# HARVESTING OF THE PIPI, DONAX DELTOIDES, IN NSW. 

Final report to<br>The Fisheries Research and Development Corporation

Project No. $95 / 152$
September 1998

## Sue Murray-Jones



PRINCIPAL INVESTIGATOR: Ms Susan Murray-Jones ADDRESS:

University of Wollongong
Australian Flora and Fauna Research Centre
Biological Sciences
Northfields Ave
WOLLONGONG NSW 2522
Ph: 0242213013 Fax: 0242214135

## OBJECTIVES:

1. To quantify levels of commercial and recreational harvesting of pipis on selected NSW beaches
2. To make preliminary estimates of the effects of harvesting

## NON TECHNICAL SUMMARY:

In order to compare the levels of recreational and commercial harvesting of the pipi, I used a voluntary log book survey to quantify catch, effort, and catch rates for the commercial fishery on Stockton Beach, NSW, over a one year period, and an onsite survey to quantify catch, effort, and catch rates for recreational food and bait harvesting on Stockton Beach on the NSW north coast and Seven Mile Beach on the south coast (which is not commercially exploited).

There were large differences between the harvesting patterns for the recreational and commercial fisheries on Stockton Beach, implying that the sectors may have very different potential impacts on local pipi stocks, even though both fisheries were restricted solely to hand gathering. I estimated that the combined recreational and commercial catch of pipis from Stockton Beach was 237.7 tonnes during the period March 1996 to February 1997 inclusive, taken in a total of 120,672 collector hours. The commercial fishery was characterised by its relatively large catch, low amount of fishing effort, and high catch rate. Commercial fishers took the bulk of the catch ( $80 \%$ of the combined commercial and recreational harvest), but accounted for only $11 \%$ of the combined fishing effort and included only 27 fishers. In contrast, the recreational fishery was characterised by a relatively small catch, many participants, high fishing effort, and extremely low catch rates. Recreational fishers took 20\% of the combined commercial and recreational catch, but accounted for $89 \%$ of the combined fishing effort, with an estimated 15,795 parties participating. Many groups had extremely low catches. Winter was the peak season for commercial
harvesters, while in the recreational fishery summer was the peak season.
When I compared north and south coast sites, I found that recreational collecting effort at Stockton Beach was more than twice that estimated for Seven Mile over the same season, summer (53,373 cf. 23,356 collector hours respectively), but at Stockton Beach catches were an order of magnitude higher ( 18.1 cf 1.6 t ) in summer due to the much higher catch rates.

At both sites, recreational collecting for food was far more extensive than bait collecting. Food gathering accounted for $93 \%$ of the total recreational catch and $96 \%$ of the total recreational effort on Stockton Beach. I found a similar pattern on Seven Mile Beach, where food collecting accounted for $88 \%$ of the total catch and $96 \%$ of effort.

I used the mean daily catch rates for each season as indices of fishing quality for each user group. For Stockton Beach the seasonal catch rates achieved in the commercial fishery were relatively high, with an overall annual catch rate of $28.8 \mathrm{~kg} /$ collector hour, and were always more than an order of magnitude greater than the comparable catch rates in the recreational food and bait fisheries. Seasonal recreational catch rates were relatively low, with overall annual catch rates for the recreational food and bait fisheries of 1.3 and $1.6 \mathrm{~kg} /$ collector hour respectively. Recreational catch rates at Seven Mile Beach were generally an order of magnitude lower again, with a catch rate of only 0.04 and $0.08 \mathrm{~kg} /$ collector hour respectively for the food and bait fisheries. Relative differences in access to good collecting sites and collecting experience probably explain much of the difference between sectors. Over 95\% of recreational harvesters accessed the beach by foot at Stockton Beach, and at least $90 \%$ of these people were collecting within the first kilometre of beach. In comparison, commercial fishers spread their collecting activities across the entire beach. Harvesters also stayed close to access points at Seven Mile Beach.

Commercial fishers and recreational bait collectors favoured large pipis and tended not to take small pipis. Recreational food collectors were less selective, often retaining small pipis, some as small as 9 mm in length. Over $25 \%$ of the recreational food catch consisted of small pipis, $<30 \mathrm{~mm}$ in length.

In order to allow preliminary estimates of the effects of harvesting, I collected information on growth rates, recruitment and reproduction. Length frequency data indicated that growth was rapid in small animals. At all sites pipis appeared to reach 37 mm (the length of sexual maturity) within 10 months. Growth clearly slowed with size. I found consistent growth rates both between and within regions, although data from tagging indicated slower growth than data from length frequency analysis. However only 6 tagged animals were retrived, from 3,700 placed in the field. Recruitment patterns were consistent both between and within sites. Mortality varied both between and within sites, with few large animals found at some sites. I found small animals all year round, although few cohorts became established. Many settlers arrived on beaches, even where
there were few adults present on the beach, suggesting that there is not a strong stock-recruit relationship in this species, and that larvae are dispersing to some degree. At least some recruits were present in all samples at all sites, sometimes in large numbers. These data imply that high post-settlement mortality is a more likely cause of recruitment variation than supply of larvae for this species.

The size at which pipis can be defined as fully mature was fairly consistent between sites and between years. At least $50 \%$ of pipis were mature by 37 mm in length, with gametes being found in animals as small as 27 mm . Size at maturity appears to be relatively constant throughout the range of this species. D. deltoides appears to partially spawn almost continuously, and I found little difference in spawning pattern between sites. Oocyte diameter measurements indicated that large oocytes were present in the gonad all year round, suggesting that spawning can occur at any time. I did not find a resting phase at any time, nor did gametes ever appear to be resorbed. I found year-to-year variation in the timing of spawning, as well as in the degree to which spawning appeared to be synchronised. I found equal numbers of males and females at all sites, and no effect of size on gender. For animals in variable environments, prolonged partial spawning may be a form of "bet-hedging", maximising the likelihood of dispersal.
Table of Contents ..... 1
Non-Technical Summary ..... 3
Background ..... 5
Need ..... 6
Objectives ..... 6
Objective 1. A comparison of the commercial and recreational fisheries of the pipi.
Introduction ..... 6
Objectives ..... 7
Methods ..... 7
Site selection ..... 7
Recreational harvesting survey ..... 9
Survey design ..... 9
Estimation methods ..... 11
Commercial fishery ..... 12
Logbook study ..... 12
Size of pipis taken ..... 13
Estimation methods ..... 13
Size frequency comparisons ..... 13
Detailed results/discussion ..... 14
Recreational fisheries ..... 14
Seven Mile Beach ..... 14
Recreational food fishery ..... 14
Recreational bait fishery ..... 15
Stockton Beach ..... 16
Recreational food fishery ..... 16
Recreational bait fishery ..... 19
Commercial fishery ..... 21
Comparisons (Discussion) ..... 23
Seasonal patterns of catch and effort ..... 24
Fishing quality comparisons ..... 25
Sizes available and sizes collected ..... 25

Objective 2. To make preliminary estimates of the effects of harvesting.
Introduction ..... 27
Methods ..... 29
Growth and mortality ..... 29
Tagging experiments ..... 29
Mortality ..... 31
Shell growth checks ..... 31
Reproduction ..... 32
Sex ratio and size at first maturity using gonad smears ..... 32
Oocyte diameters ..... 32
Reproductive output and age at first maturity, stereology ..... 33
Results Discussion ..... 35
Growth and Mortality ..... 35
Length frequency data ..... 35
Tag-recapture experiment ..... 40
Shell growth checks ..... 42
Reproduction ..... 43
Sex ratio and size at first maturity using gonad smears ..... 43
Oocyte diameters ..... 48
Reproductive output and age at first maturity, stereology ..... 50
General Discussion ..... 53
Management implications ..... 53
Implications for dispersal and recruitment ..... 54
Appropriate harvest tactics for the pipi fishery ..... 55
Specific management strategies ..... 56
Predictions ..... 58
Benefits ..... 59
Further Development ..... 59
Conclusion ..... 60
References ..... 60
Appendix 1: Intellectual property ..... 67
Appendix 2: Staff and Acknowledgments ..... 67
Appendix 3: Length frequency data ..... 68

## Non-Technical Summary

In order to compare the levels of recreational and commercial harvesting of the pipi, I used a voluntary $\log$ book survey to quantify catch, effort, and catch rates for the commercial fishery on Stockton Beach, NSW, over a one year period, and an onsite survey to quantify catch, effort, and catch rates for recreational food and bait harvesting on Stockton Beach on the NSW north coast and Seven Mile Beach on the south coast (which is not commercially exploited).

There were large differences between the harvesting patterns for the recreational and commercial fisheries on Stockton Beach, implying that the sectors may have very different potential impacts on local pipi stocks, even though both fisheries were restricted solely to hand gathering. I estimated that the combined recreational and commercial catch of pipis from Stockton Beach was 237.7 tonnes during the period March 1996 to February 1997 inclusive, taken in a total of 120,672 collector hours. The commercial fishery was characterised by its relatively large catch, low amount of fishing effort, and high catch rate. Commercial fishers took the bulk of the catch ( $80 \%$ of the combined commercial and recreational harvest), but accounted for only $11 \%$ of the combined fishing effort and included only 27 fishers. In contrast, the recreational fishery was characterised by a relatively small catch, many participants, high fishing effort, and extremely low catch rates. Recreational fishers took $20 \%$ of the combined commercial and recreational catch, but accounted for $89 \%$ of the combined fishing effort, with an estimated 15,795 parties participating. Many groups had extremely low catches. Winter was the peak season for commercial harvesters, while in the recreational fishery summer was the peak season.

When I compared north and south coast sites, I found that recreational collecting effort at Stockton Beach was more than twice that estimated for Seven Mile over the same season, summer ( 53,373 cf. 23,356 collector hours respectively), but at Stockton Beach catches were an order of magnitude higher ( 18.1 cf 1.6 t ) in summer due to the much higher catch rates.

At both sites, recreational collecting for food was far more extensive than bait collecting. Food gathering accounted for $93 \%$ of the total recreational catch and $96 \%$ of the total recreational effort on Stockton Beach. I found a similar pattern on Seven Mile Beach, where food collecting accounted for $88 \%$ of the total catch and $96 \%$ of effort.

I used the mean daily catch rates for each season as indices of fishing quality for each user group. For Stockton Beach the seasonal catch rates achieved in the commercial fishery were relatively high, with an overall annual catch rate of $28.8 \mathrm{~kg} /$ collector hour, and were always more than an order of magnitude greater than the comparable catch rates in the recreational food and bait fisheries. Seasonal recreational catch rates were relatively low, with overall annual catch rates for the recreational food and bait fisheries of 1.3 and $1.6 \mathrm{~kg} /$ collector hour respectively. Recreational catch rates at Seven Mile Beach were generally an order of magnitude lower again, with a catch rate of only 0.04 and $0.08 \mathrm{~kg} /$ collector hour respectively for the food and bait fisheries. Relative differences in access to good collecting sites and collecting experience probably explain much of the difference between sectors. Over $95 \%$ of recreational harvesters accessed the beach by foot at Stockton Beach, and at least $90 \%$ of these people were collecting within the first kilometre of
beach. In comparison, commercial fishers spread their collecting activities across the entire beach. Harvesters also stayed close to access points at Seven Mile Beach.

Commercial fishers and recreational bait collectors favoured large pipis and tended not to take small pipis. Recreational food collectors were less selective, often retaining small pipis, some as small as 9 mm in length. Over $25 \%$ of the recreational food catch consisted of small pipis, $<30$ mm in length.

In order to allow preliminary estimates of the effects of harvesting, I collected information on growth rates, recruitment and reproduction. Length frequency data indicated that growth was rapid in small animals. At all sites pipis appeared to reach 37 mm (the length of sexual maturity) within 10 months. Growth clearly slowed with size. I found consistent growth rates both between and within regions, although data from tagging indicated slower growth than data from length frequency analysis. However only 6 tagged animals were retrived, from 3,700 placed in the field. Recruitment patterns were consistent both between and within sites. Mortality varied both between and within sites, with few large animals found at some sites. I found small animals all year round, although few cohorts became established. Many settlers arrived on beaches, even where there were few adults present on the beach, suggesting that there is not a strong stock-recruit relationship in this species, and that larvae are dispersing to some degree. At least some recruits were present in all samples at all sites, sometimes in large numbers. These data imply that high post-settlement mortality is a more likely cause of recruitment variation than supply of larvae for this species.

The size at which pipis can be defined as fully mature was fairly consistent between sites and between years. At least $50 \%$ of pipis were mature by 37 mm in length, with gametes being found in animals as small as 27 mm . Size at maturity appears to be relatively constant throughout the range of this species. D. deltoides appears to partially spawn almost continuously, and I found little difference in spawning pattern between sites. Oocyte diameter measurements indicated that large oocytes were present in the gonad all year round, suggesting that spawning can occur at any time. I did not find a resting phase at any time, nor did gametes ever appear to be resorbed. I found year-to-year variation in the timing of spawning, as well as in the degree to which spawning appeared to be synchronised. I found equal numbers of males and females at all sites, and no effect of size on gender. For animals in variable environments, prolonged partial spawning may be a form of "bet-hedging", maximising the likelihood of dispersal.

## Background

Donax deltoides (the pipi) is harvested both commercially and recreationally in NSW, South Australia, and Victoria. More than 300 t were landed by commercial fishers in NSW in 1993-4, and about the same in SA. Catches were very small in Victoria and the only harvesting in Queensland was recreational. At an average retail price of $\$ 2$ per kilo (1996 value, NSW Fish Marketing Authority data base), a total catch of 600 t is worth $\$ 1.2 \mathrm{M}$ to the retail sector in Australia. Although catches and the value of the fishery vary considerably, it is generally accepted that effort is increasing, and concern over the potential impact of increased harvesting has been expressed.

At one point in the 1950s and 60s pipis were commercially harvested and canned for export on the South Coast. Overharvesting is reputed to be the cause of the collapse of this fishery. Now the only commercial harvesting in NSW is done north of Sydney. There is also a commercial fishery based around the mouth of the Murray River in SA. Little work has been done on pipis since a 1985 study by the SA Department of Fisheries, which was initiated because of concerns about overharvesting in South Australia.

Even as long ago as 1950, stocks of pipis in areas near large population centres were reported to have declined. Anglers have been complaining bitterly about the collapse of pipi populations on the north coast of NSW since the 1960s, e.g. (Anon. 1966; Cornish 1966; Dallimore 1965). There is, however, no evidence that harvesting of pipis in Australia has a deleterious effect on population structure and density. Beaches near large population centres may be particularly vulnerable to overharvesting, such as on Stockton Beach near Newcastle. In 199495, the Newcastle Fishing Co-operative handled some 137 t of pipis, of which 120 t were estimated to be from Stockton (figures from Manager, Newcastle Co-op.). This was in addition to the large, but unquantified numbers collected by recreational users. Concern about the amounts of pipis taken by non-commercial fishers has already led to the bag limit for pipis being lowered from a volume of ten litres to 50 individuals.

While commercial production information is routinely collected by many fishery agencies e.g. (ABARE 1997), comparable recreational statistics are usually not available. Recreational catch and effort data are more difficult to measure because of the large numbers of participants and the diffuse nature of many recreational fisheries, and the expense of quantifying the activities of the recreational sector is often prohibitive. For the pipi fishery there is no information available about the numbers of animals being taken from beaches, for either the commercial or recreational catch.

The valuable nature of the commercial catch, and the extensive use of pipis for bait and food, makes it important to determine whether populations are declining, and if so, why. There is no information available about the numbers of animals being taken from beaches, for either the commercial or recreational catch. Information is needed to develop appropriate management strategies, e.g. a minimum size limit, or the possibility of seasonal closing of beaches to harvesting. However, management plans cannot be more than arbitrary in the absence of knowledge. More information is needed, both about the extent of harvesting, and fisheryindependent data, such as size and age at first reproduction, and growth rate.

## Need

Prior to this survey there were suggestions that D. deltoides was vulnerable to overharvesting. There was an impression of increased effort, but no reliable estimates of either catch or effort. This was particularly the case for the recreational sector, which was thought to be large. The commercial and recreational fisheries depend on stocks of pipis, which are also an important component of the food chain. Pipis frequently have the largest biomass on sandy beaches, and are often the most abundant species. Donax form part of the diet of crabs and many species of fish, and are a favourite food of oystercatchers. A decline in the numbers of sooty oystercatchers in southern NSW may be linked to the decline in numbers of pipis. Very little was known about pipis prior to my survey. For example, there was almost no information on densities, size at first reproduction, growth rates, reproductive effort, or the levels of harvesting.

The recreational sector is likely to increase as four wheel drive vehicles become more popular, the population of NSW increases, and interest in more cosmopolitan styles of food continues, leading to a greater allocation of the pipi resource to this sector. Consequently conflict, already strong, between recreational anglers (who collect for bait), recreational food harvesters and commercial harvesters, is likely to increase. Fisheries managers are already under pressure to make decisions about allocation of this resource, however management plans cannot be more than arbitrary in the absence of knowledge.

## Objectives

1. To quantify levels of commercial and recreational harvesting of pipis on selected NSW beaches. 2. To make preliminary estimates of the effects of harvesting.

## Objective 1. A comparison of the commercial and recreational fisheries of the pipi.

## Introduction

Recreational fishing is one of the most popular activities in Australia. A national survey of participation in recreational fishing within Australia, completed in 1984, estimated that 4.5 million people over 10 years of age had fished recreationally at least once during the previous year, and that these anglers had made collectively about 48 million fishing trips (PA Management Consultants 1984). The growth of the recreational sector in Australia has led to increased conflict with the commercial sector as both user groups strive to maximise their share of fisheries resources. This conflict is widespread in fisheries in all countries (Australian National Recreational Fisheries Working Group 1994; Edwards 1990; Lal et al. 1992), particularly in beach clam fisheries which tend to be very accessible (McLachlan et al. 1996).

The pipi, Donax deltoides (Lamarck), is a large ( 80 cm in length), highly mobile clam that lives infaunally in the surf zone of high energy beaches between Fraser Island, Queensland and the mouth of the Murray River in South Australia. It has been harvested by coastal Aborigines for at least 10,000 years (Godfrey 1989), and is currently harvested by both the commercial and
recreational sectors. Most of the commercial catch of the pipi comes from New South Wales (NSW) and South Australia, each accounting for about half the annual Australian catch of about 700 tonnes (NSW Fisheries and South Australian Fisheries commercial catch statistics). In NSW, pipi collecting has been a commercial fishing operation since the early 1950s (NSW Fisheries commercial catch statistics). The declared annual commercial catch in NSW remained below 100 tonnes until 1990-91, when the catch approached a level of 300 tonnes. Annual catches during the period 1991-92 to 1995-96 ranged from 247 to 314 tonnes, and a catch of 464 tonnes was recorded in 1996-97, the most recent year for which catch records were available (NSW Fisheries commercial catch statistics). Over $99 \%$ of the commercial catch from NSW is currently carried out north of Sydney, although there was commercial harvesting on the south coast in the 1950s (Anon. 1960; MacPherson and Gabriel 1962). In addition there is believed to be a large recreational harvest, which had not been quantified. Anglers use pipis for bait when targeting finfish, and other recreational harvesters take them for food. The fishery is restricted to hand gathering, with no gear allowed in either sector, and there is no by-catch. There is no information on how the catch is partitioned between the commercial and recreational sectors, hence obtaining an accurate and precise assessment of catch and effort for both the commercial and recreational pipi fishery is a prerequisite for management and allocation of this shared resource.

## Objectives

1. I will quantify catch, effort, and catch rates for the recreational food and bait, and the commercial fishery on the most important pipi collecting site in NSW, Stockton Beach, on the north coast, over a one year period.
2. In order to compare harvesting patterns between the north and south coasts of NSW, I will quantify catch, effort, and catch rates for the recreational food and bait fishery on a noncommercially exploited beach on the south NSW coast, over one season.

## Methods

## Site selection

Stockton Beach, on the north coast of NSW, is a long beach with several access sites (Fig. 1a). The Newcastle-Nelson Bay Commercial Fishermen's Cooperative (referred to hereafter as the Newcastle Co-op) handled between 114 and 181 tonnes of pipis per year, mainly from Stockton Beach, in the period 1993-97. This represented between $28 \%$ and $73 \%$ of the entire NSW commercial pipi catch (NSW Fisheries commercial catch statistics). In addition, local NSW Fisheries Officers suggested that there was a substantial recreational harvest from Stockton Beach. These observations indicated that Stockton Beach was the most important site in NSW for both commercial and recreational pipi harvesting.

Seven Mile Beach, on the south coast, is no longer commercially harvested, although in the 1950s an export cannery existed which was based on pipis from this beach (Anon. 1960; MacPherson and Gabriel 1962). However local NSW Fisheries Officers suggested that there was still a substantial recreational harvest from this site, which also has several access points (Fig. 1b).


Figure 1 Main access points on two beaches used to estimate levels of recreational harvesting of Donax deltoides. Beaches were (a) Stockton Beach. Access points: 1. Birubi Point (foot), 2. Birubi Pt (4WD), 3. Lavis Lane (4WD), 4. Stockton (foot). Heavier shading represents Newcastle urban area. (b) Seven Mile Beach. Access points: 5. Berry Rd, 6. Berry Rd track, 7. Shoalhaven Heads track, 8. Shoalhaven Heads, all foot access only.

