated with the biomass of seagrass.

5.4.2. Experimental Manipulations of Seagrass

5.4.2.1. Biomass of Seagrass

At Site A, the experimental removal of seagrass decreased the biomass of vegetation by 86% compared with the unmanipulated controls (Table 5.3). The biomass of seagrass in the disturbance control treatment was reduced by 32% compared with the controls, even though no seagrass was directly removed during the application of the treatment. The reduction in seagrass in the disturbance control plots presumably arose from destabilisation of the sediments with subsequent loss of vegetation through erosion of the sediments under tidal and wave-driven water movement. All three treatments were significantly different from each other with respect to the biomass of seagrass present (Table 5.3A, B). There was no significant difference in the biomass of seagrass between the two times of sampling (1 and 4 weeks), nor was there an interaction between Time and Treatment suggesting that the reduction in seagrass biomass in the removal and disturbance treatments was established at, or soon after, the experiment started and there had been little in the way of recovery of seagrass over the month of the experiment.

At Site B, after 4 weeks, the biomass of seagrass was reduced by 55% in the grazed treatment and 25% in the disturbance control treatment compared with the controls. Again, all three treatments were significantly different from each other (Table 5.3).

5.4.2.2. Significant Effect of Seagrass Removal

Responses by fauna to the experimental reduction in the biomass of seagrass and the associated disturbance to the seagrass and sediments varied among the different taxa present. Four taxa showed a significant decline in abundance in the manipulated plots where seagrass biomass was reduced by 86%, but there was no significant effect of disturbance, despite the removal of up to 32% of the seagrass from disturbance control plots. Gammarid amphipods (Figure 5.8A) were reduced by 64%, gastropods (Figure 5.8B) by 58%, capitellid polychaetes (Figure 5.8C) by 48% and opheliid polychaetes by 67% in the grazed plots compared with the ungrazed control plots. The pattern of differences among the three treatments was consistent through time (no significant interaction between Time and Treatment) and, of these four taxa, only the opheliid polychaetes varied in abundance between the two times (Table 5.4).

5.4.2.3. Significant Effect of Disturbance During Seagrass Removal

Two taxa, copepods (Figure 5.9A) and terebellid polychaetes (Figure 5.9B), showed significant reductions in abundance in response to the experimental disturbance of the seagrass and sediments, but no additional effect in the grazed plots compared with the ungrazed control plots. This suggests that the disturbance to the substratum (and associated reduction in seagrass biomass) triggers the reduction in abundance for these animals although in both cases the trend was for the smallest abundances to be in the grazed plots (Figure 5.9). The abundance of copepods varied little between the two times of sampling, but there was a significant difference in the abundance of terebellids between one and four weeks after the start of the experiment. The interaction between Time and Treatment for terebellids was marginally significant ($P<0.08$) and examination of the data suggests that the abundance of these worms was smaller in the grazed plots than the control plots on both occasions, but the abundance in the disturbed plots was less than the control plots after 1 week, but not after 4 weeks.

5.4.2.4. Significant Effect of Seagrass Removal and Disturbance

The total abundance of animals (Figure 5.10A) and the abundance of tanaid crustaceans (Figure 5.10B) was significantly reduced by the disturbance to the substratum and there was an additional significant effect of seagrass removal in the grazed plots. The effect of disturbance to the substratum and the associated reduction in the biomass of the seagrass in the disturbance control plots caused a 20% reduction in the total abundance of macrofauna in these plots compared with the ungrazed control plots. Direct removal of seagrass from the grazed plots led to a 51% reduction in the abundance of animals compared with the control plots (Figure 5.10A). Compared with the control plots, the abundance of tanaids in the disturbance control plots was reduced by 39% and in the grazed plots by 76% (Figure 5.10B).

The abundance of two other taxa, bivalves (Figure 5.11A) and sabellid polychaetes (Figure 5.11B), was significantly reduced by the experimental treatments (Table 5.4), but post-hoc comparisons were unable to distinguish among the specific treatments. In both cases, there were more animals in the ungrazed control plots than the other treatments.

5.4.2.5. Significant Short-Term Effects of Seagrass Removal and Disturbance

Five different taxa showed significant short-term (1 week) effects from the experimental treatments, but these effects were not evident after 4 weeks (significant Time x Treatment interaction, Table 5.4). Ostracods (Figure 5.12A) and nematodes (Figure 5.12D) were significantly less abundant in the grazed and disturbance control plots compared with the control plots, but there was no significant difference between the grazed and disturbance control plots. In contrast, nereidid (Figure 5.12B) and syllid polychaetes (Figure 5.12C) were significantly less abundant in the grazed plots, but the disturbance control and ungrazed control plots were not different from each other. Finally, the abundance of nemerteans (Figure 5.12E) varied significantly among the three treatments, but the exact pattern of differences was unclear from the post-hoc analyses. The important result here is that however the impacts were manifested after 1 week, these effects were no longer evident after 4 weeks.

Two taxa, isopod crustaceans (Figure 5.13A) and spionid polychaetes (Figure 5.13B) were apparently unaffected by the application of either experimental treatment (Table 5.4). There was some suggestion of a short-term (1 week) effect of grazing and disturbance on the abundance of spionids but if this trend was a result of the experimental treatments, then the effect was no longer evident after 4 weeks (Figure 5.13A).

5.4.2.6. Effect of Sieve Mesh Size on Interpretation, Site A

Comparison of the results for the analyses done on the size fraction of the fauna retained on a 1 mm sieve with those discussed above for a 500 μm sieve (the entire assemblage of macrofauna), revealed few differences in interpretation or outcomes (Table 5.4). Three taxa, ostracods (Figure 5.14A), cirratulid polychaetes (Figure 5.14B) and nereidid polychaetes (Figure 5.14C) showed significant short-term (1 week) effects of the experimental removal of seagrass and/or disturbance to the seagrass and sediments when the 500 μm size fraction was analysed but these effects were not evident when the 1 mm size fraction was analysed (Table 5.4). Additionally, analysis of the >500 size fraction indicated that disturbance of the sediments and the reduction in the biomass of seagrass led to a significant reduction in the abundance of terebellid polychaetes (Figure 5.9B), but there were insufficient of these worms retained on the 1 mm mesh sieve to allow analysis.

5.4.2.7. Generality of the Results

The results of separate analyses done on the data collected after 4 weeks at Site B were compared with the results from the more extensive dataset taken at Site A to determine whether the patterns described above were consistent at another, widely separated site. It is important to note that the analyses done for Site B were based on a smaller dataset than those at Site A (two plots with 3 replicate cores per plot at Site B compared with 3 cores at each of 3 plots for Site A).

For the total number of individuals in the experimental plots, the trend among the treatments was similar at both sites (Figure 5.15A), but the relative effects of seagrass removal versus disturbance varied between the two sites. At Site A, there was a significant effect of disturbance (and the associated reduction in seagrass biomass) on the abundance of individuals but there was a further reduction in abundance with the removal of greater amounts of seagrass biomass. In contrast, at Site B, there was a clear effect of the seagrass removal, but there was little effect from the experimental disturbance to the plots, despite the removal of significant amounts of seagrass as an indirect effect of this disturbance (see Table 5.3).

The pattern of differences among the treatments in the number of gammarid amphipods was also similar at both Sites (Figure 5.15B), but in this case, post-hoc multiple comparisons (SNK tests) were unable to distinguish among the treatments at Site B, whereas these tests had indicated a significant effect of seagrass removal at Site A. The reduced number of samples collected at Site B may have led to insufficient power to detect the differences among the treatments, given the magnitude of these differences were similar at both sites. This conclusion is further supported by the analyses on the abundance of tanaid crustaceans (Figure 5.15C) and the number of capitellid polychaetes (Figure 5.15D). At Site A, the abundance of tanaids was reduced by the effects of disturbance and further by the removal of seagrass in the simulated grazing treatments, but at Site B, only the effect of seagrass removal was found to significantly impact on the abundance of the tanaids. Seagrass removal was found to significantly reduce the abundance of capitellid polychaetes (Figure 5.15D) at Site A, but there were no significant differences among the treatments at Site B (Table 5.4).

The interpretation of the relative effects of the experimental seagrass removal (grazing) and disturbance on the number of copepods varied between Site A and Site B (Figure 5.15E). At Site A, although there was a trend for a greater reduction in numbers of copepods in the grazed plots compared with the disturbance plots, these treatments were not significantly different from each other, though both had significantly fewer copepods than the control plots. At Site B, however, there was still a significant effect of grazing/seagrass removal on the abundance of copepods, but no effect of seagrass disturbance.

The experimental treatments had very little effect on the abundance of ostracods at Site A, but caused a significant reduction in their numbers in the grazed plots at Site B compared with the control plots (Figure 5.15F). A similar result was obtained for syllid polychaetes (Figure 5.15H). The opposite situation was, however, evident for sabellid polychaetes (Figure 5.15G). There was a significant effect of the experimental treatments on the abundance of sabellids at Site A, although the nature of these effects could not be distinguished, but at Site B there was no significant effect of the experimental treatments (Table 5.4).

5.4.2.8. Effect of Sieve Mesh Size on Interpretation, Site B

Interpretation of the effects of the experimental treatments varied between the two sieve mesh sizes for seven different taxa at Site B: gammarid polychaetes (Figure5.16A), copepods (Figure 5.16B), ostracods (Figure 5.16C), opheliid polychaetes (Figure 5.16D) and syllid polychaetes (Figure 5.16E). In all cases, analysis was able to detect significant differences among the treatments using the data collected across the 500 μm sieve, but no significant differences were detected among the treatments for data from the 1 mm sieve.

5.4.2.9. Effects of Grazing and Disturbance on Community Composition

The composition of the macrofaunal community at Site A was significantly affected by the application of the experimental treatments, but the differences among these treatments changed as time progressed (NPMANOVA, Table 5.5A). Initially, after 1 week, there were significant differences among all three treatments (Table 5.5B, Figure 5.17A), but after 4 weeks only the plots where the seagrass biomass had been experimentally grazed were different from the other plots (Table 5.5B, Figure 5.17B). Processing of the samples across a 1 mm sieve instead of a 500 μm sieve did not change the outcome of these analyses and interpretation was the same irrespective of sieve mesh size (Table 5.5C &D). The results of the analyses on the data from Site B after 4 weeks were similar to those obtained for Site A, with a significant effect of both grazing and experimental disturbance evident after 1 week but only an effect of grazing being evident after 4 weeks (Table 5.6, Figure 5.18).

5.4.3. Large-Scale Disturbance in Seagrass

Generally, the analyses of the data from the epibenthic beam trawls in grazed and ungrazed areas of intertidal seagrass was characterised by large variation among the three replicate sites, especially in the ungrazed areas. The analyses of variance all showed highly significant variation at the scale of Sites, and non-significant differences among the main treatments of grazed versus ungrazed. Figure 5.19A-E show examples of these analyses for the total number of individuals (Figure 5.19A), the number of fish (Figure 5.19B), the number of *Monacanthus chinensis*, a leatherjacket which was the most abundant species of fish (Figure 5.19C), the number of carid shrimp (Figure 5.19D) and the number of *Latreutes pygmaeus*, the most common species of shrimp (Figure 5.19E).

The results for multivariate analysis of the community composition of epibenthic fish and crustaceans mirrored the univariate data in that there were highly significant differences among the sites within the treatments (NPMANOVA, $P<0.002$) whereas there was no significant difference in community composition between the grazed and ungrazed areas (NPMANOVA, $P>0.478$; Figure 5.20).

Sites within each of the grazed and ungrazed areas were chosen so as to be as similar as possible in terms of seagrass cover (density, canopy height, species composition of vegetation) and other physical characteristics (depth, sediment type). At the time sampling was done, the intertidal flats at one site were covered with *Lyngbya* sp. a toxic cyanobacterium which had been in bloom proportions across Moreton Bay earlier in the year (see also Section 4). This was the site which supported the greatest abundance of epibenthic organisms during this study. *Lyngbya* was however also present in smaller amounts at the other grazed sites but no specific information was gathered on the distribution and abundance of the mats at the different sites and there is no specific information on the influence of these 'algal' blooms on the animals communities.

5.5. Discussion

Grazing by dugongs results in the removal of large amounts of seagrass and considerable disturbance to the substratum as the plants are uprooted (Wake, 1975; Preen, 1992). Sediment that is displaced during feeding forms mounds on either side of the feeding trail, potentially burying animals as it then slumps back into the trail from water movement. Taken in this context, the physical effects from grazing are similar to those resulting from digging in seagrass to catch bloodworms and other invertebrate animals.

There were between 10-85% fewer animals present in the trails compared with adjacent, ungrazed areas, although for individual taxa, the magnitude of the differences varied, and for some taxa, there was no effect of the grazing on their abundance. Similarly, the overall composition of the benthic, infaunal assemblage in the grazed areas was different from that in the ungrazed areas although there was significant small-scale (i.e. among plots) variation that masked the primary comparison between grazed and ungrazed areas. The total number of animals and the abundance of several individual taxa in the different plots was positively correlated with the biomass of the seagrass suggesting that the differences in the abundance of the these animals in the grazed and ungrazed areas was a direct response to the removal of the seagrass or to some associated factor that was closely linked to the amount of vegetation present. Previous studies (e.g. Heck & Wetstone, 1977; Lewis & Stoner, 1983; Lewis, 1984; Stoner & Lewis, 1985) have also found positive correlations between the abundance of benthic fauna and the biomass of seagrass, so this result was not surprising but it did provide further support for the contention that the loss of the vegetation is a key component in the way disturbances affect the associated fauna.

The abundance of some taxa, such as gammarid amphipods, was not correlated with the biomass of seagrass, despite the fact that there were significantly fewer animals in the grazed than ungrazed areas. This raises the possibility that amphipods were affected by some other effect associated with grazing, such as the substantial disturbance to the sediments that occurs. Many gammarids are closely associated with the vegetation (e.g. Leber, 1985; Stoner & Lewis, 1985) but others are primarily infaunal (e.g. Alldredge & King, 1980; Ambrose, 1984; Beukema et al., 1999). More detailed identification of the different groups of amphipods in the samples would be required to determine their habitat-specificity, in combination with experimental manipulations of removal and/or disturbance (see below).

The abundance of groups such as bivalves was positively correlated with the biomass of seagrass in the plots, but was not different between the grazed and ungrazed areas, despite the fact there was considerably less seagrass in the grazed than ungrazed plots. Such a pattern would result if the biomass of the seagrass affected the abundance of the bivalves at settlement, but had little influence over their subsequent patterns of distribution. Passive trapping of larvae by seagrass at different densities has been found to influence small-scale spatial variation in the distribution of infauna (e.g. Eckman, 1983; Stoner & Lewis, 1985; Peterson, 1986) due to hydrodynamic baffling of water flow.

Previous studies on the effects of mega-herbivore grazing in seagrass beds have found variable effects on the macrofaunal communities. Macia (2000) found there were no effects on the invertebrate community from natural levels of grazing by urchins. In contrast, Rose et al. (1999) found that large densities of urchins removed greater than 95% of the seagrass biomass leading to significant declines in the abundance of both infaunal and epifaunal molluscs. Similarly, in the current study, grazing by dugongs resulted in there being significantly fewer bivalves (Figure 5.4 and 5.5) and gastropods (Figure 5.5) in grazed than ungrazed areas.

Studies of the effects of mega-herbivore grazing in terrestrial pastures have demonstrated that there are two main effects of grazing, the removal of the vegetation and the associated effects of trampling and disturbance (e.g. Holt et al., 1996). Similarly, grazing by dugongs had two distinct impacts on the seagrass communities: removal of the plants and disturbance to the substratum. These different components were partitioned through the inclusion of the grazing control plots that mimicked the disturbance caused during grazing but without the removal of the plants. Comparisons of the grazing control treatment with the grazing treatment (plant removal plus disturbance) provided estimates of the magnitude of any effects due to the reduction in biomass of seagrass, over and above the physical disturbance. Simulated grazing resulted in a 86% reduction in seagrass biomass, the associated physical disturbance caused a 32% reduction. The responses of the infauna to these impacts were marked but varied considerably among the different taxa.

Gammarid amphipods, gastropods and two families of polychaetes (capitellids and opheliids) were significantly affected by the removal of the seagrass alone (i.e. no associated effect of the disturbance component). The abundance of amphipods is often highly correlated with both the biomass and surface area of seagrasses (Stoner, 1980; Lewis & Stoner, 1983; Stoner & Lewis, 1985), possibly due to habitat selectivity in response to predation pressure (Orth et al., 1984). There was, however, no correlation between the abundance of amphipods and the biomass of seagrass when grazed (trails) and ungrazed areas were compared (see above). A logical prediction would have therefore been that the abundance of amphipods would be unaffected by the experimental removal of seagrass, yet this was not the case. Results such as this highlight the importance of testing hypotheses through appropriate experiments, especially in systems where there is considerable small-scale spatial (and temporal) patchiness. The significant impacts on the abundance of gastropods and polychaetes was expected, given they were significantly less abundant in grazed (trails) than ungrazed areas.

The abundance of harpacticoid copepods and terebellid polychaetes was significantly reduced by the grazing treatment, but this effect was attributable to the disturbance component, not the removal of the vegetation. These taxa are closely associated with the sediment, so it is not surprising that the decline in abundance as a result of physical disturbance. A wide variety of different taxa has been shown to be impacted from disturbance in sediments, including copepods (Sherman & Coull, 1980) and different groups of polychaetes (Zajac & Whitlatch, 1982a; Thrush, 1986). The abundance of tanaids was affected by a component due to the removal of the vegetation and a component associated with the physical disturbance to the substrata.

There were some differences in the responses of the fauna at 4 weeks, compared with those already present after 1 week. Ostracods, nematode and nereidid and syllid polychaetes and nemerteans were all significantly impacted by the simulated grazing after 1 week but these effects were no longer evident after 4 weeks. The other taxa were still significantly impacted by either the loss of vegetation, the associated physical disturbance or both after 4 weeks. Recovery of the seagrass in areas affected by physical disturbance often takes considerably longer than 4 weeks, although some genera, including *Halophila* and *Halodule* are able to recover within a few months of being disturbed (Brouns, 1987; Fonseca et al., 1987; Poiner et al., 1989; Duarte et al., 1997). Given many of the taxa that were affected responded primarily to the loss of vegetation, recovery of these populations of animals to levels commensurate with ungrazed reference areas would probably not occur until the vegetation had recovered.

There were very few differences in the interpretation of results based on samples processed across the 1 mm compared with the 0.5 mm sieves, suggesting that for studies such as this, where there are marked changes in the physical structure of the habitat (through loss of vegetation and/or physical disturbance), significant impacts on fauna could be detected after processing across the coarser sieves, at much reduced cost (e.g. James et al., 1995). Such results need to be considered carefully though, in light of the specific questions being asked. Clearly, a large proportion of the total abundance of macrofauna is missed across the larger sieve: 19,630 individuals were collected across the 500μm sieve but only 8,163 individuals across the 1 mm sieve, a loss of over 58% of the total abundance when using the larger sieve mesh size. Many of the organisms that are not retained on the larger mesh sizes are the smaller species, so if questions are focussed on the impacts of seagrass loss and/or disturbance on patterns of biodiversity, it may not be appropriate to use the coarser sieves.

Table 5.1A: Percentage magnitude and significance of any difference in the mean abundance of taxa between the Trail and Non-trail areas of seagrass beds on Amity Banks, eastern Moreton Bay for the larger (> 1mm size) animals.

Taxon	Treatment Rank	% difference	Significance
Total animals	Non-trails > Trails	45.2 %	P < 0.004
No. Gammarids	Non-trails > Trails	52.0 %	P < 0.018
No. Ostracods	Non-trails > Trails	65.6 %	P < 0.013
No. Bivalves	Trails ≅ Non-trails	9.5 %	P > 0.652
No. Polychaetes	Non-trails > Trails	45.5 %	P < 0.020
No. Nematodes	Non-trails ≅ Trails	23.5 %	P > 0.590

Table 5.1B: Percentage magnitude and significance of any difference in the mean abundance of taxa between the Trail and Non-trail areas of seagrass beds on Amity Banks, eastern Moreton Bay for all specimens (> 500 μm size).

Taxon	Treatment Rank	% difference	Significance
Total animals	Non-trails > Trails	53.5 %	P < 0.018
No. Gammarids	Non-trails > Trails	62.3 %	P < 0.001
No. Ostracods	Non-trails > Trails	63.4 %	P < 0.045
No. Bivalves	Non-trails ≅ Trails	24.5 %	P > 0.523
No. Polychaetes	Non-trails > Trails	46.9 %	P < 0.023
No. Nematodes	Non-trails ≅ Trails	42.9 %	P > 0.230
No. Cumaceans	Non-trails ≅ Trails	64.0 %	P > 0.176
No. Tanaids	Non-trails > Trails	85.5 %	P < 0.078 *
No Gastropods	Non-trails > Trails	54.4 %	P < 0.074 *

Table 5.2: Non-parametric multivariate analyses of variance (NPMANOVA) based on Bray-Curtis distance measure for the community composition of macrofauna from cores collected in grazed (Trails) and ungrazed (Non-trail) areas of seagrass at Amity banks. Data were unstandardised and fourth root transformed; n=3 cores in each of 3 plots per treatment (Trails versus Non-trails). NPMANOVA was done using permutations of residuals (Anderson, 2001 for full details).

(A) Full model for animals larger than 1 mm size;
(B) Model for animals larger than 1 mm size with Plots and Residual pooled (see text for further details);
(C) Full model for animals larger than 500 μm size.

(A) Animals > 1 mm **Full Model**

Source	df	MS	F	P	Possible # permutations
Treatment	1	793.73	1.50	0.268	2.4×10^4
Plots (Treatment)	4	530.65	1.63	0.097	1.9×10^8
Residual	12	325.32			
Total	17				

(B) Animals > 1 mm **Plots Pooled**

Source	df	MS	F	P	Possible # permutations
Treatment	1	3173.57	4.30	0.0002	2.4×10^4
Residual	16	738.59			
Total	17				

(C) Animals > 500 μm **Full Model**

Source	df	MS	F	P	Possible # permutations
Treatment	1	794.29	3.20	0.041	2.4×10^4
Plots (Treatment)	4	248.20	1.82	0.060	1.9×10^8
Residual	12	136.61			
Total	17				

Table 5.3A: Analyses of variance on the biomass (grams DW) of seagrass in $4m^2$ plots from three different Treatments (grazed, disturbance control, control) on two different occasions after simulated grazing (1 and 4 weeks) in Site A and after 4 weeks in Site B. Data were transformed to $\log_e(x+1)$ to meet the assumption of homogeneity of variances.

SITE A

Source	df	MS	F	P
Time	1	0.007	0.12	<0.75
Treatment	2	0.852	14.50	<0.001
Treatment x Time	2	0.060	1.02	<0.40
Plots (Treatment)	12	0.059	0.99	<0.48
Residual	36	0.059		

SITE B

Source	df	MS	F	P
Treatment	2	0.515	24.33	<0.003
Plots (Treatment)	5	0.021	0.49	<0.79
Residual	16	0.044		

Table 5.3B: Post-hoc SNK tests on the biomass (grams DW) of seagrass in 4 m^2 plots from three different Treatments (grazed, disturbance control, control after simulated grazing. Data shown are means ± standard errors. Means with same letter in SNK column are not significantly different from each other at $P < 0.05$. Means with different letter in SNK column as significantly different from each other.

Treatment	**Site A**	SNK	**Site B**	SNK
Control	1.69 (± 0.15) g	A	2.35 (± 0.23) g	A
Disturbance	1.15 (± 0.14) g	B	1.76 (± 0.21) g	B
Grazed	0.23 (± 0.09) g	C	1.06 (± 0.11) g	C

Table 5.4: Summaries of analysis of variance on the abundance of different taxa in 4 m^2 plots from three different Treatments (grazed, disturbance control, control) on two different occasions after simulated grazing (1 and 4 weeks) in Site A and after 4 weeks in Site B. Interaction refers to the interaction between Treatment and Time in the ANOVAs. N=3 replicate cores from each of three plots on each occasion at Site A. N=3 replicate cores from each of two plots at Site B. Data were transformed to $\log_e(x+1)$ where necessary to meet the assumptions of homoscedasticity after Cochran's test.

	Site A				**Site B**	
Variable	**Fauna > 1.0 mm**		**Fauna > 500 μm**		**Fauna > 1.0 mm**	**Fauna > 500 μm**
	Treatment	**Interaction**	**Treatment**	**Interaction**	**Treatment**	**Treatment**
Total No. Individuals	***	ns	***	(ns)	*	**
Gammarids	***	ns	***	ns	ns	*
Isopods	ns	ns	ns	ns	na	na
Tanaids	***	ns	***	ns	*	**
Copepods	*	ns	**	ns	ns	*
Ostracods	ns	ns	-	*	ns	**
Bivalves	*	ns	*	ns	**	*
Gastropods	*	ns	***	ns	na	**
Capitellids	*	ns	*	ns	ns	ns
Cirratulids	ns	ns	-	*	na	na
Nereidids	ns	ns	-	*	na	na
Opheliids	**	ns	***	ns	(ns)	*
Phyllodocids	na	na	na	na	ns	ns
Sabellids	*	ns	*	ns	ns	ns
Spionids	*	ns	(ns)	ns	ns	ns

Table 5.4: Continued……/

	Site A				Site B	
Variable	**Fauna > 1.0 mm**		**Fauna > 500 μm**		**Fauna > 1.0 mm**	**Fauna > 500 μm**
	Treatment	**Interaction**	**Treatment**	**Interaction**	**Treatment**	**Treatment**
Syllids	-	***	-	**	ns	*
Terebellids	na	na	***	(ns)	na	na
Nematodes	-	*	-	*	(ns)	(ns)
Nemerteans	-	*	-	*	na	na
Oligochaetes	na	na	na	ns	na	ns

. * = significant at $P<0.05$, ** = significant at $P<0.01$, *** = significant at $P<0.001$, (ns) = not significant but $P<0.10$, ns = not significant at $P>0.05$, - indicates test for main effect inappropriate because of significant interaction term, na indicates insufficient animals in that taxon at that site to allow analysis.

Table 5.5: Non-parametric multivariate analyses of variance (NPMANOVA) based on Bray-Curtis distance measure for the community composition of macrofauna from cores collected in plots from three different experimental treatments (grazed, disturbance control and control) at Site A, 1 and 4 weeks since application of the treatments. Data were unstandardised and fourth root transformed; n=9 cores pooled across 3 plots per treatment.

(A) Full model for animals larger than 500 μm size
(B) Pair-wise post-hoc comparisons for interaction
(C) Full model for animals larger than 1 mm size
(D) Pair-wise post-hoc comparisons

(A) Animals > 500 μm **Full Model**

Source	df	MS	F	P	Possible # permutations
Time	1	1820.38	3.52	0.0002	1.0 x 10^{10}
Treatment	2	2060.74	3.99	0.0002	1.0 x 10^{10}
Time x Treatment	2	974.48	1.89	0.0018	1.0 x 10^{10}
Residual	48	516.65			
Total	53				

(B) 1 week	**t-value**	**P**	
Grazing vs Disturbance	1.36	0.0100	2.43 x 10^4
Grazing vs Control	2.31	0.0002	2.43 x 10^4
Disturbance vs Control	1.51	0.0098	2.43 x 10^4
4 weeks	**t-value**	**P**	
Grazing vs Disturbance	1.72	0.0006	2.43 x 10^4
Grazing vs Control	2.03	0.0002	2.43 x 10^4
Disturbance vs Control	1.07	0.2854	2.43 x 10^4

(C) Animals > 1 mm **Full Model**

Source	df	MS	F	P	Possible # permutations
Time	1	2110.86	2.70	0.0010	1.0 x 10^{10}
Treatment	2	2682.91	3.44	0.0002	1.0 x 10^{10}
Time x Treatment	2	1327.16	1.70	0.0062	1.0 x 10^{10}
Residual	48	780.61			
Total	53				

(D) 1 week	**t-value**	**P**	
Grazing vs Disturbance	1.22	0.0554	2.43 x 10^4
Grazing vs Control	2.09	0.0008	2.43 x 10^4
Disturbance vs Control	1.60	0.0034	2.43 x 10^4
4 weeks	**t-value**	**P**	
Grazing vs Disturbance	1.63	0.0016	2.43 x 10^4
Grazing vs Control	1.87	0.0002	2.43 x 10^4
Disturbance vs Control	1.03	0.3970	2.43 x 10^4

Table 5.6: Non-parametric multivariate analyses of variance (NPMANOVA) based on Bray-Curtis distance measure for the community composition of macrofauna from cores collected in plots from three different experimental treatments (grazed, disturbance control and control) at Site B, 4 weeks since application of the treatments.

(E) Full model for animals larger than 500 μm size
(F) Pair-wise post-hoc comparisons for interaction
(G) Full model for animals larger than 1 mm size
(H) Pair-wise post-hoc comparisons

(A) Animals > 500 μm **Full Model**

Source	df	MS	F	P	Possible # permutations
Treatment	2	1240.01	3.70	0.0002	2.8 x 10^6
Residual	15	334.69			
Total	17				

(B) 4 weeks	**t-value**	**P**	
Grazing vs Disturbance	1.99	0.0048	462
Grazing vs Control	2.38	0.0024	462
Disturbance vs Control	1.11	0.2064	462

(C) Animals > 1 mm **Full Model**

Source	df	MS	F	P	Possible # permutations
Treatment	2	868.53	1.55	0.0002	2.8 x 10^6
Residual	15	562.55			
Total	17				

(D) 4 weeks	**t-value**	**P**	
Grazing vs Disturbance	1.37	0.0374	462
Grazing vs Control	1.36	0.0324	462
Disturbance vs Control	0.94	0.6106	462

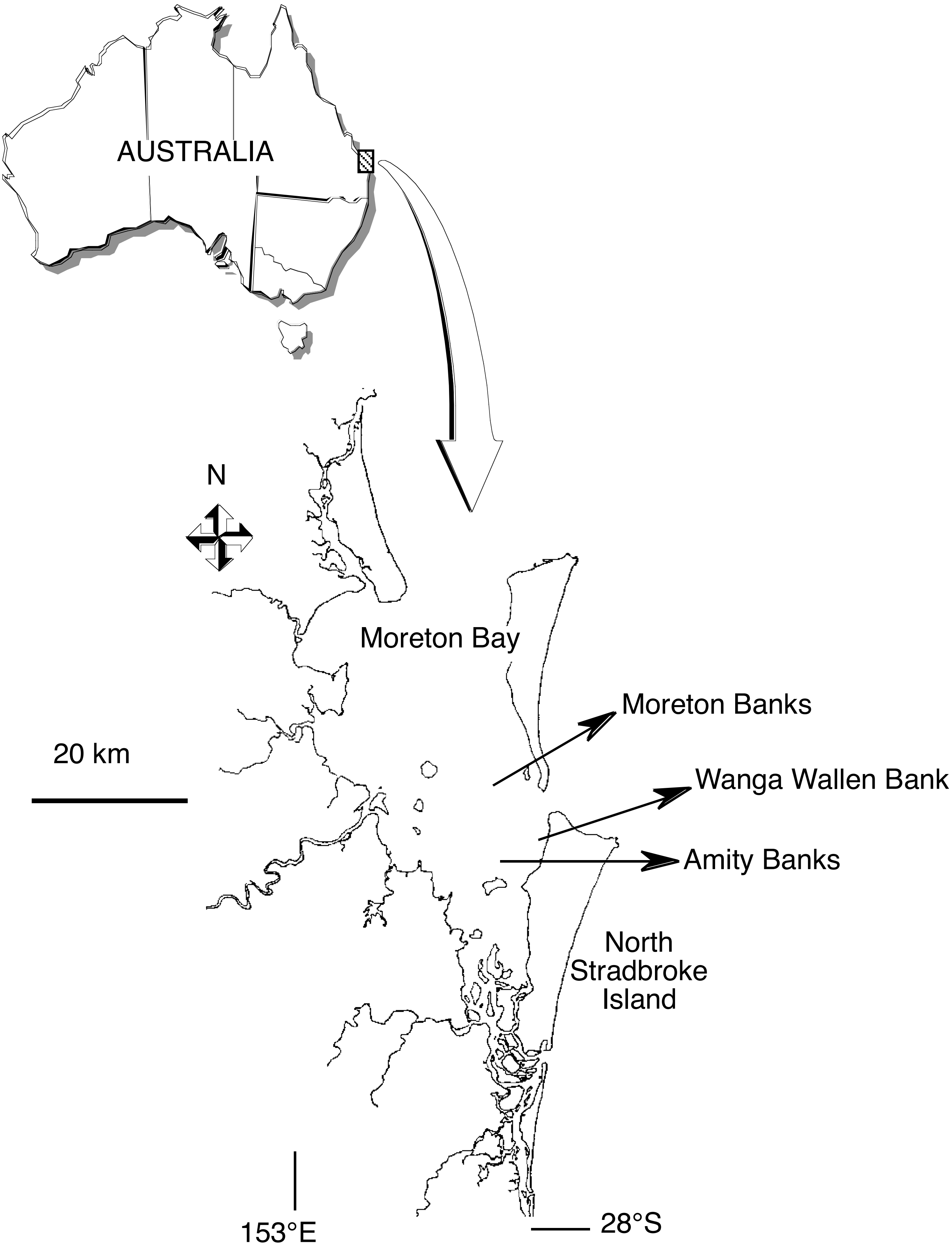


Figure 5.1: Map of Australia and the Moreton Bay region of SE Queensland showing the location of the sites in eastern Moreton Bay used for the study on the effects of dugong grazing on seagrass habitats and the associated macrofauna.

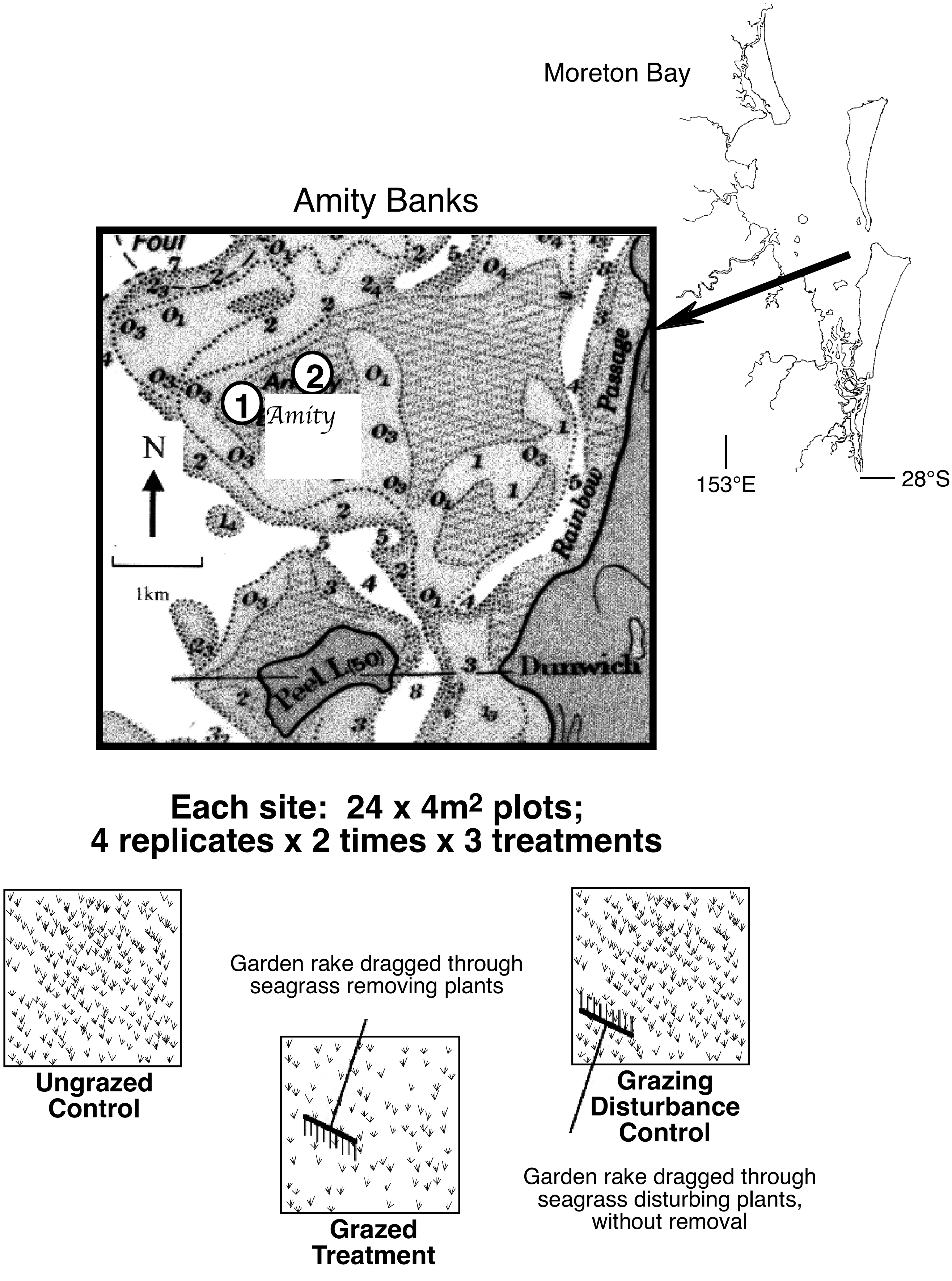


Figure 5.2: Map of Moreton Bay region showing loction of sites and a schematic representation of the experimental design used in the simulated grazing experiment (see Section 5.3.3. for further details).

