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.....
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**Ecology of Populations and Assemblages
of Temperate Reef Fish in
Port Phillip Bay, Australia**

A thesis submitted for the degree of
Doctor of Philosophy

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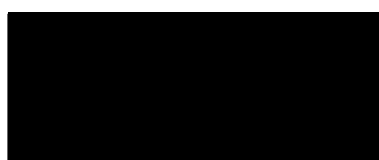
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Declaration

This thesis is submitted in accordance with the regulations of Monash University in fulfilment of the requirements for the degree of Doctor of Philosophy. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. Further, to the best of my knowledge, it does not contain material previously published or written by another person, except where due reference is made in the text.



Melissa Wheatley

April 2000

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Abstract

One of the major aims of ecological research is to understand the patterns and cause(s) of variation in the distribution and abundance of organisms. An organism's distribution may be influenced by numerous factors, one of which is environment/habitat. However, despite the potentially important role that habitat may play in determining the distribution and abundance of organisms, many ecological studies focus on the processes themselves (e.g. recruitment, competition, predation) and do not consider how an organism's habitat may mediate these processes.

Before we can determine the relative importance of different factors, such as habitat, in explaining the distribution and abundance of temperate reef fish assemblages and populations we need to have a clear understanding of the natural spatial and temporal variation in these assemblages/populations. The first part of this study provides a detailed description of spatial and temporal variation in reef fish assemblages in and around Port Phillip Bay, Victoria. Fishes were sampled using both underwater visual surveys and wire-mesh fish traps. Macroalgal assemblages were also examined to determine if there was any relationship between fish and algal assemblages. Fish assemblages varied both spatially and temporally over the scale of this study, but there was a significant positive relationship between the fish assemblages surveyed using the two methods. Reefs closer together had more similar fish assemblages than distant reefs, but this similarity was not simply related to the macroalgal assemblages present, and was most likely the result of closer sites experiencing more similar conditions (e.g. larval supply, wave action and tidal movement) than distant sites.

In addition to examining fish assemblages as a whole, it is important to consider the distribution and abundance of the component species, as the importance of factors such as habitat and movement are likely to vary not only between species, but also over the life span of individual species. Leatherjackets (Family: Monacanthidae) are some of the most common and easily recognised fish in southern Australian waters. However, despite their abundance very few studies have examined their ecology. This study examined in detail the distribution, abundance and size structure of two monacanthid species, *Meuschenia freycineti* and *Meuschenia hippocrepis*. Distinct differences were

found in the distribution and size structure of these fishes between inshore seagrass beds and offshore rocky reefs. Individuals of *M. hippocrepis* were only recorded on reefs and did not appear to recruit to inshore seagrass beds. In contrast, small *M. freycineti* (recruits and juveniles) were found exclusively in seagrass beds, while adult *M. freycineti* were largely found on reefs. Although a range of factors including recruitment, growth, mortality, habitat selection and movement may account for these patterns, evidence from this study suggests that habitat selection by settling larvae and ontogenetic movements by *M. freycineti*, are particularly important.

Movement and growth patterns were examined for adult individuals of *M. freycineti* and *M. hippocrepis* on reefs. Mean growth rates differed between the two species and between sites (*M. freycineti* only; no data for *M. hippocrepis*). Tagging/recapture data revealed no evidence of movement by *M. freycineti* or *M. hippocrepis* between reefs, and both species appear to reside permanently on reefs when in the adult phase. In addition, although evidence from this study suggests that juveniles/sub-adults of *M. freycineti* appear to undergo extensive migrations over unvegetated sand between inshore seagrass and offshore reef habitats, a large sand patch adjacent to the reef at Nepean Bay severely restricted the movements of adult individuals. These results have important implications for the management of reef-based fisheries and the allocation of Marine Protected Areas. Sand barriers should be considered in the establishment of Marine Protected Areas, particularly as these areas are often quite small.

The distinct distribution pattern of recruits/juveniles of *M. freycineti* and *M. hippocrepis* on seagrass beds and reefs, respectively, may reflect habitat selection by settling larvae. As seagrass beds tend to occur in shallow waters and reefs in deeper waters it is not known whether these settlement preferences reflect specific habitat (seagrass vs reef) or water depth preferences. The final part of this study examined the importance of habitat type and water depth in determining the distribution and abundance of temperate fishes, specifically *M. freycineti* and *M. hippocrepis*. A field experiment using artificial seagrass beds and artificial reefs at two water depths (shallow and deep) was set up at two sites. Although numbers of *M. freycineti* (no *M. hippocrepis* were recorded) were low, the distribution and size structure of individuals supported the contention that larvae of *M. freycineti* settle to shallow seagrass beds before moving to reefs at a later stage. Numerous other species were recorded on the experimental habitats and, in

general, habitat type appeared to be more important than water depth in structuring fish assemblages, with most species showing a clear preference for either seagrass (e.g. *Stigmatopora argus*) or reef (e.g. *Vincentia conspersa*) habitats.

This study provides a detailed description of temperate reef fish assemblages in and around Port Phillip Bay, Victoria, focussing on patterns in the distribution, abundance and size structure of two common species *M. freycineti* and *M. hippocrepis*. While acknowledging that a whole suite of factors will affect temperate reef fish assemblages and populations, this thesis highlights the importance of two factors, habitat and movement, and how the influence of these factors may change with fish size/age.

Chapter 1

General Introduction

One of the fundamental aims of ecological research is to determine the patterns and cause(s) of variation in the distribution and abundance of organisms. Patterns of distribution and abundance may be influenced by numerous factors. Marine ecologists have attempted to model the importance of different factors in controlling population distribution and abundance in a range of different systems, with most success coming from environments where the organisms are relatively sedentary and accessible, for example, limpets on intertidal rocky shores or fishes on tropical coral reefs. Studies of sedentary species tend to show that the patterns of distribution and abundance are determined by patterns of recruitment and survivorship (Grosberg and Levitan, 1992; Jones 1984c). However, when species utilise more than one environment over their life span, factors such as movement may become important in explaining differences in the distribution of recruits/juveniles and adults.

One important aspect of an organism's environment is the structure of the underlying habitat (Bell *et al.*, 1991). Habitat characteristics have been shown to influence the distribution and abundance of reef fishes via a number of different mechanisms. For example, habitat quality can influence recruitment and survivorship through the availability of critical resources (Jones, 1988b). Habitat structure can mediate the impacts of biological interactions, such as competition and predation, by providing refuges (Hixon and Menge, 1991). Movements associated with the selection of preferred habitats can also modify patterns of distribution (Jones, 1991). However, despite the potentially important role that habitat may play in determining the distribution and abundance of reef fishes, many ecological studies tend to focus on the processes themselves (e.g. recruitment, competition, predation) and do not consider how the fishes' habitat may mediate these processes (Jones and Syms, 1998).

Most studies examining the influence of different factors on the distribution and abundance of reef fishes have been done on tropical coral reefs. One of the most noticeable differences between temperate rocky reefs and tropical coral reefs is in the structure of the habitat. Tropical and temperate reefs are fundamentally different in the

composition of their hard substrata (i.e. rock vs coral) and in the type and amount of algal cover, with macroalgae forming a major component of the structural habitat of temperate reefs (Ebeling and Hixon, 1991). Fish-habitat interactions may be a key factor influencing the distribution and abundance of temperate reef fishes. For example, macroalgal density can vary over space and time, consequently affecting the distribution and abundance of the associated fishes (Bodkin, 1988; Holbrook *et al.* 1990a; Schmitt and Holbrook, 1990a; Anderson, 1994). Thus, habitat should be considered in any study examining variation in the distribution and abundance of reef fishes.

Many reef fish studies, particularly those on coral reefs, have tended to focus on small, sedentary, site-attached species, and as a result movement has not been considered to be an important factor influencing the distribution and abundance of reef fishes. However, fish movements have been observed over a range of spatial scales ranging from several metres (e.g. Scaly fin, *Parma victorinae*) (Norman and Jones, 1984) to 1000's of kilometres (e.g. Atlantic salmon, *Salmo salar*) (Mc Dowell, 1988). Many of these movements are related to foraging or reproductive activities, and may also encompass different habitats and/or water depths. For example, the striped parrotfish, *Scarus croicensis*, has been shown to move between shallow and deep reef areas for the purposes of feeding (Ogden and Buckman, 1973), while female spotty, *Pseudolabrus celidotus*, appear to move to deeper reef areas for spawning (Jones, 1981).

Many tropical and temperate fish species also show spatial separation in the distribution of recruits/juveniles and adults, suggesting ontogenetic movements. Size-related or ontogenetic movements, where fish move between different environments/habitats as they grow, have been reported for numerous species including *Pseudolabrus celidotus* (Jones 1984a), *Achoerodus viridis* (Gillanders, 1997a) and *Sebastes* sp. (Love *et al.* 1991). These large-scale ontogenetic movements generally arise through the dispersal of pelagic larvae from spawning to nursery areas followed by the active movement of juvenile and/or adult fish from nursery areas back to adult habitats (Bell and Worthington, 1993). Many habitats are recognised as important nursery areas (e.g. seagrass beds) and are often only used by recruits/juveniles, with adults occurring in alternative habitats (e.g. rocky reefs). Despite these observations very few studies have examined the ontogenetic movements of fishes between nursery and adult habitats. While there is strong evidence to suggest that these ontogenetic movements occur,

studies that focus on more than one life history stage and consequently more than one habitat are needed to examine the possible links between different nursery and adult habitats.

Leatherjackets (Family: Monacanthidae) are some of the most easily recognised fish in southern Australian waters due to their prominent dorsal spine and modified scales that form a tough leathery skin. Two monacanthid species that are common along the Victorian coast are the sixspine leatherjacket, *Meuschenia freycineti*, and the horseshoe leatherjacket, *Meuschenia hippocrepis*. Despite their abundance very few studies have examined the ecology of *M. freycineti* and *M. hippocrepis*; however, studies have shown that the recruits and juveniles of several monacanthid species, including *M. freycineti*, tend to occur in seagrass beds within estuaries, while adult individuals occur primarily on coastal rocky reefs (Bell *et al.*, 1978). It appears that *M. freycineti* larvae settle to shallow seagrass beds (e.g. *Zostera capricorni* and *Heterozostera tasmanica*), and remain there for approximately 12 months before migrating offshore to coastal reefs (Bell and Worthington, 1993), often via other habitats such as *Posidonia* seagrass beds (Middleton *et al.*, 1984; Jordan *et al.*, 1998). Very few studies have examined the distribution of *M. hippocrepis*, but in contrast to *M. freycineti*, there is no evidence to suggest that *M. hippocrepis* individuals recruit to seagrass beds (Jenkins *et al.*, 1993, 1996).

We are just beginning to understand the anthropogenic impacts of exploitation, pollution and habitat modification on assemblages of temperate reef fishes. With this understanding has come the realisation that we know very little about the ecological relationships among temperate reef fishes, or the relative importance of different factors, such as habitat and movement, in explaining the distribution and abundance of temperate reef fishes. This thesis provides the first detailed description of the fish assemblages on rocky reefs in and around a temperate water bay in southeastern Australia. The broad aims of this study were to examine fish-habitat associations and, in particular, to examine how these associations may change over a fish's life span. *Chapter 2* contains a detailed description of the study sites and methods, including statistical analyses, used throughout this thesis. *Chapter 3* details the spatial and temporal variation in fish assemblages on rocky reefs in and around Port Phillip Bay, and examines whether spatial variation in the fish assemblages is related to spatial

variation in macroalgal cover. *Chapter 4* examines the distribution, abundance and size structure of two common temperate fish species, *Meuschenia freycineti* and *Meuschenia hippocrepsis* (Family: Monacanthidae), on rocky reefs and in seagrass beds, and *Chapter 5* examines the movement patterns and growth of these two species on reefs. *Chapter 6* details an experimental study examining the influence of habitat (seagrass and reef) and water depth on the distribution and size structure of temperate fishes, specifically *M. freycineti* and *M. hippocrepsis*. A general discussion and synthesis of the study is provided in *Chapter 7*.