## Recreational harvesting survey

## Survey design

For both sites, I used an on-site survey to quantify the recreational food and bait fisheries. People were counted and interviewed as they left the beach, hence catch, effort and catch rates were estimated from completed trips. I chose a "bus route" design, in which multiple sites can be covered on a single day by travelling on a predetermined route for which the starting point is allocated at random (Pollock et al. 1994).

In order to identify survey strata and to set sampling probabilities for random subsampling within these strata, I used data collected during pilot studies at both sites, as well as information derived from extensive consultations with NSW Department of Fisheries officers, Council rangers, commercial fishers and local residents, and my own observations.

I used a primary sampling unit of a day, with work shift as the secondary sampling unit. I divided days into two work shifts, giving the early work shift a selection probability of $\pi_{1}=0.33$; and the afternoon shift had a selection probability of $\pi_{2}=0.67$. The length of these work shifts varied seasonally. Hence from November to March, I split the fishing day into two six hour shifts, 0800-1400, and 1400-2000, while for the rest of the year the shifts were shortened to 5.5 hours.

Pipis are available at any point of the tidal cycle, and the pilot study data indicated that collecting effort was highest on afternoons with good weather conditions regardless of tide. Hence I did not stratify sampling shifts for tide. I decided to run the main harvesting study under all weather conditions, as recreational anglers and local residents suggested that illegal collecting was quite common in wet weather, because Fisheries Inspectors were perceived as less likely to patrol in poor weather. In addition, the presence of reasonable numbers of fishers on a wet Sunday afternoon during the pilot study indicated that weather may be less important than day and time in determining usage.

In order to compare seasonal sampling patterns, I divided the year into seasonal strata (autumn: March-May; winter: June-August; spring: September-November; summer: DecemberFebruary) and allocated 15 days to each season, a total of 60 days sampled. Within each season I used two day-type strata. I assigned a site selection probability to the weekends, public and school holidays stratum of $\pi_{1}=0.70$, and $\pi_{2}=0.30$ to the non-holiday weekdays stratum. However I did not weight season strata unequally, as surveys of recreational angling in northern NSW have showed high fishing effort all year round (Steffe et al. 1994; West and Gordon 1994).

There are four main access points onto Stockton Beach (see Fig. 1a): foot access from Stockton (south end) and from Birubi Point (north end); and four wheel drive (4WD) access at Birubi Pt and Lavis Lane (approximately 20 km south of Birubi Pt). However my pilot study indicated that the majority of recreational pipi harvesters used only two access sites, which accounted for $\mathbf{> 9 8 \%}$ of the recreational harvest from this beach. Thus, I restricted the survey to these two access sites, assigning a site selection probability to the foot access site at Birubi Point (north end) of $\pi_{1}=0.70$, and $\pi_{2}=0.30$ to the main four-wheel drive (4WD) access site near Birubi Pt.

For Seven Mile Beach there are four access points, all foot access (see Fig. 1b): the main National Park picnic ground at Berry Road, a track approximately 1.5 km to the south, another track about 500 m north of Shoalhaven Heads, and the main Shoalhaven Heads access point. For this site, I used the same day-type and shift sampling probabilities, and on the basis of a plot study selected site sampling probabilities of $\pi_{1}=0.50$ (Berry Rd), $\pi_{2}=0.20$ (Berry Rd track), $\pi_{3}=$ 0.10 (Shoalhaven Heads track), and $\pi_{4}=0.20$ (Shoalhaven Heads). I restricted sampling to one season (summer) at this site, hence 15 days were sampled.

I collected data for Stockton Beach for the period 1 March 1996-28 February 1997, and for Seven Mile Beach for the period 1 December 1996-28 February 1997. At the foot access sites I approached and interviewed all people carrying containers that could hold pipis (e.g. bags, coolers, buckets), or carrying angling tackle. I was able to interview all collectors on all occasions at all foot sites site. At the 4WD access site, I stopped every car and interviewed the occupants, except on two days when traffic was very heavy. On these occasions I stopped and interviewed every third car. Thus, for these two days I assumed that people interviewed were a representative sample of pipi harvesting parties, and used a direct expansion method to account for those parties who could not be interviewed but had been counted.

For all interviews, I recorded the time harvesting was commenced and completed, the number of people collecting, and whether pipis taken were intended for bait or food. Time spent walking along the beach or searching for pipis was included, as pipis were often scarce near access points, particularly on days when large numbers of people had been collecting. I used volunteers with binoculars to confirm that pipi collectors were not attempting to avoid my weigh station.

The quality of some interviews may have been reduced by difficulty in communicating with harvesters for whom English was a second language. However this problem could not affect catch measurement as catches were weighed. Estimates of trip duration could have been biased because of language problems with some groups and because many people do not wear watches on the beach. Hence, in order to validate how accurately harvesters could recall and report trip duration, I observed independently the starting and finish times for a random sample of 50 groups, prior to an interview with them. I then compared their reported trip times with observed trip lengths by using a paired two tailed $t$-test.

Refusals and avoidance behaviour were rare, although some people initially attempted to conceal pipis. I used binoculars to find out who was collecting on the beach. Such prior knowledge often enabled me to convince parties with illegal amounts of pipis to let me weigh their catches. However, for some collectors, my presence on the beach may have increased their level of compliance with regulations (a bag limit of 50 animals per person).

To estimate the catch when people were taking pipis off the beach, I drained the animals before weighing the catch to the nearest 0.1 kg on a spring balance. However, in general, anglers use pipis on site as bait for finfish while food collectors take them off the beach. Hence I asked anglers (easily identified by their equipment) to estimate how many pipis they had used during their fishing trip, and how long they had taken to collect their bait. To quantify recall and rounding
error, I asked 20 anglers to carry bait creels and keep the shells of any pipis used as bait. I told them I needed these shells for "size analysis" to avoid making them conscious of counting. When they came off the beach, I asked them to estimate the number of pipis used for bait and obtained the shells of pipis used. I then compared their reported catch with the known number of shells retained, using a paired two tailed t-test.

In order to compare the sizes taken by recreational and commercial fishers at Stockton Beach, I measured samples to the nearest mm using a measuring board, or photographed random samples from catches being carried off the beach and used NIH Image (written by Wayne Rasband at the U.S. National Institute of Health) to obtain estimates of pipi lengths. Initially I measured 100 animals by both methods, and found no significant difference in mean length (paired twotailed t -test, $\mathrm{t}=1.11 ; \mathrm{df}=99 ; \mathrm{p}=0.27$ ), indicating that the method used did not bias the pipi length data. Thus I pooled all length data prior to plotting a size frequency histogram. For the bait fishery I measured the shells from the number verification study, and used pooled length-weight data to convert numbers into weights taken. I pooled the length data from the pipis used by anglers for bait and plotted them as a size frequency histogram.

## Estimation methods

I estimated catch and effort separately for bait and food harvesters using direct expansion (Pollock et al. 1994). For each day, I estimated catch as

$$
C=\mathrm{T} \sum_{i=1}^{n}(1 / \mathrm{w} i) \sum_{j=1}^{m}\left(\mathrm{c}_{j i} / \pi\right)
$$

where $C$ is the estimated total daily catch ( kg ), $\mathrm{c}_{j i}$ is the catch for the $j$ th fisher at the $i$ th site (with $i$ $=1, \ldots, n$ sites, $j=1, \ldots, m$ fishers), $\pi$ is the work shift sampling probability, T is the time in minutes for a complete full circuit, and $w_{i}$ is the waiting time in minutes at the $i$ th site.

I calculated mean daily catch for each day-type stratum by summing daily totals and dividing by the number of days sampled within that stratum. The total catch for that day-type stratum was then the product of the mean daily catch and the number of possible sampling days in that stratum. I summed day-type stratum totals to get seasonal catches, and then summed seasonal totals to obtain a yearly recreational total. I calculated effort (in units of collector hours) in the same way, and calculated variances according to Pollock et al. (1994). I calculated catch rates in kg/collector hour using the mean of ratios, $\mathrm{R}_{2}$ as

$$
\mathrm{R}_{2}=\sum_{i=1}^{n}\left(\mathrm{c}_{i} / \mathrm{L}_{i}\right) / \mathrm{n}
$$

where $\mathrm{c}_{i}$ is the catch of group $i$ in $\mathrm{kg}, \mathrm{L}_{i}$ is the length of the fishing trip in collector-hours for group $i$, and n is the number of groups collecting on that day. Note that collector hours in this hand gathering fishery are equivalent to angler-hours in a finfish line fishery. I then used these daily catch rates to calculate a mean daily catch rate and its variance for each season. The mean of ratios is the correct catch ratio estimator to use for completed trip data when an index of fishing quality is required (Pollock et al. 1997).

## Commercial fishery

The primary data source for my estimates of commercial catch, effort and catch rates was a voluntary logbook that I distributed to all commercial fishers that worked on Stockton Beach. Logbooks can provide a complete enumeration of on-site catch and effort if all fishers can be identified and are willing to report information describing their fishing activities. I used Newcastle Co-op records and NSW Fisheries catch statistics as secondary data sources.

I preferred to use a voluntary logbook approach even though I believed that the majority of pipis handled by the Newcastle Co-op were probably from Stockton Beach. Co-op consignment records are probably less reliable than logbook data for a variety of reasons. Many fishers work on several beaches but Co-op consignment records do not indicate the source of catches. Some local fishers do not consign all catches to the Newcastle Co-op, instead choosing to send their catches directly to the Sydney Fish Market, or sell directly interstate. Other fishers are known to travel long distances to fish Stockton Beach when pipi abundance is high, but consign their catches through their own regional Co-op.

All commercial fishers in NSW are required by law to provide a monthly record of their catch and effort to NSW Fisheries. The catch statistics compiled from these compulsory monthly records do not indicate the beach from which catches are taken and the data are self reported. The voluntary logbook approach was again the preferred method for collecting commercial fishery data for Stockton Beach.

## Logbook study

When I started this study there was no available list with which to identify the commercial pipi fishers that work on Stockton Beach. I used a variety of sources to identify these fishers. Initially, I compiled a comprehensive state wide list of all commercial pipi fishers in NSW (101 fishers) for the financial year 1993-4 from catch statistics held by NSW Fisheries. I identified 42 of these fishers as likely to be collecting pipis on Stockton Beach in the coming year, from contacting most fishers directly and by obtaining additional information about the Stockton fishery from the Newcastle Co-op. I asked these 42 fishers to fill out a voluntary logbook to quantify their fishing activities on Stockton Beach. All indicated their willingness to participate in the study. Catches were reported in kilograms and fishing effort was reported in units of collector hours, which included searching and grading times. Catch (pipis kept and released) and harvest (pipis kept) are synonymous in this fishery and I use these terms interchangeably throughout the text. There are no quotas or size limits, hence none of the catch is discarded or dumped prior to dispatch to regional Co-ops or the Fish Markets in the capital cities.

For fishers who put all their catches through the Newcastle Co-op, I obtained permission to validate reporting of catches by cross-checking against Newcastle Co-op records. In all cases, logbook catches corresponded well with Co-op records, except for some minor variations in dates. I called fishers regularly to remind them to return their records. Some fishers did not include effort data with their logbooks, but I was able to estimate the number of days spent fishing from Newcastle Co-op records and NSW Fisheries catch statistics.

During the logbook survey period, I checked Newcastle Co-op consignment records regularly, and asked active local fishers to identify any new fishers who had entered the fishery but who were not on the original list. None were found. In addition, I regularly called all commercial fishers that had worked previously on Stockton Beach but had indicated that they were unlikely to collect pipis in the coming year. None of these fishers were active on Stockton Beach during the course of the logbook study.

The logbook study was planned to run at the same time as the recreational survey, however due to a delay in obtaining a list of fishers, the start of the commercial logbook study was delayed by a month, and data were collected for the period 1 April 1996-28 February 1997. I obtained commercial monthly catch and trip information for March 1996 from NSW Fisheries catch statistics and Newcastle Co-op records, and these data were verified by contacting the fishers directly.

## Size of pipis taken

In order to obtain an estimate of the sizes taken by commercial fishers during the survey, I collected length data from the Newcastle/Nelson Bay Commercial Fishermen's Cooperative (hereafter Newcastle Co-op) and the Sydney Fish Markets for pipis consigned from the Newcastle Co-op. At approximately monthly intervals, I took scoops at random from all tubs on the market floor, sampled at least $10 \%$ of each tub, and took photographs of these samples. I scanned the photos into a computer and used NIH Image to obtain estimates of pipi lengths. I pooled the length data from the monthly samples and plotted them as a size frequency histogram.

## Estimation methods

I estimated total effort by using data from logbooks, supplemented by data from NSW Fisheries monthly catch statistics and Newcastle Co-op consignment records. Some fishers did not fill in logbooks on a daily basis, but either gave monthly catch totals or gave permission for their Newcastle Co-op records to be accessed. I have hourly effort data for most fishers who returned logbooks, while data from other sources is on a daily or trip basis. I used the mean hourly trip length, estimated from logbooks, to convert the daily Newcastle Co-op and NSW Fisheries data into hourly units of effort. I calculated catch rates in $\mathrm{kg} /$ collector hour from logbook data, using the mean of ratios estimator, $\mathrm{R}_{2}$ (Pollock et al. 1994) as for the recreational survey, but in this case $\mathrm{c}_{i}$ is the catch ( kg ) for the $i$ th fisher ( $i=1, \ldots, \mathrm{n}$ fishers), $\mathrm{L}_{i}$ is the length of the fishing trip (collector hours) for the $i$ th fisher, and n is the number of fishers on that day.

## Size frequency comparisons

For Stockton Beach, in order to make a fishery independent comparison of the sizes available on the beach with sizes taken by different groups of harvesters, I pooled sizes from downshore transects taken at approximately monthly intervals during the period of the study at three sites on Stockton Beach, at $0.6,3$ and 6 km south of Birubi Point. I used these data to construct a size frequency histogram of available sizes of pipis on the beach.

## Detailed results/discussion

## Recreational fisheries

## Seven Mile Beach

A total of 190 party groups, which consisted of 1,033 individuals, were collecting pipis during sampling shifts in the 15 days sampled between $1 \mathrm{Dec} 96-28 \mathrm{Feb} 97$. I was able to interview all of these parties. I estimated that $4,981 \pm 1,656$ groups participated in the food and bait fisheries during the summer. I estimated the total recreational harvest for food and bait as 1.6 $\pm 0.6 \mathrm{t}$ over the summer, and total effort as $23,365 \pm 7,015$ collector hours.

## Recreational food fishery

The majority of recreational harvesters were collecting pipis for food. I estimated that 1.4 $\pm 0.6 \mathrm{t}$ of pipis were taken for food (Table 1), which represented $88 \%$ of the total recreational catch. Most of the recreational food catch was taken during weekends, public and school holidays (1.3 tor $81 \%$ of total food harvest), and non-holiday weekdays had low levels of catch ( 0.1 t or $19 \%$ of total food harvest - Table 1). Recreational food harvesters made an estimated $3,599 \pm$ 1,547 party trips collected for food, which represented $72 \%$ of all recreational pipi collecting trips. These food harvesting party trips accounted for an estimated $22,462 \pm 7,010$ collector hours of effort (Table 2), which represented $96 \%$ of the total recreational effort. Most recreational food collecting occurred during weekends, public and school holidays ( 21,680 collector hours or $97 \%$ of total food effort), and non-holiday weekdays had low levels of effort ( 783 collector hours or $4 \%$ of total food effort).

The mean daily catch rates of recreational food collectors were always low, ranging from $0.02-0.09 \mathrm{~kg} /$ collector hour (Table 3). The mean daily catch rate over the entire season was 0.04 $\pm 0.2 \mathrm{~kg} /$ collector hr .

Table 1 Day-type stratum estimates of catch with standard errors, for the pipi Donax deltoides, by recreational food and bait harvesters on Seven Mile Beach, NSW, for one season, summer December 1996 to February 1997 inclusive. "days" = number of days sampled. All catches are expressed in metric tonnes.
Recreational food \&
bait catch
for each day-type

| Food |  |  |  |
| :--- | ---: | ---: | ---: |
| $\quad$ Weekends \& holidays | 11 | 1.3 | 0.6 |
| Non-holiday weekdays | 4 | 0.1 | 0.3 |
| Total | 15 | 1.4 | 0.6 |
|  |  |  |  |
| Bait |  |  |  |
| Weekends \& holidays | 11 | 0.1 | 0.0 |
| Non-holiday weekdays | 4 | 0.1 | 0.1 |
| Total | 15 | 0.2 | 0.1 |
|  |  |  |  |
|  |  |  |  |
| Food + Bait Total | 15 |  | 0.6 |

Table 2 Day-type stratum estimates of collecting effort, with standard errors, for the pipi Donax deltoides, by recreational food and bait harvesters on Seven Mile Beach, NSW, for one season, summer December 1996 to February 1997 inclusive. Figures in parentheses are the number of days sampled. All effort units are expressed as collector-hours.

|  <br> bait collecting effort <br> for each day-type | Season <br> Summer <br> days | effort | SE |
| :--- | :---: | ---: | ---: |
| Food | 11 | 21,680 | 6,996 |
| Weekends \& holidays | 4 | 783 | 366 |
| Non-holiday weekdays | 15 | 22,462 | 7,010 |
| Total |  |  |  |
|  |  | 528 | 194 |
| Bait | 11 | 366 | 196 |
| Weekends \& holidays | 4 | 895 | 506 |
| Non-holiday weekdays | 15 |  |  |
| Total | 15 | 23,356 | 7,015 |

Table 3 Day-type stratum estimates of mean daily catch rates with standard errors, for the pipi Donax deltoides, by recreational food and bait harvesters on Seven Mile Beach, NSW, for one season, summer, December 1996 to February 1997 inclusive. "days" = number of days sampled on which effort occurred. All mean daily catch rates are expressed in kilograms per collector hour. Survey days during which no interviews were obtained are excluded from catch rate calculations. These days were treated as having an indeterminate catch rate rather than a zero catch rate.

|  <br> bait catch rate <br> for each day-type | Season <br> Summer <br> days | catch rate | SE |
| :--- | :--- | :---: | :---: |
| Food <br> Weekends \& holidays <br> Non-holiday weekdays | 10 | 0.02 | 0.13 |
| Total | 3 | 0.09 | 0.05 |
|  | 13 | 0.04 | 0.02 |
| Bait |  |  |  |
| $\quad$ Weekends \& holidays | 10 | 0.05 | 0.01 |
| Non-holiday weekdays | 2 | 0.24 | 0.12 |
| Total | 12 | 0.08 | 0.03 |

## Recreational bait fishery

I estimated that only $0.2 \pm 0.1 \mathrm{t}$ of pipis were taken for bait in the summer season at Seven Mile Beach (Table 1), which represented $13 \%$ of the total recreational catch. Recreational bait harvesters made an estimated $1,382 \pm 594$ party trips which represented $28 \%$ of all recreational pipi collecting trips. These bait harvesting party trips (usually anglers collecting pipis for immediate use as bait for finfish) accounted for an estimated $528 \pm 194$ collector hours of effort (Table 2), which represented only $4 \%$ of the total recreational effort. Most recreational bait collecting was low in both day-type strata, with 528 collector hours ( $60 \%$ of total bait effort) during weekends, public and school holidays, and 366 collector hours ( $40 \%$ ) on non-holiday weekdays (Table 2).

The mean daily catch rates of recreational food collectors was $0.1 \mathrm{~kg} /$ collector hour on non-holiday weekdays, but increased to $0.2 \mathrm{~kg} /$ collector hour during weekends, public and school holidays (Table 3). The mean daily catch rate over the entire season was $0.1 \pm 0.3 \mathrm{~kg} /$ collector hour.

## Stockton Beach

A total of 1,005 party groups, which consisted of 4,945 individuals, were collecting pipis during sampling shifts in the 60 days sampled between 1 March $96-28$ Feb 97. I was able to interview 977 of these parties. Nearly all recreational fishers were cooperative. Only one party refused my request for information (a refusal rate of $0.1 \%$ ), but I had observed their time collecting and were able to estimate their catch from the volume of pipis they carried. I estimated that $15,795 \pm 2,212$ groups participated in the food and bait fisheries during the year.

I was able to validate the accuracy of trip length estimates made by recreational harvesters by comparing reported estimates of trip times with independent observations of actual trip times. I found no significant difference between reported and actual trip lengths (paired two-tailed $t$-test: $t=$ 1.82; $\mathrm{df}=49 ; \mathrm{p}=0.07$ ).

I estimated the total recreational catch for food and bait as $46.5 \pm 5.3 \mathrm{t}$ which was $20 \%$ of the combined recreational and commercial catch of 237.7 t , and the total recreational effort for the food and bait fisheries as $107,049 \pm 15,508$ collector hours, which represented $89 \%$ of the combined recreational and commercial effort ( 120,672 collector hours).

## Recreational food fishery

The majority of recreational harvesters were collecting pipis for food. I estimated that $43.1 \pm 5.3 \mathrm{t}$ of pipis were taken for food (Table 4), which represented $18 \%$ of the total commercial and recreational catch, and $93 \%$ of the total recreational catch. The largest recreational catches for food were taken during summer and autumn, 17.3 t and 13.3 t respectively, representing $40 \%$ and $31 \%$ of the total annual food harvest. Catches declined markedly during spring and winter to 7.2 t and 5.3 t respectively ( $17 \%$ and $12 \%$ of total food harvest - Table 4). Most of the recreational food catch was taken during weekends, public and school holidays ( 39.1 t or $91 \%$ of total food harvest), and non-holiday weekdays had low levels of catch ( 4.0 t or $9 \%$ of total food harvest Table 4).