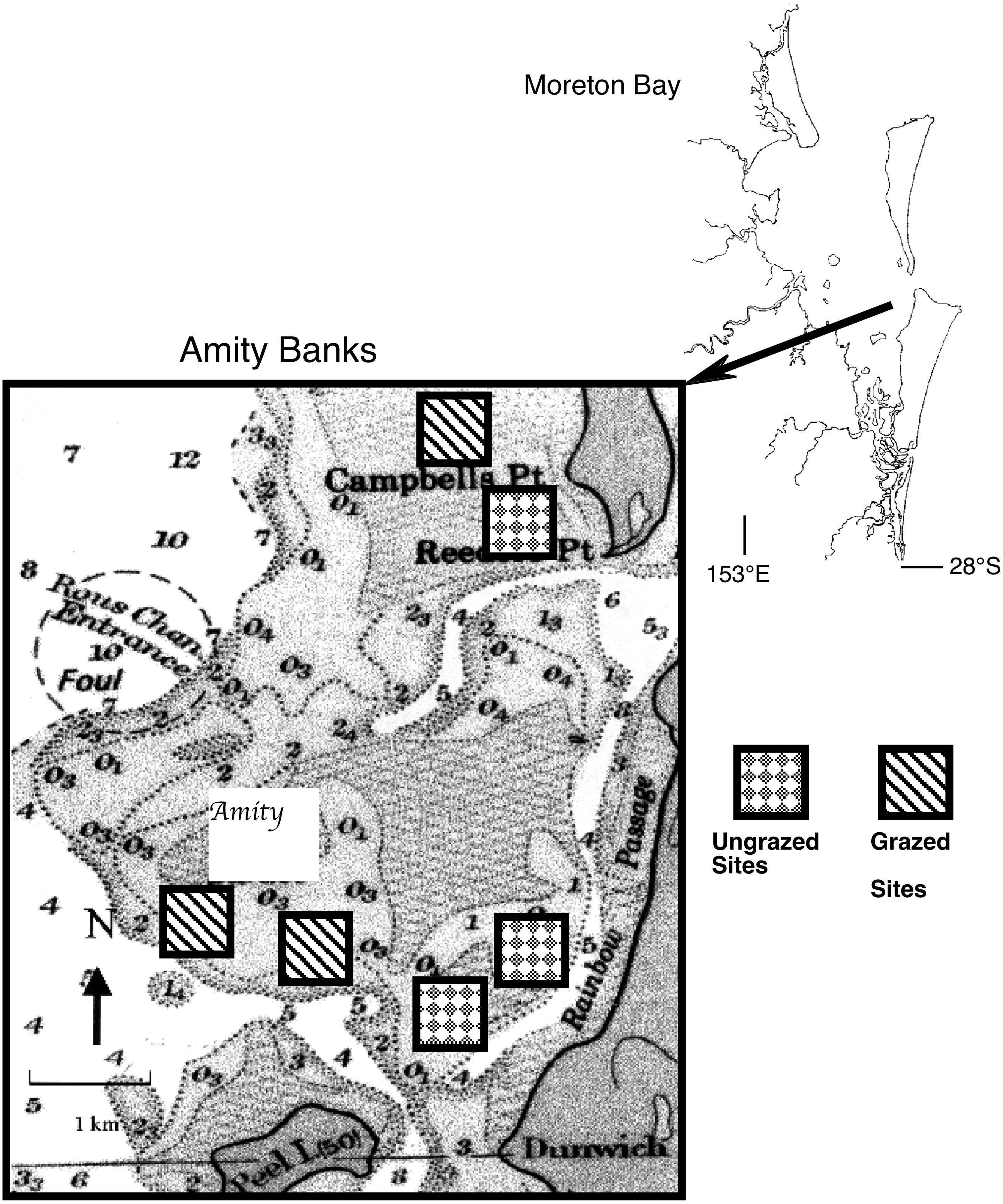


Figure 5.3: Map of Moreton Bay region of SE Queensland showing the location of the sites in eastern Moreton Bay used for the study comparing the composition of the epibenthic fish and crustacean community in grazed and ungrazed areas of seagrass habitat.

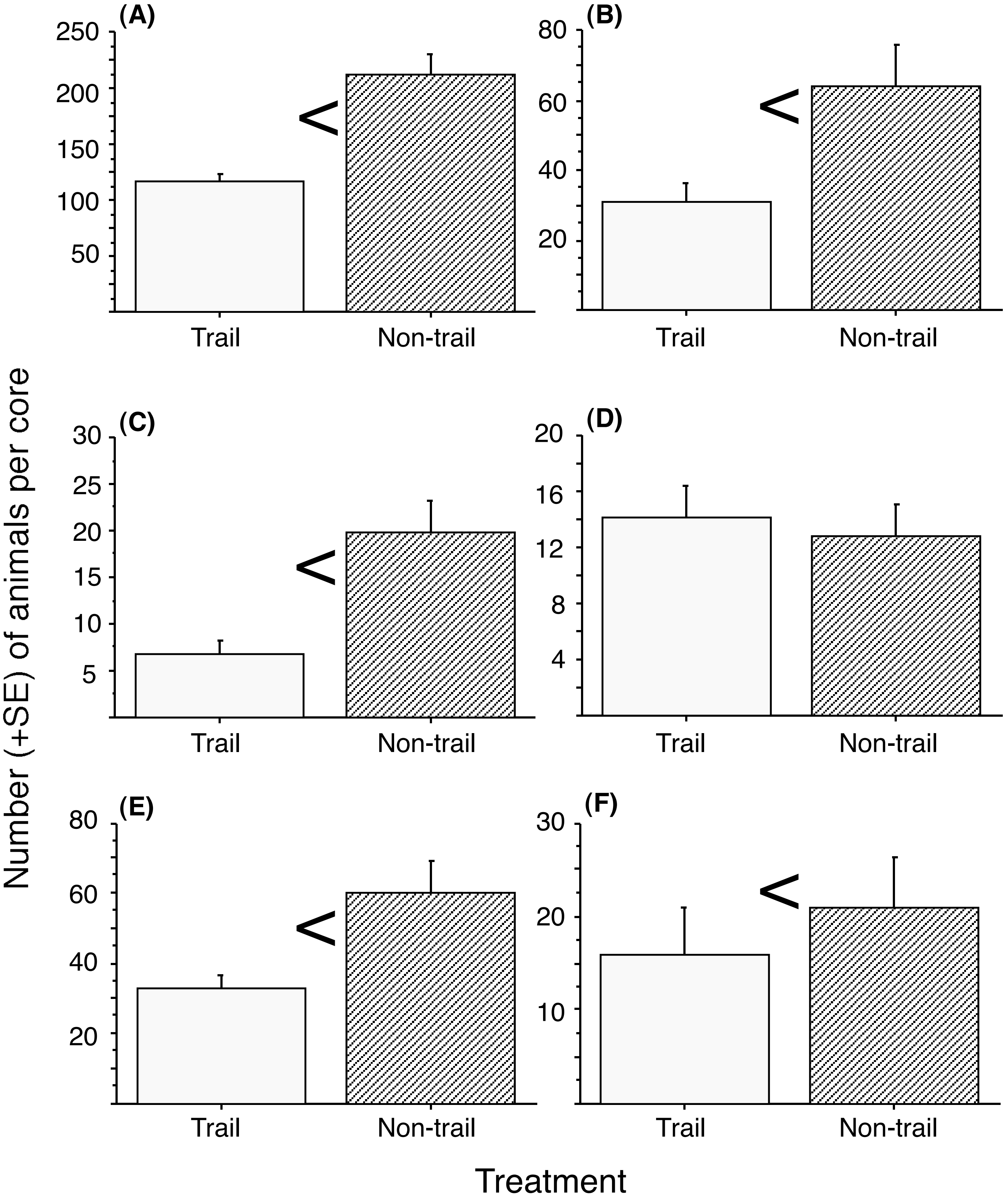


Figure 5.4: Mean (± SE) number of (A) all animals, (B) gammarid amphipods, (C) ostracods, (D) bivalves, (E) polychaetes and (F) nematodes, greater than 1 mm in size, in tracks recently grazed by dugongs (Trail) and nearby ungrazed patches of seagrass (Non-trail). N=9 cores for each treatment (3 replicate cores from each of 3 trails or ungrazed patches). > indicates significant difference between treatments after ANOVA (see text for further details).

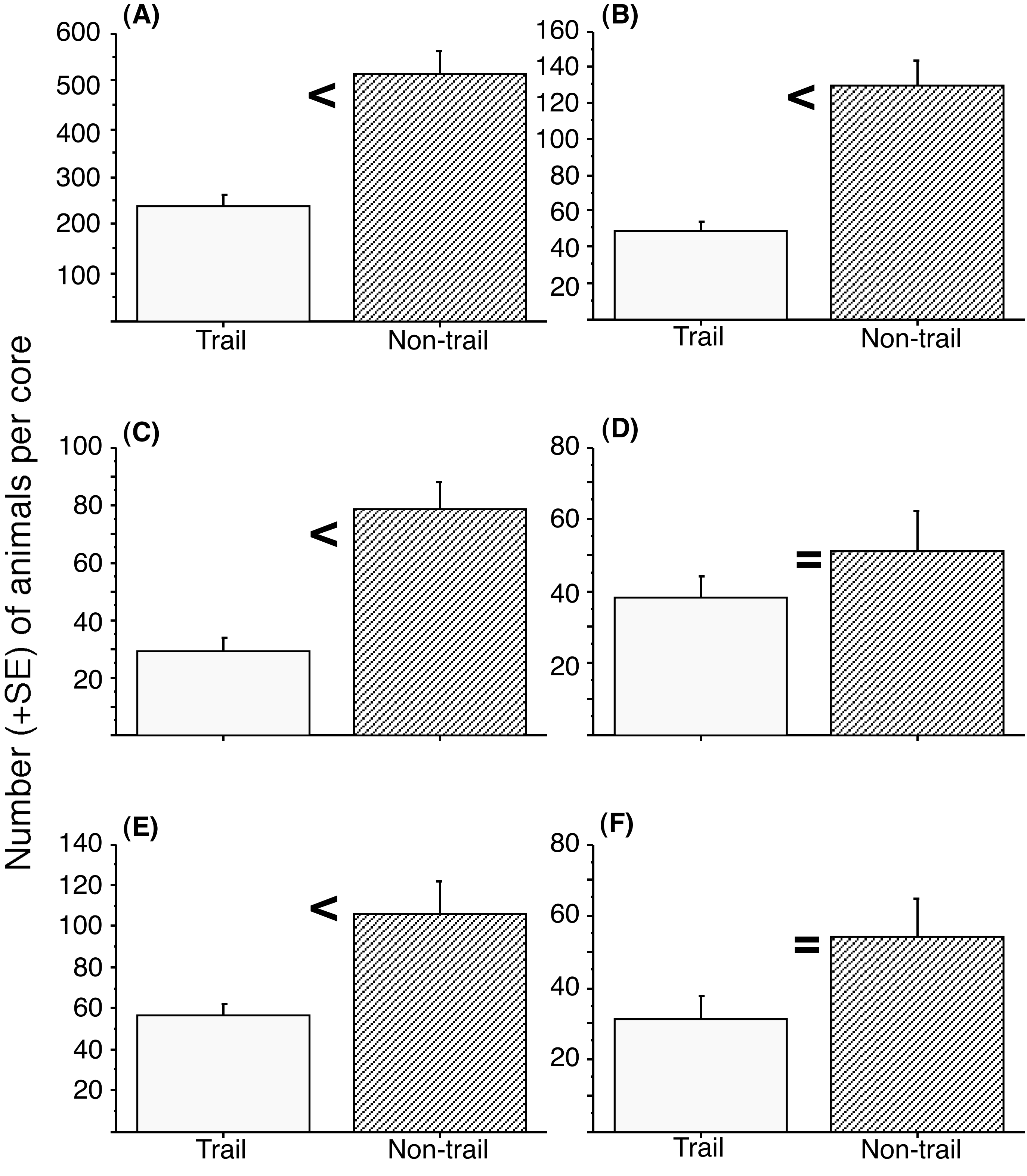


Figure 5.5: Mean (± SE) number of (A) all animals, (B) gammarid amphipods, (C) ostracods, (D) bivalves, (E) polychaetes and (F) nematodes, greater than 500 μm in size, in tracks recently grazed by dugongs (Trail) and nearby ungrazed patches of seagrass (Non-trail). N=9 cores for each treatment (3 replicate cores from each of 3 trails or ungrazed patches).
< indicates significant difference between treatments, = indicates no significant difference between treatments after ANOVA (see text for further details).

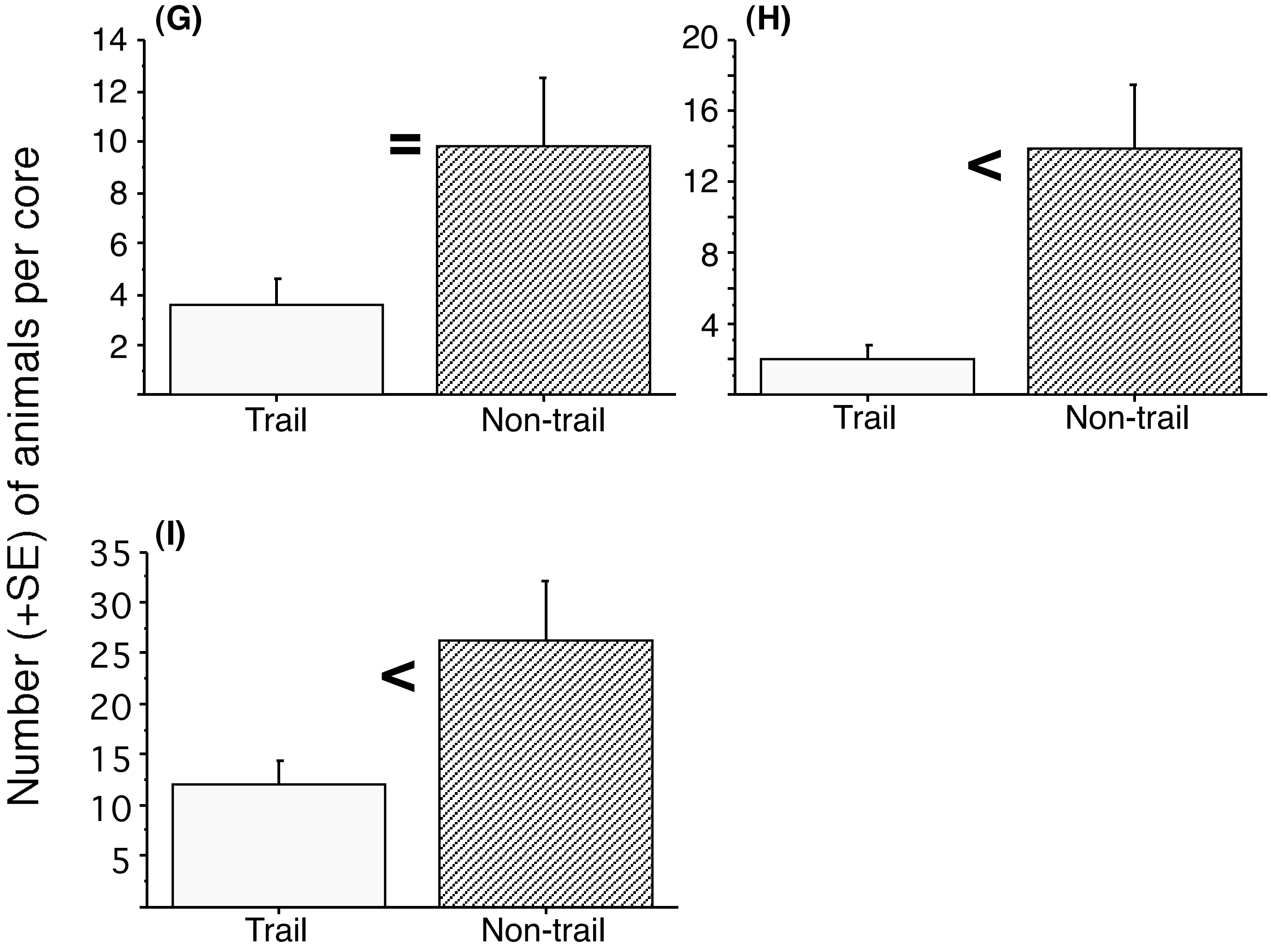


Figure 5.5 continued: Mean (± SE) number of (G) cumaceans, (H) tanaids and (I) gastropods, greater than 500 μm in size, in tracks recently grazed by dugongs (Trail) and nearby ungrazed patches of seagrass (Non-trail). N=9 cores for each treatment (3 replicate cores from each of 3 trails or ungrazed patches). < indicates significant difference between treatments, = indicates no significant difference between treatments after ANOVA (see text for further details).

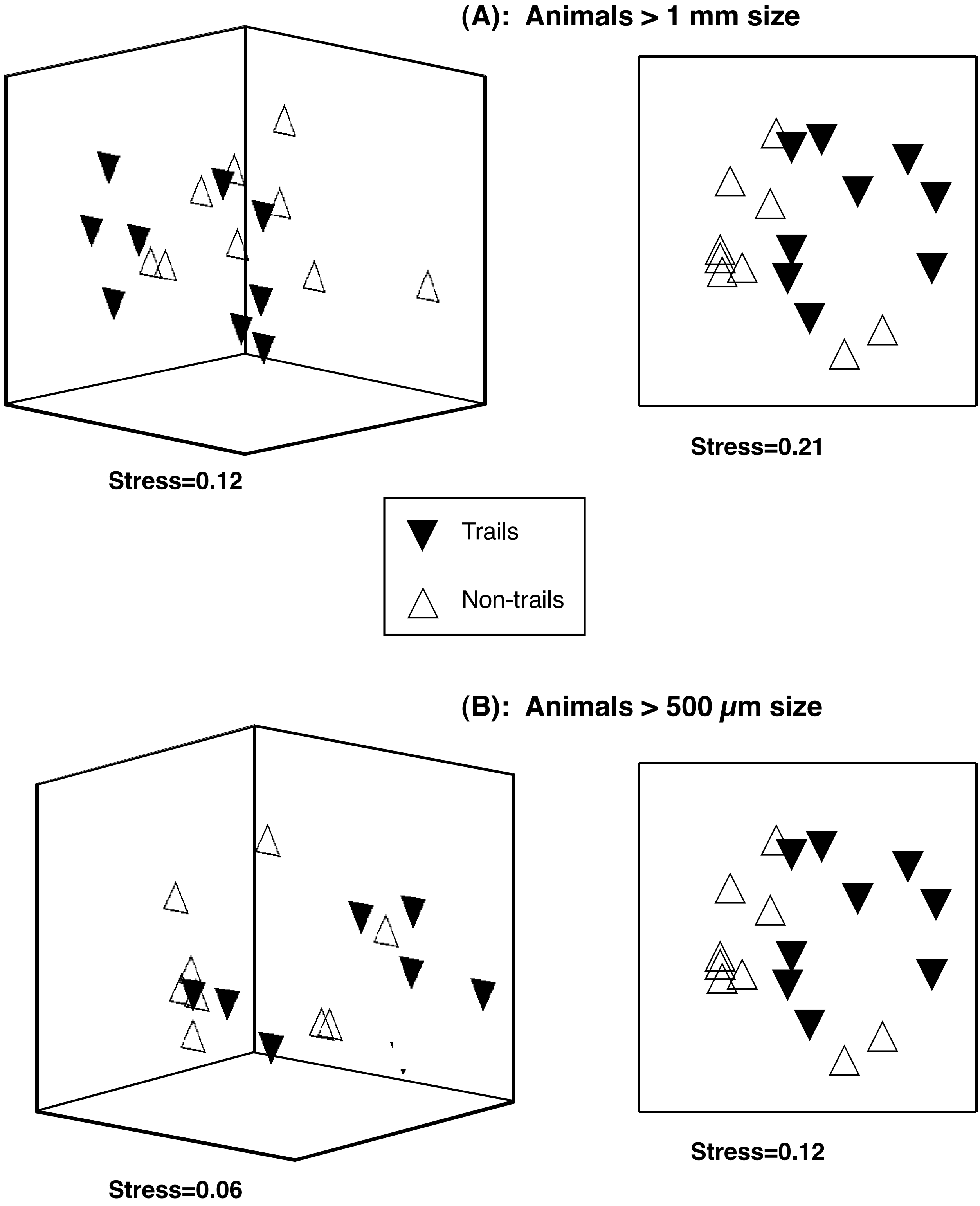


Figure 5.6: nMDS ordinations on forth root transformed abundance data for (A) animals > 1mm size and (B) animals > 500 μm size from cores taken within grazed areas (Trails) and ungrazed areas (Non-trails). There were n=3 replicates from each of three plots in the Trail and Non-trail areas.

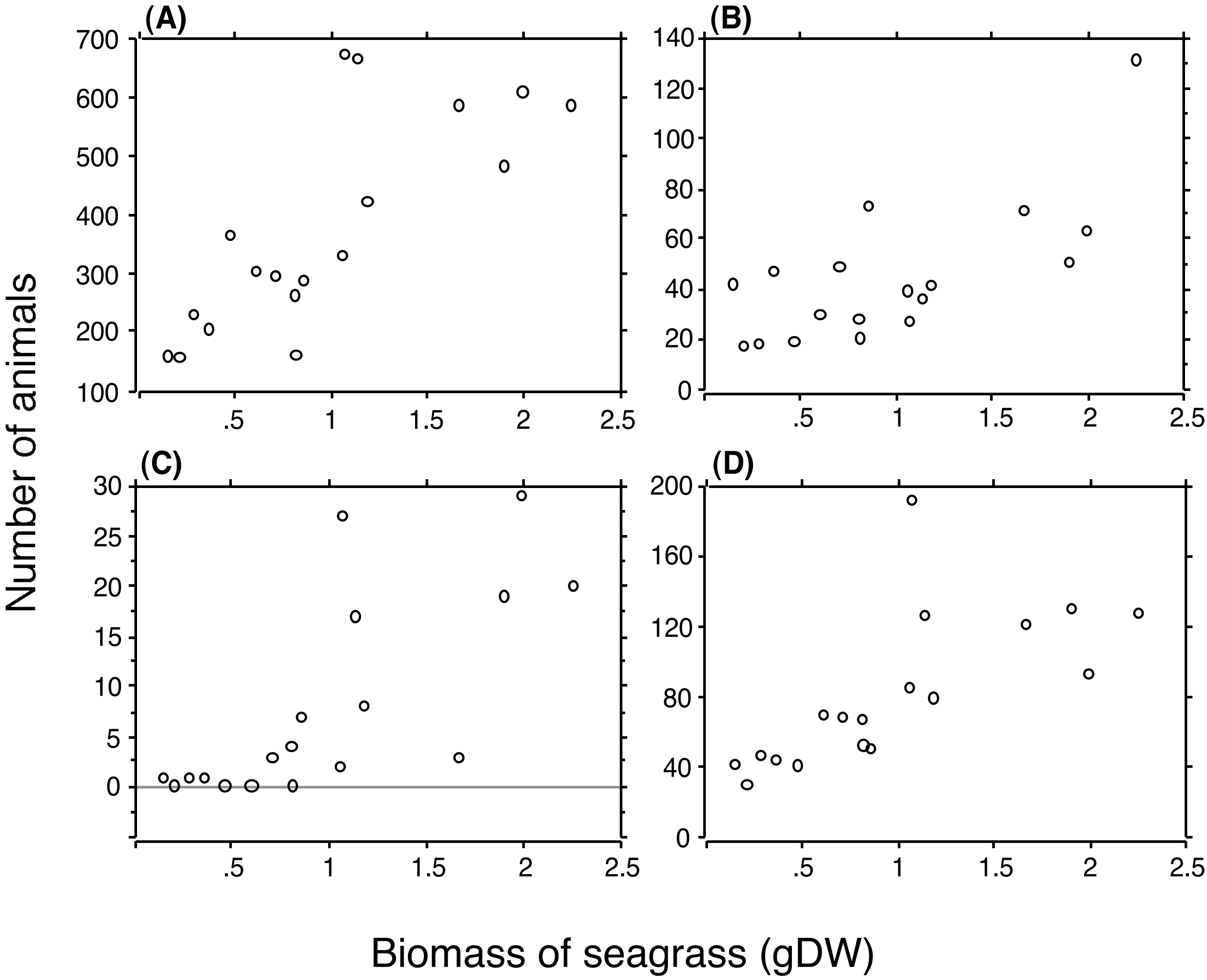


Figure 5.7: Scatter plots showing the correlations between the abundance of different taxa and the biomass of seagrass in samples collected inside and outside of dugong grazing trails. N=18 for each plot (9 samples from trails and 9 samples from non-trails). (A) total number of individuals; (B) number of bivalves; (C) number of tanaids; (D) number of polychaetes.

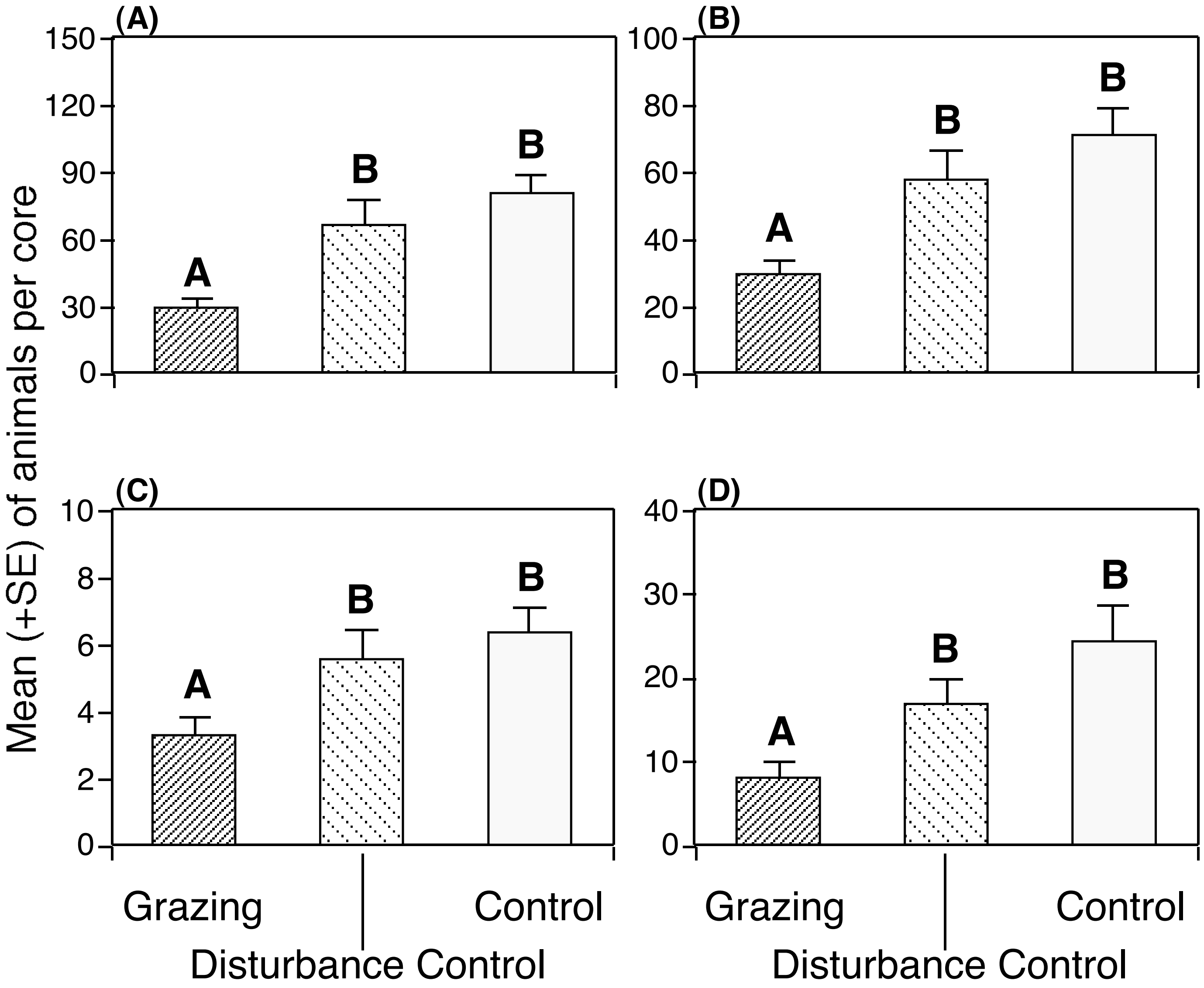


Figure 5.8: Mean (+SE) number of (A) gammarid amphipods, (B) gastropods, (C) capitellid polychaetes and (D) opheliid polychaetes (>500 μm) significantly affected by the experimental reduction of seagrass biomass. Three treatments were examined: 4 m^2 plots where the biomass of seagrass was reduced (Grazing), seagrass and sediments were disturbed (Disturbance Control) or unmanipulated (Control). N=18 cores pooled across 3 plots x 2 times. Data were transformed to $\log_e(x+1)$ to stabilise variances after Cochran's tests.

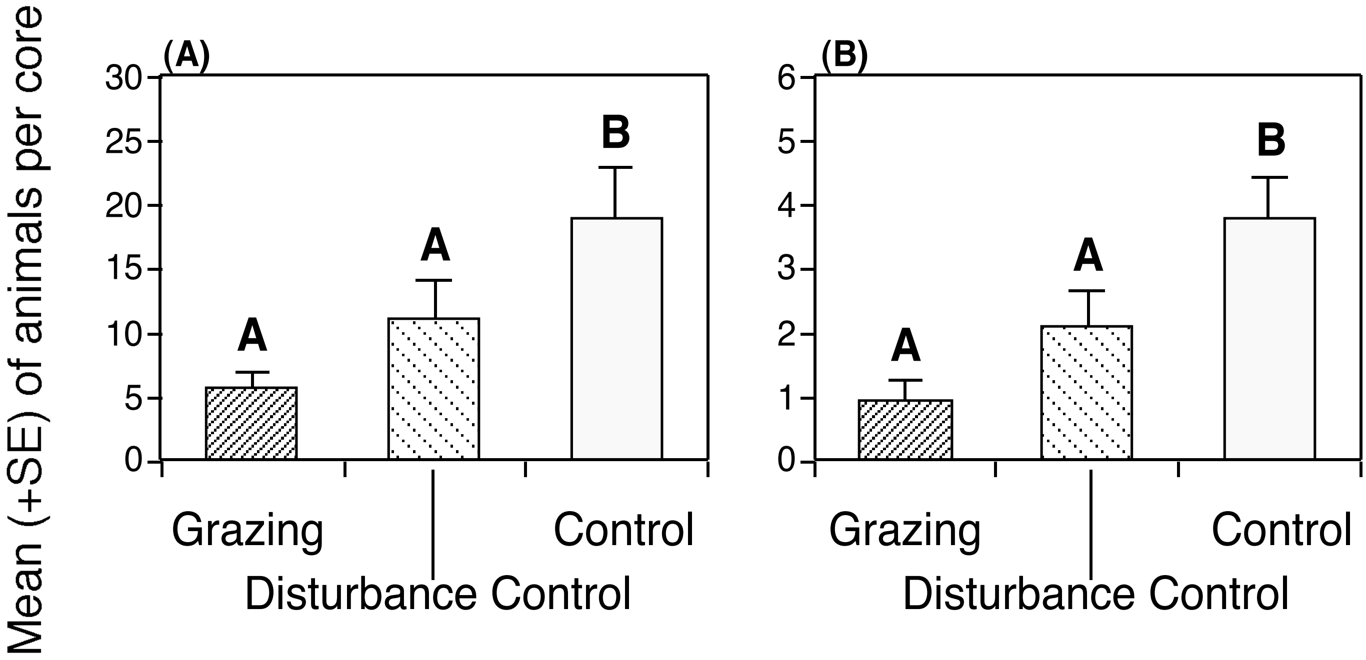


Figure 5.9: Mean (+SE) number of (A) copepods and (B) terebelillid polychaete (>500 μm) which were significantly affected by the experimental disturbance in seagrass and sediments. Other details as in Figure 5.8.

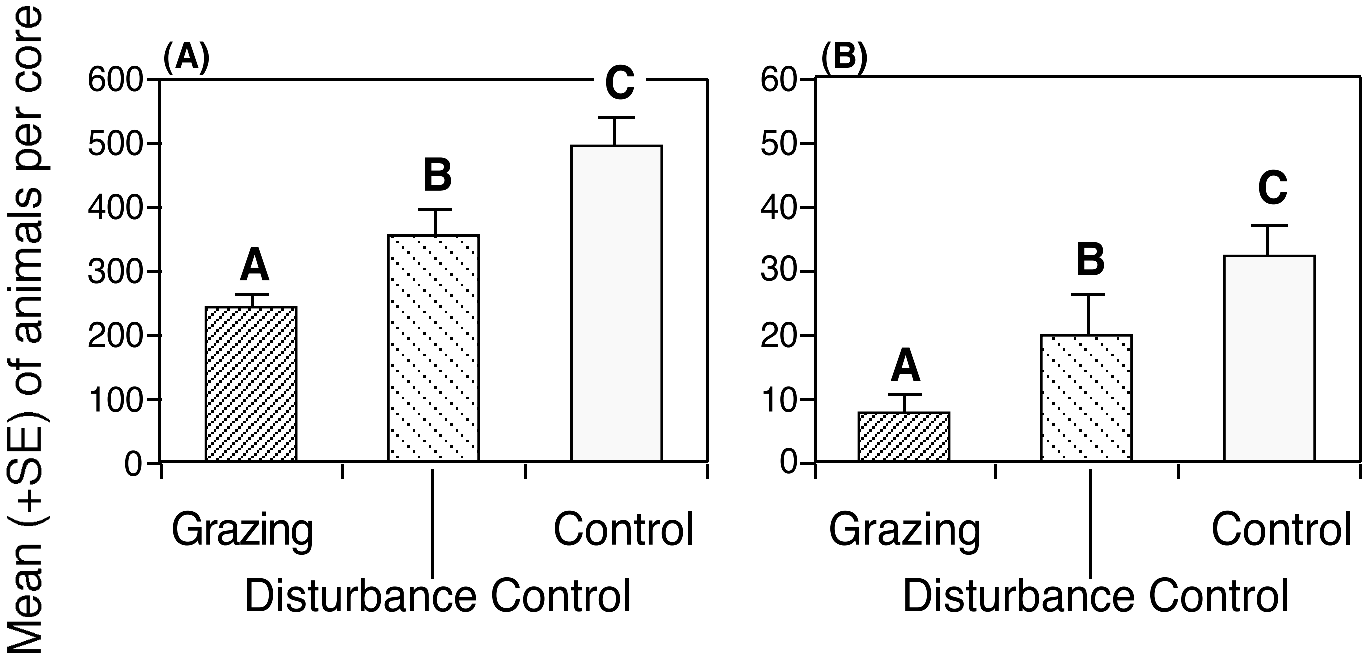


Figure 5.10: Mean (+SE) number of (A) individuals and (B) tanaids (>500 μm) which were significantly affected by the experimental reduction of seagrass biomass and by the disturbance to seagrass and sediments. Other details as in Figure 5.8.

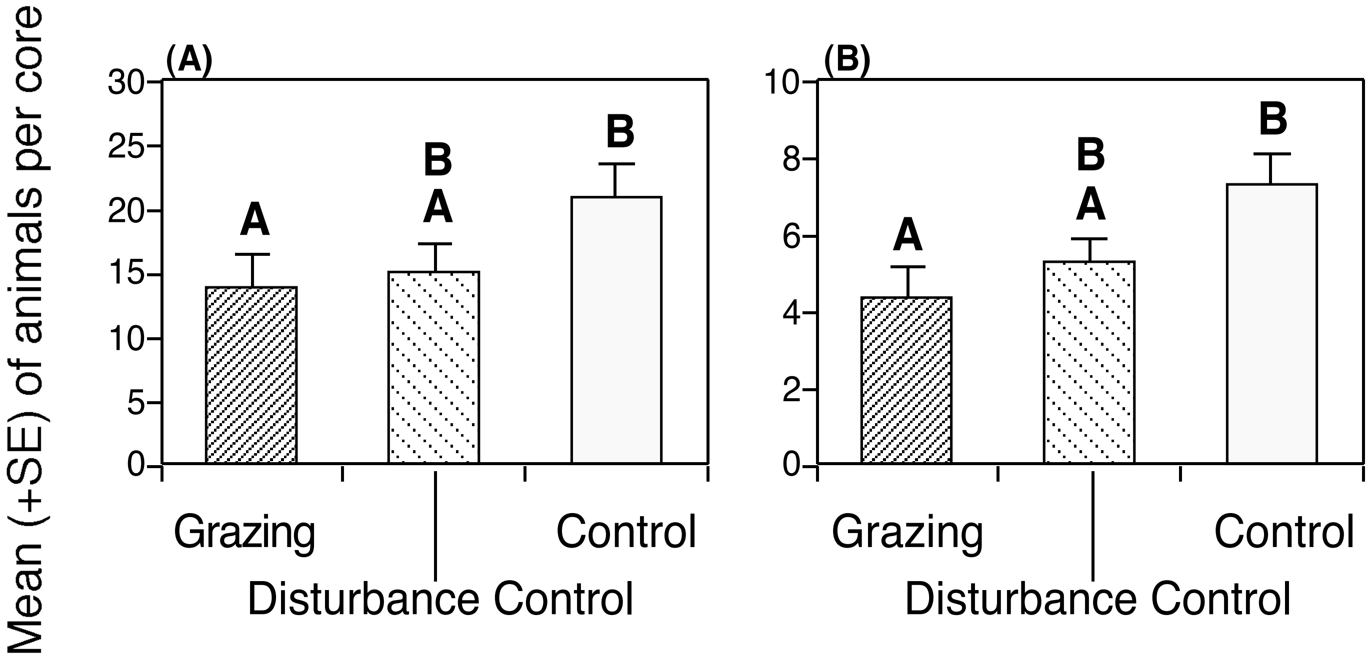


Figure 5.11: Mean (+SE) number of (A) bivalves and (B) sabellid polychaetes (>500 μm) which were significantly affected by either the experimental reduction of seagrass biomass or by the disturbance to seagrass and sediments, but specific patterns were unclear in the analyses. Other details as in Figure 5.8.

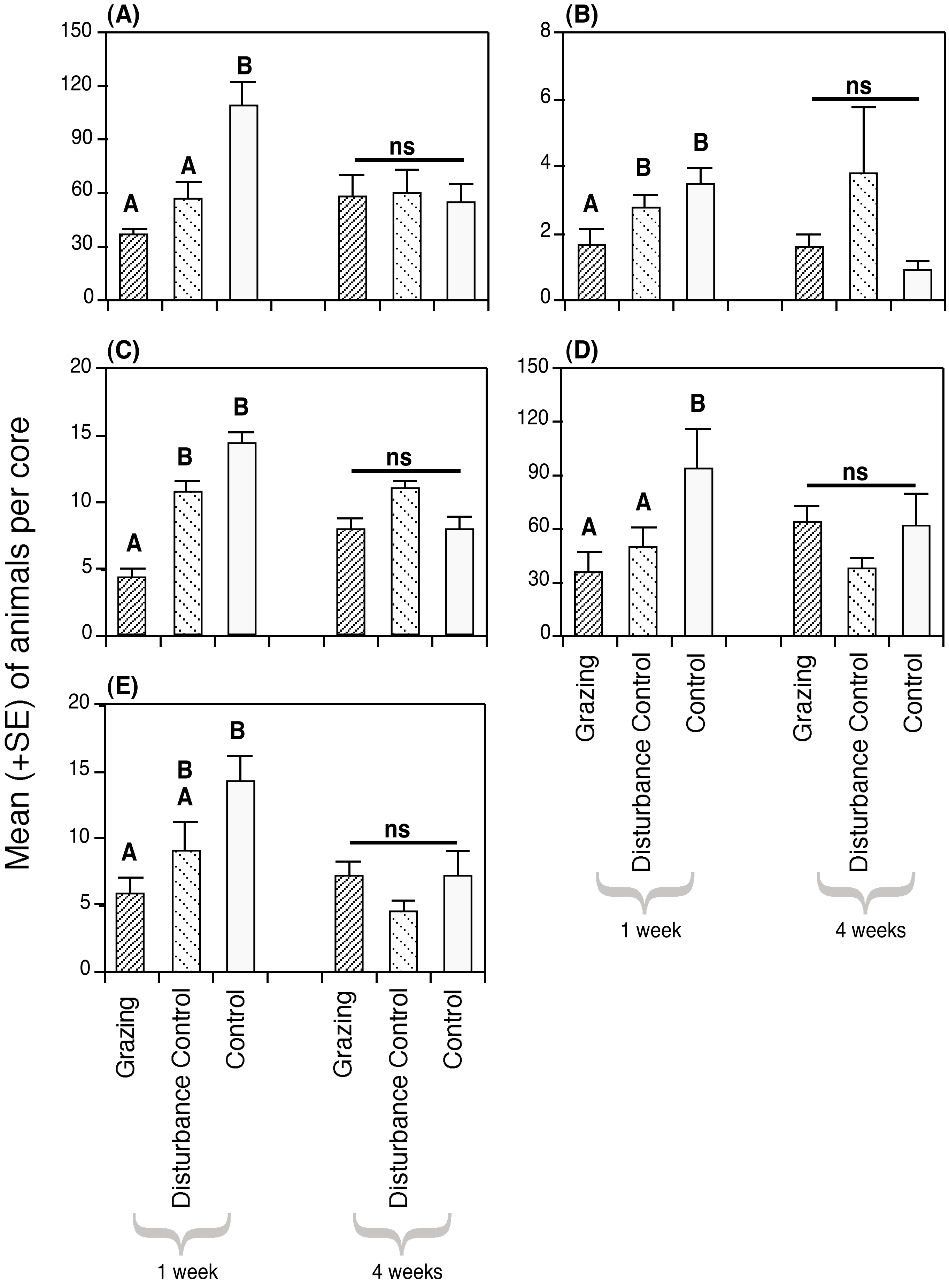


Figure 5.12: Mean (+SE) number of (A) ostracods, (b) nereidid polychaetes, (C) syllid polychaetes (D) nematodes and (E) nemerteans (>500 μm) all of which showed a significant short-term (1 week) response to either the experimental reduction of seagrass biomass or by the disturbance to seagrass and sediments but any effect had gone after 4 weeks. Other details as in Figure 5.8.