Definition: In general, *community* defines all species occupying a particular habitat that either directly or indirectly interact with each other, while *assemblage* is used to define a group of species occupying a particular habitat with no implied interaction (*sensu* Menge, 1976). Throughout this thesis the term assemblage is used when referring to tropical and temperate reef fishes.

Chapter 2

General Methods

Study Sites

The southeastern coast of Australia possesses numerous bays and inlets that contain many different subtidal habitats including sandy beaches, seagrass beds and rocky reefs. Although not as species-rich and diverse as tropical waters, temperate waters off the southern coast of Australia harbour over 700 different fish species, many of which are endemic to the area (Gomon *et al.*, 1994).

Port Phillip Bay is a large (1950 km²) semi-enclosed embayment on the coast of Victoria, and is linked to Bass Strait by a narrow entrance. Although Port Phillip Bay has a relatively small tidal range (approx. 1 m), current flow near its entrance is high (Black *et al.*, 1993). The hydrodynamics of Port Phillip Bay can be characterised into three separate regions: the entrance, where fast ebb and flood currents dominate (approx. 3 ms⁻¹); a large flood-tidal delta extending into the middle of the bay, where strong currents occur in the major channels; and an inner zone encompassing the northern half of the bay, where tidal currents are weak and wind currents dominate (Black *et al.*, 1993).

Throughout this thesis, fish assemblages from two different habitats within Port Phillip Bay, seagrass beds and rocky reefs, were surveyed. The dominant seagrass species in the bay, and that surveyed in this study, was the subtidal eelgrass, *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog. *H. tasmanica* beds along both the Bellarine and Mornington Peninsula areas of Port Phillip Bay generally consist of 20 m-wide bands of seagrass running parallel to the shoreline. Over the course of this study, fishes were surveyed at five seagrass sites: Grand Scenic, Grassy Point, Indented Head, St Leonards and Blairgowrie (Fig. 2.1; see Chapters 4 and 6).

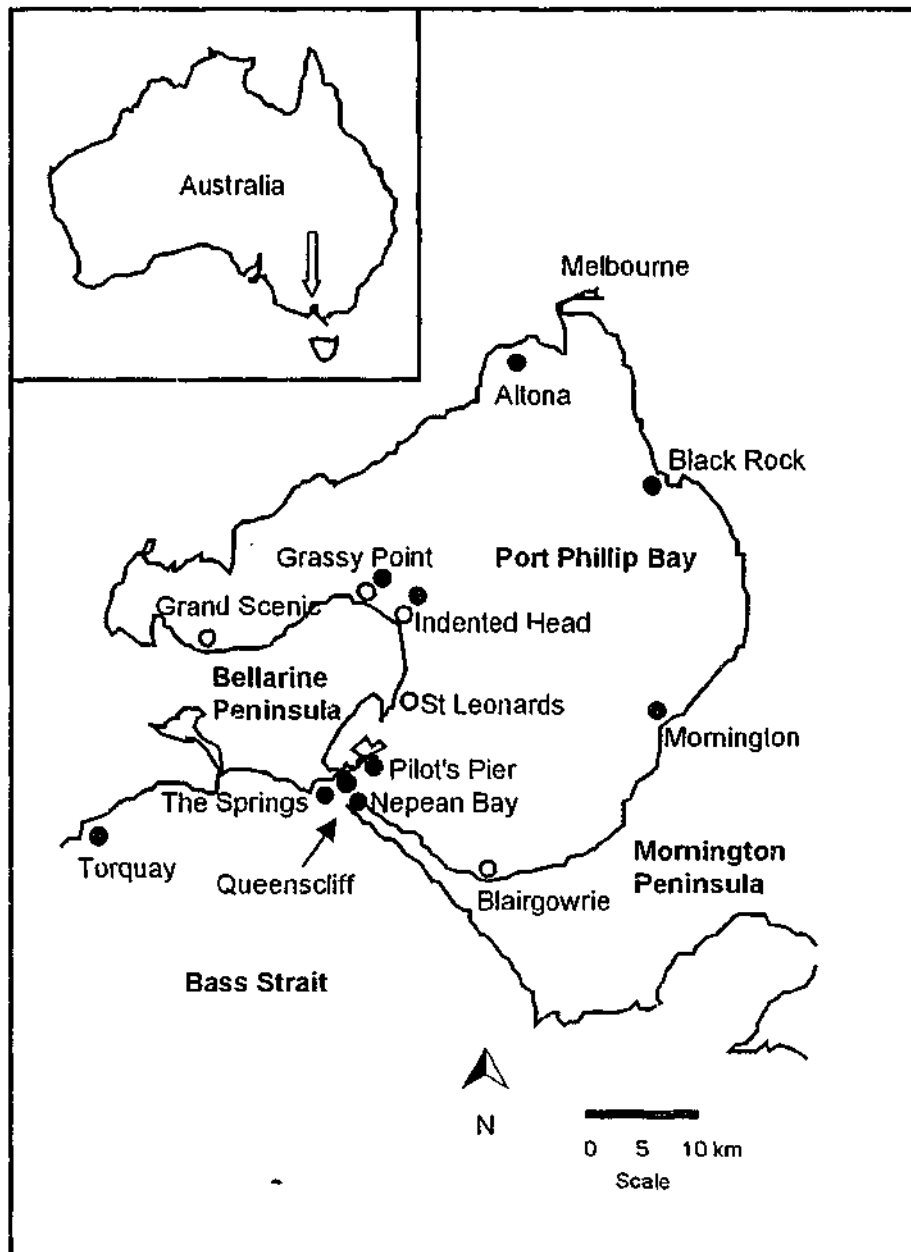


Figure 2.1: Location of the main study sites surveyed in and around Port Phillip Bay throughout this thesis. Inset: location of Port Phillip Bay on the Australian coast. Closed circles = reef sites; open circles = seagrass sites.

Port Phillip Bay has a maximum depth of 24 m, but in general, subtidal rocky reefs within the bay occur in depths of <10 m. Ten reefs were surveyed during this study; nine reefs were located inside the bay and one (Torquay) was approximately 28 km west of the entrance to the bay (Fig. 2.1; see Chapter 3). These sites were considered representative of rocky reef habitats in and around Port Phillip Bay (Table 2.1). All reefs surveyed

were covered by a variety of small canopy-forming and turfing macroalgal taxa (see Chapter 3)

Table 2.1: Habitat characteristics of the reef sites surveyed in and around Port Phillip Bay.

Site	Rock Type	Depth (m)
Torquay	Sandstone	6
The Springs	Limestone Sandstone	6
Queenscliff	Limestone Sandstone	5
Pilot's Pier	Limestone Sandstone	2-3
Nepean Bay	Limestone Sandstone	5
Mornington	Sandstone	5
Indented Head	Basalt	2-3
Grassy Point	Basalt	5
Black Rock	Sandstone	2-3
Altona	Basalt	2-3

Selection of reef sites was based primarily on accessibility, water depth and reef size; the method used to survey reefs in the early part of this study required large continuous reef areas. Where possible, seagrass sites were selected on the basis of proximity to reef sites. Only five seagrass sites were selected, because seagrass beds further from the entrance into Port Phillip Bay were not close to any rocky reefs. In the latter part of this thesis, site selection was restricted to sites with relatively consistent catch rates of *Meuschenia freycineti* and *Meuschenia hippocrepis* (Chapters 4 and 5), and to locations where both inshore seagrass beds and offshore reefs were present (Chapter 6)

Sampling Methodology

Quantitative studies of fishes are logistically difficult due to factors such as fish mobility and behaviour (i.e. schooling). These factors may contribute to the patchiness in fish abundance observed over space and time (Kimmel, 1985). Three techniques were used to survey fish assemblages: visual surveys, fish traps and seine nets. The selection of these methods was based on the objectives of each particular component of the study, the characteristics of the fish, and the habitat being surveyed

Visual Surveys

Numerous methods have been used to sample tropical and temperate reef fish assemblages, including visual strip transects, explosives, rotenone, trapping, gill netting and hand lines. Visual surveys provide a relatively quick and efficient method for estimating population sizes with minimal disturbance to the fish assemblage, and have been used to estimate densities of reef fish since 1954 (Brock, 1982). Strip or belt transects are the most commonly used visual survey technique, and have become an important method in determining the distribution and abundance of temperate rocky reef fish (St John *et al.*, 1990). There are, however, assumptions and constraints to this method, and it is generally believed that visual transects underestimate fish densities (Thresher and Gunn, 1986). Another constraint in the use of visual transects is that they are restricted to relatively clear and moderately shallow (<30 m) water (Turner and Mackay, 1985). Visual surveys tend also to be insensitive to cryptic fish, and to those that actively avoid divers, but do give reliable estimates of diurnally active fishes (Brock, 1982). In general, temperate reef fish assemblages are less diverse than coral reef fish assemblages, so methods such as visual transects are more reliable in temperate waters (DeMartini and Roberts, 1982). Despite their limitations, underwater visual surveys remain the best non-destructive method available for surveying reef fish populations and assemblages (Kulbicki, 1998).

Visual surveys of the fish assemblages in the first part of this study were carried out during the day using the strip/belt transect method. Five replicate transects, each 50 m in length, were haphazardly laid out over the reef at each site. Two trained divers, each surveying a 2 m-wide strip either side of the measuring tape, recorded the number of individuals of each species on underwater slates. To minimise the impact of diver presence, all counts were conducted as the tape was laid out, and divers maintained a constant speed along each replicate transect (approx. 10 min/transect). Visibility exceeded 4 m on all sampling trips. It is acknowledged that the densities of cryptic and nocturnal species on temperate rocky reefs in and around Port Phillip Bay are likely to have been underestimated.

Fish Traps

Fish traps are used worldwide in commercial fisheries, and in many areas such as the Caribbean, trapping is the primary method used to catch reef fish (Recksiek *et al.*, 1991). Fish traps have also become an increasingly popular method of quantitatively sampling tropical and temperate reef fish assemblages. Traps are a very convenient method for surveying reef fish as they can fish unattended over a large area (Miller and Hunte, 1987). They are also relatively inexpensive to construct, are robust, and can sample areas that are otherwise inaccessible to other survey techniques due to habitat complexity, or water depth and clarity (Miller and Hunte, 1987). In addition, traps offer the advantage of retaining live specimens that can be used for accurate size/age measurements, and for studies of reproductive biology, movement and growth.

A major limitation of fish traps is that they only provide an index of fish abundance, and only when it is assumed that the area fished by each trap is the same at different times and sites (Miller and Hunte, 1987). Both the design of fish traps and their mode of operation can also severely influence the number and species of fish caught (Sheaves, 1995). Trap shape, volume, mesh size and entrance type (straight vs 'horsehead' funnel) can each affect catch rates, as does the type and amount of bait, and the time the traps are left to sample (soak time). Catch rates tend to be higher when mesh size is small (Sheaves, 1995; Robichaud *et al.*, 1999), when bait containers are flexible with numerous small holes (Sheaves, 1995), and when soak times are relatively short (Whitelaw *et al.*, 1991). 'Horsehead' funnels also tend to have reduced rates of egress, and possibly reduced rates of ingress, when compared to straight funnels (Sheaves, 1995). Chevron traps, which are similar in shape to the traps used in this study, are more effective than many other standard trap designs (Collins, 1990). Efficient traps and fishing techniques will yield higher catch rates per unit effort, thus providing a better index of fish abundance. The fish traps used in this study were designed to maximise catch rates.

