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Links between seagrass habitats, piscivorous fishes and their fish prey

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Title

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1999/215 Links between seagrass habitats, piscivorous fishes and their fish prey

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Objectives:

1. Quantify the contribution of fishes, which may or may not be economically valuable, within seagrass beds to the dietary composition of piscivorous fish, some of which e.g. Yank flathead (*Platycephalus speculator*), Rock flathead (*Platycephalus laevigatus*) and Australian Salmon (*Arripis* sp.) form commercially valuable fisheries.
2. Identify how piscivorous fish influence the abundance of juvenile fish within seagrass beds, some of which, e.g. the King George whiting, form valuable commercial and recreational fisheries.
3. Describe and quantify, using carbon and nitrogen isotope analysis, the strength of links between seagrass beds, juvenile fish inhabitants and their fish predators.

Non Technical Summary

Outcomes Achieved

This project has increased our understanding of the importance of seagrass habitats to larger, commercially valuable, species of fish by combining experimental and correlative scientific principles. We found that many small fish use seagrass habitats for nutrition and to avoid predation by large predatory fish. Some of these small fish also form important parts of the diets of commercially important species, such as Australian Salmon. The importance of predatory fish varied, however, from site to site, suggesting that seagrass habitats may need to be evaluated individually. The primary outcomes of this study will be important in identifying seagrass habitats that are especially valuable as feeding and nursery sites for commercially valuable fish in Port Phillip Bay. The type of information presented in this study will help understand how and why various nearshore marine habitats may be used by various species of fish, and how best to ensure their protection and future sustainability.

The importance of predation by fish in determining the population structure of juvenile King George whiting (Sillaginidae: *Sillaginodes punctata*, Cuvier) was examined at multiple locations in Port Phillip Bay, Australia, by manipulating the abundance of piscivorous fish in unvegetated sand and seagrass habitats using exclusion cages. Additional information regarding the local abundances of, and habitat use by, a transient predatory fish, Western Australian salmon (Arripidae: *Arripis truttacea*, Cuvier) was attained using netting surveys and underwater video. *S. punctata* were generally more abundant inside exclusion cages over unvegetated sand than partial cages or uncaged areas, which contained similar numbers of fish. In seagrass, however, there was generally no effect of excluding predatory fish; uncaged, partially caged and fully caged areas of seagrass contained similar numbers of *S. punctata.* While the patterns in cage use for each habitat were consistent between sites, the relative difference in the abundance of *S. punctata* between habitats was site specific. Abundances of *S. punctata* also varied inconsistently between sites through time. Juvenile *A. truttacea* were most abundant at Blairgowrie and their abundances did not vary between Kilgour and Grand Scenic, where they were generally low. Captured *A. truttacea* consumed a variety of epibenthic fishes including atherinids, clupeids, gobiids, syngnathids and pleuronectids. At Blairgowrie, *A. truttacea* occurred more commonly in patches of unvegetated sand than seagrass, and over unvegetated sand, the abundance of *A. truttacea* varied little between partial cages and uncaged areas. The importance of predation by fish in determining abundances of juvenile *S. punctata* within and amongst locations is discussed in relation to habitat complexity, the provision of artificial structure and the local abundances of predatory fish.

The temporal (between seasons) variability in abundances and isotopic compositions of predatory fish and their teleost prey were measured in seagrass beds at two locations in Port Phillip Bay, Australia. Samples of tissue from predatory fish and their teleost prey, as well as sediment and seagrass, were analysed for $\delta^{13}C$ and $\delta^{15}N$, and dietary analyses were undertaken on predatory fish. The assemblage structure of predatory fish and small fish depended strongly on the site from which they were sampled, but varied little between seasons. Regardless of species, predatory fishes were generally more abundant at St Leonards than

Grand Scenic, but varied little between months or seasons. Western Australian salmon, and Pike-headed hardyhead (Atherinidae: *Kestratherina esox,* Klunzinger) were the numerically dominant large fishes at St Leonards and Grand Scenic. The numbers of *A. truttacea* did not vary significantly between seasons at Grand Scenic, where overall, their abundances were low, but at St Leonards, abundances of *A. truttacea* were higher during autumn and winter than spring and summer. Small fish were more abundant at Grand Scenic than St Leonards, and this pattern was mirrored by abundances of atherinids, but syngnathids did not vary between sites. The stomachs from 11 species of large fish contained fish remains. Non-fish stomach contents of large fishes included benthic and pelagic crustaceans, cephalopods, polychaetes, gastropods, plant material and terrestrial insects. *Arripis truttacea* and *Kestratherina esox* were the most abundant piscivores, and they consumed both benthic and epibenthic fish prey. Stomachs of *A. truttacea* from Grand Scenic contained a higher proportion of fish than those from St Leonards. The amount of fish in the guts of *A. truttacea* at St Leonards did not appear to vary in any discernible way between months. The amount of fish in guts of *K. esox* at Grand Scenic increased monthly between late summer and early autumn, and decreased during winter and spring. Stable isotope analyses separated environment and fish samples into four general categories which were relatively consistent between sites and through time: 1) seagrass, *Heterozostera tasmanica,* 2) sediment and algae, 3) fishes eating mainly benthic invertebrates, 4) fishes eating mainly pelagic invertebrates and other fishes. Stable isotope analyses appeared to differentiate fish and habitat samples according to the sites but not the seasons in which they were sampled. Values of δ^{15}N and δ^{13}C in seagrass (*Heterozostera tasmanica*) and sediments were often higher and more negative respectively at St Leonards compared with Grand Scenic. Piscivorous fishes generally had greater δ^{15}N (>11 ‰) and lower δ^{13}C (< -15 ‰) than fishes that consumed mainly crustaceans, although these differences were location specific. Fishes that consumed mainly invertebrates had δ^{15}N and δ^{13}C values between 6 and 12 ‰, and -5 and -17 ‰ respectively. Higher trophic level in fishes appeared to coincide with a change in the base of nutritional support from seagrass to plankton. Our results suggest that predatory fishes associated with seagrasses habitats potentially impact on abundances of juvenile fishes, and seagrass beds are both a source of nutrition and an area of refuge for smaller prey fish. However, the strength and nature of this link may vary with the location.

KEYWORDS: seagrass, isotope analysis, piscivory, fish, diet analysis

2. Background

Seagrass beds are widely acknowledged as valuable nursery habitats for early post-settlement and juvenile fish, many of which form commercially valuable fisheries (Jenkins *et al.*, 1997a, Jenkins *et al.*, 1993). However, there is some debate as to why seagrass beds are important. The provision of refuge from predation (Orth *et al.*, 1984, Summerson and Peterson, 1984), the mediation of physical disturbance (Bell and Pollard, 1989, Pollard, 1984) and greater food availability (Heck and Weinstein, 1989, Bell and Westoby, 1986) dominate contemporary theories as to why seagrass beds are beneficial to the settlement and survival of early post-settlement and juvenile fishes. Understanding the links between seagrass and feeding, protection from predators and amelioration of physical disturbance is important for increasing our capacity to predict the effects of changes in seagrass extent on commercial fish (Connolly *et al.*, 1999).

Previous studies have evaluated the importance of larval supply and broad-scale hydrodynamic features in structuring fish assemblages amongst seagrass beds within Port Phillip Bay (Jenkins *et al.*, 1997b, Jenkins and Black, 1994). Hydrodynamic models, in which pre-settlement pelagic fish larvae were modelled as passive particles explained more than 66% of the broad-scale, amongst sites, variability in recruitment patterns (Jenkins *et al.*, 1997b).

Epifauna, which are more diverse and abundant within seagrass beds compared to other habitats (Edgar and Robertson, 1992, Edgar, 1990, Bell and Westoby, 1986), are an important food source for early post-settlement and juvenile fish (Bell and Pollard, 1989, Robertson, 1980). Subsequently, larval fish are more likely to settle and survive in habitats such as seagrass which have the greatest levels of food. The role of food in the facilitating settlement and survival of young fish with seagrass beds in Port Phillip bay is currently being investigated. Research is evaluating how broad-scale, amongst sites, differences in food availability influences recruitment patterns in post-settlement stage King George Whiting (*Sillaginodes punctata*) (Jenkins *et al.*, current research).

It is also likely that predation by fish, and the mediation of this predation by structural characteristics of seagrass beds, generates variability in the abundance and diversity of juvenile fishes amongst and within seagrass beds in Port Phillip Bay.

Seagrass beds harbour a diverse assemblage of predatory fishes, many of which are piscivorous, consuming fish (Edgar and Shaw, 1995, Hettler, 1989, Burchmore *et al.*, 1984, Orth *et al.*, 1984, Klumpp and Nichols, 1983, Robertson, 1982). Piscivory by fish is important in structuring fish assemblages on tropical and temperate reefs, and sandy beaches (Connell, 1996, Gibson and Robb, 1996, Choat, 1982), however there is a paucity of data regarding the role of piscivory in structuring fish assemblages within seagrass beds. Most research into food habits of piscivorous fish within seagrass beds has been conducted in similar, localised (Connolly *et al.*, 1999), regions (Edgar and Shaw, 1995, Robertson, 1982). More research is needed to determine the role of piscivory by fish in structuring fish assemblages within seagrass habitats in other locations (Connolly *et al.*, in 1999). These studies should evaluate the importance of juvenile fishes in the diets of piscivorous fishes and quantify the strength of links between seagrass beds, and the fishes, many of which form commercially and recreationally valuable fisheries, which inhabit them.

Recent research within seagrass beds, *Heterozostera tasmanica*, in Port Phillip Bay (J. Hindell, University of Melbourne, Ph.D. Project) has found that broad-scale, amongst sites, spatial patterns in the abundance of early post-settlement and juvenile fish corresponds inversely with the abundance of piscivorous fishes, particularly Australian Salmon (*Arripis* sp.). Dietary analysis identified eight piscivorous species of fish; rock flathead (*Platycephalus laevigatus*), yank flathead (*Platycephalus speculator*), Australian salmon (*Arripis* sp.), pike-headed hardy head (*Kestratherina esox*), Tommy Ruff (*Arripis georgiana*), southern crested weedfish (*Cristiceps australis*), long-nose weedfish (*Heteroclinus tristis*) and the stargazer (*Kathetostoma laeve*). The Australian salmon and the flathead species currently contribute substantially to Fisheries in SE Australia (Kailola *et al.*, 1993). These piscivorous species consumed larvae and juveniles from seven families of fish. This represented 47 % of the total fish families within seagrass beds, and included juveniles of important commercial species such as King George whiting (*Sillaginodes punctata*), and greenback flounder (*Rhombosolea tapirina*) (Kailola *et al.*, 1993).

Experimental manipulation of predator densities using cages to enclose or exclude predators is a powerful way to examine the importance of particular species in structuring marine communities (Hall *et al.*, 1990). Where caging experiments are carefully planned to elucidate artefacts which may confound the interpretation of treatment effects (Connell, 1997), field experiments are the least equivocal way of assessing the importance of fish predation in marine systems (Hall *et al.*, 1990). Indeed, these types of manipulative experiments remain the only valid test of hypotheses pertaining to the role of predation in structuring marine fish assemblages (Hall *et al.*, 1990).

Preliminary experiments, using exclusion cages, are currently being trialed to assess their effectiveness in elucidating fine- (within bed) and broad- (amongst beds) scale patterns in the effects of piscivory by fish on juvenile fish abundance and diversity within seagrass. The experimental caging component of this project builds on preliminary caging experiments (J. Hindell. pers. comm.), and compliments previous and present research (Jenkins *et al.*, 1997b, Jenkins and Wheatley, 1998), providing a holistic view of the importance of seagrass beds as habitats for temperate marine fishes and their predators. More precisely, this aspect of the project addresses a need for small scale manipulative experiments conducted over large enough spatial scales such that we can make generalisations about the nature of the links between seagrass habitats and the processes which shape fish assemblages within them (Connolly *et al.*, 1999).

A comprehensive understanding about the strength of links between seagrass, prey fish and their fish predators can only be achieved by combining manipulative experimentation with descriptive studies.

Observational techniques are one of the most commonly employed methods of determining the importance of different prey types in the diets of predators (Rau *et al.*, 1992). However, results from studies which depend solely on stomach content analyses, based on an instant in time, are susceptible to the limitations of both temporal and spatial scaling (Hobson and Welch, 1992). The accuracy with which the strength in links between habitats and inhabitants can be measured is limited. Conversely, descriptive measurement of the abundance's of naturally occurring isotopes of carbon and nitrogen are useful in elucidating feeding relationships in a variety of marine settings (Rau *et al.*, 1992) and provide accurate quantitative trophic level information in marine food webs (Harrigan *et al.*, 1989, Hobson and Welch, 1992). The utility of such measurements for marine food web studies lies in the fact that stable carbon and nitrogen in animals are largely determined by the isotope abundance in the animals food (Rau *et al.*, 1992, Nichols *et al.*, 1985). Therefore, measurement of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in animal biomass is advantageous over stomach content analysis because the trophic level information is based on assimilated, not just ingested foods, and trophic positions therefore represent long-term averages (Rau *et al.*, 1992, Hobson and Welch, 1992).

Despite the identification of apparent associations between fishes and seagrass, the dependence of fishes on seagrass is difficult to establish (Harrigan *et al.*, 1989). Several studies have identified an association between fishes, their prey and seagrass habitats (Klumpp, 1982, Edgar and Shaw, 1992), however these studies are based on dietary analysis only. Stable isotope studies have been used to describe the strength in links between invertebrates and seagrass (Boon *et al.*, 1997, Loneragan *et al.* 1997), however very little research has established dependence by attempting to identify the links between seagrass beds and the fishes which utilise them using isotope analysis (Nichols *et al.*, 1985). This project provides a quantitative and qualitative estimate of the dependence of predatory fish on seagrass and seagrass associated fish assemblages through dietary and isotope studies, thereby filling a gap in our understanding (Connolly *et al.*, 1999). Connolly *et al.* (1999) suggested that "further dietary and isotope studies of piscivorous fish are required".

3. Need

The FRDC recently commissioned a review of the importance of seagrass habitats to fisheries sustainability in which Connolly *et al.* (1999) identified the “gaps in our understanding and future research needs” and made “recommendations for future research”.

Connolly *et al.* (1999) suggest that the nature of the links between fish and processes such as “feeding, protection from predators and amelioration of physical disturbance” within seagrass habitats are “poorly known”. “Hard data on links between seagrass and fishery species are needed urgently”. Connolly *et al.* (1999) identify a need for “small scale manipulative experiments”, “conducted over a large enough spatial scale” so that we can increase our capacity “to predict the effects of changes in seagrass extent on commercial fish”. It is important to understand the “processes linking seagrass with fish” in order to be “able to predict the effects of seagrass changes on fisheries”(Connolly *et al.*, 1999).

Connolly *et al.* (1999) also suggest that “dietary and isotope studies of piscivorous fish are required” because the role of small, non-commercial species in food chains for commercial species is only known in localised areas”. Isotope studies will address the need for research which compares the ecology (e.g. extent of assimilation of food from seagrass beds) of fishery species that spend all or only a part of their life associated with seagrass (Connolly *et al.*, 1999).

Cappo et al (1998) reiterate Connolly *et al.* (1999) in suggesting that information is needed about the role of predation in structuring fish assemblages within seagrass beds. “There is a surprising lack of basic life-history information for most of the major fishery species in Australia”, and “consequently a paucity of information on ‘critical’ habitat requirements and processes such as post-recruitment mortality”.

4. Objectives

4. Quantify the contribution of fishes, which may or may not be economically valuable, within seagrass beds to the dietary composition of piscivorous fish, some of which e.g. Yank flathead (*Platycephalus speculator*), Rock flathead (*Platycephalus laevigatus*) and Australian Salmon (*Arripis* sp.) form commercially valuable fisheries.
5. Identify how piscivorous fish influence the abundance of juvenile fish within seagrass beds, some of which, e.g. the King George whiting, form valuable commercial and recreational fisheries.
6. Describe and quantify, using carbon and nitrogen isotope analysis, the strength of links between seagrass beds, juvenile fish inhabitants and their fish predators.

5. Methods

5.1. Study Sites

The caging experiments and predator surveys were carried out at three sites in Port Phillip Bay: Blairgowrie, Grand Scenic and Kilgour (Fig. 1). Surveys of fish abundances were carried out at St Leonards and Grand Scenic (Fig. 1). Port Phillip Bay is a large, semi-enclosed embayment that is joined to Bass Strait bay a narrow rocky entrance (Fig. 1). At each site there are large contiguous beds of *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog, which are interspersed with patches of unvegetated sand and rocky reef in shallow (<3 m) water close to the shoreline. These beds of seagrass become progressively more extensive further inside Port Phillip Bay, probably as a function of reduced disturbance regimes. Historically, the locations in this study contain different assemblages of fish (Jenkins *et al.* 1993, Jenkins and Wheatley 1998), and this is also thought to be related to variable disturbance regimes as well as larval supply (Jenkins *et al.* 1997a). The currents around Grand Scenic and Kilgour are weak ($\approx$10 cm s^{-1}), but currents in the vicinity of Blairgowrie may reach 100-200 cm s^{-1} (the range of current velocities in the channel proximal to this study site), depending on the local wind direction (Black *et al.* 1993). The substrates at each site strongly reflect these exposure regimes, with fine silty clays at Grand Scenic and well sorted 'gravely' sand at Blairgowrie (Anon. 1973). All of these sites have a northerly orientation and are protected from the prevailing southwesterly winds. Currents in the vicinity of St Leonards are generally stronger ($\approx$ 0.5 m s^{-1}) (Black *et al.* 1993) and the sediments are a gravely sand with low amounts of organic material (Anon. 1973). Tides throughout Port Phillip Bay are semidiurnal with a range of less than 1 m. Jenkins and Wheatley (1998) have shown that despite the variation in assemblage structure of fishes between sites, relatively high, but inter-annually variable, numbers of *Sillaginodes punctata* settle to all sites during spring.

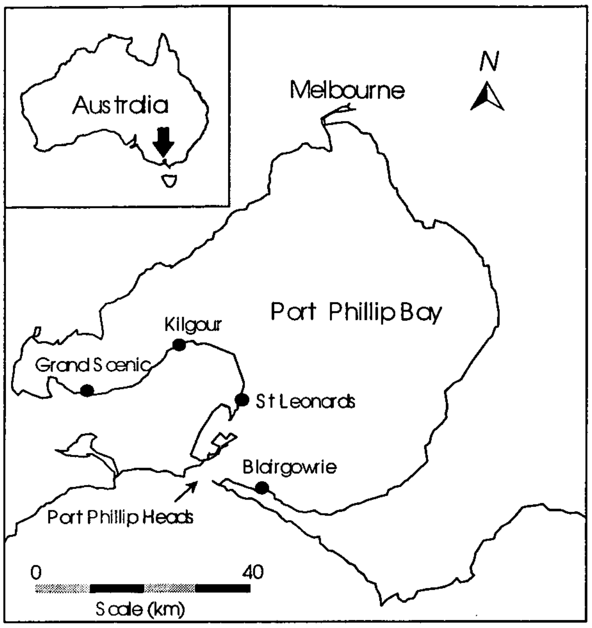

Figure 1. Locations of study sites in Port Phillip Bay. Inset: Location of Port Phillip Bay within Australia.

5.2. Experimental assessment of predation impacts

5.2.1. Design of exclusion cages and cage controls

To assess whether a) predatory fish alter abundances of *Sillaginodes punctata*, and b) seagrass alters the influence of fish predation compared with unvegetated sand, piscivorous fishes, primarily juvenile *Arripis truttacea*, were excluded from 16 m^2 (4 × 4 m) patches of unvegetated sand and seagrass at each site using cages during spring, 1999. Predatory fish that occur in beds of seagrass along the Victorian coast are well described (Robertson 1984, Edgar and Shaw 1995, Hindell *et al.* 2000). *Arripis truttacea* is a perennially abundant predatory fish in Port Phillip Bay and consumes juvenile fishes associated with seagrass (Robertson 1982, Hindell *et al.* 2000). Other predatory fishes include Pike-headed hardyheads, *Kestratherina esox* (Atherinidae) Klunzinger, *Arripis truttacea*, Yank flathead (*Platycephalus speculator*) Klunzinger, and Rock flathead (*Platycephalus laevigatus*) Cuvier, but *A. truttacea* was the most abundant predatory fish across all three sites in this study.