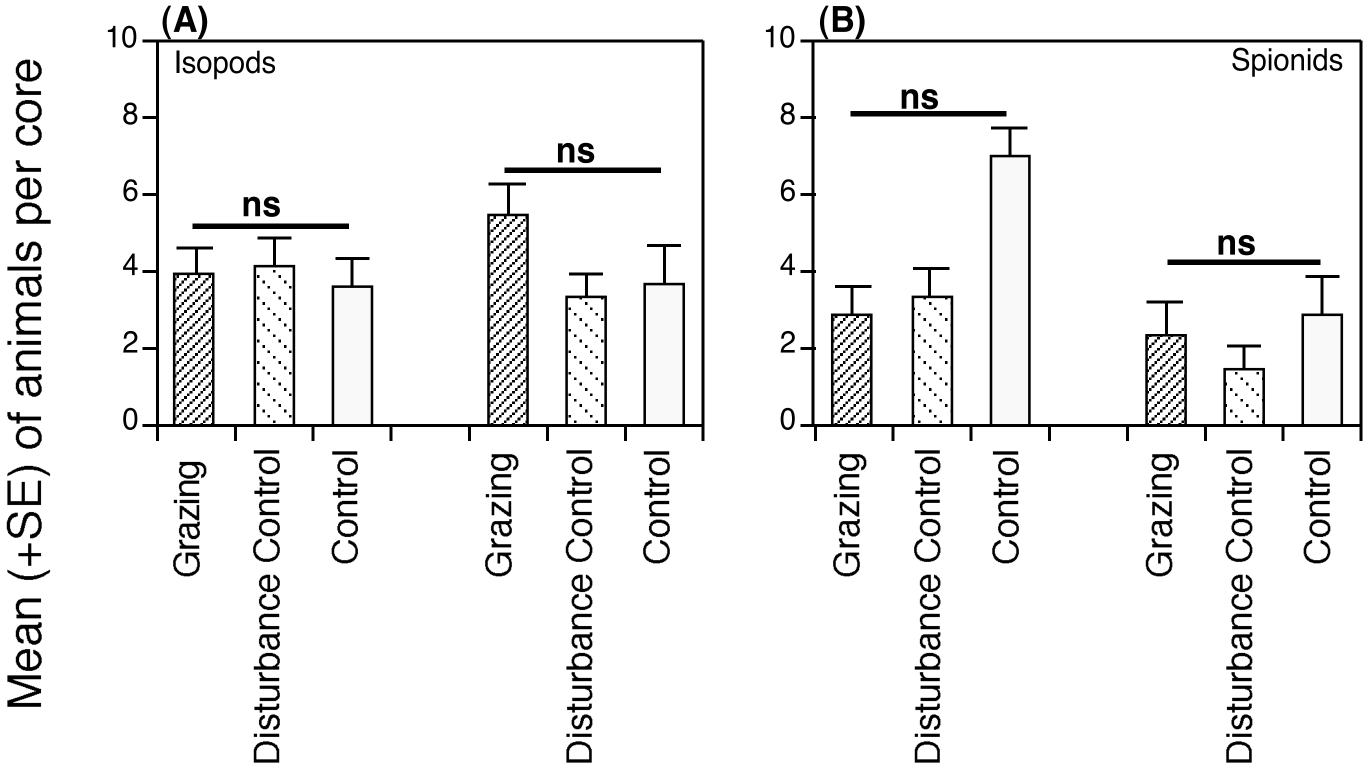


Figure 5.13: Mean (+SE) number of (A) isopods and (B) spionid polychaetes (>500 μm) which did not show a significant response to either the experimental reduction of seagrass biomass or by the disturbance to seagrass and sediments. Other details as in Figure 5.8.

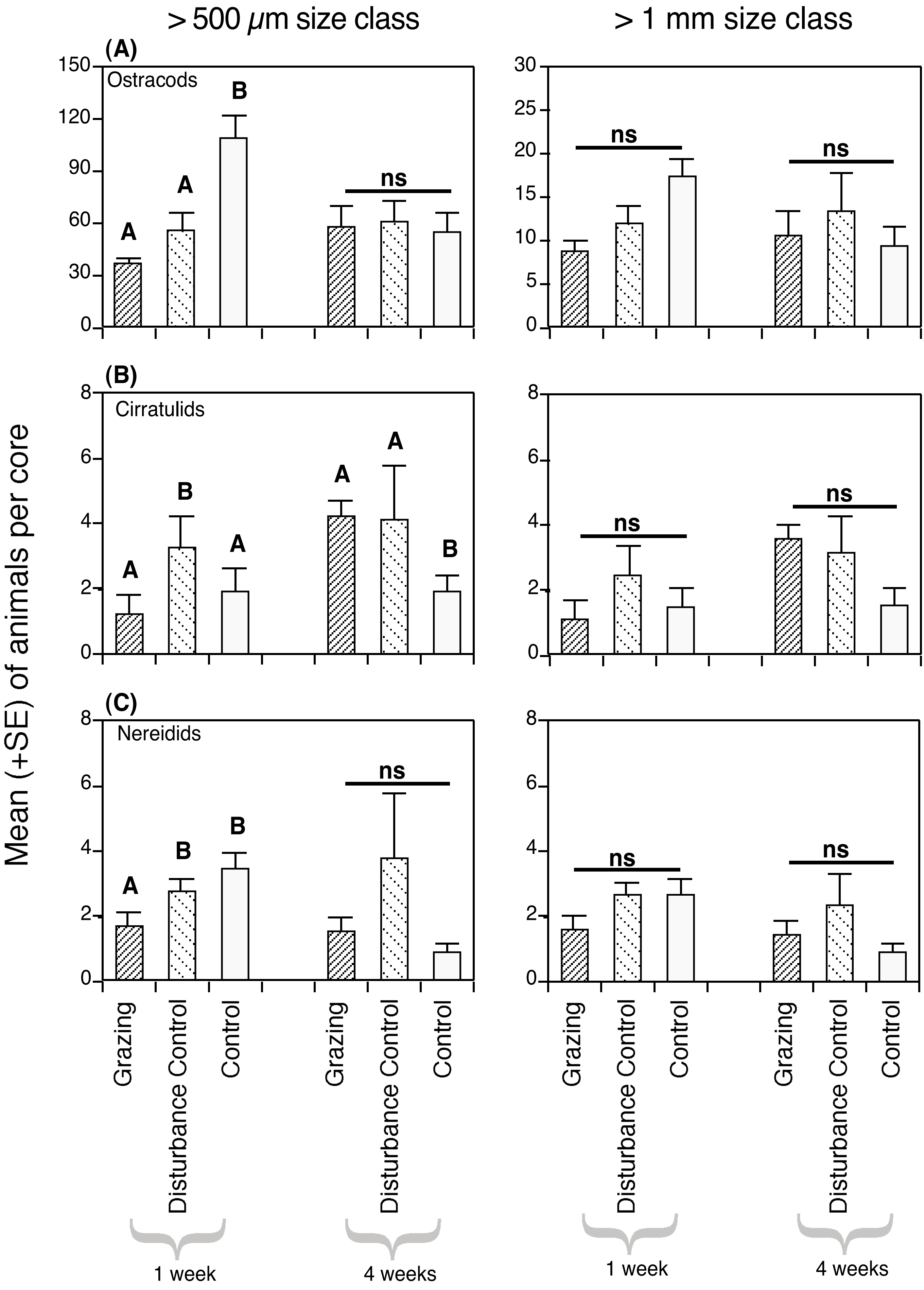


Figure 5.14: Mean (±SE) abundance of (A) ostracods, (B) cirratulid polychaetes and (C) nereidid polychaetes where the interpretation of analytical results varied between the two size classes (>500μm and >1mm) at Site A. Other details as in Figure 5.8.

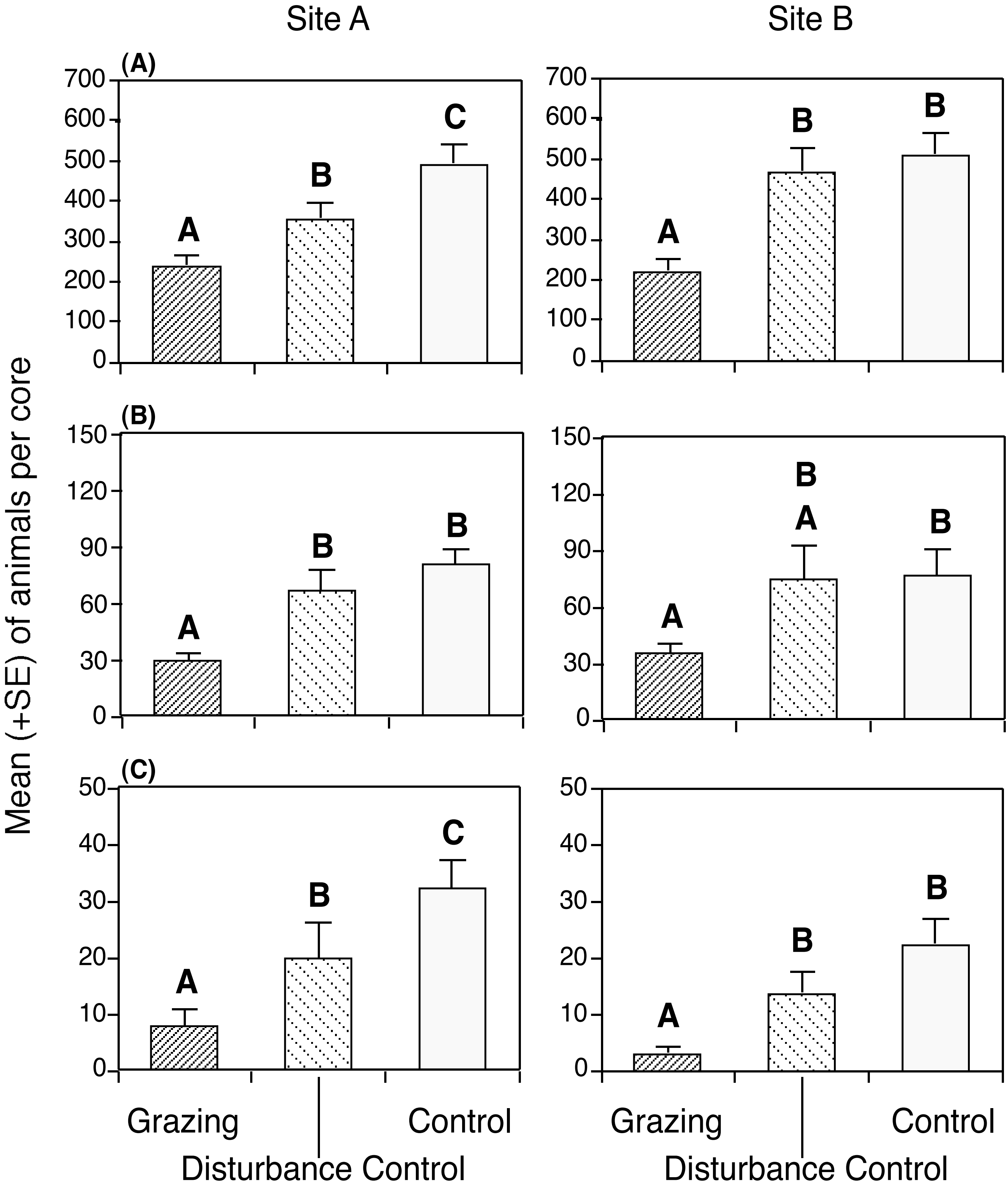


Figure 5.15: Mean (±SE) abundance of (A) individuals, (B) gammarids and (C) tanaids where the interpretation of analytical results varied between the two different sites. Other details as in Figure 5.8.

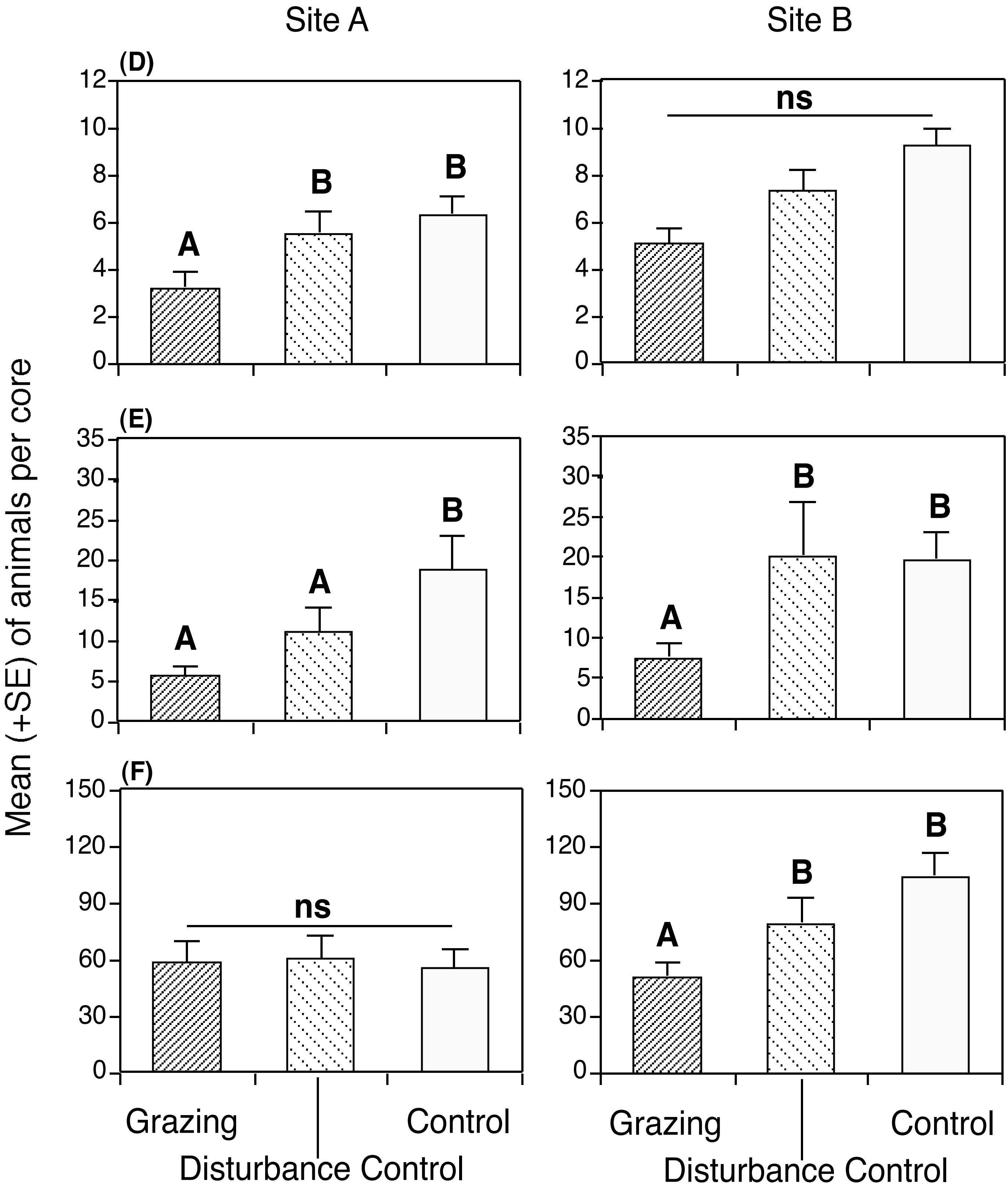


Figure 5.15 continued: Mean (±SE) abundance of (D) capitellid polychaetes, (E) copepods and (F) ostracods where the interpretation of analytical results varied between the two different sites. Other details as in Figure 5.8.

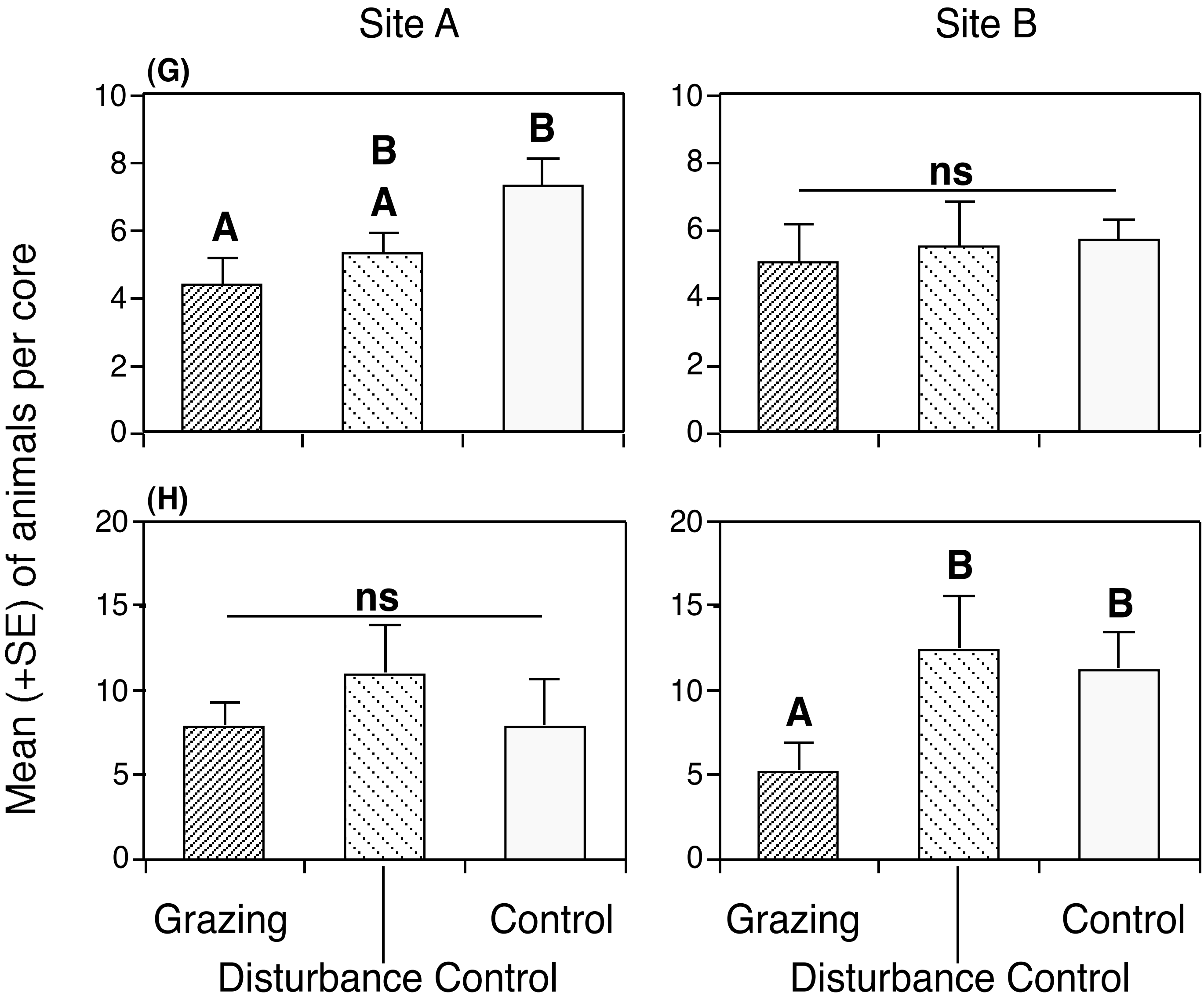


Figure 5.15 continued: Mean (±SE) abundance of (I) sabellid polychaetes and (H) syllid polychaetes where the interpretation of analytical results varied between the two different sites. Other details as in Figure 5.8.

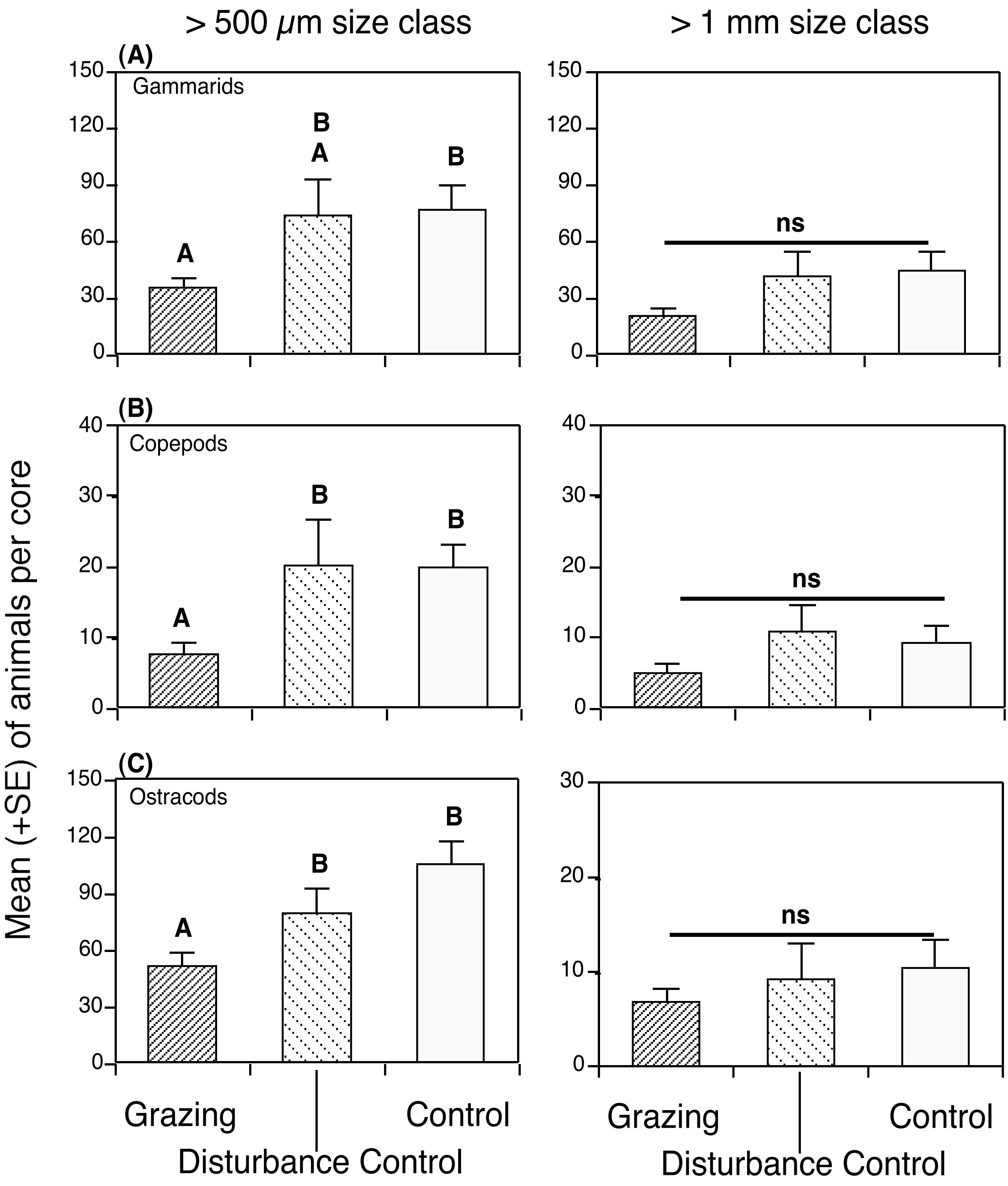


Figure 5.16: Mean (±SE) abundance of (A) gammarid amphipods, (B) copepods and (C) ostracods where the interpretation of analytical results varied between the two size classes (>500μm and >1mm) at Site B. Other details as in Figure 5.8.

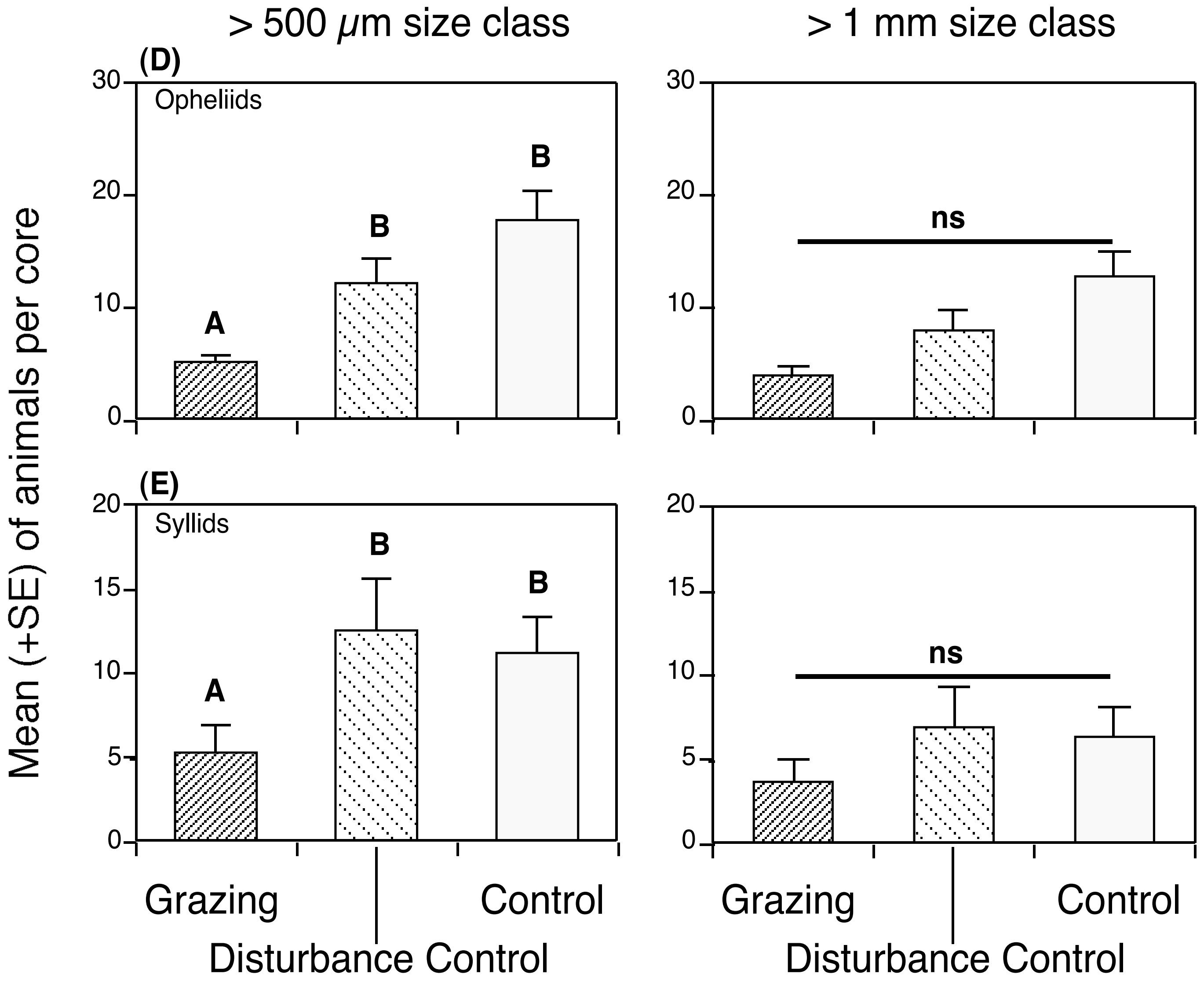
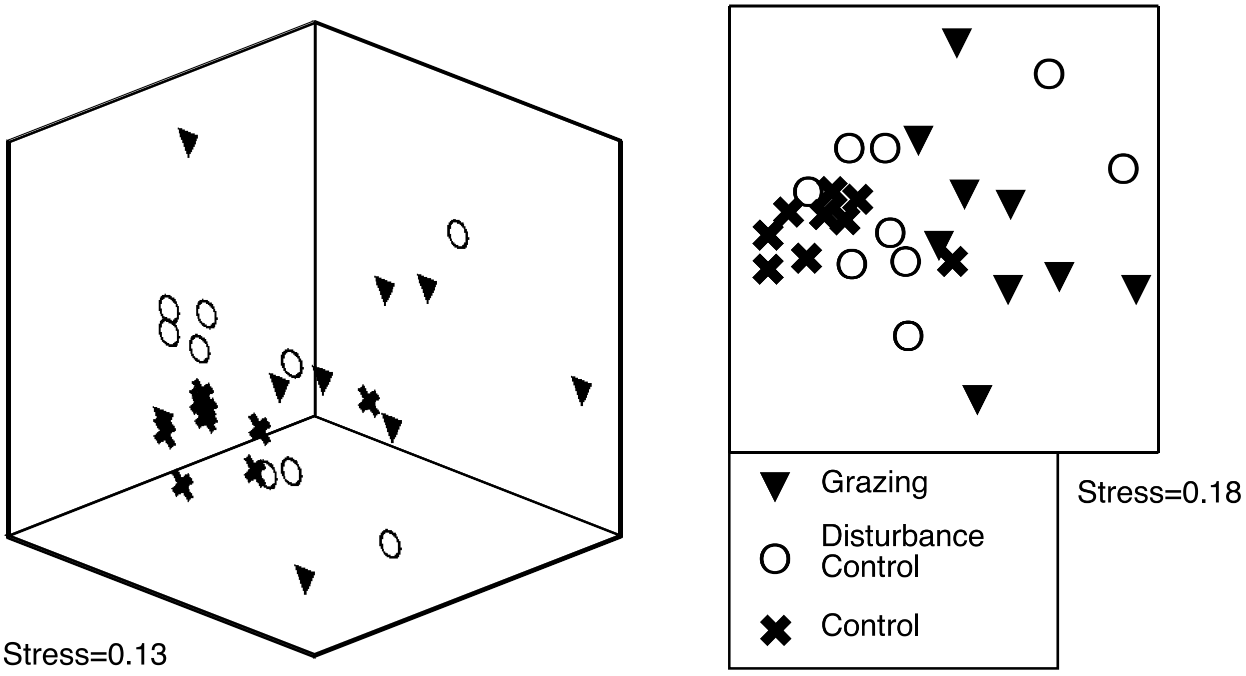


Figure 5.16 continued: Mean (±SE) abundance of (D) opheliid polychaetes and (E) syllid polychaetes where the interpretation of analytical results varied between the two size classes (>500μm and >1mm) at Site B. Other details as in Figure 5.8.

(A) Site A, 1 week after start of experiment



(B) Site A, 4 weeks after start of experiment

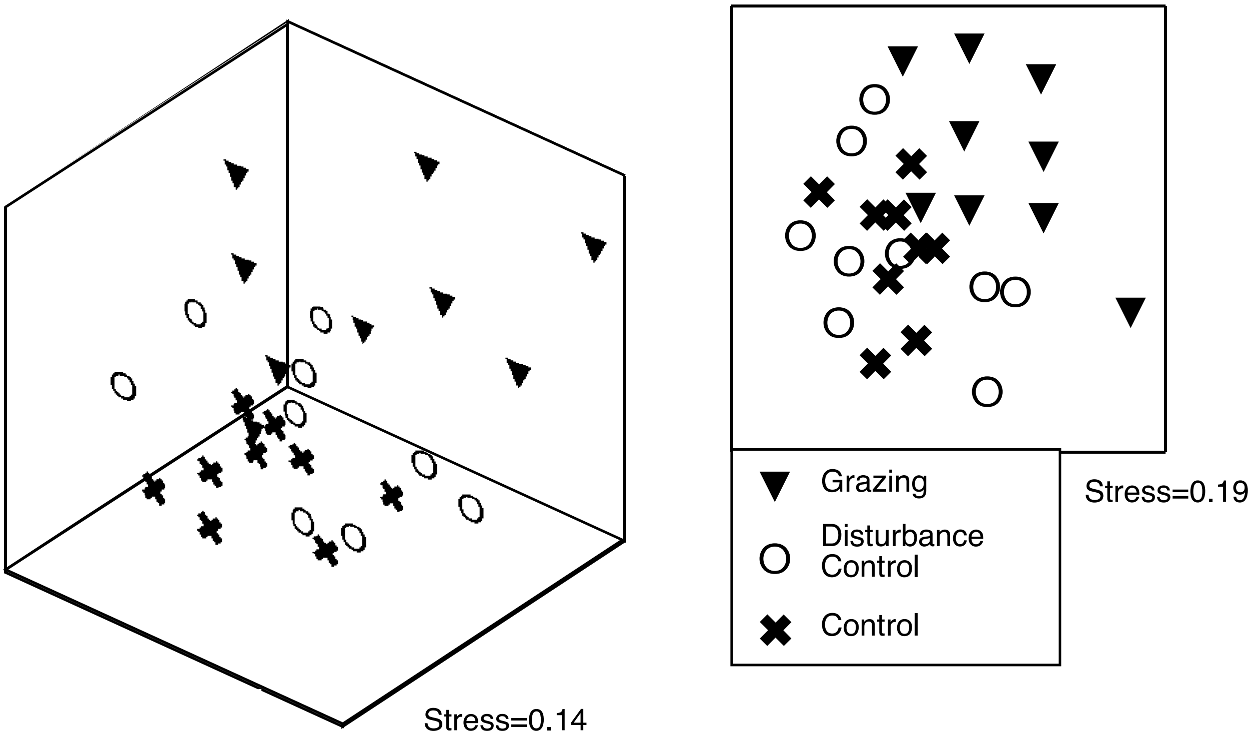


Figure 5.17: nMDS ordinations on fourth root transformed data for the abundance of macrofauna in plots from three experimental treatments (grazed, disturbance control and control) at Site A, 1 and 4 weeks since the application of the treatments. Data are for 3 replicates from each of 3 plots per treatment.

Section 6: Implications of Harvesting for Higher Trophic Levels-Migratory Shorebirds

6.1. Preamble

Intensive harvesting of intertidal invertebrates for use as bait may lead to the depletion of the population levels of the targeted species and/or indirect effects on other organisms that live in the same habitats (see previous sections). These indirect effects could include impacts on organisms at higher trophic levels which are dependent on benthic animals as prey.

Many estuarine intertidal areas, including those that are used heavily for bait-harvesting, provide staging and/or overwintering grounds for millions of Holarctic breeding shorebirds (e.g. Bay of Fundy in North America and the Dutch Wadden Sea in Western Europe; Smit, 1984a, b; Hicklin, 1987). Large-scale human use, modification and alteration of intertidal areas may have direct and indirect effects on populations of shorebirds utilising these sites for feeding. There has been some work on this problem in northern temperate areas. Shepherd (1994) found that the collection of bait in the Bay of Fundy led to a 20% decline in the size of populations of bloodworms (*Glycera dibranchiata*) and there was an associated significant decline in the rate of prey capture of the black-bellied plover (*Pluvialis squatarola*) that primarily feeds on this polychaete. Loss of habitat or a reduction in the quality of a habitat as a staging/wintering area may also lead to a decrease in the winter survivorship of shorebirds. The widespread decline in populations of migratory North American passerines has been partly attributed to the removal of large areas of habitat in their tropical wintering grounds (Askins et al., 1990; Rappole and McDonald, 1994).

It is not only intertidal areas in the northern hemisphere that are important for migratory shorebirds. Many wintering and staging grounds important for migratory waders lie south of the equator (Hockey et al., 1992; Tulp and de Goeij, 1994). As is the case in the north, many of these southern hemisphere intertidal areas occur close to human population centres and are frequently used for the collection of bait. There is little information though on the influence of bait-harvesting on shorebird populations utilising southern hemisphere wintering and staging areas.

Moreton Bay is presently recognised as the 11th most important site for waders in Australia (Lane, 1987; Thompson, 1990). During the austral summer and migration period, sites around Moreton Bay are known to accommodate in excess of 50,000 waders (Thompson, 1992) including between 20 and 40% of the total population of Far Eastern Curlew in Australia (Watkins, 1993; Congdon and Catterall, 1994). Some other long-distance migrants also reach large numbers in Moreton Bay, including the Grey-tailed Tattler (approximately 22,000 animals), Bar-tailed Godwit (~10,000 animals) and Red Knot (~5000 animals).

Many of the medium to large sized Holarctic waders wintering in Australia are thought to cross the Western Pacific in a single giant leap (Tulp and de Goeij, 1994). No intermediate staging grounds are used. A number of key intertidal areas in Australia may, therefore, be of critical importance to the shorebirds allowing them to accumulate energy reserves before their northward migration. Shorebirds exploiting food resources of intertidal areas may be affected by bait-harvesting if their food base is undermined due to direct and indirect impacts associated with bait-harvesting. Such a situation may arise if the collection of yabbies for bait leads directly or indirectly to changes in the availability or accessibility of prey used as food by the shorebirds.

A large-scale experimental manipulation of the abundance of yabbies was begun on the 15th October, 1998 to determine whether the direct and indirect effects of bait-harvesting affected the abundance and size-structure of populations of *Trypaea australiensis*, the abundance and composition of the remaining benthic macrofauna and the feeding activity and behaviour of migratory shorebirds. The primary goals of this component of the project were to: (i) determine the impact from harvesting of yabbies from intertidal mudflats on the abundance and size-structure of the yabbies; (ii) determine the impact of harvesting of yabbies on other benthic macrofauna in the sediments, particularly those species which are preyed on by migratory shorebirds; and (iii) determine the impact of yabby harvesting on shorebird feeding rates using the Bar-tailed Godwit and Far Eastern Curlew as model species. The results for goals (i) and (ii) are presented in earlier sections. The specific effects on foraging of migratory shorebirds are presented and discussed here as two separate sections, the first dealing with bar-tailed godwits, the second with Far-eastern curlews.

Depletion of benthic invertebrates by bar-tailed godwits *Limosa lapponica* in a subtropical estuary

(Mar. Ecol. Prog. Ser. (2003), Vol. 254: pp. 151-162)

6.2. Introduction

Local densities and intake rates of shorebirds (Charadrii) spending the non-breeding season on intertidal flats and estuaries are determined primarily by the instantaneously available stock of benthic prey (Goss-Custard, 1984; Piersma, 1987). However, during a non-breeding season intake rates can be reduced by at least three factors, that, when they operate over a large area, may eventually lead to shorebirds' starvation and/or emigration from a wintering site. These factors are (i) interference competition among foraging birds (e.g. Goss-Custard et al., 1984; Triplet et al., 1999), (ii) deterioration of the nutritional value of individual prey items (e.g. Zwarts & Wanink, 1993; Zwarts & Ens, 1999) and (iii) depletion of the available prey stocks (e.g. Goss-Custard et al. ,1996; Zwarts et al., 1996).