Food harvesters made an estimated $12,854 \pm 2,141$ party trips, which represented $81 \%$ of all recreational pipi collecting trips. These food harvesting party trips accounted for an estimated $102,255 \pm 15,443$ collector hours of effort (Table 5), which represented $85 \%$ of total commercial and recreational effort, and $96 \%$ of the total recreational effort. Recreational food collecting effort was highest in summer at 51,038 collector hours (representing $50 \%$ of total annual recreational food effort), at an intermediate level in autumn with 26,576 collector hours expended ( $26 \%$ of total food effort), and was lowest during the spring and winter, with 13,292 and 11,349 collector hours respectively ( $13 \%$ and $11 \%$ of total food effort - Table 5).

Table 4 Annual, seasonal and day-type stratum estimates of catch with standard errors, for the pipi Donax deltoides, by recreational food and bait harvesters on Stockton Beach, NSW, March 1996 to February 1997 inclusive. Figures in parentheses are the number of days sampled. All catches are expressed in metric tonnes.


Table 5. Annual, seasonal and day-type stratum estimates of collecting effort with standard errors, for the pipi Donax deltoides, by recreational food and bait harvesters on Stockton Beach, NSW, March 1996 to February 1997 inclusive. Figures in parentheses are the number of days sampled. All effort units are expressed as collector hours.

| Recreational food \& | Season |  |  |  |  |  |  |  |  |  |  | Total |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| bait collecting effort for each day-type | Autumn |  | Winter |  |  | Spring |  |  | Summer |  |  |  |  |  |
| Food |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Weekends \& holidays | (10) 23,959 | 8,401 | (10) | 8,677 | 2,970 | (10) | 11,721 | 3,292 | (12) | 50,596 | 11,991 | (42) | 94,953 | 15,298 |
| Non-holiday weekdays | ( 5) 2,617 | 1,026 | ( 5) | 2,672 | 1,659 | ( 5) | 1,571 | 684 | ( 3) | 442 | 442 | (18) | 7,302 | 2,114 |
| Total | (15) 26,576 | 8,464 | (15) | 11,349 | 3,402 | (15) | 13,292 | 3,362 | (15) | 51,038 | 12,000 | (60) | 102,255 | 15,443 |
| Bait |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Weekends \& holidays | (10) 947 | 411 | (10) | 311 | 73 | (10) | 347 | 133 | (12) | 2,305 | 1,303 | (42) | 3,910 | 1,375 |
| Non-holiday weekdays | (5) 421 | 294 | ( 5) | 159 | 33 | ( 5) | 274 | 129 | ( 3) | 30 | 30 | (18) | 884 | 323 |
| Total | (15) 1,368 | 506 | (15) | 470 | 81 | (15) | 621 | 185 | (15) | 2,335 | 1,303 | (60) | 4,794 | 1,412 |
| Food + Bait Total | (15) 27,944 | 8,511 | (15) | 11,819 | 3,510 | (15) | 13,913 | 3,422 | (15) | 53,373 | 12,015 | (60) | 107,049 | 15,508 |

Most recreational food collecting occurred during weekends, public and school holidays ( 94,953 collector hours or $93 \%$ of total food effort), and non-holiday weekdays had low levels of effort ( 7,302 collector hours or $7 \%$ of total food effort - Table 5).

The mean daily catch rates of recreational food collectors were relatively low throughout the year and across all day-type and seasonal strata, ranging from $0.4-2.4 \mathrm{~kg} /$ collector hour (Table 6). The mean daily catch rate over the entire year was $1.3 \pm 0.2 \mathrm{~kg} /$ collector hour (Table 6). Seasonal catch rates were highest in autumn ( $1.8 \mathrm{~kg} /$ collector hour) and winter ( $1.9 \mathrm{~kg} /$ collector hour), and were very low in spring and summer ( 0.9 and $0.6 \mathrm{~kg} /$ collector hour respectively). I found that non-holiday weekdays ( $1.2 \mathrm{~kg} /$ collector hour) had similar catch rates to public and school holidays and weekends ( $1.3 \mathrm{~kg} /$ collector hour - Table 6).

## Recreational bait fishery

A considerable number of recreational harvesters were collecting pipis for bait. I estimated that $3.4 \pm 0.6 \mathrm{t}$ of pipis were taken for bait (Table 4), which represented $2 \%$ of the total commercial and recreational catch, and $7 \%$ of the total recreational catch. The largest recreational catches for bait were taken during autumn ( 1.5 t representing $44 \%$ of the total annual bait harvest). Catches were much lower during summer ( 0.8 t or $24 \%$ of annual bait harvest), spring ( 0.6 t , $18 \%$ of total bait harvest) and winter ( $0.5 \mathrm{t}, 15 \%$ of total bait harvest - Table 4). Most of the recreational bait catch was taken during weekends, public and school holidays ( 2.3 t or $68 \%$ of total bait harvest), and non-holiday weekdays had low levels of catch ( 1.1 t representing $32 \%$ of annual bait harvest - Table 4).

Recreational bait harvesters made an estimated $2,941 \pm 555$ party trips which represents $19 \%$ of all recreational pipi collecting trips. These bait harvesting party trips (usually anglers collecting pipis for immediate use as bait for finfish) accounted for an estimated $4,794 \pm 1,412$ collector hours of effort (Table 5), which represented $4 \%$ of total commercial and recreational effort, and $5 \%$ of the total recreational effort. Recreational bait collecting effort was highest in summer with 2,335 collector hours (representing $49 \%$ of total annual recreational bait effort), at an intermediate level in autumn at 1,368 collector hours ( $29 \%$ of total bait effort), and lowest during the spring and winter with 621 and 470 collector hours respectively ( $13 \%$ and $10 \%$ of total bait effort - Table 5). Most recreational bait collecting occurred during weekends, public and school holidays ( 3,910 collector hours or $82 \%$ of total bait effort), and non-holiday weekdays had low levels of effort ( 884 collector hours representing $18 \%$ of total bait effort - Table 5).

The mean daily catch rates of recreational bait collectors were relatively low throughout the year and across all day-type and seasonal strata, ranging from $0.7-2.6 \mathrm{~kg} /$ collector hour (Table 6 ). The mean daily catch rate of recreational bait harvesters over the entire year was $1.6 \pm 0.2$ $\mathrm{kg} /$ collector hour (Table 6). Seasonal catch rates were highest in autumn ( $2.1 \mathrm{~kg} /$ collector hour), winter ( $1.8 \mathrm{~kg} /$ collector hour), and spring ( $1.8 \mathrm{~kg} /$ collector hour) but were very low in summer ( $0.9 \mathrm{~kg} /$ collector hour). Non-holiday weekdays ( $1.9 \mathrm{~kg} /$ collector hour) had similar catch rates to holidays and weekends ( $1.6 \mathrm{~kg} /$ collector hour - Table 6).

Table 6 Annual, seasonal and day-type stratum estimates of mean daily catch rates with standard errors, for the pipi Donax deltoides, by recreational food and bait harvesters on Stockton Beach, NSW, March 1996 to
February 1997 inclusive. Figures in parentheses are the number of days sampled on which effort occurred. All mean daily catch rates are expressed in kilograms per collector hour. Survey days during which no interviews were obtained are excluded from catch rate calculations. These days were treated as having an indeterminate catch rate rather than a zero catch rate. NA: Standard error cannot be calculated when sample size is restricted to one day.

Recreational food \& $\qquad$

## Total

bait catch rates Autumn Winter Spring Summer
for each day-type

## Food

| Weekends \& holidays | (10) 2.4 | 0.1 | (10) 2.0 | 0.1 | (10) 0.8 | 0.1 | (12) 0.6 | 0.1 | (42) 1.3 | 0.2 |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Non-holiday | weekdays | (5) 1.7 | 0.9 | ( 2) 1.6 | 0.3 | (3) 1.4 | 0.2 | (1) 0.4 | NA | (11) 1.2 | 0.4 |
|  |  | (15) 1.8 | 0.5 | (12) 1.9 | 0.5 | (13) 0.9 | 0.2 | (13) 0.6 | 0.1 | (53) 1.3 | 0.2 |

Total
$\begin{array}{llllll}\text { (15) } & 1.8 & 0.5 & \text { (12) } 1.9 & 0.5 & \text { (13) } 0.9 \\ 0.2\end{array}$
(13) 0.60 .1
(53) $1.3 \quad 0.2$

Bait

| Weekends \& holidays | (10) 2.6 | 0.5 | (10) 1.7 | 0.5 | (10) 2.1 | 0.6 | (12) 0.9 | 0.4 | (42) 1.6 | 0.2 |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Non-holiday | weekdays | (4) 2.0 | 0.8 | ( 5) 2.1 | 0.1 | (4) 1.6 | 0.1 | (2) 0.7 | 0.2 | (15) 1.9 | 0.4 |
| Total |  | (14) 2.1 | 0.4 | (15) 1.8 | 0.5 | (14) 1.8 | 0.4 | (14) 0.9 | 0.1 | (57) 1.6 | 0.2 |

I was able to validate the accuracy of recreational anglers' estimates of pipi numbers used for bait by comparing reported numbers of pipis used for bait with the number of shells retained in the containers provided. I found no significant difference between the reported numbers of pipis used for bait and the actual number of retained shells (paired two-tailed $t$-test: $t=1.82 ; \mathrm{df}=19 ; \mathrm{p}$ $=0.08$ ).

## Commercial fishery

Of the 42 commercial fishers participating in the voluntary logbook program, 27 worked at least once on Stockton Beach during the study. All commercial fishers were co-operative and provided information about their fishing activities on Stockton Beach. Hence the logbook study provided a full coverage or census of the commercial catch and effort on Stockton Beach during the study period. I estimated that the commercial catch for the period 1 March 1996-28 February 1997 was 191.2 t (Table 7). This represents $80 \%$ of the total commercial and recreational catch from Stockton Beach. The commercial catch peaked in autumn and winter at 58.5 t and 103.3 t respectively (representing $31 \%$ and $54 \%$ of the total annual commercial catch), declined in spring to 22.5 t ( $12 \%$ of commercial catch). The lowest level of catch recorded was 6.9 t in summer ( $4 \%$ of commercial catch - Table 7). The low catches taken during the summer season were due to a scarcity of pipis at Stockton Beach which led many fishers to concentrate their collecting activities at other beaches in the region. The highest catch for an individual fisher in one day was 0.9 t , taken in June. Note that I have derived estimates of catch and effort for the commercial survey from summing census data using a complete sampling frame, hence it is not appropriate to calculate standard errors.

I estimated that commercial fishers accounted for 13,623 collector hours of effort, which represented only $11 \%$ of the combined commercial and recreational effort (Table 7). The bulk of the commercial collecting effort was in winter with 10,348 collector hours ( $76 \%$ of total commercial effort). Intermediate levels of collecting effort occurred in autumn and spring with 1,440 and 1,423 collector hours respectively ( $11 \%$ and $10 \%$ of commercial effort), and the lowest level was in summer with 416 collector hours (representing only $3 \%$ of commercial effort).

The mean daily catch rate for the commercial fishery on Stockton Beach was initially high during autumn ( $36.7 \mathrm{~kg} /$ collector hour) and winter ( $36.1 \mathrm{~kg} /$ collector hour), declined sharply in spring (to $22.0 \mathrm{~kg} /$ collector hour) and was lowest in summer ( $16.1 \mathrm{~kg} /$ collector hour - Table 7). The summer catch rate was less than half that recorded during the autumn and winter seasons, and was associated with the low abundance of pipis reported during the summer on Stockton Beach. The overall mean daily catch rate, calculated across the entire year, was $28.8 \mathrm{~kg} /$ collector hour, which is relatively high (Table 7). The highest catch rate on any day for an individual fisher was $172 \mathrm{~kg} /$ collector hour, and in June and July several fishers were routinely collecting at a rate of $>100 \mathrm{~kg} /$ collector hour. The lowest catch rate reported by an individual fisher was $0.5 \mathrm{~kg} /$ collector hour, during the summer season.

| Commercial catch statistics for each day-type stratum | Season |  |  |  | Total |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Autumn | Winter | Spring | Summer |  |  |
| Catch (metric tonnes) | 58.5 | 103.3 | 22.5 | 6.9 | 191.2 |  |
| Collecting effort (collector hours) | 1,440 | 10,348 | 1,423 | 416 | 13,623 |  |
| Mean daily catch rates (kg.collector hour- ${ }^{-1}$ ) | $\text { (55) } 36.7 \quad 1.5$ | (91) 36.12 .5 | $\begin{aligned} & \text { (69) } 22.0 \quad 1.2 \end{aligned}$ | (49) 16.10 .9 | $\text { (264) } 28.8$ |  |

My overall estimates of commercial harvesting of 191.2 t was in good agreement with the total of 179.1 t for the same period recorded by Newcastle Co-op, although the proportion of pipis from Stockton Beach handled by the Coop varied from month to month (Fig. 2). My logbook survey suggested that substantial numbers of pipis taken from Stockton Beach were not sold through the Co-op in the first half of the year. In June and July, higher estimates from my survey were due to fishers from other regions collecting on Stockton Beach but selling catches directly through the Sydney Fish Markets or their own regional Co-ops. Later in the year, as numbers of pipis on Stockton Beach declined, many fishers collected on other beaches but continued to consign their catches through the Newcastle Co-op

## Comparisons (Discussion)

For the pipi fishery at Stockton Beach, on the north coast of NSW, most of the catch was taken by commercial fishers, but far more effort was expended by recreational harvesters, who had generally low catch rates. On the south coast, recreational effort was high at Seven Mile Beach but catches and catch rates were extremely low in comparison to Stockton Beach.

I found large differences between the harvesting patterns for the recreational and commercial fisheries on Stockton Beach, implying that the sectors may have very different potential impacts on local pipi stocks, even though both fisheries were restricted solely to hand gathering. The commercial fishery was characterised by its relatively large catch, low amount of fishing effort, and high catch rate. Commercial fishers took the bulk of the catch ( $80 \%$ of the combined commercial and recreational harvest), but accounted for only $11 \%$ of the combined fishing effort and included only 27 fishers. In contrast, the recreational fishery was characterised by a relatively small catch, high fishing effort, and extremely low catch rates. Recreational fishers took $20 \%$ of the combined commercial and recreational catch, but accounted for $89 \%$ of the combined fishing effort, with an estimated 15,795 parties participating.

When I compared north and south coast sites, I found that effort at Stockton Beach was more than twice that estimated for Seven Mile over the same season, summer, but both catches were an order of magnitude higher at Stockton due to the much higher catch rates.

At both sites, recreational collecting for food was far more extensive than bait collecting. Food gathering accounted for $93 \%$ of the total recreational catch and $96 \%$ of the total recreational effort on Stockton Beach, and $88 \%$ of the total catch and $96 \%$ of effort at Seven Mile Beach. This contrasts strongly with the recreational fishery for Donax serra, a similar surf clam from South Africa, in which only $47 \%$ of the catch was taken for food (Schoeman 1996).


Figure 2 Commercial harvest of Donax deltoides in NSW recorded from two sources. Monthly catch in metric tonnes from (a) $\boxtimes$ a logbook survey of commercial fishers; (b) $\mathbb{Z}$ catches handled by the Newcastle/Nelson Bay Commercial Fishermen's Cooperative.

## Seasonal patterns of catch and effort

The commercial and recreational sectors had very different seasonal harvesting patterns. Winter was the peak season for commercial harvesters, while the lowest commercial catch and effort occurred in summer. In contrast, in the recreational fishery, winter had the lowest catch and effort while summer was the peak season, with $39 \%$ of total recreational catch and $50 \%$ of effort. These different harvesting patterns can be explained by the different behaviours of commercial and recreational collectors. Commercial collectors were most active when large numbers of pipis were present on the beach, regardless of weather. However, low densities of pipis on Stockton Beach during the summer forced many commercial collectors to move their activities to other beaches in the region, and many engaged in other activities during summer.

It is not surprising that the majority of the recreational catch and effort occurred during the summer holiday season when weather conditions and water temperature were most suitable for recreational pursuits. The reasons why people participate in recreational fisheries are diverse and the catching of fish is often a secondary factor (Henry and Virgona 1984; Matlock et al. 1991; Miranda and Frese 1991). The high recreational effort observed during summer suggests that the low densities of pipis found on Stockton Beach during that season did not greatly deter recreational participation in the fishery. People came to the beach for a fun day out, and fishing was often secondary. People were less likely to visit the beach in winter, hence my finding that recreational effort and catch were lowest during winter, despite the presence of large concentrations of pipis on the beach.

## Fishing quality comparisons

I used the mean daily catch rates for each season as indices of fishing quality for each user group. For Stockton Beach the seasonal catch rates achieved in the commercial fishery were relatively high, with an overall annual catch rate of $28.8 \mathrm{~kg} /$ collector hour, and were always more than an order of magnitude greater than the comparable seasonal and annual catch rates observed in the recreational food and bait fisheries. Seasonal recreational catch rates were relatively low, with overall annual catch rates for the recreational food and bait fisheries of 1.3 and $1.6 \mathrm{~kg} /$ collector hour respectively. Catch rates at Seven Mile Beach were generally an order of magnitude lower again, with a catch rate of 0.04 and $0.08 \mathrm{~kg} /$ collector hour respectively for the food and bait fisheries.

It is surprising to find such large differences in catch rates for an animal that is hand collected by both sectors. I believe that relative differences in access to good collecting sites and collecting experience explain much of the difference between sectors. The exploitation of the pipi population on Stockton Beach was not uniform along its entire length. Pipis were more heavily exploited at sites adjacent to major access points and I found relatively low catch rates at these heavily used sites. Over $95 \%$ of recreational harvesters accessed the beach by foot at Birubi Point, and at least $90 \%$ of these people were collecting within the first kilometre of beach. I also noted that the majority of recreational food collectors using 4WD vehicles to access the beach generally stayed within two kilometres of the car access point (which is only 600 meters from Birubi Point). These findings are consistent with those of Schoeman (1996) who reported that more than $85 \%$ of people collecting Donax serra stayed within one kilometre of the access points, even when 4WD vehicles were used. In comparison, commercial fishers spread their collecting activities across the entire beach. Harvesters also stayed close to access points at Seven Mile Beach.

## Sizes available and sizes collected

The fishery independent transects provided evidence of a polymodal size distribution for the pipi population, indicative of multiple cohorts available to harvesters on Stockton Beach (Fig. 3a). The pipi population on Stockton Beach was dominated by small animals ( $<30 \mathrm{~mm}$ ) and showed a strong cohort in the $45-55 \mathrm{~mm}$ size range. The median size of pipis on the beach was 27 mm ( $\mathrm{n}=5,142$ ) and the interquartile range was $12-48 \mathrm{~mm}$. I found pipis up to 74 mm in length in low numbers during the transect work, but these cannot be seen in Fig. 3a as large pipis ( $>65 \mathrm{~mm}$ ) comprised $<0.01 \%$ of the sample.

The commercial catch consisted mainly of large pipis (Fig. 3b). The median size of pipis in the commercial catch was $53 \mathrm{~mm}(\mathrm{n}=4,227)$, the interquartile range was $48-60 \mathrm{~mm}$, and no pipis smaller than 26 mm were taken. The catch of recreational food collectors contained a high proportion of small pipis, including animals as small as 9 mm in length. The median size of pipis in the recreational food catch was $45 \mathrm{~mm}(\mathrm{n}=1502)$ and the interquartile range was $28-50 \mathrm{~mm}$ (Fig. 3c). The catch of recreational bait collectors consisted mainly of large pipis (Fig. 3d). The median size of pipis in the recreational bait catch was $52 \mathrm{~mm}(\mathrm{n}=205)$ and the interquartile range was $48-58 \mathrm{~mm}$ (Fig. 3d).


Figure 3 Size frequency distributions for Donax deltoides taken from Stockton Beach, NSW by (a) commercial harvesters, data from samples on market floor, $\mathrm{n}=4227$; recreational collectors for (b) food, data from photographs and measurements on site, $\mathrm{n}=1502$; (c) bait, data from shells collected by anglers, $\mathrm{n}=205$; and ( d ) sizes available along the beach ( $\mathrm{n}=5142$, pooled data from transects at each of three sites on Stockton Beach, at 0.6, 3 and 6 km from Birubi Point).

Over $25 \%$ of the recreational food catch consisted of small pipis, $<30 \mathrm{~mm}$ in length. I believe that recreational food collectors were less selective than the other user groups because the great majority of them gain access to the beach on foot, concentrate most of their effort within walking distance of heavily fished access points, and have difficulty in locating patches of pipis under some conditions. Many complained that they could not find large pipis.

## Objective 2. To make preliminary estimates of the effects of harvesting.

## Introduction

In fisheries biology, decisions to regulate catches of a stock are usually based on estimates of potential yield, which presuppose accurate knowledge of growth and mortality, while correct aging of animals is required for stock production models. For animals which are difficult to cage or keep in captivity, growth rates and age-specific mortality can be estimated by direct measurement from tag-and-recapture methods, or inferred from length frequency data or the presence of growth rings in the bivalve shell (Hilborn and Walters 1992; Rhoads and Lutz 1980).