Each exclusion cage was constructed from four steel stakes hammered into the substrate at each corner of a 4 × 4 m square plot. Around this, a 16 m length of black polypropylene netting, 1.5 m high with a mesh size of 15 mm, was attached (Fig. 2 a). The top of each cage was not enclosed with mesh, but the height of the cage (1.5 m) precluded the cage from being submerged even during spring high tides and thus prevented predatory fish entering the cage. To prevent predatory fish swimming between the substrate and the cage walls, the bottom of each mesh wall was weighted using a 3 m length of steel rod (10 mm diameter). Cage controls were built from exactly the same materials, and in the same dimensions, as exclusion cages. But, to allow predatory fish access to the interior of cage controls while controlling for any effect of cage structure, the top or bottom half of each wall was filled-in alternatively around the four sides (Fig. 2 b). Uncaged areas were simply 16 m^2 plots without cage structure.

At each site, 4 replicates of each cage treatment (exclusion cage, cage control and uncaged) were applied to haphazardly chosen plots of unvegetated sand and seagrass. All cages were constructed at all sites within 8 days and left for one week prior to sampling juvenile fish.

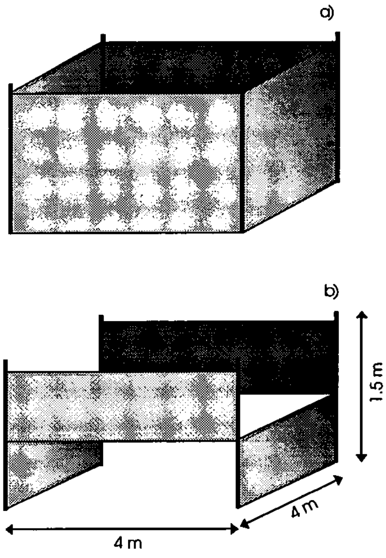

Figure 2. Design of a) exclusion cage used to exclude predatory fish from areas of seagrass and unvegetated sand, and b) partial cage used to assess artefacts associated with the structure of the cage *per se*.

5.2.2. Sampling of Sillaginodes punctata

Juvenile *Sillaginodes punctata* within a particular site were sampled on the same day during low tide. The remaining sites were sampled on consecutive days within the same week. This sampling protocol was repeated weekly for four consecutive weeks.

Sillaginodes punctata in each caging treatment were sampled using a large dip net, 4 m wide × 1.5 m high × 1.5 m deep, with 0.5 mm black mesh. The net was attached to a solid (4 × 1.5 m) rectangular frame made from 20 mm PVC pipe. The net was placed inside, and at one end, of the 16 m^2 area, and hauled through to the opposite end by two people, where it was lifted from the water and returned to a boat so that the fish could be removed. Captured fish were anaesthetised in Benzocaine and preserved in ethanol. Pilot studies showed that >90 % of the *S. punctata* in a plot were caught on the first haul, therefore only one haul was conducted per plot on any given sampling occasion, and visual estimates of netting effectiveness showed that *S. punctata* rarely avoided capture by swimming outside the sampling area (J. Hindell pers. obs.). In the laboratory, the standard length (SL), the length in mm from the tip of the snout to the posterior end of the caudal peduncle, of all fish was measured and fish were counted.

5.2.3. Sampling of predatory fish

Abundances of *Arripis truttacea*, as well as any other predatory fishes in the vicinity, were measured using a beach seine net, 100 m long × 2 m high with 20 mm mesh in the wings and 15 mm mesh in the bag and middle, with 50 m long hauling ropes attached to each end, during spring 1999. The seine net was set parallel to the shoreline, 50 m offshore and was hauled directly onto the beach. Three replicate 'shots' of the seine net were conducted in haphazardly selected areas on two separate occasions at each site. All *A. truttacea* were retained for dietary analysis. In the laboratory the SL of each *A. truttacea* was measured, and their stomachs, not including intestines, were excised and preserved in ethanol.

5.2.4. Dietary analysis of predatory fish

The stomach contents of each *A. truttacea* were identified, and individual dietary items were counted, and their categories weighed. The importance of a dietary component can vary with its weight, abundance and frequency of occurrence (Hyslop 1980), therefore the percentage of these parameters was calculated for each dietary item found and expressed as;

$$N = N_s / N_t \times 100,$$

where N is the percentage number, N_s is the number of individuals of a prey category or species, and N_t is the total number of prey individuals;

$$M = M_s / M_t \times 100,$$

where M is the percentage mass, M_s is the total mass of a prey category or species, and M_t is the total mass of prey; and

$$F = F_s / F_t \times 100,$$

where F is the percentage frequency occurrence, F_s is the number of stomachs containing a prey category or species, and F_t is the total number of stomachs, including empty ones (Hyslop 1980).

5.2.5. Underwater observations of Arripis truttacea

Sony standard 8 mm Handycam video recorders, enclosed in underwater housings, were used to measure the variability in abundances of *Arripis truttacea* between cage treatments and habitats (unvegetated sand and seagrass). In either unvegetated sand or seagrass, depending on what was randomly chosen, a single replicate of each caging treatment (as in exclusion experiment) was set-up. A single video camera was placed inside each cage treatment, and the videos were linked using Cameratalk software, JK instruments Ltd, which enables the user to pre-program recording regimes. Videos were set to simultaneously begin recording 3 hr before mean high water, and to record the first 10 minutes of each half hour time interval for 6 hr so that they 'captured' the movement of fish during flood and ebb tides. This procedure was replicated twice in each habitat only at Blairgowrie. Video analysis was conducted over the same period as the predator survey. After all sites had been videoed, the numbers of *A. truttacea* observed in each combination of habitat and cage were counted.

5.3. Evaluating links between fish and seagrass using isotope analyses and measures of abundance

Sampling was conducted at St. Leonards and Grand Scenic over twelve months between October 1998 and October 1999.

5.3.1. Sampling predatory fishes

On two randomly chosen days each month, for twelve consecutive months, predatory fishes were sampled diurnally at each site, on the same day within 3 hours each side of mean high water. Predatory fish were caught using a beach seine-net (60 m long × 3 m high, and 15 mm mesh). The net was set 50 m offshore and parallel to the shoreline over the bow of a small boat, and hauled onto the shore. Fish were preserved on ice until they could be frozen (-80°C) at the Queenscliff Marine Station.

5.3.2. Sampling small fishes

On a randomly chosen day each month for 12 consecutive months, small fishes (either juveniles or adults <15 cm total length) at each location were sampled at low tide on the same day using a beach seine net (10 m wide × 2 m deep × 1 mm mesh). The steps undertaken in setting and retrieving this net are described by Jenkins and his colleagues (Jenkins *et al.* 1997a). An overdose of benzocaine was used to kill small fish, and they were stored on ice until they were returned to the Queenscliff Marine Station and preserved by freezing (-80°C).

5.3.3. Collection of habitat samples

On three randomly chosen replicate days each season (spring, summer, autumn and winter), at each site, three haphazardly selected samples of *Heterozostera tasmanica* were taken. Each sample of seagrass was taken by removing ≈ 30 fronds just above the sediment. The samples of seagrass often contained fronds of algae, samples of which were also analysed. Sediment samples were collected at each site on 3 randomly selected days during summer and winter. On each day, 500 ml of sand was collected subtidally from unvegetated patches within the seagrass matrix. All samples were stored on ice to reduce biodegradation and preserved at the laboratory by freezing (-80°C). In subsequent analyses, samples of sediments and seagrass collected on replicate days were pooled prior to isotope analyses.

5.3.4. Dietary composition of predatory fishes

The dietary composition, % mass (*M*) and % abundance (*N*) of taxonomic categories of prey in the stomachs (excluding intestines), of predatory fish was described quantitatively. Where possible, teleost remains were identified to family. If the number of a single species of predatory fish in a sample exceeded 10, only stomachs from 10 haphazardly chosen fish were excised for stomach contents analyses.

5.3.5. Isotope analysis and sample preparation

Isotopic compositions of carbon and nitrogen are expressed in terms of δ, which are parts per thousand differences from a standard:

$$\delta X = [(R\text{sample}/R\text{standard})-1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N. The δ values, which are measures of the relative amounts of heavy isotopes, were measured in samples of sediment, seagrass, and in species of algae and fish.

Values of δ^{13}C and δ^{15}N vary between tissue types in fish (Sholto *et al.* 1991). However, Pinnegar and Pulunin (2000) have shown that values of δ^{13}C and δ^{15}N in white muscle tends to be less variable than other tissues, and therefore, muscle tissue from just ventral to the anterior end of the dorsal fin was used for isotope analysis. Where the small size of fish precluded such sampling of tissue, whole animals were used. Each tissue sample was washed in distilled water and dried to constant weight (24 hr at 40°C). The sample was then ground to a fine powder using a pestle and mortar, and between 1.5 – 2 mg was placed into a foil capsule for analysis.

The organic matter in sediment samples was elutriated off the sediment component and washed, first in distilled water, then in 5 % hydrochloric acid (to remove carbonates), then rinsed finally in distilled water. Organic material was dried to constant weight (24 hr at 40°C), ground, and up to 5 mg was placed in foil capsules. Samples of seagrass and algae were prepared in the same way as organic material, although frond and leaf were scraped clean of epibionts and epiphytes using a razor blade.

Prior to analysis, all samples were stored at -80°C to reduce the likelihood of decomposition. Analyses of stable isotopes were carried out at CSIRO Land and Water, Adelaide Laboratory, by Automated Nitrogen Carbon Analysis-Mass Spectrometry (ANCA-MS). Dried and finely ground samples were sealed into tin capsules and combusted, and the reaction products were separated by GC to give pulses of pure nitrogen and carbon dioxide for analysis of total N and C, and ^{15}N and ^{13}C isotopic contents by the mass spectrometer (20-20. Europa Scientific, Crewe, U.K.).

5.4. Statistical analysis

5.4.1. Univariate analysis

Assumptions of homogeneity of variance and normality were assessed by viewing box plots and plots of residuals. Non-normal data or data with heterogeneous variances were transformed ($\log_{10}$) and reassessed.

Variability in abundances of *Sillaginodes punctata* was analysed using a 4-factor repeated measures analysis of variance (ANOVA). Site, habitat and caging were treated as fixed factors, and each replicate was measured repeatedly over four consecutive times. The assumption of sphericity was assessed using the Greenhouse-Geisser (G-G) epsilon value (ε). G-G adjusted probability (P) values were used to reduce the potential for sphericity to influence our results, but where the adjusted P-value did not alter the significance of the un-adjusted P-value, the unadjusted P-value is presented. Variability in abundances of *Arripis truttacea*, both for netting and underwater video measures, were analysed using 2-factor partially nested analyses of variance in which site and day were treated as fixed and random factors respectively. Where interactions were found between main effects, separate one factor ANOVAs and *a-priori* planned comparisons were conducted for a main effect to determine where the levels of the interacting main effect varied. *A-priori* planned comparisons were used to determine how the levels of the cage effect varied. Initially we compared abundances of fish in uncaged areas to those associated with partial cages to assess for a cage effect. If there was no statistical difference (P=0.05), and therefore no cage effect, then the average of these was compared to exclusion cages. If however, abundances of fish varied significantly between partially and uncaged areas, abundances of fish in exclusion cages were compared to those inside partial cages to provide some measure of the importance of predation versus cage structure in determining abundances of fish. Tukey's tests were used to determine which sites differed. Low replication (n=1) in some habitat × cage treatments precluded a fully orthogonal analysis of the variability in sizes of *S. punctata* between sites, caging and habitats, and subsequently, we only compared variability in sizes of *S. punctata* between a) exclusion cages in unvegetated sand and seagrass, cage controls and uncaged areas in seagrass separately at Blairgowrie and Kilgour, and between exclusion cages in seagrass and unvegetated sand at each of the three sites; all main effects were treated as fixed factors.

For the isotope and fish abundance analyses, data that failed to meet assumptions of normality and homogeneity of variances were transformed and reassessed. Variability in abundances of predatory and prey fishes was analysed using three-factor partially nested analyses of variance (ANOVAs). Season, site and month were treated as fixed factors, and month was nested within season. Replicate samples of predatory fish within each month enabled an additional term, site × month{season}, to be added to the model. Variability in $\delta^{15}N$ and $\delta^{13}C$ in the environment (seagrass, algae and sediment) and fish (large and small) samples was analysed using either one- or two-factor analyses of variance (ANOVAs). Site and season were treated as fixed factors. *A-posteriori* Tukey's tests were used to determine how the levels of a main effect differed. Where interactions were found between main effects, separate one-factor ANOVAs and *a-posteriori* Tukey's tests were conducted for each level of one main effect to determine where the levels of the second, interacting main effect varied. Regression analyses were used to measure the degree by which the isotopic measures varied with the size of fish.

All analyses were conducted using SYSTAT statistical software (Wilkinson *et al.* 1992).

5.4.2. Multivariate analyses

The relationships between sites and seasons, based on the frequencies of species of predatory and small fishes, were examined using linear, non-metric multidimensional scaling (nMDS). Similarity matrices on abundances of species of fish were constructed using the Bray-Curtis similarity coefficient. Data were $\sqrt{}^4$ transformed to reduce the influence of numerically dominant species. Two-dimensional ordinations were produced (Clarke 1993). Stress values less than 0.20 allowed interpretable nMDS patterns (see Anderson and

Underwood (1994) and Clarke (1993). Analysis of similarities (ANOSIM) was used to test whether sites varied significantly ($P<0.05$) in their assemblages of fish (Clarke 1993). Where the number of *a priori* tests exceeded the degrees of freedom (*df*) for the effect being tested, the significance level (α) was Bonferroni adjusted. All multivariate analyses were carried out using PRIMER v4.0 computer program (Carr and Clarke 1994).

6. Results

6.1. Experimental assessment of predation impacts

*6.1.1. Variability in abundances of King George whiting (*Sillaginodes punctata*) amongst predator treatments*

Sillaginodes punctata varied in a complex way between sites, habitats and caging treatments (Table 1).

Table 1. Three-factor repeated measures analysis of variance comparing the numbers of *Sillaginodes punctata* at each site (Blairgowrie, Kilgour and Grand Scenic) within each cage treatment (exclusion cage, cage control and uncaged) in each of seagrass and unvegetated sand habitats through time (n=288). Data were log(x+1) transformed prior to statistical analysis. Greenhouse-Geisser Epsilon value was 0.8322. *df* degrees of freedom. The table shows, for *S. punctata*, the probabilities (*P*) and MS associated with each of the terms in the model (SOURCE).

Between Subjects			
Source	*df*	MS	*P*
Site (S)	2	5.310	**<0.001**
Habitat (H)	1	4.285	**<0.001**
Cage (C)	2	1.364	**<0.001**
S × H	2	3.380	**<0.001**
S × C	4	0.210	**0.049**
H × C	2	1.298	**<0.001**
S × H × C	4	0.451	**0.001**
Error	54	0.082	
Within Subjects			
Time (T)	3	0.055	0.221
T × S	6	0.121	**0.005**
T × H	3	0.044	0.319
T × C	6	0.022	0.731
T × S × H	6	0.043	0.329
T × S × C	12	0.056	0.130
T × H × C	6	0.068	0.098
T × S × H × C	12	0.043	0.315
Error	162	0.037	

There was a significant 3-way interaction between sites, caging and habitats, pooling data across times (Table 1, Figs. 3 a-c). At Blairgowrie, while there was no effect of caging in seagrass ($df_{2,54}$, MS=0.084, *P*=0.826), caging strongly influenced the abundance of fish over unvegetated sand habitats ($df_{2,54}$, MS=2.279, *P*=0.008)(Fig. 3 a); the abundance of *S. punctata* did not vary between uncaged areas and partial cages ($df_{1,54}$, MS=0.004, P=0.926) but they were much more abundant inside exclusion cages than the average of cage controls and uncaged areas ($df_{1,54}$, MS=4.555, P=0.002)(Fig. 3 a). At Grand Scenic, more fish were associated with seagrass than unvegetated sand.

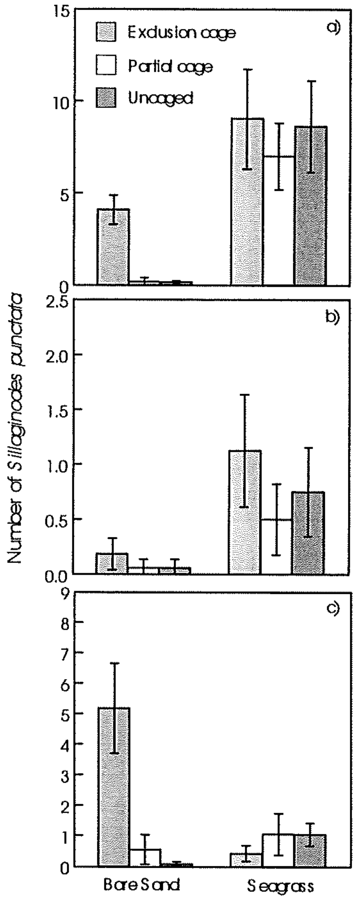

Figure 3. Mean abundance (±SE) of *Sillaginodes punctata* at a) Blairgowrie, b) Grand Scenic and c) Kilgour associated with exclusion cages, partial cages, and uncaged areas in seagrass and unvegetated sand habitats.

In seagrass, the abundance of *S. punctata* did not vary between cage treatments ($df_{2,54}$, MS=0.071, P=0.850)(Fig. 3 b). Despite a higher number of *S. punctata* in exclusion cages compared with cage controls or uncaged areas (Fig. 3 b), this pattern was not statistically significant in unvegetated sand at Grand Scenic ($df_{2,54}$, MS=0.006, P=0.986)(Fig. 3 b). The abundance of *S. punctata* at Kilgour varied greatly between habitats; more *S. punctata* occurred over unvegetated sand than seagrass (Fig. 3 c). In seagrass at Kilgour there was no difference in the abundance of *S. punctata* between cage treatments ($df_{2,54}$, MS=0.132, P=0.739)(Fig. 3 c), but there was a strong caging effect in unvegetated sand ($df_{2,54}$, MS=2.707, P=0.004). Partial cages over unvegetated sand contained similar numbers of fish to uncaged areas ($df_{1,54}$, MS=0.131, P=0.586). Exclusion cages over unvegetated sand at Kilgour (Fig. 3 b) contained significantly more fish than the average of partial cages and uncaged areas ($df_{1,54}$, MS=5.283, P=0.001)(Fig. 3 c).

There was also an interaction between site and time (Table 1), which did not follow any particular pattern, and the rank order of site was always the same, with most fish at Blairgowrie followed by Kilgour and Grand Scenic (Fig. 4).

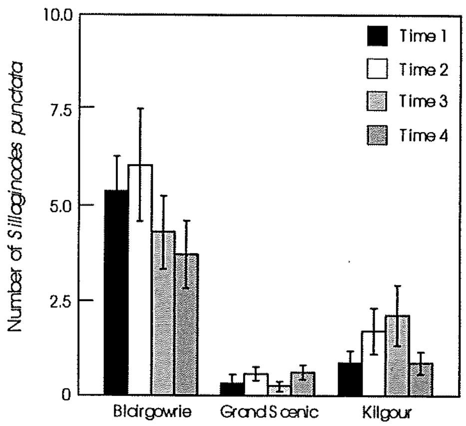

Figure 4. Mean abundance (±SE) of *Sillaginodes punctata* at Blairgowrie, Grand Scenic and Kilgour at time 1, time 2, time 3 and time 4.