Prey depletion by wintering shorebirds has received much attention over the past two decades and is known to depend on a range of factors including initial prey and predator densities, predator residency period and prey (re)production (reviewed by Székely & Bamberger, 1992; Meire et al., 1994; Zwarts & Ens, 1999; van der Meer et al., 2001). Wolff & Smit (1990) and Wolff (1991) compared prey exploitation by shorebirds between two of the most important wintering areas along the East Atlantic Flyway, the temperate Wadden Sea (54° N) and subtropical Banc d'Arguin (19° N). The authors estimated that shorebirds remove annually 17% of the standing stock of benthos in the former and 83 – 133% in the latter. They argued that annual predictability of the food supply in the north temperate estuaries is low (e.g. Zwarts et al., 1992; Zwarts & Wanink, 1993; Beukema et al., 1993; but see Beukema et al., 2001) because of frequent stochastic mortality of benthos (e.g. due to severe winters, Camphuysen et al., 1996), absence of reproduction in the winter and irregular recruitment. Consequently, food available to shorebirds may be plentiful in some years but scarce in others (Meire et al., 1994; Zwarts & Ens, 1999). Thus, shorebird populations may be maintained via e.g. density-dependent mortality mechanisms at such levels so as to not overexploit food stocks in poor years (e.g. Wolff, 1991). In this case, on average, consumption by shorebirds should be independent from benthic production (or the initially available prey stock) (e.g. Fig. 15.5 in van der Meer et al., 2001). In other words, the 'safety margin' between shorebird consumption and benthic production (or the standing stock at the onset of a non-breeding season) has to be high. On the local scale, at least at prime feeding sites because of the initially large prey stocks, shorebird intake rates can be independent of densities of their primary prey (e.g. Goss-Custard, 1977; Gill et al., 2001; Goss-Custard et al., 2001) unless a considerable proportion of the harvestable (sensu Zwarts & Wanink, 1993) fraction is removed (e.g. Goss-Custard et al., 2001) or dies off (e.g. Zwarts & Ens, 1999).

It has not been decisively resolved whether or not ecologically significant depletion of benthic prey by shorebirds over their residence period occurs at warm-climate non-breeding sites (e.g. Schneider, 1985; Kalejta, 1993; Mercier & McNeil, 1994). By contrast to the north temperate region, warm-climate wintering sites have more stable abiotic conditions, benthic (re)production during periods of intensive shorebird predation (Alongi ,1990; Kalejta & Hockey, 1991) and they also support higher shorebird densities (Summers, 1977; Zwarts et al., 1990; Hockey et al., 1992; Kalejta, 1993). Currently, these sites are hypothesised to allow for a higher level of exploitation of benthic stocks by the shorebirds and consequently, have relatively low standing benthic biomass densities (Wolff & Smit, 1990; Wolff, 1991; but see van der Meer et al., 2001). If the purported low ratio between the benthic stocks and shorebird consumption indeed exists in a warm-climate wintering area, a converse local scale foraging situation should be true. The intake rate achieved by an individual forager should be in the vicinity of the functional response gradient, i.e. it should be directly limited by the prey density throughout a non-breeding season.

Three lines of evidence can be used to test the hypothesis of the lower ratio between the benthic stock and shorebird predation pressure in warm climates as compared to the cold-climate wintering areas. (i) Initial benthic stocks and their depletion (exploitation level) over a non-breeding season can be compared. However, in the absence of data on long-term annual fluctuations in the benthic food supply, shorebird consumption (Kalejta & Hockey, 1991; Dittmann & Vargas, 2001) and the proportion of the standing stock that can actually be harvested by the birds in tropics/subtropics, such comparisons may be unreliable at present (Piersma et al., 1993a). (ii) Functional response curves can be measured directly (e.g. Gill et al., 2001) to determine if the rate of intake is indeed limited by the density of prey as would be expected in a predator – prey system with a quick turn-over of matter and energy. However, such responses are often difficult to measure in the field and our ability to predict the shape of a functional response curve from the generally available field data (e.g. prey type and size, handling time, forager density) is currently limited (Ens et al., 1994). (iii) The third line of evidence can come from experiments manipulating prey densities in the field (e.g. Cummings et al., 1997). This approach uses a converse logic as compared to (ii).

Specifically, if the rate of intake is in the vicinity of the gradient of a functional response curve, then depleting food densities in the field should negatively affect intake rates or lead to emigration of predators from the impacted areas. This is the approach taken in this study, although data pertinent to points (i) and (ii) have also been collected and are presented.

In this study numerical (density) and functional (capture rate and feeding success) responses of bar-tailed godwits *Limosa lapponica* to changes in prey densities were studied in a manipulative field experiment conducted at a spatial scale roughly corresponding to the local scale of movements of the birds (e.g. Cummings et al., 1997; Chamberlain & Fuller, 1999). Sediment disturbance due to manual removal of the callianassid shrimp *Trypaea australiensis* (see Section 2) resulted in a decrease in densities of several other benthic organisms that constitute the bulk of diet of the godwit. It was predicted that if the intake rate is limited by the density of prey available to the birds, a reduction in prey density will cause rapid numeric (emigration out of the impacted plots) and functional (decrease in capture rate and/or foraging success) responses by the birds.

6.3. Methods

6.3.1. Study area

The study was carried out on the western shore of North Stradbroke Island, Moreton Bay, Queensland, Australia (27°25'S, 153°25'E) between October 1998 and November 1999 (Figure 6.1). Moreton Bay is a large estuarine system with semidiurnal tides exposing the intertidal area on average for 5.5 to 6.5 hours per low tide. Moreton Bay supports up to 80,000 wintering shorebirds including more than 20,000 bar-tailed godwits (Thompson, 1990a). The study area is known to support godwit densities considerably higher than elsewhere in the Bay (Thompson 1990b) and thus can be considered a “preferred site”. This minimised the chance of obtaining a significant relationship between foraging rates and prey densities by virtue of sampling at a site with already poor feeding conditions (e.g. Goss-Custard et al., 1984). The intertidal flats on the western (estuarine) side of the island are characterised by three broad zones: a mangrove fringe along the upper shore (primarily Avicennia marina), an essentially unvegetated mid-intertidal zone and extensive seagrass (*Zostera capricorni, Halophila ovalis*, and *Syringodium isoetifolium*) beds along the lower intertidal zone.

All experimental manipulations and observations of godwits were done in the middle (unvegetated) sandy zone of the intertidal. The substratum in the study area consists of fine sand (mean grain size 0.204 mm) with small (2%) silt (grain size < 0.063 mm) fraction and it has a micro-relief of intermingling elevated ridges and pools (Thompson, 1992). The possible affect of manipulations on sediment grain size was not investigated because the size of the prey normally consumed by the godwits was considerable larger than the sediment grain size (cf. Quammen, 1982). Therefore, no confounding effect on godwit foraging efficiency was anticipated.

6.3.2. Experimental manipulations and assessment of the densities of benthos

Mechanical perturbation of soft sediments inevitably leads to significant amounts of disturbance with effects on the associated infauna (e.g. Skilleter, 1996). At larger scales, artificial removal of benthic invertebrates (e.g. for bait) has been shown to significantly reduce the abundance of non-target macrofauna (e.g. Wynberg & Branch, 1994; Ambrose et al., 1998). This study used the expected effects of sediment disturbance associated with harvesting of the burrow-dwelling callianassid shrimp *Trypaea australiensis* (McPhee & Skilleter, 2002) on non-target macrofauna (crabs, polychaetes and bivalves) to examine the responses of bar-tailed godwits, which rely on these smaller invertebrates as prey.

Six 100 x 100 m (1 ha) study plots were permanently marked with 40 cm long wooden stakes. The plots were located at the same tidal height along a visually uniform stretch of the mudflat without natural barriers. Adjacent plots were separated by 75 – 100 m. Three of the plots were designated at random for experimental manipulations involving direct removal of *Trypaea australiensis* using a hand-operated suction pump and the remaining three plots served as undisturbed controls, apart from sampling of benthic fauna. *Trypaea* removals were carried out in November 1998, January, March, May, June, July, September and December 1999. The procedure for harvesting *Trypaea* with a pump (a 0.70 m-long, 0.05 m-diameter tube with a handle and a plunger) is to push the unit into the substratum with visible *Trypaea* holes and extract the sediment, which is then dumped onto the substratum to collect animals. The pump is pushed into the substratum at the same point several times, after which the harvester begins the process again at a new point. Teams of two people (a pumper and a collector) gradually worked through each experimental plot walking from one side of the plot to another and pumping in areas with visible *Trypaea* holes. This insured that all of an experimental plot was subjected to pumping as the plots were laid out in the typical *Trypaea* habitat (Hailstone & Stephenson, 1961). The sampling effort was uniform among the three experimental plots and equaled ca. 4 hours per plot per harvesting event. All captured *Trypaea* with a carapace length of >7 mm were removed from the plots.

Core samples were collected using hand-held cores just before the start of *Trypaea* removal, in October 1998, and then on three more occasions in January, May and November 1999 (Times 1-4) to determine the abundance of benthic macrofauna in the plots. On each occasion, 5 replicate cores were collected from each of two different depths, 5 cm and 15 cm into the substratum, at three randomly selected sites within a plot, using a 15 cm diameter PVC core. Collecting sites were at least 10 metres apart.

All cores were preserved in 4% Rose Bengal-stained formaldehyde solution, sieved across a 1.0 mm-mesh sieve and the retained organisms identified to various taxonomic levels. The following taxa, given in the order of their importance in the godwit diet as determined from faecal analysis (Zharikov & Skilleter ,2002) and visual observations, were analysed in this study: soldier crabs *Mictyris longicarpus*, macrophthalmid crabs (*Macrophthalmus crassipes*, M. *punctulatus*, *Macrophthalmus* sp. and *Enigmaplax* sp. combined), polychaetes (Capitellidae, Cirratulidae, Maldanidae, Nephtyidae, Nereididae, Opheliidae, Orbiniidae, Spionidae, and Syllidae families combined), and bivalves (unidentified tellinids and mactrids).

6.3.3. Shorebird observations

Godwits were normally present in the study area from early October until mid-April (Thompson, 1992; personal observations). Godwit observations were conducted over one complete low tide period per plot per month starting in 1998 with the post-breeding arrivals of these shorebirds in October, and ending in late March 1999, shortly before their northward departure. Additional density and foraging activity data were collected in the subsequent season, in early November 1999. Due to logistical constraints, it was not always possible to conduct shorebird observations immediately after *Trypaea*-removal (disturbance) sessions when the strongest impact of the experimental manipulations on the benthos and its predators would have been expected. As we were interested in the immediate responses of the shorebirds to the manipulations of their prey densities, only the data collected within two – three weeks after a disturbance event were included in formal statistical analyses. This provided for three sets of density data and behavioural observations for the godwits: November 1998, February and March 1999 (Times 1-3). However, the entire shorebird data set is presented to show the overall trends in density and foraging behaviour.

Bar-tailed godwits were observed from the mangrove edge through a 20-40x spotting scope at distances of 50 – 150 m. Observations were conducted during daylight hours, on days with published low water heights of 0.42 – 0.88 m, during periods without rain apart from an occasional shower, and moderate breeze. The particular plot watched on any day was picked at random. As the density of birds in the plots could be affected by the total intertidal area available for foraging, a comparison was made of published low water heights between the days of experimental and control plot observations included in the formal analyses. The mean (±SD) heights were not significantly different, experimental = 0.64±0.12 m, control = 0.63±0.10 m (F1,16=0.04, P=0.85). Observations always started when half of the plot became exposed and terminated when half of the plot was flooded by the rising tide. One to 5 min observations (n=12 per plot per day) on randomly selected actively foraging birds were used. For each focal bird, the numbers of probes and prey captured were dictated onto a cassette recorder to derive capture rates and foraging success. Since capture rate was used as a proxy for the rate of intake, it was important to know that sizes of individual prey did not differ between the treatments. This was the case e.g. for Trypaea (Skilleter, unpublished). No data was available for the other benthos. Godwit density data were obtained on the same days as the focal observations by counting birds present in the plot every 20 min.

6.3.4. Statistical analyses

The abundances of *Mictyris*, and of the three other benthic taxa considered prey of bar-tailed godwits, estimated from the cores taken to 5 cm and 15 cm depth into the substratum, were analysed using a four factor mixed model ANOVA with factors Time (fixed, a=4 levels), Treatment (fixed, b=2 levels), Plot (random, nested in Treatment, c=3 levels), Site (random, nested within Time * Plot (Treatment), d=3 levels) with n=5 cores sampled per site at each depth on each occasion. Although analysed separately, the data from the two depths may not be independent because the 15 cm cores also include the top 5 cm of sediment, and consequently estimates of the abundance of benthos to this depth. The two estimates of abundance are presented here, however, because some crabs do burrow below 5 cm into the substratum and bar-tailed godwits are able to probe beyond this depth when foraging. Godwit data were analysed with three factor, hierarchical mixed model ANOVAs, with factors Time (fixed, a=3 levels), Treatment (fixed, b=2 levels), Plot (random, nested in Treatment, c=3 levels).

Seasonal removal of prey (*Mictyris* per m^2 per season) by the godwits was calculated as a product of mean seasonal capture rates assuming that 38% of all prey captured were Mictyris (Zharikov & Skilleter, 2002), proportion of time spent foraging, godwit density, duration of a season and duration of a low tide period assuming equal capture rates by day and night (e.g. Scheiffarth et al. 2002). Also, mean in-plot prey densities were plotted against mean in-plot capture rates to assess the shape of the relationship between these two variables.

The analysed variables were the numbers of select invertebrate taxa (see above) per 5 or 15 cm-deep core (surface area of 0.07 m^2), overall capture rates of prey per min of time spent actively foraging, foraging success (proportion of successful probes) and density in birds per ha. All count, capture rate and density data were $\log_e(x+1)$ transformed to conform to the ANOVA assumptions. Foraging success data did not need to be transformed. When appropriate, post-hoc pooling of mean square estimates was used to increase the power for specific terms in the ANOVAs following Winer et al. (1991).

6.3. Results

6.3.1. Benthic prey responses to the experimental disturbance

6.3.1.1. Abundance of Crabs

The benthic cores tended to contain small *Mictyris longicarpus* with carapace length (CL) < 10 mm as the larger animals (max. CL=22 mm) were foraging on the surface at the time sampling was done. At both depths (i.e. 5 cm and 15 cm), the *in situ* density of small *Mictyris* showed a significant temporal decrease from October 1998 to January 1999 and then an increase from May 1999 to November 1999 (Time, $F_{3,12}$-values > 10.71, P-values < 0.001, Figure 6.2). There were initially significantly more *Mictyris* in the experimental plots than the control plots, but by January 1999, the abundances of crabs had decreased markedly and were then similar in both treatments. After that time, the temporal trends in the two treatments diverged with more crabs occurring in the control plots than the harvested plots. This was highly significant for the 5 cm cores (Time * Treatment interaction, $F_{3,12} = 4.96$, $P < 0.004$), but not significant for the 15 cm cores even after post-hoc pooling ($F_{3,60} = 1.69$, $P > 0.18$). However, the temporal trends in the data for both depths of sediment were similar suggesting that overall there was a significant impact from harvesting on the abundance of *Mictyris*. The decrease in *Mictyris* abundance associated with the experimental manipulations was 35% in the upper 5 cm of the sediment and 17% in the upper 15 cm of the sediment.

The other group of crabs that were relatively abundant in the cores were the macrophthalmids. At least four species (see Methods) occurred in the area, but these species could not be identified individually from the examination of godwit faecal samples (Zharikov & Skilleter 2002), so data were combined for analysis. There was a significant treatment effect detected for the 5 cm deep cores ($F_{1,52} = 6.42$, $P < 0.02$) with significantly more of the macrophthalmids occurring in the control plots than the harvested plots (Figure 6.3A). A similar trend was evident for the data from the 15 cm cores, but there was substantially more small-scale variation (Sites, $F_{48,288} = 1.44$, $P < 0.04$) for these deeper cores and the treatment effect was not significant (Figure 6.3B). Importantly, by chance, the abundance of macrophthalmids was greater in the control plots than experimental plots before the beginning of *Trypaea* removal, so the difference cannot be attributed to the harvesting. No significant seasonal trend was apparent in the density of macrophthalmids (P-values > 0.17).

6.3.1.2. Abundance of Polychaetes and Bivalves

The abundance of polychaetes showed a significant seasonal increase in the 5 cm cores (Time, $F_{3,12} = 19.54$, $P < 0.002$). No significant temporal trend was detected in the 15 cm cores (Time, $F_{3,12} = 3.05$, $P < 0.07$) (Figure 6.3C-D). For the 5 cm cores, the abundance of polychaetes was initially similar in each treatment, but diverged once experimental manipulations began, with more polychaetes present in the control plots (Treatment, $F_{1,52} = 3.63$, $P < 0.062$). The Time * Treatment interaction was significant ($P < 0.002$) after three replicate cores with extremely high numbers of polychaetes at one site in a single control plot, which occurred in a small patch of seagrass, were replaced with the average of all other cores (Underwood, 1997) collected from control plots in May 1999. The interaction suggested that the experimental manipulations had significantly depressed the abundance of polychaetes in the harvested plots. In 5 cm cores, the decrease in the abundance of polychaetes associated with the experimental impact was 46%. For the 15 cm cores, there was a significant treatment effect, with more polychaetes occurring in the control plots throughout the experiment ($F_{1,52} = 5.99$, $P < 0.02$) but there was no response to *Trypaea* harvesting. The temporal patterns of abundance of bivalves were similar in the 5 cm and 15 cm cores (Time, $F_{3,12}$ values > 5.70, P-values < 0.011) and between the treatments with an increase in density over time (Figure 6.3E-F). There was no effect of harvesting on the abundance of bivalves though (all P-values > 0.23).

6.3.2. Godwit responses to the experimental manipulations

Habitat disturbance due to *Trypaea* removal had a rather dramatic effect on the godwits. All the three variables (density, capture rate and foraging success) examined with ANOVAs showed significantly lower values in the experimental plots (Table 6.1). All the variables started off being roughly equal between the treatments but then showed a strong response to the experimental manipulations. However, the strength of the response apparently diminished over time (Figure 6.4). The density, capture rate and foraging success were respectively 58.5, 22.2 and 17.6% lower in the plots from which *Trypaea* were being removed than in the controls. The time of sampling contributed significantly to the overall variability in the capture rate and foraging success. Both behavioural parameters gradually decreased over time. The density of godwits remained unchanged within and between the seasons, but varied considerably at the scale of Plots within Treatment.

6.3.2.1. Relationship between prey densities and capture rates

If the godwit capture rates were determined directly by the prey densities, a strong linear relationship between these two variables would have been expected. At first, linear regression of the mean monthly in-plot godwit capture rate against *Mictyris* density (15 cm cores) produced a poor relationship ($R^2 = 0.12$, $P < 0.08$, $n = 24$). However, when the October 1998 data, collected at the time of godwit arrival from their breeding grounds, i.e. before any depletion of prey density could take place, were taken out of the equation, the linear fit ($y = 1.18x + 1.75$) improved greatly ($R^2 = 0.52$, $P < 0.001$, $n = 18$). Addition of other prey types (bivalves, macrophthalmid crabs and polychaetes) into the equation did not improve the fit.

6.3.2.2. Estimated proportion of prey removed by the godwits

Bar-tailed godwits, foraging for 96% of the low tide time available to them at a rate of 4.54 prey * min^{-1} and the density of 4.85 bird * ha^{-1} (Zharikov & Skilleter 2002), would have removed 116 *Mictyris* * m^{-2} * season^{-1} assuming that 38% of the prey taken were these crabs and the godwits' wintering season lasted from early October to mid-April. The density of *Mictyris* in 15-cm cores at the start of the season in October 1998 was 132 crabs * m^{-2}. Therefore, 88% of the initial stock would have been removed by the godwits. The *in situ Mictyris* density decreased by 90% over the same period (Fig. 2).

6.4. Discussion

During a wintering season in the north temperate region, depletion of stocks of benthic organisms by shorebirds on average does not exceed 25 – 40% of the initial, start-of-the-season levels (Székely & Bamberger, 1992; Meire et al., 1994; Zwarts & Ens, 1999) and appears to be independent of production/standing stock (van der Meer et al., 2001). Due to the high local densities of prey at the onset of a season, intake rates can remain invariable across a range of prey densities and such a level of depletion may not be sufficient to affect intake rates noticeably (e.g. Dolman & Sutherland, 1997). When depletion in excess of these values occurs, it is usually brought about by cold spells (e.g. Camphuysen et al., 1996; Zwarts et al., 1996), infestation of prey by parasites (Jonsson & André, 1992) causing considerable background mortality, or by a decrease in the area available for foraging (Evans et al., 1979). In the near absence of benthic production in the northern estuaries during boreal winter, a large (> 50%) decrease in the density of food stocks leads to emigration of shorebirds from the heavily depleted sites/estuaries (e.g. Zwarts et al., 1996) into areas where comparatively higher intake rates can be achieved. The relatively frequent occurrence of high background prey mortality events in the northern estuaries (Camphuysen et al., 1996, cf. Moverley et al., 1986 for a subtropical site) coupled with generally irregular recruitment patterns of benthos (Beukema, 1982; Beukema et al., 1993, 2000) necessitates the maintenance of a high ratio between benthic stock and shorebird consumption to insure against prey overexploitation in poor years (Wolff, 1991). How do the results of this study in SE Queensland compare with those from the northern hemisphere?

6.4.1. Disturbance experiment

Physical perturbation of intertidal sediment often leads to a decrease in the densities of benthic fauna (e.g. Wynberg & Branch, 1994; Beukema, 1995; Ambrose et al., 1998) and can be used to assess the relationship between shorebird intake rate, densities and prey abundance. In one published study, a decrease in the density of a benthic amphipod *Corophium volutator* caused by sediment disturbance, reduced capture rates and foraging success of a flock-foraging shorebird, the semipalmated sandpiper *Calidris pusilla* (Shepherd & Boates, 1999). Unfortunately, no information on the densities of the sandpipers in control and disturbed areas was available precluding any insight into whether or not the birds emigrated out of the impacted areas. The present study provides appropriate information for a warm subtropical estuary.

Sediment disturbance significantly reduced in situ densities of two important godwit prey, soldier crabs, *Mictyris longicarpus* and polychaetes, which comprise 73% and <5% of godwit dry weight intake in the sandy habitat respectively (Zharikov & Skilleter, 2002). The numeric and functional responses of the godwits associated with the impact were in agreement with the original prediction. The initial decrease in godwit density, capture rate and foraging success in the experimental plots occurred soon after an impact event (Figure 6.4). The significance of ANOVA tests that used only the data obtained shortly after impacts also attests to the rapidity of shorebird response. This suggests that prey density in the plots was limiting intake rates of the birds throughout the non-breeding season. As discussed earlier, this is often not the case in the north temperate region, where prey densities may vary broadly without affecting shorebird intake rates.

Godwits leaving the experimental plots appeared to forage, at least partially, in the control plots suggesting that moving farther away would not improve their feeding conditions. Otherwise, it seems likely the birds would have left the general study area. Also, bar-tailed godwits that were colour-flagged in a different study appeared to use the same sites (100's m scale) within the study area day after day for the duration of a wintering season (6 months) (personal observations). These observations contrast with many north temperate estuaries, where non-territorial shorebirds use areas of > 1 – 10 km^2 in search of suitable foraging sites, e.g. red knot *Calidris canutus* (e.g. Zwarts et al., 1992; Piersma et al., 1993b), western sandpiper *Calidris mauri* (Warnock & Takekawa 1996), dunlin Calidris alpina (Shepherd 2001) and black-tailed godwit *Limosa limosa* (Shubin, 1999). In the absence of prey reproduction, this roaming may be caused by local prey depletion, but one should keep in mind that northern estuaries are usually much larger and thus have more surface area available (e.g. Hockey et al., 1992) than those in the southern hemisphere.

An unexpected outcome of the experiment was that godwit densities in the harvested and control plots merged after three months without further *Trypaea* harvesting. One explanation for this pattern could be that the stocks of benthic prey recovered from such disturbance rather quickly (McLusky et al., 1983; van den Heiligenberg, 1987; but see Wynberg & Branch, 1994). Whereas this suggestion was not supported by the benthic sampling data, unfortunately benthic sampling occurred on a coarser temporal scale than shorebird observations. Therefore, short-term pulses in benthos abundance could be missed. Alternatively, godwits could learn to use different prey in the impacted plots, e.g. bivalves, densities of which did not differ between the treatments, thus offsetting the decrease in the density of the other prey (*Mictyris*, polychaetes). Although visual observations cannot help in resolving this suggestion (> 95% of prey items could not be identified individually), it appeared that godwits, for example, were capturing 10 times more large surface-dwelling *Penaeus* prawns in control (1.1 % of visual diet) as opposed to the experimental plots (0.1 % of visual diet) following the start of the experiment – no prawns were consumed in October.

The godwits not only achieved a smaller capture rate in the experimental plots, but their foraging success was also smaller than in the controls. Temporal fluctuations in foraging success showed a pattern similar to that of the density (Figure 6.4A, C). It is possible the birds were attempting to compensate for a drop in prey density by increasing their probing rate. As the increase in the probing rate did not fully cancel out the decrease in foraging success, immigration of godwits out of the impacted plots occurred. Also, it can be suggested that godwits were making more mistakes while foraging. This could either be due to obliteration of some important visual cues on the surface (Velasquez & Navarro, 1993) or a change in the spatial aggregation of prey (Warwick & Clarke, 1993).

Small-scale spatial aggregation of benthos is commonly associated with micro-relief features of the flats (e.g. Hogue & Miller, 1987; Sun & Fleeger, 1994) and topography may be used by shorebirds as foraging cues (e.g. Sutherland et al., 2000). Therefore, a disruption of this spatial arrangement even without a decrease in the overall density of prey would result in a drop in foraging success until the new spatial distribution of prey is memorised by the predators. If the new pattern persists over time, obviously its effect on the predator foraging efficiency will decline. Other data indicate that *Trypaea*-pumping changed the degree of spatial aggregation in the small-scale distribution of *Mictyris*, which may have resulted from changes to the topography and sediment structure of the substratum caused by this type of harvesting (Curley, 1996). If the *in situ* aggregation of *Mictyris* is linked to any micro-relief features, then the obliteration of these features may lead to both (i) removal of important visual cues used by the godwits and (ii) a less clumped, i.e. predictable distribution of prey (e.g. Fauchald, 1999) causing the godwits to have to travel greater distances between successive captures (e.g. Sutherland et al., 2000). In either case, the rate of prey capture will be compromised.

6.4.2. Functional response in bar-tailed godwits and estimated depletion of *Mictyris* stocks

In addition to the rapid functional and numerical responses of bar-tailed godwits to the experimental decrease in their prey density, there were two more lines of evidence pointing to the birds' capture rate being directly limited by the instantaneously available stocks of the prey. First, regression of mean monthly in-plot godwit capture rates against mean *Mictyris* density initially produced a poor relationship but when the October 1998 data were taken out of the equation, the linear fit improved greatly. This suggests that if an excess of prey for these birds existed in the system, it was only for a short period soon after their arrival in October and subsequent removal of this excess took place very quickly. Second, estimated seasonal depletion of *Mictyris* stocks was 88% of the initial (October) level. Indeed, between the start and the end of a shorebird wintering season densities of *Mictyris* in the substratum decreased by a similar value (90%). This suggests that even if the *in situ* stocks of *Mictyris* were being replenished through recruitment (Cameron, 1966), predation pressure coupled with other factors was exceeding it. However, to show that godwit predation controls in situ density of *Mictyris* would require an appropriately designed (Sewell, 1996) exclosure experiment (e.g. Quammen, 1984; Székely & Bamberger, 1992).

6.4.3. Seasonal trends in godwit density and foraging behaviour and prey densities

A significant seasonal decrease in the capture rate and foraging success suggest that fewer prey were becoming available to the godwits as the time progressed. However, neither the density of godwits in the plots nor the total mudflat population, ca. 2,400 individuals per 250 ha mudflat, decreased between October (1998/99) and April (1999/2000) (personal observations). This has been explained by a seasonal increase in the size of consumed prey, which resulted in an apparent increase in the intake rate (sandy habitat: 0.88 kJ * min^{-1} in December to 1.20 kJ * min^{-1} in March, Zharikov & Skilleter, 2002) despite a lower capture rate. The explanation to the seemingly paradoxical situation: virtual disappearance of *Mictyris* from sediment samples versus the stable local godwit population size and apparently, small contributions of the other prey types to the energy intake of the birds (Zharikov & Skilleter, 2002) may lie in the life history of *Mictyris*.

Cameron (1966) reported that reproduction in *Mictyris longicarpus* takes place year-round. However, further north on the Queensland coast Dittmann (1998) reported a large peak in the number of juvenile (< 7 mm CL) individuals only in September, about the same time of the year as our samples containing large densities of *Mictyris* were collected, but not during other months of the year. Furthermore, pilot samples of surface-active *Mictyris* collected in the study area in October 2000 and March 2001 had 67 and 27% of juvenile *Mictyris* respectively. These observations do not exclude year-round reproduction because in this study juvenile individuals were found in all sets of benthic samples (Figure 6.2). However, they do suggest that regular recruitment events may take place in September – October, the time of mass arrival of Pale- and Nearctic shorebirds to the East Australian coast (Thompson, 1992).

Mictyris forage on the mudflat surface (Quinn, 1983; Dittmann, 1993). Although the exact relationship between the body size of the crabs and the proportion of time they spend foraging remains known, adult individuals forage for longer and move over larger distances than juveniles (Cameron, 1966; Quinn, 1983). Therefore, while on the one hand the fraction of small individuals in the population present in the sediment is reduced by predators, on the other hand *Mictyris* grow and recruit into the surface-active population, which is not effectively sampled by benthic cores. The combination of these two processes may explain the steep seasonal decrease in the in situ density of these crabs. However, as stated above, it needs to be determined experimentally whether predation by the godwits, who typically consume *Mictyris* < 10 mm carapace length (Zharikov, 2002), plays an important role in the decline.

To conclude, the observed functional and numerical responses to the experimental reduction of prey density, the strong linear relationship between prey densities and capture rate and the high estimated depletion of the initial stock of Mictyris demonstrate that: (i) bar-tailed godwits wintering in subtropical Moreton Bay may achieve a high exploitation level of their food resources and (ii) the rate of intake achieved by these birds is limited by prey density. This finding may tie together (i) the low intake rates observed in this population (0.88 – 1.62 kJ * min-1, Zharikov & Skilleter 2002) as compared to the populations wintering and/or staging in Europe (1.21 – 2.38 kJ * min-1, Smith 1975; 1.5 – 1.8 kJ * min-1, Scheiffarth et al. 2002) with (ii) the low rate of body mass gain (2.9 g * day-1) and the generally prolonged period of pre-migratory preparations reported in bar-tailed godwits elsewhere in Australia (M. Barter, J. Wilson, pers. comm.).

6.4.4. Utility of large-scale experiments in shorebird–prey interaction studies

When an experiment directed at studying spatial distribution of a mobile predator is to be conducted, its scale has to correspond to the scale of movements of the study species (e.g. Cummings et al., 1997) otherwise, any potentially important interactions may be overshadowed by the background variability. Shorebirds frequently range over large distances (e.g. Zwarts et al., 1992; Piersma et al., 1993b) but generally respond numerically to the densities of their prey from scales of 100's m and up (Colwell & Landrum, 1993). In this study area, bar-tailed godwits appeared to range over distances of 100's m. Therefore, the scale of 1 ha was chosen to investigate responses of the shorebirds to manipulations of their prey densities. This choice was appropriate for the godwits as can be seen from the significant correlations between the shorebird capture rates and densities of their principal prey and the variability in their density at the level of plots (Table 6.1). It seems that the optimal approach to studies of shorebird predator-benthic prey interactions in the intertidal habitats is application of large scale controlled manipulative experiments that would account for both large scale shorebird movements and small scale spatial and temporal variability in benthos (Thrush 1991; Sewell 1996) distribution irrelevant to the distribution of the birds.

Potential interactions between humans and non-breeding shorebirds on a subtropical intertidal flat

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6.5. Introduction

During the non-breeding season, shorebirds (Suborder: Charadrii) occurring on coastal and estuarine intertidal flats world-wide often utilise the same areas and prey on the same species of benthic invertebrates that are used by humans for bait and for consumption (Hanekom & Baird, 1982; de Boer & Longamane, 1996; Goss-Custard et al., 1996; Norris et al., 1998; Shepherd & Boates, 1999). Such co-existence may lead to numerous direct and indirect interactions between people and the birds. For example, the harvesting of benthic animals by humans may disturb the birds, displacing them from their foraging sites and thus affect them even without specifically changing the abundance of any prey (de Boer, 2001). Probably more importantly though, birds may be affected via the focussed harvesting of stocks of their benthic prey (Norris et al., 1998; Stillman et al., 2001), or due to increased mortality of their prey occurring as a by-product of harvesting (Shepherd & Boates, 1999). In either case, since the size of non-breeding shorebird populations is thought to be balanced against the average size of multi-annual stocks of their prey (Wolff, 1991; Meire et al., 1994), any such increase in the mortality of benthos may lead, especially during adverse weather events (Moverley et al., 1986; Günther & Niesel, 1999), to increased mortality rates in non-breeding shorebird populations (Goss-Custard & Durell, 1990; Camphuysen et al., 1996). The harvesting of intertidal invertebrates by humans, due to its widespread nature, therefore represents a potentially important interaction between people and migratory shorebirds especially at key non-breeding sites. While such interactions have been investigated in the Northern Hemisphere (Shepherd & Boates, 1999; Stillman et al., 2001 and references therein), so far, few comparable experimental or even observational studies have addressed this issue at warm-climate (tropical or subtropical) sites, where many Artic-breeding shorebirds spend the boreal winter (but see Zharikov & Skilleter, 2003a).

In Australia, the seasonal home to ca. 3 million non-breeding shorebirds migrating annually from Siberia and Alaska, the collection of intertidal invertebrates for bait is a common fishery (Underwood, 1993). One bait organism frequently harvested both commercially and recreationally is a burrowing shrimp from the family Callianassidae *Trypaea australiensis* (also known locally as the yabby). *Trypaea* inhabits sandy intertidal estuarine sediments all along the eastern seaboard of Australia (Hailstone & Stephenson, 1961; Inglis, 1995; Rotherham & West, 2003). These shrimp are typically obtained from the substratum using a manual suction device known as the 'yabby-pump' (Hailstone & Stephenson, 1961; Rotherham & West 2003 and see Section 1). This method of harvesting, broadly applied in Australia and in other countries with abundant burrowing shrimp populations, e.g. South Africa (Wynberg & Branch, 1991; Hodgson et al., 2000), has been shown to cause marked, small-scale (1-12 m^2) direct and indirect negative effects on the populations of the shrimps (Wynberg & Branch, 1994, 1997). It is, however, unclear from such studies whether the impacts of shrimp-harvesting at these smaller scales translate to effects over larger scales on higher trophic-level predators that prey on these decapods.

In Moreton Bay, Queensland, Australia collection of *Trypaea* for bait is widespread in areas not specifically covered by habitat protection regulations (McPhee & Skilleter, 2002a, b). *Trypaea* and another abundant decapod crustacean, a mictyrid crab, *Mictyris longicarpus*, represent important prey for a large Siberia-breeding shorebird, the eastern curlews, *Numenius madagascariensis*, during the non-breeding season (Lane, 1987; Rohweder & Baverstock, 1996; Zharikov & Skilleter, 2003b). This raises the potential for the harvesting of *Trypaea* for bait to reduce the stocks of prey for the curlew, through the combined effect of direct removal and additional indirect mortality due to sediment disturbance (Wynberg & Branch, 1994, 1997). As ≈ 13% of the global population of the protected (Collar et al., 1994) shorebird species spend their non-breeding season in Moreton Bay (Thompson, 1990; del Hoyo et al., 1996) any reduction in prey levels to the extent that the foraging efficiency and abundance of these birds are affected may have important conservation implications (Goss-Custard & Durell, 1990).

The primary aim of this study was to investigate whether bait harvesting with all its inherent effects resulted in an impact on a migratory shorebird, the eastern curlew. In a large-scale manipulative study, stocks of *Trypaea* were experimentally harvested simulating the technique and the levels of harvesting intensity per unit area of this decapod by bait-collectors observed in Moreton Bay (McPhee & Skilleter, 2002b) and other parts of the world (Wynberg & Branch, 1991; Hodgson et al., 2000). In assessing the impacts of harvesting of *Trypaea*, we examined whether there was a detectable decrease in the overall abundance of the shrimp, but also in the abundance of the size-cohort of the shrimp population specifically preyed upon by the curlews. We also examined if the *in situ* densities of *Mictyris* were affected as an indirect consequence of *Trypaea* harvesting. We predicted that if bait harvesting caused a decrease in the densities of *Trypaea* and/or *Mictyris*, the key prey for the curlews, then we would observe a decrease in foraging efficiency of the birds and possibly their emigration from the harvested areas.

In the course of the study it also became apparent that the curlews themselves were removing large numbers of *Trypaea* from the mudflats. Therefore, a secondary aim of the study was to assess indirectly the extent of the impact of the bird predation on the local standing stocks of *Trypaea* through the course of a non-breeding season. To achieve this, the predation pressure exerted by eastern curlews on *Trypaea australiensis*, expressed as the estimated seasonal percent removal of the prey stock present at the start of a non-breeding season was calculated (Schneider, 1992; Székely & Bamberger, 1992). The seasonal trends in curlew diet and density were recorded as well. We predicted that if the curlews deplete local *Trypaea* stocks then (1) a seasonal decrease in densities of *Trypaea* within the size range taken by the birds would be observed, (2) a gradual seasonal diet shift to another abundant prey (e.g. *Mictyris*) would occur or, alternatively (3) if no diet shift is possible, emigration out of the area would occur resulting in a seasonal decrease in local curlew densities (Székely & Bamberger, 1992).

6.6. Methods

6.6.1. Study area

The study was done on the western shore of North Stradbroke Island, Moreton Bay, Queensland, Australia (27°25'S, 153°25'E) between October 1998 and February 2000. Moreton Bay is a large estuarine embayment with semidiurnal tides exposing the intertidal zone on average for 5.5 to 6.5 hours per low tide and the maximal tidal range of 2.7 m. During the austral summer, Moreton Bay accommodates up to 80,000 non-breeding Arctic shorebirds including ≈ 5,000 eastern curlews (Thompson, 1990). The immediate study area is known to support curlew densities considerably greater than the average across the Bay (Finn et al., 2001) and thus can be considered a "preferred site" for the birds. The intertidal flats on the western (estuarine) side of the island are characterised by three broad zones: a mangrove (primarily *Avicennia marina*) fringe along the upper shore; an essentially unvegetated mid-intertidal zone; and extensive seagrass (*Zostera capricorni*, *Halophila ovalis* and *Syringodium isoetifolium*) beds along the lower intertidal zone (Abal et al. 1998). All experimental manipulations and observations of shorebird foraging activity were done in a 20-ha segment of the sandy (unvegetated) section of the intertidal flat. The substratum consisted of fine sand (mean grain size = 0.204 mm, sorting coefficient = 0.38) with a small (2%) silt (grain size < 0.063 mm) fraction and a micro-relief of elevated ridges and water-pools (Thompson, 1992).