In the absence of tagging data, the collection of length frequency data is one of the most commonly used methods of estimating growth and mortality. However in order to allow the estimation of length and mortality estimates from length frequency data, most commonly used methods of analysis utilise some or all of the following assumptions: (i) that each mode represents one year class or that recruitment comes from one or two discrete events, (ii) that the distribution of sizes of each cohort is normally distributed and there is a fixed relationship between cohort mean size and standard deviation, (iii) that growth follows the von Bertalanffy growth equation, (iv) that all year classes are equally represented in the sample, (v) that all ages are equally vulnerable to sampling, (vi) that sampling is random and unbiased, (vii) that rates of growth and mortality are constant during a year and the population structure is stable with a stationary age structure, and (viii) that modal groups can be associated with age groups (Barry and Tegner 1990; Ebert 1973; Grant et al. 1987; Green 1970; MacDonald and Pitcher 1979; Schnute and Fournier 1981; Wilbur and Owen 1983). Despite these restrictions, length frequency analysis may be the only method available to obtain growth and mortality data.

Data about recruitment and reproduction are central to fisheries management. It is generally accepted that the collapse of many of the world's fisheries have been due to recruitment failure (Cushing 1973). Variable recruitment in particular can be a major problem in fisheries management, because large fluctuations in recruitment can lead to the rapid collapse of a fishery, particularly if recruitment is independent of stock size (Gulland 1973; Sainsbury and Polacheck 1994). When recruitment is variable, particularly when abundances fluctuate, it is not always easy to tell if overfishing is occurring, especially in the case of recruitment overfishing (Gulland 1989; Hilborn and Walters 1992; Hirshfield and Tinkle 1975). In some instances yields from a population with variable recruitment may be stabilised by a "storage effect", where adults have a relatively long life span, i.e. successful recruitments are "stored" as long-lived adults and the fishery is supported by one predominant size class (Chesson 1986).

In order to make predictions about the likely dispersal of larvae, particularly on a coast subject to erratic current flows as in eastern Australia, an understanding of basic reproductive biology is required. The timing of the release of eggs and the provisioning of larvae will affect the distance larvae will be able to travel. Knowledge of the timing and degree of synchronisation of spawning for a harvested species will enable the introduction of management tactics focused
on measures such as seasonal closures or the imposition of a minimum or maximum size limit in order to ensure a sufficient supply of recruits.

In some species of the genus Donax, the gonads remain active all year round, the spawning cycle is not strongly synchronised and spawning may be partial and incomplete. Mean oocyte diameter in samples of animals can be correlated with stages of gonad development such as oogenesis, maturation and spawning (Sastry 1979). Large egg diameters are taken to indicate ripeness, and a decrease in mean egg diameter is taken to imply spawning, as the largest eggs are probably released first, hence changes in oocyte diameter are often used to look at the timing and duration of the gametogenic cycle, e.g. (Grant and Tyler 1983a; Kanti et al. 1993; Sastry 1966). Large changes in the mean oocyte diameter of consecutive samples are taken to imply synchronisation of spawning within that group of animals (Grant and Tyler 1983b), while nonsignificant changes indicate that all animals within the group are not spawning at the same time. Asynchronous spawners typically show high variation in oocyte diameter within samples compared to the amount of variation between sample dates (Grant and Tyler 1983b). I am using "asynchronous" spawning here to imply that the majority of individuals within a sample or population do not release most of their gametes at the same time, although obviously some animals on a local scale must spawn at the same time, particularly males and females.

Fecundity or reproductive output ( RO ) is some measure of gamete production over a biologically meaningful length of time (e.g. lifetime, a year, a spawning season). For species which spawn once per year, RO is estimated as the number of eggs or sperm spawned, e.g. (MacDonald and Thompson 1985), and is usually estimated by collecting spawned products, or by calculating the number of eggs in the gonad. These methods assume that the gonad can be weighed separately, and/or that the population spawns only once, synchronously, and that gametes can be collected and weighed. However for many bivalves, some or all of the following may be true: the gonad may form an integral part of the visceral mass and cannot be excised and weighed separately; spawning may be incomplete; spawning may be serial i.e. occur several times per year; and spawning may not be synchronised between individuals in a given period (Lucas 1982). My preliminary studies implied that all of these were true for Donax deltoides, hence I used the method of Morvan and Ansell (1985) to obtain an estimate of the number of eggs held by females.

In this section I describe studies with the specific aim of estimating growth rates, length-at-age, and mortality for Donax deltoides at several sites. In addition I describe studies designed to enable me to make predictions about the likely dispersal capabilities of $D$. deltoides and the implications of its reproductive biology for management. Specifically I describe size at both first and full maturity, whether sex ratios varied with body size, the timing of gametogenesis and spawning and size specific fecundity.

## Methods

## Growth and mortality

In order to estimate growth rates, the timing of recruitment and mortality, I collected approximately monthly samples from several sites, using shore normal transects. I used a $0.03 \mathrm{~m}^{2}$ quadrat to take two replicate cores every two metres from the high water mark (HWM), to as far into the surf zone as possible under prevailing surf conditions, and sieved the contents through a 5 mm mesh screen. Where numbers of pipis were low, I collected additional animals haphazardly until I had a total of 200 animals in order to allow accurate determination of the mode of each size class. I sampled between July 1993 and November 1997 from Seven Mile Beach, and from two sites on Stockton Beach between July 1995 and November 1997, although not all sites were sampled on all occasions. In order to assess temporal variation in length frequency, I made occasional additional collections at random intervals. This also avoided any bias from changes in behaviour linked to the lunar or tidal cycle.

I used simple modal analysis to estimate growth. I used modes rather than means, because the first cohort was often truncated as my sieve only retained animals $\geq 6 \mathrm{~mm}$. In addition, where cohorts overlap, methods of analysis which separate the tails of the distributions to enable an estimation of means are all fairly subjective and hence introduce bias. Using modes is less subjective, as no such separation of the tails is required, provided that the modes are fairly clear.

To ensure that the modes were unambiguous, I did not include cohorts which had $<10$ animals in a length grouping. I grouped animals into 2 mm length classes. By convention, size class intervals between 1 and $5 \%$ of the size of the largest specimen found are widely used (Cerrato 1980), and 2 mm was $2.5 \%$ of the largest pipi length ( 79 mm ) found during the study. I picked modes by eye, using the mid-point of the most frequently occurring size grouping as the mode, e.g. when the largest number of animals were in the size group $8-9.9 \mathrm{~mm}$, I used 9 mm as the mode.

I plotted modal length for each size class over time. For apparent cohorts, in which I was able to follow the progression of modes, I fitted lines using the least squares method. I selected data after close examination of sequential length frequency plots and the modal curves themselves to ensure that these data sets did appear to be cohorts. I extrapolated these lines of best fit backwards to zero size in order to obtain an estimate of settlement date. (Note that I did not assume that growth in this part of the growth curve was linear, nor that pipis settle at zero size, however I did assume that growth was fairly constant between settlement and 6 mm in length, hence this extrapolation allowed me to look for differences in the timing of settlement from year to year, rather than the real settlement date.)

## Tagging experiments

I conducted a preliminary caging experiment, with an initial field trial in the shallow subtidal using mesh covered trays in an estuarine environment, just inside the Port Stephens, NSW ( $32^{\circ} 43^{\prime} \mathrm{S}, 152^{\circ} 9^{\prime} \mathrm{E}$ ), but all animals died within two weeks. Hence I selected the more
exposed Red Rock Beach in Jervis Bay ( $35^{\circ} 1^{\prime} \mathrm{S}, 150^{\circ} 42^{\prime} \mathrm{E}$ ) for caging trials. This beach was moderately sheltered, difficult to access, and supported a population of adult pipis. I collected 480 animals, $>25 \mathrm{~mm}$ in length, and allocated three animals from eight different tagging treatments into each of 20 cages, however all cages were vandalised and removed within three weeks.

I placed 400 animals tagged with Hallprint $4 \times 8 \mathrm{~mm}$ plastic tags on Stockton Beach in order to look at short term longshore movement, but was unable to locate any one week later.

In order to measure growth in the field, I conducted a non-caged tag-recapture experiment, selecting Connor's Beach and Third Beach within the Hat Head National Park, in close proximity to beaches where commercial quantities of pipis occur (Crescent Head, NSW, $30^{\circ} 59^{\prime} \mathrm{S}, 153^{\circ} 4^{\prime} \mathrm{E}$ ). These beaches were relatively short ( 800 and 500 m in length), and difficult to access. I found large pipis on these beaches, which were not commercially harvested (pers. comm. NSW Fisheries personnel and commercial fishers). Advice from the local branch of the Mid-North Coast Amateur Deep Sea Fishing Association indicated that there was little or no recreational harvesting from those beaches except for bait, and all members of the local fishing club (the main users) agreed to re-release any tagged animals found. I selected short beaches to assist in relocating released animals.

On 1/5/96 I placed 2000 animals, all tagged with numbered $4 \times 8 \mathrm{~mm}$ Hallprint plastic tags to allow easy identification onto these beaches. In addition, I double-tagged 900 animals in order to test other tagging methods, uncaged, in the field. On the basis of the preliminary caging trial, I did not use aluminium tags or cold-treatment. Of 2000 animals with plastic tags, I treated 200 animals with notches, and 200 with neo-iridium magnets, which give a strong signal in response to a metal detector. In addition I treated 500 pipis with tetracycline- $\mathrm{HCl}(\mathrm{T}-\mathrm{HCl})$ which induces a fluorescent mark in the shell. I released two thirds of the pipis at Connor's Beach, and the remainder at Third Beach on 3/5/96. I collected a second set of 1500 pipis from Hat Head Beach on 16/8/96, measured and tagged them with plastic tags only, and released them on 17/8/96 with the same proportion on each beach.

Retrieval: Six people spent a total of 100 person-hours on 14/8/96 and four people spent a total of 80 person-hours on 14/6/97 searching for pipis, using a Fisher FX-3 FerroProbe to look for animals tagged with neo-iridium magnets, as well as a variety of hooks, hoes, and yabbie pumps to search for other tagged animals. Searching was begun at high tide and continued until two hours after low water, and included the intertidal, swash and subtidal region. I measured and replaced any tagged pipis found, with the exception of one $\mathrm{T}-\mathrm{HCl}$ tagged individual, and inspected any untagged pipis found for unusual growth checks, any sign that the plastic tag had become detached (e.g. a paler spot on the right valve), and any notches. I plastic tagged all untagged pipis found and returned them to the beach, an additional 248 tagged pipis.

Analysis: I used a Gulland-Holt plot to estimate the von Bertalanffy growth parameters (Gulland and Holt 1959), as the more usual Petersen method assumes that data are collected a year apart.

In a Gulland-Holt plot, growth increment is plotted against mean length (i.e. [length at release + length at recapture]/2). The X-intercept of a line fitted to these data gives a crude estimate of $\mathrm{L}_{\infty}$, and the slope provides an estimate of K . This method assumes that all animals are following the same growth trajectory (Kaufmann 1981), and that animals are exhibiting von Bertalanffy growth, where the equation $L_{t}=L_{\infty}\left(1-\exp \left[-K\left(t-t_{0}\right)\right]\right)$ describes growth, with $L_{t}$ as the length at age $t, L_{\infty}$ is the theoretical maximum (or asymptotic) length, $K$ is a growth coefficient which gives a measure of the rate at which maximum size is reached, and $t_{0}$ is the theoretical age at zero length (Beverton and Holt 1957).

## Mortality

Mortality can be estimated in a number of ways. The instantaneous total mortality rate, Z can be calculated from the exponential decay expression $N_{t} / N_{0}=e^{-Z t}$, where $N_{0}$ is the number of individuals at time $t=0$ and $N_{t}$ is the number remaining at time $t$, and can be estimated from a survivorship curve. Each size class is assumed to represent a year class, and the number present in each class are plotted against age (King 1995). In a fished species, if accurate growth data are available, Z can also be calculated from the length frequency distribution of the catch (Pauly 1983). A length-converted catch curve is constructed, which involves plotting $\ln (\mathrm{f} / \mathrm{dt})$ against T , where $f$ is the number of individuals in each age class, $T$ is relative age, and dt is the time taken to grow through a particular size class. Z is then approximated by the slope of the regression line of the descending portion of this graph (Pauly 1983).

All of the methods available to estimate mortality rely on the assumption that all portions of the population have an equal chance of being sampled, that the age distribution is stationary, that recruitment is invariant from year to year and that mortality is constant over time (Barry and Tegner 1990; Ebert 1973; Green 1970).

I used length frequency data from transects to obtain an estimate of total mortality by pooling monthly samples for a 12 month period, assuming that the age distribution was stable. In order to compare estimates of mortality from different methods, I collected length data from the Newcastle/Nelson Bay Commercial Fishermen's Cooperative (hereafter Newcastle Co-op) as previously described.

## Shell growth checks

In order to estimate growth rates from periodic checks in the shell I collected 40 pipis across a wide range of sizes from a small patch on Stockton Beach on 1/4/96 and made thin radial sections from a subsample, following the detailed methods given by (Clark 1980), then examined these with a Nikon microscope at $400 \times$ magnification to look for periodic disturbance lines. I also kept shells from regular collections in order to follow gross disturbance rings in shells from a single cohort.

## Reproduction

I collected 50 animals where possible approximately monthly from Comerong Island (July 1993-July 1997) and Stockton Beach, NSW (July 1995-July 1997), from downshore transects, and kept appropriate sizes for the different reproductive analyses. When required, I collected additional animals haphazardly from the same area of the beach. Not all procedures were carried out on all animals. After collecting, I rinsed animals and kept them in filtered sea water (Millipore $0.8 \mu \mathrm{~m}$ ) at $10^{\circ} \mathrm{C}$ for 48 hr , changing the water every 12 hr in order to eliminate sand and pseudofaeces. I measured all animals to the nearest 0.1 mm with vernier callipers, and opened them by slicing through the adductor muscles. Prior to histological sectioning, I placed the visceral mass in $10 \%$ formalin in sea water for two days, before transferring to $70 \%$ ethanol. Sections were then embedded in paraffin, dehydrated with alcohol, cleared with xylene, embedded in wax, sectioned to $7 \mu \mathrm{~m}$ and stained with Ehrlich's haematoxylin eosin.

## Determination of sex ratio and size at first maturity using gonad smears

In order to detect the presence of gametes, I used gonad smears in which a scraping of fresh material from the gonad was suspended in filtered seawater, covered and examined at up to $400 \times$ magnification. Gonad smears provide a cheap and rapid method in which a fresh preparation of gonadal material is examined, e.g. (Branch 1974; Griffiths 1977; Harvey and Vincent 1989; Wade 1967a). Length at sexual maturity is commonly accepted to be the length class at which $50 \%$ have visible sexual products (Harvey and Vincent 1989). I scored animals for presence/absence of apparently mature sexual products (i.e. motile sperm or nucleated oocytes).

## Oocyte diameters

I used measurements of oocyte diameters (OD) to examine the sequence and timing of events in the reproductive cycle. I sectioned animals from collections at Stockton Beach from May 1996 - May 1997. I videotaped sections of gonad and transferred the images into a Power Macintosh computer using the software Apple Video Player with a National WV-CD video camera mounted on an microsope at $400 \times$ magnification. I used NIH Image to measure oocyte area. I only measured eggs in which the nucleus and nucleolus were clearly visible, making the assumption that cells with a visible nucleolus were sectioned through or near the centre, in order to avoid the problem of tangential measurements. Nested ANOVA allowed quantification of the seasonality of gonad development as well as differences in developmental stages between individuals and between samples (Grant and Tyler 1983b).

Preliminary sectioning indicated that mean egg size did not vary significantly among animals, among slices or among fields of view (FOV) within a collection. I found more variation within than among slices or among animals, hence I used a single slice to measure egg diameter.

I collected 20 females monthly from Stockton Beach between May 1996 and May 1997. For each collection, I measured the area of 25 eggs in randomly chosen FOVs. I calculated a mean OD for each date. I used a two-factor nested mixed model ANOVA to test for
heterogeneity in OD among sample dates, and among animals within dates, and partitioned the variances between these factors. I used Tukey's HSD to determine which differences between mean ODs were significant for each sampling date (Zar 1984).

## Reproductive output and age at first maturity using stereological methods

Stereological techniques have been applied to histological sections by a number of authors in order to determine the volume fraction of different components within the gonad (Beninger 1987; Lowe et al. 1982; Morvan and Ansell 1988; Newell et al. 1982; Sundet and Lee 1984), as well as for generating accurate size frequency distributions of developing oocytes in situ (Morvan and Ansell 1988). Quantitative stereological methods are used to derive threedimensional information from two-dimensional images (Briarty 1975; Williams 1977 ). By measuring the 2-D or areal proportion of gonad:total body tissue through the body of individual pipis, I was able to estimate a 3-D volume fraction, and hence could make a point in time approximation of the number of eggs held in females for Donax deltoides.

On 23/11/96, I collected 500 animals from the subtidal and swash zone of Stockton Beach, New South Wales. Previous histological collections, gonad smears and condition indices suggested that the animals had not yet spawned and should be in good condition. While the contribution of males to the reproductive effort is not negligible, it is usually ignored in such studies, with the implicit assumption that the development of ovaries and testes are synchronous, e.g. (Crisp 1984; Morvan and Ansell 1988; Nakaoka 1994). Hence after a preliminary gonad smear, I discarded any males. I included some animals which were too small to sex by gonad smear to look at development of the gonad, and discarded any that had differentiated and contained sperm after sectioning. I then measured length, total wet weight and total wet tissue weight as described above, as well as the total volume of soft tissue (to the nearest 0.1 ml , determined by gravimetry) and the body (visceral mass and foot) weight (to the nearest 0.01 g ). I excised the visceral mass from the foot and weighed it separately to determine what proportion of the body the visceral mass comprised.

I took three sections through the gonad, and outlined and measured the actual areas of (a) the visceral mass, and (b) gonad (the area occupied by alveoli and gametes, including alveoli that were just beginning to differentiate, but excluding blood vessels and muscle). I first summed the total area of the visceral mass and the area of gonad for each of the three slices through the gut to obtain an areal fraction, $\mathrm{A}_{\mathrm{r}} / \mathrm{A}_{v m}$, where $\mathrm{A}_{\mathrm{r}}$ is the area of reproductive tissue within the visceral mass and $\mathrm{A}_{\mathrm{vm}}$ is the total visceral mass area (Underwood 1970). I used this areal fraction to calculate the number of eggs held. This provided a 'snap-shot' of fecundity, and allowed the relative contribution of animals of different sizes to be estimated, by assuming that different sized females were storing similar proportions of their annual egg production at any given time.

Using the Delesse Principle, I assumed that the areal fraction $A_{r} / A_{v m}$ provides an unbiased estimate of the volume fraction $\mathrm{V}_{\mathrm{r}} / \mathrm{V}_{\mathrm{vm}}$. Hence the volume of the gonad, $\mathrm{V}_{\mathrm{r}}$, for each animal could be estimated, as I had previously estimated directly the total tissue volume, the
visceral mass weight and the total tissue weight. I used the method of Williams (1977) to estimate the number of oocytes within the volume of the gonad by combining estimates of the number of oocytes per unit area, and the relative volume and mean diameter of oocytes within the gonad.

To estimate fecundity, I measured all oocytes, those sectioned through the nucleus and nucleolus as well as those sectioned tangentially, in order to obtain an estimate of the number of oocytes per unit volume. I estimated the areas (A) of all the oocyte profiles contained in randomly chosen fields of view until 25 oocytes had been measured for each of 15 animals, and used a single factor Model 2 ANOVA to test for heterogeneity in mean oocyte area among animals. I converted areas into equivalent circle diameters (ECD) where $E C D=2 \sqrt{ }(\mathrm{~A} / \pi)$, assuming that oocytes were approximately spherical. I pooled these ECDs to generate a size frequency distribution of oocyte profiles. Diameters vary from a maximum if sectioned through the centre, and approach zero if sectioned tangentially. To provide an estimation of the real oocyte diameter, I grouped ECDs into $5 \mu \mathrm{~m}$ size classes and calculated a mean oocyte diameter, D, using a profile reconstruction technique via the Fullman formula as described by Williams (1977), in which

$$
\mathrm{D}=(\pi / 2) \times \mathrm{N} / \sum_{\mathrm{i}=1}^{\mathrm{h}}\left(\mathrm{n}_{\mathrm{i}} / \mathrm{d}_{\mathrm{i}}\right)
$$

where $n_{i}$ is the number in the $i$ th size class, $d_{i}$ is the mean diameter of the ith size class, $h$ is the number of size classes and $N$ is the total number of profiles measured. Variance around D was estimated using a Taylor expansion (Kendall and Stuart 1969), with

$$
\left.\operatorname{Var}(\mathrm{D}) \approx \sum_{\mathrm{i}=1}^{\mathrm{h}}\left\{\left\{\mathrm{~N} \pi / 2 \times \mathrm{n}_{\mathrm{i}} / \mathrm{d}_{\mathrm{i}}^{2} \times \sum_{\mathrm{i}=1}^{\mathrm{h}}\left(\mathrm{n}_{\mathrm{i}} / \mathrm{d}_{\mathrm{i}}\right)\right]^{-1}\right\}^{2} \times \operatorname{Var}\left(\mathrm{d}_{\mathrm{i}}\right)\right\}
$$

where $\operatorname{Var}\left(\mathrm{d}_{\mathrm{i}}\right)$ is the variance of the mean oocyte diameter for the ith size class and is estimated by $\mathrm{s}_{\mathrm{i}}{ }^{2} / \mathrm{n}_{\mathrm{i}}$. Subsequent terms can be ignored as the number of oocyte profiles is large and derived from many different animals.