During all times there was significant variability between sites in the abundance of *S. punctata* (time one - $df_{2,162}$, MS=12.201, $P<0.001$; time two - $df_{2,162}$, MS=6.958, $P<0.001$; time 3 - $df_{1,162}$, MS=7.184, $P<0.001$; time 4 - $df_{1,162}$, MS=3.733, $P<0.001$)(Fig. 4). The inconsistency in the abundance of *S. punctata* between sites through time, as shown in Table 1, was a reflection of the temporal variability in the abundances of *S. punctata* between Grand Scenic and Kilgour. Blairgowrie consistently had much higher numbers of *S. punctata* than Grand Scenic (time one - $df_{1,162}$, $P<0.001$; time two - $df_{1,162}$, $P<0.001$; time three - $df_{1,162}$, $P<0.001$; time four - $df_{1,162}$, $P<0.001$)(Fig. 4) or Kilgour (time one - $df_{1,162}$, $P<0.001$; time two - $df_{1,162}$, $P<0.001$; time three - $df_{1,162}$, $P<0.001$; time four - $df_{1,162}$, $P<0.001$)(Fig. 4). But the numbers of *S. punctata* were rarely significantly different between Kilgour and Grand Scenic, even though there appears to be a pattern of greater abundance of *S. punctata* at Kilgour than Grand Scenic for each of the sampling times (time 1 - $df_{1,162}$, P=0.056; time 2 - $df_{1,162}$, P=0.070; time

3 - $\text{df}_{1,162}$, $P<0.001$; time 4 - $\text{df}_{1,162}$, $P=0.840$)(Fig. 4). Only during the third sampling time was the abundance of *S. punctata* significantly greater at Kilgour than Grand Scenic.

The SLs of *S. punctata* varied little inside exclusion cages either between sites ($\text{df}_{2,12}$, MS=13.883, $P=0.070$) or between seagrass and unvegetated sand ($\text{df}_{1,12}$, MS=15.040, $P=0.081$)(Fig. 5).

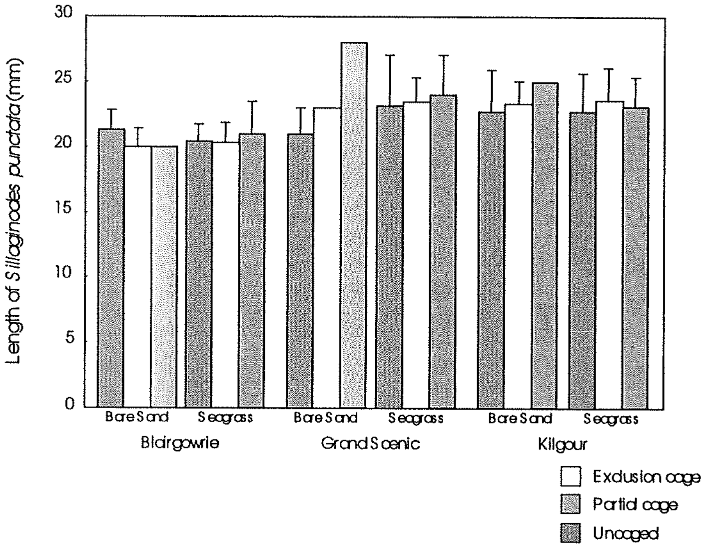

Figure 5. Mean length (±SE) of *Sillaginodes punctata* associated with exclusion cages, partial cages and uncaged areas at Blairgowrie, Grand Scenic and Kilgour in seagrass and unvegetated sand.

The SLs of *S. punctata* varied significantly between cage treatments (exclusion cages, partial cages and uncaged) in seagrass at Blairgowrie ($\text{df}_{2,9}$, MS=0.0002, $P=0.030$). This variability in SLs of fish between cage treatments in seagrass at Blairgowrie was partly driven by larger fish in uncaged than partially caged areas ($\text{df}_{1,9}$, MS=0.0002, $P=0.021$). *S. punctata* were similarly sized in exclusion cages and cage controls in seagrass ($\text{df}_{1,9}$, MS<0.0000, $P=0.933$), and there was no significant difference in the SLs of *S. punctata* in exclusion cages over unvegetated sand compared with the average SLs of fish in exclusion cages and cage controls in seagrass ($\text{df}_{1,12}$, MS<0.0002, $P=0.074$). At Kilgour, the SLs of *S. punctata* were similar across caging treatments in seagrass ($\text{df}_{2,6}$, MS=0.0007, $P=0.757$), and the SLs of fish in this habitat across cages was similar to that found in *S. punctata* inside exclusion cages over unvegetated sand ($\text{df}_{1,8}$, MS=0.002, $P=0.356$). Overall, the exclusion of predatory fishes from areas of habitat appeared to have little effect on the sizes of *S. punctata.*

6.1.2. Broad-scale (between sites) spatial variability in abundances and dietary composition of Arripis truttacea

Abundances of *Arripis truttacea* varied significantly between sites (Table 2, Fig. 6 a).

Table 2. Two-factor nested analysis of variance comparing the numbers of *Arripis truttacea* caught at each site (Blairgowrie, Kilgour and Grand Scenic), and during each sampling time within each site (n=6). Data were log(x+1) transformed prior to statistical analysis. df^N numerator degrees of freedom. df^D denominator degrees of freedom. The table shows, for *Arripis truttacea*, the probabilities (*P*) and MS associated with each of the terms in the model (SOURCE).

Source	df^N	df^D	MS	*P*
Site	2	3	2.700	**0.008**
Day{Site}	3	12	0.077	0.982
Error	12		1.408	

Much higher numbers of *A. truttacea* were caught at Blairgowrie than either Kilgour ($df_{1,3}$, *P*=0.010) or Grand Scenic ($df_{1,3}$, *P*=0.012)(Fig. 6 a), but the number of *A. truttacea* did not vary significantly between Kilgour and Grand Scenic ($df_{1,3}$, *P*=0.953).

Crustaceans, mysids and euphausids, dominated the dietary composition of *A. truttacea* only at Blairgowrie and Grand Scenic (Table 3). *A. truttacea* from Kilgour did not consume any crustaceans at all. Instead, the diet of *A. truttacea* from this region was composed exclusively of atherinid larvae. The contribution of fish to the diets of *A. truttacea* decreased successively at Grand Scenic and Blairgowrie. At Grand Scenic, pleuronectids and unknown fish contributed only 3.3 or 29.4 and 10 or 40.3 by % abundance and % mass respectively to the total diet (Table 3). *A. truttacea* at Blairgowrie consumed a more diverse assemblage of fish, although the overall contribution of fish was low. Atherinids, clupeids, gobiids and syngnathids all contributed to the dietary composition, but unknown fish were the most abundant dietary component of fish consumed (Table 3). In contrast to Hindell *et al.* (2000), none of the *A. truttacea* sampled during this study could be positively identified as having consumed juvenile *Sillaginodes punctata.*

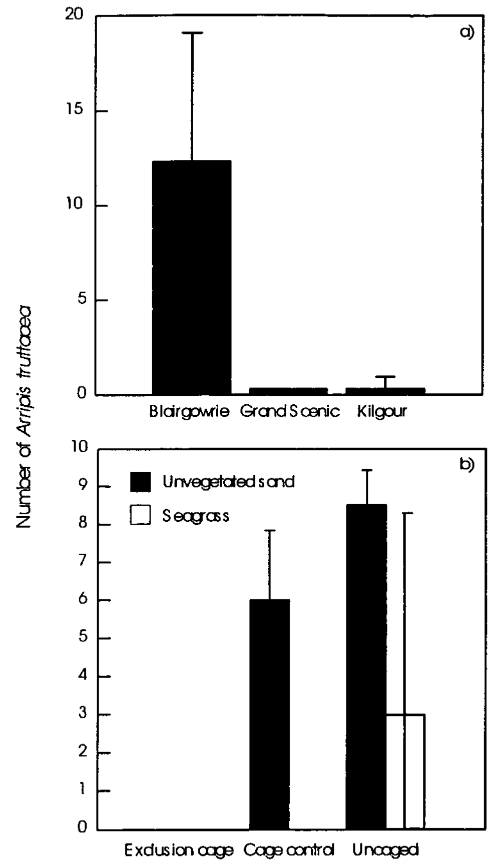

Figure 6. Mean abundance (±SE) of *Arripis truttacea* a) caught using a seine net at Blairgowrie, Grand Scenic and Kilgour, and b) observed using underwater videos' in exclusion cages, partial cages and uncaged areas within seagrass and unvegetated sand habitats at Blairgowrie.

Table 3. The number of *Arripis truttacea* caught at each site (n), their mean standard length ± standard error (SL±SE), and the % abundance (*N*), % mass (*M*) and % frequency of occurrence (*F*) of their stomach contents.

	Site Blairgowrie			Grand Scenic			Kilgour		
n	70			2			2		
SL (±SE)	16			15			19 (2)		
Prey items	*N*	*M*	*F*	*N*	*M*	*F*	*N*	*M*	*F*
Fish									
Atherinidae	0.3	3.7	4.6	-	-	-	100	100	100
Clupeidae	0.9	24.9	10.8	-	-	-	-	-	-
Rhombosolea	-	-	-	3.3	29.4	50.0	-	-	-
Gobiidae	0.2	2.6	4.6	-	-	-	-	-	-
Syngnathidae	0.1	0.2	1.5	-	-	-	-	-	-
Unknown fish	1.2	11.3	23.1	10.0	40.3	100	-	-	-
Other									
Crustaceans	97.3	57.4	75.4	86.7	30.3	50.0	-	-	-

6.1.3. Within-site variability in the use of habitats and cage treatments by Arripis truttacea

Abundances of *Arripis truttacea* varied significantly between cage treatments (Table 4, Fig. 6 b).

Table 4. Two-factor partially nested analysis of variance comparing the numbers of *Arripis truttacea* observed at Blairgowrie in each cage treatment (exclusion cage, cage control and un-caged) within seagrass and unvegetated sand habitats. Raw data used in statistical analysis. df^N numerator degrees of freedom. df^D denominator degrees of freedom. The table shows, for *A. truttacea*, the probabilities (*P*) and MS associated with each of the terms in the model (SOURCE).

Between Subjects Source	df^N	df^D	MS	*P*
Habitat (H)	1	2	40.333	0.067
Cage (C)	2	4	30.333	**0.044**
H × C	2	4	10.333	0.190
Day{H}	2	4	3.000	0.529
Error	4		4.000	

Underwater video showed that *A. truttacea* occurred in seagrass only once in 480 minutes of video time taken over 24 hours on four separate days. In this case, the small school of *A. truttacea* (n=6) passed through the field of vision in less than 1.5 seconds. Therefore, we re-analysed our data for unvegetated sand habitats only. In this habitat, abundances of *A. truttacea* varied significantly between cage treatments ($df_{2,4}$, MS=2.764, *P*=0.025). The design of our cages ensured that no *A. truttacea* were observed inside exclusion cages. There were clearly more fish in partial cages and uncaged areas than exclusion cages (Fig. 6 b), and abundances of *A. truttacea* inside partial cages did not differ to those inside uncaged areas over unvegetated sand ($df_{1,4}$, MS=4.000, *P*=0.374)(Fig. 6 b, Appendix 3). Importantly, neither *A. truttacea* nor their potential prey, such as atherinids, clupeids, appeared to congregate around the walls of cages.

6.2. Evaluating links between fish and seagrass using isotope analyses and measures of abundance

6.2.1. Temporal variability in numbers of fishes

A diverse assemblage of large fishes, 11 species from 9 families, was sampled in this study. These large fishes included benthic (Platycephalidae), demersal (Odacidae) and pelagic (Arripidae and Carangidae), species. Many of these fishes, such as arripids, clinids and platycephalids, are piscivorous (Hindell *et al.* 2000) (Table 5). The small fish assemblage was composed of at least 19 species, representing 16 families. Some of these species of small fish, such as sillaginids, monacanthids and pleuronectids, were composed exclusively of juveniles, while fish from the families Syngnathidae and Odacidae were primarily adult fish (Table 6).

The assemblage structure of both large and small fish showed a relatively high degree of site specificity, regardless of the time of year (Table 7, Fig. 7 a & b), but varied little between seasons (Table 7, Fig. 7 a & b).

Abundances of large fishes, regardless of species, varied only between sites; more large fish were captured at St Leonards than Grand Scenic (Table 8, Fig. 8 a). The two most abundant large fishes were *Arripis truttacea* and *Kestratherina esox*, which represented 48.7 and 23.4 % of the total number of large fish captured respectively (Table 5). *A. truttacea* varied differently between seasons at each site (Table 8). There was little variability in abundances of *A. truttacea* between seasons at Grand Scenic (df$_{3,24}$, MS=0.034, P=0.246)(Fig. 8 b), and overall, numbers of fish were low at this site (Fig. 8 b). Conversely, abundances of *A. truttacea* were much larger at

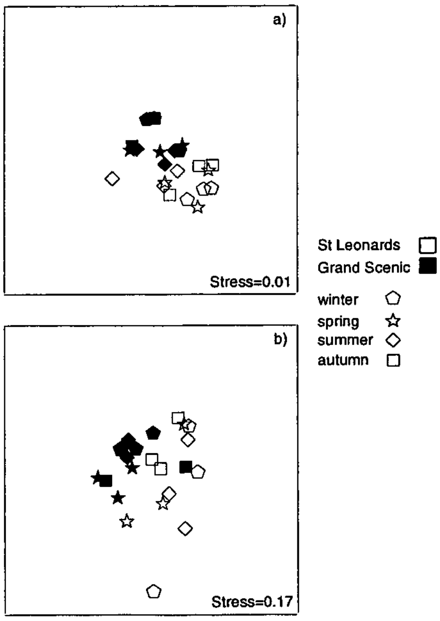

Figure 7. Multidimensional ordination plot of assemblages of a) predatory and b) small fishes in each regime of site (St Leonards and Grand Scenic) and season (winter, summer, spring and autumn)

Table 5. Abundance of predatory fishes during each month at each site, Grand Scenic (GC) and St Leonards (SL)

Species	June		July		August		September		October		November		December		January		February		March		April		May	
	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL
Arripidae																								
Arripis georgiana	-	-	-	-	25	13	-	-	-	-	-	-	-	-	-	15	-	-	-	2	-	-	-	-
Arripis truttacea	-	55	-	35	1	28	-	-	1	15	4	11	5	11	-	11	-	15	-	3-	-	29	-	25
Atherinidae																								
Kestratherina esox	5	-	11	-	3	-	5	-	7	-	11	-	2	-	37	-	14	-	19	-	4	-	-	-
Clinidae																								
Cristiceps australis	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	1	-	-	-	-	-	-	-	2
Carangidae																								
Pseudocaranx wrighti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	11	-	-	-	-
Odacidae																								
Haletta semifasciata	-	-	-	-	-	-	1	1	-	1	1	-	-	1	1	-	4	-	2	-	-	-	-	-
Platycephalidae																								
Platycephalus laevigatus	-	-	-	-	-	1	-	-	-	-	-	3	-	-	-	-	-	3	-	3	-	-	-	-
Platycephalus speculator	-	-	-	-	-	1	-	-	-	1	1	1	-	1	-	-	-	-	-	1	-	-	-	1
Ophidiidae																								
Genypterus tigerinus	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sparidae																								
Acanthopagrus butcherii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	3	-	-
Uranoscopidae																								
Kathetostoma laeve	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total no. fish	5	55	11	35	29	44	6	1	8	19	17	16	7	13	40	28	18	19	21	49	4	32	-	28

Table 6. Abundance of small, seagrass associated fishes during each month at each site, Grand Scenic (GC) and St Leonards (SL)

Species	Summer				Autumn						Winter						Spring						Summer	
	January		February		March		April		May		June		July		August		September		October		November		December	
	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL	GC	SL
Arripidae																								
Arripis truttacea	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Atherinidae	74	-	58	-	59	-	45	2	-	-	70	-	3	-	40	-	9	-	1	-	55	-	27	1
Clupeidae																								
Spratelloides robustus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
Cheilodactylidae																								
Dactylophora nigricans	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	1	-	-
Clinidae																								
Heteroclinus perspicilatus	1	-	1	-	-	-	-	-	3	-	1	1	-	-	-	-	-	-	-	-	-	-	1	-
Cristiceps australis	1	-	-	2	3	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Enoplosidae																								
Enoplosus armatus	-	-	-	-	-	2		6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Gobiidae																								
Favonigobius lateralis	-	-	1	-	-	1	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1
Gobiesocidae																								
Genus *C* sp. 1	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monacanthidae																								
Meuschenia freycineti	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	4	-	-	1	-
Acanthaluteres	-	-	2	-	-	-	2	-	-	-	11	-	-	-	-	-	2	-	1	-	-	-	-	-
Mugilidae																								
Aldrichetta forsteri	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Odacidae																								
Neoodax balteatus	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	1	-	1	1	-	-	-	-
Pleuronectidae																								
Rhombosolea tapirina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Scorpaenidae																								
Gymnapistes marmoratus	-	-	4	-	2	-	-	1	-	-	-	-	-	-	-	-	-	2	-	1	-	1	-	-
Sillaginidae																								
Sillaginodes punctata	32	-	2	1	-	3	-	-	-	-	-	-	-	-	-	-	4	-	3	-	3	-	2	-
Syngnathidae																								
Stigmatopora sp.	-	2	58	15	-	48	12	70	3	4	9	1	2	1	115	-	5	2	35	15	8	-	-	-
Sparidae																								
Acanthopagrus butcherii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
Total no. fish	110	2	126	35	64	55	61	79	11	6	92	5	5	1	155	4	21	4	42	24	67	3	32	4

Table 7. Two-factor multivariate analysis of similarity (ANOSIM) comparing assemblages of predatory and small fish between sites (Grand Scenic and St Leonards) and seasons (winter – Wi, spring – Sp, summer – Su, autumn – Au). *R* sample statistic/Global R. *P* significance level. ^{ns} not significant after Bonferroni adjustment (*P*<0.008).

	Predatory		Small Fish	
Stress	0.01		0.17	
Source	*R*	*P*	*R*	*P*
Season	-0.074	0.786	0.240	**0.006**
Wi vs Sp	0.009	0.480	0.333	0.070
Wi vs Su	-0.167	0.780	0.204	0.140
Wi vs Au	-0.093	0.730	0.148	0.120
Sp vs Su	-0.185	0.940	0.343	0.060
Sp vs Au	-0.028	0.590	0.389	0.030^{ns}
Su vs Au	-0.093	0.730	0.065	0.330
Site	0.667	**<0.001**	0.472	**0.040**

Table 8. Three-factor partially nested analysis of variance (ANOVA) comparing the abundances of predatory fish, *Arripis truttacea*, *Kestratherina esox*, small fish, atherinids and syngnathids between sites (St Leonards and Grand Scenic) and seasons (Winter, Spring, Summer, Autumn). Data $\log_{10}(x+1)$ transformed prior to statistical analysis. – interaction term not valid in model

		Predatory fish		*Arripis truttacea*		*Kestratherina esox*			Small fish		Atherinidae		Syngnathidae	
Source	*df*	MS	*P*	MS	*P*	MS	*P*	*df*	MS	*P*	MS	*P*	MS	*P*
Season	3	0.317	0.213	0.228	0.206	0.032	0.791	3	0.191	0.219	252.556	0.646	0.194	0.538
Site	1	1.416	**0.013**	7.266	**<0.001**	3.709	**<0.001**	1	2.936	**0.001**	7993.500	**0.003**	0.186	0.413
Site × Season	3	0.333	0.195	0.502	**0.028**	0.032	0.791	3	0.304	0.100	244.500	0.657	0.916	0.063
Month{Season}	8	0.342	0.141	0.087	0.748	0.157	0.142	8	0.352	0.052	436.667	0.502	0.583	0.126
Site × Month{Season)	8	0.128	0.730	0.061	0.883	0.157	0.142	–	–	–	–	–	–	–
Error	24	0.197		0.139		0.091		8	0.104		438.000		0.250	

St Leonards than Grand Scenic, and while they varied significantly between seasons ($df_{3,24}$, MS=0.696, P=0.008), this result was driven primarily by significantly lower numbers of *A. truttacea* in spring than either autumn ($df_{1,24}$, P=0.030) or winter ($df_{1,24}$, P=0.008)(Fig. 8 b). *Kestratherina esox* only occurred at Grand Scenic, and despite a trend that suggests they are more abundant during summer, their numbers did not vary significantly across seasons (Table 8, Fig. 8 c).