6.6.2. Simulation of *Trypaea* harvesting

Six square, permanent 1 ha plots were marked out with inconspicuous wooden poles on a visually uniform stretch of the intertidal flat at the same tidal elevation, each contiguous pair separated by 75-100 m. Three of the plots were designated at random for experimental harvesting and the remaining three plots served as undisturbed controls, apart from sampling to determine the abundance of benthic fauna. The study area was sufficiently (> 2 km) remote from any known *Trypaea* collection site to preclude any uncontrolled harvesting within the experimental area. In fact, in the course (15 months) of the experiment, people (on-foot or landing from boats) were only seen in the study area on a few occasions and they were either shell-fish collectors or fishermen (funnel-netters), but not *Trypaea*-collectors.

Trypaea australiensis build permanent burrows in unvegetated sediment and typically do not occur on the surface (Hailstone & Stephenson, 1961). We harvested *Trypaea* from the experimental plots using *Trypaea* harvesting techniques identical to those employed by recreational harvesters (McPhee & Skilleter, 2002b). Specifically, we used the 'yabby-pump', a manual suction device consisting of a stainless-steel pipe (length = 0.75 m, diameter = 0.05 m) with a handle and plunger, widely employed by bait-collectors (Hailstone & Stephenson, 1961; Hodgson et al., 2000; Rotherham & West, 2003). The usual procedure for collecting *Trypaea* with a 'yabby-pump' is to push the unit into the substratum over visible *Trypaea* holes every 4 – 5 steps and extract the sediment, which is then dumped onto the substratum to collect suitable-sized animals. As a rule, the pump is pushed into the substratum at the same point several times, after which the harvester begins the process again at a new point.

Similar to Wynberg & Branch (1994), the goal was to apply the combined effects associated with *Trypaea* harvesting (i.e. removal of yabbies, sediment trampling and disturbance, destruction of burrow systems, etc.) fully across each experimental plot. To achieve this goal, one or two teams of two people (a pumper and a collector) walked experimental plots perpendicular or parallel to the water line from side to side in a shuttle fashion pumping in areas with visible *Trypaea* holes every few steps. Because of a large area that had to be covered (cf. 12 m^2 plots harvested by Wynberg & Branch (1994) and 10,000 m^2 plots harvested here), the natural differences in fitness and motivation levels of participants, in addition to the need to sometimes deploy two harvesting teams in one plot simultaneously, the exact harvesting effort (e.g. the number of pumps) per plot was not estimated. However, ultimately, harvesting activities were limited by the duration of a low tide, and so our harvesting effort equaled 4-5 pumper-hours per plot per harvesting event. All captured *Trypaea* (= 8,338 individuals) with the carapace length (CL) ≥ 7 mm, the size usually taken by bait-collectors (McPhee & Skilleter, 2002b), were removed from the plots and subsequently counted. The smaller-sized animals were left in the plots so that they could re-burrow. Naturally, 55% of bait-collectors harvest *Trypaea* at least once a month while the remainder do so less regularly (McPhee and Skilleter 2002b). Due to logistic constrains associated with delivering harvesting teams to the study sites and processing large numbers of samples, we could not always conduct harvesting at this (monthly) frequency. The harvesting events took place once every month or every two months, in November 1998, January, March, May, June, July 1999 and then in December 1999 and February 2000 (Figure 6.5).

6.6.3. Stock assessment of *Trypaea* and *Mictyris*

The abundance of *Trypaea* in the six study plots was estimated by sampling the shrimp using 'yabby-pumps' in 10 randomly placed 4 m^2 quadrats per plot. The amount of pumping required to harvest all *Trypaea* in a 4 m^2 quadrat was determined from a pilot experiment where the cumulative percentage of *Trypaea* harvested from a quadrat was plotted against the number of sets of 7 pumps per given point completed (McPhee & Skilleter, 2002a). Specifically, complete (100%) harvesting of a 4 m^2 quadrat required 18 sets of 7 pumps, i.e. approximately 0.74 m^3 (24.7% of volume) of sediment was removed out of 3.0 m3 available in a 4 m^2 quadrat to the depth of 0.75 m (it should be noted, though, that a pump rarely fills with sediment completely). Sediment collected from each of the quadrats was passed through a 2.0 mm sieve in the field and the retained *Trypaea* were stored. In the laboratory, *Trypaea* were counted and their carapace length (from the postorbital cavity to the dorsal end of the cephalothorax) measured with calipers to the nearest 1 mm. The density of *Trypaea* was estimated in each of the plots at the beginning of the experiment in October 1998, i.e. just before experimental harvesting commenced and on five, subsequent occasions (Figure 6.5). Sampling of *Trypaea* resulted in removal of 4,210 animals from the control plots and 3,643 *Trypaea* from the harvested plots. Thus, the actual total harvest from the manipulated plots was ≈ 50% greater due to sampling. However, given similar numbers of animals were removed from control and experimental plots to estimate the population size, this sampling could not confound the experimental comparisons associated with the effects of harvesting.

The soldier crab, *Mictyris longicarpus*, was the only other common, large decapod found in the substratum. Since larger specimens of these crabs are also a prey item of the curlews, their densities were estimated using the same method as used for *Trypaea*. Unlike *Trypaea*, *Mictyris* do not form permanent burrows and do not always remain underground. At each low tide, diurnal or nocturnal, a variable proportion of the crab population emerges onto the flats to forage in 'armies' of many thousand individuals ranging over hundreds of metres of the intertidal zone (Cameron, 1966; Dittmann, 1993, 1998). The fraction of the *Mictyris* population remaining burrowed at low tide appears to be determined by the weather as few crabs may emerge on rainy days, but under other circumstances it seems to be rather small (≈ 10%; personal observation). After a period of surface feeding and usually 0.5-1 hour before the flats are flooded, the crabs corkscrew themselves directly into the substratum at a new location and remain there until the next emergence. The pump method of sampling used here captured all *Trypaea* with carapace length (CL) ≥ 2 mm and the fraction of the *Mictyris* population remaining underground with CL ≥ 5 mm. Smaller individuals passed through the sieve. In the study area, curlews consumed *Trypaea* 5 to 11 mm CL (mean = 6.8±1.2, n = 366) and *Mictyris* 5 to 21 mm CL (mean = 11.6 ± 3.0, n = 2110) (Zharikov, unpublished). Therefore this method of sampling was expected to capture the range of sizes taken by the birds. It is important to note that estimates of the abundance of the size range of *Mictyris longicarpus* preyed on by godwits (see above) was using benthic cores because this provided more reliable estimates of these smaller sizes while the stock assessment method used in the curlew study was more appropriate for the larger members of the population.

6.6.4. Spatial scale of the experiment

With rare exceptions (McLusky et al., 1983), due to their labour-intensive nature, manipulative experiments in marine systems are conducted at spatial scales of only a few square metres (Sewell, 1996; van der Meer et al., 2001). Over the past few years, it has been repeatedly argued that in studies of shorebird-prey (or any large mobile predator-prey) interactions (Sewell, 1996; Cummings et al., 1997; Thrush, 1999; van der Meer, 2001) the spatial scale of investigation (experiment) should correspond to the spatial scale at which the organism(s) in question experiences its environment. If this condition is not fulfilled, either inconclusive (Sewell, 1996) or negative (no-response) (Cummings et al., 1997) results may be obtained. Also, the relevance to real-life ecological interactions of the results from experiments done at inappropriate spatial scales may be rather limited (Thrush, 1999).

The two important components of spatial scale relevant to the design of ecological experiments are the extent and the grain. Extent corresponds to the total area over which replicate samples are collected, i.e. for example an individual organism's home range or territory or an experimental plot. Grain corresponds to the area of a single sample of the environment taken by an individual animal and/or a researcher (Thrush, 1999). To produce ecologically meaningful results from a study on mobile predators, the extent and the grain of the study must correspond, at least approximately, to the extent and the grain, characterising the interaction between the predator and its environment (prey). This experiment fulfilled both conditions. (1) Individual eastern curlew territory size (= extent) ranges from 0.22 to 0.87 ha (Zharikov & Skilleter, 2003c) and non-breeding shorebirds in general have home ranges and respond to variability in prey abundances at scales ≥ 100 m (Colwell & Landrum, 1993; Piersma et al., 1993). Therefore, the experimental unit (extent) for examining the effects of *Trypaea* harvesting on eastern curlew foraging efficiency and density was a 1 ha plot. (2) Based on unpublished data, an eastern curlew, on average, samples (probes) the substratum every 5 seconds walking at 0.30 m^*s^{-1} (cf., the smaller Eurasian curlew *Numenius arquata* walks with the average speed of 0.22 m^*s^{-1}; Zwarts & Esselink, 1989). If we assume that it scans a path 0.5 – 1.0 m on either side of the line of movement, then the grain at which a curlew samples its environment is approximately 1.5-3 m^2. Thus, the methodology for assessing the abundance of *Trypaea* in these habitats based on 4 m^2 quadrats represents the appropriate unit of replication (grain) to sample curlew prey (*Trypaea* and *Mictyris*) densities in the study plots.

6.6.5. Curlew observations

Curlew observations started with the post-breeding arrival of the birds in October 1998 and ended with their departure in mid-March 1999. Additional data were collected in October 1999 and February 2000. Birds were observed over one complete low tide period (day) per study plot per month, except for November 1998, when two sets of observations were obtained, one just before and one just after the very first *Trypaea* harvesting event (Figure 6.5). Curlews were observed from the mangrove edge through a 20-40x spotting scope at distances of 50–150 m. Observations were made during daytime hours, on days with published low water heights of 0.42 – 0.88 m, during periods without rain apart from a brief shower and moderate breezes. Observations started 20-30 min after mudflats began to open and terminated 20-30 min before they were fully flooded, i.e. when the upper half of the plot became exposed and the lower half of the plot was covered, respectively. Thus, a plot was observed for 4 to 5 hours per day. We usually attempted to cover all six plots within a contiguous set of diurnal low tides in a random sequence. However, on some days due to the lack of time a pair of adjacent plots was observed by alternating between them. To estimate curlew density, the number of curlews present in a plot under observation was recorded at every available 20 min mark (e.g. 9:20, 9:40, 11:20, etc.) when the observer was free from focal bird observations (see below). As the density of birds in the plots could be affected by the total intertidal area available for foraging due to variation in the tidal height, a comparison of published low water heights between the days of experimental and control plot observations was included in the formal analyses. The mean (± SD) heights were not significantly different from each other (experimental = 0.67 ± 0.14 m, control = 0.67 ± 0.12 m - $F_{1,22} = 0.01$, $P > 0.96$). Only one to four different curlews used a 1 ha plot at any time potentially making estimates of abundance collected on a given day non-independent. Therefore, the mean of all the counts per plot per day (mean number of counts per plot per day = 9 ± 2, n = 54 plot-days) was used as a replicate estimate of curlew density.

To estimate curlew foraging efficiency, 1 to 5 min focal observations of randomly selected birds actively foraging in the plots were used (Altmann, 1974). For each focal bird, the numbers of probes and prey captured were dictated onto a cassette recorder to subsequently derive capture rates (prey captured per 1 min time spent foraging) and foraging success (proportion of probes that resulted in capture of prey). Curlews primarily foraged on large prey (*Mictyris* and *Trypaea*), which were easily identifiable from a distance (Zharikov & Skilleter, 2003b), therefore prey-specific capture rates could be determined. Small unidentifiable prey were also recorded, and, although excreta analyses showed most of them to be small (CL = 5-10 mm) *Mictyris* (Zharikov & Skilleter, 2003b), for the purposes of this study we treated them as a separate prey type. We used capture rate as a proxy for the rate of intake. Therefore, it was important to know that sizes of individual prey did not differ between the treatments. This was the case for *Trypaea*: mean carapace length was identical between the treatments (7.0 ± 2.9 mm, n = 3,643 for the experimental plots and 7.0 ± 2.9 mm, n = 4,210 for the control plots). No comparable data on *Mictyris* were available but given the high mobility of these animals (Cameron, 1966) we assumed the same was true. As with the density, the mean of all the curlew foraging efficiency estimates per plot per day (mean number of focal bird observations per plot per day = 11 ± 5, n = 54 plot-days) was used as an independent data point.

6.6.6. Seasonal removal of *Trypaea* by eastern curlews

Following (Schneider, 1992), seasonal removal of *Trypaea* (individuals per m^2 per season) by eastern curlews was calculated as a product of the overall mean seasonal *Trypaea*-capture rate, proportion of time spent foraging, curlew density, duration of a non-breeding season and duration of a low tide period assuming equal capture rates by day and night (inferred from Rohweder & Baverstock, 1996). The mean seasonal *Trypaea*-capture rate was derived from focal bird observations as described above. The proportion of time spent foraging by the curlews was determined by scan sampling all curlews within ≈ 250 m radius of an observer using a spotting scope and describing their state as either foraging or non-foraging (standing, sleeping, preening, territorial, vigilant). It is assumed here that the proportion of individuals in the population engaged in a particular activity at a given point in time, estimates the proportion of time an individual in this population allocates to this activity (Altmann, 1974). Scans were carried out alongside counts of curlews in the plots. Mean seasonal curlew density was estimated by conducting plot counts as above. Duration of a season, based on the curlews' arrival to and departure from the study area was estimated at 6 months, October to March (Lane, 1987). Mean duration of a low tide period, i.e. a period when the mudflats were free of water and thus available to the birds, was estimated at 358 ± 17 min (n = 22) (Zharikov, unpublished data).

6.6.7. Statistical analyses

Data on the abundances of *Trypaea* (total and size-cohort taken by the curlews) and *Mictyris*, estimated from the stock assessments, were analysed with a three-factor, hierarchical mixed-model ANOVA, with factors Time (fixed: 6 levels), Treatment (fixed: 2 levels), and Plot (random, nested in Treatment: 3 levels) with n = 10 quadrats sampled per plot on each occasion. Time was treated as a fixed factor, as opposed to, for example, a repeated-measure factor because at each sampling occasion the combined area of all samples (40 m^2) represented only 0.4% of the area of a plot (10,000 m^2), thus making any effect of prior sampling (and therefore non-independence of data) *per se* highly unlikely. For these analyses, when nested factors (Plot) did not contribute significantly to the overall ANOVA model, post-hoc pooling of nested levels was carried out to increase the power of the test for specific differences between the Treatments (Underwood, 1981; Winer et al., 1991). In this design, a significant Treatment * Time term would indicate an effect of harvesting on abundance of the decapod crustaceans as their population trends in the control and experimental plots would be expected to diverge following the commencement of *Trypaea* harvesting.

Similar to the other long-lived shorebirds (e.g. Ens & Goss-Custard, 1986), non-breeding *Numenius* curlews in general (Marks & Redmond, 1996) and eastern curlews in particular (Finn et al., 2001) display a large degree of within and between season site fidelity, which had three important implications for this study. (1) Short-term displacement of the birds from the plots during harvesting and sampling sessions was unlikely to confound any effects of harvesting *per se* as individual curlews re-occupied their territories within a few minutes after our withdrawal from the area (personal observations). (2) Times (months) of sampling are likely to have been non-independent. (3) In general, site-faithful individuals may show a delayed numerical response to any habitat alteration (Milsom et al., 2000 and references therein) even if their foraging efficiency is immediately affected. To account for possible non-independence in the curlew foraging efficiency and density data here, Time was treated as a repeated-measure. To investigate the possibility of existence of both short-term and delayed responses by the curlews to *Trypaea* harvesting, firstly we tested for any short-term effects associated with the very first harvesting event in this relatively pristine system. A BACI (Before/After-Control/Impact) design (Green, 1979) was applied to the data collected approximately within one month BEFORE and within one month AFTER the start of *Trypaea* harvesting on 13-14 November 1998 (Figure 6.5), with factors Period (fixed: 2 levels), Treatment (fixed: 2 levels), Time (repeated-measure: 2 levels). The numbers of replicates (i.e. mean Plot estimates) was n = 3. In this test, a significant Treatment * Period term would indicate a short-term effect of harvesting on the curlews. Subsequently seven more harvesting events were carried out potentially allowing for accumulation of effects in the system resulting in a delayed response by the birds. Here, we analysed only the curlew data collected AFTER the start of harvesting using a two-way ANOVA with, Treatment (fixed; 2 levels) and Time (repeated-measure; 7 levels) and n = 3 replicates. In this test a significant Treatment * Time term would indicate a delayed effect of harvesting on the curlews.

The measured variables were the numbers of *Trypaea* or *Mictyris* per 4 m^2 quadrat, prey-specific (*Trypaea*, *Mictyris*, and “small-prey”) capture rates in prey per min of time the curlews spent actively foraging, foraging success (proportion of successful probes) and density in birds per ha. Where necessary, $\log_e(x+1)$ transformations of abundance and capture rate data were used to meet the assumption of homogeneity of variances after Cochran’s C-test (Underwood, 1981).

6.7. Results

6.7.1. Abundance of *Trypaea*

A total of 8,338 *Trypaea* was removed from the experimental plots during eight harvesting events between October 1998 and February 2000. However, harvesting did not result in a significant impact on the total abundance of the shrimp in the experimental plots (Table 6.2, Figure 6.6A). The overall density of *Trypaea* decreased significantly from October 1998 to July 1999 (Times 1 – 3, Tukey's HSD test $P < 0.001$ after post-hoc pooling of the Plot (Treatment) and residual mean square estimates) but remained virtually unchanged thereafter (July 1999 – February 2000, Times 3 – 6, Tukey's HSD test $P > 0.12$). When the abundance of large (CL = 5 to 11 mm) *Trypaea* (size-cohort taken by the curlews) was analysed separately, similarly non-significant Treatment * Time and Treatment effects and a significant Time effect were obtained. Post-hoc pooling was not done due to the significant Plot (Treatment) term. However, the trend was for the October 1998 and March 1999 densities to be slightly higher than July-December 1999 densities (Figure 6.6A).

6.7.2. Abundance of *Mictyris*

The *in situ* abundance of *Mictyris* was greater in the harvested plots than in the control plots (significant Treatment effect), but the Treatment * Time interaction was not significant even after post-hoc pooling of the Plot (Treatment) and residual mean square estimates ($F_{5,348}=1.95$, $P<0.08$). The effect of Time was highly significant reflecting large seasonal fluctuations in the ≥ 5 mm CL *Mictyris* density in the substratum (Table 6.2, Figure 6.6B). Specifically, the *in situ* abundance of *Mictyris* tended to be greater at or before the start of a season (October 1998, July 1999) than towards the end of a season (March 1999, February 2000) (Tukey's HSD tests $P < 0.04$ after post hoc pooling of the Plot (Treatment) and residual mean square estimates).

6.7.3. Eastern curlew foraging efficiency and density

As five variables (*Trypaea* capture rate, *Mictyris* capture rate, "small-prey" capture rate, foraging success and individual density) were analysed using two ANOVA designs (see Methods) resulting in a large number of statistics, only the statistics for the significant terms are presented (Table 6.3, 6.4). The overall temporal and between-treatment trends in curlew foraging behaviour and density can be assessed in Figure 6.7A-D.

There was no short-term response in the curlew foraging efficiency or abundance that could be attributed to *Trypaea* harvesting. The rate, with which the curlews took "small-prey" declined by ca. 50 % between the BEFORE and AFTER periods, while the density of the birds was significantly lower in the experimental plots regardless of the Period (Table 6.3).

There was no delayed response in the curlew foraging efficiency or abundance that could be attributed to *Trypaea* harvesting. However, there was a highly significant Time effect on all the variables except the small-prey capture rate (Table 6.4). Post-hoc analyses showed that *Trypaea*-capture rate was significantly greater in February-March 1999 than during all the other months

(Tukey's HSD tests, $P < 0.05$). *Mictyris*-capture rate tended to be greater at the start of a non-breeding season (November 1998 and October 1999) than during the rest of the year (Tukey's HSD tests, $P < 0.04$). Foraging success generally tracked *Mictyris*-capture rate (Fig. 3C). Foraging success was significantly higher in November 1998 than in March 1999 and also in October 1999 than in February 2000, i.e. the start and the end of both non-breeding seasons (Tukey's HSD tests, $P < 0.04$). Finally, the significant temporal trend in the curlew density was primarily driven by the March 1999 counts which were lower than any other Times due to the start of northward migration (Tukey's HSD tests, $P < 0.01$).

6.7.4. Estimated seasonal depletion of the *Trypaea* stock by the curlews

Overall, eastern curlews were more abundant in the plots with higher *Trypaea* densities (Figure 6.8). At the same time, the abundance of the birds was not related to the *in situ* abundance of *Mictyris* ($R^2 = 0.01$, $P > 0.05$). Based on observations of 612 focal birds (n = 2690 individual prey items) collected in the course of the study, *Mictyris longicarpus* comprised 44 ± 42% of eastern curlew diet, unidentified small prey, 31 ± 35%, and *Trypaea australiensis* comprised 17 ± 28% of diet. The remaining 8% consisted of *Macrophthalmus*, *Penaeus* and echiuran proboscises. The mean, seasonal capture rates of *Trypaea* achieved by eastern curlews in 1998-99 and 1999-2000 were 0.31 ± 0.51, (n = 480) and 0.16 ± 0.28 (n = 132) *Trypaea* * min^{-1}, respectively. The mean, seasonal densities of curlews in 1998-99 and 1999-2000 were 1.83 ± 1.18 (n = 319) and 2.02 ± 1.02 (n = 115) birds * ha^{-1}, respectively. These estimates can be used to calculate the average number of *Trypaea* removed per unit area per season. Curlews spent ca. 180 days in the study area (October to March) with 716 min (two x 358 min low tides) per day available for foraging, of which 65.1 ± 19.6% (n = 347 scans) was spent engaged in foraging activity. Thus, the curlews would have removed 4.8 and 2.7 Trypaea * m^{-2} * season^{-1} in 1998-99 and 1999-2000, respectively. Considering that the overall density of *Trypaea* was 12.9 individuals * m^{-2} at the start of the season in October 1998 and 3.4 *Trypaea* * m^{-2} just before the start of the season in August 1999, this removal estimate represents 37.2% and 79.4% of the initial stock, respectively. If only the *Trypaea* size-cohort taken by the curlews (5-11 mm CL) are considered, with a density of 4.7 and 2.8 individuals * m^{-2} for the same periods, the corresponding estimated seasonal removal values increase to ≈ 100%.

Removal of the *Mictyris* stock was not estimated because only a small proportion of the overall population remained buried at low tide and thus was effectively sampled in this study. Consequently, curlews tended to capture most of these crabs on the surface rather than from the sediment and unlike *Trypaea*, *Mictyris* roamed widely at low tide moving in and out of the plots.

6.8. Discussion

The design of the experiment was intended to mimic the levels of intensity and spatial scale of harvesting of a callianassid shrimp (*Trypaea australiensis*) by bait-collectors operating in SE Australia (and elsewhere) and therefore provide a realistic indication of whether such harvesting causes impacts on migratory shorebirds. The intended goals were achieved and the results obtained here suggest that, presently, collection of burrowing shrimp for bait does not produce strong impacts either on the shrimp themselves or on wading birds using the shrimp as prey.

6.8.1. Harvesting intensity levels

Several lines of evidence indicate that the intensity of harvesting applied to the experimental plots was of the correct magnitude. First, on average, 347 *Trypaea* (range 115-834 individuals) were removed from each of the 1 ha experimental plots on each harvesting event. The pattern of the experimental harvesting was modelled on the patterns exhibited by recreational harvesters collecting bait for a regular fishing tournament (McPhee & Skilleter, 2002b). There, individual bait collectors harvested 84 *Trypaea* per fishing event (range 30-300 individuals), covering an average distance of 700 metres in doing so. Assuming that the width of the path of an individual collector is about 4 m (McPhee & Skilleter, 2002b), the intensity of harvest of *Trypaea* by recreational collectors equates to (84 * 10,000)/(700 * 4) = 300 Trypaea * ha^{-1} per fishing event. Bait-collectors in South Africa (Knysna estuary) fishing for the mud-prawn *Upogebia africana* collected a similar number of animals (59 to 101) per fishing event (Hodgson et al., 2000), probably resulting in a similar level of harvesting intensity per unit area. It is a reasonable assumption that individual bait collectors will fish once a day (Hodgson et al., 2000; McPhee & Skilleter, 2002b). Second, based on the total number of harvesters collecting *Trypaea* (Table 1, McPhee & Skilleter ,2002b), 4,500 and 3,900 *Trypaea* were removed from the two most heavily used collection sites over 7 days. The areal extent of these sites was 4.1 ha and 1.6 ha respectively (personal observation), equating to a total harvest of between 160 and 350 *Trypaea* * ha^{-1} * day^{-1}. Third, Wynberg & Branch (1991) estimated the maximal annual harvest of callianassids *Callianassa kraussi* in Langebaan Lagoon, South Africa to be approximately 800,000 from a 20-ha area. Since, similarly to SE Australia (McPhee & Skilleter, 2002b), most bait-harvesting in South Africa occurs on week-ends and public holidays (Hodgson et al., 2000), this latter number scales down to ~300 – 350 burrowing shrimp removed per ha per day. Thus, the intensity of harvesting employed in this study was of the same magnitude as occurs in areas frequented by bait collectors. It is remarkable that the estimates of harvesting intensity from such a broad geographical and temporal range appear to be so similar. This is likely because the harvesting of burrowing shrimp is limited by the equipment (manual pump) and physical capacity of an average fisher and thus does not allow for much variability.

6.8.2. Importance of appropriate spatial scale

In this study, the experimental manipulations were done at the spatial scale that would be relevant to both the scale of disturbance by bait collectors and the scale at which the response of shorebirds would likely be detectable, i.e. the scale of hectares. To demonstrate the importance of using the appropriate scale in studies similar to this one it is useful to compare this approach and results to the approach and results of a very similar experiment done in South Africa by Wynberg & Branch (1994) (see also Wynberg & Branch, 1997). The South African study, conducted in Langebaan Lagoon, experimentally simulated effects of bait harvesting (pumping and digging) in the intertidal zone on two species of burrowing shrimp (*Callianassa kraussi* and *Upogebia africana*) and the associated infaunal biota. The study aimed at examining how the response of benthos would vary between two methods of harvesting and over time. Experimental units in the study were 12 m^2 plots (= extent). Several hundred (244-726 depending on the method and individual plot) shrimp were removed from each impact plot and the recovery of these plots was compared over time with reference areas. Results of the impacts were rather dramatic decreases in the densities of shrimp and associated biota. These results suggest that under certain conditions, the impact from this type of harvesting on the community structure of the whole estuary may be quite high, but such a conclusion may be erroneous. Wynberg & Branch conceded that the actual frequency of bait-harvesting events in the Lagoon was too low and sparsely distributed to result in any large scale effects. Indeed, if the number of shrimp removed in their study is scaled from a 12 m^2 plot to 1 ha, estimates of 200,000-600,000 shrimp removed in just one harvesting event are obtained. Yet, Wynberg & Branch (1991) estimated the maximal annual harvest of burrowing shrimp in the whole of Langebaan Lagoon at only 1,200,000 (or 800,000 from the most heavily used 20 ha area). This latter number, as shown above, scales down to 300-350 shrimp removed per ha per day. Therefore, while the design employed in Wynberg & Branch's (1994) experimental study does show what happens at a very small scale after rather destructive harvesting, it provides little information about the broad scale (community-level) implications of what in general appears to be a rather low-intensity bait fishery (0.001 – 3.2% removal of the annual standing stock). However, it is precisely the (potential) broad-scale effects of a particular disturbance that are most relevant for any management or conservation initiatives. Indeed, a study from another South African estuary with a long history of bait harvesting of this type showed no broad-scale impacts on the populations of burrowing shrimp (Hodgson et al., 2000 and references therein). Our experimental results agree with the observational findings of Hodgson et al. (2000). The discrepancy with the small-scale study described above may be explained by the fact that small-scale effects of intensive disturbance do not scale up to larger areas due to sparse distribution of bait collectors on the one hand and resilience of burrowing shrimp (Thalassinidea) to high rates of predation (see below) on the other.

6.8.3. *Trypaea* harvesting and eastern curlews

Eastern curlews responded numerically to the spatial patterns of *Trypaea* abundance signifying, independently from direct visual observations, (1) the importance of this decapod as prey for the birds and (2) the appropriateness of the selected spatial scale for the experiment (Gill et al., 2001). Removal of *Trypaea* from the experimental plots aimed to test whether foraging efficiency and/or density of eastern curlews would be affected by harvesting of an important component of their diet. Experimental harvesting occurred at the intensity levels commensurate with recreational bait-collection. These levels on average were almost 2 times higher than the intensity of curlew predation over the same time period (Table 6.5). However, if the frequency of the harvesting events is also taken into account, the number of *Trypaea* that was harvested appears relatively small compared with what was taken by the curlews. Experimental harvesting removed 1.27 ± 0.93% (n = 6 events that occurred when the curlews were present in the area) of the *Trypaea* population from the manipulated plots per day (Table 6.5). Eastern curlews consumed 0.76 ± 0.64% (n = 4) of the *Trypaea* population per day in the manipulated plots (Table 6.5). This means that each of the removal sessions resulted in almost trebling of the predation pressure on the harvested *Trypaea* population but for only one day whereas curlew predation was continuous. Such an increase in the removal of prey is probably ecologically trivial compared with the more intense and continuous effect of the birds and would be extremely difficult to detect statistically. In this context, it is noteworthy that at two South

African estuaries (Swartkops Estuary, Hanekom & Baird, 1982; Knysna Estuary, Hodgson et al., 2000)) supporting sizable populations of bait collectors, burrowing shrimp and shorebirds, bird consumption of the shrimp was also shown or suggested to far outweigh levels of human harvesting.

The important result here from a conservation and management perspectives is that, unlike commercial harvesting of benthos (Norris et al., 1998; Stillman et al., 2001), recreational harvesting at its present levels of intensity is unlikely to be a significant problem for maintaining stocks of prey used by non-breeding shorebirds. Either intensity and/or frequency of bait-collection have to increase considerably (e.g. due to mechanisation of pumping) to impact migratory shorebirds preying on benthos collected for bait. Any potential impact on the eastern curlews in Moreton Bay from bait harvesting is more likely to come from the disturbance of these birds by bait collectors present on the mudflats (Cornelius et al., 2001; but see de Boer 2001) than from the removal of their prey per se.

6.8.4. Eastern curlews and their *Trypaea* food supply

Although the experimental harvesting did not impact on the curlews, the data obtained provide an insight into the relationship between the predator and an important component of its diet, *Trypaea* and thus serve as an example of predator-prey dynamics at a warm-climate non-breeding shorebird site.

Given the rate of consumption of *Trypaea* by eastern curlews in this study, ≈ 100% of the size-cohort of the *Trypaea* population taken by the birds, present at the start of a non-breeding season (October), would have been removed by the time of the birds' departure (March). Despite this, there was no evidence of a long-term decrease in the *in situ* abundance of *Trypaea*. In fact, the population trend of *Trypaea* of the sizes taken by the curlews showed little temporal variability. Corresponding to this stable trend in their prey densities, curlew densities in the study area varied little among the months of a season and from season to season, in agreement with Finn et al. (2001), who also observed temporally stable curlew densities across a range of sites in Moreton Bay. Curlew consumption of *Trypaea* increased towards the end of a season (i.e. there was a seasonal diet shift to rather than from *Trypaea*) also suggesting that the availability of *Trypaea* did not decrease as the season progressed.

The overall density of *Trypaea* decreased two-fold between October 1998 and March 1999 when the curlews were feeding on the flats. This decrease continued at roughly the same rate into July, when no curlews were present in the study area and thus it could not be attributed to predation by the birds (see Figure 6.6A, Table 6.5). This implies that important mortality factors other than curlew predation affected the *Trypaea* population. Specifically, in October 1998, when the greatest standing stock estimate of *Trypaea* was obtained, most of the shrimp in the samples (62%) were individuals with the carapace length < 5 mm. The percentage of these immature (McPhee & Skilleter, 2002a) *Trypaea* subsequently decreased and from March 1999 varied between 5 and 19% of the population. Therefore, most of the mortality during the period from October to March occurred in the < 5 mm size-cohort of the *Trypaea* population (Fig. 2A), whereas curlews consume *Trypaea* ≥ 5 mm CL. Indeed, such high mortality of young recruits of benthic organisms is not uncommon and often occurs in a density-dependent fashion, regardless of shorebird predation (van der Meer et al., 2001). Importantly though, since presence of potential recruits is thought to have a stabilising effect on the density of adult benthos populations (Beukema & de Vlas, 1979; André & Rosenberg, 1991; Beukema et al., 2001), the presence of immature *Trypaea* through most of the year (McPhee & Skilleter, 2002a), may be one factor responsible for the stable seasonal trend in the local adult *Trypaea* densities. Another factor contributing to the stability of local shorebird food supply is the density-dependent nature of recruitment patterns in for many benthic animals (Schneider, 1985). Apart from the post-recruitment period (after October 1998) there was little or no temporal modal shift in size structure in the *Trypaea* population (see also Hailstone and Stephenson, 1961). These findings suggest that recruitment into the population of *Trypaea* probably takes place in a density-dependent fashion as happens in other benthic invertebrates (Kent & Day, 1983; Wilson, 1989; Kalejta, 1993; Flach & Beukema, 1994; Goss-Custard et al., 1996).

It is also possible that replenishment of the exploited *Trypaea* population results from local (secondary) redistribution of individuals rather than from the settlement directly out of the water column, especially if juveniles initially settle in different parts of the intertidal zone (Schneider, 1985; Dittmann & Vargas, 2001). However, existence of such an additional (proximal) step in the maintenance of the stable density of the adult (= curlew prey) population would still require temporal predictability and density-dependence in the recruitment patterns of these invertebrates.

A number of studies of non-breeding shorebird foraging behaviour and distribution, using methods similar to ours, demonstrated considerable seasonal decreases in local densities of their benthic prey (Baird et al., 1985; Schneider, 1992; Székely & Bamberger, 1992; Meire et al., 1994 and references therein). Such decreases, attributed to shorebird predation, were usually followed by reductions in local bird densities and/or switching to alternative prey types (Székely & Bamberger,1992; Zwarts & Wanink, 1993). The difference between our predator-prey system and the systems in which considerable depletion of local prey densities was detected is that, as shown above, in our warm-climate subtropical environment, prey reproduction and recruitment run parallel to prey removal by predators. By contrast, most previous work of this kind was carried out in north temperate areas in which benthic reproduction is strongly seasonal and no or little stock replenishment takes place over a course of a shorebird non-breeding season (Beukema et al., 1993; Beukema et al., 2001). This fundamental difference in the rates and timing of replenishment of food stocks (Schneider, 1985; Wolff, 1991) is the most likely explanation for the observed greater carrying capacity (in shorebirds per unit area) between warm-climate (tropical/subtropical) and cold-climate (temperate) non-breeding sites (Hockey et al., 1992). Thus, one could speculate that all else equal, any negative large-scale effect resulting in the reduction of shorebird food base at a warm-clime non-breeding site is likely to have stronger global consequences on the species/population, than a similar-magnitude effect occurring at a northern site (Goss-Custard et al., 1994).

Table 6.1. Analyses of variance of the bar-tailed godwit density, capture rate and foraging success (all $\log_e(x+1)$ transformed except for success, see Methods for design details) in control and experimental plots. Degrees of freedom for F, Treatment=1,4; Plot(Treatment)=4,161; Time=2,8; Time * Treatment=2,8; and Time * Plot(Treatment)=8,161. Significant P-values highlighted.

FACTOR	Treatment		Plot(Tr)		Time		Time * Tr		Time * Pl(Tr)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Density	8.11	**0.046**	2.32	0.06	0.70	0.53	2.20	0.17	0.92	0.50
Capture rate	11.43	**0.028**	0.80	0.53	14.92	**0.002**	0.68	0.53	2.56	**0.011**
For. success	17.10	**0.014**	0.19	0.94	12.94	**0.003**	1.07	0.39	1.92	0.06

Table 6.2. Analyses of variance of the effects of *Trypaea* harvesting on (1) the total abundance of *Trypaea australiensis*, (2) the *Trypaea* size-cohort (carapace length = 5 – 11 mm) consumed by the eastern curlews, and (3) *in situ* abundance of *Mictyris longicarpus*. $\text{Log}_e(x+1)$ transformed data were used to stabilise variance following significant Cochran C-tests for homogeneity of variance on raw data.

FACTOR	Total *Trypaea*	CL=5-11 mm *Trypaea*	*Mictyris*
Treatment ($F_{1,4}$, P)	3.72, 0.13	1.11, 0.35	20.76, 0.01
Time ($F_{5,20}$, P)	16.85, <0.001	7.12, <0.001	12.88, <0.001
Plot (Treatment) ($F_{4,324}$, P)	1.44, 0.22	2.59, 0.031	0.54, 0.71
Treatment*Time ($F_{5,20}$, P)	0.84, 0.53	1.33, 0.29	1.72, 0.18
Time*Plot (Treat.) ($F_{20,324}$, P)	1.58, 0.056	1.32, 0.16	1.14, 0.30

Table 6.3. Analyses of variance of short-term effects of *Trypaea* harvesting on the eastern curlew (1) prey-specific capture rates (prey * min^{-1}), (2) foraging success and (3) density (birds * ha^{-1}). Raw data were used, except for *Trypaea* capture rate which was $\log_e(x+1)$ transformed to stabilise variance following a significant Cochran C-test for homogeneity of variance.

FACTOR	*Trypaea*	*Mictyris*	"Small-prey"	Success	Density
Treatment (C/I)	NS	NS	NS	NS	$F_{1,8}=8.3$, $P=0.02$
Period (B/A)	NS	NS	$F_{1,8}=12.2$, $P<0.01$	NS	NS
Time	NS	NS	NS	NS	NS
Treat. * Period	NS	NS	NS	NS	NS
Treat. * Time	NS	NS	NS	NS	NS
Treat.*Period*Time	NS	NS	NS	NS	NS

Table 6.4. Analyses of variance of delayed effects of *Trypaea* harvesting on the eastern curlew (1) prey-specific capture rates (prey * min^{-1}), (2) foraging success and (3) density (birds *ha^{-1}). Raw data were used following non-significant Cochran C-tests for homogeneity of variance.

FACTOR	*Trypaea*	*Mictyris*	"Small-prey"	Success	Density
Treatment (C/I)	NS	NS	NS	NS	NS
Time	$F_{6,24}=8.3$	$F_{6,24}=6.8$	NS	$F_{6,24}=4.3$	$F_{6,24}=7.4$
	$P<0.001$	$P<0.001$		$P=0.005$	$P<0.001$
Treat. * Time	NS	NS	NS	NS	NS

Table 6.5. *Trypaea australiensis* population size in the experimental (harvested) and control plots, the absolute numbers of *Trypaea* and proportions of the population experimentally removed per each harvesting event (day) and the estimated numbers of *Trypaea* and proportions of the population consumed by the eastern curlews per day during the same time period.