After some preliminary sectioning to test for heterogeneity among animals, I used 10 animals to estimate the mean number of oocytes per $\mu \mathrm{m}^{2}$ among animals, $\mathrm{N}_{\mathrm{A}}$. I also calculated the area occupied by oocytes in the gonad, obtaining an areal fraction of oocyte area:gonad area for a different set of 10 animals. I then combined these ratios to give an estimate of the relative volume fraction of oocytes in the gonad, $\mathrm{V}_{\mathrm{v}}$.

I used the method of Weibel and Gomez as described by Williams (1977) to calculate the mean number of oocytes per unit area, $\mathrm{N}_{\mathrm{A}}$, as it is a flexible method and has been previously used for estimating potential fecundity in bivalves (Morvan and Ansell 1988). In this instance, $N_{V}=\left\{\mathrm{K}\left(\mathrm{N}_{\mathrm{A}}\right)^{3 / 2}\right\} /\left\{\beta\left(\mathrm{V}_{\mathrm{V}}\right)^{1 / 2}\right\}$ where K is a constant depending on the size distribution of the particles and $\beta$ is a shape constant. I used the formula of Weibel as given by Williams (1977) to calculate K , in which $\mathrm{K}=\left(\mathrm{M}_{2} / \mathrm{M}_{1}\right)^{3 / 2}$ with $\mathrm{M}_{1}=\Sigma\left(\mathrm{D}_{\mathrm{h}}\right) / \mathrm{n}$ and $\mathrm{M}_{2}=\left[\Sigma\left\{\left(\mathrm{D}_{\mathrm{h}}\right)^{3}\right\} / \mathrm{n}\right]^{1 / 3}$, where $\mathrm{D}_{\mathrm{h}}=$ the mean diameter of the hth size class and $n=$ the number of size classes from the size frequency distributions of oocyte profiles. Oocyte shape varied between spherical, and ellipsoid
with a 2.0 length/diameter ratio when constrained by packing in alveoli, hence I have used $\beta$ $=1.29$, intermediate between these two shapes (Williams 1977).

I calculated the variance for $\mathrm{N}_{\mathrm{V}}$ after Kendall and Stuart (1969), using
$\operatorname{Var}\left(\mathrm{N}_{\mathrm{v}}\right)=\left[3 \mathrm{k} / 2 \times\left(\mathrm{N}_{\mathrm{A}} / \mathrm{V}_{\mathrm{V}}\right)^{1 / 2}\right]^{2} \times \operatorname{var}\left(\mathrm{N}_{\mathrm{A}}\right)+\left[-\mathrm{k} / 2 \times\left(\mathrm{N}_{\mathrm{A}} / \mathrm{V}_{\mathrm{V}}\right)^{3 / 2}\right] \times \operatorname{var}\left(\mathrm{V}_{\mathrm{V}}\right)$
where $k=K / \beta$. As estimates of $N_{A}$ and $V_{V}$ were made from different animals, I assumed the covariance term was zero. As I had already calculated $V_{r}$, the gonad volume, for each female, the total number of oocytes in the gonad and hence in each female was simply $\mathrm{NV}_{\mathrm{V}} \times \mathrm{V}_{\mathrm{r}}$.

## Results /Discussion

## Growth and Mortality

For convenience I have divided the population up into several components on the basis of length. I have defined recruits as animals between 6 and 15.9 mm in length, juveniles as between $16-37 \mathrm{~mm}$, and adults as those individuals that are sexually mature as $>37 \mathrm{~mm}$. These divisions are somewhat arbitrary, and I am defining recruitment by size, but in fact "recruits" may disappear from the system at quite large sizes. Hence I will refer to "successful recruitment" as those animals which survive to form a strong cohort.

## Length frequency data

Modal progression indicated that initial growth was rapid at all sites (Fig. 4), and with large numbers of animals $<8 \mathrm{~mm}$ in length at nearly all times of the year. Settlement was clearly not confined to a discrete pulse per year. Additional length frequency collections replicated at short time intervals ( $<2$ days apart) showed various modes completely or partially missing from one sample, but present in the other (Murray-Jones 1998). These age classes reappear, implying that "disappearance" was due to migration, not mortality. Hence animals collected from a given transect are unlikely to be a representative sample of the population. Continuous recruitment and unrepresentative sampling violate the assumptions of computer models such as ELEFAN, MIX, and MULTIFAN which are frequently used to estimate growth. I therefore used simple modal analysis to estimate growth, by plotting the modes of each cohort against time (Fig. 4).
Growth: Initial growth (i.e. from 6 mm to 30 mm ) was rapid at all sites, and appeared to be initially linear. I have fitted lines of best fit to the clearer modal progressions, after examination of length frequency data. I have been conservative in fitting curves e.g. over five years at Seven Mile Beach, my interpretation suggests that settlement was successful i.e. appeared to generate only three distinct cohorts (curves (i), (ii) and (iii) in Fig. 4a). Two other cohorts are less clear or have fewer data points ((iv) and (v)). Using the lines of best fit, I estimated how many months it would have taken for cohorts to increase within the range marked by the solid regression line in Fig. 4, and I have given an equivalent monthly growth rate (Table 8), which I will use to compare growth. Note that I am assuming that modal progression does imply growth.

Figure 4 Plots of the modes of sequential length frequency distributions of Donax deltoides collected from downshore transects on two beaches in NSW. Lines of best fit (numbered) have been fitted by least squares regression to some portions of the data (selected by eye) in which the progression of modes could be tracked, in order to estimate growth rates. Vertical scale is the same for all graphs, but horizontal scales reflect different sampling periods.




Table 8 Growth rates of Donax deltoides estimated from modal analysis of size frequency data for two beaches. Growth rates were calculated from a line of best fit, and "cohort" indicates which data set (numbered in Fig. 4) these figures pertain to. "Months" is the time pipis appeared to take to grow from size a to size b , " $\mathrm{mm} \mathrm{mth}^{-1 "}$ represents the monthly growth rate within the range of the regression, and $\mathrm{r}^{2}$ is the correlation coefficient of the fitted regression lines shown in Fig. 4. In addition, an approximate time of settlement is given, estimated by extending the line of best fit to a size of zero where appropriate, to allow comparisons between sites.

| cohort | months | to grow from |  | mm | $\mathbf{r}^{2}$ | est. time |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  | a to $\quad$ b | $\mathbf{m t h}^{-1}$ |  | settled |  |  |


| (a) Seven Mile (Fig. 4a) |  |  |  |  |  |  |  |  |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| (i) | 5.6 | 6 | 30 | 4.3 | 0.98 | Sept 93 |  |  |  |  |  |  |
| (ii) | 6.7 | 6 | 30 | 3.6 | 0.98 | July 94 |  |  |  |  |  |  |
| (iii) | 8.3 | 6 | 30 | 2.9 | 0.95 | Aug 95 |  |  |  |  |  |  |
| (iv) | 3.8 | 6 | 30 | 6.4 | 1.00 | Nov 96 |  |  |  |  |  |  |
| (v) | 7.3 | 6 | 30 | 3.3 | 1.00 | Dec 96 |  |  |  |  |  |  |

## Sites on Stockton Beach

(b) $\mathbf{3} \mathbf{~ k m}$ (Fig. 4b)

| (i) | 10.3 | 40 | 50 | 1.3 | 0.90 |  |
| :--- | :---: | ---: | :--- | :--- | :--- | :--- |
| (ii) | 4.8 | 6 | 30 | 5.0 | 0.93 | Aug 95 |
| (iii) | 4.4 | 6 | 30 | 5.5 | 0.94 | Aug 96 |
|  |  |  |  |  |  |  |
| (c) $\mathbf{6}$ km (Fig. 4 c ) |  |  |  |  |  |  |
| (i) | 3.9 | 50 | 60 | 2.6 | 0.97 |  |
| (ii) | 3.9 | 50 | 60 | 2.6 | 0.99 |  |
| (iii) | 3.0 | 50 | 60 | 3.4 | 0.99 |  |
| (iv) | 4.1 | 6 | 30 | 5.9 | 0.95 | Sept 96 |

For Seven Mile Beach, all modes increased rapidly (Fig. 4a), implying growth rates of 2.9-6.4 mm mth ${ }^{-1}$ in the range $6-30 \mathrm{~mm}$ (Table 8a). Large animals were rare at this site, hence I was unable to estimate growth for animals $>35 \mathrm{~mm}$.

Large animals were more common at Stockton Beach and I found clear differences in growth rates between small and large animals. At the 3 km site, small animals (cohorts (ii) and (iii), $6-30 \mathrm{~mm}$ ) had equivalent growth rates of $5.0-5.5 \mathrm{~mm} \mathrm{mth}^{-1}$ (Table 8b, Fig. 4b), while larger animals (cohort (i), 40-50 mm) had an equivalent growth rate of $1.3 \mathrm{~mm} \mathrm{mth}^{-1}$. Further along the beach, at the 6 km site, I frequently found large animals but there was an almost complete lack of intermediate sized pipis (20-45 mm) between June 1996 and January 1997 (Fig. 4c). Larger animals (cohorts (i), (ii), (iii), $50-60 \mathrm{~mm}$ ) had equivalent growth rates of $2.6-3.4 \mathrm{~mm} \mathrm{~m}^{-1}$, while smaller animals (cohort (iv), $6-30 \mathrm{~mm}$ ) had an equivalent growth rate of $5.9 \mathrm{~mm} \mathrm{mth}^{-1}$.

I found few differences in inferred growth rates within or between sites, at distances up to nearly 300 km . My two sites on Stockton Beach returned very similar results, although the size of cohorts varied between sites. I found fairly consistent, fast growth rates both between and within regions. Length frequency data, indicated that growth was rapid in small animals. Pipis appeared to reach 37 mm in $<10$ months at all sites. Data from other sites not included in this report were in close agreement (Murray-Jones 1998). Growth appeared to slow in larger animals, but I found more variation in growth rates between sites with increasing size. A slowing of growth with size is common in bivalves, particularly as animals reach sexual maturity and begin to channel energy into reproduction (Wilbur and Owen 1983). Fast initial growth rates are typical of the genus Donax in their first year (Ansell 1983), with growth typically slowing around the age of sexual maturation. Growth is generally slower and seasonal differences more pronounced in species from higher latitudes (Ansell and Lagardère 1980; Bodoy 1982; Guillou and Le Moal 1980). My estimate of around 50 mm in the first year for $D$. deltoides was high, however other sandy beach species of comparable size show growth rates similar to this. For example, in Uruguay the yellow clam, Mesodesma mactroides, also reached around 50 mm by the end of its first year (Defeo et al. 1992) Growth then slowed (length frequency analysis and counting growth rings), with the yellow clam taking 3 years to reach its full size of around 85 mm . King (1985) estimated that D. deltoides in South Australia took six months to reach a size of 18 mm , and 3.5 years to reach its maximum length of 58 mm (length frequency data), both slower growth and a smaller maximum size than my figures. This may be due to colder water in South Australia, or undersampling of large clams, as King restricted sampling to the intertidal.

Sampling problems such as I encountered for pipis, such as the occasional "disappearance" of a size class, or the movement of larger animals to the subtidal on occasions meant that sampling was not representative, and that the mean length of a sample could change from day to day. I attempted to fit growth curves to my length frequency data with the maximum likelihood computer program MULTIFAN (Fournier et al. 1989), however parameters failed to converge and gave nonsensical estimates. Hence I restricted my analysis to a plot of modes against time because of the prolonged recruitment, sampling problems, and often non-normal data demonstrated by my data set.

Pattern of recruitment: I found large numbers of recruits at all sites for most of the year. For example, over all sites, the smallest age group ( $6-7.9 \mathrm{~mm}$ ) was represented in $>90 \%$ of collections, and $>70 \%$ of samples contained at least $5 \%$ of this size grouping. These settlers rarely established substantial cohorts. Through all sites and all times sampled there were no occasions on which I found no animals $<16 \mathrm{~mm}$ in length. An examination of the proportion of recruits, juveniles and adults for each month sampled did not reveal any clear seasonal pattern, with recruitment possible at all times of the year.

Cohorts at Seven Mile Beach appeared to be initiated by settlement only in the last half of the year, but not in the same month every year (Fig. 4a). At the Stockton Beach 3 km site, cohorts (ii) and (iii) settled in August of 1995 and 1996 respectively (Fig. 4b) while at the 6 km site the only successful settlement I observed was in September 1996 (Fig. 4c).

Sequential waves of settlement make interpretation of recruitment events difficult. An examination of the proportion of recruits, juveniles and adults for each month sampled did not reveal any clear seasonal pattern. On many occasions the mode of the length frequency distribution was comprised of animals $<10 \mathrm{~mm}$ in length (see Fig. 4). However, not all of these modes established cohorts. I have interpreted these events as unsuccessful recruitment, however it is equally possible that at high densities, growth may have slowed greatly, leading to a merging of cohorts. In addition some animals may have recruited onto the beach before moving offshore. I found very high densities for some of these waves of settlers, and it is interesting that so many settlers arrive on the beach but so few cohorts become established. These data imply that high post-settlement mortality is a more likely cause of recruitment variation than supply of larvae for this species.

I have estimated possible settlement dates by extrapolating back to zero size from the lines of best fit in Fig. 4, for cohorts that appear clear in these graphs. Of course, settlement does not occur at zero size, but it does appears to be at relatively small sizes in this species e.g. other Donax species metamorphose between 245-350 $\mu \mathrm{m}$ after a larval life of 3-4 weeks (Chanley 1969; Frenkiel and Mouëza 1979; Wade 1968), implying that spawning precedes settlement by about a month. No data are available for D. deltoides, although King (1985) suggested a larval life of six weeks. For my data, extrapolation of the lines of best fit to modal progressions to zero size implies that pipis take around 3-4 weeks from time of spawning to 6 mm , but this may overestimate early growth. I included estimates of settlement dates from extrapolation of cohorts in Fig. 4 in order to compare sites, rather than to estimate actual settlement times. I have assumed that the time it takes to settle and reach 6 mm in length does not vary between sites or times, which also may not be true.

Mortality: The degree of variability in the length frequency data that I found for all sites precluded any simple estimation of mortality based on length frequency data. Length frequency distributions sometimes varied dramatically from day to day, hence, as for growth estimates, any given transect was unlikely to provide a representative sample of the population. The intermittent disappearance of some size classes, particularly larger animals would bias mortality
estimates based on the exponential decay model. The age distribution was not stable from year-to-year and there was clearly more than one recruitment pulse p.a. These violations in assumptions applied to both transect data and commercial catch samples and meant that formal estimations of mortality were inappropriate. Indeed pooled data over 12 months from my Stockton Beach 6 km site imply negative mortality, as I found more large animals than small (Fig. 5).

When I pooled transect data for each site across a 12 month period (July 1996-1997), the two beaches show apparent differences in mortality (Fig. 5). I found almost no animals large enough to be sexually mature ( $\geq 37 \mathrm{~mm}$ ) at Seven Mile Beach during this period (Fig. 5a), suggesting very high mortality. Data from the sites on Stockton Beach show apparent differences in mortality (Fig. 5b, c) at relatively short spatial scales, and I found very few juveniles at the Stockton 6 km site (Fig 5c). This may be due to a movement offshore of this age class rather than high mortality. However if mortality was high amongst juvenile animals in this period, there may be implications for future commercial catches.

## Tag-recapture experiment

I retrieved very few tagged pipis. In August 1996, I found four tagged animals on Third Beach, and two on Connor's Beach. All had retained the plastic tag, and one was double-tagged with T-HCl. I kept this animal to determine whether the chemical had been incorporated into the shell, and replaced the other five. In June 1997, I found no tagged animals on either beach. The mean growth of the six tagged pipis was $2.4 \pm 2.1 \mathrm{~mm}$ over the 104 days ( 3.4 months) they were in the field (a rate of $0.7 \pm 0.6 \mathrm{~mm} \mathrm{mth}^{-1}$ ). This was lower than the mean monthly equivalent estimated from length frequency data for animals $>30 \mathrm{~mm}$ in length ( $1.8 \pm 1.1 \mathrm{~mm} \mathrm{mth}^{-1}$ ). These estimates were significantly different $(t=2.32, \mathrm{df}=11, \mathrm{p}=0.04$ ). Tagged adult animals ( $>37$ mm ) grew more slowly than recruits ( $16-37 \mathrm{~mm}$ ). A Gulland-Holt plot (Fig. 6) suggested a value of $\mathrm{L}_{\infty}=64.6$ and $\mathrm{k}=0.6 \mathrm{yr}^{-1}$ for the von Bertalanffy growth parameters. All animals retrieved had a strong disturbance check, which was associated with the T-HCl mark in the chemically tagged animal.

At least part of the reason for the low recapture rates of tagged pipis (only $0.3 \%$ of animals from the first release, and none from the second) was a bad storm on the northern NSW coast immediately after releasing the first 2000 pipis. High seas so soon after handling and placement on the beach probably caused high mortality. In addition, these beaches became severely eroded after this storm, and may not have remained suitable pipi habitat. There was also a bad storm shortly after I released the second set of tagged animals. Other attempts to tag this species have also been unsuccessful.


Figure 5 Combined monthly length frequency data for Donax deltoides collected from downshore transects from three sites (two beaches) in NSW. Data have been pooled for the period July 1996 - June 1997. Hence each graph represents 12 months of size frequency data.


Figure 6 A Gulland-Holt plot from tag-and-recapture data for tagged Donax deltoides retrieved from Hat Head, NSW. Mean length (mm) was plotted against growth rate per week (mm per week) for six pipis retrieved after 104 days in the field. The line of best fit, calculated by least squares regression, was of the form $y=0.6463-0.0106 x$, and growth parameters were estimated from the numerical value of the slope and X -axis intercept respectively as $\mathrm{K}=0.01 \mathrm{wk}^{-1}$ and $\mathrm{L}_{\infty}=64.6 \mathrm{~mm}$.

My estimate of growth rate for the six tagged animals that I was able to retrieve ( $0.7 \pm$ $0.6 \mathrm{~mm} \mathrm{mth}^{-1}$ ) was significantly lower than my estimate for larger animals from length frequency data ( $1.8 \pm 1.1 \mathrm{~mm} \mathrm{mth}^{-1}$ ). My growth estimates from this method may have been low due to tagging effects, handling shock, lack of food or unsuitable habitat, as pipis were collected from different beaches prior to release. In addition, this type of cross sectional data requires large numbers of individuals (Kaufmann 1981), and should be estimated over a longer period of time (a year is customary) to minimise the effects of initial handling shock, and to ensure that seasonal fluctuations in growth do not affect estimates of growth parameters.

My estimates of growth from length frequency data were remarkably consistent, between regions subject to different patterns of current flow and temperature, and between years. My estimates from length frequency data are more likely to be closer to the true growth rate than the slower values from tagged animals, and I offer the following in support of this contention. 1. I have length frequency data from several sites, with large sample sizes (generally $\geq 200$ ), over a long period of time (up to five years), while tagging data were only for 6 animals over 3.4 months, despite the placement of $>3,700$ tagged pipis in the field. 2 . Length frequency data come from populations on long, flat beaches where pipis were frequently found in large quantities. While I ensured that the beaches where I placed the tagged animals did in fact support adult pipis, densities were lower, and these beaches were closer to reflective. Given the consistency of my estimates of growth from length frequency data in the range $6-30 \mathrm{~mm}$, I feel that it is reasonable to assume that pipis grow rapidly initially, taking between 4-8 months to reach 30 mm .

## Shell growth checks

I found that naturally occurring growth checks were difficult to interpret, with even quite large external marks, which appeared to be disturbance checks, present on some animals but not others within a single patch of animals. In addition, pipis did not show strong annuli, and I was not able to age animals using this technique. The growth rings of shallow water bivalves are often difficult to interpret, possibly because rapid temperature fluctuations or high wave activity such as those experienced by intertidal bivalves can cause the formation of pseudoannuli (Jones 1981; McCuaig and Green 1983). The lack of strong annual rings in pipis may be due to the fact that growth does not appear to stop in the relatively mild winter of the east coast of Australia. Weak annual rings may be also due to the lack of synchronisation of the spawning cycle in pipis, while variation in the timing of spawning behaviour may also lead to differences in the formation of deposition bands within populations. In any case, visible rings on the shells of bivalves cannot always be easily related to annual events, even where bands appear clear (Krantz et al. 1984; Young 1990).