Fish traps were triangular in shape, measuring 1 m in length \times 0.8 m in width \times 0.5 m in height (Plate 2.1). Trap frames were constructed from 6 mm steel rods, which were bent and welded into shape. Each trap was covered with 1.3 mm thick galvanised steel mesh, with a square mesh size of 25 mm. Each trap had one 'horsehead'-shaped inlet funnel with an aperture measuring 200 \times 60 mm. Traps were baited with approximately 250 gm

of squid. This was placed in plastic mesh bags (240×200 mm) that were perforated with numerous small holes, and suspended mid-way between the top and base of the trap. A polystyrene buoy (surface marker) was attached to each trap by 10 m of rope. Traps were oriented so the entrance funnel faced down-current, as fish tend to approach traps from down current in response to the bait plume (Whitelaw *et al.*, 1991). Fish traps were set during daylight hours only. After a soak time of approximately 1 hr all traps were retrieved and emptied. All captured fish were identified, counted, and total length was measured (TL: tip of head to tip of tail). Aside from individuals of *Meuschenia freycineti* that were required for gonad analysis (Chapter 4), all fish were released directly after measurement and/or tagging (Chapter 5).



Plate 2.1: Design of the wire-mesh fish traps used throughout this thesis.

Beach Seine Nets

Shallow water seagrass beds provide an important habitat for many fishes, particularly juveniles (Pollard, 1984). Various methods have been used to survey these assemblages, including visual surveys, poisoning, trawling and netting, and the composition and abundance of fish reported will depend on the method used. Beach seines have been very effectively used to surveying seagrass fishes, particularly when comparing the abundance of a single species between locations (Connolly, 1994). However, data collected on the whole fish assemblage should be interpreted with caution, as seine nets can provide inaccurate information on the rank order of species abundance (Connolly, 1994). Data collected using seine nets will be more informative if presented in conjunction with information on the catching efficiency of the net (Connolly, 1994). The catching efficiency of nets that were of a similar design to the one used in this study has been examined previously (Connolly, 1994; Jenkins and Sutherland, 1997). In these studies seine nets were shown to efficiently survey species that occur in the water column within the seagrass canopy (e.g. *Sillaginodes punctata*, *Atherinosoma microstoma*, *Stigmatopora argus* and *Acanthaluteres* sp.), but did not effectively sample species intimately associated with the sediment (e.g. *Favonigobius lateralis* and *Cristiceps australis*).

In this study, fish in seagrass beds were sampled with a beach seine net measuring 10 m in length, with a 3 m drop, and a mesh size of 1 mm. The net was weighted along the bottom with leads and had a series of small floats along the top edge. Netting was conducted during daylight hours, and all surveys were conducted within one hour of low tide, at water depths between 50–100 cm. Two 10 m ropes were attached to each end. Each haul was conducted by feeding out one of the 10 m ropes while walking directly offshore, setting the net parallel to shore, and then letting the second 10 m rope out while walking back to the initial position (Plate 2.2). The seine net was then hauled into a plastic bin, carried to shore and the contents were sorted. In general, all fish caught were recorded and the total length (TL) of individuals of *Meuschenia freycineti* and *Meuschenia hippocrepis* noted (Chapters 4 and 6). All fish were released as soon as possible after counting and/or measuring. Replicate hauls were taken within the same

seagrass bed at each site, and each haul was separated by approximately 5 m to ensure that hauls did not overlap.

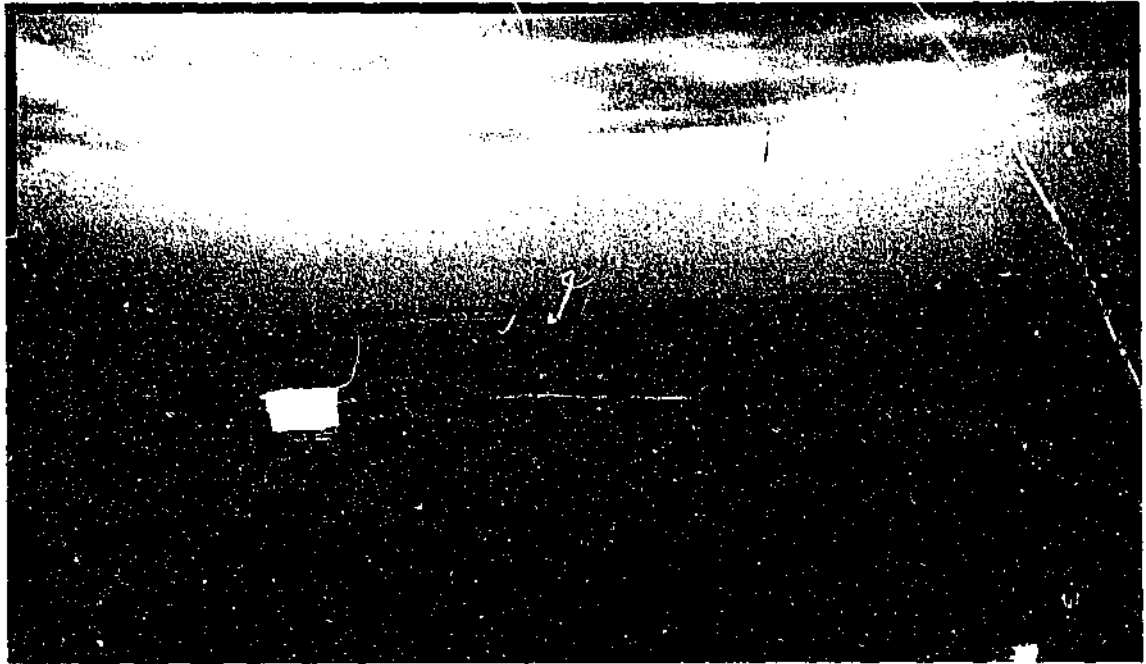


Plate 2.2: Setting the beach seine net to capture fishes in seagrass.

Statistical Analyses

Univariate Analyses

Univariate data (e.g. number of species, density of individual fish species) were analysed using Analyses of Variance (ANOVAs). For all univariate analyses, assumptions of normality and homogeneity of variances were examined using box and residual plots. Data were rarely normally distributed and were $\log_{10}(x+1)$ transformed when necessary. All transformations are recorded in the table captions. The null hypotheses tested with ANOVAs were that there were no differences between treatment or group means for single factor ANOVAs, and for multiple factor ANOVAs that there were no differences between treatment/group means, and that there were no interactions between the factors.

When a significant interaction term did occur, the cause of the interaction was examined using simple main effects contrasts using the mean square residual from the original

analysis as the error term. Unplanned comparisons were done after ANOVAs using Tukey's (HSD) tests. All univariate data were analysed using Systat v7.01.

Multivariate Analyses

Differences in fish assemblages between groups or between experimental treatments were determined using Non-metric Multi-Dimensional Scaling (NMDS) and Analysis of Similarities (ANOSIM) (Clarke, 1993). NMDS was based on Bray-Curtis dissimilarity matrices for replicate samples (Clarke, 1993), which are considered one of the most reliable distance measures for ecological data (Faith *et al.*, 1987). Each NMDS was repeated six times from random starting configurations, and stress values were compared before an ordination was accepted. Stress values estimate how well the configuration plot fits the true dissimilarities; the lower the stress value the better the fit. Clarke (1993) recommended that stress values be at least <0.20 and preferably <0.10 , guidelines that were followed here. Ordinations were plotted in 2-dimensions wherever possible, although to reduce the stress values it was often necessary to plot in 3-dimensions. In general, ordinations were plotted for the entire data set. However, for the fish assemblage and macroalgal assemblage data (Chapter 3), and for the comparison of sampling methodologies (Chapter 3), means for each site were plotted to allow subsequent comparisons between the assemblages. Plots of means were derived from NMDS on the group means.

In this thesis the null hypothesis that there is no relationship between two multivariate patterns (e.g. between fish assemblages surveyed using two different methods) was examined by comparing the two similarity matrices using a randomisation/permutation test (e.g. 'RELATE'). If there is no correlation between the two similarity matrices Global RHO = 0. The test involves recomputing Global RHO for a random subset (5000) of permutations of the sample labels in one of the two similarity matrices. If the observed value of Global RHO surpasses that found in 95% of the permutations, then the null hypothesis can be rejected ($\alpha = 0.05$) (Clarke and Warwick, 1994).

Following each NMDS ordination, when possible, ANOSIMs were performed to test the significance of any groupings observed from the ordination plot (Clarke, 1993). The null hypotheses tested using ANOSIM were that there were no differences between fish

assemblages in the different groups and/or treatments, and that there were no differences between pairs within groups or treatments. Probabilities derived from ANOSIM were subject to a Holm's (1979) sequential-Bonferroni P -value adjustment to account for multiple pairwise comparisons. All multivariate analyses were conducted using Primer v4.0 from the Plymouth Marine Laboratory.

All analyses were tested for significance at $\alpha = 0.05$, and throughout this thesis MS = mean square, df = degrees of freedom, F = F-ratio, R = R-statistic, P^* = Holm's adjusted P -value.

Chapter 3

Patterns in Temperate Reef Fish Assemblages: the Influence of Macroalgae and Methodology

Introduction

The distribution and abundance of temperate fishes may reflect a range of different factors, including habitat characteristics and the movement patterns of the fishes themselves. However, before we can determine the importance of habitat and ontogenetic movements we need to have an idea of the natural spatial and temporal variation in the distribution and abundance of temperate fishes, as the relative importance of these factors may depend on the spatial and temporal scales examined. For example, studies of fish movement over small scales often reveal limited movement; however, when the spatial and/or temporal scale of the study is increased, extensive migrations have been observed (e.g. Hyndes *et al.*, 1996).

Many studies have considered spatial and temporal variation in temperate fish assemblages in seagrass beds (Middleton *et al.*, 1984; McNeill *et al.*, 1992; Jenkins *et al.*, 1993) and rocky reefs (Ebeling *et al.*, 1980; Choat *et al.*, 1988; Holbrook *et al.*, 1994 and review by Jones (1988a)). However, while numerous studies examining spatial and temporal variation in temperate seagrass fish assemblages have been conducted in Australia, including Port Phillip Bay, the majority of work examining variation in temperate reef fishes has been conducted in the United States and New Zealand, with comparatively few studies in Australia (but see Jones and Andrew, 1990; Jones, 1992; Holbrook *et al.*, 1994; Jenkins and Wheatley, 1998).

Almost without exception previous studies have reported significant differences in the abundance and species composition of temperate reef fish assemblages at all spatial and temporal scales examined (Jones, 1988a). Variation in the distribution and abundance of fish at small spatial scales, such as between nearby reefs or within a single reef, is typical of many species, and may result from spatial variation in the abiotic and biotic aspects of the reef. Biotic characteristics, such as macroalgal cover, can vary considerably both spatially and temporally (Dayton *et al.*, 1984; Schiel and Foster,

1986), consequently affecting the abundance of associated fish species (Russell, 1977; Bodkin, 1988; Holbrook *et al.*, 1990a, b; Schmitt and Holbrook, 1990a; Anderson, 1994). Macroalgae are often a major source of shelter and/or food for fishes, especially on temperate reefs. Canopy-forming kelps such as *Macrocystis pyrifera* can directly affect the densities of fish species that use the kelp as a nursery area and/or adult habitat (Ebeling and Laur, 1985; Bodkin, 1988; Holbrook *et al.*, 1990a; Carr, 1994). Kelps can also affect fish species indirectly by reducing the presence of other understory algal species that may serve as important sources of food (Holbrook *et al.*, 1990a; Schmitt and Holbrook, 1990a) and shelter (Carr, 1989).