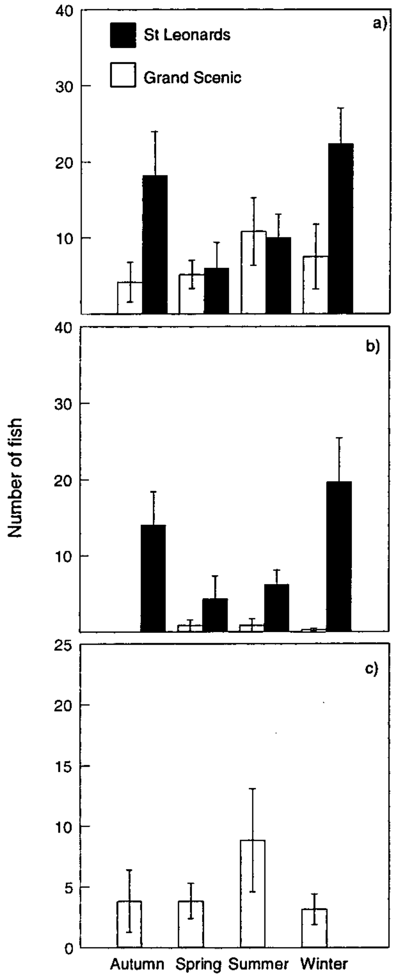

Figure 8. Mean (±SE) numbers of a) predatory fish, regardless of species, b) *Arripis truttacea* and c) *Kestratherina esox* in each season at St Leonards and Grand Scenic

Abundances of small fish varied only between sites; Grand Scenic contained significantly more fish than St Leonards (Table 8, Fig. 9 a). Atherinids and syngnathids dominated the catches of small fish, representing 44.1 and 40.2 % respectively (Table 6). Atherinids were more abundant at Grand Scenic than St Leonards, and these site differences were relatively consistent across seasons (Table 8, Fig. 9 b). Syngnathids were generally highly variable between months, and varied neither with site nor season, despite a trend which suggests that they were more abundant at Grand Scenic (Table 8, Fig. 9 c).

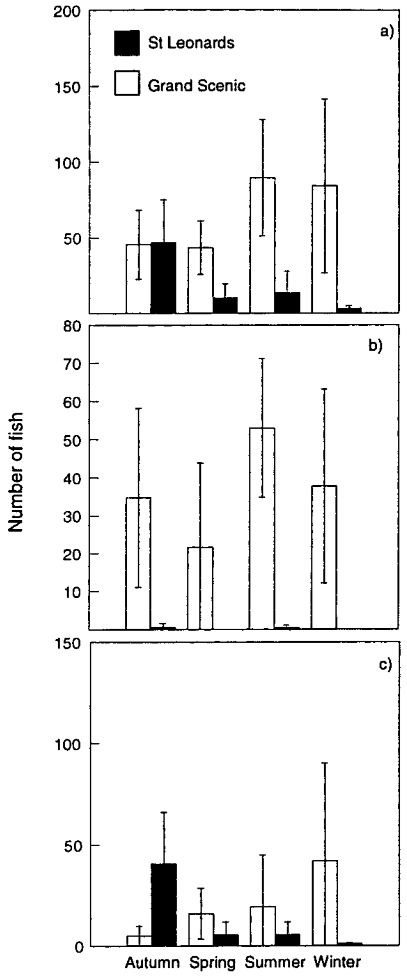

Figure 9. Mean (±SE) numbers of a) small fish, regardless of species, b) Atherinidae and c) *Stigmatopora* sp. in each season at St Leonards and Grand Scenic.

6.2.2. Dietary composition of large fish

Twelve species of large fish were sampled in this study (Table 9). The most common dietary items in the guts of these fish were other fish and small benthic crustaceans, such as amphipods (Table 9). Other crustaceans, such as pelagic mysids and euphausids, shrimps and crabs, as well as cephalopods, polychaetes, gastropods, plant material and terrestrial insects, contributed to the dietary composition of large fishes (Table 9). Guts from 11 species contained fish remains (Table 10). These remains included fish from at least 9 different families, including those with demersal and pelagic life histories. Unknown fish remains contributed the greatest proportion of the teleost prey (Table 10).

The two most abundant piscivorous fishes, *Arripis truttacea* and *Kestratherina esox*, consumed a range of fishes (Fig. 10). Despite *A. truttacea* rarely occurring at Grand Scenic, when they did, their stomachs contained a higher proportion of fish than when they occurred at St Leonards. The composition of fish in guts of *A. truttacea* at St Leonards did not appear to vary in any discernible way with month (Fig. 10). Conversely, *K. esox* appeared to show a trend of increasing contribution by fish in late summer/early autumn, and this pattern was driven primarily by increases in the contribution by atherinids (Fig. 10). Interestingly, gobiids, which are almost exclusively benthic, were consumed by both of these large fish, which implies that pelagic large fishes forage close to the substrate for at least some of the time.

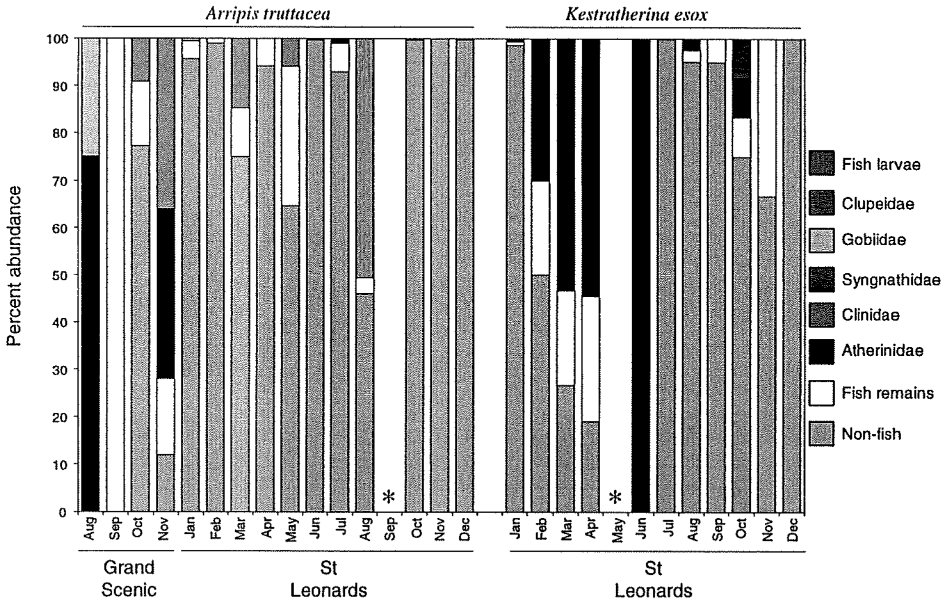

Figure 10. Site-specific proportions of the stomach contents of *Arripis truttacea* and *Kestratherina esox* in each month. * no fish caught in this month.

6.2.3. Temporal and spatial variability in the isotopic composition of fish and habitat samples

Regardless of the time-of-year, clear patterns were discernible in relative trophic positions of fishes, their teleost prey, and the habitats within which they were sampled, and these patterns were relatively consistent between locations (Table 11, Fig. 11 a & b). The most obvious result from our study was that measures of $\delta^{13}C$ and $\delta^{15}N$ in our samples were quite variable within species/habitat samples. Despite this variability, average measures of $\delta^{13}C$ and $\delta^{15}N$ showed four general groupings. Seagrasses appeared to form the first group; they had the lowest $\delta^{15}N$ and least negative $\delta^{13}C$. A second group consisted of the various algae and sediments, which generally had $\delta^{13}C$ values close to –15 ‰ and $\delta^{15}N$ values of about 5 ‰. A third group consisted predominantly of juvenile fish that consume invertebrates; the $\delta^{13}C$ and $\delta^{15}N$ values of this group ranged between ≈ -10 and ≈ -15 ‰ and 7 and 12 ‰ respectively. The fourth group consisted of piscivorous fishes such as *Arripis truttacea*, *Arripis georgiana* and *Platycephalus speculator*, although the degree to which this group was separated from the third group of fishes varied with site. Overall, levels of $\delta^{13}C$ and $\delta^{15}N$ were generally higher and lower respectively, by between 2 and 5 ‰, in samples from Grand Scenic compared with St Leonards. This difference was relatively consistent across samples.

Measures of $\delta^{13}C$ and $\delta^{15}N$ in samples of *Heterozostera tasmanica* averaged -10.5 and 3 ‰ respectively at Grand Scenic, and –12.4 and 4.7 ‰, respectively at St Leonards. $\delta^{13}C$ varied inconsistently between seasons at each location (Tables 12 & 13, Fig. 12 a & b). At Grand Scenic, $\delta^{13}C$ in seagrass did not vary seasonally, but at St Leonards, levels of $\delta^{13}C$ were greater in autumn than spring (P=0.001) or summer (P=0.028), and $\delta^{13}C$ in seagrass during spring was more negative than in winter (Fig. 7a). $\delta^{15}N$ varied differently through time between locations (Table 13). At St Leonards, $\delta^{15}N$ values in seagrass were higher during winter than spring (P=0.008) or summer ($P<0.001$) (Fig. 12 b). Similarly, seagrass samples from autumn also contained higher values of $\delta^{15}N$ than spring ($P<0.001$) or summer ($P<0.001$).

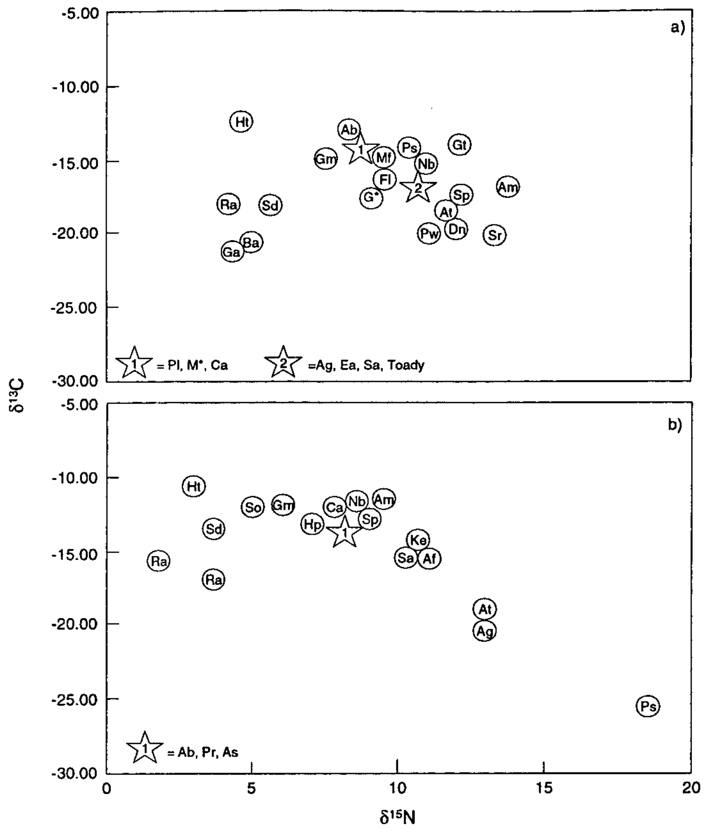

Figure 11. Variability in the relative trophic positions of fishes and habitats sampled at a) St Leonards and b) Grand Scenic. Each point corresponds to one species, the key to which is in Table 7.

Values of $\delta^{15}N$ and $\delta^{13}C$ in sediments appeared to be slightly different at Grand Scenic (mean $\delta^{15}N=4.6$ ‰, $\delta^{13}C=-13.2$ ‰) compared with St Leonards (mean $\delta^{15}N=5.2$ ‰, $\delta^{13}C=-18.4$ ‰). Values of $\delta^{13}C$ were slightly less negative at Grand Scenic than St Leonards, but did not vary significantly between seasons (Table 12, Fig. 12 c). $\delta^{15}N$ varied inconsistently between winter and summer at both locations (Table 13, Fig. 12 d). At St Leonards, $\delta^{15}N$ did not vary seasonally (Table 13), but at Grand Scenic, winter sediments had significantly lower $\delta^{15}N$ than those sampled during summer (Table 13, Fig. 12 d).

Table 9. Dietary composition of predatory fishes. no. number of predatory fish. *N* percentage abundance. *M* percentage mass. * percentage <0.5. - absent. L length (± standard error). W weight (± standard error).

				Fish		Pelagic		Benthic		Macro-Crustaceans		Cephalopods		Polychaetes		Gastropods		Unknown crustaceans		Plant material		Insects	
no.	Species	L (cm)	W (g)	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*
	Grand Scenic																						
5	*Arripis georgiana*	18 (±0.4)	97 (±30)	-	-	-	-	91	31	3	25	-	-	6	44	-	-	-	-	-	-	-	-
11	*Arripis truttacea*	9 (±3)	18 (±32)	62	86	28	2	4	*	6	12	-	-	-	-	-	-	-	-	-	-	-	-
2	*Cristiceps australis*	10 (±1)	5 (±2)	33	30	-	-	67	70	-	-	-	-	-	-	-	-	-	-	-	-	-	-
115	*Kestratherina esox*	11 (±1)	11 (±2)	5	44	32	6	59	38	2	8	*	1	1	2	*	*	-	-	1	*	-	-
9	*Neoodax balteatus*	10 (±1)	12 (±2)	-	-	16	3	6	11	-	-	-	-	1	1	77	84	-	-	1	*	-	-
1	*Platycephalus*	29	225	37	80	-	-	-	-	62	20	-	-	-	-	-	-	-	-	-	-	-	-
	St Leonards																						
5	*Acanthopagrus*	21 (±7)	291 (±299)	17	3	-	-	-	-	33	30	-	-	-	-	50	67	-	-	-	-	-	-
30	*Arripis georgiana*	13 (±4)	49 (±41)	*	1	6	3	94	78	*	1	-	-	*	17	-	-	-	-	-	-	*	*
190	*Arripis truttacea*	9 (±2.3)	12 (±12)	3	43	45	19	50	24	1	11	-	-	*	4	-	-	-	-	*	*	-	-
4	*Cristiceps australis*	11 (±1)	13 (±7)	50	47	-	-	25	1.73	25	52	-	-	-	-	-	-	-	-	-	-	-	-
2	*Genypterus tigerinus*	30 (±5)	310 (±173)	50	78	-	-	-	-	50	22	-	-	-	-	-	-	-	-	-	-	-	-
2	*Haletta semifasciata*	25 (±4)	208 (±112)	-	-	-	-	55	2	-	-	3	5	15	34	-	-	24	59	3	*	-	-
1	*Kathetostoma laeve*	15	135	67	100	-	-	-	-	33	*	-	-	-	-	-	-	-	-	-	-	-	-
1	*Neoodax balteatus*	11	22	50	45	-	-	-	-	-	-	-	-	-	-	50	55	-	-	-	-	-	-
10	*Platycephalus*	31 (±13)	434 (±348)	19	13	-	-	-	-	69	86	-	-	6	*	-	-	6	*	-	-	-	-
5	*Platycephalus*	17 (±6.4)	65 (±51.7)	4	19	-	-	48	13	35	62	-	-	13	6	-	-	-	-	-	-	-	-
12	*Pseudocaranx wrighti*	9 (±1.4)	13 (±5)	7	68	12	8	77	23	-	-	-	-	-	-	1	*	4	*	-	-	-	-

Table 10. Dietary composition of piscivorous fishes. *N* percentage abundance. *M* percentage mass. * percentage <0.5. - absent.

Predatory fish	Prey fish																					
	Atherinidae		Clinidae		Clupeidae		Engraulidae		Gobiidae		Monacanthi-		Mugilidae		Pleuronecti-		Syngnathi-		Larval fish		Unknown	
	N	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*	*N*	*M*
Grand Scenic																						
Arripis truttacea	36	47	-	-	-	-	-	-	3	24	-	-	-	-	-	-	33	5	-	-	27	23
Cristiceps australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	100
Kestratherina esox	50	54	3	12	3	17	-	-	3	2	-	-	-	-	-	-	-	-	-	-	40	15
Platycephalus speculator	-	-	-	-	-	-	-	-	-	-	33	12	-	-	-	-	-	-	-	-	67	88
St Leonards																						
Acanthopagrus butcherii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	100
Arripis georgiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	86	50	-	-	14	50
Arripis truttacea	1	*	-	-	1	2	3	65	1	5	-	-	-	-	-	-	11	7	41	1	42	19
Cristiceps australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	100
Genypterus tigerinus	-	-	-	-	-	-	-	-	50	27	-	-	-	-	50	73	-	-	-	-	-	-
Kathetostoma laeve	-	-	-	-	-	-	-	-	-	-	-	-	50	80	50	20	-	-	-	-	-	-
Neoodax balteatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	100	-	-	-	-
Platycephalus laevigatus	-	-	-	-	-	-	-	-	33	37	-	-	-	-	-	-	-	-	-	-	67	63
Platycephalus speculator	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	100
Pseudocaranx wrighti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	100

Table 11. Isotope measures in fish and habitat samples at each site. - no measurement

		Grand Scenic				St Leonards			
Key	Sample	δ15N	seδ15N	δ13C	seδ13C	δ15N	seδ15N	δ13C	seδ13C
	Environmental								
Ba	Brown algae	-	-	-	-	5.00	0.04	-20.56	0.66
Ga	Green Algae	-	-	-	-	4.38	0.28	-20.99	0.39
Ra	Red Algae	3.74	0.12	-16.75	0.11	4.17	0.79	-17.98	2.84
Sd	sediment	5.11	0.17	-12.02	0.31	5.59	1.33	-18.14	3.64
Ht	*Heterozostera tasmanica*	3.04	0.30	-10.61	0.91	4.74	0.44	-12.52	0.84
							-	-	
	Fish								
Ab	*Acanthopagrus butcherii*	8.2		-13.99		8.27	0.82	-12.93	1.04
Af	*Aldrichetta forsteri*	11.12	0.04	-15.48	0.10	-	-	-	-
Am	Atherinidae	9.50	0.97	-11.56	1.17	13.69	3.30	-16.67	2.74
As	*Acanthaluteres spilomelanurus*	7.87	0.49	-13.11	0.95	-	-	-	-
Ag	*Arripis georgiana*	13.01	1.33	-20.31	4.35	11.19	0.60	-16.10	5.13
At	*Arripis truttacea*	12.99	0.47	-18.96	4.62	11.94	0.98	-18.47	3.52
Ca	*Cristiceps australis*	7.87	0.42	-11.90	1.52	9.00	1.35	-14.14	1.49
Dn	*Dactylophora nigricans*	-	-	-	-	11.97	1.03	-19.21	2.11
Ea	*Enoplosus armatus*	-	-	-	-	10.94	0.23	-17.47	0.79
Fl	*Favonigobius lateralis*	-	-	-	-	9.64	0.95	-16.88	1.53
G*	Genus *C* sp. 1	-	-	-	-	9.34		-17.63	
Gt	*Genypterus tigerinus*	-	-	-	-	12.14	0.12	-13.86	1.12
Gm	*Gymnapistes marmoratus*	6.11	0.51	-11.71	0.16	7.47	0.42	-15.01	1.11
Hp	*Heteroclinus perspicilatus*	7.07	0.50	-13.12	0.86	10.96	-	-16.45	-
Ke	*Kestratherina esox*	10.73	0.93	-14.27	4.35	-	-	-	-
M*	*Macrobrachium* sp.					9.04	1.21	-14.43	1.09
Mf	*Meuschenia freycineti*	-	-	-	-	9.52	1.29	-14.90	2.20
Nb	*Neoodax balteatus*	8.17	0.49	-14.00	0.99	10.7		-17.09	
No	*Neoodax balteatus*	8.45	0.53	-11.91	2.51	10.80	0.56	-15.18	3.58
Pl	*Platycephalus laevigatus*	-	-	-	-	8.81	1.12	-14.29	2.66
Ps	*Platycephalus speculator*	18.59		-25.61		10.47	1.04	-14.77	2.76
Pd	*Pseudocaranx wrighti*	-	-	-	-	11.09	0.75	-19.86	3.29
Rt	*Rhombosolea tapirina*	7.96		-13.58		-	-	-	-
Sp	*Sillaginodes punctata*	8.95	1.88	-12.55	2.92	12.18	1.95	-17.47	1.10
Sr	*Spratelloides robustus*	-	-	-	-	13.30	0.62	-20.1	0.32
Sa	*Stigmatopora* sp.	10.30	1.87	-15.37	1.45	11.00	1.35	-17.24	1.09