In order to determine the relationship between size and age for this species, I constructed an age-length key (Fig. 7), based on length frequency data. The key is speculative, particularly for larger pipis, and I have made no attempt to smooth the curve. Animals appear to reach sexual maturity within 6-10 months. At the end of their first year, they are between 51 and 54 mm in length, and have reached the asymptotic length of 75 mm before their third year (in 18-22 months). For section (a), I used the mean of the slopes of the lines of best fit for all cohorts of smaller animals from the 3 and 6 km sites at Stockton, and have plotted $95 \%$ confidence intervals around this mean calculated as $\mathrm{SE} \times \mathrm{t}_{\mathrm{df}, 0.05}$. While I have included the range $0-6 \mathrm{~mm}$ in Fig. 7, I have no information about animals of this length as my 3 mm sieve mesh only retained animals $\geq 6 \mathrm{~mm}$ in length. Section (b) of the age-length key consists of data from the 6 km Stockton Beach site (Fig. 4c). These cohorts are close together, and other interpretations are possible. Section (c) of the key comes from a cumulative frequency plot of sizes recorded on Stockton Beach during my study, which indicates an asymptote at 75 mm . The maximum size found during this study was 79 mm , larger than the maximum size of 60 mm estimated by King (1985) for this species in South Australia, however King did not sample subtidally.

The age-length relationship of Donax deltoides may over-estimate growth in the latter part of life. My data indicate a slowing of growth as pipis got larger. Growth may slow more after reaching sexual maturity, as in D. serra (Donn 1986). Because animals of $35-45 \mathrm{~mm}$ were missing in many samples, I lack sufficient evidence to accurately determine the relationship. Bivalves can show large variation in individual growth rates, among individuals, within sites, and between regions e.g. (Cerrato 1992; Koehn et al. 1988; Peterson and Beal 1989). Density dependent effects can cause variation in growth rates in bivalves e.g. (Christensen and Kanneworff 1985; Sastre 1984), however site effects are often much larger than density effects in infaunal clams e.g. (Peterson and Black 1987; Peterson and Black 1993). Competition and density dependence may be less important for mobile species.

## Reproduction

## Determination of sex ratio and size at first maturity using gonad smears

Sex ratios were consistent both across sites and times. I found no significant deviation from a 1:1 sex ratio in any year, and found no significant differences between sites or years using heterogeneity chi-square ( $\chi^{2}=1.33, \mathrm{df}=3, \mathrm{p}=0.7$, Table 9 ). I could not always find 50 animals at all sites and have only included results from collections that contained at least 10 animals. Overall, of 4128 individuals sexed, 2044 were female and 2084 male, a ratio of 1:1.02 (not significantly different to $1: 1, \chi^{2}=0.37, \mathrm{df}=1, \mathrm{p}=0.5$ ). I pooled animals into 3 mm size classes to avoid low or zero numbers in expected cells, and found no significant effect of size on sex for these animals $\left(\chi^{2}=18.21 ; \mathrm{df}=12 ; \mathrm{p}=0.1 ; \mathrm{n}=4128\right)$, and the size frequency distributions of males and females were almost identical (Fig. 8). I found no hermaphrodites, and no indication of sequential hermaphroditism among approximately 5,000 animals examined, in either fresh or histological preparations. Sex ratios of $1: 1$ appear characteristic of surf clams (reviewed by McLachlan et al. 1996), and particularly for Donax species (Ansell 1983).


Figure 7 Age-length key for Donax deltoides constructed from growth data from Stockton Beach, NSW. Section (a) was based on the mean of the slopes of five cohorts of smaller animals from three sites at Stockton Beach, section (b) from the means of the slopes of three cohorts from the Stockton Beach 6 km site, and Section (c) from the inflection point of a cumulative frequency plot of all sizes collected from Stockton Beach. Dotted lines are $95 \%$ confidence intervals generated as the mean of the slopes $\pm\left(\mathrm{SE} \times \mathrm{t}_{\mathrm{df}, 0.05}\right)$.

Table 9 Numbers of male and female Donax deltoides from approximately monthly collections made at Comerong Island in 1994-5, and at Stockton Beach, NSW in 1996-7. Overall, differences in sex ratios between sites and years were not significant ( $\chi 2=1.33 ; \mathrm{df}=3 ; \mathrm{p}=0.7$ ). All collections from each site contained $\geq 10$ animals.

| site | year | females | males | ratio |
| :--- | :---: | :---: | :---: | :---: |
| Comerong Island | 1994 | 652 | 658 | $1: 0.98$ |
| Comerong Island | 1995 | 526 | 541 | $1: 1.03$ |
| Stockton Beach | 1996 | 397 | 382 | $1: 0.96$ |
| Stockton Beach | 1997 | 469 | 503 | $1: 1.07$ |
| Total |  | 2044 | 2084 | $1: 1.02$ |



Figure 8 Size frequency of Donax deltoides that contained active sperm ( $\square$ ) or nucleated oocytes (区), based on examination of smears of fresh gonadal tissue from pooled collections from Comerong Island, NSW, in 1994 and 1995 and Stockton Beach, NSW, in 1996 and 1997. There was no significant effect of size on sex when pooled into 3 mm size classes $\left(\chi^{2}=18.21\right.$; $\mathrm{df}=12 ; \mathrm{p}=0.1 ; \mathrm{n}=4128$ ).

The probability of sexual maturity varied in a consistent manner with body length at all sites. Animals $<27 \mathrm{~mm}$ in length were always immature and most pipis became mature between 33 and 37 mm in length (Fig. 9 and Table 10), using Harvey and Vincent's (1989) definition of maturity as the length at which $50 \%$ of the length class contains visible sexual products.

Animals appeared to contain apparently mature gametes for most of the year, and I rarely found substantial numbers of large animals with empty gonads, except in July of 1993 and July of 1995 (Fig. 10). A similar pattern may have occurred for July 1994, but shortages of large animals meant that only one sample could be obtained during this period. There was also a decrease in the percentage of animals with gametes just prior to winter in 1996 for both sites, but no such decline for pipis at Stockton Beach for the winter of 1997. The proportion of animals with gametes varied significantly across sampling dates for each site, determined by heterogeneity chi-square tests (Comerong Island, $\chi 2=416.25, \mathrm{df}=22, \mathrm{p}<0.0001$; Stockton Beach, $\chi^{2}=470.0, \mathrm{df}=19, \mathrm{p}<0.0001$ ). Note that as gonad smears cannot differentiate between recently spawned or developing animals, and immature animals, I have only included animals > 40 mm in length in this analysis, in order to avoid bias from large numbers of immature animals. Note that the lines in Figs. 9 and 10 are merely to guide the eye and do not imply knowledge about the proportion of mature animals between sampling events.
(a) Comerong Island, 1994-5

(b) Stockton Beach, 1996-7


Figure 9 The percentage of Donax deltoides that contained active sperm or nucleated oocytes based on examination of fresh gonadal tissue for: (a) Comerong Island, 1994 (『), 26 collections, $\mathrm{n}=1310$; and $1995\left(^{*}\right.$ ), 14 collections, $\mathrm{n}=1067$; and (b) Stockton Beach, 1996 (『), 15 collections, $\mathrm{n}=779$; and $1997(*), 13$ collections, $\mathrm{n}=972$. Only collections with $\geq 10$ animals are included. Dotted lines indicate size at maturity i.e the size at which $50 \%$ have visible sexual products.

Table 10 Size at first and full maturity for Donax deltoides estimated by different methods, including a comparison with D. serra. Size at first maturity ( 1 st M ) was the size in mm at which females contained apparently mature gametes (fully formed sperm or oocytes with a nucleus), while full maturity (full M) was defined as the size at $\geq 50 \%$ of animals had visible sexual products. For comparison I have included the only other estimate of these parameters for this species, as well as an estimate for the similar sized Donax serra.

| species | method | date | 1st M | full M | max. length | site |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Current study |  |  |  |  |  |  |
| D. deltoides | smear | 1994 | 27 | 33 | 79 mm | Comerong Is. |
|  | smear | 1995 | 30 | 34 |  | Comerong Is. |
|  | smear | 1996 | 29 | 36 |  | Stockton |
|  | smear | 1997 | 28 | 34 |  | Stockton |
|  | histology | 1996 | 25 | 29 |  | Stockton |
|  | histology | 1997 | 25 | 29 |  |  |
| Other studies | histology | 1985 | 29 | 36 | 58 mm | S. Australia |
| D. deltoides <br> (King 1985) | histology | 1975 | 33 | 39 | 80 mm | S. Africa |
| D. serra <br> (de Villiers 1975) |  |  |  |  |  |  |



Figure 10 The percentage of Donax deltoides in approximately monthly collections containing apparently mature eggs or sperm (as identified by gonad smear) from Comerong Island, NSW, (■) and Stockton Beach, NSW ( $\bullet$ ), plotted against time. Numbers vary but are always $>10$. Only animals $>37 \mathrm{~mm}$ in length were included. The proportion of animals with gametes varied significantly across sampling dates for each site (heterogeneity chi-square test (a) Comerong Island, $\chi^{2}=416.25 ; \mathrm{df}=22 ; \mathrm{p}<0.0001$, and (b) Stockton Beach, $\chi 2=469.93 ; \mathrm{df}=19 ; \mathrm{p}<$ 0.0001 ).

## Oocyte diameters

Oocyte diameters varied greatly, from $<10$ up to $80 \mu \mathrm{~m}$ in diameter, both within monthly samples and within some individuals. A mixed model two-factor nested ANOVA showed highly significant heterogeneity in mean OD both among sample dates and among animals within dates (Table 11). Within animal variance explained nearly $50 \%$ of the total variance, with the remaining variance fairly evenly partitioned among animals within dates and among dates (Table 11). Such high within animal variation compared to variation between samples is typical of asynchronous spawners (Grant and Tyler 1983b).

Over the 12 months sampled, mean monthly OD increased significantly in May and June 1996, to $33.6 \pm 0.3 \mu \mathrm{~m}$ in July (Fig. 11) before decreasing steeply, reaching the minimum mean diameter in August of $19.1 \pm 0.2 \mu \mathrm{~m}$. Tukey's HSD indicates that this value was significantly lower than all other monthly means (Table 11). Mean OD increased significantly in November and March 1996, reaching a maximum of $41.1 \pm 0.4 \mu \mathrm{~m}$ in April 1997 (Fig. 11).

I found very few large oocytes in samples in August and November, 1996, indicating that most animals had spawned by those dates, but in the rest of the year I found a wide range of sizes. Microscopic examination of specimens confirmed that individuals held mature and immature oocytes simultaneously, and that different individuals in the sample could be at different stages. No oocyte atresia (degeneration within the ovary) was observed. I observed some fragmentation of oocytes in a few animals, but this appeared to be an artefact due to sectioning.

These data suggest that pipis are partial, incomplete spawners. In fully synchronous spawners, mean oocyte diameter declines sharply during spawning, often reaching zero during the resting phase e.g. in Spisula solidissima, mean OD declined by approximately $75 \%$ in one month, and then dropped to zero (Kanti et al. 1993). Oocyte diameter values have only been published for one species of Donax, D. trunculus, which showed a drop in mean diameter of $100 \%$ over two months in the Mediterranean, followed by a resting phase, implying good synchronisation of spawning (Neuberger-Cywick et al. 1990). In my study, the sharpest decline in mean OD was $42 \%$ in one month, and ODs did not continue to decline but increased in the following month. Mean ODs can vary in bivalves with time, geographic location and environmental condition (Barber and Blake 1983; Sastry 1979), so that my data may have reflected unusual environmental conditions rather than real spawning patterns. However I found highly significant differences in mean ODs both among animals and between sample dates, with most of the variance explained by variation within animals rather than between sampling dates, which implies that, in general, oocytes within individuals did not ripen at the same time, and that animals are at different developmental stages within each monthly sample (Grant and Tyler 1983b).

Table 11 Analysis of variance among oocytes for Donax deltoides collected from Stockton beach, NSW in 1996-7. The diameters of 25 oocytes in each of 20 pipis for 12 approximately monthly sampling dates were measured and a mixed model two-factor nested ANOVA used to test for heterogeneity. The factors were date (fixed) and animals nested within dates (random), with the null hypothesis of no difference in oocyte diameters between or within samples. Tukey's HSD test was used a posteriori to determining which differences between sample dates were significant.

| Source | df | SS | MS | F | p |
| :--- | ---: | ---: | ---: | ---: | ---: |
| among sample dates | 11 | 186,370 | 16,942 | 260.78 | $<0.0001$ |
| among animals within dates | 228 | 197,970 | 868 | 13.37 | $<0.0001$ |
| error | 5,760 | 361,038 | 65 |  |  |
| total | 5,999 | 758,563 |  |  |  |

Cochran's C $=0.1205, \mathrm{p}>0.05$

## Partitioning variances

## Source of variance

within animal, $\mathrm{s}^{2}$
among animals within dates, $\mathrm{s}^{2} \mathrm{~A} \subset \mathrm{D}$
among dates, $\mathrm{s}^{2} \mathrm{D}$
total variance

| Calculated as | Value | \% tot. |
| :--- | ---: | ---: |
| MS $_{\text {error }}$ | 65.0 | 49.7 |
| $\left(\mathrm{MS}_{\mathrm{A} \subset \mathrm{D}}-\mathrm{MS}_{\text {error }}\right) / \mathrm{n}$ | 32.1 | 24.5 |
| $\left(\mathrm{MS}_{\mathrm{D}}-\mathrm{MS}_{\text {error }}\right) / \mathrm{nb}$ | 33.8 | 25.8 |
| $\mathrm{~s}^{2}+\mathrm{s}^{2} \mathrm{~A}_{\text {A }}+\mathrm{s}^{2} \mathrm{D}$ | 130.9 | 100.0 |

where $\mathrm{n}=$ number of replicate oocytes $(=25)$ and $\mathrm{b}=$ number of animals for each date $(=20)$.
Mean
$\begin{array}{llllllllllll}19.0 & 27.8 & 28.3 & 30.4 & 31.3 & 33.6 & 34.1 & 35.5 & 35.9 & 36.1 & 38.3 & 41.2\end{array}$

## Sample date

$\begin{array}{lllllllllllllll}18 / 8 & 11 / 5 & 23 / 11 & 7 / 6 & 10110 & 1017 & 1 / 3^{1} & 6 / 9 & 30 / 12 & 26 / 1^{1} & 13 / 5^{1} & 13 / 4^{1}\end{array}$
Tukey's HSD $=2.021$. Lines indicate differences of $>2.021$ between means; dates marked ${ }^{1}$ are 1997, all others are 1996.


Figure 11 Mean oocyte diameters from female Donax deltoides collected from Stockton Beach, NSW. Each data point is the mean diameter of 25 oocytes from 20 animals ( $\mathrm{n}=500$ ) from approximately monthly collections. Bars are standard error. Arrowheads represent significant differences determined by Tukey's HSD.

Donax deltoides appears to spawn almost continuously, and I found little difference in spawning pattern between sites. My gonad smear data indicate that there were only a few months in more than four years in which $<50 \%$ of the population had ripe gametes, typically in winter, and every collection included at least some individuals that contained sexual products. Oocyte diameter measurements indicated that large oocytes were present in the gonad all year round, which implies that spawning can occur at any time.

My estimates of oocyte diameter made from different methods were all within the range published for the genus and for other free-spawning members of class Heterodonta with planktotrophic larvae. These eggs sizes are consistent with a planktotrophic pattern of development, and hence allow the prediction that this species will have high fecundity and short generation times, with high mortality early in life and a relatively prolonged larval life (Levin et al. 1987; Stearns 1976; Strathmann 1980; Thorson 1950)

I found year-to-year variation in the timing of spawning, as well as in the degree to which spawning appeared to be synchronised. My examination of gonad smears showed that the majority of the population were in a spent state in July of 1993 and 1995, representing some degree of synchronisation of spawning activity. However in July of 1994 and 1996, over >70\% of animals contained gametes. A rise in the percentage of the population containing gametes after April 1996 for both sites implied a peak of activity in late summer in that year. The timing of events appeared very similar for both sites when I was able to obtain enough data for comparison. The only decline in the proportion of ripe animals in 1997 was in March, and this was only a $2 \%$ decrease.

Prolonged spawning, with multiple stages present simultaneously and the lack of a defined resting stage is widespread among Donax species, which frequently show several peaks of spawning intensity. King (1985) found similar results for D. deltoides in South Australia, with large oocytes present for most of the year, and no inactive or resting phase. In general, freespawning members of Class Heterodonta (to which Donax belongs) have prolonged spawning periods (Strathmann 1987).

## Reproductive output and age at first maturity using stereological methods

No animals $<25 \mathrm{~mm}$ had begun to develop gonadal material. Animals appeared to start to develop gonads from 25 mm onward, but many had not fully differentiated at smaller size and could not be reliably sexed.

Fecundity and size at maturity: I did not find significant heterogeneity in the distribution of oocyte areas among animals, hence I pooled these data to give a mean ECD of $28.0 \pm 0.3 \mu \mathrm{~m}$ and calculated the mean adjusted diameter and the standard error around the mean, $\mathrm{D}=46.3 \pm$ $0.1 \mu \mathrm{~m}$, larger than the maximum monthly mean of $41.1 \pm 0.4 \mu \mathrm{~m}$ recorded for April 1997 using only oocytes sectioned through nucleus and nucleolus. An approximate Normal-based test indicated that this difference was significant $(\mathrm{Z}=12.6 ; \mathrm{p}<0.0001$ for all pairs $)$.

Mean numbers of oocyte per $\mathrm{mm}^{-2}$ of gonad did not vary significantly among animals in this collection, hence I pooled measurements to give an estimate of the mean number of oocytes per unit area, $\mathrm{N}_{\mathrm{A}}=133.3 \pm 3.0$ oocytes $\mu \mathrm{m}^{-2}$ for this collection. Similarly the ratio of the area occupied by oocytes:area of gonad did not vary significantly between animals, hence I used the overall mean ratio of oocyte area:gonad area as the areal proportion, which, utilising the Delesse Principle, approximates the volume fraction, $\mathrm{V}_{\mathrm{V}}$, (in this instance the relative volume of oocytes in the gonad) for this collection, with $\mathrm{V}_{\mathrm{V}}=0.21 \pm 0.01$. I calculated the constant $\mathrm{K}=0.97$. Hence $\mathrm{NV}=2520.0 \pm 33.0$ oocytes $\mathrm{mm}^{-3}$ of gonad.

I estimated that the mean number of oocytes contained in any animal was $2758.0 \pm 237.2$, and the maximum was 7,724 oocytes, in an animal of 70.5 mm in length (Fig. 12). The range of oocyte numbers within similar sized animals was large e.g. the number of oocytes within animals between 40 and 50 mm in length varied from $<400$ to nearly 6,000 . Unless smaller animals contained nucleated oocytes, I treated them as if they had no gonad, hence they were plotted as having zero eggs. The length at which females began to hold mature eggs is 25 mm , and length at maturity ( $50 \%$ containing eggs) was 29 mm .

My estimates of fecundity support my contention that pipis are incomplete, partial spawners. My estimate of a maximum 7,724 number of eggs held per female was much lower than estimates from other studies. Bivalves are typically highly fecund, although estimates of fecundity often show high variability (Griffiths 1981; Thompson 1979). Estimates for other species of clam include 24.3 M eggs spawned by an individual Venus mercenaria in a single event (Davis and Chanley 1956), a release of $30,000-7 \mathrm{M}$ oocytes during a summer spawning for Tapes rhomboides (Morvan and Ansell 1988), and between 1,000 to 50,000 eggs were spawned at a time, with several ovulations per season in D. gouldi, (Coe 1955). In comparison my estimate of $<20$ to $>7,500$ oocytes held per female is low. The true number may well have varied even more, as I did not calculate all parameters for all animals, but used averages of a random sample. However oocyte densities appeared fairly uniform throughout this collection. All animals showed empty spaces in the gonad, indicating that the bulk of the population appeared to have recently partially spawned, which would lead me to underestimate fecundity. I observed these empty spaces within all collections, indicating that partial spawning is common at all times of the year. As the spawning season appears prolonged, females may not store eggs for a "big bang" spawning event, but instead may release smaller numbers more frequently (commonly called dribble spawning). Fecundity is likely to be extremely high despite the relatively low numbers of eggs found in each animal in my "snap-shot" estimate of fecundity at one point in time.


Figure 12 Number of eggs ( $\square$ ) contained in female Donax deltoides of different sizes from a collection made on 23/11/96 from Stockton Beach, using stereological techniques. $\mathrm{n}=172$.

The size at which pipis can be defined as fully mature was fairly consistent between sites and between years. Gonad smears indicated that at least $50 \%$ of pipis were mature by 37 mm in length, with gametes being found in animals as small as 27 mm . Histological preparations indicated smaller sizes both for first ( 25 mm ) and full maturity ( 29 mm ). I attribute this to differences in technique rather than spatial or temporal variation. Under microscopic examination, even animals with one mature follicle were scored as mature, however I would be unlikely to detect so few gametes with the gonad smear technique. As small animals held few oocytes (e.g. animals $\leq 35 \mathrm{~mm}$ in length held a mean number of $59 \pm 12$ oocytes per female), it may be more useful for management purposes to class them as mature when they have enough sexual products to be detected via gonad smear. Gonad smears appear to give reproducible and biologically meaningful estimates of size at maturity for this species, and provide a quick and cheap method of obtaining information. My estimates of size at maturity were in close agreement with the only other published estimate for Donax deltoides, of 36 mm (King 1985). Such similar values for my two sites ( 250 km apart), as well as for a South Australian site, an area influenced by very different current and temperature regimes, indicates that size at maturity is relatively constant throughout the range of $D$. deltoides. A comparison of size at maturity for Donax deltoides with other species of Donax, as well as other bivalves, suggests rapid initial growth and an early onset of sexual maturity in pipis (McLachlan et al. 1996).