The factors important in determining spatial patterns in fish assemblages may be distinct from those resulting in temporal changes (Jones, 1988a). Within-year sampling has revealed that some fish species show marked seasonal changes in abundance (Kingett and Choat, 1981). However, these differences were not related to the reef habitat, but were the result of a summer influx of recruits, and older individuals showed no such seasonal trends. Seasonal fluctuations in water temperature may also result in temporal changes in the abundance of fishes on temperate reefs (Parker, 1990). Evidence from Parker (1990) suggests that many species move off reefs and into deeper water when the water temperature drops, and only return when the temperature increases again.

To examine spatial and temporal variation in reef fish assemblages, we require accurate information on the abundance of the component species. Reef fish assemblages can be difficult to survey accurately due to the variety of behaviours exhibited by the fish, and to the complexity of the habitat (Cappo and Brown, 1996). In fisheries research, catch per unit effort (CPUE) is commonly used to estimate fish abundance, although very few studies have compared CPUE with independent estimates of abundance (but see Richards and Schnute, 1986; Connell *et al.*, 1998). Fish traps are used worldwide in commercial fisheries, and provide useful CPUE data for species susceptible to traps (Reese, 1973). However, the design and mode of operation of fish traps can severely affect the species and numbers of fish caught (Sheaves, 1995). Underwater visual transects provide an efficient and non-destructive method for surveying reef fish, and have been used extensively in fisheries-independent studies to estimate abundance of temperate reef fishes. Abundance estimates derived from visual surveys are considered accurate for non-cryptic diurnally active species (Brock, 1982). Previous studies have

shown very little overlap in the species of fish caught in fish traps and surveyed visually, largely due to the size selectivity of traps (Ferry and Kohler, 1987; Miller and Hunte, 1987).

Port Phillip Bay provides a unique environment in which to examine variation in the distribution and abundance of temperate fishes as habitats, such as seagrass beds and rocky reefs, within the bay fall along an exposure gradient in terms of wave action and tidal movement (refer to Chapter 2). While detailed studies examining spatial and temporal variation in seagrass fish assemblages have been conducted within the bay (Jenkins *et al.*, 1993; Jenkins *et al.*, 1996), very few studies have examined variation in reef fish assemblages (but see Jenkins and Wheatley, 1998). The aims of this chapter were to: (i) detail spatial and within-year temporal variation in temperate reef fish assemblages, and in particular in the densities of *Meuschenia freycineti* and *Meuschenia hippocrepis*, on reefs in and around Port Phillip Bay; (ii) determine whether spatial variation in fish assemblages was related to either the macroalgal assemblage present or to the distance between the sites; and (iii) examine the relative species selectivities of underwater visual transects and fish traps.

Methods

Study Sites

To examine spatial and temporal variation in fish assemblages in and around Port Phillip Bay, three subtidal reefs were selected for detailed study: two sites (Queenscliff and Nepean Bay) were within the bay, and one (Torquay) was approximately 28 km west of the entrance to the bay (Fig. 3.1). To further examine spatial variation in fish assemblages, ten sites around Port Phillip Bay (including Torquay, Queenscliff and Nepean Bay) were also surveyed (Fig. 3.1). Refer to Chapter 2 for a detailed description of the study sites.

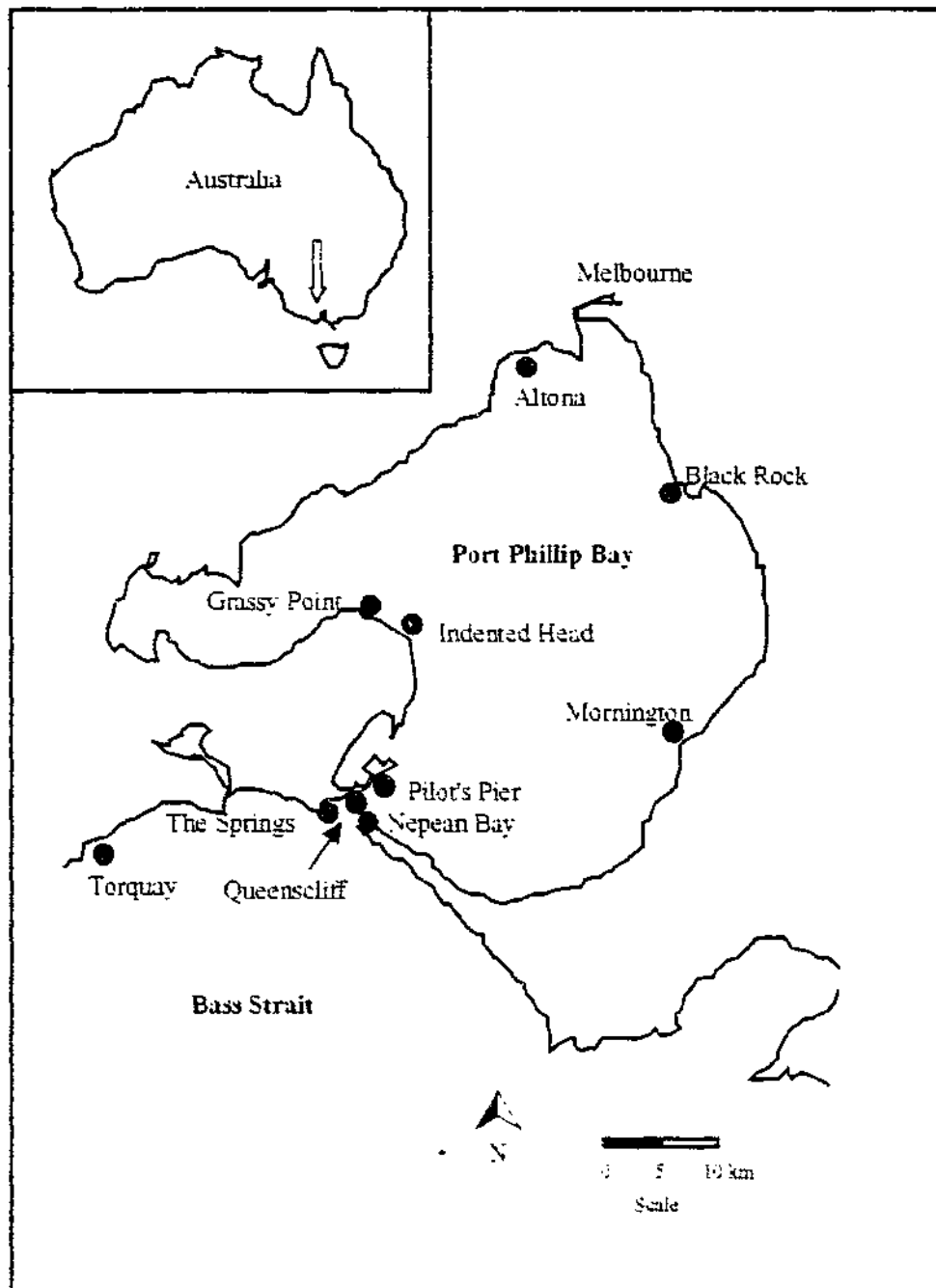


Figure 3.1: Location of study sites in and around Port Phillip Bay, Victoria, Australia. Inset: location of Port Phillip Bay on the Australian coast.

Fish Assemblage Surveys

Visual Transects

Monthly visual surveys were done at Torquay, Queenscliff and Nepean Bay from January to December 1996. Due to adverse weather conditions, surveys were not possible in some months. Visual surveys were also done once only at nine sites

between December 1997 and April 1998. Visual surveys were not done at Pilot's Pier because this reef consisted of numerous discrete patches that were too small to run 50 m transects. The monthly surveys at the three sites and the once-off surveys at the nine sites were done using the same method. At each site, five 50 m transects were sampled by haphazardly positioning a measuring tape over the reef. Two SCUBA divers, each surveying a 2 m lane either side of the transect line, recorded the number of individuals of all species encountered. Refer to Chapter 2 for a detailed description of the visual survey methodology.

Fish Traps

To compare the effectiveness of different methods in surveying temperate reef fish assemblages, once-off surveys using fish traps were also conducted. Surveys were conducted at all ten sites between December 1997 and April 1998. Where possible, visual and trap surveys were done on the same day. Fish traps were set at the completion of the visual surveys as bait plumes emanating from traps may have increased fish numbers in the area, and thus biased the visual surveys. Six traps were set on the reef at each site, and after a soak time of approximately 1 hr all traps were retrieved and emptied. Traps were then rebaited and reset for a further 1 hr, at all sites except Pilot's Pier (insufficient reef area). All captured fish were identified and released. Refer to Chapter 2 for a detailed description of the fish trapping methodology.

Macroalgal Surveys

To examine whether there was any relationship between the fish and macroalgal assemblages, once-off surveys of the dominant macroalgal taxa were done at nine sites (excluding Pilot's Pier) between December 1997 and April 1998. Where possible, fish and macroalgal surveys were conducted on the same day. At each site, the percentage cover of the dominant macroalgal taxa were estimated from 40 haphazardly placed 1.35 m \times 1.35 m quadrats. Macroalgal specimens were collected to confirm identification in the laboratory.

Statistical Analyses

Non-metric multi-dimensional scaling (NMDS) was used to graphically represent the differences in fish assemblages between sites and months. Ordinations were either

plotted for the entire data set, or for the means of each group (for visual simplicity). Plots of means were derived from NMDS on the group means.

A two-factor crossed analysis of similarity (ANOSIM) was used to compare fish assemblages between sites and months for the spatial and temporal investigation at the three sites: Torquay, Queenscliff and Nepean Bay. Months when all three sites were not surveyed were omitted from this analysis (i.e. April/May, August and September). To include all months surveyed, separate one-factor ANOSIMs were used to compare months at each site. A one-factor ANOSIM was also used to compare fish assemblages, survey visually, over the larger spatial scale. Probabilities derived from ANOSIM were subjected to a Holm's (1979) sequential-Bonferroni *P*-value adjustment to account for multiple pairwise comparisons. Because most adjusted *P*-values were non-significant, due to the conservative nature of the adjustment and the number of comparisons, significant differences before adjustment are also discussed. It was not possible to perform ANOSIM on the macroalgal data because the amount of data (i.e. number of quadrats) exceeded the capabilities of Primer v4.0, so a dissimilarity matrix could only be constructed from the means.

To test whether there were any differences in the fish assemblages surveyed using visual transects and fish traps, comparisons were made between the two similarity matrices. To determine whether spatial variation in fish assemblages was related to the macroalgal assemblage present and/or the distance between the sites, separate comparisons were made between the fish assemblage similarity matrix (generated from the visual survey data), and the similarity matrices of the macroalgal assemblage and site distance data. All comparisons of similarity matrices were conducted using 'RELATE' (Primer v4.0).

For the fish assemblage data, separate univariate analyses were conducted on the number of species and total number of fishes (total density) for each of the survey methods. Separate analyses were also conducted on the abundance of bluelthroat wrasse, *Notolabrus tetricus* (visual transects) and sixspine leatherjackets, *Meuschenia freycineti* (fish traps). Analyses for other species were not possible, as their densities were too low and variable and violated analysis of variance (ANOVA) assumptions. Two-factor ANOVAs were used to examine variation between sites and over time at Torquay, Queenscliff and Nepean Bay. Months when all three sites were not surveyed

were omitted from this analysis (i.e. April/May, August and September). When a significant site \times month interaction term occurred, the cause of the interaction was examined using simple main effects contrasts, comparing months for each site separately. One-factor ANOVAs were used to examine spatial variation in fish assemblages across nine sites for the visual survey data, and across all ten sites for the fish trapping data. For the macroalgal data, spatial variation in the number of taxa and the percentage cover of the most common taxa (*Ecklonia radiata* and *Sargassum* sp.) were analysed using one-factor ANOVAs.