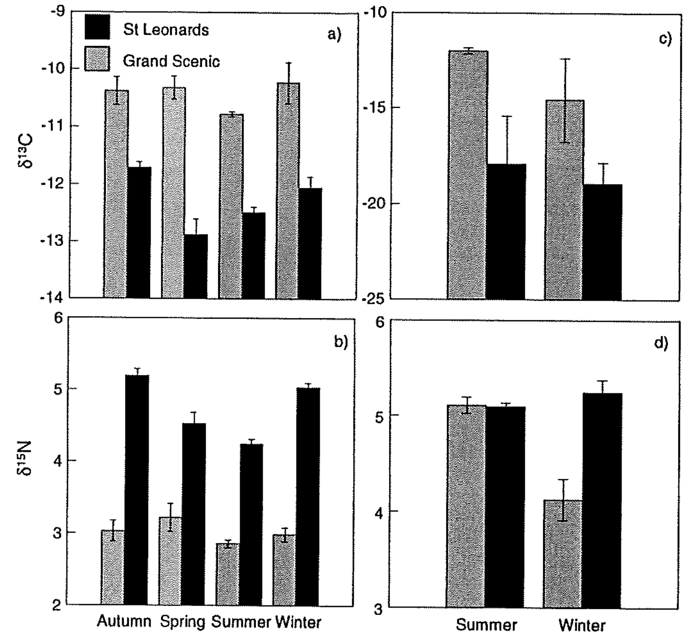

Figure 12. Mean (±SE) isotopic measures for a) $\delta^{13}C$ and b) $\delta^{15}N$ in *Heterozostera tasmanica* during each season, and c) $\delta^{13}C$ and d) $\delta^{15}N$ in sediment during summer and winter at St Leonards and Grand Scenic

The most abundant small fishes sampled in our study were from the families Syngnathidae and Atherinidae (Table 6). For each of these families, we measured $\delta^{15}N$ and $\delta^{13}C$ in *Stigmatopora* sp. (mean $\delta^{15}N$=10.3 ‰, $\delta^{13}C$=-15.3 ‰ at Grand Scenic and mean $\delta^{15}N$=11 ‰, $\delta^{13}C$=-17.2 ‰ at St Leonards), and Atherinidae (*Leptatherina presbyteroides* and *Atherinasoma microstoma*) (mean $\delta^{15}N$=9.5 ‰, $\delta^{13}C$=-11.5 ‰ at Grand Scenic and mean $\delta^{15}N$=13.7 ‰, $\delta^{13}C$=-16.6 ‰ at St Leonards). For the atherinids, $\delta^{13}C$ varied significantly between seasons at Grand Scenic (Table 12, Fig. 13 b); tissues in spring had more negative values for $\delta^{13}C$ than those in autumn ($df_{1,21}$, P=0.007) or summer ($df_{1,21}$, P=0.012) (Fig 13 b). Tissue samples from *Stigmatopora* sp. varied significantly between sites only for $\delta^{13}C$; they were less negative at Grand Scenic than St Leonards (Table 12, Fig. 13 c & d). Measures of $\delta^{15}N$ and $\delta^{13}C$ varied significantly between seasons at both locations (Tables 12 & 13, Fig. 13 c & d). Values of $\delta^{15}N$ were lower in spring than either autumn ($df_{1,33}$, P=0.001) or summer ($df_{1,33}$, P=0.020) and lower in autumn than winter ($df_{1,33}$, P=0.036); values of $\delta^{13}C$ were more negative in spring than either summer ($df_{1,33}$, P=0.001) or winter ($df_{1,33}$, P=0.019), and more negative in autumn than spring ($df_{1,33}$, $P<0.001$) (Fig. 13 c & d).

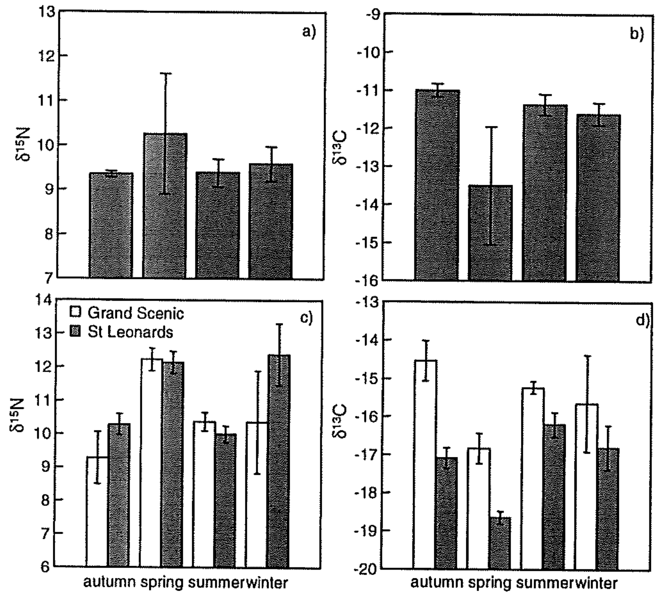

Figure 13. Seasonal patterns in the mean (±SE) isotope measures for a) $\delta^{15}N$ and b) $\delta^{13}C$ from atherinids, and c) $\delta^{15}N$ and d) $\delta^{13}C$ from syngnathids at St Leonards and Grand Scenic

Kestratherina esox (mean $\delta^{15}N=10.7$ ‰, $\delta^{13}C=-14.2$ ‰ – only sampled from Grand Scenic) and *Arripis truttacea* (mean $\delta^{15}N=13$ ‰, $\delta^{13}C=-18.9$ ‰ at Grand Scenic and mean $\delta^{15}N=11.9$ ‰, $\delta^{13}C=-18.5$ ‰ at St Leonards) were the most abundant large fishes sampled in our study. Neither isotopic measure varied significantly in samples of *Kestratherina esox* between seasons (Tables 12 & 13, Fig. 14 a & b), nor with the length of fish ($\delta^{15}N$ – $df_{1,38}$, MS=1.220, $P=0.244$, $\delta^{13}C$ – $df_{1,38}$, MS=6.106, $P=0.577$)(Figs. 14 c & d). At St Leonards, neither isotope measure varied seasonally in *Arripis truttacea* (Tables 12 & 13, Fig. 15 a & b). When each isotope measure was compared in *A. truttacea* during spring and summer at each site, $\delta^{15}N$ was found to be higher in fishes at Grand Scenic than St Leonards (Table 13, Fig. 15 d) and $\delta^{13}C$ was less negative during summer than spring (Table 12, Fig. 15 c). While the measure of $\delta^{13}C$ did not change with size ($df_{1,59}$, MS=4.343, $P=0.563$), there was a significant and positive relationship between $\delta^{15}N$ and length ($df_{1,59}$, MS=10.731, $P<0.001$)(Fig. 16).

Table 12. One- and two-factor analyses of variance comparing δ^{13}C in samples of seagrass, sediment and fishes between seasons and sites. – no test for this term in model. [a] at St Leonards only. [b] at both sites but only spring and summer seasons.

	Seagrass		Sediment		Atherinidae		*Stigmatopora* sp.		*Kestratherina*		*Arripis truttacea*[a]		*Arripis truttacea*[b]	
Source	*df*	P	*df*	P	*df*	P	*df*	P	*df*	P	*df*	P	*df*	*P*
Season	3	**0.004**	1	0.245	3	**0.010**	3	**0.001**	3	0.997	3	0.086	1	**0.011**
Site	1	**<0.001**	1	**0.004**		–	1	**<0.001**		–		–	1	0.400
Site × Season	3	**0.020**	1	0.602		–	3	0.243		–		–	1	0.420
St Leonards														
Season	3	**0.001**		–		–		–		–		–		–
Grand Scenic														
Season	3	0.291		–		–		–		–		–		–
Error	32	0.175	12	8.584	21	0.931	33	0.945	6	5.549	7	3.550	12	11.775

Table 13. One- and two-factor analyses of variance comparing δ^{15}N in samples of seagrass, sediment and fishes between seasons and sites. – no test for this term in model. [a] at St Leonards only. [b] at both sites but only spring and summer seasons.

	Seagrass		Sediment		Atherinidae		*Stigmatopora* sp.		*Kestratherina*		*Arripis truttacea*[a]		*Arripis truttacea*[b]	
Source	*df*	*P*	*df*	P	*df*	P	*df*	P	*df*	P	*df*	P	*df*	P
Season	3	**<0.000**	1	**0.003**	3	0.565	3	**0.001**	3	0.207	3	0.144	1	0.197
Site	1	**<0.000**	1	**<0.001**		–	1	0.140		–		–	1	**0.008**
Site × Season	3	**<0.000**	1	**<0.001**		–	3	0.236		–		–	1	0.981
St Leonards														
Season	3	**<0.001**	1	0.374		–		–		–		–		–
Grand Scenic														
Season	3	0.119	1	**<0.001**		–		–		–		–		–
Error	32	0.054	12	0.051	21	0..994	33	1.625	6	0.384	7	0.366	12	0.261

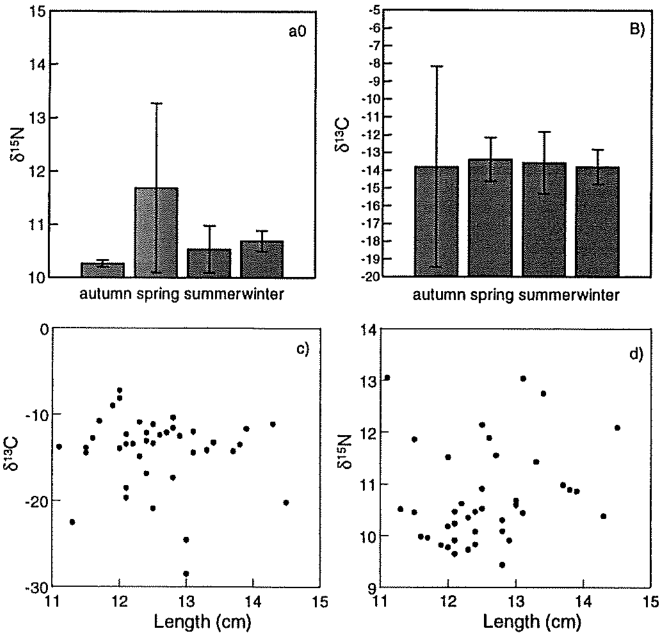

Figure 14. Isotope measures in *Kestratherina esox* for a) δ^{15}N and b) δ^{13}C during each season, and the relationship between c) δ^{13}C and d) δ^{15}N and the size (length) of fish only at Grand Scenic

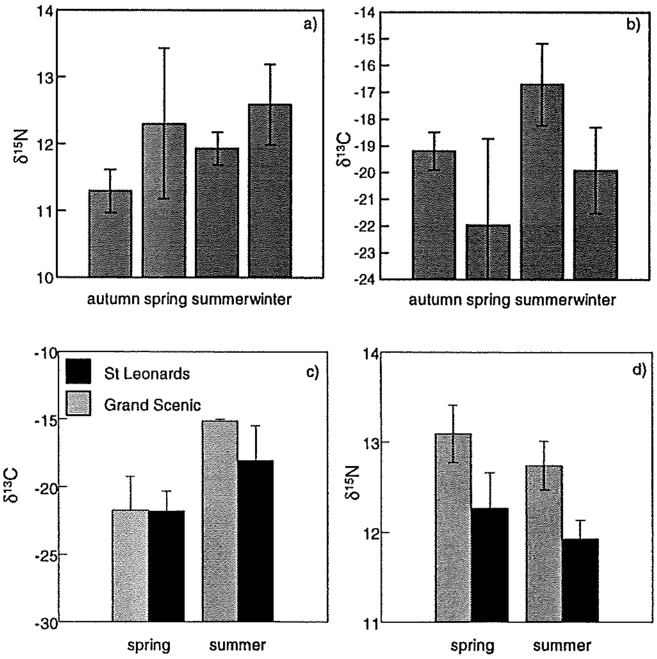

Figure 15. Isotope measures in *Arripis truttacea* for a) δ^{15}N and b) δ^{13}C during each season at St Leonards, and c) δ^{13}C and d) δ^{15}N in spring and summer at St Leonards and Grand Scenic

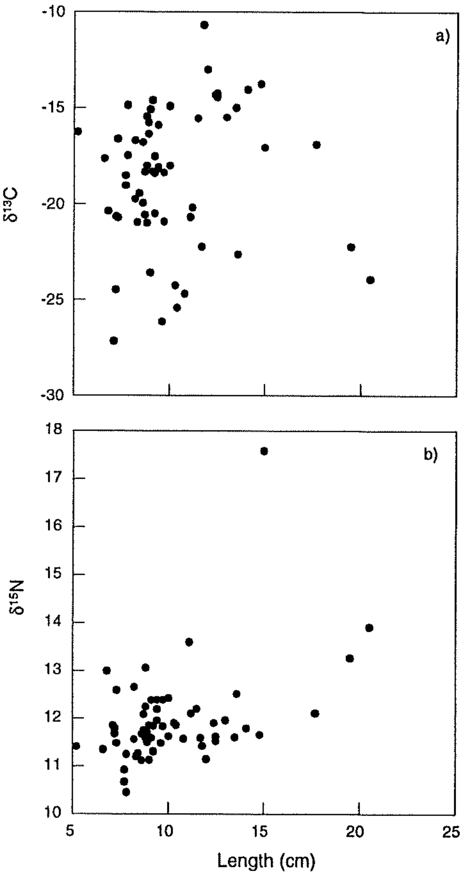

Figure 16. Relationship between a) $\delta^{13}C$ and b) $\delta^{15}N$ and the size (standard length) of *Arripis truttacea* (pooled across sites)

7. Discussion

7.1. Experimental assessment of the effects of piscivorous fish on juvenile fish in seagrass beds

Seagrass habitats generally contain a richer and more abundant fish fauna than alternative, especially unvegetated, habitats (Pollard 1984, Bell and Pollard 1989, Kemp 1989, Connolly *et al.* 1999). These patterns are thought to be a reflection of selection by juvenile fish for areas that offer high levels of food and/or refuge from environmental disturbance (Bell and Westoby 1986a, Jenkins *et al.* 1997a). Alternatively, the positive correlation between the abundance of fishes and aspects of seagrass beds may relate to variability in predation pressure (Orth *et al.* 1984). Encounter rates between fish and their teleost predators are lower, or predator success is reduced and latency to capture is higher, in areas with seagrass (Sweatman and Robertson 1994, Gotceitas *et al.* 1997). Where predation does not influence variability in abundances of fish, it may alter the size structure of fish in structurally variable habitats (Levin *et al.* 1997). Behaviourally mediated avoidance of predators may also explain differential use of habitats by prey (Jordan *et al.* 1996). At our study locations, *S. punctata* rarely occurred over unvegetated sand except where predatory fish were excluded. This implies that predation by fish may be an important determinant of small-scale (between habitat types) spatial variability. In contrast to Levin *et al.* (1997), there did not appear to be any trend of increasing size of sillaginid recruits inside predator exclusions, nor between habitat types within a site. Therefore, we contend that the importance of seagrass beds as nursery areas for small fish is related, at least partially, to their provision of refuge from predation by fishes.

Structural aspects of the environment, regardless of whether they are biogenic or not, often provide small fish with a refuge from predation (Heck and Crowder 1991, Beukers and Jones 1997), and thereby influence patterns in survival and recruitment (Steele 1999). Predation risk, as a reflection of survival and latency to capture, is lower in habitats with significant levels of structural complexity (Gotceitas and Brown 1993, Tupper and Boutilier 1997). In estuarine environments, the high association of juvenile fish with seagrass beds, relative to unvegetated sand, might partially reflect the provision of refuge, via structural complexity, by 'actively' interfering with predator foraging. The ability of small fish to avoid capture and the interference to foraging by predatory fish is often related to structural characters of seagrass including leaf density and morphology (Stoner 1982, Mattila 1992, 1995, Gotceitas *et al.* 1997). The results from our study imply that structural complexity, regardless of whether it is provided naturally, seagrass, or via artificial materials, exclusion cages, is important in determining predation patterns. At Blairgowrie, comparisons of the abundance of *S. punctata* between cage treatments within each habitat implied that seagrass beds were somehow mediating predation. However, our observations of habitat preference in predatory fish show that predatory fish actually foraged very little in seagrass habitats. Video recordings of predatory fish showed that *A. truttacea* occurred in seagrass only once during 480 minutes of video footage, while over unvegetated sand, *A. truttacea* were recorded in cage controls and uncaged areas during each recording event. This result is interesting, because, regardless of the potential for the structural complexity in seagrass beds to mediate predation, in fact, predatory fish were using this type of habitat only rarely. Therefore, differences in the numbers of *S. punctata* between seagrass and unvegetated sand do not necessarily reflect the interference of predation by aspects of the seagrass, but are more likely to be related to habitat preferences of predatory fish and greater mortality with increasing predation pressure, and/or selection by juvenile fishes for areas with low numbers of predators. This situation is alluded to by Peterson and Black (1994), who identified problems in interpreting results from studies where processes, in our case predation activity, potentially interact with treatments, habitats, seagrass and unvegetated sand. Why predatory fish occur less in seagrass could reflect some adaptive behaviour to restrict foraging to areas where prey are easiest to catch, or as Sweatman and Robertson (1994) suggested, to avoid the risk of predation to themselves from still larger piscivores. More research is now needed which assesses how the habitat complexity generated by seagrass interacts with predator activity, and why predator activity varies amongst habitats of variable structure.

Dietary composition, together with measures of local abundance, can provide correlative evidence on the potential for predatory fish to influence the assemblage structure of their prey (Hall *et al.* 1995, Connell and Kingsford 1997), and this information is an important prerequisite for manipulative experiments that are designed to assess the importance of piscivores (Connell and Kingsford 1997). In our study, *Arripis truttacea* consumed a variety of fishes including clupeids, atherinids, pleuronectids and gobiids, but in contrast to what might be expected given the variability in abundance of *S. punctata* between cage treatments, *S. punctata* were conspicuously absent from the diets of *A. truttacea*, even though previous research has shown that sillaginids are consumed by juvenile *A. truttacea* (Hindell *et al.* 2000). Unless *S. punctata* contributed exclusively to the 'unidentified' dietary component of *A. truttacea* diets, which is possible in view of the likely rapid rate of digestion for these early post-settlement fish, then it is likely that our results represent anti-predator behaviour, selection of areas with low numbers of predators, rather than variability in direct mortality. Patterns in recruitment of fish within mosaics of unvegetated sand and seagrass have previously been shown to be due to behaviourally mediated predator avoidance by recruits rather than the depredations of predatory fish (Sweatman and Robertson 1994, Jordan *et al.* 1996). Alternatively, atherinids and clupeids represented large proportions in the diets of *A. truttacea*, and these fish displayed strong associations with exclusion cages (J. Hindell unpublished data), so it is plausible that direct predation influences small-scale spatial patterns in some fishes. More information about microsite selection with respect to the local abundance of predatory fish is required in order to apportion contributions of direct predation induced mortality versus antipredator behaviour to the spatial variability in abundance of *S. punctata*.

The importance of recruitment variability, spatial and temporal variability in the input and settlement of juveniles, in determining the observed distributions of fishes, particularly adults, is debatable (Caley *et al.* 1996, Hixon 1998). However, recruitment patterns are often considered to strongly influence broad-scale patterns in abundances of juveniles and adults (Doherty and Williams 1988, Gutierrez 1998, Ohman *et al.* 1998). In seagrass habitats, broad-scale (between sites) variability in the abundance of juvenile fish can be explained by environmental processes that influence larval supply (Eggleston 1995, Jenkins *et al.* 1998). Bell and Westoby (1986b) suggest that larval supply is the proximate cause of spatial variability in abundances of juvenile fish soon after settlement, but preliminary distributions may then be modified by redistribution of juvenile fish to microsites which favour survival. For our study, this would be areas with low numbers of predators and/or sufficient refuge from predation. Therefore, measuring the local abundances of predatory fishes potentially affords researchers an estimate of their predation potential. Theoretically, if predation is important in structuring assemblages of fish prey at the scale of amongst-sites, then sites with the most predatory fish would correspond to sites with the fewest prey fish, (Hixon 1986, 1991, Connell and Kingsford 1997). In our study, predation patterns, differences in the abundance of *S. punctata* between exclusion cages, cage controls and uncaged regions, were relatively consistent within habitats, seagrass or unvegetated sand, regardless of the site. Additionally, predatory fish were most abundant at Blairgowrie, but there were very low numbers of *A. truttacea* at the other locations. Interestingly, *S. punctata* were also most abundant at Blairgowrie. Despite the apparently strong effects of predation, indicated by the between cage patterns in sillaginid abundance in unvegetated sand, the overall effect of predation did not appear to be influencing the abundance of fish at the site level. Although our study was conducted at relatively few sites, the results suggest that predation effects *per se*, although consistent between habitats across sites, are less important determinants of large-scale spatial variability in the abundance of small fish. Bell *et al.* (1987) suggested that abundances of fish in isolated seagrass units were not due to settlement preferences based on physical complexity of seagrass, or on post-settlement predation, but were due to the availability of larvae prepared to settle indiscriminately into any shelter. Our results support the paradigms promoted by Bell and his colleagues (Bell and Westoby 1986a, Bell and Pollard 1989), whereby larval supply probably drives the initial broad-scale spatial patterns in small fish abundances, but, at least in our study, processes such as predation strongly contribute to the inter-habitat variability within a site. More specifically, the effects of predation by *Arripis truttacea* on the inter-habitat variability in abundances of *S. punctata* shows that, within a location, processes related to predation are restricting the distribution of *S. punctata* to habitats where predation pressure is 'low', and this impact is consistent between sites.