Trypaea stock assessment	Total (CL=5-11 mm) *Trypaea* population[1]	*Trypaea* (% total) removed per harvesting event[2]	Estimated *Trypaea* (% total and % CL=5-11 mm population) consumed by eastern curlews per day[3]
Time 1 (Oct 1998)			
Experimental	387,750 (157,000)	816 (0.21)	80 (0.02, 0.05)
Control	384,500 (125,250)		120 (0.03, 0.10)
Time 2 (Mar. 1999)			
Experimental	153,250 (142,250)	693 (0.45)	2328 (1.52, 1.64)
Control	211,500 (199,500)		2598 (1.23, 1.30)
Time 3 (July 1999)			
Experimental	101,750 (88,250)	1460 (1.43)	
Control	90,250 (82,500)		
Time 4 (Aug. 1999)			
Experimental	80,500 (68,250)	1255 (1.56)	
Control	121,000 (100,250)		
Time 5 (Dec. 1999)			
Experimental	61,000 (47,500)	1723 (2.81)	308 (0.50, 0.65)
Control	91,000 (73,750)		362 (0.40, 0.49)
Time 6 (Feb. 2000)			
Experimental	90,750 (69,250)	1029 (1.13)	888 (0.98, 1.28)
Control	63,500 (47,750)		800 (1.26, 1.68)

[1] The total *Trypaea* population per stock assessment per treatment was estimated following Schneider (1992) as:

$$T_t = \sum^{N_t} a \sum^{N_s} T_s$$

where T_t is the total *Trypaea* population; $N_t = 3$ is the number of plots per treatment; _ is the reciprocal of the proportion of a 1 ha plot sampled per stock assessment; $N_s = 10$ is the number of 4 m^2 samples (quadrats) taken per plot and T_s is the number of *Trypaea* per sample.

[2] Only those harvesting events that occurred within a month of a stock assessment are included here. Thus, harvesting events that occurred in January and May 1999 (Fig. 1) we omitted from the table.

[3] The number of *Trypaea* consumed by the eastern curlews per day was estimated as the product of the average monthly treatment-specific *Trypaea* capture rate (Fig. 3A), the average monthly treatment-specific curlew density (Fig. 3D) and the proportion of time spent foraging and the duration of a diurnal low tide given in the Results. No estimates were made for the austral winter months because no or very few eastern curlews were present then in the study area.

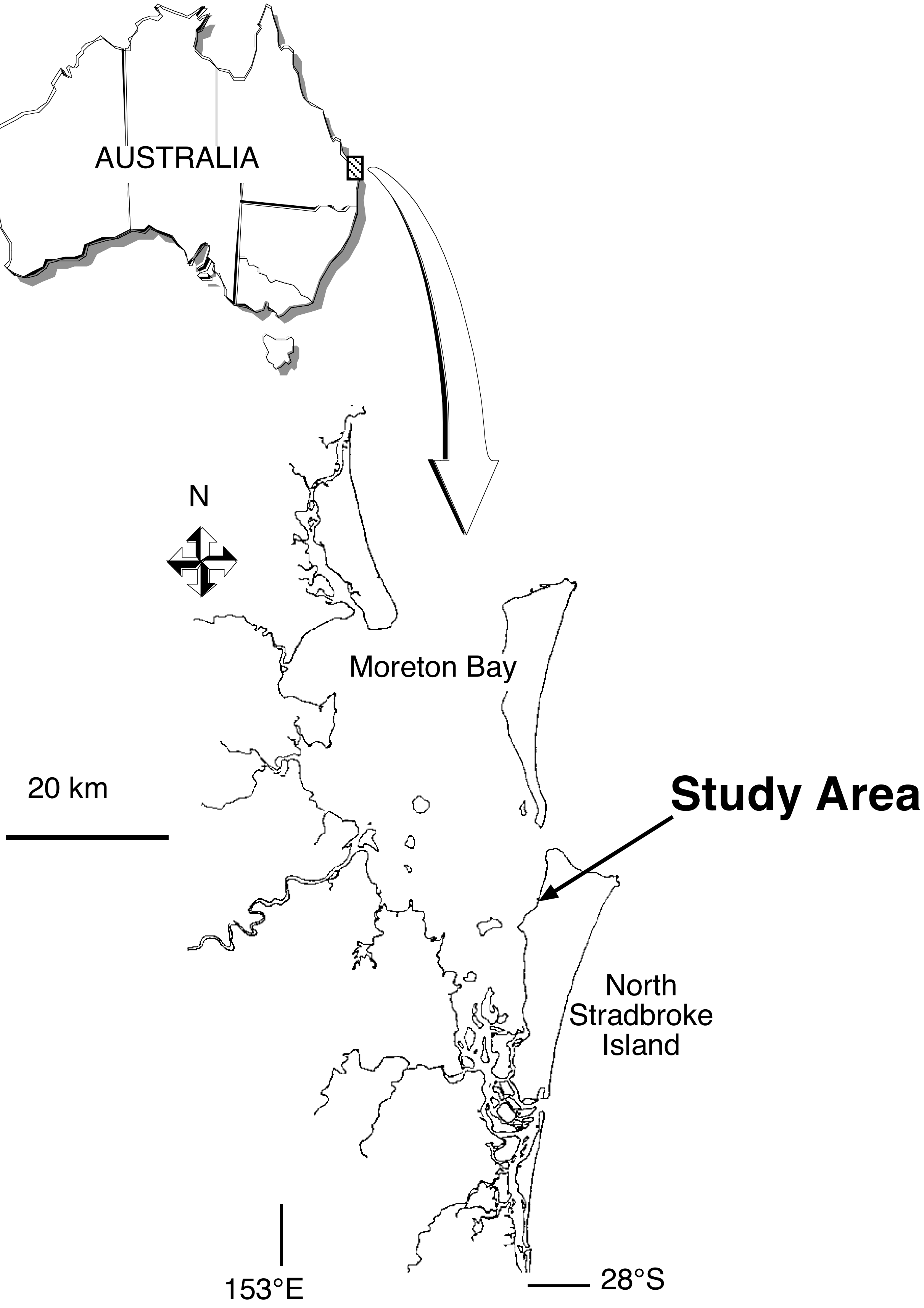


Figure 6.1: Map of Australia and Moreton Bay, showing North Stradbroke Island and the study site at Chiggill Chiggill where the studies on shorebirds were done

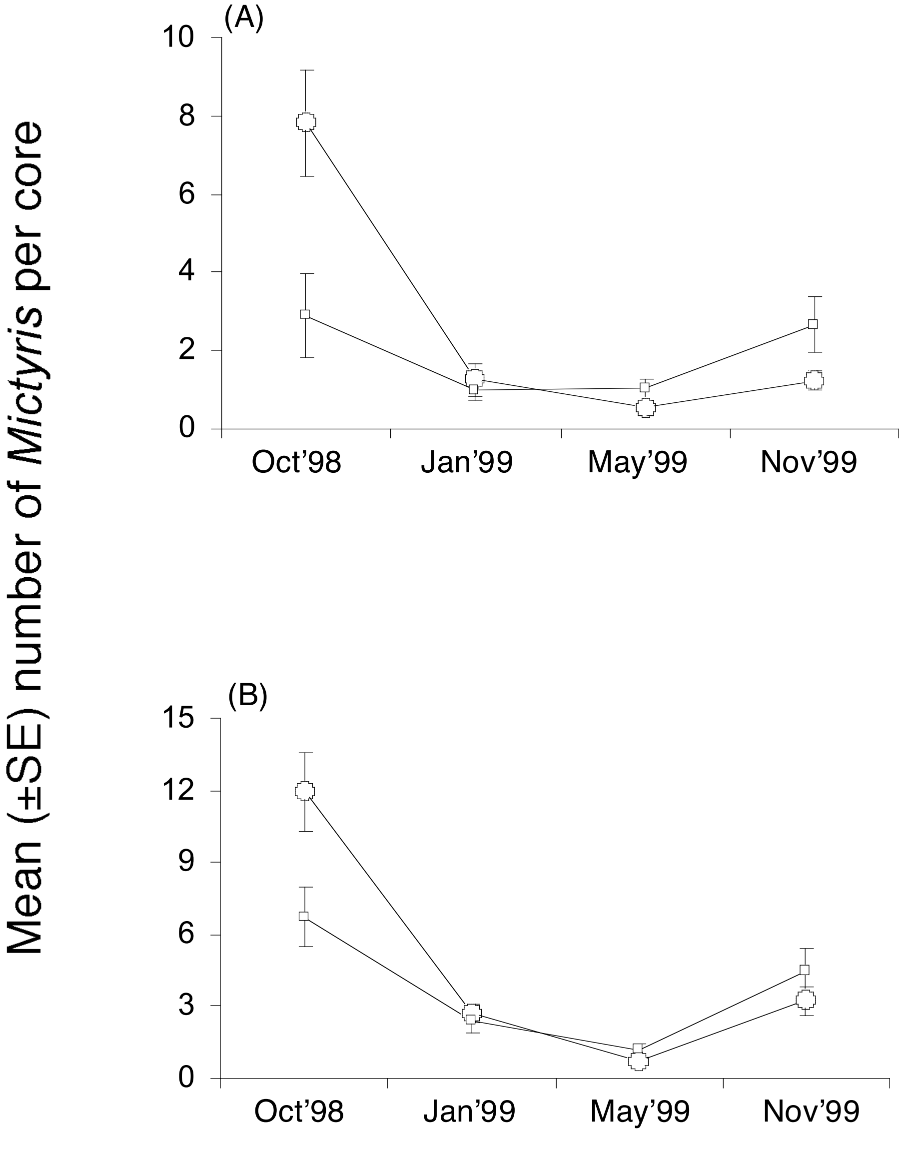


Figure 6.2: Mean (±SE) abundances of *Mictyris longicarpus* in control (square) and experimental (circle) plots estimated per 5 cm deep (A) and 15 cm deep (B) benthic cores. First *Trypaea* removal took place between the October and November 1998 sampling sessions.

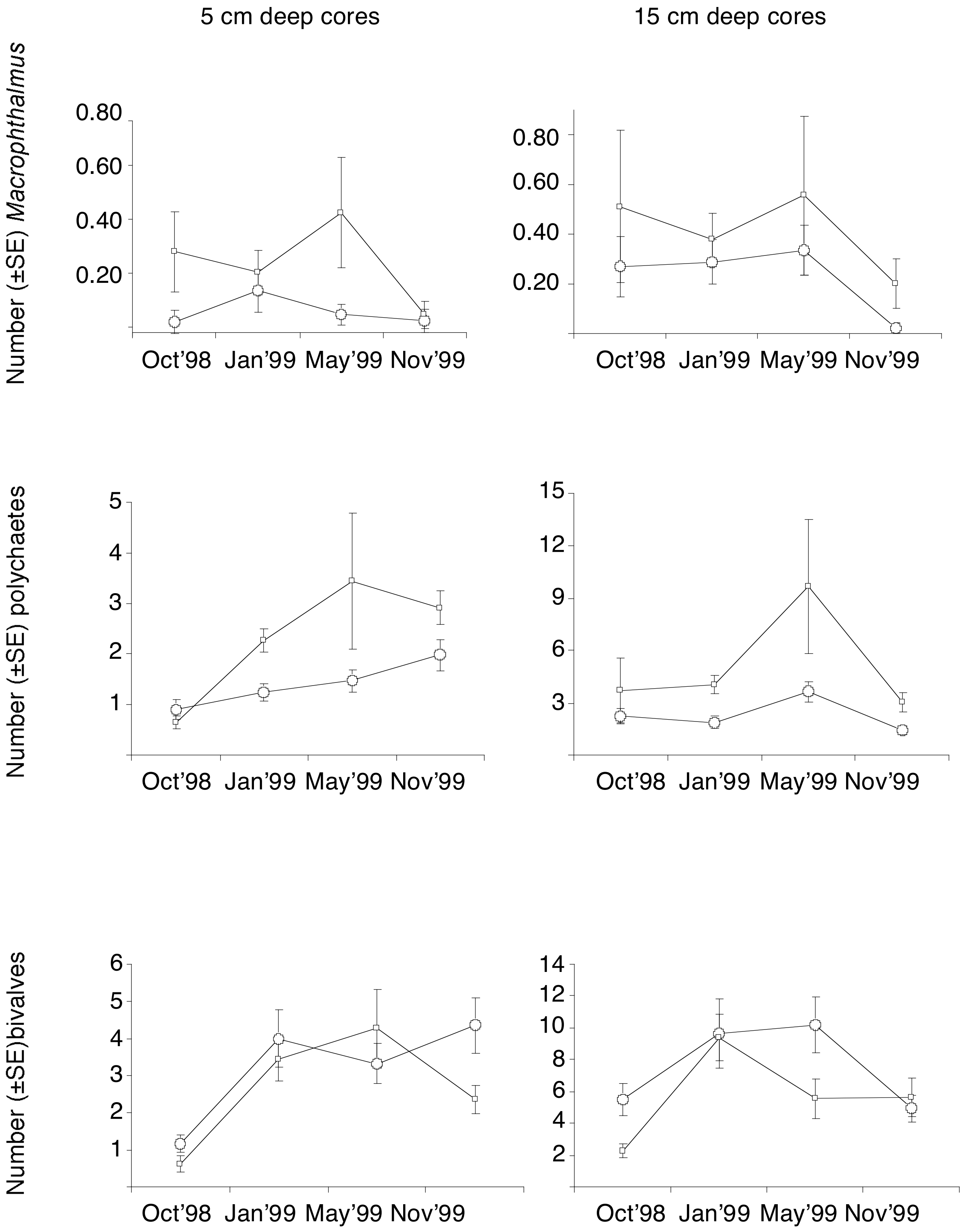


Figure 6.3: Mean (±SE) number of macrophthalmid crabs, polychaetes and bivalves in control (squares) and harvested (circle) plots in 5 cm deep (A, C, E) and 15 cm deep (B, D, F) cores. First removal took place between the October and November 1998 sampling sessions. Note the different scales on the Y-axes.

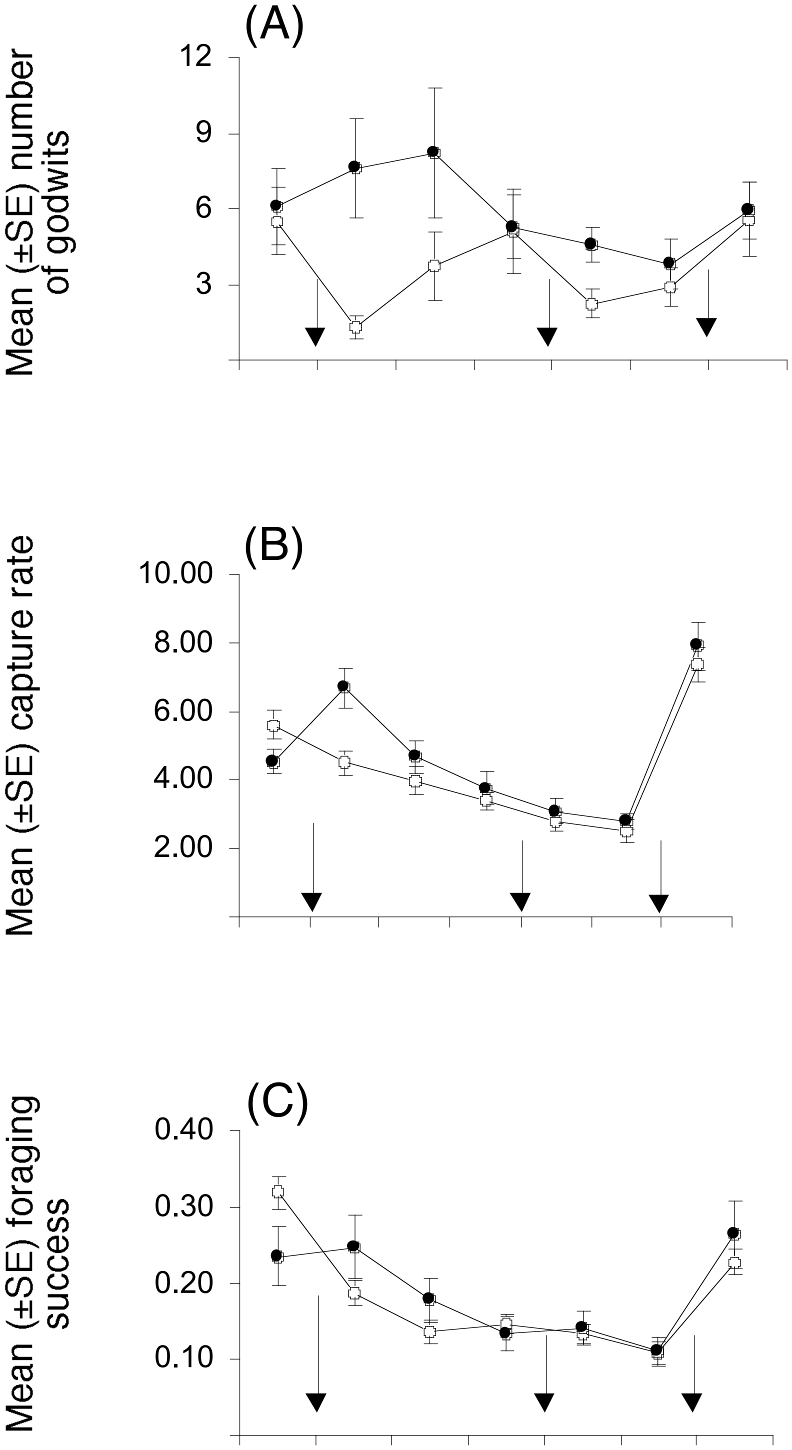


Figure 6.4: Mean (±SE) number of godwits (A), capture rate (B) and foraging success (C) for bar-tailed godwits, Limosa lapponica in control (square) and harvested (circle) plots during the study period. Arrows indicate the dates when experimental harvesting was applied. (A) Sample sizes for counts of the numbers of birds for each month in control and harvested plots respectively were: October 98 - 30, 55; November 98 - 27, 28; December 98 - 8, 30; January 99 - 29, 31; February 99 - 33, 28; March 99 - 32, 31; October/November 99 - 32, 27; February 2000 - 28, 28. (B, C) Capture rate and foraging success sample size for each month x treatment combination = 36. Within season (1998/99) correlations were: month and density: r_p=-0.01, p>0.85, n=382; capture rate: r_s=-0.42, p<0.001, n=432; and foraging success: r_s=-0.46, p<0.001, n=432.

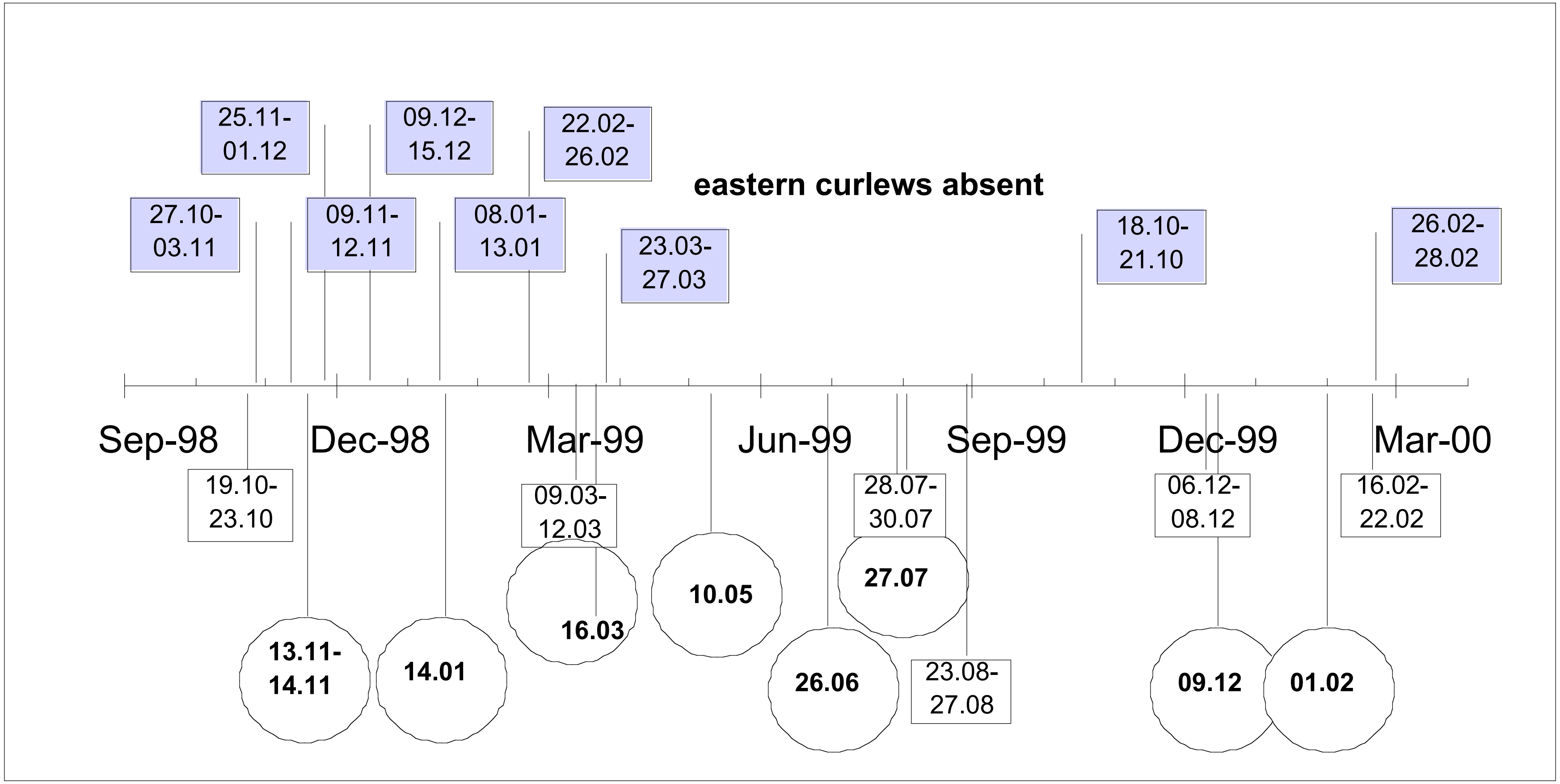


Figure 6.5: The temporal sequence and exact dates for each of the *Trypaea* harvesting events (circles below the time-line), *Trypaea* and *Mictyris* stock assessments (rectangles below the time-line) and periods of eastern curlew counts and focal observations (grey-shaded rectangles above the time-line) that occurred during the course of the experimental study.

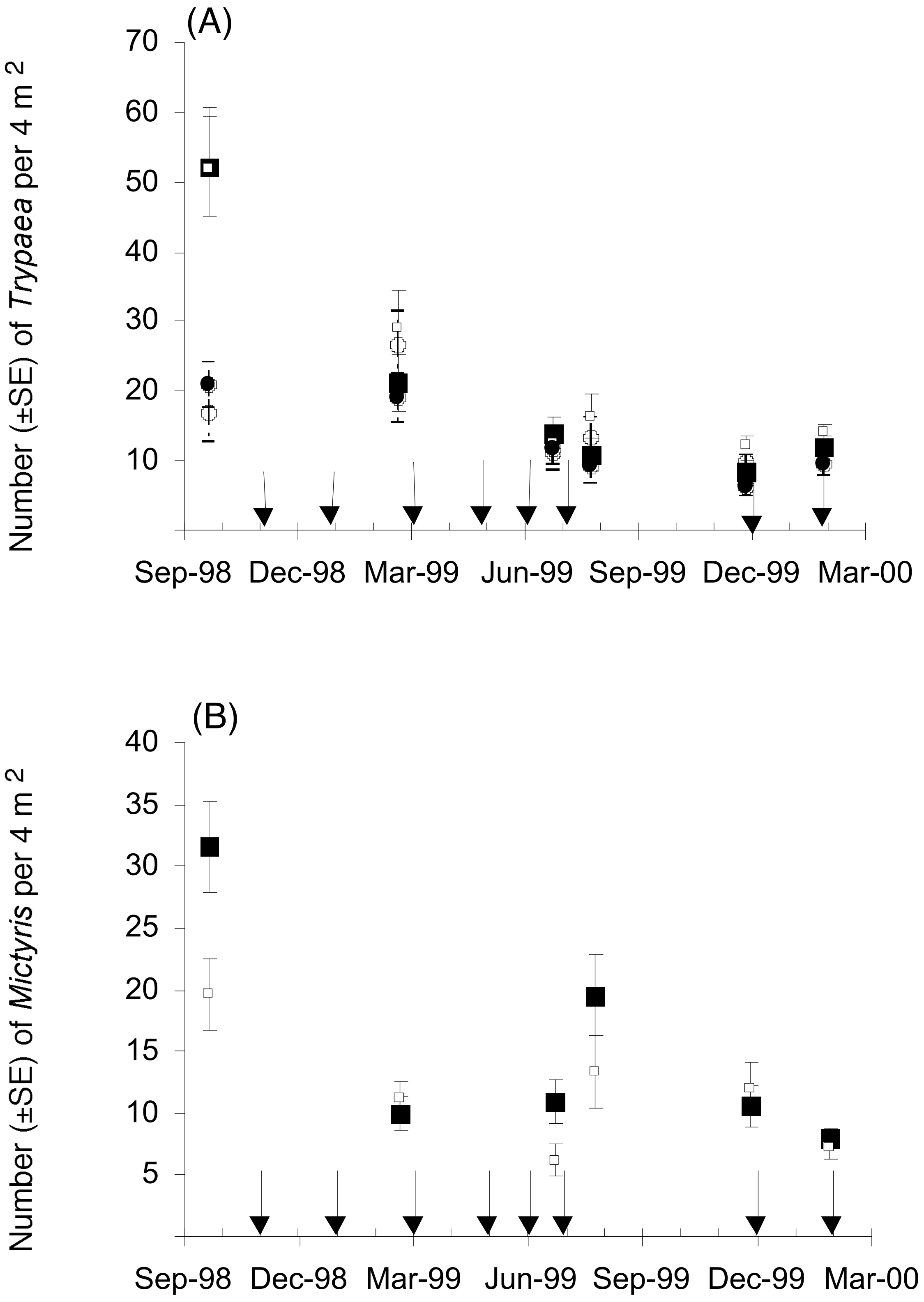
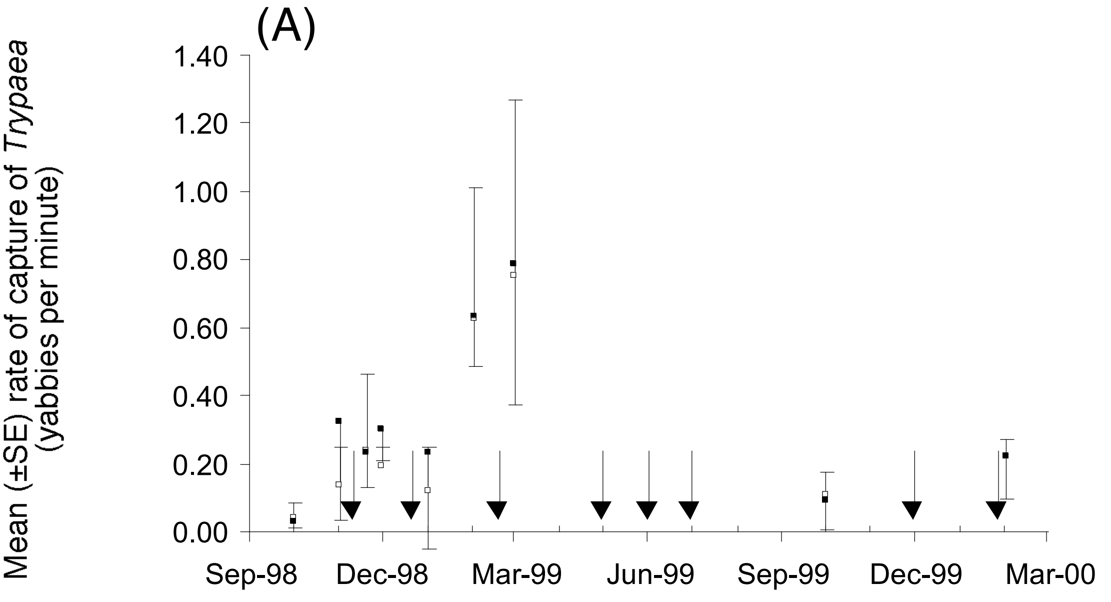


Figure 6.6: Mean (±SE) in situ abundances of (A) *Trypaea australiensis* and (B) *Mictyris longicarpus* in 4 m2 quadrats in control (open symbols) and harvested (solid symbols) plots. Squares in (A) represent the total *Trypaea* population while circles represent the 5 to 11 mm carapace length size-cohort. Arrows indicate the timing of harvesting events (see Methods for further details).



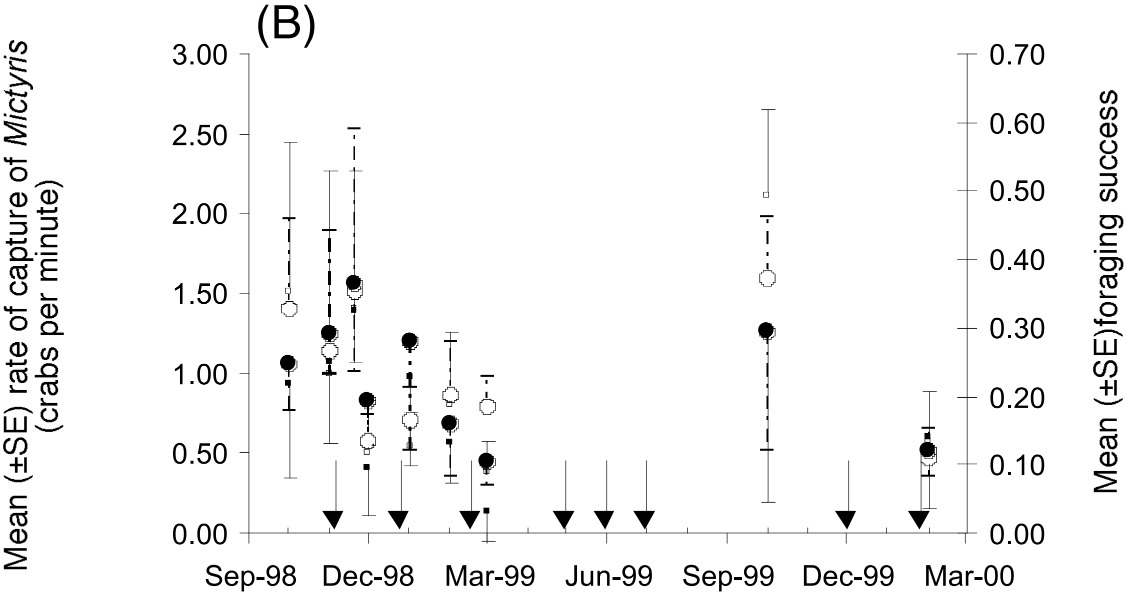


Figure 6.7: Mean (±SD) (A) rate of capture of *Trypaea*, (B) rate of capture of *Mictyris* (squares) and foraging success on *Mictyris* (circles), (C) rate of capture of 'small-prey' and (D) abundance of eastern curlews, *Numenius madagascariensis*, foraging in control (open symbol) and harvested (solid symbol) plots. The mean and error estimates are based on the averages of three plots per day obtained for each treatment each month for each of the five variables except for in November 1998, when two plots per day were sampled (see Methods for more details).

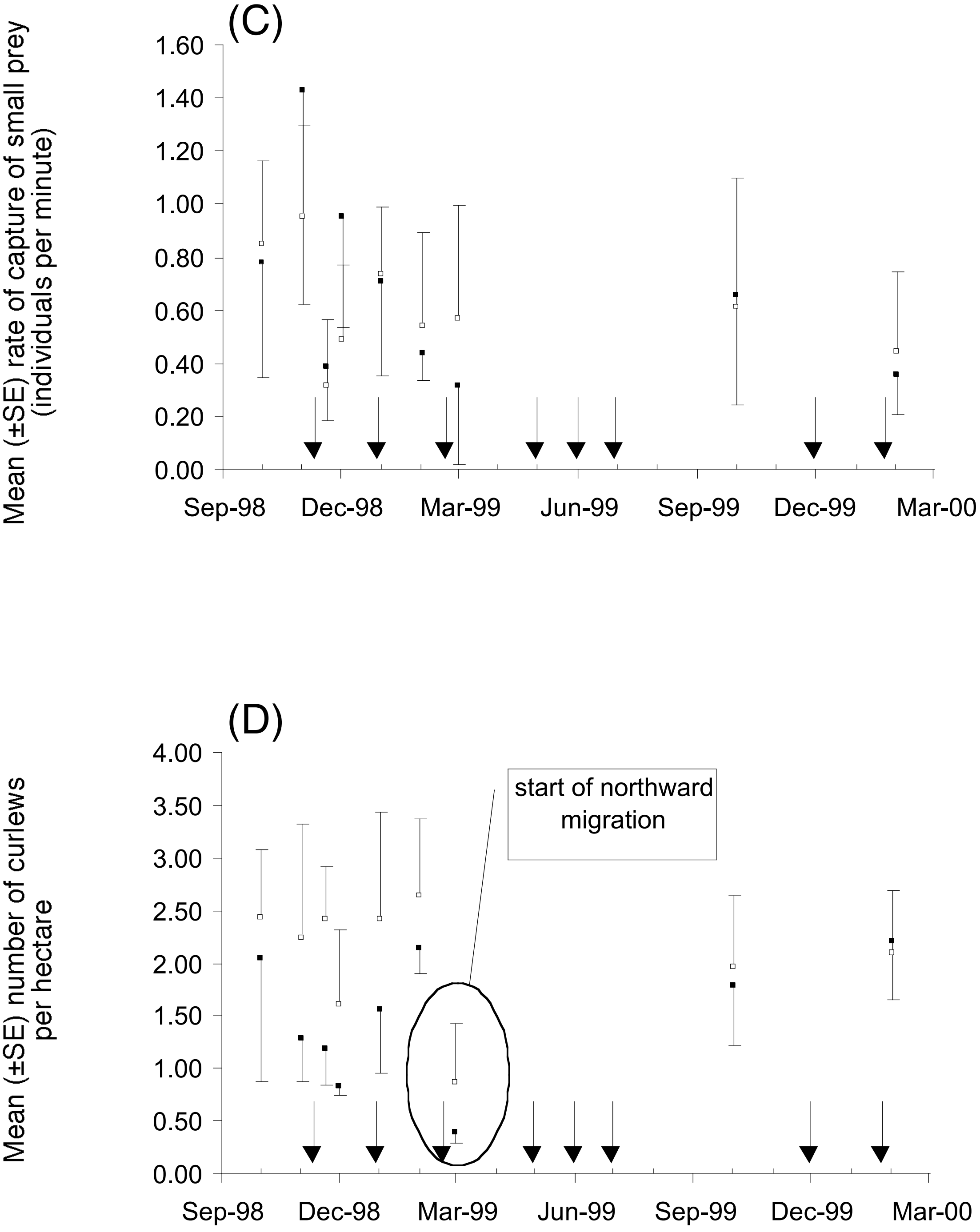


Figure 6.7 continued: Mean (±SD) (C) rate of capture of 'small-prey' and (D) abundance of eastern curlews, *Numenius madagascariensis*, foraging in control (open symbol) and harvested (solid symbol) plots. The mean and error estimates are based on the averages of three plots per day obtained for each treatment each month for each of the five variables except for in November 1998, when two plots per day were sampled (see Methods for more details).

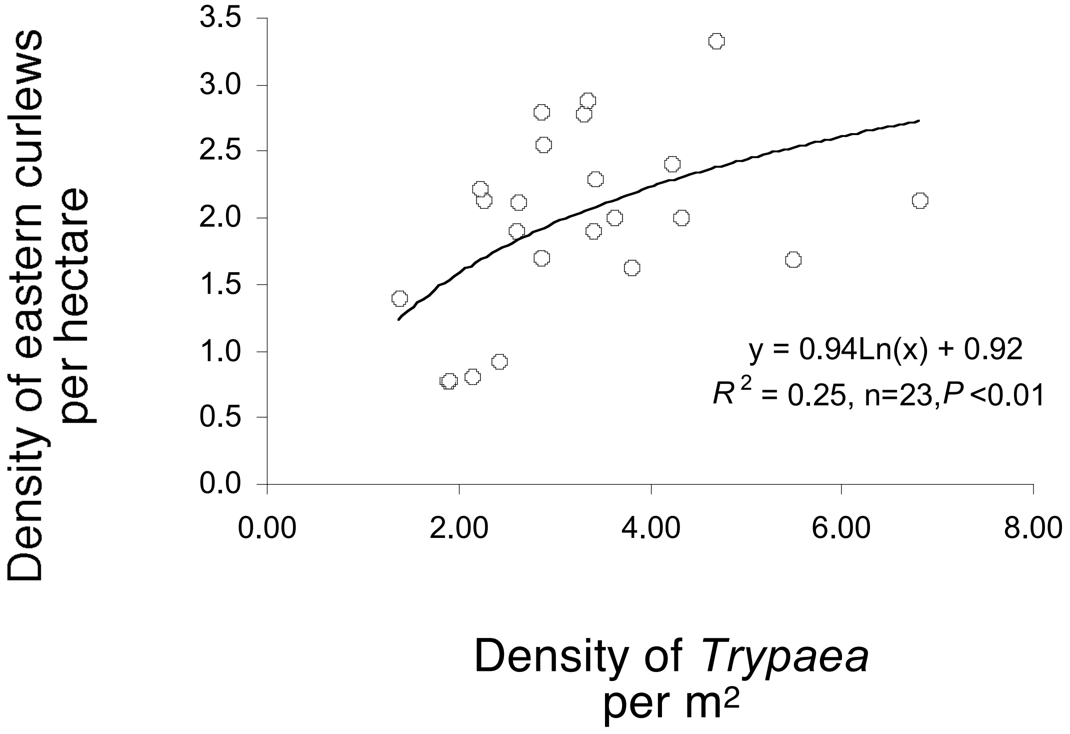


Figure 6.8: A relationship between the mean in-plot density of eastern curlews density and mean in-plot density of *Trypaea* with carapace length of 5 to 11 mm. The figure combines the *Trypaea* density estimates from four stock assessments made in October 1998, March 1999, December 1999 and February 2000, with the eastern curlew density estimates obtained during the same or immediately preceding (February 1999) months. The dataset excludes one data point (an experimental plot from October 1998) with an unusually small mean density of eastern curlews that may have been the result of a high level of local activity of raptors on that day.

Section 7: Conclusions

There were five objectives in this study:

1. To assess the ecological impacts associated with commercial and recreational harvesting of yabbies and bloodworms on other components of the ecosystem;
2. To assess the impacts of bait-harvesting activities on the sustainability of populations of yabbies (*Trypaea australiensis*) and bloodworms (*Marphysa* sp.);
3. To develop a population assessment technique for yabbies and bloodworms;
4. Determine levels of recruitment of these species and assess whether harvesting affects recruitment;
5. Obtain estimates of the recreational harvest of these species.

Ecological Impacts: There was clear evidence that recreational and commercial harvesting of yabbies (from intertidal mudflats) and bloodworms (from intertidal seagrass beds) impacted on the other invertebrates found in these habitats. These effects included direct impacts on the habitat (loss of vegetation, changes to sediment compaction etc.) and indirect effects on the abundance and diversity of animals.