Pearson's correlation coefficients were used to examine the relationships between water visibility and species richness and total density of fishes. Correlations were also used to examine the relationships between fish densities and the percentage cover of macroalgae (total algal cover and individual taxa).

Refer to Chapter 2 for a detailed description of the multivariate and univariate analyses used throughout this chapter.

Results

Fish Assemblages

Spatial differences were apparent between the fish assemblages at the three sites: Torquay, Queenscliff and Nepean Bay (Table 3.1). *Notolabrus tetricus* and *Meuschenia flavolineata* were very common at Torquay, while *Odax cyanomelas*, *Aplodactylus arcidens*, *Meuschenia hippocrepis* and *Enoplosus armatus* were the most abundant species at Nepean Bay (Table 3.1). Several species were common to both Nepean Bay and Queenscliff, but were rarely recorded at Torquay, such as *Dactylophora nigricans*, *Pempheris multiradiata* and *Girella zebra* (Table 3.1). Spatial differences were also very apparent between the fish assemblages across all ten sites, and between survey methods within a site (Table 3.2). While most species occurred in low numbers, there were some notable exceptions. *Trachinops caudimaculatus* was extremely abundant on the visual transects at both Grassy Point and Mornington, but was not caught in the fish traps, or recorded at any other site (Table 3.2). *Acanthaluteres spilomelanurus* was also very abundant at Grassy Point relative to the other sites, however, only one individual was caught in the traps at this site compared to 455 individuals surveyed visually (Table 3.2). *Siphaemia cephalotes* was extremely abundant on the visual transects at

Queenscliff, and to a lesser extent at Grassy Point and Indented Head, but was virtually absent from the remaining sites (Table 3.2). *N. tetricus* was again most abundant at Torquay, and most individuals were recorded visually (Table 3.2). In contrast, the majority of *Meuschenia freycineti* individuals recorded were caught in fish traps (Table 3.2). Despite differences in the fishes surveyed using visual transects and fish traps, there was a significant correlation between the fish assemblages surveyed using the two methods (Global RHO = 0.572, $P = 0.001$).

The NMDS and ANOSIM for the fish assemblages at Torquay, Queenscliff and Nepean Bay revealed significant differences between sites and months (Fig. 3.2; Table 3.3). Fish assemblages at all three sites were significantly different from each other (Fig. 3.2a; Table 3.3), but the differences between months could not be further resolved by pairwise comparisons (Fig. 3.2b; Table 3.3). However, before the P -values were adjusted there were significant differences between months, with fish assemblages tending to differ between summer and winter (Table 3.3). Separate NMDS plots for each site showed very little clustering of months (Figs. 3.3, 3.4 and 3.5). ANOSIMs revealed no effect of month at Queenscliff ($R = 0.009$; $P = 0.385$), and although months were significantly different at Torquay and Nepean Bay, these differences could not be further elucidated by pairwise comparisons between months (Tables 3.4 and 3.5, respectively). However, before adjustment there were significant differences between months, and in general, fish assemblages differed between summer and winter/spring at both Torquay and Nepean Bay (Tables 3.4 and 3.5, respectively).

Table 3.1: Fish species recorded during monthly visual surveys at Torquay (T), Queenscliff (Q) and Nepean Bay (NB). The total number of sightings was pooled across months (January - December 1996).

Taxon	Common name	Site		
		T	Q	NB
Parascyllidae				
<i>Parascyllium variolatum</i>	Varied catshark	0	0	1
Urolophidae				
<i>Urolophus gigas</i>	Spotted stingaree	0	3	0
Syngnathidae				
<i>Pyglopteryx taeniolatus</i>	Common seadragon	0	1	0
Serranidae				
<i>Caesioperca rasor</i>	Barber perch	0	1	0
Plesiopidae				
<i>Trachinops caudimaculatus</i>	Southern hulafish	0	4	0
Apogonidae				
<i>Siphaemia cephalotes</i>	Woods siphon fish	0	40	15
<i>Vincentia conspersa</i>	Southern cardinalfish	0	4	0
Dinolestidae				
<i>Dinolestes lewini</i>	Longfin pike	0	0	1
Mullidae				
<i>Upeneichthys vlamingii</i>	Red mullet	0	17	12
Pempherididae				
<i>Pempheris multiradiata</i>	Common bullseye	5	50	61
Girellidae				
<i>Girella zebra</i>	Zebrafish	3	52	50
Scorpididae				
<i>Scorpius aequipinnis</i>	Sea sweep	6	12	0
<i>Tilodon sexfasciatum</i>	Moonlighter	0	11	2
Enoplosidae				
<i>Enoplosus armatus</i>	Old wife	9	7	42
Chironemidae				
<i>Chironemus marmoratus</i>	Kelpfish	1	1	3
<i>Threpterus maculosus</i>	Silver spot	0	0	2
Aplodactylidae				
<i>Aplodactylus arctidens</i>	Southern seacarp	0	0	47
Cheilodactylidae				
<i>Cheilodactylus nigripes</i>	Magpie perch	54	65	36
<i>Dactylophora nigricans</i>	Dusky morwong	8	28	48
Latrididae				
<i>Latridopsis forsteri</i>	Bastard trumpeter	0	2	8
Pomacentridae				
<i>Parma victoriae</i>	Scalyfin	77	61	83
Labridae				
<i>Notolabrus fucicola</i>	Saddled wrasse	0	0	6
<i>Notolabrus tetricus</i>	Bluethroat wrasse	557	390	385
<i>Notolabrus</i> sp. (hybrid)	Bluethroat/Saddled wrasse	11	0	2
<i>Pictilabrus laticlavus</i>	Senator wrasse	6	4	38
Unidentified wrasse		0	0	1
Odacidae				
<i>Haletta semifasciata</i>	Blue rock whiting	0	0	1
<i>Odax acroptilus</i>	Rainbow cale	2	0	6
<i>Odax cyanomelas</i>	Herring cale	13	20	197
<i>Siphonognathus beddomei</i>	Pencil weed whiting	0	0	6
Clinidae				
Unidentified clinidae		0	0	1

Table 3.1: cont.

Taxon	Common name	Site		
		T	Q	NB
Callionymidae				
<i>Forsterypes calauropomus</i>	Common stinkfish	0	1	0
Monacanthidae				
<i>Acanthaluteres spilomelanurus</i>	Bridled leatherjacket	0	0	2
<i>Acanthaluteres vittiger</i>	Toothbrush leatherjacket	2	0	0
<i>Meuschenia australis</i>	Brownstriped leatherjacket	1	0	0
<i>Meuschenia flavolineata</i>	Yellowstriped leatherjacket	91	14	24
<i>Meuschenia freycineti</i>	Sixspine leatherjacket	2	28	3
<i>Meuschenia galii</i>	Bluelined leatherjacket	3	0	7
<i>Meuschenia hippocrepis</i>	Horseshoe leatherjacket	11	26	62
<i>Meuschenia trachylepis</i>	Yellow-finned leatherjacket	0	1	0
<i>Scobinichthys granulatus</i>	Rough leatherjacket	2	3	15
Unidentified leatherjacket		3	2	7
Aracidae				
<i>Aracana aurita</i>	Shaws cowfish	0	0	1
Tetraodontidae				
<i>Tetractenos glaber</i>	Smooth toadfish	0	0	1
Diodontidae				
<i>Diodon nictemerus</i>	Globefish	3	3	5
Unidentified fish		3	1	52
Total number of species		20	27	31

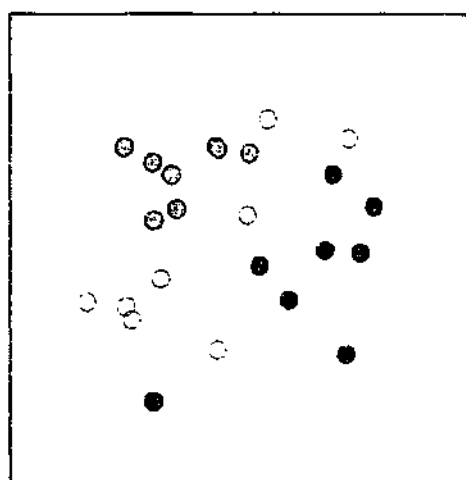
See Appendix 3.1 for species authorities

Table 3.2: cont.

Taxon	T		TS		Q		PP		NB		M		IH		GP		BR		A	
	V	T	V	T	V	T	V	T	V	T	V	T	V	T	V	T	V	T	V	T
Cheilodactylidae																				
<i>Cheilodactylus nigrripes</i>	13	0	0	0	3	0	ND	0	1	0	1	0	1	0	3	0	0	0	0	0
<i>Dactylophora nigricans</i>	0	0	0	0	1	0	ND	0	1	0	1	0	1	0	5	0	0	0	3	0
Pomacentridae																				
<i>Parma victoriae</i>	11	0	4	0	4	1	ND	0	1	0	9	1	3	0	4	1	0	0	0	0
Labridae																				
<i>Notolabrus fucicola</i>	1	0	0	0	0	0	ND	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Notolabrus tetricus</i>	105	15	26	2	32	8	ND	0	30	3	12	0	55	0	19	0	0	0	0	0
<i>Pictilabrus latilavus</i>	3	0	3	0	1	0	ND	0	1	1	4	0	1	0	3	2	0	0	0	0
Odacidae																				
<i>Neodax balteatus</i>	0	0	0	0	0	0	ND	0	0	0	1	0	1	0	21	0	7	0	24	0
<i>Odax acroptilus</i>	0	0	0	0	0	0	ND	0	2	0	0	0	0	0	0	0	0	0	0	0
<i>Odax cyanomelas</i>	3	0	14	0	0	0	ND	0	34	0	0	0	0	0	0	0	0	0	0	0
Clinidae																				
<i>Heteroclinus wilsoni</i>	0	0	0	0	0	1	ND	0	0	0	0	0	0	0	0	0	0	0	0	0
Monacanthidae																				
<i>Acanthaluteres vittiger</i>	8	27	1	0	0	0	ND	0	0	0	0	6	0	0	0	0	1	0	0	0
<i>A. spilomelanurus</i>	3	0	4	0	0	0	ND	0	0	0	0	0	7	0	455	1	0	0	2	0
<i>Brachaluteres jacksonianus</i>	0	0	0	0	0	0	ND	0	0	0	0	0	0	0	0	0	1	0	1	0
<i>Meuschenia australis</i>	0	0	0	0	0	0	ND	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Meuschenia flavolineata</i>	11	1	0	0	0	0	ND	0	1	0	3	0	0	0	0	0	0	0	0	0
<i>Meuschenia freycineti</i>	0	1	1	4	0	16	ND	11	0	14	2	7	0	20	0	11	0	0	0	1
<i>Meuschenia galii</i>	1	0	0	0	0	0	ND	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Meuschenia hippocrepis</i>	4	13	0	2	6	0	ND	0	0	5	1	7	0	0	0	0	2	0	1	0
<i>Scobinichthys granulatus</i>	1	0	0	0	0	0	ND	0	0	0	0	9	0	5	0	0	1	1	1	0
Tetraodontidae																				
<i>Contusus brevicaudus</i>	0	0	0	0	0	0	ND	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Tetraodon glaber</i>	0	0	0	0	0	0	ND	0	2	0	0	0	2	1	1	0	5	5	0	0
Diodontidae																				
<i>Diodon nicthemerus</i>	0	0	0	0	1	0	ND	0	0		4	0	3	0	0	0	0	0	1	0
Total number of species	18	6	11	3	11	4	ND	2	12	5	13	5	11	4	12	7	7	2	11	1