Predatory fish are commonly size selective with regards their prey, and therefore, predation potentially influences the size structure of juvenile fishes (Folkvord and Hunter 1986, Pepin and Shears 1995, Manderson *et al.* 1999). Levin *et al.* (1997) showed that the presence of predatory fishes was associated with a higher mean size of fish recruits, which they attributed to size selective predation. Similarly, Connell (1998) found that growth increased in prey fish released from predation, although Jaquet and Raffaelli (1989) showed that predation did not alter the size structure of prey. Within sites, lengths of *Sillaginodes punctata* did not vary between cage treatments or habitats in ways that were consistent with either predatory fishes influencing their size distributions or juveniles changing their habitat selection ontogenetically, even at Blairgowrie, where, given the large numbers of predators, a strong effect should have been observed if predation was size-selective . In view of the apparent importance of behaviour rather than depredation in determining habitat patterns in relation to predation pressure, our results additionally suggest that antipredator behaviour is not size-specific with regards *S. punctata.* We contend that the slight variability in SLs of *S. punctata* between sites is more likely to be related to the supply of larvae and their size at settlement, which generally varies positively with distance into Port Phillip Bay (Jenkins *et al.* 1996, Jenkins and Wheatley 1998). Juvenile *S. punctata* enter Port Phillip Bay from Bass Strait, and there is no breeding stock inside the bay (Kailola *et al.* 1993). Blairgowrie is the closest site to the source of larvae and therefore, is the first of our three sites to receive larvae. The other sites receive juvenile *S. punctata* later, by which time, as our results suggest, they are generally larger in size.

Steele (1999) showed that magnitude and patterns of recruitment for a reef fish were similar among shelter treatments regardless of whether they were open to predation or not, and suggested other mechanisms not related to the impact of predation were important. Between sites in our study, the numbers of *Sillaginodes punctata* varied inconsistently between areas of unvegetated sand and seagrass where predatory fish were excluded. The numbers of *S. punctata* were equal between seagrass and unvegetated sand protected from predators at Blairgowrie, but numbers of *S. punctata* were higher and lower, in unvegetated sand compared with seagrass, at Kilgour and Grand Scenic respectively. This implies that the provision of refuge from predation was not the only role of seagrasses, at least at Kilgour and Grand Scenic, and other processes, such as food availability are likely to interact to determine observed patterns (Kemp 1989, Keough and Jenkins 1995). Connolly (1994a) demonstrated that patterns in *S. punctata* were consistent with a model stressing the importance of prey availability in the role seagrass plays as habitat for small fish. Numbers of *S. punctata* were positively correlated with abundances of epifauna, which were highest in seagrass, intermediate in cleared patches and lowest in unvegetated sand. Conversely, Holbrook and Schmitt (1988) showed that, regardless of food levels, fish preferred to forage in areas that provided a refuge from predation. Therefore, at Kilgour, where more *S. punctata* were sampled in areas of unvegetated sand than seagrass from which predators had been excluded, unvegetated sand may actually be a 'preferred' foraging habitat, but *S. punctata* are restricted to foraging in seagrass, probably because of predatory fish and the associated risk to survival. Further research is needed to determine how *S. punctata* respond to predatory fish by altering their foraging habitats, but from this preliminary data, we contend that local abundances of *S. punctata* are a reflection of a combination of processes, including food availability and predation, and the relative importance of these processes varies between the sites investigated in our study.

Cage effects may strongly complicate the interpretation of effects due to predation by fish (Kennelly 1991, Steele 1996, Connell 1997). Unmeasured processes related to the provision of structure via the materials used to construct cages could promote a predation effect, even though it does not actually exist, in effect, an ecological type I error. For example, differential baffling effects between the structure of partial and exclusion cages might facilitate changes to the composition of meiofauna or sediment (Kennelly 1991), which may subsequently attract small fish and thereby generate a predation effect. Bell *et al.* (1987) showed that the numbers of labrids were highly related to the amount of cage structure. In thinned seagrass, labrids were most abundant in exclusion cages, least abundant in uncaged areas and intermediately abundant in cage controls. Over unvegetated sand, labrids were higher in exclusion cages than uncaged areas, but the numbers of labrids in partial cages was the same as exclusion cages. Examples such as these were the reason for Connell's (1997) suggestion that predation studies be augmented with additional data, using both published studies and complimentary novel experiments, which help to clarify our understanding of the importance of cage effects resulting from differential structure between treatments, and enable researchers to more convincingly interpret patterns between cage treatments in relation to predation.

Previous research indicates that the partial cages used in our study were appropriate controls for structural artefacts pertaining to the modification of hydrodynamic features or biological processes. The mesh size used in our cages did not inhibit the movement of small fishes, so there was no retention effect of the predator exclusion mesh (Bell and Westoby 1986a). Jaquet and Raffaelli (1989) showed that mesh as small as 4 mm (the mesh used in our cages was 15 mm) did not modify the sediment regime inside cages, and Virnstein (1978) suggested that increasing the size of the cage (we used large, 16 m^2 cages) reduces the ratio of cage structure to internal area and therefore should reduce the impact of effects associated with the cage structure. In fact, if the patterns between caging treatments over unvegetated sand were related to the mediation of environmental disturbance by cage structure, then similar caging patterns would have been unlikely at sites that clearly vary in their disturbance regimes. The substrate at Grand Scenic is composed of fine sand and high levels of organic material because this area is located in a region where the currents are weak (Longmore *et al.* 1990, Black *et al.* 1993). Conversely, Blairgowrie is situated at a location where the currents are relatively strong and the wave action is considerably greater (Longmore *et al.* 1990, Black *et al.* 1993), and the sand in this region is coarser and contains less organic material.

While Martin-Smith (1993) and Schmidt and Warner (1984) showed that cage effects alter the abundance of epifauna, Schrijers *et al.* (1998) found that abundances of meiofauna, which in our study were the main food of juvenile *S. punctata* (Jenkins *et al.* 1996), were unaffected by the differential structure in cage treatments, nor the fouling or sedimentation associated with these, even after 5 months. And Mattila and Bonsdorff (1989) found that normal biological exchange was maintained between the cages and the external environment using similarly sized mesh to ourselves. Research carried out contemporaneously to this work showed that cage structure did not modify any one of five size components or the organic content of the sediment, or abundances of meiofauna (J. Hindell unpublished data). Therefore, we do not believe that the structure of cages used in our study complicates the interpretation of predation effects by altering environmental or biological parameters.

Additional structure in marine environments may act as a type of fish attraction device (Kingsford 1993, Clarke and Aeby 1998), around which predatory fish and their teleost prey may congregate, and these effects can partially obscure, or prevent the interpretation of, predation effects. Cage structure is widely acknowledged as important in attracting macrofauna (Reise 1985), however, the numbers of *Sillaginodes punctata* were not linearly related to the amount of cage structure. Furthermore, underwater observations showed that other epibenthic/pelagic fishes, such as atherinids and clupeids, as well as *S. punctata*, did not congregate around cage walls. Therefore, differences in the numbers of *S. punctata* between cage treatments can be interpreted more unequivocally in terms of predation rather than cage artefacts related to the attraction of fishes that respond positively to habitat structure.

The successful interpretation of results from studies that use partial cages to control for cage effects are generally bound in their conclusions by the usually untested assumption that predatory animals forage inside cage controls with similar frequency to that which they forage over uncaged regions. However, it is important to measure how predator impact is modified by different mechanisms of predator manipulation because, as Virnstein (1978) observed, it is difficult to conceive of a cage control that provides all the structure of an exclusion cage, but allows access to predatory animals. Connell (1996, 1997) measured abundances of predatory fishes visually, but diver observations potentially underestimate abundances of fast-swimming and transient predatory fishes which are difficult to observe and count (Hickford and Schiel 1995, Connell *et al.* 1998, Tupper and Hunte 1998), and therefore, less intrusive techniques, such as underwater video cameras, may be quantitatively more accurate in measuring local abundances of predatory fishes and their prey (Burrows *et al.* 1994). In our study, underwater observations showed that *Arripis truttacea* occurred inside partial cages over unvegetated sand in similar numbers to those observed over uncaged areas, and therefore, it is reasonable to conclude that the foraging pressure inside partially caged areas is similar to that over uncaged areas. Interestingly, despite the potential for cage controls to partially alter abundances of predatory fishes, Connell (1997) also showed that abundances of large predatory fishes were unaffected by partial cages, and predation pressure between open plots and partial cages was commensurable. The predation patterns suggested by the variability in abundances of *S. punctata* between cage treatments in our study is unlikely to be driven by either differential predator use of uncaged areas compared with cage controls, or variable attraction of fishes to different levels of cage structure. Subsequently, our results can be attributed more convincingly to predation by fish, and underwater videos are useful in elucidating the importance of artificial structure in determining patterns in abundances of fishes.

7.2. Evaluating links between fish and seagrass using isotope analyses and measure of abundance

Understanding the nature and strength of links between fishes and the habitats within which they occur is important in managing different habitats. Seagrass beds are thought to be important in the provision of foraging habitats for juvenile and adult fishes, however, the strength and nature of this relationship is equivocal because few studies have assessed abundances of large fishes in relation to their prey while simultaneously measuring the strength of these links using dietary and stable isotope analyses. Our study measured abundances of large and prey fishes, and quantitatively detailed the trophic structure and nutritional base of fishes in relation to their teleost prey and various habitat types using a combination of gut contents and stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$). We also measured the spatial (between sites) and temporal (between seasons) variability in the nature of these links.

Abundances of fish associated with seagrass beds vary between seasons and different locations (Ferrell *et al.* 1993, Jenkins *et al.* 1997b), probably because of the seasonality in recruitment of larval fishes (Kingsford 1988, Neira *et al.* 1992), and movements of adults fishes (Hyndes *et al.* 1999) in response to spawning, feeding or environmental disturbance. Regardless of species, abundances of large fish in our study varied little between seasons, and this appeared to be manifested at the assemblage level, which similarly varied little between seasons. However, at both the assemblage and individual levels (for total fish and the two most common species), large fish varied strongly between locations. These patterns appeared to be a reflection of the higher abundances of *Arripis truttacea* at St Leonards and the exclusive association of *Kestratherina esox* with Grand Scenic, although higher numbers of platycephalids (*Platycephalus laevigatus* and *P. speculator*) at St Leonards also contributed to the broad-scale spatial variability in assemblage structure of fishes. Whether abundances of large fishes varied seasonally depended on the species and the site; abundances of *A. truttacea* varied seasonally seasonal at Grand Scenic but not at St Leonards, while abundances of *K. esox* and other large fishes (regardless of species) varied little between seasons. The lack of seasonal effect is partially a reflection of the inherent high variability in the large fish sampled; *A. truttacea* and *K. esox* are highly gregarious and their abundances are subsequently very patchy both spatially and temporally. However, the fact remains that these two species of fish generally occurred throughout the year at the sites within which they were most abundant. Our results imply that the potential impact of piscivorous fishes is likely to be relatively consistent throughout the year, however at some sites during certain times, predation pressure may increase due to an influx of large fishes from elsewhere. Broad-scale spatial (between sites) variability in abundances of piscivorous fishes, and subsequent predation impact, is likely to influence the utility of spatially disparate sites containing seagrass as nursery areas for juvenile (prey) fishes.

Recruitment variability can influence seasonal patterns in the assemblage structure of fish (Neira *et al.* 1992, Nash and Santos 1998, Power *et al.* 2000), particularly in seagrass habitats where a large proportion of the fishes are juveniles and their abundances reflect larval supply and ontogenetic habitat shifts (Ferrell *et al.* 1993, Eggleston 1995, Jenkins and Wheatley 1998, Hyndes *et al.* 1999). However, in our study, neither abundances nor the assemblage structure of small fish varied between seasons. In the year of this study, the normally large recruitment of some fishes, for example *Sillaginodes punctata* (Jenkins and Wheatley 1998), was low (J. Hindell personal observation), perhaps because of the low number of zonal west winds (Thresher 1994). Coupled with the high relative numbers of permanent resident fish in seagrass (Burchmore *et al.* 1984), the dampened recruitment events could not be detected against the background variability in resident fish abundances. Jackson and Jones (1999) similarly found little variability between months at the year level in the assemblage structure of fish. They suggested that the consistent presence of the dominant species of fish throughout the year might mask the influence of monthly immigrations and emigrations. Conversely, there was a significant degree of site-specificity in the structure of fish assemblages. Variability in abundances of small fishes between sites is probably influenced by variable disturbance regimes and larval supply. For *S. punctata*, Jenkins *et al.* (1997a) have show that around 70 % of the variability in abundances of fish between locations within Port Phillip Bay can be explained by larval supply and disturbance regimes. Therefore, variability between sites in abundances of fish is likely to be influenced strongly by differential disturbance regimes, the supply of fish and habitat preferences following recruitment.

Burchmore *et al.* (1984) found that large fish in seagrass often consume prey that inhabit similar microsites; for example, benthic fishes commonly consume invertebrates associated with the substrate such as crustaceans and polychaetes while pelagic fishes mostly consume animals in the water column. In our study, most large fishes were demersal in nature and consumed crustaceans that were closely associated with seagrass. However, two pelagic fishes, *Arripis truttacea* and *Kestratherina esox*, commonly consumed benthic prey. This implies that pelagic fish probably forage throughout the water column. This ability to forage between microsites, together with their dietary flexibility and relatively large numbers, implies that these pelagic large fishes may be important determinants of the assemblage structure of juvenile fishes in seagrass.

The preferential excretion of ^{14}N via metabolism in animals and the subsequent increases in $\delta^{15}N$ by between 3 and 5 ‰ per trophic level (Peterson and Fry 1987), has been used extensively to describe the nature of trophic interactions (Hobson and Welch 1992, Rau *et al.* 1992, Hansson *et al.* 1997). Large fish that consume mostly teleost prey have a higher trophic position, greater $\delta^{15}N$, than fishes that consume mostly invertebrates (Thomas and Cahoon 1993, Beaudoin *et al.* 1999). The trophic relationships demonstrated between fishes and habitat samples in our study were slightly site specific, but overall they suggested that there were two trophic levels in the fish/seagrass system studied: fishes that consume mainly benthic invertebrates and those that are commonly piscivorous or consume planktonic animals. Piscivorous fishes such as *Arripis truttacea* and *Arripis georgiana* had the highest $\delta^{15}N$ values, while fishes such as *Gymnapistes marmoratus*, which are documented as consuming mainly benthic crustaceans (Edgar and Shaw 1995, Hindell *et al.* 2000) had values of $\delta^{15}N$ only slightly higher than those of seagrass.

The trophic positions of animals commonly vary between locations (Deegan and Garritt 1997, Jennings *et al.* 1997, Thompson *et al.* 1999), and between alternative habitats at particular locations (Fry *et al.* 1999). In fact, variability in isotopic signatures within species may be largely determined by site differences (Thomas and Cahoon 1993). Jennings *et al.* (1997) imply that some of the variability in trophic position between sites is caused by spatially variable feeding strategies; there is a degree of plasticity in feeding strategies that provide predatory animals with greater adaptive flexibility to respond to site specific changes in food availability. Recently, Fry *et al.* (1999) showed that the trophic levels of fish caught in a littoral marsh zone were lower than those caught offshore. In our study, the trophic level varied between fishes caught in shallow seagrass habitats, and this variability appeared to be related to whether they fed primarily on benthic animals, or on pelagic prey. At each location, some of the species of fish with the highest values of $\delta^{15}N$ consumed mostly pelagic micro-crustacea; at St Leonards, atherinids and *Spratelloides robustus* had higher $\delta^{15}N$ than piscivorous fish (*A. truttacea* and *P. speculator*); at Grand Scenic, *Stigmatopora* sp., which consume a large proportion of planktonic calanoid copepods (Howard and Keohn 1985, Edgar and Shaw 1995, Jenkins and Sutherland 1997) had similar $\delta^{15}N$ to the piscivorous *Kestratherina esox*, which feed on fish and benthic macro-crustaceans. *Aldrichetta forsteri*, which has a broad omnivorous diet (Edgar and Shaw 1995), had similar mean $\delta^{15}N$ to both *K. esox* and *Stigmatopora* sp. Our data suggests that benthic fishes, such as *Stigmatopora* sp., potentially provide a strong coupling between open-water ecosystems and benthic habitats (Edgar and Shaw 1995), and trophic position of fishes feeding on pelagic invertebrates may be similar to piscivorous fishes.

Predatory fishes that forage in seagrass habitats are considered to be generalists; they consume a variety of prey types (Orth *et al.* 1984, Bell and Pollard 1989). Piscivorous fishes are a relatively common element of the fauna of seagrass habitats, and they commonly compliment the teleost component of their diet with a range of invertebrates including polychaetes, macro- and micro-crustaceans (Edgar and Shaw 1995, Hindell *et al.* 2000). The conspicuous absence of exclusively piscivorous species is probably a reflection of the large numbers of alternative (primarily crustacean) prey present in seagrass (Hutchings 1981) and the temporally variable nature of juvenile (prey) fishes (Neira *et al.* 1992, Ferrell *et al.* 1993, Hyndes *et al.* 1999). The generalist nature of fishes in seagrass beds implies that fish will most likely consume abundant prey preferentially, although this is likely to be influenced by behavioural and morphological aspects of the predator and prey (Hambright 1991, Boubee and Ward 1997, Michaletz 1997). In our study, the utility of $\delta^{15}N$ in matching dietary preferences appeared to vary spatially but not through time, depending on the species of predatory fish. For example, Grand Scenic contained higher numbers of small 'prey' fish than St Leonards, and *Arripis truttacea* and *Arripis georgiana* appeared to have a higher trophic level, and their stomachs contained more fish, than at St Leonards, where small fish, particularly atherinids, which are commonly preyed upon (Hindell *et al.* 2000), were far less abundant. For these predatory fishes, the broad-scale spatial differences in abundances of fish in their diets appeared to support their relative trophic position. Similarly, Beaudoin *et al.* (1999) found that fish feeding mainly on invertebrates in areas depauperate of fish prey had lower trophic levels than those that feed mainly on fish, in fish rich areas. Conversely, at Grand Scenic, even though *K. esox* consumed higher numbers of fish at some times of the year, this did not appear to translate into a higher trophic position, nor did it appear to relate to the availability of prey fish.. While the trophic position of fish appears to vary in a predictable manner with the availability of prey at different sites and stomach contents between locations, within a location, temporal variability in dietary composition and availability of different prey may not necessarily translate into variability in trophic position.