Sustainability and recruitment: Intensive harvesting of yabbies, at levels commensurate with current recreational and commercial harvesting, failed to suppress populations of these animals. This resilience to harvesting appears to arise from a combination of the patterns of recruitment and redistribution of adults. Recruitment tends to be greater in areas with greater densities of adults (gregariousness), but immediately after harvesting, adults redistribute themselves into areas of sediment that have been harvested. Recruitment appears to be continuous throughout the year, albeit with some defined peaks in spring and late summer. There was no evidence that harvesting reduced the levels of recruitment to areas that had been recently and/or repeatedly harvested over an extended period of time. The mobility of the animals within the sediment (i.e. their capacity to redistribute themselves through a network of interconnected tunnels) allows for a rapid redistribution of yabbies into localised areas that have been harvested. If sufficient adults were removed from a very large area, this may then result in a reduction in recruitment to that area because of the loss of appropriate cues from adults, but there is no indication that the current patterns of harvesting would result in this. In terms of the sustainability of harvesting in a context of the broader ecosystem, direct effects were generally restricted to a few taxa that appeared to recover rapidly after disturbance. The longer-term consequences for the indirect effects of harvesting on shorebird foraging is difficult to assess without more detailed information on the broader availability of suitable habitats within the region for the species affected. At the present levels of harvesting though, it seems unlikely the dynamics of shorebirds would be affected adversely because they are able to move to other areas that are not being harvested. Again, if the levels of harvesting were to increase markedly, reducing the access by shorebirds to areas that had not been harvested, the longer-term sustainability of yabby harvested would need to be re-assessed.

It was difficult to assess sustainability of bloodworms directly because of the problems in obtaining a fishery-independent measure of their abundance (see below). Two pieces of evidence suggest, however, that current levels of commercial harvesting on Fisherman Islands are sustainable. First, at any time, only approximately 20% of each of the commercial plots is being dug over. A period of 18-24 months is required for recovery of the vegetated component of the habitat (i.e. the seagrass and algal cover) and there is also some indication that the populations of other invertebrates in the area have started to recover by this time. Current self-regulation by the commercial operators means that areas tend not to be dug in less than a 18-24 month period. Second, despite extensive and intensive sampling of the intertidal seagrass beds, only a few recruits of bloodworms were detected. It has been suggested elsewhere that recruitment occurs primarily in the shallow subtidal areas of the seagrass beds. If this is the case, and it seems likely given the lack of recruits found in the intertidal, then harvesting occurs in different areas from where recruitment happens. The subtidal recruits would therefore provide a refuge population for recovery of areas that had been harvested. The sustainability of recreational harvesting of bloodworms is far less likely to be sustainable given the large number of worms being taken from even relatively small areas and the fact that most people engaging in recreational harvesting were either unaware of, or ignored, regulations relating to bag limits and protection of the habitat. Further, recreational harvesters tended not to leave fallow areas that had been previously dug, meaning that adequate time may not have elapsed for recovery of habitat and associated fauna. The lack of resources available for enforcement of regulations as applied to recreational harvesting is a concern for the longer-term sustainability of populations of bloodworms and other components of the ecosystem.

Population assessment: A method for rapidly assessing the stock sizes of yabbies was developed and tested. Previous methods, based on counts of burrow openings, were validated but found to be inappropriate. No method was devised for a fishery-independent stock assessment for bloodworms. Despite application of several different methods for obtaining estimates of the abundance of bloodworms in intertidal seagrass, none was found to be cost-effective or reliable. The time and cost associated with processing benthic cores is prohibitive and requires a high degree of taxonomic expertise. Furthermore, standard techniques of benthic coring are inappropriate for sampling deep-dwelling animals, such as bloodworms. A portable suction dredge was trialed and found to be far more effective than hand-based coring, allowing suitably large areas of seagrass to be dug rapidly, but the resultant damage to the habitat and time required to extract the worms meant that such an approach would be impractical as a general technique for stock assessment.

Recreational harvest: Direct estimates of the recreational harvest of yabbies collected for commercialised fishing tournaments were obtained. Attempts to obtain more widespread information on the levels of recreational harvesting of yabbies proved to be difficult given the large number of sites that were available to fishers. It would require a very large team of people, simultaneously surveying many of the sites in order to obtain reliable estimates of the catch. Even sites that were considered as being favoured by fishers, were only irregularly visited. A method for assessing the recreational harvest of yabbies was tested and validated, providing an appropriate approach for assessing the catch associated with focussed fishing tournaments, or more general recreational harvesting (assuming resources were available to do such studies).

The recreational harvest of bloodworms tends to be more restricted in spatial distribution, given a tendency for harvesting to be focussed in areas with intertidal seagrass and with easy access from the shoreline. A method for assessing the magnitude of the recreational harvest was shown to be effective and could easily be implemented at those sites indicated as being used extensively for harvesting of bloodworms. This method provides reliable estimates of catch and also an indication of whether groups are adhering to regulations pertaining to the harvesting of bloodworms.

Section 8: References

Abal, E.G., Dennison, W.C. and O'Donohue, M.J.H. 1998. Seagrasses and mangroves of Moreton Bay. In: Moreton Bay and Catchment. Tibbetts, I.R., Hall, N.J. and Dennison, W.C. (ed). School of Marine Science, University of Queensland, Brisbane. pp. 269-278.

Abrams, P., Nyblade, C. and Sheldon, S. 1986. Resource partitioning and competition for shells in a subtidal hermit crab species assemblage. Oecologia 69: 429-445.

Abrams, P.A. 1980. Resource partitioning and interspecific competition in a tropical hermit crab community. Oecologia 46: 365-379.

Alldredge, A.L. and King, J.M. 1980. Effects of moonlight on the vertical migration patterns of demersal zooplankton. J. Exp. Mar. Biol. Ecol. 44: 133-156.

Alongi, D.M. 1990. The ecology of tropical soft-bottom benthic ecosystems. Oceanogr. Mar. Biol. Annu. Rev. 28: 381-496.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behavior 79: 227-263.

Ambrose, W.G. (Jr.) 1984. Increased emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. J. Exp. Mar. Biol. Ecol. 80: 67-75.

Ambrose, W.G. (Jr.) 1986. Estimate of removal rate of *Nereis virens* (Polychaeta: Nereidae) from an intertidal mudflat by gulls (*Larus* spp.) Mar. Biol. 90: 243-247.

Ambrose, W.G. (Jr.), Dawson, M., Gailey, C., Ledkovsky, P., O'Leary, S., Tassinari, B., Vogel, H. and Wilson, C. 1998. Effects of baitworm digging on the soft-shelled clam, *Mya arenaria,* in Maine: Shell damage and exposure on the sediment surface. J. Shellfish Res. 17: 1043-1049.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Aust. J. Ecol. 26: 32-46.

André, C. and Rosenberg, R. 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria.* Mar. Ecol. Prog. Ser. 71: 227-234.

Andrew, N.L. and Pepperell, J.G. 1992. The by-catch of shrimp trawl fisheries. Oceanogr. Mar. Biol. Annu. Rev. 30: 527-565.

Anonymous. 2000. Management directions for Western Australia's recreational fisheries. Fisheries Management Papers. No. 136. Fisheries Department of Western Australia, 68 pp.

Aragones, L.V. 1996. Dugongs and green turtles: grazers in the tropical seagrass ecosystem. Ph.D Thesis, James Cook University, Townsville, Queensland.

Armstrong, D.A., Dinnel, P.A., Iribarne, O.O., Fernandez, M.E. and McGraw, K. 1992. Use of intertidal oyster shell to enhance 0+ Dungeness crab production in Grays Harbor estuary (WA). In: International Crab Rehabilitation and Enhancement Symposium. Kodiak, Alaska. Alaska Department of Fish & Game and Kodiak College, pp. 125-140.

Arnold, W.S. 1984. The effect of prey size, predator size, and sediment composition on the role of predation of the blue crab, *Callinectes sapidus* Rothbun, on the hard clam, *Mercenaria mercenaria* (Linné). J. Exp. Mar. Biol. Ecol. 80: 207-219.

Askins, R.A., Lynch, J.F. and Greenberg, R. 1990. Population declines in migratory birds in eastern North America. Current Ornithology 7: 1-57.

Baines, D., Sage, R.B. and Baines, M.M. 1994. The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. J. Appl. Ecol. 31: 776-783.

Baird, D., Evans, P.R., Milne, H. and Pienkowski, M.W. 1985. Utilisation by shorebirds of benthic invertebrate production in intertidal areas. Oceanogr. Mar. Biol. Annu. Rev. 23: 573-597.

Barshaw, D.E. and Able, K.W. 1990. Deep burial as a refuge for lady crabs *Ovalipes ocellatus*: comparisons with blue crabs *Callinectes sapidus*. Mar. Ecol. Prog. Ser. 66: 75-79.

Beal, B.F. and Vencile, K.W. 2001. Short-term effects of commercial clam (*Mya arenaria* L.) and worm (*Glycera dibranchiata* Ehlers) harvesting on survival and growth of juveniles of the soft-shell clam. J. Shellfish Res. 20: 1145-1157.

Beauchamp, K.A. and Gowing, M.M. 1982. A quantitative assessment of human trampling effects on a rocky intertidal community. Mar. Environ. Res. 7: 279-293.

Bell, J.D. and Pollard, D.A. 1989. Ecology of fish assemblages and fisheries associated with seagrasses. In: Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region. Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. (ed). Elsevier Science Publishers, Amsterdam. pp. 565-609.

Bender, E.A., Case, T.J. and Gilpin, M.E. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65: 1-13.

Best, R.C. 1981. Foods and feeding habits of wild and captive Sirenia. Mammal Review 11: 3-29.

Beukema, J.J. 1982. Annual variation in reproductive success and biomass of the major macrozoobenthic species living in a tidal flat area of the Wadden Sea. Neth. J. Sea Res. 16: 37-45.

Beukema, J.J. 1995. Long-term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. Neth. J. Sea Res. 33: 219-227.

Beukema, J.J. and de Vlas, J. 1979. Population parameters of the lugworm *Arenicola marina*, living on the tidal flats of the Dutch Wadden Sea. Neth. J. Sea Res. 13: 331-353.

Beukema, J.J., Dekker, R., Essink, K. and Michaelis, H. 2001. Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. Mar. Ecol. Prog. Ser. 211: 143-155.

Beukema, J.J., Essink, K. and Dekker, R. 2000. Long-term observations on the dynamics in 3 species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator-prey interactions. J. Anim. Ecol. 69: 31-44.

Beukema, J.J., Essink, K., Michaelis, H. and Zwarts, L. 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: How predictable is this food source for birds? Neth. J. Sea Res. 31: 319-330.

Beukema, J.J., Flach, E.C., Dekker, R. and Starink, M. 1999. A long-term study of the recovery of the macrozoobenthos on large defaunated plots on a tidal flat in the Wadden Sea. J. Sea Res. 42: 235-254.

Blaber, S.J.M. and Blaber, T.G. 1980. Factors affecting the distribution of juvenile estuarine and inshore fish. J. Fish. Biol. 17: 143-162.

Blake, R.W. 1979a. Exploitation of a natural population of *Arenicola marina* (L.) from the north-east coast of England. J. Appl. Ecol. 16: 663-670.

Blake, R.W. 1979b. On the exploitation of a natural population of *Nereis virens* Sars from the north-east coast of England. Estuarine Coastal Mar. Sci. 8: 141-148.

Boon, P.I., Bird, F.L. and Bunn, S.E. 1997. Diet of the intertidal callianassid shrimps *Biffarius arenosus* and *Trypea australiensis* (Decapoda: Thalassinidea) in Western Port (Southern Australia), determined with multiple stable-isotope analyses. Mar. Freshw. Res. 48: 503-511.

Bowden, D.A., Rowden, A.A. and Attrill, M.J. 2001. Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. J. Exp. Mar. Biol. Ecol. 259: 133-154.

Branch, G.M. and Pringle, A. 1987. The impact of the sand prawn *Callianassa kraussi* Stebbing on sediment turnover and on bacteria, meiofauna and benthic microflora. J. Exp. Mar. Biol. Ecol. 107: 219-236.

Brenchley, G.A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom communities. J. Mar. Res. 39: 767-790.

Bristow, G.A. and Vadas, R.L. 1991. Genetic variability in bloodworm (*Glycera dibranchiata*) populations in the Gulf of Maine. Mar. Biol. 109: 311-319.

Broham, L., Cardillo, M., Bennett, A.F. and Elgar, M.A. 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Aust. J. Ecol. 24: 199-207.

Brouns, J.J.W.M. 1987. Growth patterns in some Indo-West-Pacific seagrasses. Aquat. Bot. 28: 39-61.

Brown, B. 1993. Maine's baitworm fisheries: Resources at risk? Amer. Zool. 33: 568-577.

Brown, B.J. and Ewel, J.J. 1987. Herbivory in complex and simple tropical ecosystems. Ecology 68: 108-116.

Buchanan, J.B. 1963. The bottom fauna communities and their sediment relationships off the coast of Northumberland. Oikos 14: 155-175.

Butler, A.J. and Jernakoff, P. 1999. Seagrass in Australia: Strategic Review and Development of an R & D Plan. FRDC 98/223. CSIRO Publishing, Collingwood, Victoria.

Cameron, A.M. 1966. Some aspects of the behaviour of the soldier crab, *Mictyris longicarpus*. Pacific Sci. 20: 224-234.

Camphuysen, C.J., Ens, B.J., Heg, D., Hulscher, J.B., Vandermeer, J. and Smit, C.J. 1996. Oystercatcher *Haematopus ostralegus* winter mortality in the Netherlands: the effect of severe weather and food supply. Ardea 84A: 469-492.

Carriker, M.R. 1967. Ecology of estuarine benthic invertebrates: a perspective. In: Estuaries. Publication No. 83. American Association for the Advancement of Science (AAAS), Washington, DC. pp. 442-487.

Carriker, M.R. 1986. Influence of suspended particles on biology of oyster larvae in estuaries. Amer. Malacol. Bull. Spec. Edn. 3: 41-49.

Castilla, J.C. and Durán, L.R. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). Oikos 45: 391-399.

Castilla, J.C., Luxoro, C. and Navarrete, S.A. 1989. Galleries of the crabs *Acanthocyclus* under intertidal mussel beds: their effects on the use of primary substratum. Revista Chilena de Historia Natural 62: 199-204.

Catterall, C.P. and Poiner, I.R. 1984. Distribution, abundance and resilience of macro-molluscs in the seagrass beds of North Stradbroke Island. In: Coleman, R.J., Covacevich, J. and Davie, P. (ed). Focus on Stradbroke: New Information on North Stradbroke Island and Surrounding Areas, 1974-1984. Point Lookout, North Stradbroke Island. Boolarong Publications, Brisbane. pp. 291-299.

Catterall, C.P. and Poiner, I.R. 1987. The potential impact of human gathering on shellfish populations, with reference to some NE Australian intertidal flats. Oikos 50: 114-122.

Cebrian, J. and Duarte, C.M. 1994. The dependence of herbivory on growth rate in natural plant communities. Functional Ecol. 8: 518-525.

Chamberlain, D.E. and Fuller, R.J. 1999. Density-dependent habitat distributions in birds: issues of scale, habitat definition and habitat availability. J. Avian Biol. 30: 427-436.

Chipman, B.D. and Helfrich, L.A. 1988. Recreational specializations and motivations of Virginia River anglers. N. Am. J. Fish. Manag. 8: 390-398.

Clarke, J.R. and Buxton, C.D. 1989. A survey of the recreational rock-angling fishery at Port Elizabeth, on the south-east coast of South Africa. S. Afr. J. mar. Sci. 8: 183-194.

Clarke, S.M. and Kirkman, H. 1989. Seagrass dynamics. In: Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region. Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. (ed). Elsevier Science Publishers, Amsterdam. pp. 304-345.

Coen, L.D., Heck, K.L. and Abele, L.G. 1981. Experiments on competition and predation among shrimps of seagrass meadows. Ecology 62: 1484-1493.

Coles, R.G., Lee Long, W.J., Squire, B.A., Squire, L.C. and Bibby, J.M. 1987. Distribution of seagrasses and associated juvenile commercial penaeid prawns in north-eastern Queensland waters. Aust. J. Mar. Freshwater Res. 38: 103-119.

Coles, R.G., Lee Long, W.J., Watson, R.A. and Derbyshire, K.J. 1993. Distribution of seagrasses and their fish and penaeid prawn communities, in Cairns Harbour, a tropical estuary, northern Queensland, Australia. Aust. J. Mar. Freshwater Res. 44: 193-210.

Collar, N.J., Crosby, M.J. and Staffersfield, A.J. 1994. Birds to Watch. 2: The World List of Threatened Birds. Birdlife International, Oxford.

Colwell, M.A. and Landrum, S.L. 1993. Non-random shorebird distribution and fine-scale variation in prey abundance Condor 94-103:

Congdon, B.C. and Catterall, C.P. 1994. Factors influencing the Eastern Curlew's distribution and choice of foraging sites among tidal flats of Moreton Bay, south-eastern Queensland. Wildlife Res. 21: 507-518.

Connolly, R.M. 1994. Removal of seagrass canopy: effects on small fish and their prey. J. Exp. Mar. Biol. Ecol. 184: 99-110.

Connolly, R.M. 1997. Differences in composition of small, motile invertebrate assemblages from seagrass and unvegetated habitats in a southern Australian estuary. Hydrobiologia 346: 137-148.

Constable, A.J. 1995. Impacts of bait collection using hand-pumps on the range and distribution of feeding habitat of the endangered Eastern Curlew, *Numenius madagascariensis*, in Moreton Bay, Queensland. Report to: Queensland Department of Environment and Heritage, Memorial Grant No. 207840. Griffith University, Brisbane. 58 pp.

Cornelius, C., Navarrete, S.A. and Marquet, P.A. 2001. Effects of human activity on the structure of coastal marine bird assemblages in central Chilé. Conserv. Biol. 15: 1396-1404.

Creaser, E.P. 1973. Reproduction of the bloodworm (*Glycera dibranchiata*) in the Sheepscott Estuary. J. Fish. Res. Bd. Can. 30: 161-166.

Creaser, E.P. and Clifford, D.A. 1986. The size frequency and abundance of subtidal bloodworms (*Glycera dibranchiata* Ehlers) in Montsweag Bay, Woolwich-Wiscasset, Maine. Estuaries 9: 200-207.

Creaser, E.P., Clifford, D.A., Hogan, M.J. and Sampson, D.B. 1983. A commercial sampling program for sandworms, *Nereis virens* Sars, and bloodworms, *Glycera dibranchiata* Ehlers, harvested along the Maine coast. NOAA Technical Report. NMFS SSRF-767. US Dept. of Commerce, NMFS, Maine. 56 pp.

Creed, J.C. and Amado Filho, G.M. 1999. Disturbance and recovery of the macroflora of a seagrass (*Halodule wrightii* Ascherson) meadow in the Abrolhos Marine National Park, Brazil: an experimental evaluation of anchor damage. J. Exp. Mar. Biol. Ecol. 235: 285-306.

Cryer, M., Whittle, G.N. and Williams, R. 1987. The impact of bait collection by anglers on marine intertidal invertebrates. Biol. Conserv. 42: 83-93.

Cummings, V.J., Schneider, D.C. and Wilkinson, M.R. 1997. Multiscale experimental analysis of aggregative responses of mobile predators to infaunal prey. J. Exp. Mar. Biol. Ecol. 216: 211-227.

Curley, F.J. 1996. Assessment of the macrofaunal assemblage of an intertidal sandflat exposed to activities associated with a boating facility. B.Sc. (Appl. Sci.) Honours Thesis, University of Queensland, Brisbane.

Cyr, H. and Pace, M.L. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature 361: 148-150.

Davis, A.R. 1995. Over-exploitation of *Pyura chilensis* (Ascidiacea) in southern Chile: The urgent need to establish marine reserves. Revista Chilena de Historia Natural 68: 107-116.

Dawes, C.J., Andorfer, J., Rose, C.U.C. and Ehringer, N. 1997. Regrowth of the seagrass *Thalassia testudinum* into propeller scars. Aquat. Bot. 59: 139-155.

Day, J.H. 1967. Polychaeta of southern Africa. Part 1. Errantia. Part 2. Sedentaria. British Museum of Natural History, London.

Dayton, P.K. 1971. Competition, disturbance and community organization: the provision and utilization of space in rocky intertidal community. Ecol. Monogr. 41: 351-389.

Dayton, P.K. and Oliver, J.S. 1980. An evaluation of experimental analyses of population and community patterns in benthic marine environments. In: Marine Benthic Dynamics. Tenore, K.R. and Coull, B.C. (ed). University of South Carolina Press, Columbia, South Carolina. pp. 93-120.

de Boer, W.F. 2001. The shorebird community structure at an intertidal mudflat in southern Mozambique. Ardea 90: 81-92.

de Boer, W.F. and Longamane, F.A. 1996. The exploitation of intertidal food resources in Inhaca Bay, Mozambique, by shorebirds and humans. Biol. Conserv. 78: 295-303.

de Boer, W.F. and Prins, H.H.T. 2002. Human exploitation and benthic community structure on a tropical intertidal flat. J. Sea Res. 48: 225-240.

de Iongh, H.H., Wenno, B.J. and Meelis, E. 1995. Seagrass distribution and seagrass biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. Aquat. Bot. 50: 1-19.

del Hoyo, J., Elliot, A. and Sargatal, J. 1996. Handbook to the Birds of the World. Lynx, Barcelona.

den Hartog, C. 1977. Structure, function and classification in seagrass communities. In: Seagrass Ecosystems: a scientific perspective. McRoy, C.P. and Helfferich, C. (ed). Marcel Dekker Inc., USA. pp. 89-122.

Dennison, W.C., O'Neill, J.M., Duffey, E.J., Oliver, P.E. and Shaw, G.R. 1999. Blooms of the cyanobacterium *Lyngbya majusculum* in coastal waters of Queensland, Australia. Bull. Inst. Oceanogr. (Monaco) 501-506.

Dirnberger, J.M. 1994. Influences of larval settlement location and rate on later growth and mortality in a sessile marine invertebrate population (*Spirorbis spirillum*). Northeast Gulf Science 13: 65-78.

Dittmann, S. 1990. Mussel beds - amensalism or amelioration for intertidal fauna? Helgoländer Meersunters. 44: 335-352.

Dittmann, S. 1993. Impact of foraging soldier crabs (Decapoda: Mictyridae) on meiofauna in a tropical tidal flat. Rev. Biol. Trop. 41: 627-637.

Dittmann, S. 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. Mar. Ecol. Prog. Ser. 134: 119-130.

Dittmann, S. 1998. Behaviour and population structure of soldier crabs *Mictyris longicarpus* (Latrielle): observations from a tidal flat in tropical North Queensland, Australia. Senckenbergiana marit. 28: 177-184.

Dittmann, S. and Vargas, J.A. 2001. Tropical tidal flat benthos compared between Australia and Central America. In: Ecological comparisons of sedimentary shores. Ecological Studies, v. 151. Reise, K. (ed). Springer, Berlin, New York. pp. 275-293.

Ditton, R.B., Loomis, D.K. and Choi, S. 1992. Recreation specialisation: re-conceptualisation from a social world's perspective. Journal of Leisure Research 24: 33-51.

Dobbs, F.C. and Guckert, J.B. 1988. *Callianassa trilobata* (Crustacea: Thalassinidae) influences abundance of meiofauna and biomass, composition, and physiological state of microbial communities within its burrow. Mar. Ecol. Prog. Ser. 45: 69-79.

Dolman, P.M. and Sutherland, W.J. 1997. Spatial pattern of depletion imposed by foraging vertebrates: theory, review and meta-analysis. J. Anim. Ecol. 66: 481-494.

Duarte, C.M., Terrados, J., Agawin, N.S.R., Fortes, M.D., Bach, S. and Kenworthy, W.J. 1997. Response of a mixed Philippine seagrass meadow to experimental burial. Mar. Ecol. Prog. Ser. 147: 285-294.

Dumbauld, B.R., Armstrong, D.A. and McDonald, T.L. 1993. Use of oyster shell to enhance intertidal habitat and mitigate loss of Dungeness crab (*Cancer magister*) caused by dredging. Can. J. Fish. Aquat. Sci. 50: 381-390.

Durán, L.R. and Castilla, J.C. 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. Mar. Biol. 103: 555-562.

Dye, A.H. 1992. Experimental studies of succession and stability in rocky intertidal communities subject to artisanal shellfish gathering. Neth. J. Sea Res. 30: 209-217.

Eckman, J.E. 1983. Hydrodynamic processes affecting benthic recruitment. Limnol. Oceanogr. 28: 241-257.

Eckrich, C.E. and Holmquist, J.G. 2000. Trampling in a seagrass assemblage: direct effects, response of associated fauna, and the role of substrate characteristics. Mar. Ecol. Prog. Ser. 201: 199-209.

Edgar, G.J. 1992. Patterns of colonization of mobile epifauna in a Western Australian seagrass bed. J. Exp. Mar. Biol. Ecol. 157: 225-246.

Engel, J. and Kvitek, R. 1998. Effects of otter trawling on a benthic community in Monterey Bay national marine sanctuary. Conserv. Biol. 12: 1204-1214.

Ens, B.J. and Goss-Custard, J.D. 1986. Piping as a display of dominance in wintering oystercatchers *Haematopus ostralegus*. Ibis 128: 382-391.

Ens, B.J., Piersma, T. and Drent, R. 1994. The dependence of waders and waterfowl migrating along the East-Atlantic flyway on their coastal food supplies: what is the most profitable research programme? Ophelia Suppl. 6: 127-151.

Evans, P.R., Herdson, D.M., Knights, P.J. and Pienkowski, M.W. 1979. Short-term effects of reclamation of part of the Seal Sand Teesmouth, on wintering waders and Shelduck. Oecologia 41: 183-206.

Fairweather, P.G. 1991. A conceptual framework for ecological studies of coastal resources: an example of a tunicate collected for bait on Australian seashores. Ocean & Shoreline Management 15: 125-142.

Fauchald, K. 1977. The Polychaete Worms: Definitions and keys to the Orders, Families and Genera. Science series 28/ Natural History Museum of Los Angeles County. Natural History Museum of Los Angeles County, Los Angeles. 188 pp.

Fauchald, P. 1999. Foraging in hierarchical patch systems. Am. Nat. 153: 603-613.

Fedler, A.J. and Ditton, R.B. 1994. Understanding angler motivations in fisheries management. Fisheries 19: 6-13.

Finn, P.G., Driscoll, P.V. and Catterall, C.P. 2002. Eastern curlew numbers at high-tide roosts versus low-tide feeding grounds: a comparison at three spatial scales. Emu 102: 233-239.

Flach, E.C. and Beukema, J.J. 1994. Density-governing mechanisms in populations of the lugworm *Arenicola marina* on tidal flats. Mar. Ecol. Prog. Ser. 115: 139-149.

Fonseca, M.S. 1989. Sediment stabilization by *Halophila decipiens* in comparison to other seagrasses. Estuarine Coastal Shelf Sci. 29: 501-507.

Fonseca, M.S. and Kenworthy, W.J. 1987. Effects of current on photosynthesis and distribution of seagrasses. Aquat. Bot. 27: 59-78.

Fonseca, M.S., Kenworthy, W.J., Colby, D.R., Rittmaster, K.A. and Thayer, G.W. 1990. Comparisons of fauna among natural and transplanted eelgrass *Zostera marina* meadows: criteria for mitigation. Mar. Ecol. Prog. Ser. 65: 251-264.

Fonseca, M.S., Thayer, G.W. and Kenworthy, W.J. 1987. The use of ecological data in the implementation and management of seagrass restorations. Fla. Mar. Res. Publ. 42: 175-187.

Fonseca, M.S., Zieman, J.C., Thayer, G.W. and Fisher, J.S. 1983. The role of current velocity in structuring eelgrass (*Zostera marina* L.) meadows. Estuarine Coastal Shelf Sci. 17: 367-380.

Forbes, A.T. 1984. The Bait Worm Fishery in Moreton Bay. Project Report Q08009. Queensland Department of Primary Industries , Brisbane.

Gabric, A.J., McEwan, J. and Bell, P.R.F. 1998. Water quality and phytoplankton dynamics in Moreton Bay, south-eastern Queensland. I. Field survey and satellite data. Mar. Freshw. Res. 49: 215-225.

Garcia, R.B. and Mantelatto, F.L.M. 2001. Shell selection by the tropical hermit crab *Calcinus tibicen* (Herbst, 1791) (Anomura, Diogenidae). J. Exp. Mar. Biol. Ecol. 265: 1-14.

Gigliotti, L.M. and Taylor, W.W. 1990. The effect of illegal harvest on recreational fisheries. N. Am. J. Fish. Manag. 10: 106-110.

Gill, J.A., Sutherland, W.J. and Norris, K. 2001. Depletion models can predict shorebird distribution at different spatial scales. Proc. Roy. Soc. Lond. Ser. B 268: 369-376.

Ginsburg, R.N. and Lowenstam, H.A. 1958. The influence of marine bottom communities on the depositional environment of sediments. J. Geol. 66: 310-318.

Goss-Custard, J.D. 1977. The ecology of the Wash III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). J. Anim. Ecol. 14: 721-739.

Goss-Custard, J.D. 1984. Intake rates and food supply in migrating and wintering shorebirds. In: Shorebirds: migration and foraging behaviour. Burger, J. and Olla, B.L. (ed). Plenum Press, New York. pp. 233-270.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A.L.d. and West, A.D. 1994. Population consequences of habitat loss and change in wintering migratory birds: predicting the local and global effects from studies of individuals. Ibis 137 (Suppl.): 56-66.

Goss-Custard, J.D., Clarke, R.T. and Durrell, S.E.A.L.d. 1984. Rates of food intake and aggression of oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe estuary. J. Anim. Ecol. 53: 233-245.

Goss-Custard, J.D. and Durell, S.E.A.L.d. 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. Ibis 132: 273-289.

Goss-Custard, J.D., McGrorty, S. and Durell, S.E.A.L.d. 1996. The effect of oystercatchers *Haematopus ostralegus* on shellfish populations. Ardea 84A: 453-468.

Goss-Custard, J.D., West, A.D., Stillman, R.A., Durrell, S.E.A.L.d., Caldow, R.W.G., McGrorty, S. and Nagarajan, R. 2001. Density-dependent starvation in a vertebrate without significant depletion. J. Anim. Ecol. 70: 955-964.

Grant, J. 1983. The relative magnitude of biological and physical sediment reworking in an intertidal community. J. Mar. Res. 41: 673-689.

Green, R.H. 1979. Sampling Design and Statistical Methods for Environmental Biologists. John Wiley and Sons, New York. 257 pp.

Greenway, M. 1995. Trophic relationships of macrofauna within a Jamaican seagrass meadow and the role of the echinoid *Lytechinus variegatus* (Lamarck). Bull. Mar. Sci. 56: 719-736.

Günther, C.P. and Niesel, V. 1999. Effects of the ice winter 1995/96. In: The Wadden Sea Ecosystem. Stability Properties and Mechanisms. Dittman, S. (ed). Springer-Verlag, Berlin. pp. 193-206.

Hailstone, T.S. and Stephenson, W. 1961. The biology of *Callianassa* (*Trypaea*) *australiensis* Dana 1852 (Crustacea, Thalassinidea). University of Queensland papers - v.1., no. 12. University of Queensland, Brisbane, Queensland. pp. 261-282.

Hall, S.J. and Harding, M.J.C. 1997. Physical disturbance and marine benthic communities: the effects of mechanical harvesting of cockles on non-target benthic infauna. J. Appl. Ecol. 34: 497-517.

Hanekom, N. and Baird, D. 1982. Growth, reproduction and consumption of the thalassinid prawn *Upogebia africana* (Ortmann) in the Swartkops Estuary. S. Afr. J. Zool. 27: 130-139.

Hazlett, B.A. 1996. Assessments during shell exchanges by the hermit crab *Clibanarius vittatus*: the complete negotiator. Anim. Behav. 51: 567-573.

Heck, K.L. and Thoman, T.A. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. J. Exp. Mar. Biol. Ecol. 53: 573-596.

Heck, K.L. and Wetstone, G.S. 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J. Biogeogr. 4: 135-142.

Heinsohn, G.E. and Spain, A.V. 1974. Effects of a tropical cyclone on littoral and sub-littoral biotic communities and on a population of dugongs (*Dugong dugon* (Muller). Biol. Conserv. 6: 143-152.

Hicklin, P.W. 1987. The migration of shorebirds in the Bay of Fundy. Wilson Bull. 99: 540-570.

Higgs, J. 1999. Experimental recreational catch estimates for Queensland residents. RFISH Technical Report No. 2. Queensland Fisheries Management Authority, Brisbane. 55 pp.

Hilborn, R. 1985. Fleet dynamics and individual variation. Why some people catch more fish than others. Can. J. Fish. Aquat. Sci. 42: 2-13.

Hines, A.H. and Comtois, K.L. 1985. Vertical distribution of estuarine infauna in sediments in a subestuary of central Chesapeake Bay. Estuaries 8: 296-304.

Hockey, P.A.R. and Bosman, A.L. 1986. Man as an intertidal predator in Transkei: disturbance, community convergence and management of a natural food resource. Oikos 46: 3-14.

Hockey, P.A.R., Navarro, R.A., Kalejta, B. and Velasquez, C.R. 1992. The riddle in the sands: why are shorebird densities so high in southern estuaries. Am. Nat. 140: 961-979.

Hocking, M. and Twyford, K. 1997. Assessment and management of beach camping impacts within Fraser Island World Heritage Area, south-east Queensland. Aust. J. Env. Manag. 4: 26-39.

Hodgson, A.N., Allanson, B.R. and Cretchley, R. 2000. The exploitation of *Upogebia africana* (Crustacea: Thalassinidae) for bait in the Knysna Estuary. Trans. Roy. Soc. S. Afr. 55(2): 197-204.

Hogue, E.W. and Miller, C.B. 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. J. Exp. Mar. Biol. Ecol. 53: 181-191.

Holt, J.A., Bristow, K.L. and McIvor, J.G. 1996. The effects of grazing pressure on soil animals and hydraulic properties of two soils in semi-arid tropical Queensland. Aust. J. Soil Res. 34: 69-79.

Hopper, G.A. 1994. The reproductive ecology and biology of *Marphysa sanguinea* (Annelida; Polychaeta), a fisheries resource. Honours thesis, University of Queensland, Brisbane. 79pp.

Hughes, D.J., Ansell, A.D. and Atkinson, R.J.A. 1994. Resource utilization by a sedentary surface deposit feeder, the echiuran worm *Maxmuelleria lankesteri*. Mar. Ecol. Prog. Ser. 112: 267-275.

Hughes, D.J., Ansell, A.D. and Atkinson, R.J.A. 1996a. Distribution, ecology, and life-cycle of *Maxmuelleria lankesteri*. (Echiura: Bonellidae): A review with notes on field identification. J. mar. biol. ass. U.K. 76: 897-908.

Hughes, D.J., Ansell, A.D. and Atkinson, R.J.A. 1996b. Sediment bioturbation by the echiuran worm *Maxmuelleria lankesteri* (Herdman) and its consequences for radionuclide dispersal in Irish Sea sediments. J. Exp. Mar. Biol. Ecol. 195: 203-220.

Hunt, J.H., Ambrose, W.G. and Peterson, C.H. 1987. Effects of the gastropod, *Ilyanassa obsoleta* (Say), and the bivalve, *Mercenaria mercenaria* (L.), on larval settlement and juvenile recruitment of infauna. J. Exp. Mar. Biol. Ecol. 108: 229-240.

Inglis, G. 1995. Intertidal muddy shores. In: Coastal Marine Ecology of Temperate Australia. Underwood, A.J. and Chapman, M.G. (ed). University of New South Wales Press, Sydney, Australia. pp. 171-186.

Irlandi, E.A. and Peterson, C.H. 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. Oecologia 87: 307-318.

Iwasaki, K. 1995. Comparison of mussel bed community between two intertidal mytilids *Septifier virgatus* and *Hormomya mutabilis*. Mar. Biol. 123: 109-119.

Jackson, M.J. and James, R. 1979. The influence of bait digging on cockle, *Cerastoderma edule*, populations in north Norfolk. J. Appl. Ecol. 16: 671-679.

James, R.J., Smith, M.P.L. and Fairweather, P.G. 1995. Sieve mesh size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. Mar. Ecol. Prog. Ser. 118: 187-198.

Jamieson, G.S. 1993. Marine invertebrate conservation: Evaluation of fisheries over-exploitation concerns. Amer. Zool. 33: 551-567.

Johnson, R.G. 1970. Variations in diversity within benthic marine communities. Am. Nat. 104: 285-300.

Jonsson, P.R. and André, C. 1982. Mass mortality of the bivalve *Cerastoderma edule* on the Swedish west coast caused by infestation with the digenean trematode *Cercaria cerastoderma* I. Ophelia 36: 151-157.

Kalejta, B. 1993. Intense predation cannot always be detected experimentally: a case study of shorebirds predation on nereid polychaetes in South Africa. Neth. J. Sea Res. 31: 385-393.

Kalejta, B. and Hockey, P.A.R. 1991. Distribution, abundance and productivity of benthic invertebrates at the Berg River estuary, South Africa. Estuarine Coastal Shelf Sci. 33: 175-191.

Kent, A.C. and Day, R.W. 1983. Population dynamics of an infaunal polychaete: the effect of predators and an adult-recruit interaction. J. Exp. Mar. Biol. Ecol. 73: 185-203.

Keough, M.J. 1986. The distribution of a bryozoan on seagrass blades: settlement, growth and mortality. Ecology 67: 846-857.

Keough, M.J., Quinn, G.P. and King, A. 1993. Correlations between human collecting and intertidal mollusc populations on rocky shores. Conserv. Biol. 7: 378-390.

Kingsford, M.J., Underwood, A.J. and Kennelly, S.J. 1991. Humans as predators on rocky reefs in New South Wales, Australia. Mar. Ecol. Prog. Ser. 72: 1-14.

Kirkman, H. and Young, P.C. 1981. Measurement of health, and echinoderm grazing on *Posidonia oceanica* (L.) Delile. Aquat. Bot. 10: 329-338.

Kitner, K.R. and Maiolo, J.R. 1988. On becoming a billfisherman: a study of enculturation. Human Organisation 47: 213-223.

Klawe, W.L. and Dickie, L.M. 1957. Biology of the bloodworm *Glycera dibranchiata* Ehlers, and its relation to the bloodworm fishery of the maritime provinces. Bull. Fish. Res. Board Can. 115: 1-37.

Klumpp, D.W., Salita-Espinosa, J.T. and Fortes, M.D. 1993. Feeding ecology and trophic role of sea urchins in a tropical seagrass community. Aquat. Bot. 45: 205-230.

Koike, I. and Mukai, H. 1983. Oxygen and inorganic nitrogen contents and fluxes in burrows of the shrimps *Callianassa japonica* and *Upogebia major*. Mar. Ecol. Prog. Ser. 12: 185-190.

Laegdsgaard, P. and Johnson, C.R. 1995. Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Mar. Ecol. Prog. Ser. 126: 67-81.

Lake, P.S. 1990. Disturbing hard and soft bottom communities: A comparison of marine and freshwater environments. Aust. J. Ecol. 15: 477-488.

Landsberg, J., James, C. and Morton, S. 1997. Assessing the effects of grazing on biodiversity in Australia's rangelands. Aust. Biol. 10: 153-162.

Lane, B. 1987. Shorebirds of Australia. Nelson Publishers, Melbourne, Australia.

Lanyon, J.M. 2003. Distribution and abundance of dugongs in Moreton Bay, south-east Queensland. Wildlife Res. 30: 397-409.

Lanyon, J.M., Limpus, C.J. and Marsh, H. 1989. Dugongs and turtles: grazers in the seagrass system. In: Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region. Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. (ed). Elsevier Science Publishers, Amsterdam. pp. 610-634.

Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. 1989. Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region. Elsevier Science Publishers, Amsterdam.

Leber, K.M. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. Ecology 66: 1951-1964.

Levin, R., Petri, K.R. and Malone, J. 1997. Interactive effects of habitat selection, food supply and predation on recruitment of estuarine fish. Oecologia 112: 55-63.

Levinton, J.S. 1979. Deposit-feeders, their resources, and the study of resource limitation. In: Ecological Processes in Coastal and Marine Systems. Livingston, R.J. (ed). Plenum Press, New York. pp. 117-141.

Levinton, J.S. 1989. Deposit-feeding and coastal oceanography. In: Ecology of Marine Deposit Feeders. Lopez, G.R., Taghon, G.L. and Levinton, J.S. (ed). Springer-Verlag, New York. pp. 1-23.

Lewis (III), F.G. 1984. Distribution of macrobenthic crustaceans associated with *Thalassia*, *Halodule* and bare sand substrata. Mar. Ecol. Prog. Ser. 19: 101-113.

Lewis (III), F.G. and Stoner, A.W. 1983. Distribution of macrofauna within seagrass beds: an explanation for patterns of abundance. Bull. Mar. Sci. 33: 296-304.

Loomis, D.K. and Ditton, R.B. 1987. Analysis of motive and participation differences between saltwater sport and tournament. N. Am. J. Fish. Manag. 7: 482-487.

Macia, S. 2000. The effects of sea urchin grazing and drift algal blooms on a subtropical seagrass bed community. J. Exp. Mar. Biol. Ecol. 246: 53-67.

Marks, J.S. and Redmond, R.L. 1996. Demography of bristle-thighed curlews *Numenius tahitensis* wintering on Laysan Island. Ibis 138:

Marsh, H. 1988. An ecological basis for dugong conservation in Australia. In: Marine Mammals of Australia. Augee, M.L. (ed). Royal Zoological Society of NSW, Sydney, Australia. pp. 9-21.

Marsh, H., Corkeron, P.J., Limpus, C.J., Shaughnessy, P.D. and Ward, T.M. 1995. The reptiles and mammals in Australian seas: their status and management. In: State of the Marine Environment Report for Australia - Technical Annex 1. Zann, L.P. and Kailola, P. (Eds). Department of the Environment, Sport and Territories, Canberra. pp. 151-166.

Marsh, H. and Lefebvre, L.W. 1994. Sirenian status and conservation efforts. Aquatic Mammals 20: 155-170.

Marsh, H. and Saalfeld, W.K. 1989. The distribution and abundance of dugongs in the northern Great Barrier Reef Marine Park. Australian Wildlife Research 16: 429-440.

Maurer, D., Keck, R.T., Tinsman, J.C. and Leatham, W.A. 1981. Vertical migration and mortality of benthos in dredged material. Part I. Mollusca. Mar. Environ. Res. 4: 299-319.

Maurer, D., Keck, R.T., Tinsman, J.C. and Leatham, W.A. 1981. Vertical migration and mortality of benthos in dredged material. Part II. Crustacea. Mar. Environ. Res. 5: 301-317.

Maurer, D., Keck, R.T., Tinsman, J.C. and Leatham, W.A. 1982. Vertical migration and mortality of benthos in dredged material. Part III. Polychaeta. Mar. Environ. Res. 6: 49-68.

May, E.B. 1973. Environmental effects of hydraulic dredging in estuaries. Alabama Marine Resources Bull. 9: 1-85.

McGlennon, D. 1992. Recreational boatfishing: The 1990-91 metropolitan survey. Safish 4: 4-10.

McLusky, D.S., Anderson, F.E. and Wolfe-Murphy, S. 1983. Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait-digging. Mar. Ecol. Prog. Ser. 11: 173-179.

McNaughton, S.J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. 113: 691-703.

McNulty, J.K., Work, R.C. and Moore, H.B. 1962. Some relationships between the infauna of the level bottom and the sediment in South Florida. Bull. Mar. Sci. Gulf and Caribbean 12: 322-332.

McPhee, D.P., Leadbitter, D. and Skilleter, G.A. 2002. Swallowing the bait: is recreational fishing ecologically sustainable? Pacif. Conserv. Biol. 8: 40-51.

McPhee, D.P. and Skilleter, G.A. 2002. Harvesting of intertidal animals for bait for use in a recreational fishing competition. Proc. R. Soc. Qld. 110: 19-27.

McPhee, D.P. and Skilleter, G.A. 2003. Aspects of the biology of the yabby *Trypaea australiensis* (Dana) (Decapod: Thalassinidea) and the potential of burrow counts as an indirect measure of population density. Hydrobiologia In Press:

McShane, P.E., Black, K.P. and Smith, M.G. 1988. Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. J. Exp. Mar. Biol. Ecol. 124: 175-203.

Meire, P.M., Schekkerman, H. and Meininger, P.L. 1994. Consumption of benthic invertebrates by waterbirds on the Oosterschelde estuary, SW Netherlands. Hydrobiologia 282/283: 525-546.

Mercier, F. and McNeil, R. 1994. Seasonal variations in intertidal density of invertebrate prey in a tropical lagoon and effects of shorebird predation. Can. J. Zool. 72: 1755-1763.

Milsom, T.P., Langton, S.D., Parkon, W.K., Peel, S., Bishop, J.D., Hart, J.D. and Moore, N.P. 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. J. Appl. Ecol. 37: 706-727.

Moran, P.J. 1991. The effects of dredging on the larval settlement and community development of fouling organisms in Port Kembla Harbour, Australia. Wat. Res. 25: 1151-1155.

Moreno, C.A., Lunecke, K.M. and Lepez, M.I. 1986. The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from man in Southern Chile and the effects on benthic sessile assemblages. Oikos 46: 359-364.

Morrisey, D.J., Howitt, L., Underwood, A.J. and Stark, J.S. 1992. Spatial variation in soft-sediment benthos. Mar. Ecol. Prog. Ser. 81: 197-204.

Morton, J.W. 1977. Ecological effects of dredging and dredge spoil disposal: A literature review. Tech. Pap. U.S. Fish Wildl. Serv. No. 94. 33 pp.

Morton, R.M., Pollock, B.R. and Beumer, J.P. 1987. The occurrence and diet of fishes in a tidal inlet to a saltmarsh in southern Moreton Bay, Queensland. Aust. J. Ecol. 12: 217-237.

Moverley, J.H., Saenger, P. and Curtis, M.A. 1986. Patterns of polychaete recolonization in Queensland (Australia) subtropical estuaries following severe flooding. Hydrobiologia 134: 227-236.

Murphy, R.C. 1985. Factors affecting the distribution of the introduced bivalve, *Mercenaria mercenaria*, in a California lagoon - the importance of bioturbation. J. Mar. Res. 43: 673-692.

Murphy, R.C. and Kremer, J.N. 1992. Benthic community metabolism and the role of deposit-feeding callianassid shrimp. J. Mar. Res. 50: 321-.

Murray-Jones, S. and Steffe, A.S. 2000. A comparison between commercial and recreational fisheries of the surf clam, *Donax deltoides*. Fisheries Res. 44(3): 219-233.

Nagle, D.G. and Paul, V.J. 1998. Chemical defense of a marine cyanobacterial bloom. J. Exp. Mar. Biol. Ecol. 225: 29-38.

Nishiwaki, M., Kasuya, T., Miyazaki, N., Tobayama, T. and Kataoka, T. 1979. Present distribution of the dugong in the world. Scientific Reports of the Whales Research institute (Tokyo) 31: 133-141.

Norris, K., Bannister, R.C.A. and Walker, P.W. 1998. Changes in the number of oystercatchers *Haematopus ostralegus* wintering in the Burry Inlet in relation to the biomass of cockles *Cerastoderma edule* and its commercial exploitation. J. Appl. Ecol. 35: 75-85.

Novinger, G.D. 1984. Observations on the use of size limits for black basses in large impoundments. Fisheries 9(4): 2-6.

O'Neill, M. Fishery Assessment of the Burnett River, Maroochy River and Pumicestone Passage. Queensland Department of Primary Industries Project Report Q099012. 112 pp.

Olff, H. and Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. TREE 13(7): 261-265.

Oliva, D. and Castilla, J.C. 1986. The effect of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. P.S.N.Z.I. Mar. Ecol. 7: 201-217.

Olive, P.J.W. 1993. Management of the exploitation of the lugworm *Arenicola marina* and the ragworm *Nereis virens* (Polychaeta) in conservation areas. Aquatic Conservation 3: 1-24.

Orth, R.J. 1977. The importance of sediment stability in seagrass communities. In: Ecology of Marine Benthos. Coull, B.C. (ed). University Of South Carolina Press, Columbia, South Carolina. pp. 281-300.

Orth, R.J., Heck, K.L. and van Montfrans, J.V. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7: 339-350.

Osborne, N.J.T., Webb, P.M. and Shaw, G.R. 2001. The toxins of *Lyngbya majuscula* and their human and ecological health effects. Environment International 27: 381-392.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65-75.

Paine, R.T. 1974. Intertidal community structure: Experimental studies on the relationships between a dominant competitor and its principle predator. Oecologia 15: 93-120.

Paine, R.T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus - Pisaster* interaction. Ecology 57: 858-873.

Paine, R.T. and Levin, S.A. 1981. Intertidal landscapes: disturbance and dynamics of pattern. Ecol. Monogr. 51: 145-178.

Peterson, C.H. 1976. Relative abundance of living and dead molluscs in two California lagoons. Lethaia 9: 137-148.

Peterson, C.H. 1977. Competitive organisation of the soft bottom macrobenthic communities of Southern California Lagoons. Mar. Biol. 43: 343-359.

Peterson, C.H. 1982. The importance of predation and intra- and inter- specific competition in the population biology of two infaunal suspension-feeding bivalves *Protothaca staminea* and *Chione undatella*. Ecol. Monogr. 52: 437-475.

Peterson, C.H. 1985. Patterns of lagoonal bivalve mortality after heavy sedimentation and their paleological significance. Paleobiology 11: 139-153.

Peterson, C.H. 1986. Enhancement of *Mercenaria mercenaria* densities in seagrass beds: Is pattern fixed during settlement season or altered by subsequent differential survival? Limnol. Oceanogr. 31: 200-205.

Peterson, C.H. and Black, R. 1988b. Density-dependent mortality caused by physical stress interacting with biotic history. Am. Nat 131: 257-270.

Peterson, C.H. and Summerson, H.C. 1992. Basin-scale coherence of population dynamics of an exploited marine invertebrate, the Bay scallop: implications of recruitment limitation. Mar. Ecol. Prog. Ser. 90: 257-272.

Peterson, C.H., Summerson, H.C. and Luettich Jr., R.A. 1996. Response of bay scallops to spawner transplants: a test of recruitment limitation. Mar. Ecol. Prog. Ser. 132: 93-107.

Piersma, T. 1987. Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. Mar. Ecol. Prog. Ser. 38: 187-196.

Piersma, T., de Goeij, P. and Tulp, I. 1993a. An evaluation of intertidal habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. Neth. J. Sea Res. 31: 503-512.

Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P. and Wiersma, P. 1993b. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. Neth. J. Sea Res. 31: 331-357.

Poiner, I.R., Walker, D.I. and Coles, R.G. 1989. Regional studies-seagrasses of tropical Australia. In: Biology of Seagrasses. Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. (ed). Elsevier Press, Amsterdam. pp. 279-303.

Pollock, K.H., Jones, C.M. and Brown, T.L. 1994. Angler survey methods and their application in fisheries management. American Fisheries Society Special Publication 25. American Fisheries Society , Bethesda, Maryland. 371 pp.

Posey, M.H. 1986. Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. Mar. Ecol. Prog. Ser. 31: 15-22.

Posey, M.H., Lindberg, W., Alphin, T. and Vose, F. 1996. Influence of storm disturbance on an offshore benthic community. Bull. Mar. Sci. 59: 523-529.

Preen, A. 1992. Interactions between dugongs and seagrasses in a subtropical environment. Ph.D. Thesis, James Cook University, Townsville, Queensland.

Preen, A. 1995. Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. Mar. Ecol. Prog. Ser. 124: 201-213.

Preen, A. and Marsh, H. 1995. Response of dugongs to large-scale loss of seagrass from Hervey Bay, Queensland, Australia. Wildlife Res. 22: 507-519.

Preen, A.R., Long, W.J.L. and Coles, R.G. 1995. Flood and cyclone related loss, and partial recovery, of more than 1000 km^2 of seagrass in Hervey Bay, Queensland, Australia. Aquat. Bot. 52: 3-17.

Quammen, M.L. 1982. Influence of subtle substrate differences on feeding by shorebirds on intertidal mudflats. Mar. Biol. 71: 339-343.

Quammen, M.L. 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. Ecology 65: 529-537.

Queensland Fisheries Management Authority (QFMA). 1996a. Queensland Subtropical Inshore Finfish Fishery. Discussion Paper No. 3. Queensland Fish Management Authority, Brisbane, Queensland. 50 pp.

Queensland Fisheries Management Authority (QFMA). 1996b. Queensland Trawl Fishery. Discussion Paper No. 5. Queensland Fish Management Authority, Brisbane, Queensland. 100 pp.

Queensland Fisheries Management Authority (QFMA). 1997a. Moreton Bay Fishery. Discussion Paper No. 6. Queensland Fish Management Authority, Brisbane, Queensland. 146 pp.

Queensland Fisheries Management Authority (QFMA). 1997b. Research needs and priorities for the management of Queensland's fisheries. Queensland Fish Management Authority, Brisbane, Queensland. 16 pp.

Queensland Fisheries Management Authority (QFMA). 1998. Experimental Recreational Catch Estimates for Queensland Residents. Queensland Fish Management Authority, Brisbane, Queensland.

Quinn, R.H. 1980. Mechanisms for obtaining water for flotation feeding in the soldier crab, *Mictyris longicarpus* Latreille 1806 (Decapoda, Mictyridae). J. Exp. Mar. Biol. Ecol. 43: 49-60.

Quinn, R.H. 1983. Water uptake and feeding in the soldier crab, *Mictyris longicarpus* Latrielle, 1806 (Decapoda, Mictyridae). Ph.D. Thesis, University of Queensland, Brisbane, Queensland.

Quinn, R.H. 1992. Fisheries Resources of the Moreton Bay Region Queensland Fish Management Authority, Brisbane. 52 pp.

Rappole, J.H. and McDonald, M.V. 1994. Cause and effect in population declines of migratory birds. Auk 111: 652-660.

Rasheed, M.A. 1999. Recovery of experimentally created gaps within a tropical *Zostera capricorni* (Aschers.) seagrass meadow, Queensland Australia. J. Exp. Mar. Biol. Ecol. 235: 183-200.

Reise, K. 1983. Experimental removal of lugworms from marine sand affects small zoobenthos. Mar. Biol. 74: 327-332.

Reynard, T.S. and Hilborn, R. 1986. Sports angler preferences for alternative regulatory methods. Can. J. Fish. Aquat. Sci. 43: 240-242.

Rhoads, D.C. 1974. Organism-sediment relationships on the muddy sea-floor. Oceanogr. Mar. Biol. Annu. Rev. 12: 263-300.

Rhoads, D.C. and Young, D.K. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28: 150-178.

Rhoads, D.C. and Young, D.K. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by *Molpadia oolitica* (Holothuroidea). Mar. Biol. 11: 255-261.

Riddle, M.J. 1988. Cyclone and bioturbation effects on sediments from coral reef lagoons. Estuarine Coastal Shelf Sci. 27: 687-695.

Roberts, H.H., Wiseman, W.J. and Suchanek, T.H. 1981. Lagoon sediment transport: the significant effect of *Callianassa* bioturbation. Proc. 4th Internat. Coral Reef Symp., Manila. pp. 459-465.

Rohweder, D.A. and Baverstock, P.R. 1996. Preliminary investigation of nocturnal habitat use by migratory waders (Order Charadriiformes) in northern New South Wales. Wildlife Res. 23: 169-184.

Rose, C.D., Sharp, W.C., Kenworthy, W.J., Hunt, J.H., Lyons, W.G., Prager, E.J., Valentine, J.F., Hall, M.O., Whitfield, P.E. and Fourqurean, J.W. 1999. Overgrazing of a large seagrass bed by the sea urchin *Lytechinus variegatus* in Outer Florida Bay. Mar. Ecol. Prog. Ser. 190: 211-222.

Rotherham, D. and West, R.J. 2003. Comparison of methods for sampling populations of ghost shrimp, *Trypaea australiensis* (Decapoda: Thalassinidea: Callianassidae). Fisheries Res. 60: 585-591.

Saila, S.B., Pratt, S.D. and Polgar, T.T. 1972. Dredge spoil disposal in Rhode Island Sound. Mar. Tech. Rep. No. 2. University of Rhode Island, Rhode Island. 48 pp.

Sainsbury, K.J., Campbell, R.A. and Whitelaw, A.W. 1993. Effects of trawling on the marine habitat on the North West Shelf of Australia and implications for sustainable fisheries management. In: Hancock, D.A. (ed). Sustainable Fisheries through Sustaining Fish Habitat, Australian Society for Fish Biology Workshop. Victor Harbor, SA. Australian Government Publishing Service, Canberra. pp. 137-145.

Sand-Jensen, K. 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. Ophelia 14: 185-201.

Sanders, H.L. 1958. Benthic studies in Buzzard Bay. I. Animal-sediment relationships. Limnol. Oceanogr. 3: 245-253.

Sanders, H.L. 1960. Benthic studies in Buzzard Bay. III. The structure of the soft-bottom community. Limnol. Oceanogr. 5: 138-153.

Scheiffarth, G., Wahls, S., Ketzenberg, C. and Exo, K.M. 2002. Spring migration strategies of 2 populations of bar-tailed godwits, *Limosa lapponica,* in the Wadden Sea: time minimizers or energy minimizers. Oikos 96: 346-354.

Schill, D.J. and Kline, P.A. 1995. Use of random response to estimate angler noncompliance with fishing regulations. N. Am. J. Fish. Manag. 15: 721-731.

Schlacher, T.A. and Wooldridge, T.H. 1996. Origin and trophic importance of detritus - evidence from stable isotopes in the benthos of a small, temperate estuary. Oecologia 106: 382-388.

Schneider, D.C. 1985. Migratory shorebirds: resource depletion in the tropics? Ornithol Monogr. 36: 546-558.

Schneider, D.C. 1992. Thinning and clearing of prey by predators. Am. Nat. 139: 148-160.

Schoeman, D. 1996. An assessment of a recreational beach clam fishery: current fishing pressure and opinions regarding the initiation of a commercial clam harvest. S. Afr. J. Wildl. Res. 26: 160-170.

Schramm Jr, H.L., Armstrong, M.L., Fedler, A.J., Funicelli, N.A., Green, D.M., Hahn, J.L., Lee, D.P., Manns Jr., R.E., Taubert, B.D. and Waters, S.J. 1991a. Sociological, economic, and biological aspects of competitive fishing. Fisheries 16: 13-21.

Schramm Jr, H.L., Armstrong, M.L., Fedler, A.J., Funicelli, N.A., Green, D.M., Hahn, J.L., Lee, D.P., Manns Jr., R.E., Taubert, B.D. and Waters, S.J. 1991a. The status of competitive sport fishing in North America. Fisheries 16: 4-12.

Schramm Jr, H.L. and Dennis, J.A. 1993. Characteristics and perceptions of users and nonusers of an urban fishery program in Lubbock, Texa. N. Am. J. Fish. Manag. 13: 210-216.

Schramm Jr, H.L. and Edwards, G.B. 1994. The perspective on urban fisheries management. Fisheries 19(10): 9-15.

Sewell, M.A. 1996. Detection of the impact of predation by migratory shorebirds: an experimental test in the Fraser River estuary, British Columbia (Canada). Mar. Ecol. Prog. Ser. 144: 23-40.

Shaw, M. and Jenkins, G.P. 1992. Spatial variation in feeding, prey distribution and food limitation of juvenile flounder *Rhombsolea tapirina* Gunther. J. Exp. Mar. Biol. Ecol. 165: 1-21.

Shepherd, P.C.F. 1994. Effects of baitworm harvesting on the prey and feeding behaviour of shorebirds in the Minas Basin Hemispheric Shorebird Reserve. M.Sc. Thesis, Acadia University, Wolfville, Canada.

Shepherd, P.C.F. 2001. Space use, habitat preferences, and time activity budgets of Dunlin (*Calidris alpina pacifica*) in the Fraser River Delta, B.C. Ph.D. Thesis, Simon Fraser University, Burnaby, B.C.

Shepherd, P.C.F. and Boates, J.S. 1999. Effects of a commercial baitworm harvest on semipalmated sandpipers and their prey in the Bay of Fundy hemispheric shorebird reserve. Conserv. Biol. 13: 347-356.

Shepherd, S.A., McComb, A.J., Bulthuis, D.A., Neverauskas, V., Steffensen, D.A. and West, R. 1989. Decline of seagrasses. In: Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region. Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. (ed). Elsevier Science Publishers, Amsterdam. pp. 346-387.

Sherman, K.M. and Coull, B.C. 1980. The response of meiofauna to sediment disturbance. J. Exp. Mar. Biol. Ecol. 46: 59-71.

Short, F.T. and Wyllie-Echeverria, S. 1996. Natural and human-induced disturbance of seagrasses. Environ. Conserv. 23: 17-27.

Shubin, A.O. 1999. Feeding and aggressive behaviour of waders (Charadriiformes, Charadrii) as evidence of competition in areas of their concentration on the south-west shore of the Caspian Sea. Zool. Zh. 78: 382-397 (in Russian).

Siegfried, W.R., Hockey, P.A.R. and Crowe, A.A. 1985. Exploitation and conservation of brown mussel stocks by coastal people of Transkei. Environ. Conserv. 12: 303-307.

Skilleter, G.A. 1994. Refuges from predation and the persistence of estuarine clam populations. Mar. Ecol. Prog. Ser. 109: 29-42.

Skilleter, G.A. 1996. An experimental test of artifacts from repeated sampling in soft-sediments. J. Exp. Mar. Biol. Ecol. 205: 137-148.

Skinner, J.L., Gillam, E. and Rohlin, C.-J. 1998. The demographic future of the Moreton Bay region. In: Moreton Bay and Catchment. Tibbets, I.R., Hall, N.J. and Dennison, W.C. (ed). School of Marine Science, University of Queensland, Brisbane. pp. 67-78.

Smit, C.J. 1984a. Importance of the Wadden Sea for estuarine birds. In: Ecology of the Wadden Sea, 2, part 6. Wolff, W.J. (ed). Balkema, Rotterdam. pp. 290-301.

Smit, C.J. 1984b. Production of biomass by invertebrates and consumption by birds in the Dutch Wadden Sea areas. In: Ecology of the Wadden Sea, 2, part 6. Wolff, W.J. (ed). Balkema, Rotterdam. pp. 290-301.

Smith, P.C. 1975. A study of the winter feeding ecology and behaviour of the bar-tailed godwit (*Limosa lapponica*). Ph.D Thesis, University of Durham,

Steffe, A.S., Murphy, J.J., Chapman, D.J., Tarlinton, B.E., Gordon, G.N.G. and Grinberg, A. 1996. An assessment of the impact of offshore recreational fishing in New South Wales on the management of commercial fisheries. Final Report to the Fisheries Research and Development Corporation. Project 94/053. 112 pp.

Stillman, R.A., Goss-Custard, J.D., West, A.D., Durell, S.E.A.L.d., McGrorty, S., Caldow, R.W.G., Norris, K.J., Johnstone, I.G., Ens, B.J., van der Meer, J. and Triplet, P. 2001. Predicting shorebird mortality and population size under different regimes of shellfishery management. J. Appl. Ecol. 38: 857-868.

Stoner, A.W. 1982. The influence of benthic macrophytes on the foraging behaviour of pinfish, *Lagodon rhomboides* (Linnaeus). J. Exp. Mar. Biol. Ecol. 58: 271-284.

Stoner, A.W. and Lewis, F.G. 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. J. Exp. Mar. Biol. Ecol. 94: 19-40.

Sturkie, C. 1996. Human impacts associated with the harvesting of *Trypaea australiensis* (Dana, 1852). PG.Dip. Thesis, University of Queensland, Brisbane.

Suchanek, T.H. 1983. Control of seagrass communities and sediment distribution by *Callianassa* (Crustacea, Thalassinidae) bioturbation. J. Mar. Res. 41: 281-298.

Suer, A.L. 1984. Growth and spawning of *Urechis caupo* in Bodega Harbor, California. Mar. Biol. 78: 275-284.

Summers, R.W. 1977. Distribution, abundance and energy relationships of waders (Aves: Charadrii) at Langebaan Lagoon. Trans. Roy. Soc. S. Afr. 42: 483-494.

Summerson, H.C. and Peterson, C.H. 1984. Role of predation in organising benthic communities of a temperate-zone seagrass bed. Mar. Ecol. Prog. Ser. 15: 63-77.

Sun, B. and Fleeger, J.W. 1994. Field experiments on the colonization of meiofauna into sediment depressions. Mar. Ecol. Prog. Ser. 110: 167-175.

Supanwanid, C. 1996. Recovery of the seagrass *Halophila ovalis* after grazing by dugong. In: Kuo, J., Phillips, R.C., Walker, D.I. and Kirkman, H. (ed). Seagrass Biology: Proceedings of an International Workshop. Rottnest Island, Western Australia. University of Western Australia, Nedlands, WA. pp. 315-318.

Sutherland, T.F., Shepherd, P.C.F. and Elner, R.W. 2000. Predation on meiofaunal and macrofaunal invertebrates by western sandpipers (*Calidris mauri*): evidence for dual foraging modes. Mar. Biol. 137: 983-993.

Székely, T. and Bamberger, Z. 1992. Predation of waders (Charadrii) on prey populations: an exclosure experiment. J. Anim. Ecol. 61: 447-456.

Thayer, G.W., Bjorndal, K.A., Ogden, J.C., Williams, S.L. and Zieman, J.C. 1984a. Role of larger herbivores in seagrass communities. Estuaries 7: 351-376.

Thayer, G.W., Kenworthy, J.W. and Fonseca, M.S. 1984b. The ecology of eelgrass meadows of the Atlantic Coast: A community profile. FWS/OBS-84/02. Fish and Wildlife Service, U.S. Dept. of the Interior, pp. 1-147.

Thistle, D. 1981. Natural physical disturbances of marine soft-bottoms. Mar. Ecol. Prog. Ser. 6: 223-228.

Thompson, J.J. 1990. The sex and age-related distribution of bar-tailed godwits in Moreton Bay, Queensland, during the northward migration. Emu 169-174:

Thompson, J.J. 1990a. A reassessment of the importance of Moreton Bay to migrant waders. Sunbird 20: 83-88.

Thompson, J.J. 1992. Spatial and temporal patterns of shorebird habitat utilisation in Moreton Bay, Queensland. Ph.D. thesis, University of Queensland, Brisbane, Queensland. 258pp.

Thrush, S.F. 1986. Spatial heterogeneity in subtidal gravel generated by the pit-digging activities of *Cancer pagurus*. Mar. Ecol. Prog. Ser. 30: 221-227.

Thrush, S.F. 1991. Spatial patterns in soft-bottom communities. TREE 6: 75-79.

Thrush, S.F. 1999. Complex role of predators in structuring soft-sediment macrobenthic communities: implications of changes in spatial scale for experimental studies. Aust. J. Ecol. 24: 344-354.

Thrush, S.F., Pridmore, R.D., Hewitt, J.E. and Cummings, V.J. 1991. Impact of ray feeding disturbances on sandflat macrobenthos: Do communities dominated by polychaetes or shellfish respond differently? Mar. Ecol. Prog. Ser. 69: 245-252.

Thwaites, A.J. and Williams, L.E. 1994. The summer whiting fishery in southeast Queensland. Mem. Qld. Mus. 35: 249-254.

Triplet, P., Stillman, R.A. and Goss-Custard, J.D. 1999. Prey abundance and the strength of interference in a foraging shorebird. J. Anim. Ecol. 68: 254-265.

Tulp, I. and de Goeij, P. 1994. Evaluating wader habitats in Roebuck Bay (North-western Australia) as a springboard for northbound migration in waders, with a focus on great knots. Emu 94: 78-95.

Underwood, A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Annu. Rev. 19: 513-605.

Underwood, A.J. 1989. The analysis of stress in natural populations. Biol. J. Linn. Soc. 37: 51-78.

Underwood, A.J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable world. J. Exp. Mar. Biol. Ecol. 161: 145-178.

Underwood, A.J. 1993. Ecological research and the management of human exploitation on the rocky coast of New South Wales. Ivanovici, A.M., Tarte, D. and Olson, M. (ed). Protection of marine and estuarine areas - a challenge for Australians: Proceedings of the fourth Fenner conference on the environment. Canberra. Australian Committee for IUCN, Sydney. pp. 122-128.

Underwood, A.J. 1997. Experiments in ecology. Their logical design and interpretation using analysis of variance. Cambridge University Press, London. 504 pp.

Underwood, A.J. and Chapman, M.G. 2003. Power, precaution, Type II error and sampling design in assessment of environmental impacts. J. Exp. Mar. Biol. Ecol. 296: 49-70.

Underwood, A.J. and Kennelly, S.J. 1990. Pilot studies for designs of surveys of human disturbance of intertidal habitats in New South Wales. Aust. J. Mar. Freshwater Res. 41: 165-173.

Valentine, J.F. and Heck Jr., K.L. 1991. The role of sea urchin grazing in regulating subtropical seagrass meadows: evidence from field manipulations in the northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. 154: 215-230.

Valentine, J.F., Heck, K.L., Harper, P. and Beck, M. 1994. Effects of bioturbation in controlling turtlegrass (*Thalassia testudinum* Banks ex König) abundance: evidence from field enclosures and observations in the Northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. 178: 181-192.

Van den Heiligenberg, T. 1987. Effects of mechanical and manual harvesting of lugworms *Arenicola marina* L. on the benthic fauna of tidal flats in the Dutch Wadden Sea. Biol. Conserv. 39: 165-177.

Van der Elst, R.P. 1989. Marine recreational angling in South Africa. In: Oceans of Life off South Africa. Payne, A.J.L. and Crawford, R.J.M. (ed). Vlaeberg Publishers, Cape Town. pp. 164-176.

van der Meer, J., Piersma, T. and Beukema, J.J. Population dynamics of benthic species on tidal flats: the possible roles of shorebird predation. In: Ecological comparisons of sedimentary shores. Ecological Studies, v. 151. Reise, K. (ed). Springer, Berlin, New York. pp. 317-335.

Velasques, C.R. and Navarro, R.N. 1993. The influence of water depth and sediment type on the foraging behaviour of Whimbrels. J. Field Ornithol. 64: 149-157.

Vermaat, J.E., Agawin, N.S.R., Duarte, C.M., Fortes, M.D., Marbá, N. and Uri, J.S. 1995. Meadow maintenance, growth and productivity of a mixed Philippine seagrass bed. Mar. Ecol. Prog. Ser. 124: 215-225.

Vigliano, P.H., Lippolt, G., Denegri, A., Alonso, M., Macchi, P. and Dye, C.O. 2000. The human factors of the sport and recreational fishery of San Carlos de Bariloche, Rio Negro, Argentina. Fisheries Res. 49: 141-153.

Wackernagel, M. and Rees, W. 1996. Our Ecological Footprint: Reducing Human Impact on the Earth. New Society Publishers, New York. 159 pp.

Wake, J.A. 1975. A study of the habitat requirements and feeding biology of the dugong, *Dugong dugon* (Muller). B.Sc. Honours Thesis, James Cook University, Townsville, Queensland.

Walker, D.I. and McComb, A.J. 1992. Seagrass degradation in Australian coastal waters. Mar. Pollut. Bull. 25: 191-195.

Warburton, K. and Blaber, S.J.M. 1992. Patterns of recruitment and resource use in a shallow-water fish assemblage in Moreton Bay, Queensland. Mar. Ecol. Prog. Ser. 90: 113-126.

Ward, T.J. 1989. The accumulation and effects of metals in seagrass habitats. In: Biology of Seagrasses. Larkum, A.W.D., McComb, A.J. and Shepherd, S.A. (ed). Elsevier Press, Amsterdam. pp. 797-820.

Warnock, S.E. and Takekawa, J.Y. 1996. Wintering site fidelity and movements patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. Ibis 138: 160-167.

Warwick, R.M. and Clarke, K.R. 1993. Increased variability as a symptom of stress in marine communities. J. Exp. Mar. Biol. Ecol. 172: 215-226.

Waslenchuk, D.G., Matson, E.A., Zajac, R.N., Dobbs, F.C. and Tramontano, J.M. 1983. Geochemistry of burrow waters vented by a bioturbating shrimp in Bermudian sediments. Mar. Biol. 72: 219-225.

Watkins, D. 1993. A National Plan for Shorebird Conservation in Australia. RAOU Report No. 90. Australasian Wader Studies Group, Royal Australasian Ornithologists Union and World Wide Fund for Nature, Melbourne, Australia.

Watling, L. and Norse, E.A. 1998. Disturbance of the seabed by mobile fishing gear: A comparison to forest clear cutting. Conserv. Biol. 12: 1180-1197.

WBM Oceanics . 1993. The Fisherman Islands Baitworm Fishery Brisbane's Port Environmental Study. Port of Brisbane Authority, Brisbane. pp. 193-204.

West, R.J. and Gordon, G.N.G. 1994. Commercial and recreational harvest of fish from two Australian rivers. Aust. J. Mar. Freshwater Res. 45: 1259-1279.

Wilde, G.R., Riechers, R.K. and Ditton, R.B. 1998. Differences in attitudes, fishing motives, and demographic characteristics between tournament and nontournament black bass anglers. N. Am. J. Fish. Manag. 18: 422-431.

Wilson (Jr.), W.H. 1981. Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete *Abarenicola pacifica.* J. Mar. Res. 39: 735-748.

Wilson (Jr.), W.H. 1989. Predation and the mediation of interspecific competition in an infaunal community in the Bay of Fundy. J. Exp. Mar. Biol. Ecol. 132: 221-245.

Winer, B.J., Brown, D.R. and Michels, K.M. 1991. Statistical Principles in Experimental Design. McGraw-Hill Kogakusha, Tokyo. 1057 pp.

Wolff, W.J. The interaction of benthic macrofauna and birds in tidal flat estuaries: A comparison of the Banc d'Arquin, Mauritania, and some estuaries in the Netherlands. In: Estuaries and Coasts: Spatial and Temporal Intercomparisons. Elliot, M. and Ducrotoy, J.-P. (ed). Olsen & Olsen, Fredensborg. pp. 299-306.

Wolff, W.J. Fredensborg, Denmark. The interaction of benthic macrofauna and birds in tidal flat estuaries: a comparison of the Banc d'Arguin, Mauritania, and some estuaries in the Netherlands. In: Estuaries and coasts: Spatial and temporal intercomparisons. Elliot, M. and Ducroty, J.-P. (ed). Olsen and Olsen, 1991. pp. 299-306.

Wolff, W.J. and Smit, C.J. 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. Ardea 78: 17-38.

Woodin, S.A. 1979. Settlement phenomena: The significance of functional groups. In: Reproductive Ecology of Marine Invertebrates. Stancyk, S.E. (ed). University of South Carolina Press, Columbia, South Carolina. pp. 99-106.

Wynberg, R.P. and Branch, G.M. 1991. An assessment of bait-collecting for *Callianassa kraussi* Stebbing in Langebaan Lagoon, and of associated avian predation. S. Afr. J. Mar. Sci. 11: 141-152.

Wynberg, R.P. and Branch, G.M. 1994. Disturbance associated with bait-collection for sandprawns (*Callianassa krausii*) and mudprawns (*Upogebia africana*): long-term effects on the biota of intertidal sandflats. J. Mar. Res. 52: 523-558.

Wynberg, R.P. and Branch, G.M. 1997. Trampling associated with bait-collection for sandprawns *Callianassa kraussi* Stebbing: effects on the biota of an intertidal sandflat. Environ. Conserv. 24: 139-148.

Yates, M.G., Goss-Custard, J.D., McGroty, S., Lakhani, K.H., Durell, S.E.A.L.d., Clarke, R.T., Rispin, W.E., Moy, I., Yates, T., Plant, R.A. and Frost, A.J. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. J. Appl. Ecol. 30: 599-614.

Young, G.C., Wise, B.S. and Ayvazian, S.G. 1999. A tagging study on tailor (*Pomatomus saltatrix*) in Western Australian waters: their movement, exploitation, growth and mortality. Mar. Freshw. Res. 50: 633-642.

Young, P.C. 1978. Moreton Bay, Queensland: A nursery area for juvenile penaeid prawns. Aust. J. Mar. Freshwater Res. 29: 55-75.

Zajac, R.N. and Whitlatch, R.W. 1982a. Responses of estuarine infauna to disturbance. I. Spatial and temporal variation of initial recolonisation. Mar. Ecol. Prog. Ser. 10: 1-14.

Zharikov, Y. 2002. Feeding ecology of shorebirds (Charadrii) spending the non-breeding season on an Australian subtropical estuarine flat. Ph.D. Thesis, University of Queensland, Brisbane, Queensland.

Zharikov, Y. and Skilleter, G.A. 2002. Sex-specific intertidal habitat use in subtropically wintering bar-tailed godwits. Can. J. Zool. 80: 1918-1929.

Zharikov, Y. and Skilleter, G.A. 2003a. Depletion of benthic invertebrates by bar-tailed godwits *Limosa lapponica* in a subtropical estuary. Mar. Ecol. Prog. Ser. 254: 151-162.

Zharikov, Y. and Skilleter, G.A. 2003b. Nonbreeding eastern curlews *Numenius madagascariensis* do not increase the rate of intake of digestive efficiency before long-distance migration because of an apparent digestive constraint. Physiol. Biochem. Zool. 76: 704-715.

Zharikov, Y. and Skilleter, G.A. 2003c. A relationship between prey density and territory size in non-breeding eastern curlews *Numenius madagascariensis.* Ibis 145: In Press.

Zwarts, L., Blomert, A.-M., Ens, B.J., Hupkes, R. and van Spanje, T.M. 1990. Why do waders reach high feeding densities on the intertidal flats of the Banc d'Arguin, Mauritania. Ardea 78: 39-52.

Zwarts, L., Blomert, A.-M. and Wanink, J.H. 1992. Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. Mar. Ecol. Prog. Ser. 83: 129-140.

Zwarts, L. and Ens, B.J. 1999. Predation by birds on marine tidal flats. In: Adams, N.J. and Slotow, R.H. (ed). Proc. 22 Intl. Ornithol. Congr. Durban, South Africa. Birdlife South Africa, Johannesburg, South Africa. pp. 2309-2327.

Zwarts, L. and Esselink, P. 1989. Versatility of male curlews (*Numenius arquata*) preying upon *Nereis diversicolor* deploying contrasting capture modes dependent on prey availability. Mar. Ecol. Prog. Ser. 56: 255-269.

Zwarts, L. and Wanink, J. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth. J. Sea Res. 31: 441-476.

Zwarts, L., Wanink, J.H. and Ens, B.J. 1996. Predicting seasonal and annual fluctuations in the local exploitation of different prey by oystercatchers *Haematopus ostralegus*: a ten-year study in the Wadden Sea. Ardea 84A: 401-440.

Appendix 1

Staff:

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