See Appendix 3.1 for species authorities

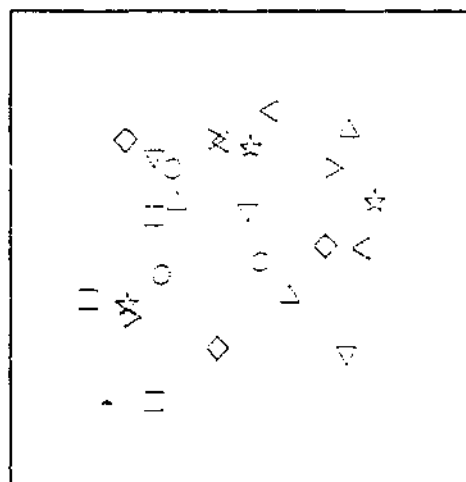
a)



Site

 T	 Q	 NB
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b)



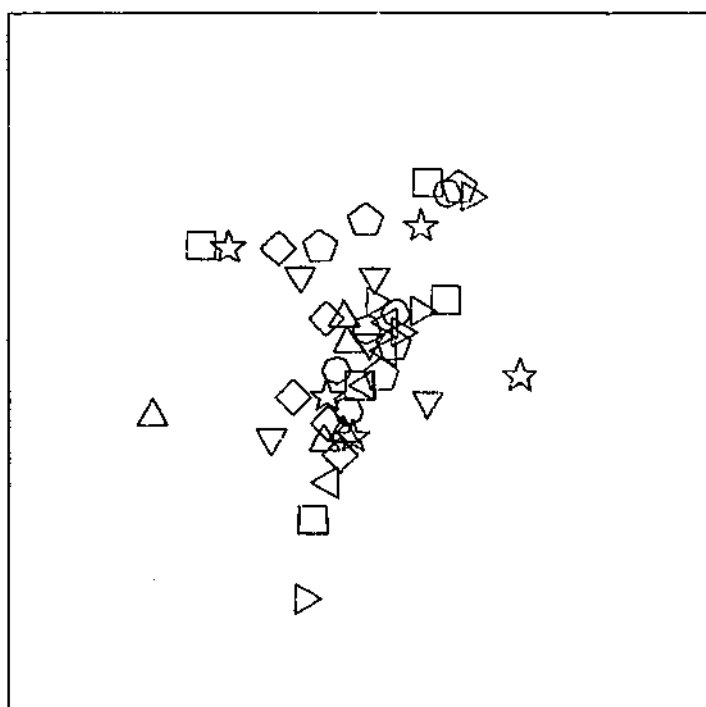
Month

 Jan	 Feb	 Mar	 Jun	 Jul	 Oct	 Nov	 Dec
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Figure 3.2: Two-dimensional NMDS ordinations of the fish assemblages at Torquay (T), Queenscliff (Q) and Nepean Bay (NB) showing a) mean data set differentiating sites (stress = 0.15) and b) mean data set differentiating months (stress = 0.15).

Table 3.3: Two-factor crossed ANOSIM comparing fish assemblages between sites (Torquay, Queenscliff and Nepean Bay) from January - December 1996 (no data for April/May, August and September). T = Torquay, Q = Queenscliff and NB = Nepean Bay. P^* Holm's adjusted P -value.

Source	R	P	P^*
Site	0.273	<0.001	
T v Q	0.168	<0.001	<0.001
T v NB	0.398	<0.001	<0.001
Q v NB	0.284	<0.001	<0.001
Month	0.087	0.040	
Mar v Jul	0.317	0.002	0.056
Mar v Jun	0.251	0.006	0.162
Mar v Oct	0.266	0.009	0.234
Feb v Jun	0.197	0.011	0.275
Feb v Oct	0.226	0.012	0.288
Feb v Jul	0.182	0.023	0.529
Jan v Jun	0.111	0.038	0.836
Jul v Oct	0.153	0.047	0.987
Jan v Feb	-0.071	0.810	1.000
Jan v Mar	0.019	0.366	1.000
Jan v Jul	0.010	0.415	1.000
Jan v Oct	0.125	0.050	1.000
Jan v Nov	-0.069	0.828	1.000
Jan v Dec	-0.070	0.860	1.000
Feb v Mar	0.057	0.241	1.000
Feb v Nov	0.129	0.058	1.000
Feb v Dec	0.045	0.259	1.000
Mar v Nov	0.139	0.070	1.000
Mar v Dec	0.047	0.258	1.000
Jun v Jul	0.031	0.316	1.000
Jun v Oct	-0.011	0.524	1.000
Jun v Nov	0.001	0.472	1.000
Jun v Dec	0.077	0.122	1.000
Jul v Nov	0.105	0.090	1.000
Jul v Dec	0.047	0.218	1.000
Oct v Nov	0.031	0.316	1.000
Oct v Dec	0.137	0.071	1.000
Nov v Dec	0.010	0.406	1.000



Month

▽	Jan	ND	Aug
△	Feb	ND	Sep
□	Mar	◇	Oct
◇	Apr/May	☆	Nov
▷	Jun	○	Dec
◁	Jul		

Figure 3.3: Two-dimensional NMDS ordination of the fish assemblages recorded over 12 months at Queenscliff. This plot represents the entire data set and each point depicts a single transect.

ND = no data. Stress = 0.14.

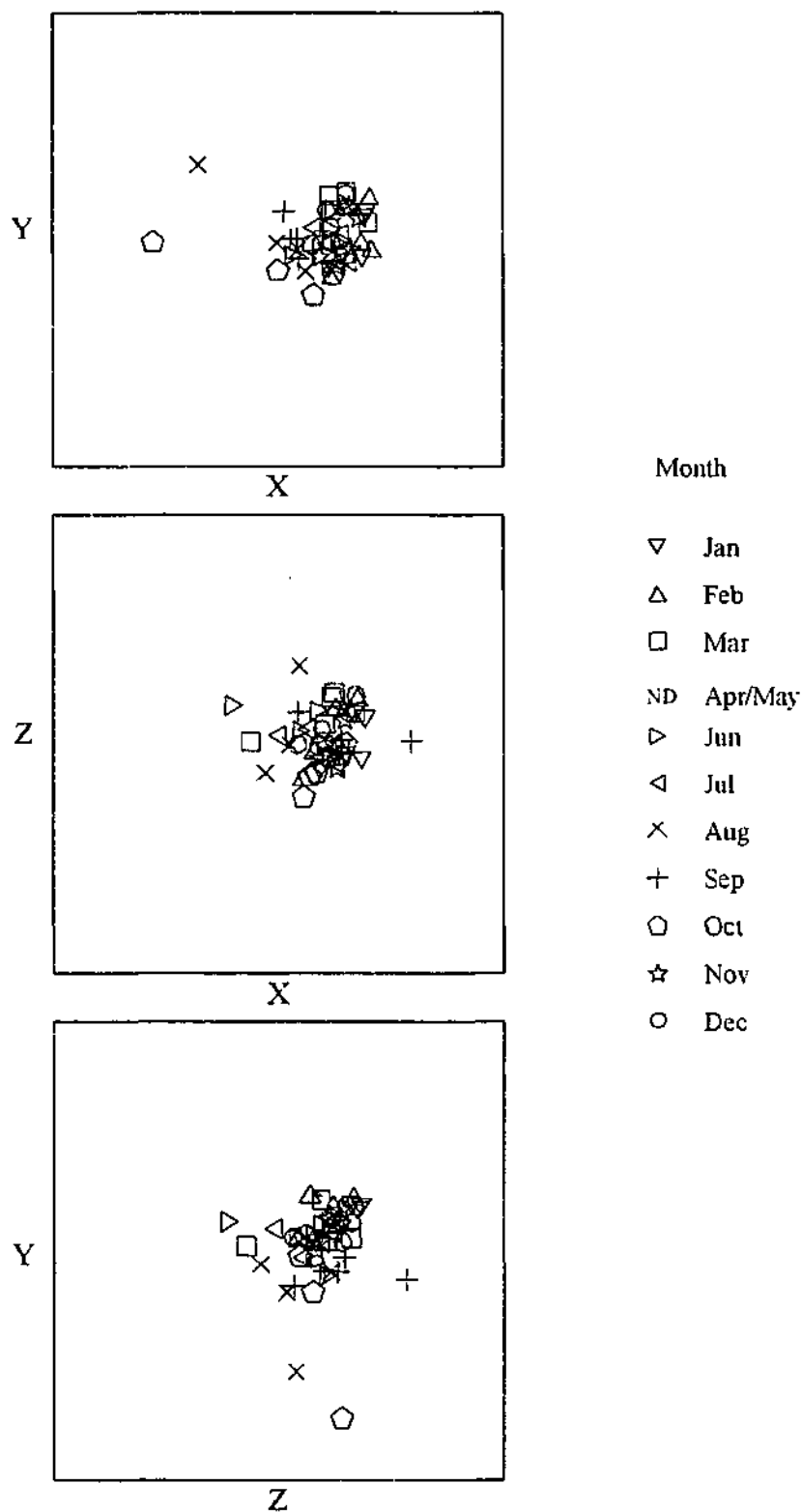


Figure 3.4: Three-dimensional NMDS ordination of the fish assemblages recorded over 12 months at Torquay. These plots represent the entire data set and each point depicts a single transect.

ND = no data. Stress = 0.10.