The fractionation of $\delta^{13}C$ rarely exceeds 1 ‰ between trophic levels (DeNiro and Epstein 1978), therefore $\delta^{13}C$ values have been to used to identify the source of nutritional support in a given system. In our study, for small fish which are known to consume benthic crustaceans associated with seagrass beds (Burchmore *et al.* 1984, Edgar and Shaw 1995, Hindell *et al.* 2000), seagrass, *Heterozostera tasmanica*, appeared to be the primary source of nutrition. However, as the trophic position of fishes increased, particularly at Grand Scenic, there was a trend for the values of $\delta^{13}C$ to become more negative. This suggests that either the base for nutrition shifts away from seagrass as the trophic level increases or the fractionation of $\delta^{13}C$ is greater than previously thought. Values of $\delta^{13}C$ have been used to distinguish between pelagic and benthic feeding in fishes (Jennings *et al.* 1997, Vander Zanden *et al.* 1998). ^{13}C was enriched in pelagic and depleted in benthic food chains, and while not a useful indicator of trophic position, it does indicate inshore/benthic versus offshore/pelagic feeding preferences (Hobson 1993), regardless of whether the animals are feeding at similar trophic levels (Thomas and Cahoon 1993). For example, pelagic/benthic feeding fishes had $\delta^{13}C$ values close to -24‰, while primarily benthic feeding fishes had levels around -21‰, and the similarity between the $\delta^{13}C$ levels in phytoplankton and the pelagic food web is evidence for the phytoplankton being the primary source of carbon in this food web (Yoshii *et al.* 1999). In our study, fishes such as *Gymnapistes marmoratus*, *Neoodax balteatus* and *Platycephalus laevigatus* consume mostly macro-crustaceans and gastropods associated with seagrass (see also Hindell *et al.*, 2000) and subsequently have different values of $\delta^{13}C$ compared with fishes such as *Pseudocaranx wrightii* and *Dactylophora nigricans,* which consume mainly benthic infauna closely associated with unvegetated sand. Pelagic fishes such as *Arripis truttacea* and *Arripis georgiana* at Grand Scenic mainly feed on juvenile and larval fishes that consume planktonic crustacea, and subsequently the base of nutritional support for this trophic level is associated more closely with the plankton. Therefore, while seagrass beds appear to be important as a foraging base for several species of fish, they may be less important to fishes at higher trophic levels whose values of $\delta^{13}C$ imply that the base of nutritional support is outside the seagrass system, probably pelagic based. Therefore, the association of pelagic fishes with seagrass beds may be a reflection of the provision of refuge from perturbation, both biological and environmental.

Measures of $\delta^{13}C$ are useful in differentiating between locations for samples from animals and habitats (Jennings *et al.* 1997, Thompson *et al.* 1999). For example, Marguillier *et al.* (1997) differentiated fish communities from different locations on the basis of $\delta^{13}C$. In the present study, *Heterozostera tasmanica* and sediments generally had less negative values of $\delta^{13}C$ at Grand Scenic than St Leonards. Similarly, fish such as *Sillaginodes punctata* and *Gymnapistes marmoratus* had more negative values of $\delta^{13}C$ at St Leonards than Grand Scenic. Our study implies that site-specific differences can be identified in fishes even within the same form of habitat, and this information has potential applications in following broad-scale spatial movements of fish that forage in similar habitats amongst locations.

The literature is replete with examples of how the trophic level of animals varies with age (Cowen 1986, Hambright 1991, Eggleston *et al.* 1998). Ontogenetic shifts in diet may also be accompanied by shifts in trophic level and the base of nutritional support, and a positive relationship between total length and values of $\delta^{15}N$ in fish, which may be reflected in the stomach contents by increasing amounts of fish prey, is common (Gu *et al.* 1996, Lindsay *et al.* 1998, Vander Zanden *et al.* 1998, Yoshii *et al.* 1999). In our study the relationship between the size of the predatory fish and the isotope value was dependant on the isotope measured and the species of fish. There was no relationship between length and either $\delta^{15}N$ or $\delta^{13}C$ for *Kestratherina esox*, which suggested that their base of nutritional support and trophic position did not vary with the changes in length observed, although the range observed was relatively narrow. Conversely, $\delta^{15}N$ increased significantly with length in *Arripis truttacea*, but values of $\delta^{13}C$ did not vary with the size of fish. This information suggests that while the base of nutrition for *A. truttacea* does not change with length – regardless of length *A. truttacea* consume mostly pelagic crustacea and fish larvae, larger *A. truttacea* consume higher numbers of fish and subsequently have a higher trophic position. Stable isotope analysis appears to be a useful tool for differentiating ontogenetic patterns in trophic level and habitat links for some species of fish.

Temporal variation in isotope ratios for fish can be interpreted by visual gut contents analyses (Yoshioka and Wada 1994). However, stable isotope measures in environmental parameters and habitats may vary seasonally, potentially complicating any interpretation of trophic linkages. For example, $\delta^{13}C$ values in seagrass may vary between seasons as a result of changes in source carbon, irradiance levels and temperature (McMillan 1980, Hemminga and Mateo 1996). Our study measured the variability in $\delta^{15}N$ and $\delta^{13}C$ over four seasons, and the extent to which seagrass samples varied seasonally depended on the site. Seagrasses varied seasonally only at St Leonards, where generally there was a trend for $\delta^{15}N$ and $\delta^{13}C$ to be lower during spring and summer than winter and autumn. A review of the literature by Hemminga and Mateo (1996) suggests that lower temperatures and irradiance levels are associated with more negative values of $\delta^{13}C$, however, more negative values in our study occurred during seasons when temperatures and irradiance were greatest. Therefore, the contrast between our results and those discussed by Hemminga and Mateo (1996) requires further attention. Interestingly, the variability in isotope values of fish appeared to be unrelated to the changes occurring in either of the habitats. Therefore, while seasons can potentially influence stable isotope measures, in our study, seasonality appears to be less important than location in determining values of $\delta^{15}N$ or $\delta^{13}C$ in fishes, particularly where the fishes concentrate on prey which probably have little trophic relationship with, in our case, seagrass beds.

8. Benefits

This project has benefited fisheries and habitat management by increasing our understanding of the strength of links between spatially discrete seagrass beds and juvenile and adult commercially and recreationally valuable fishes. This information can be used to protect sites that are important in the provision of resources that enhance associated fisheries.

Commercial and recreational fisheries sectors have benefited from increasing our understanding about how predatory fish and prey fish interact amongst each other and with seagrass habitats. Understanding these links is important to increasing our capacity to predict how commercial fish populations will change as a consequence of changes to the extent of seagrass (Connolly *et al.*, 1999).

This project has directly complimented and enhanced information gained from other projects (Jenkins *et al.*, 1997, Jenkins *et al.*, current research) which have/are investigating how other processes, such as food availability or hydrodynamic features, influence spatial patterns in the abundances and diversity of fishes in seagrass habitats.

9. Further Development

This project presented some interesting and novel research from two complementary aspects of a project, which should be developed further.

The results from the experimental predation study showed that areas containing seagrass are important in the provision of habitat for juvenile King George whiting, probably because of the low numbers of predatory fishes. Abundances of predatory fish, particularly Western Australian salmon, were highly variable between locations, and within a location, predatory fish appeared to avoid vegetated areas. A logical extension of this aspect of the project would be to assess the generality of variable habitat use by predatory fish over larger spatial scales. Further, it would be interesting to assess the nature of predation in alternative vegetated aquatic habitats, such as rocky reefs and mangroves, and to assess, using pluralistic manipulative experiments, the relative importance of predation compared with alternative processes such as physical disturbance, food availability and larval supply. Information gleaned from this type of research will be useful in evaluating the relative importance of alternative habitats.

The second aspect of this project demonstrated the utility of using isotope analyses in combination with measures of abundance and dietary information to accurately describe the variability and diversity in the nature of fish/habitat links within seagrass beds. However, this type of data is largely descriptive and correlative. Further research should focus on experimentally evaluating how the isotopic composition of fish changes under specific environmental conditions. For example, standardised fish (fish with the same or similar isotopic composition) could be caged in different types of habitat for different lengths of time to determine the specificity of fish-habitat links. This type of approach will provide a much less equivocal assessment of how fish interact with habitats.

By integrating the two approaches presented in this project, experimental and descriptive, scientists and mangers will have a better understanding of the importance of the habitat specific nature of various processes. Subsequently, they will be better able to manage different marine environments so that the associated fisheries are sustainable.

10. Conclusions

The following conclusions individually address each of the primary objectives outlined in Section 4.

10.1. Contribution of seagrass associated fishes to the diets of commercially valuable predatory fishes

Several commercially and recreationally important predatory fishes, such as rock flathead (*Platycephalus laevigatus*), yank flathead (*Platycephalus speculator*) and Australian salmon (*Arripis* spp.) were captured in the vicinity of seagrass beds during this study. These were found to consume a diverse assemblage of small, often juvenile, fishes associated with seagrass beds. All of the fishes found to be consumed were non-commercially important species such as atherininds, syngnathids, gobiids and clupeids. No single group of small, seagrass associated fish appeared to be differentially important in the diets of predatory fishes, and no exclusively piscivorous species of fish were found. Instead, predatory fish supplemented their diet with large numbers of crustacean and polychaete prey. For example, rock flathead consumed fish rarely; most of its diet was composed of the red swimmer crab (*Nectocarcinus integrifrons*). Overall, seagrass beds are an important habitat for many non-commercial species of fish which make an important contribution to the diets of larger, economically valuable species. While seagrass habitats may not necessarily be important in the provision of foraging areas for exclusively piscivorous species of fish, they are important to species of fish, such as yank flathead, which commonly consume seagrass-associated fishes.

10.2. Effects of predatory fishes on abundances of juvenile fishes of economic importance in seagrass beds

The importance of predation by fish in structuring populations and assemblages of small fish in seagrass beds is somewhat controversial. For juveniles of King George whiting (*Sillaginodes punctata*), predation strongly influences their inter-habitat distribution within a location, probably by affecting their behaviour rather than direct mortality, and these impacts are consistent over relatively large (10's of km) spatial scales. However, video evidence suggested that predatory fish rarely used vegetated habitats, relative to unvegetated areas.

While seagrass beds are important in reducing the mortality of juvenile King George whiting compared with unvegetated sand, it appears that it is the avoidance of these habitats by predatory species, rather than the physical mediation of predatory foraging *per se* by aspects of the seagrass beds, which determines the importance of seagrass beds as nursery habitats.

10.3. The strength of links between piscivorous fish, their fish prey and seagrass beds described using stable isotope values

Measures of abundance, together with analyses of stomach contents and isotopic composition, are thought to provide a thorough description of the trophic structure and base of nutritional support in seagrass/fish associations, particularly where these measures are taken through time and at more than one location. The results of this study show that there is a relatively high degree of variability in the results from carbon and nitrogen stable isotope analyses; this variability is partially a reflection of differences between sites and times of the year. Most of the small fishes captured appeared to have high affinities with seagrass beds *per se* based on their abundances. Several groups of these small fish had stable isotope compositions that were consistent with 'close' nutritional associations with seagrass, e.g. the clinids and a scorpaenid. However, these groups of fish were not commonly consumed by predatory fishes. The species of fish most commonly consumed by predatory fish such as *A. truttacea* and *P. speculator*, e.g. the atherinids and clupeids, had isotope compositions consistent with nutritional reliance on pelagic food webs, not seagrass beds. Therefore, even though small fishes and their predators may be associated with seagrass beds, the strength of this link is not always based strongly on nutritional elements, but rather may be a function of protection from predation or other forms of physical disturbance such as wave action.

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12. References

Anon. 1973. Environmental study of Port Phillip Bay. Report on phase one, 1968-1971. Melbourne and Metropolitan Board of Works and Fisheries and Wildlife Department of Victoria, Melbourne.

Anderson, M. J., and A. J. Underwood 1994. Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. Journal of Experimental Marine Biology and Ecology **184**:217-236.

Beaudoin, C. P., W. M. Tonn, E. E. Prepas, and L. I. Wassenaar 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. Oecologia **120**:386-396.

Bell, J. D. and D. A. Pollard 1989. Ecology of fish assemblages and fisheries associated with seagrasses. In: Larkum, A. W. D., McComb, A. J., and Shepherd, S. (Eds.) Biology of seagrasses: a treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, pp. 565-609.

Bell, J. D., and M. Westoby 1986a. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia **68**:205-209.

Bell, J. D., and M. Westoby 1986b. Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. Journal of Experimental Marine Biology and Ecology **104**:275-295.

Bell, J. D., A. S. Steffe, and M. Westoby 1985. Artificial seagrass: How useful is it for field experiments on fish and macroinvertebrates. Journal of Experimental Marine Biology and Ecology **90**:171-177.

Bell, J. D., M. Westoby, and A. S. Steffe 1987. Fish larvae settling in seagrass: do they discriminate between beds of different leaf density ? Journal of Experimental Marine Biology and Ecology **111**:133-144.

Bell, J. D., A. S. Steffe, and M. Westoby 1988. Location of seagrass beds in estuaries: effects on associated fish and decapods. Journal of Experimental Marine Biology and Ecology **122**:127-146.

Beukers, J. S., and G. P. Jones 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecologia **114**:50-59.

Black, K., D. Hatton, and M. Rosenberg 1993. Locally and externally-driven dynamics of a large semi-enclosed bay in southern Australia. Journal of Coastal Research **9**:509-538.

Bohnsack, J. A., A. Ecklund, and A. M. Szmant 1997. Artificial reef research: is there more than the attraction-production issue. Fisheries **22**:14-23.

Booth, D. J., and G. Wellington 1998. Settlement preferences in coral-reef fishes: effects on patterns of adult and juvenile distributions, individual fitness and population structure. Australian Journal of Ecology **23**:274-279.

Boon, P. I., F. L. Bird, and S. E. Bunn 1997. Diet of the intertidal Callianassid shrimps *Biffarius arenosus* and *Trypea australiensis* (Decapoda: Thalassinidae) in Western Port (southern Australia), determined with multiple stable-isotope analyses. Marine and Freshwater Research **48**: 503-511

Boubee, J. T., and F. J. Ward 1997. Mouth gape, food size, and diet of the common smelt *Retropinna retropinna* (Richardson) in the Waikato River system, North Island, New Zealand. New Zealand Journal of Marine and Freshwater Research **31**:147-154.

Brewer, D. T., S. J. M. Blaber, J. P. Salini, and M. J. Farmer 1995. Feeding ecology of predatory fishes from Groote Eylandt in the Gulf of Carpentaria, Australia, with special reference to predation on penaeid prawns. Estuarine, Coastal and Shelf Science **40**:577-600.

Browman, H. I. 1995. Introduction: Commentaries on current research trends in recruitment studies. Marine Ecology Progress Series **128**:305-310.

Burchmore, J. J., D. A. Pollard, and J. D. Bell 1984. Community structure and trophic relationships of the fish fauna of an estuarine *Posidonia australis* seagrass habitat in Port Hacking, New South Wales. Aquatic Botany **18**:71-87.

Burrows, M. T., R. N. Gibson, L. Robb, and C. A. Comely 1994. Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. Journal of Experimental Marine Biology and Ecology **177**:251-268.

Butler, A., and P. Jernakoff 1999. Seagrass in Australia: Strategic review and development of an R & D plan. CSIRO, Melbourne.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge 1996. Recruitment and the local dynamics of open marine populations. Annual Review of Ecology and Systematics **27**:477-500.

Cappo, M., D. M. Alongi, McB. Williams and N. Duke 1998. A Review and Synthesis of Australian Fisheries Habitat Research. Major threats, issues and gaps in knowledge of marine and coastal fisheries habitats - a prospectus of opportunities for the FRDC "Ecosystem Protection Program". Australian Institute of Marine Science: Project No. 95/055: 433 pp.

Carr, M. H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology **75**:1320-1333.

Carr, M. R., and K. R. Clarke 1994. Primer v4.0. Plymouth Marine Laboratories (NERC), UK.

Carr, M. H., and M. A. Hixon 1997. Artificial reefs: the importance of comparisons with natural reefs. Fisheries **22**:28-33.

Chesson, P. 1998. Recruitment limitation: a theoretical perspective. Australian Journal of

Ecology **23**:234-240.

Choat, J. H. 1982. Fish feeding and the structure of benthic communities in temperate waters. Annual Review of Ecology and Systematics **13**:423-449.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117-143.

Clarke, T. A., and G. S. Aeby 1998. The use of small mid-water attraction devices for investigation of the pelagic juveniles of carangid fishes in Kaneohe Bay, Hawaii. Bulletin of Marine Science **62**:947-955.

Connell, S. D. 1996. Variations in mortality of a coral-reef fish: links with predator abundance. Marine Biology **126**:347-352.

Connell, S. D. 1997. Exclusion of predatory fish on a coral reef: the anticipation, pre-emption and evaluation of some caging artefacts. Journal of Experimental Marine Biology and Ecology **213**:181-198.

Connell, S. D. 1998. Effects of predators on growth, mortality and abundance of a juvenile reef-fish: evidence from manipulations of predator and prey abundance. Marine Ecology Progress Series **169**:251-261.

Connell, S. D., and M. J. Kingsford 1997. The utility of descriptive information for assessing the impact of coral reef piscivores on their prey. Proceedings 8th International Coral Reef Symposium **1**:999-1004.

Connell, S. D., M. A. Samoilys, M. P. Lincoln Smith, and J. Leqata 1998. Comparisons of abundance of coral-reef fish: Catch and effort surveys vs visual abundance. Australian Journal of Ecology **23**:579-586.

Connolly, R. M. 1994a. Removal of seagrass canopy: effects on small fish and their prey. Journal of Experimental Marine Biology and Ecology **184**:99-110.

Connolly, R. M. 1994b. Comparison of fish catches from a buoyant pop net and a beach seine net in a shallow seagrass habitat. Marine Ecology Progress Series **109**: 305-309

Connolly, R., G. Jenkins, and N. Loneragan 1999. Links between seagrass dynamics and fisheries sustainability. Pages 36-68 *in* A. J. Butler and P. Jernakoff, editors. Seagrass Strategic Review and Development of an R&D Plan. CSIRO.

Cortes, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Science B**54**: 726-738.

Cowen, R. K. 1986. Site specific differences in the feeding ecology of a California sheephead, *Semicossyphus pulcher* (Labridae). Contemporary studies on fish feeding: the proceedings of GUTSHOP '84:193-203.

Deegan, L. A., and R. H. Garritt 1997. Evidence for spatial variability in estuarine foodwebs. Marine Ecology Progress Series **147**:31-47.

DeNiro, M. J., and S. Epstein 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim Comoschim **42**:495-506.

Doherty, P. J., and P. F. Sale 1985. Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs **4**:225-234.

Doherty, P. J., and D. McB. Williams 1988. The replenishment of coral reef fish populations. Oceanography and Marine Biology Annual Review **26**:487-551.

Edgar, G. J. 1990. The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass. Journal of Experimental Marine Biology and Ecology **137:** 215-240

Edgar, G. J. and A. I. Robertson 1992. The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian Amphibolis bed. Journal of Experimental Marine Biology and Ecology **160**: 13-31

Edgar, G. J., and C. Shaw 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. Journal of Experimental Marine Biology and Ecology **194**:83-106.

Ellis, M. J. and B. C. Coull 1989. Fish predation on meiobenthos: field experiments with juvenile spot *Leiostomus xanthurus*. Journal of Experimental Marine Biology and Ecology. **130**: 19-32

Eggleston, D. B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. Marine Ecology Progress Series **124**:9-22.

Eggleston, D. B., J. J. Grover, and R. N. Lipcius 1998. Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. Bulletin of Marine Science **63**:111-126.

Ferrell, D. J., S. E. McNeill, D. G. Worthington, and J. D. Bell 1993. Temporal and spatial variation in the abundance of fish associated with the seagrass *Posidonia australis* in south-eastern Australia. Australian Journal of Marine and Freshwater Research **44**:881-899.

Folkvord, A., and J. R. Hunter 1986. Size-specific vulnerability of Northern anchovy, *Engraulis mordax*, larvae to predation by fishes. Fishery Bulletin **84**:859-869.

Friedlander, A. M., and J. D. Parrish 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology **224**:1-30.

Fry, B., P. L. Mumford, F. Tam, D. D. Fox, G. L. Warren, K. E. Havens, and A. D. Steinman 1999. Trophic position and individual feeding histories of fish from lake Okeechobee, Florida. Canadian Journal of Fisheries and Aquatic Science **56**:590-600.

Gannes, L. Z., D. M. O'Brien, and C. Martinez del Rio 1997. Stable isotopes in animal ecology: assumptions, caveats and a call for more laboratory experiments. Ecology **78**:1271-1276.

Gibson, R. N. and L. Robb 1996. Piscine predation on juvenile fishes on a Scottish sandy beach. Journal of Fish Biology **I49**: 120-138

Gillanders, B. M., and M. J. Kingsford 1998. Influence of habitat on abundance and size structure of a large temperate-reef fish, *Acheorodus viridis* (Pisces:Labridae). Marine Biology **132**:503-514.

Gotceitas, V., and J. A. Brown 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia **93**:31-37.

Gotceitas, V., S. Fraser, and J. A. Brown 1997. Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Science **54**:1306-1319.