## General Discussion

## Management implications

Management of beach clam fisheries is complicated by the interaction of human behaviour and the biological characteristics of the animals. The large episodic fluctuations in distribution and abundance that characterise beach clams make stock estimation and management difficult, particularly in pipis (Murray-Jones 1998). However pipis have planktonic larvae which may disperse widely (Ansell 1983). My data suggest that the spawning season is prolonged, and I found recruits on beaches at all times of the year. These characteristics are typical of beach clams (McLachlan et al. 1996) and may act to mitigate the effects of harvesting. Even so, many beach clam fisheries in other areas of the world have shown a trend towards declining catches over time which is believed to be the result of overharvesting by both the commercial and recreational sectors (McLachlan et al. 1996).

The different harvesting patterns that characterise the commercial and recreational fisheries make it difficult to balance the management needs of both sectors whilst ensuring the maintenance of a sustainable pipi fishery. The commercial sector is extremely efficient at harvesting pipis. The bulk of the pipi catch from Stockton Beach was taken by the commercial sector, and it seem likely that the commercial sector accounts for the majority of pipis on a state wide scale. Historical data indicate that state wide commercial pipi catches have been increasing steeply since the late 1980s, reaching 464 tonnes in 1996-97 (NSW Fisheries catch statistics). The unrestricted growth of commercial pipi catches in NSW should be monitored closely because of the potential risks of overfishing this shared resource.

I found comparatively high levels of effort in the recreational fishery, but most participants were inefficient and had very low catch rates. Despite the high effort, the recreational catch from Stockton Beach was only about $20 \%$ of the total catch, most of which was taken for food. Any increase in collecting efficiency by the recreational sector, due to collectors gaining experience in locating patches of pipis or having better access to productive sites on beaches, would undoubtably lead to an increase in recreational catches and a greater allocation of the pipi resource to the recreational sector. In addition, any future increase in the population of NSW, allied to an increasing trend towards more cosmopolitan styles of food, could lead to increases in recreational collecting effort for pipis. At present, further expansion of the recreational fishery in NSW is at least partially restricted by the current bag limit regulation of 50 pipis per person per day (Lynch and Prokop 1993).

Competition between the commercial and recreational sectors for the shared pipi resource in NSW is likely to increase over time, thus it is important to develop an appropriate management strategy that includes consideration of the different harvesting patterns of the commercial and recreational sectors and incorporates relevant biological information about pipi populations.

My data from widely separated sites clearly indicate that growth is asymptotic, very rapid up to the age of sexual maturity, and that settlement is prolonged and prolific. In terms of fisheries management, fast growth and abundant settlement imply that sustainable harvesting
should be possible. However due to sampling difficulties experienced with this species, more work is required in order to validate the age-length relationship and estimate mortality. Another tagging trial might yield this information, possibly by mass tagging large numbers of very small animals with tetracycline. The recovered tetracycline tagged pipi had a strong fluorescence line which could be read externally, hence this method was successful. In addition, because large numbers of recruits on the beach were often present which did not form cohorts, a study of postsettlement recruitment processes would be interesting in order to differentiate between mortality and migration. Also of interest is the source of recruits, and the degree to which populations are genetically isolated.

The spawning pattern of Donax deltoides is poorly defined, and shows considerable variation in the timing of reproduction from year to year both within individuals and between years. Populations at both locations showed very prolonged spawning, with some peaks in activity. At both sites, mature females ( $\geq 37 \mathrm{~mm}$ ) contained apparently mature eggs for nearly all of the year. The proportion of the body which was gonad increased with size, but the true relationship was probably obscured by prolonged spawning. The number of eggs held per female was low overall, but also varied greatly between individuals. These findings appear typical of surf clams worldwide (e.g. McLachlan et al. 1996), and particularly for other Donax species (e.g. Ansell 1983).

## Implications for dispersal and recruitment

There are some particular challenges facing infauna on sandy beaches, such as the turbulence of the water, the semi-closed nature of the rip circulation cells formed off sandy beaches (McLachlan 1980; Talbot and Bate 1987) and the erratic nature of the connecting currents. Dispersal in Donax deltoides will depend greatly on the timing of spawning and the degree to which spawning is triggered by oceanographic cues. These factors will determine whether populations are effectively closed, with a strong stock-recruitment relationship, or more open, with high gene flow and little genetic differentiation between populations. Pipis on the east coast of Australia show little genetic differentiation, and effectively form a single, panmictic stock (Murray-Jones and Ayre 1997). I did not find evidence for a strong relationship between stock and recruitment. Hence recruits to a beach may be coming from other locations, or perhaps from reservoirs offshore.

Although I found considerable variation in the timing of reproduction from year to year both within individuals and among years, in general at all sites spawning was prolonged, with recruitment all year round. However not all recruits survived to enter the fishery. There appeared to be high post-settlement mortality at all sites, with few recruits appearing to establish cohorts. High variability in the survival of recruits generally implies differential mortality (Keough and Downes 1982), and survival in surf clams may be a stochastic event, with large storms removing the bulk of settlers so that only those which have reached a sufficient size can survive high wave activity and hence recruit.

For species with delayed maturity and low fecundity, even moderate increases in fishing intensity can decrease the supply of larvae (recruitment overfishing). However for fast maturing, highly fecund animals, recruitment may not decrease greatly until stock sizes are very low. This tendency increases the risk of collapse. Any tendency to harvest animals before they have made a contribution to reproductive output will increase the likelihood of recruitment overfishing. Pipis appeared to grow fast, reaching sexual maturity within six to nine months, however they begin to be harvested well before they reach sexual maturity. Pipis $<45 \mathrm{~mm}$ in length did not contain large numbers of eggs at any one time (Fig. 12). However they had been recruited into the fishery at this size and hence were subject to considerable fishing pressure (Fig. 3). While the majority of animals targeted by harvesters were large, recreational food collectors often took very small animals, down to 10 mm in length. Even commercial harvesters took animals as small as 26 mm at times, although all groups expressed a preference for larger animals. Nearly $60 \%$ of the recreational food harvest, and $14 \%$ of the combined recreational and commercial harvest, was $<37 \mathrm{~mm}$, the size that my data suggest that $D$. deltoides reaches sexual maturity. This contrasts with the recreational fishery for Donax serra (similar in size and appearance to $D$. deltoides) in which only $1.3 \%$ of the total catch was $<45 \mathrm{~mm}$, the estimated size of sexual maturity for this species (Schoeman 1996). There is enormous potential for increases in both catch rates and numbers of participants in the recreational harvesting sector. In addition, commercial fishers will take small animals when no large are available. Given the fact that such large numbers of pre-reproductive individuals are taken, and the potential for the proportion of small animals taken to grow if the fishery expands or if larger animals become scarce, there appears to be a real risk of recruitment overfishing, although this must depend on the relationship between adults and recruitment levels (Gulland 1973).

## Appropriate harvest tactics for the pipi fishery

Management concerns in the pipi fishery include conserving the resource, the sustainability of harvesting, partitioning of the resource between user groups, and resolving conflict between commercial fishers, recreational harvesters for food, recreational anglers, local residents and other recreational beach users (pers. comm. Manager, Newcastle/Nelson Bay Fishing Co-op; Secretary, Master Fish Merchants' Association of NSW; NSW Fisheries officers; Secretary, Mid North Coast Amateur Deep Sea Fishing Association; and John Prosser, NSW Fishing Clubs Association). Harvest tactics that can be employed to address specific management concerns and to implement management strategies include quotas and bag limits, gear restrictions, effort controls and restricted entry, stock enhancement, size limits, area and seasonal closures, and the maintenance of unfished areas to act as reserves (Jamieson 1986). These tactics are not mutually exclusive. Some of these are already in place in the pipi fishery including gear restrictions and bag limits. No implement may be used to locate, dig, or sieve pipis by either sector, and the recreational bag limit is 50 pipis per person per day (Lynch and Prokop 1993). Most beach clams do not appear to be good candidates for aquaculture (McLachlan et al. 1996), so stock enhancement is probably not an option. As previously
mentioned, there is so much variability in the distribution and abundance of this species that neither my data, nor other studies, yield enough information to assert that management tactics need to be immediately applied. However there appears to be some risk of recruitment overfishing, hence the precautionary principle applies.

## Specific management strategies

There are four main harvesting strategies commonly used in fisheries management (stock size dependence, yield-per-recruit (YPR) and egg-per-recruit (EPR) models. Most of these are not appropriate for the pipi fishery in NSW.

1. Stock-size dependent strategies. Stock size dependent strategies are reliant on an accurate assessment of stock. However my estimates of biomass at the transect level were very different over along-shore distances as small as 20 m (Murray-Jones 1998). Pipis were also likely to move offshore and out of sampling range and showed day-to-day variation in location on shore and differences in abundance over very short spatial and temporal scales. These factors mean that obtaining accurate stock assessment would require very intensive (and perhaps prohibitively expensive) sampling. My estimates of biomass varied over short temporal scales, due to rapid changes in distribution both along the shore or down the shore, hence stock assessments would need to be well replicated in time as well, adding to the cost e.g. my preliminary stock estimates for a small part of Stockton Beach increased from 2.6 to $12.9 \mathrm{t} \mathrm{km}^{-1}$ over only five months (Murray-Jones 1998).

The variation in distribution and abundance common in this species was reflected in large changes in catch, and catch rates, in the commercial and recreational fisheries. Varying catches are characteristic of beach clam fisheries world wide (McLachlan et al. 1996), which suggests that there is variation in either the absolute numbers available, or the accessibility of targeted animals.

In some fisheries, catch per unit effort (CPUE) is used as an index of population abundance. However CPUE is really estimating the abundance of older stock, and can remain high until the stock is seriously depleted, hence is not a particularly useful indicator of abundance for management purposes (Jamieson 1986). In any case, in the pipi fishery CPUE fluctuates greatly with position on shore, as well as with short term fluctuations in abundance, hence CPUE cannot be reliably standardised to provide an index of abundance (Klaer 1994; Szarzi et al. 1995).

For the pipi fishery, it would not be appropriate to base management decisions on models that require estimates of biomass and stock abundance, as these may be unreliable and obtaining precise estimates is likely to prove prohibitively expensive.
2. Yield-Per-Recruit and Egg-Per-Recruit models. These models rely on accurate estimates of the age-length relationship, mortality, and knowledge about longevity. I have little information about longevity. I found considerable differences in mortality between the north coast and south coast, with animals large enough to be sexually mature being rare throughout the study at the Seven Mile Beach, while at Stockton Beach, large animals were generally present,
however I was not able to obtain accurate estimates of mortality from my data. I was also unable to satisfactorily age animals, although I was able to obtain a reasonable estimate of growth rates until about the size of sexual maturity. In addition, fecundity is difficult to measure in asynchronous spawners in which the gonad cannot be separated from the visceral mass.

Because the relevant input parameters are imprecise, YPR and EPR models based on my data are unlikely to generate sensible information for making management decisions about fishing effort for the pipi fishery. In any case, YPR calculations can be misleading when fluctuating abundances mean that the equilibrium assumptions underpinning such models are not being met (Jamieson and Caddy 1986). In addition, optimum yield methods do not consider recruitment so can be problematical when recruitment is variable (Sainsbury and Polacheck 1994). High recruitment variability creates particular management difficulties in a fishery, and in the long run it may prove economic to forgo the maximum potential yield from a strong year class when yields are likely to oscillate (Murawski and Serchuk 1989)
3. Pulse or periodic strategies. Pulse strategies are those in which fishing grounds are rotated or areas left unfished for some period of time in order to allow animals to grow to marketable size. These strategies are effective when older animals fetch a higher price, or it is more economic to collect large numbers at a time. However this is not the case in the pipi fishery. This is a low cost fishery, with no equipment requirements, and large pipis do not fetch a higher price. Although the Master Fish Merchant's Association of NSW has in place a system of grading by size, there is no mean difference in sale price between sale lots of extra large (<30 pipis per kg ), large ( $31-40$ ) or small ( $\geq 40$ ) pipis (Fish Marketing Authority of NSW data base). To some degree, pulse fishing happens naturally in the pipi fishery, as commercial fishers will tend to target other beaches, often in different geographic regions, if local stocks decline.
4. Size limit strategies. The imposition of a minimum size limit would prevent the heavy harvest of small animals, and avoid some conflict over resources, as local residents resent tourists who are perceived as taking very small animals (pers. comm. Manager, Birubi Point Caravan Park). I have listened to many complaints from different users groups over this issue, and indeed observed violence. Size limits would be relatively easy to enforce for the commercial sector (which accounts for $80 \%$ of the total harvest), as most fishers grade their catch by size already. A minimum size limit may be more difficult to enforce for the recreational sector due to the large numbers of recreational harvesters participating. The recreational fishery in South Africa for Donax serra employs a minimum legal width of 35 mm , corresponding to a length of 55 mm (Schoeman 1996). Schoeman found that as much as $38 \%$ of the recreational catch was smaller than the legal length, rising to nearly $50 \%$ during holidays and weekends. Any size limit imposed for $D$. deltoides should prohibit the taking of animals $<45 \mathrm{~mm}$ in length, as prior to this point few eggs are held, and would prevent the removal of large numbers of immature animals.

A maximum size limit is sometimes thought to be of benefit in preventing recruitment overfishing. However, while I found that the number of eggs held per female clearly increased with size for small pipis, I found little or no correlation between size and number of eggs held in larger animals (Fig. 12). Large animals may, of course, recover faster and produce more eggs
over a prolonged spawning period, but I have no data on which to base the imposition of a maximum size limit.

In addition, ensuring that some areas of long sandy beaches which support a large population of pipis are set aside as reserves may offer protection from the limitations of managing variable recruitment fisheries, perhaps enhancing long term sustainability (Lauck et al. 1998). Such area closures in the form of intertidal protected areas have been under discussion in NSW for some time (Anon. 1991), and are intended to include parts of sandy beaches, but these have not yet been formalised.

## Predictions

In general, in the absence of precise stock abundance estimates, only general predictions can be made about the effects of any future increases in harvesting. Pipi prices are generally low, fluctuating between 80 c and $\$ 5$ per kilogram over the past few years, with an average price on the Fish Market floor of $\$ 2$ per kilogram during the commercial harvesting survey (1996-7) (Fish Marketing Authority data base). If further fishing decreased stock abundance, collecting pipis would quickly become uneconomical for commercial fishers (who took $80 \%$ of the catch in 1996-7). Indeed in late 1996, commercial fishers began targeting other beaches as numbers declined on Stockton Beach, or switched back to other finfishing activities. While rarity value could force the price up, pipis are not regarded as a particular delicacy, and never fetch the high prices of other shellfish such as abalone (average price $\$ 24.60$ per kilogram during 1996-7, Fish Marketing Authority data base). In any case, NSW Fisheries are currently proposing a management strategy involving limited fishing licences which will greatly reduce the number of participants in the fishery.

In the recreational sector, fishing effort was far higher than in the commercial sector. Recreational harvesters accounted for $89 \%$ of total effort, although their catch rates were very low even when abundances were high. As long as the majority of recreational harvesters continue to access beaches on foot, declines in abundance on a long beach such as Stockton Beach will serve to limit individuals' catches. However there is the potential for the recreational catch to increase substantially, particularly if harvesters become more experienced at collecting. Decreasing the recreational bag limit would be a suitable method of further limiting the catch if the proportion of the catch taken by recreational harvesters became larger.

## Benefits

The main beneficiaries will be NSW commercial and recreational fishers. The results of this study could be used by fisheries managers and research scientists in State and Commonwealth Departments in a number of ways. Prior to this study there was little information on the basic biology of the pipi, and none on harvesting rates. Recreational catch and effort data can be used (a) to describe total resource use, (b) to provide a baseline to monitor harvests, (c) to estimate the relative impacts of the different sectors on pipi stocks, and (d) to minimise resource conflicts. Data on the recreational harvest can be used by managers in considering the effectiveness of harvest controls such as minimum length or bag limits, and in public forums to support the decisions of managers on allocation of the resource and to educate the public. Basic biological data can be used to make predictions about the effects of harvesting. Given the Australian Government's commitment to ecological sustainability, I would argue that the next generation will also be a direct beneficiary of careful management of this species. Of less direct benefit is the maintenance of food chains, as these bivalves provide food for crabs and other invertebrates, as well as many species of fish and birds. Many recreational anglers link low catches of finfish on beaches like Stockton with perceived declines in abundance.

This study also validates efforts of the Master Fish Merchant's Association and the Newcastle/Nelson Bay Fishermen's Cooperative to grade pipis and discourage fishers from taking small animals.

## Further Development

I would suggest that a copy of this report be sent to appropriate fisheries management agencies in NSW, South Australia, Victoria, and Queensland, and in abbreviated form be disseminated to commercial and recreational fishers.

This fishery probably requires little management other than monitoring. It is not cost effective for fishers to continue collecting from beaches on which stocks are low, and they tend to move to other fisheries or shift location. As stock assessment is both difficult and expensive for this species, the most cost-effective method of monitoring the fishery would be to keep data on the sizes of catches coming through the fish markets. Another tag-recapture study would be beneficial in obtaining a more reliable estimate of growth rates and age at size.

## Conclusion

The primary objective of this project was to quantify the levels of harvesting on selected NSW beaches. This objective has been achieved. Working in conjunction with NSW Fisheries personnel, I decided to collect precise information for a limited number of beaches, rather than diffuse information for many sites. Hence I restricted the study to two sites: Stockton Beach, the most important commercially harvested site in NSW, with a large recreational harvest; and Seven Mile Beach on the NSW south coast, which is no longer commercially harvested but has a large recreational fishery. I used a voluntary log book survey to quantify catch, effort, and catch rates for the commercial fishery, and an onsite survey to quantify catch, effort, and catch rates for recreational food and bait harvesting.

For the pipi fishery at Stockton Beach, most of the catch was taken by commercial fishers, but far more effort was expended by recreational harvesters, who had generally low catch rates. On the south coast, recreational effort was high at Seven Mile Beach but catches and catch rates were extremely low. I estimated that the combined recreational and commercial catch of pipis from Stockton Beach was 237.7 tonnes during the period March 1996 to February 1997 inclusive, taken in a total of 120,672 collector hours. Commercial fishers took the bulk of the catch, but accounted for only a small amount of the combined fishing effort. In contrast, the recreational fishery was characterised by a relatively small catch, many participants, high fishing effort, and extremely low catch rates. At both sites, recreational collecting for food was far more extensive than bait collecting. Catch rates were high for the commercial fishery, but relatively low in the recreational sector.

Commercial fishers and recreational bait collectors favoured large pipis and tended not to take small pipis. Recreational food collectors were less selective than these other user groups, often retaining small pipis, some as small as 9 mm in length. Over $25 \%$ of the recreational food catch consisted of small pipis, $<30 \mathrm{~mm}$ in length.

The secondary objective was to make preliminary estimates of the effects of harvesting. As specified I collected information to allow a description of growth, size at first reproduction, and the nature of the spawning cycle. This objective was also met. Growth was rapid in small animals, with pipis reaching 37 mm (sexual maturity) within 10 months. Growth slowed with size. Recruitment patterns were consistent both between and within sites. Mortality varied both between and within sites, with few large animals found at some sites. I found small animals all year round, although few cohorts became established. D. deltoides appears to partially spawn all year round, although there was year-to-year variation in the timing and degree of synchronisation of spawning. My data suggest that this fishery is unlikely to be recruitment limited.

## References

ABARE. 1997 Australian Fisheries Statistics. ABARE (Australian Bureau of Agricultural and Resource Economics). Canberra

Anon. 1960 1959-1960 Annual Report. New South Wales Fisheries. Sydney
Anon. 1966 Harvesting of pipis - Council right to refuse. Northern Star, Oct 20th p. 9
Anon. 1991 Managing harvesting in intertidal habitats: A discussion paper. NSW Agriculture \& Fisheries. Sydney

Ansell, A. D. 1983 The biology of the genus Donax. In Sandy Beaches as Ecosystems. (ed. A. McLachlan \& T. Erasmus), pp. 607-635 D R W Junk. The Hague

Ansell, A. D. \& Lagardère, F. 1980 Observations on the biology of Donax trunculus and D. vittatus at Ile d'Oléron (French Atlantic coast). Mar. Biol. 57: 287-300

Australian National Recreational Fisheries Working Group. 1994 Recreational fishing in Australia: A national policy. Australian National Recreational Fisheries Working Group, Dept. Primary Industries and Energy. Canberra

Barber, B. J. \& Blake, N. J. 1983 Growth and reproduction of the bay scallop, Argopecten irradians (Lamarck) at its southern distributional limit. J. Exp. Mar. Biol. Ecol. 66: 247-456

Barry, J. P. \& Tegner, M. J. 1990 Inferring demographic processes from size-frequency distributions. Simple models indicate specific patterns of growth and mortality. Fish. Bull. 88: 13-19

Beninger, P. G. 1987 A qualitative and quantitative study of the reproductive cycle of the giant scallop, Placopecten magellanicus, in the Bay of Fundy (New Brunswick, Canada). Can. J. Zool. 65: 495-498

Beverton, R. J. H. \& Holt, S. J. 1957 On the dynamics of exploited fish populations. Fishery Invest. Lond. Ser. 2 19: 1-533

Bodoy, A. 1982 Croissance saisonnière du bivalve Donax trunculus (L) en Méditerranée Nordoccidentale. Malacologia 22: 353-358

Branch, G. M. 1974 The ecology of Patella linnaeus from the Cape Peninsula, South Africa. 2. Reproductive cycles. Trans. Roy. Soc. S. Afr. 41: 111-160

Briarty, L. G. 1975 Stereology: methods for quantitative light and electron microscopy. Sci. Prog., Oxf. 62: 1-32

Cerrato, R. M. 1980 Demographic analysis of bivalve populations. In Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change. (ed. D. C. Rhoads \& R. A. Lutz), pp. 417-463 Plenum Press. NY, Lond.