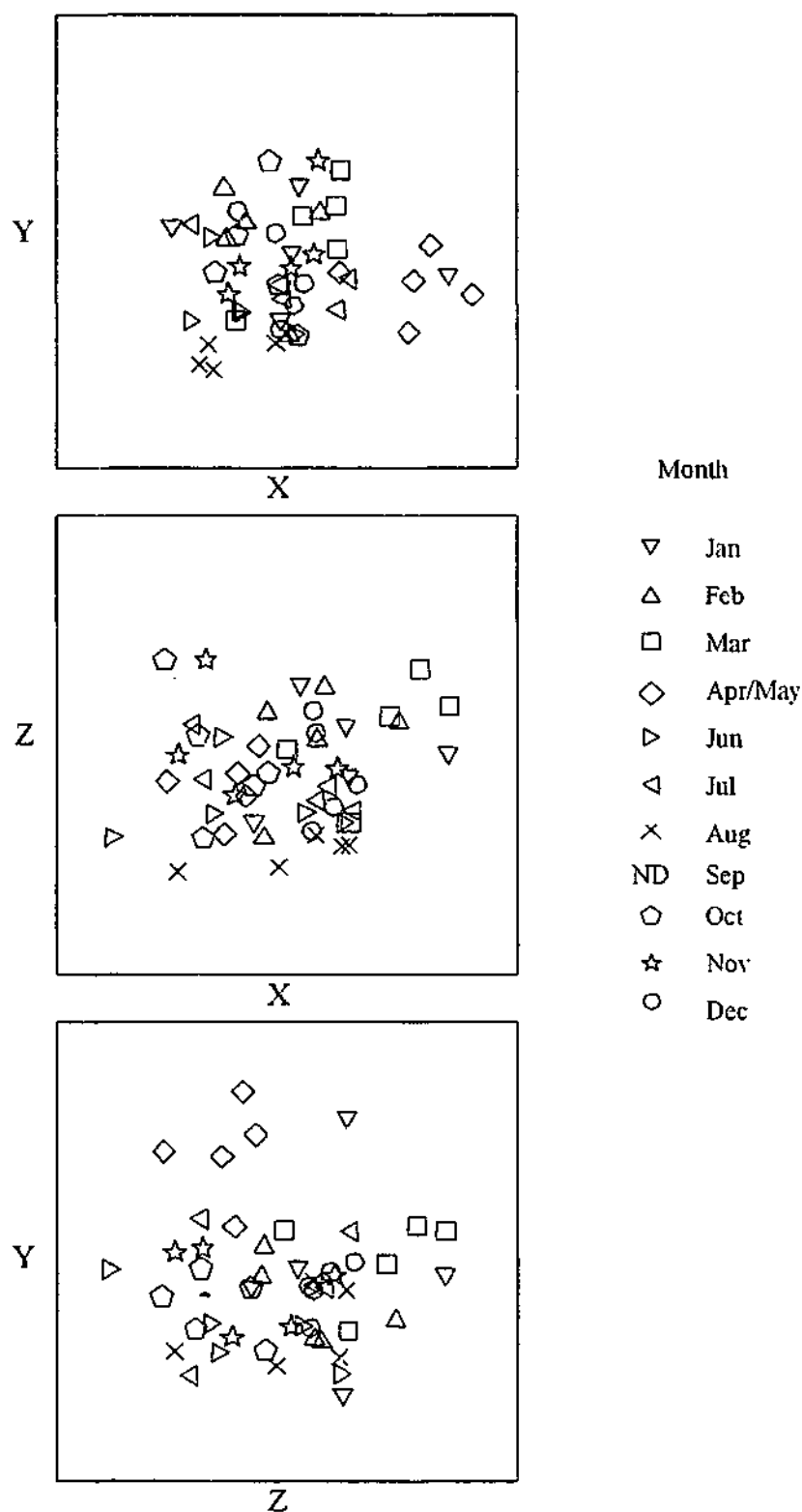


Figure 3.5: Three-dimensional NMDS ordination of the fish assemblages recorded over 12 months at Nepean Bay. These plots represent the entire data set and each point depicts a single transect.

ND = no data. Stress = 0.13.

Table 3.4: One-factor ANOSIM comparing fish assemblages over time at Torquay (January - December 1996, no data for April-May). P^* Holm's adjusted P -value.

Source	R	P	P^*
Month	0.194	<0.001	
Jan v Aug	0.655	0.008	0.560
Jan v Sept	0.576	0.008	0.560
Mar v Sept	0.582	0.008	0.560
Aug v Nov	0.572	0.008	0.560
Sept v Nov	0.466	0.008	0.560
Feb v Aug	0.541	0.016	0.640
Feb v Sept	0.392	0.016	0.640
Aug v Dec	0.355	0.016	0.640
Mar v Aug	0.481	0.024	0.888
Mar v Oct	0.340	0.024	0.888
Sept v Dec	0.248	0.024	0.888
Jan v Feb	-0.052	0.587	1.000
Jan v Mar	0.294	0.048	1.000
Jan v Jun	0.242	0.032	1.000
Jan v Jul	0.260	0.071	1.000
Jan v Oct	0.250	0.040	1.000
Jan v Nov	0.116	0.175	1.000
Jan v Dec	0.162	0.151	1.000
Feb v Mar	0.034	0.357	1.000
Feb v Jun	0.052	0.278	1.000
Feb v Jul	0.020	0.429	1.000
Feb v Oct	0.150	0.151	1.000
Feb v Nov	-0.064	0.605	1.000
Feb v Dec	0.030	0.333	1.000
Mar v Jun	0.038	0.341	1.000
Mar v Jul	0.398	0.032	1.000
Mar v Nov	0.276	0.071	1.000
Mar v Dec	0.170	0.119	1.000
Jun v Jul	-0.182	0.092	1.000
Jun v Aug	0.188	0.075	1.000
Jun v Sept	0.152	0.095	1.000
Jun v Oct	0.060	0.262	1.000
Jun v Nov	0.096	0.190	1.000
Jun v Dec	-0.096	0.325	1.000
Jul v Aug	0.297	0.056	1.000
Jul v Sept	0.258	0.056	1.000
Jul v Oct	0.084	0.222	1.000
Jul v Nov	0.072	0.278	1.000
Jul v Dec	0.034	0.333	1.000
Aug v Sept	0.194	0.056	1.000
Aug v Oct	0.019	0.357	1.000
Sept v Oct	0.126	0.087	1.000
Oct v Nov	0.124	0.145	1.000
Oct v Dec	0.256	0.032	1.000
Nov v Dec	0.088	0.216	1.000

Table 3.5: One-factor ANOSIM comparing fish assemblages over time at Nepean Bay (January - December 1996; no data for September). P^* Holm's adjusted P -value.

Source	R	P	P^*
Month	0.330	<0.001	
Jan v Apr/May	0.508	0.008	0.360
Jan v Oct	0.370	0.008	0.360
Feb v Apr/May	0.730	0.008	0.360
Feb v Aug	0.510	0.008	0.360
Mar v Apr/May	0.758	0.008	0.360
Mar v Jun	0.548	0.008	0.360
Mar v Oct	0.636	0.008	0.360
Apr/May v Jun	0.716	0.008	0.360
Apr/May v Jul	0.526	0.008	0.360
Apr/May v Aug	0.822	0.008	0.360
Apr/May v Oct	0.706	0.008	0.360
Apr/May v Nov	0.530	0.008	0.360
Apr/May v Dec	0.768	0.008	0.360
Oct v Dec	0.500	0.008	0.360
Jan v Aug	0.414	0.016	0.496
Jan v Jun	0.252	0.024	0.720
Feb v Jul	0.270	0.024	0.720
Feb v Oct	0.394	0.024	0.720
Mar v Jul	0.380	0.024	0.720
Mar v Aug	0.410	0.024	0.720
Jun v Dec	0.272	0.024	0.720
Aug v Nov	0.348	0.024	0.720
Feb v Jun	0.360	0.032	0.736
Mar v Nov	0.400	0.032	0.736
Aug v Oct	0.420	0.032	0.736
Jan v Feb	0.036	0.365	1.000
Jan v Mar	0.176	0.119	1.000
Jan v Jul	-0.132	0.881	1.000
Jan v Nov	0.132	0.159	1.000
Jan v Dec	0.020	0.397	1.000
Feb v Mar	0.314	0.056	1.000
Feb v Nov	0.232	0.063	1.000
Feb v Dec	0.132	0.159	1.000
Mar v Dec	0.174	0.135	1.000
Jun v Jul	0.134	0.159	1.000
Jun v Aug	0.148	0.143	1.000
Jun v Oct	0.152	0.135	1.000
Jun v Nov	0.026	0.365	1.000
Jul v Aug	0.262	0.056	1.000
Jul v Oct	0.258	0.079	1.000
Jul v Nov	0.052	0.254	1.000
Jul v Dec	0.012	0.421	1.000
Aug v Dec	0.218	0.056	1.000
Oct v Nov	-0.026	0.579	1.000
Nov v Dec	0.188	0.079	1.000

The NMDS and ANOSIM comparing fish assemblages at the nine sites visually surveyed revealed a significant effect of site (Fig. 3.6; Table 3.6). The ordination plot of the data means shows some site clustering, with sites in the north, centre and south of the bay grouping together (Fig. 3.6). Although the site effect could not be further resolved by pairwise comparisons between the sites, before *P*-value adjustments were made, the fish assemblages differed significantly between all sites except The Springs and Queenscliff, The Springs and Nepean Bay, and Queenscliff and Indented Head (Table 3.6).

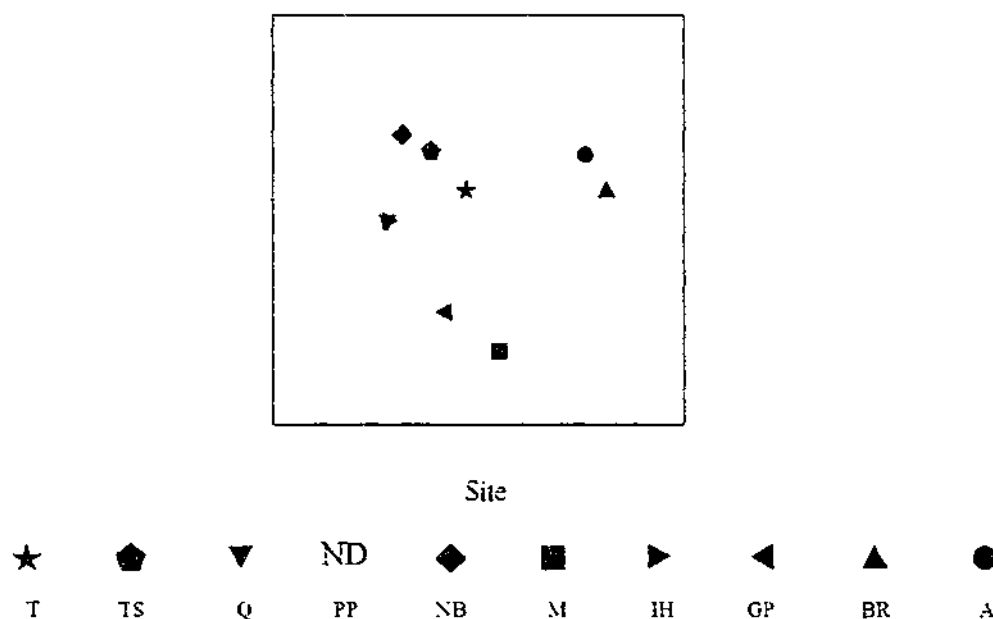


Figure 3.6: Two-dimensional NMDS ordination of the mean fish assemblage data recorded once only at the nine sites surveyed using visual transects (stress = 0.10). T = Torquay, TS = The Springs, Q = Queenscliff, PP = Pilot's Pier, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona.

Table 3.6: One-factor ANOSIM comparing fish assemblages at all nine sites surveyed visually (once-off surveys between December 1997 - April 1998). *P** Holm's adjusted *P*-value. T = Torquay, TS = The Springs, Q = Queenscliff, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona.

Source	<i>R</i>	<i>P</i>	<i>P</i> *
Site	0.692	<0.001	
T v TS	0.644	0.008	0.288
T v IH	0.736	0.008	0.288
T v GP	0.876	0.008	0.288
T v A	1.000	0.008	0.288
T v BR	1.000	0.008	0.288
T v M	0.500	0.008	0.288
T v NB	0.676	0.008	0.288
TS v GP	0.928	0.008	0.288
TS v A	0.992	0.008	0.288
TS v BR	1.000	0.008	0.288
TS v M	0.562	0.008	0.288
Q v A	0.908	0.008	0.288
Q v BR	0.968	0.008	0.288
Q v M	0.508	0.008	0.288
IH v GP	0.716	0.008	0.288
IH v A	0.980	0.008	0.288
IH v BR	1.000	0.008	0.288
IH v M	0.584	0.008	0.288
IH v NB	0.780	0.008	0.288
GP v A	0.932	0.008	0.288
GP v BR	0.992	0.008	0.288
GP v NB	0.988	0.008	0.288
A v M	0.796	0.008	0.288
A v NB	1.000	0.008	0.288
BR v M	0.890	0.008	0.288
BR v NB	1.000	0.008	0.288
M v NB	0.660	0.008	0.288
T v Q	0.436	0.016	0.288
TS v IH	0.618	0.016	0.288
Q v GP	0.504	0.016	0.288
Q v NB	0.450	0.016	0.288
GP v M	0.308	0.024	0.288
A v BR	0.306	0.048	0.288
TS v Q	0.320	0.079	0.288
TS v NB	-0.018	0.532	1.000
Q v IH	-0.060	0.556	1.000

Number of Species and Total Density of Fishes

Over this study 41 species were recorded on the visual transects at Torquay, Queenscliff and Nepean Bay (Table 3.1). There was significant temporal variation in the number of species, but the pattern was not consistent between the three sites (Fig. 3.7; Table 3.7). Comparisons across months for each site revealed no significant difference between

months at either Queenscliff or Torquay, but at Nepean Bay significantly more species were recorded in January and March than in October (Fig. 3.7; Table 3.7).