Gu, B., C. L. Schelske, and M. V. Hoyer 1996. Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure of the fish community in a shallow hyper-eutrophic lake. Journal of Fish Biology **49**:1233-1243.

Gutierrez, L. 1998. Habitat selection by recruits establishes local patterns of adult distribution in two species of damselfishes: *Stegastes dorsopunicans* and *S. planifrons*. Oecologia **115**:268-277.

Hall, S. J., D. Raffaelli, and W. R. Turrell 1990. Predator-caging experiments in marine systems: A re-examination of their value. The American Naturalist **136**:657-672.

Hall, S. J., W. S. C. Gurney, H. Dobby, D. J. Basford, S. D. Heaney, and M. R. Roberston 1995. Inferring feeding patterns form stomach contents data. Journal of Animal Ecology **64**:39-62.

Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: Role of predator mouth width and prey body depth. Transactions of the American Fisheries Society **120**:500-508.

Hansson, S. 1998. Methods of studying fish feeding: a comment. Canadian Journal of Fisheries and Aquatic Science **55**:2706-2707.

Hansson, S., J. E. Hobbie, R. Elmgren, U. Larsson, B. Fry, and S. Johansson 1997. The stable nitrogen isotope ratio as a marker of food web interactions and fish migration. Ecology **78**:2249-2257.

Harrigan, P., J. C. Zieman, and S. A. Macko 1989. The base of nutritional support for the Gray snapper (*Lutjanus griseus*): An evaluation based on a combined stomach content and stable isotope analysis. Bulletin of Marine Science **44**:65-77.

Heck, K. L., and L. B. Crowder 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. Pages 281-299 *in* S. S. Bell, E. D. McCoy and H. R. Mushinsky, editors. Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London, UK.

Heck, K. L., and R. J. Orth 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring assisted fish and motile macroinvertebrate assemblages. Pages 449-464 *in* V. S. Kennedy, editors. Estuarine Perspectives. Academic Press, New York.

Heck, K. L., and T. A. Thoman 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. Journal of Experimental Marine Biology and Ecology **53**:125-134.

Heck, K. L. and M. P. Weinstein 1989. Feeding habits of juvenile reef fishes associated with Panamanian seagrass meadows. Bulletin of Marine Science **45**: 629-636

Heck, K. L., and K. A. Wilson 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. Journal of Experimental Marine Biology and Ecology **107**:87-100.

Hemminga, M. A., and M. A. Mateo 1996. Stable carbon isotopes in seagrasses: variability in ratios and use in ecological studies. Marine Ecology Progress Series **140**:285-298.

Hesslein, R. H., M. J. Capel, D. E. Fox, and K. A. Hallard 1991. Stable isotopes of sulphur, carbon and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River Basin, Canada. Canadian Journal of Fisheries and Aquatic Science **48**:2258-2265.

Hettler, W. F. 1989. Food habits of juveniles of spotted seatrout and gray snapper in western Florida bay. Bulletin of Marine Science **44**: 155-162

Hickford, M. J. H., and D. R. Schiel 1995. Catch vs count: Effects of gill-netting on reef fish populations in southern New Zealand. Journal of Experimental Marine Biology and Ecology **188**:215-232.

Hindell, J. S., G. P. Jenkins, and M. J. Keough 2000. Variability in the abundances of fishes associated with seagrass habitats in relation to the diets of predatory fishes. Marine Biology **136**:725-737.

Hixon, M. A. 1986. Fish predation and local prey diversity. *In* C. A. Simenstad and G. M. Calliet, editors. Contemporary studies on fish feeding: the proceedings of gutshop '84. Dr. W. Junk Publishers, Boston.

Hixon, M. A. 1991. Predation as a process structuring coral reef fish communities. *In* P. F. Sale, editors. The Ecology of Fishes on Coral Reefs. Academic Press, Inc., San Diego, California.

Hixon, M. A. 1998. Population dynamics of coral-reef fishes: controversial concepts and hypotheses. Australian Journal of Ecology **23**:192-201.

Hixon, M. A., and M. H. Carr 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science **277**:946-949.

Hobson, K. A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series **95**:7-18.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia **120**:314-326.

Hobson, K. A., and H. E. Welch 1992. Determination of trophic relationships within a high Arctic marine food web using d13C and d15N analysis. Marine Ecology Progress Series **84**:9-18.

Holbrook, S. J., and R. J. Schmitt 1988. The combined effects of predation risk and food reward on patch selection. Ecology **69**:125-134.

Howard, R. K., and J. D. Keohn 1985. Population dynamics and feeding ecology of pipefish (Syngnathidae) associated with eelgrass beds of Western Port, Victoria. Australian Journal of Marine and Freshwater Research **36**:361-370.

Hutchings, P. 1981. The fauna of Australian Seagrass Beds. Proceedings of the Linnean Society of NSW **106**:181-200.

Hyndes, G. A., M. E. Platell, I. C. Potter, and R. C. J. Lenanton 1999. Does the composition of the demersal fish assemblages in temperate coastal waters change with depth and undergo consistent seasonal changes. Marine Biology **134**:335-352.

Hyslop, E. J. 1980. Stomach contents analysis- a review of methods and their application. Journal of Fish Biology **17**:411-429.

Jackson, G., and G. K. Jones 1999. Spatial and temporal variation in nearshore fish and macroinvertebrate assemblages from a temperate Australian estuary over a decade. Marine Ecology Progress Series **182**:253-268.

Jaquet, N., and D. Raffaelli 1989. The ecological importance of the sand goby *Pomatoschistus minatus* (Pallus). Journal of Experimental Marine Biology and Ecology **128**:147-156.

Jenkins, G. P., and K. P. Black 1994. Temporal variability in settlement of a coastal fish (*Sillaginodes punctata*) determined by low-frequency hydrodynamics. Limnology and Oceanography **39**:1744-1754.

Jenkins, G. P., and C. R. Sutherland 1997. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: colonisation and turnover rate of fishes associated with artificial macrophyte beds of varying physical structure. Journal of Experimental Marine Biology and Ecology **218**:103-125.

Jenkins, G. P., and M. J. Wheatley 1998. The influence of habitat structure on nearshore fish assemblages in a southern Australian embayment: comparison of shallow seagrass, reef algal and unvegetated sand habitats, with emphasis on their importance to recruitment. Journal of Experimental Marine Biology and Ecology **221**:147-172.

Jenkins, G. P., G. F. Watson, and L. S. Hammond 1993. Patterns of utilisation of seagrass (*Heterozostera*) - dominated habitats as nursery areas by commercially important fish. (Victorian Institute of Marine Sciences: Technical Report 19: 100 pp)

Jenkins, G. P., M. J. Wheatley, and A. G. B. Poore 1996. Spatial variation in recruitment, growth and feeding of post-settlement King George whiting, Sillaginodes punctata, associated with seagrass beds of Port Phillip Bay, Australia. Canadian Journal of Fisheries and Aquatic Science **53**:350-359.

Jenkins, G. P., K. P. Black, M. J. Wheatley, and D. N. Hatton 1997a. Temporal and spatial variability in recruitment of a temperate, seagrass-associated fish is largely determined by physical processes in the pre- and post-settlement phases. Marine Ecology Progress Series **148**:23-35.

Jenkins, G. P., H. M. A. May, M. J. Wheatley, and M. G. Holloway 1997b. Comparison of fish assemblages associated with seagrass and adjacent unvegetated habitats of Port Phillip Bay and Corner Inlet, Victoria, Australia, with emphasis on commercial species. Estuarine, Coastal and Shelf Science **44**:569-588.

Jenkins, G. P., M. J. Keough, and P. A. Hamer 1998. The contribution of habitat structure and larval supply to broad-scale recruitment variability in a temperate zone, seagrass-associated fish. Journal of Experimental Marine Biology and Ecology **226**:259-278.

Jennings, S., O. Renones, B. Morales-Nin, N. V. C. Polunin, J. Moranta, and J. Coll 1997. Spatial variation in the ^{15}N and ^{13}C stable isotope composition of plants, invertebrates and fishes on Mediterranean reefs: implications for the study of trophic pathways. Marine Ecology Progress Series **146**:109-116.

Jones, G. P. 1988. Ecology of rocky reef fish of north-eastern New Zealand. New Zealand Journal of Marine and Freshwater Research **22**:445-462.

Jones, G. P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. *In* P. F. Sale, editors. The ecology of fishes on coral reefs. Academic Press, San Diego, California.

Jordan, F., M. Bartolini, C. Nelson, P. E. Patterson, and H. L. Soulen 1996. Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). Journal of Experimental Marine Biology and Ecology **208**:45-56.

Kailola, P. J., M. J. Williams, P. C. Stewart, R. E. Reichelt, A. McNee, and C. Grieve 1993. Australian Fisheries Resources. Bureau of Resource Sciences, Department of Primary Industries and Energy, and Fisheries Research and Development Corporation, Canberra, Australia.

Kemp, W. M. 1989. Estuarine Seagrasses. *In* J. W. Day, C. A. S. Hall, W. M. Kemp and A. Yanez-Arancibia, editors. Estuarine Ecology. John Wiley and Sons, New York.

Kennelly, S. J. 1991. Caging experiments to examine the effects of fishes on understorey species in a sublittoral kelp community. Journal of Experimental Marine Biology and Ecology **147**:207-230.

Keough, M. J., and B. J. Downes 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia **54**:348-352.

Keough, M. J., and G. P. Jenkins. 1995. Seagrass meadows and their inhabitants. *In* A. J. Underwood and M. G. Chapman, editors. Coastal Marine Ecology of Temperate Australia. University of NSW Press, Sydney.

Kingsford, M. J. 1988. The early life history of fish in coastal waters of northern New Zealand: a review. New Zealand Journal of Marine and Freshwater Research **22**:463-479.

Kingsford, M. J. 1993. Biotic and abiotic structure in the pelagic environment: importance to small fish. Bulletin of Marine Science **53**:393-415.

Kingsford, M. J. 1998. Reef fishes. *In* M. J. Kingsford and C. Battershill, editors. Studying temperate marine environments: a handbook for ecologists. Canterbury University Press, Christchurch.

Klumpp, D. W. and P. D. Nichols 1983. A study of food chains in seagrass communities II. Food of the Rock Flathead, *Platycephalus laevigatus* Cuvier, a major predator in a *Posidonia australis* seagrass bed. Australian Journal of Marine and Freshwater Research **34**: 745-754

Levin, P., R. Petrik, and J. Malone 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. Oecologia **112**:55-63.

Lindholm, J. B., P. J. Auster, and L. S. Kaufman 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhau*. Marine Ecology Progress Series **180**:247-255.

Lindsay, D. J., M. Minagawa, I. Mitai, and K. Kawaguchi 1998. Trophic shift in the Japanese anchovy *Engraulis japonicus* in its early life history stages as detected by stable isotope ratios in Sagami Bay, Central Japan. Fisheries Science **64**:403-410.

Longmore, A. R., R. A. Cowdell, and C. F. Gibbs 1990. Monitoring Port Phillip Bay water quality 1985-86. Environmental Protection Authority Victoria, Scientific Report Series 89/003.

Loneragan, N. R., S. E. Bunn, and D. M. Kellaway 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. Marine Biology **130**:289-300.

Manderson, J. P., B. A. Phelan, A. J. Bejda, L. L. Stehlik, and A. W. Stoner 1999. Predation by striped searobin (*Prionotus evolans*, Triglidae) on young-of-the-year winter flounder (*Psedopleuronectes americanus*, Walbaum): examining prey size selection and prey choice using field observations and laboratory experiments. Journal of Experimental Marine Biology and Ecology **242**:211-231.

Marguillier, S., G. van der Velde, M. A. Hemminga, and S. Rajagopa 1997. Trophic relationships in an interlinked mangrove seagrass ecosystem as traced by d13C and d15N. Marine Ecology Progress Series **151**:115-121.

Martin-Smith, K. M. 1993. Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. Journal of Experimental Marine Biology and Ecology **174**:243-260.

Mattila, J. 1992. The effect of habitat complexity on predation efficiency of perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus*. Journal of Experimental Marine Biology and Ecology **157**:55-67.

Mattila, J. 1995. Does habitat complexity give refuge against fish predation? Some evidence from two field experiments. *In* A. Eleftheriou, A. Ansell and C. J. Smith, editors. Biology and Ecology of Shallow Coastal Waters. Olsen and Olsen, Fredensborg.

Mattila, J., and E. Bonsdorff 1989. The impact of fish predation on shallow soft bottoms in brackish waters (SW Finland): an experimental study. Netherlands Journal of Sea Research **23**:69-81.

McMillan, C. 1980. $^{13}C/^{12}C$ ratios in seagrass. Aquatic Botany **9**:237-249.

Michaletz, P. H. 1997. Influence of abundance and size of age-0 gizzard shad on predator diets, diet overlap, and growth. Transactions of the American Fisheries Society **126**:101-111.

Morrisey, D. J., S. J. Turner, and A. B. MacDiarmid 1998. Subtidal assemblages of soft substrata. *In* M. Kingsford and C. Battershill, editors. Studying Temperate Marine Environments. Canterbury University Press, Christchurch.

Nash, R. D. M., and R. S. Santos 1998. Seasonality in diel catch rate of small fishes in a shallow-water fish assemblage at Porto Pim Bay, Faial, Azores. Estuarine, Coastal and Shelf Science **47**:319-328.

Neira, F. J., I. C. Potter, and J. S. Bradley 1992. Seasonal and spatial changes in the larval fish fauna within a large temperate Australian estuary. Marine Biology **112**:1-16.

Nichols, P. D., D. W. Klumpp, and R. B. Johns 1985. A study of food chains in seagrass communities III. Stable carbon isotope ratios. Australian Journal of Marine and Freshwater Research **36**:683-690.

Ohman, M. C., P. L. Munday, G. P. Jones, and M. J. Caley 1998. Settlement strategies and distribution patterns of coral-reef fishes. Journal of Experimental Marine Biology and Ecology **225**:219-238.

Orth, R. J. 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. *In* D. M. John, S. J. Hawkins and J. H. Price, editors. Plant-animal interactions in the Marine Benthos. Clarendon Press, Oxford.

Orth, R. J., K. L. Heck, and J. von Montfrans 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.

Pain, S. 1997. Swimming for dear life. New Scientist **155**:28-32.

Pepin, P., and T. H. Shears 1995. Influence of body size and alternate prey abundance on the risk of predation to fish larvae. Marine Ecology Progress Series **128**:279-285.

Peterson, C., and R. Black 1994. An experimentalists challenge: when artefacts of intervention interact with treatments. Marine Ecology Progress Series **111**:289-297.

Peterson, B. J., and B. Fry 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics **18**:293-320.

Pinnegar, J. K., and N. V. C. Polunin 2000. Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia **122**:399-409.

Pollard, D. A. 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquatic Botany **18**:3-42.

Power, M., M. J. Attrill, and R. M. Thomas 2000. Environmental factors and interactions affecting the temporal abundance of juvenile flatfish in the Thames Estuary. Journal of Sea Research **43**:135-149.

Raffaelli, D., and H. Moller 2000. Manipulative field experiments in animal ecology: do they promise more than they can deliver. Advances in Ecological Research **30**:299-338.

Rangeley, R. W., and D. L. Kramer 1998. Density-dependent antipredator tactics and habitat selection in juvenile pollock. Ecology **79**:943-952.

Rau, G. H., D. G. Ainley, J. L. Bengston, J. J. Torres and T. L. Hopkins 1992. $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure.

Marine Ecology Progress Series **84**: 1-8

Reise, K. 1985. Tidal Flat Ecology: An Experimental Approach to Species Interactions, Ecological Studies, Vol. 54. Springer-Verlag, Berlin.

Robertson, A. I. 1980. The structure and organisation of an eelgrass fish fauna. Oecologia **47**: 76-82

Robertson, A. I. 1982. Population dynamics and feeding ecology of juvenile Australian salmon (*Arripis trutta*) in Western Port, Victoria. Australian Journal of Marine and Freshwater Research **33**:369-375.

Robertson, A. I. 1984. Trophic interactions between the fish fauna and macrobenthos of an eelgrass community in Western Port, Victoria. Aquatic Botany **18**:135-153.

Robertson, D. R., and K. W. Kaufmann 1998. Assessing early recruitment dynamics and its demographic consequences among tropical reef fishes: accommodating variation in recruitment seasonality and longevity. Australian Journal of Ecology **23**:226-233.

Sale, P. F. 1991. Habitat structure and recruitment in coral reef fishes. *In* S. S. Bell, E. D. McCoy and H. R. Mushinsky, editors. Habitat Structure: the arrangement of objects in space. Chapman and Hall, London, UK.

Schmidt, G. H., and G. F. Warner 1984. Effects of caging on the development of a sessile epifaunal community. Marine Ecology Progress Series **15**:251-263.

Schrijvers, J., M. G. Camargo, R. Pratiwi, and M. Vincx 1998. The infaunal macrobenthos under East African Ceriops tagal mangroves impacted by epibenthos. Journal of Experimental Marine Biology and Ecology **222**:175-193.

Sholto, D. A. D., J. G. Field, A. G. James, and N. J. Van Der Merwe 1991. Carbon-13 carbon-12 and nitrogen-15 nitrogen-14 isotope ratios in the southern Benguela ecosystem. Indicators of food web relationships among different size-classes of plankton and pelagic fish differences between fish muscle and bone collagen tissues. Marine Ecology Progress Series **78**:23-31.

Steele, M. A. 1996. Effects of predators on reef fishes: separating cage artefacts from effects of predation. Journal of Experimental Marine Biology and Ecology **198**:249-267.

Steele, M. A. 1999. Effects of shelter and predators on reef fishes. Journal of Experimental Marine Biology and Ecology **233**:65-79.

Stoner, A. W. 1982. The influence of benthic macrophytes on the foraging behaviour of pinfish, *Lagodon rhomboides* (Linnaeus). Journal of Experimental Marine Biology and Ecology **58**:271-284.

Summerson, H. C. and C. H. Peterson 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Marine Ecology Progress Series **15**: 63-77

Sydeman, W. J., K. A. Hobson, P. Pyle, and E. B. McLaren 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. Condor **99**:327-336.

Sweatman, H., and D. R. Robertson 1994. Grazing halos and predation on juvenile Caribbean surgeonfishes. Marine Ecology Progress Series **111**:1-6.

Thomas, C. J., and L. B. Cahoon 1993. Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. Marine Ecology Progress Series **95**:19-24.

Thompson, D. R., K. Lilliendahl, J. Solmundsson, R. W. Furness, S. Waldron, and R. A. Phillips 1999. Trophic relationships among six species of Icelandic seabirds as determined through stable isotope analysis. Condor **101**:898-903.

Thresher, R. 1994. Climatic cycles may help explain fish recruitment in south east Australia. Australian Fisheries 2:20-22.

Tupper, M., and R. G. Boutilier 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Marine Ecology Progress Series **151**:225-236.

Tupper, M., and W. Hunte 1998. Predictability of fish assemblages on artificial and natural reefs in Barbados. Bulletin of Marine Science **62**:919-935.

Vander Zanden, M. J., M. Hulshof, M. S. Ridgeway, and J. B. Rasmussen 1998. Application of stable isotope techniques to trophic studies of age-0 smallmouth bass. Transactions of the American Fisheries Society **127**:729-739.

Virnstein, R. W. 1978. Predator caging experiments in soft sediments: caution advised. Pages 261-273 *in* M. L. Wiley, editors. Estuarine interactions. Academic Press Inc., New York.

Wilkinson, L., M. Hill, J. P. Welna, and G. K. Birkenbeuel 1992. SYSTAT for Windows: Statistics, Version 5 Edition. SYSTAT, Inc., Evanston, IL.

Yoshii, K., N. G. Melnik, O. A. Timoshkin, N. A. Bondarenko, P. N. Anoshka, T. Yoshioka, and E. Wada 1999. Stable isotope analyses of the pelagic food web in Lake Baikal. Limnology and Oceanography **44**:502-511.

Yoshioka, T., and E. Wada 1994. A stable isotope study on seasonal food web dynamics in a eutrophic lake. Ecology **75**:835-846.

Appendix 1: Intellectual Property

The FRDC's theoretical share of project income, based on the relative value of contribution is 50.88%.

Appendix 2: Staff

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