Cerrato, R. M. 1992 Age structure, growth and morphometric variations in the Atlantic surf clam, Spisula solidissma, from estuarine and inshore waters. Mar Biol 114: 581-593

Chanley, P. 1969 Larval development of the Coquina clam, Donax variabilis Say, with a discussion of the structure of the larval hinge in the Tellinacea. Bull. Mar. Sci. 19: 214-244

Chesson, P. L. 1986 Environmental variation and the coexistence of species. In Community Ecology. (ed. J. M. Diamond \& T. Case), pp. 240-256 Harper and Rowe. NY

Christensen, H. \& Kanneworff, E. 1985 Sedimenting phytoplankton as a major food source for suspension and deposit feeders in the Øresund. Ophelia 24: 223-44

Clark, G. R. I. 1980 Appendix 1. Preparation and examination of skeletal materials for growth studies. Part A. Molluscs. 2. Study of molluscan shell structure and growth lines using thin sections. In Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change. (ed. D. C. Rhoads \& R. A. Lutz), pp. 603-611 Plenum Press. NY, Lond.

Coe, W. R. 1955 Ecology of the bean clam Donax gouldi on the coast of Southern California. Ecology 36: 512-514

Cornish, T. E. 1966 Save the Pipi! A fisherman's plea. Anglers' Digest pp. 28-30
Crisp, D. J. 1984 Energy flow measurements. In Methods for the Study of Marine Benthos. (ed. N. A. Holme \& A. D. McIntyre), pp. 284-372 Blackwell. Oxford \& Edinburgh

Cushing, D. H. 1973 Recruitment and parent stock in fishes. Washington Sea Grant Publication. University of Washington, Seattle

Dallimore, M. 1965 Keep pipis please. Northern Star, 28/10/65 pp. 26
Davis, H. C. \& Chanley, P. E. 1956 Spawning and egg production of oysters and clams. Proc. Natl. Shellfish Assoc. 46: 40-58

Defeo, O., Arreguín-Sánchez, F. \& Sánchez, J. 1992 Growth studies of the yellow clam Mesodesma mactroides: a comparative analysis of three length-based methods. Sci. Mar. 56: 53-59
de Villiers, G. 1975 Reproduction of the white sand mussel Donax serra Röding. Investl.
Rep. Sea Fish. Brch. S. Afr. 102: 1-33
Donn, T. E. 1986 Growth, production and distributional dynamics of the white mussel, Donax serra, in the Eastern Cape. In Workshop on the biology of the genus Donax in South Africa. (ed. T. E. Donn), pp. 34-41 University of Port Elizabeth, Institute for Coastal Research Report \# 5. Port Elizabeth

Ebert, T. A. 1973 Estimating growth and mortality rates from size data. Oecologia 11: 281298

Edwards, S. F. 1990 An economic guide to allocation of fish stocks between commercial and recreational fisheries. NOAA Technical Report NMFS 94.

Fournier, D. A., Sibert, J. R., Majkowski, J. \& Hampton, J. 1989 MULTIFAN, a likelihoodbased method for estimating growth parameters and age composition from multiple length frequency data sets with an application to southern bluefin tuna. Otter Software.

Frenkiel, L. \& Mouëza, M. 1979 Développment larvaire de deux Tellinacea, Scrobicularia plana (Semelidae) et Donax vittatus (Donacidae). Mar. Biol. 55: 187-195

Godfrey, M. C. S. 1989 Shell bed midden chronology in SW Victoria. Arch. in Oceania. 24: 65-69

Grant, A., Morgan, P. J. \& Olive, P. J. W. 1987 Use made in marine ecology of methods for estimating demographic parameters from size/frequency data. Mar. Biol. 95: 201-208

Grant, A. \& Tyler, P. A. 1983a The analysis of studies of invertebrate reproduction: I. Introduction and statistical analysis of gonad indices and maturity indices. Int. J. Invert. Rep. 6: 259-269

Grant, A. \& Tyler, P. A. 1983b The analysis of studies of invertebrate reproduction: II. The analysis of oocyte size/frequency data, and comparison of different types of data. Int. J. Invert. Rep. 6: 271-283

Green, R. H. 1970 Graphical estimation of rates of mortality and growth. J. Fisheries Res. Board Canada 27: 204-208

Griffiths, R. J. 1977 Reproductive cycles in littoral populations of Choromytilus meridonalis (Kr.) and Aulacomya ater (Molina) with a quantitative assessment of gamete production in the former. J. Exp. Mar. Biol. Ecol. 30: 53-71

Griffiths, R. J. 1981 Production and energy flow in relation to age and shore level in the bivalve Choromytilus meridionalis (Kr.). Est. Coast. Shelf Sci. 13: 477-493

Guillou, J. \& Le Moal, Y. 1980 Aspects de la dynamique des populations de Donax vittatus et Donax trunculus en Baie de Douarnenez. Ann. Inst. Océanogr. 56: 55-64

Gulland, J. A. 1973 Can a study of stock and recruitment aid management decisions? Rapp. PV. Reun. Cons. Int. Explor. Mar. 169: 368-372

Gulland, J. A. 1989 Fish Stock Assessment: A Manual of Basic Methods. John Wiley \& Sons.
Gulland, J. A. \& Holt, S. J. 1959 Estimation of growth parameters for data at unequal time intervals. J. Cons. Perm. Int. Expl. Mer. 25: 47-49

Harvey, M. \& Vincent, B. 1989 Spatial and temporal variations of the reproduction cycle and energy allocation of the bivalve Macoma balthica (L) on a tidal flat. J. Exp. Mar. Biol. Ecol. 129: 199-217

Henry, G. \& Virgona, J. 1984 Why is angling so popular? Australian Fisheries May 1984: 32-33

Hilborn, R. \& Walters, C. J. 1992 Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman \& Hall. London

Hirshfield, M. F. \& Tinkle, D. W. 1975 Natural selection and the evolution of RE. Proc. Natl. Acad. Sci. USA 72: 2227-2231

Jamieson, G. S. 1986 A perspective on invertebrate fisheries management - the British Colombia experience. In North Pacific Workshop on Stock Assessment and Management of Invertebrates. Nanaimo, B.C. May 1984. (ed. G. S. Jamieson \& N. Bourne), pp. 57-74 Dept. Fisheries and Oceans. Ottawa

Jamieson, G. S. \& Caddy, J. F. 1986 Research advice and its application to management of invertebrate resources: an overview. In North Pacific Workshop on Stock Assessment and Management of Invertebrates. Nanaimo, B.C. May 1984. (ed. G. S. Jamieson \& N. Bourne), pp. 416-424 Dept. Fisheries and Oceans. Ottawa

Jones, D. S. 1981 Repeating layers in the molluscan shell are not always periodic. J. Paleontol. 55: 1076-1082

Kanti, A., Heffernan, P. B. \& Walker, R. L. 1993 Gametogenic cycle of the southern surfclam, Spisula solidissima similis (Say), from St. Catherine's Sound, Georgia. J. Shellfish Res. 12: 255-261

Kaufmann, K. W. 1981 Fitting and using growth curves. Oecologia 49: 293-299
Kendall, M. G. \& Stuart, A. 1969 The Advanced Theory of Statistics. Griffin. London

Keough, M. J. \& Downes, B. J. 1982 Recruitment of marine invertebrates: The role of active larval choices and early mortality. Oecologia 54: 348-342

King, M. G. 1985 The life history of the Goolwa cockle Donax (Plebidonax) deltoides (Bivalvia: Donacidae) on an ocean beach, South Australia. South Australian Dept. of Fisheries, Adelaide.

King, M. 1995 Fisheries Biology, Assessment and Management. Fishing News Books, Blackwell Science Ltd. Oxford

Klaer, N. L. 1994 Methods for standardisation of catch/effort and data requirements. In Population dynamics for fisheries management, Australian Soc. for Fish Biology Workshop Proceedings. (ed. D. A. Hancock), pp. 86-90. Australian Soc. for Fish Biology Perth

Koehn, R. K., Diehl, W. J. \& Scott, T. M. 1988 The differential contribution by individual enzymes of glycolysis and protein catabolism to the relationship between heterozygosity and growth rate in the coot clam, Mulinia lateralis. Genetics, Austin, Tex. 118: 121-130

Krantz, D. E., Jones, D. S. \& Williams, D. F. 1984 Growth rate of the sea scallop, Placopecten magellanicus, determined from the 18O/O record in shell calcite. Biol. Bull. 167: 186-199

Lal, P., Holland, P. \& Power, P. 1992 Competition between recreational and commercial fishers. Aust. Bureau of Agricultural \& Resource Economics. Canberra

Lauck, T., Clark, C. W., Mangel, M. \& Munroe, G. 1998 Implementing the precautionary principle in fisheries. Management through marine reserves. Ecol. Appl. Supplement 8: S72S78

Levin, L. A., Caswell, H., DePatra, K. D. \& Creed, E. L. 1987 Demographic consequences of larval development mode: Planktotrophy vs. lecithotrophy in Streblospio benedicti. Ecology 68: 1877-1886

Lowe, D. M., Moore, M. N. \& Bayne, B. L. 1982 Aspects of gametogenesis in the marine mussel Mytilus edulis L. J. Mar. Biol. Ass. U. K. 62: 133-145

Lucas, A. 1982 Evaluation of RE in bivalve molluscs. Malacologia 22: 183-187
Lynch, P. \& Prokop, F. 1993 Fishnote: Intertidal invertebrates - regulations. NSW Fisheries. Sydney

MacDonald, B. A. \& Thompson, R. J. 1985 Influence of temperature and food availability on the ecological energetics of the giant scallop Placopecten magellanicus. II Reproductive output and total production. Mar. Ecol. Prog. Ser. 25: 295-303

MacDonald, P. D. M. \& Pitcher, T. J. 1979 Age-groups from size-frequency data: A versatile \& efficient method of analysing distribution mixtures. J. Fish. Res. Bd Canada 36: 987-1001

MacPherson, J. H. \& Gabriel, C. J. 1962 Marine Molluscs of Victoria. Melbourne University Press. Melbourne

Matlock, G. C., Osburn, H. R., Riechers, R. K. \& Ditton, R. B. 1991 Comparison of response scales for measuring angler satisfaction. American Fisheries Society Symposium 12: 413-422

McCuaig, J. M. \& Green, R. H. 1983 Unionoid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie. Can. J. Fish. Aquat. Sci. 40: 436-442

McLachlan, A. 1980 Exposed sandy beaches as semi-closed ecosystems. Mar. Envt. Res. 4: 59-63

McLachlan, A., Dugan, J. E., Defeo, O., Ansell, A. D., Hubbard, D. M., Jaramillo, E. \& Penchaszadeh, P. E. 1996 Beach clam fisheries. Oceanog. Mar. Biol. Ann. Rev. 34: 163-232

Miranda, L. E. \& Frese, W. 1991 Can fishery scientists predict angler preferences? American Fisheries Society Symposium 12: 375-379

Morvan, C. \& Ansell, A. D. 1988 Stereological methods applied to reproductive cycle of Tapes rhomboides. Mar. Biol. 97: 355-364

Murawski, S. A. \& Serchuk, F. M. 1989 Mechanical shellfish harvesting and its management: The offshore clam fishery of the eastern U.S. In Marine Invertebrate Fisheries: Their Assessment and Management. (ed. J. F. Caddy), pp. 479-95 Wiley \& Sons. New York

Murray-Jones, S. E. 1998 Conservation and management in variable environments: The surf clam, Donax deltoides. PhD Thesis. Biological Sciences. pp. 254. University of Wollongong. Wollongong

Murray-Jones, S. E. \& Ayre, D. J. 1997 High levels of gene flow in the surf bivalve, Donax deltoides (Bivalvia: Donacidae) on the east coast of Australia. Mar. Biol. 128: 83-89

Nakaoka, M. 1994 Size-dependent reproductive traits of Yoldia notabilis (Bivalvia: Protobranchia). Mar. Ecol. Prog. Ser. 114: 129-137

Neuberger-Cywick, L., Achituv, Y. \& Mizrahi, L. 1990 The ecology of Donax trunculus Linnaeus and $D$. semistriatus Poli from the Mediterranean coast of Israel. J. Exp. Mar. Biol. Ecol. 134: 203-220

Newell, R. I. E., Hilbish, T. J., Koehn, R. K. \& Newell, C. J. 1982 Temporal variation in the reproductive cycle of Mytilus edulis L. (Bivalvia, Mytilidae) from localities on the east coast of the United States. 162: 299-310

PA Management Consultants. 1984 National survey of participation in recreational fishing. . Melbourne

Pauly, D. 1983 Length-converted catch curves: a powerful tool for fisheries research in the tropics (Part 1). Fishbyte 1: 9-13

Peterson, C. H. \& Beal, B. F. 1989 Bivalve growth and higher order interactions: Importance of density, site and time. Ecology 70: 1390-1404

Peterson, C. H. \& Black, R. 1987 Resource depletion by active suspension feeders on tidal flats: Influence of local density and tidal elevation. Limol. Ocean. 32: 143-166

Peterson, C. H. \& Black, R. 1993 Experimental tests of the advantages and disadvantages of high density for two coexisting cockles in a Southern Ocean lagoon. J. Anim. Ecol. 62: 614633

Pollock, K. H., Hoenig, J. M., Jones, C. M., Robson, D. S. \& Greene, C. J. 1997 Catch rate estimation for roving and access point surveys. N. Am. J. Fish. Management 17: 11-19

Pollock, K. H., Jones, C. M. \& Brown, T. L. 1994 Angler survey methods and their applications in fisheries management. American Fisheries Society, Special Publication 25. Bethesda, Maryland

Rhoads, D. C. \& Lutz, R. A. (ed.) 1980 Skeletal Growth of Aquatic Organisms: Biological Records of Environmental Change. Plenum Press. NY
Lond.
Sainsbury, K. \& Polacheck, T. 1994 The use of biological reference points for defining recruitment overfishing, with an application to southern bluefin tuna. In Population dynamics
for fisheries management, Australian Soc. for Fish Biology Workshop Proceedings. (ed. D. A. Hancock), pp. 265-274. Australian Soc. for Fish Biology Perth

Sastre, M. P. 1984 Relationships between environmental factors and Donax denticulatus populations in Puerto Rico. Est. Coast. Shelf Sci. 19: 217-230

Sastry, A. N. 1966 Temperature effects in reproduction of the bay scallop, Aequipecten irradians Lamarck. 130: 118-134

Sastry, A. N. 1979 Pelecypoda (excluding Ostreidae). In Reproduction of marine invertebrates. (ed. A. C. Giese \& J. S. Pearse), pp. 113-292 Academic Press. NY

Schnute, J. \& Fournier, D. 1981 A new approach to length-frequency analysis: Growth structure. Can. J. Fish. Aquat. Sci. 37: 1137-1351

Schoeman, D. 1996 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

Stearns, S. C. 1976 Life-History tactics: A review of the ideas. Quart. Rev. Biol. 51: 3-47
Steffe, A. S., Staines, J. F. \& Murphy, J. 1994 Recreational use of fisheries resources in northern NSW. NSW Fisheries Research Institute. Sydney

Strathmann, M. F. 1987 ()Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press. Washington

Strathmann, R. R. 1980 Why does a larva swim so long? Palaeobiology 6: 373-376
Sundet, J. H. \& Lee, J. B. 1984 Seasonal variations in gamete development in the Icelandic Scallop, Chlamys islandica. J. Mar. Biol. Assoc. U.K. 64: 411-416

Szarzi, N. J., Quinn, T. J. I. \& McBride, D. N. 1995 Assessment of shallow-water clam resources: case study of razor clams, eastern Cook Inlet, Alaska. ICES Mar. Sci. Symp. 199: 274-286

Talbot, M. M. B. \& Bate, G. C. 1987 Rip current characteristics and their role in the exchange of water and surf diatoms between the surf zone and nearshore. Est. Coast. Shelf Sci. 25: 707720

Thompson, R. J. 1979 Fecundity and reproductive effort in the blue mussel (Mytilus edulis), the sea urchin (Strongylocentrotus drobachiensis), and the snow crab (Chionoecetes opilo) from populations in Nova Scotia and Newfoundland. J. Fish. Res. Bd. Can. 36: 955-964

Thorson, G. 1950 Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25: 1-45

Underwood, E. E. 1970 Quantitative Stereology. Metallurgy and Materials. Reading, Mass.
Wade, B. A. 1967a Studies on the biology of the West Indian beach clam, Donax denticulatus Linné. I. Ecology. Bull. Mar. Sci. 17: 149-174

Wade, B. A. 1968 Studies on the biology of the West Indian beach clam, Donax denticulatus Linné. II. Life history. Bull. Mar. Sci. 18: 876-901

West, R. J. \& Gordon, G. N. G. 1994 Commercial and recreational harvest of fish from two Australian coastal rivers. Aust. J. Mar. Freshwat. Res. 45: 1259-1279

Wilbur, K. M. \& Owen, G. 1983 Growth. In The Mollusca Vol IV Physiology. (ed. K. M. Wilbur \& A. S. M. Saleuddin), pp. 211-231 Academic press. New York

Williams, M. A. 1977 Pt II Quantitative methods in biology. In Practical Methods in Electron Microscopy. (ed. A. M. Glauert), pp. 1-234 North Holland Pub. Co. Amsterdam, NY, Oxford

Young, P. C. 1990 Ageing of scallops. In The measurement of age and growth in fish and shellfish. Proceedings \#12. Aust. Soc. for Fish Biology Workshop. (ed. D. A. Hancock), pp. 9395 Dept. Primary Industries \& Energy. Lorne, Victoria

Zar, J. H. 1984 Biostatistical Analysis. Prentice-Hall International, Inc.

## Appendix 1: Intellectual property

There will be no patents arising from this research, and all results will be published in the public domain literature and as a PhD Thesis.

## Appendix 2: Staff and Acknowledgments

The only person directly employed on this project was the principle investigator. However many people contributed to this project. Firstly I would like to thank my supervisors, David Ayre and Andy Davis for their help and advice. I am particularly indebted to Neil Andrew (formerly of the NSW Fisheries Research Institute (FRI), Cronulla). Many people helped with the job of sieving sand -thanks to Ed Chambers, Michelle Crowder, Andy Davis; Carla Ganassin, Ian Murray-Jones, Chris Outteridge, Trish Shannon, Jenny Tyler, Ross Vickers, Valèrie Villière, David, Pat, Terry, Jane, and the 1994 Population Ecology class from Wollongong University.

I would particularly like to thank Allan Holloway and Margaret Hood of the Mid-North Coast Amateur Deep Sea Fishing Association and John Prosser of the NSW Fishing Clubs Association. Thanks also to Justine Cox, Carl Gosper, Sue Fyfe, and Ross Vickers for help with the tagging phase. Aldo Steffe and Jeff Gordon of the FRI helped with the harvesting survey design. Also thanks to Dennis Read, Bruce Pease, and Doug Ferrell from the FRI. Maria Byrne of The University of Sydney helped with identification of various reproductive stages. Christy Patterson of the NSW Fisheries Brackish Water Field Station placed trays of pipis in the field.

From the University of Wollongong, Ken Russell worked out the novel method for estimating variances around oocyte diameters reconstructed from profile sections. Thanks also to staff at the Newcastle Commercial Fishermen's Cooperative Ltd (in particular Des Dye, Bill Pearce, Mark and Peter); Wayne Curry of NSW Fisheries for escorting me through the Fish Markets (at 3.30 am ); Brett Ryan, Fisheries Officer from Nelson Bay, for information; Sam Gordon from the Master Fish Merchant's Association for information on grading and selling pipis; Nick Patton and Joshua Jusef from the Fish Markets Data Base for supplying data in useable form; and Samantha Dawes at FRI for Catch Data Base information.

I could not have done the commercial harvesting survey without the support of the commercial fishers who gave me information and filled in log sheets. Particularly worthy of note were Bruce Heynatz and Alfie Patane, who weren't collecting from Stockton at the time but gave vast amounts of information, as well as Eric Glenn, Tony Mellows, and Douglas Cupit.

## Appendix 3

Size frequency histograms of length of Donax deltoides at (a) Seven Mile Beach, and Stockton Beach at (b) 3 km and (c) 6 km from the north headland. Data from collections made using downshore transects using a $0.03 \mathrm{~m}^{2}$ corer and sieving through a 3 mm mesh, and lengths grouped into 5 mm size classes.
a. Seven Mile Beach

a. Seven Mile Beach continued

b. Stockton Beach, 3 km site

c. Stockton Beach, 6 km from Birubi Point