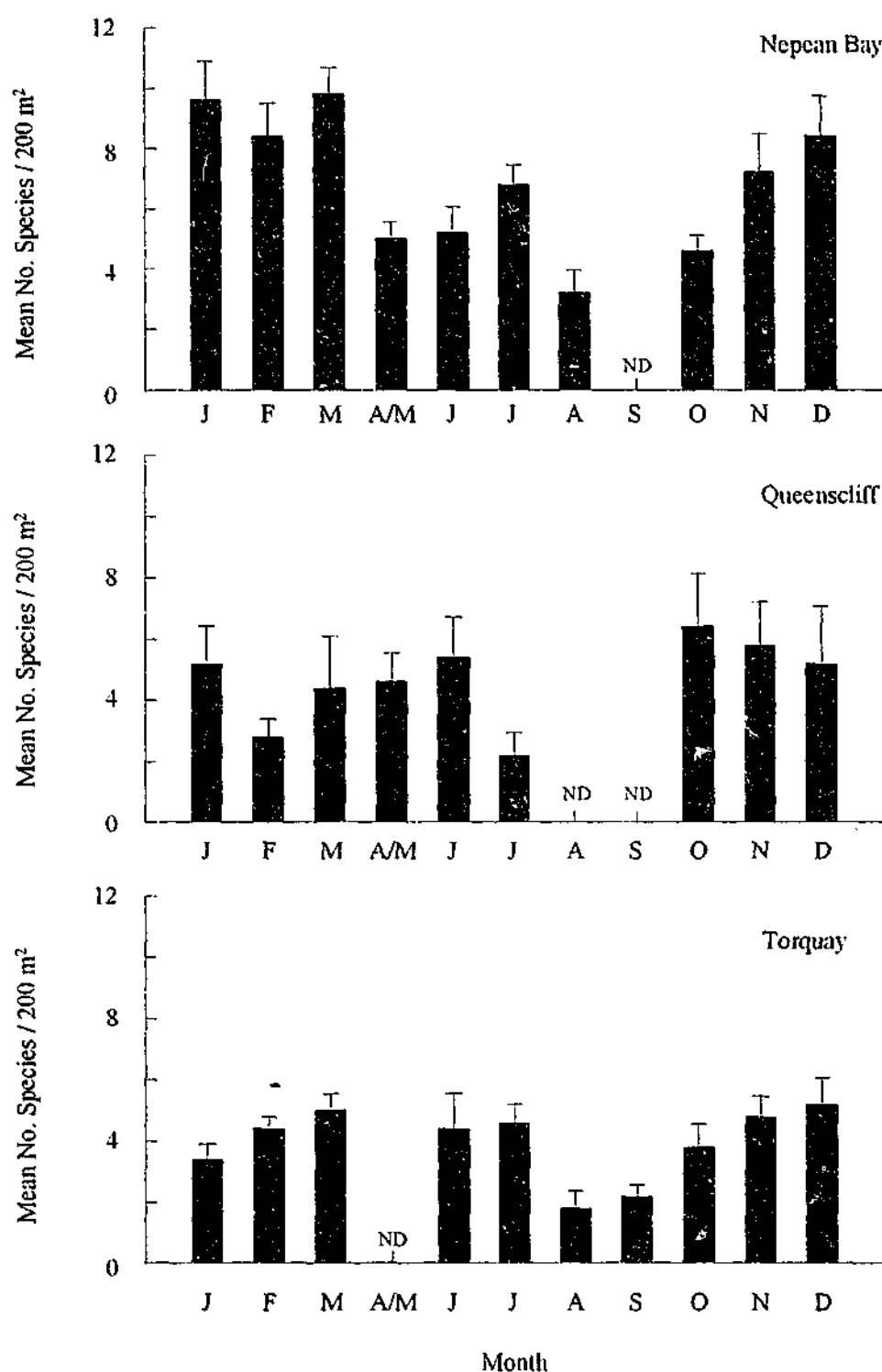


Figure 3.7: Number of fish species (mean \pm SE; $n = 5$) recorded monthly at Torquay, Queenscliff and Nepean Bay from January – December 1996. ND = no data.

Table 3.7: Two-factor ANOVAs comparing number of species, total density of fishes and densities of *Notolabrus tetricus*, across sites (Torquay, Queenscliff and Nepean Bay), and months (January, February, March, June, July, October, November and December 1996). Months when all three sites were not sampled were excluded from the analyses.

Source	MS	df	F	P
No. of Species^u				
Month	7.475	7	1.289	0.264
Site	115.558	2	19.924	<0.001
Month*Site	11.682	14	2.014	0.024
<u>Torquay</u>				
Month	1.814	7	0.313	0.947
<u>Queenscliff</u>				
Month	10.739	7	1.852	0.086
<u>Nepean Bay</u>				
Month	18.286	7	3.153	0.005
Error	5.800	96		
Total Density^l				
Month	0.202	7	2.786	0.011
Site	0.277	2	3.832	0.025
Month*Site	0.104	14	1.432	0.153
Error	0.072	96		
<i>N. tetricus</i>^l				
Month	0.098	7	1.807	0.095
Site	0.429	2	7.876	0.001
Month*Site	0.081	14	1.490	0.130
Error	0.054	96		

^u = untransformed data, ^l = $\log_{10}(x+1)$ transformed data

Fish assemblage surveys over the broad spatial scale recorded 31 species from sites visually surveyed, but only 18 species from fish traps (Table 3.2). The number of species differed significantly across all nine sites visually surveyed (Fig. 3.8a; Table 3.8). There were significantly fewer species at Black Rock and Altona than at Grassy Point and Torquay, and also at Queenscliff than at Torquay (Fig. 3.8a). The number of species also varied between the ten sites surveyed using fish traps, with significantly fewer species recorded at Altona compared with Queenscliff, Nepean Bay and Grassy Point (Fig. 3.8b; Table 3.8). At all sites, more species were recorded on the visual surveys than in fish traps (Figs. 3.8a and b).

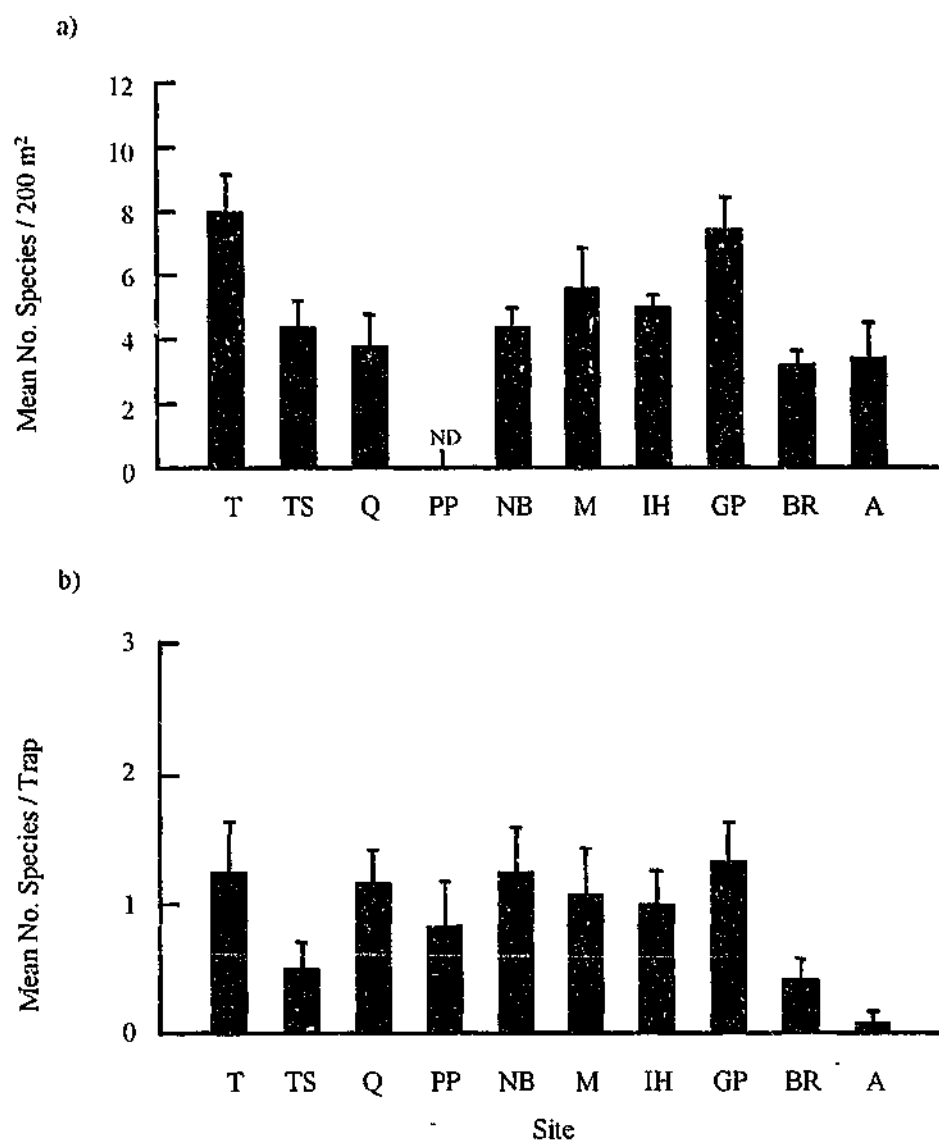


Figure 3.8: Number of fish species (mean \pm SE) recorded from all sites using a) visual transects ($n = 5$) and b) fish traps ($n = 12$ at all sites except PP where $n = 6$). Sites were surveyed once only between December 1997 – April 1998. T = Torquay, TS = The Springs, Q = Queenscliff, PP = Pilot's Pier, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona. ND = no data. Note: maximum Y-value differs between survey methods.

Table 3.8: One-factor ANOVAs comparing number of species, total density of fishes and densities of *Notolabrus tetricus* (visual surveys) and *Meuschenia freycineti* (fish trap surveys), across all sites surveyed once only between December 1997 - April 1998. Note: visual surveys were not conducted at Pilot's Pier.

Source	Visual Transects				Fish Traps			
	MS	df	F	P	MS	df	F	P
No. of Species^a								
Site	14.422	8	4.652	0.001	0.112	9	2.803	0.005
Error	3.100	36			0.040	104		
Total Density[†]								
Site	1.299	8	8.018	<0.001	0.337	9	3.242	0.002
Error	0.162	36			0.104	104		
<i>N. tetricus</i>[†]								
Site	0.945	8	16.340	<0.001				
Error	0.058	36						
<i>M. freycineti</i>[†]								
Site					0.181	9	3.610	0.001
Error					0.050	104		

^a = untransformed data, [†] = log₁₀(x+1) transformed data

Total density varied significantly between sampling months, and also between the three sites: Torquay, Queenscliff and Nepean Bay (Fig. 3.9; Table 3.7). Total density was significantly lower in July than March at all sites, and significantly lower at Queenscliff than Nepean Bay (Fig. 3.9).

Total density was extremely variable over all nine sites visually surveyed (Fig. 3.10a; Table 3.8), with densities significantly lower at Black Rock and Altona than Queenscliff, Mornington and Grassy Point (Fig. 3.10a). Total density also varied significantly between the ten sites surveyed using fish traps, with significantly fewer fish recorded at Altona than at Torquay and Grassy Point (Fig. 3.10b; Table 3.8). At all sites, more fish were recorded visually than by using fish traps (Figs. 3.10a and b).

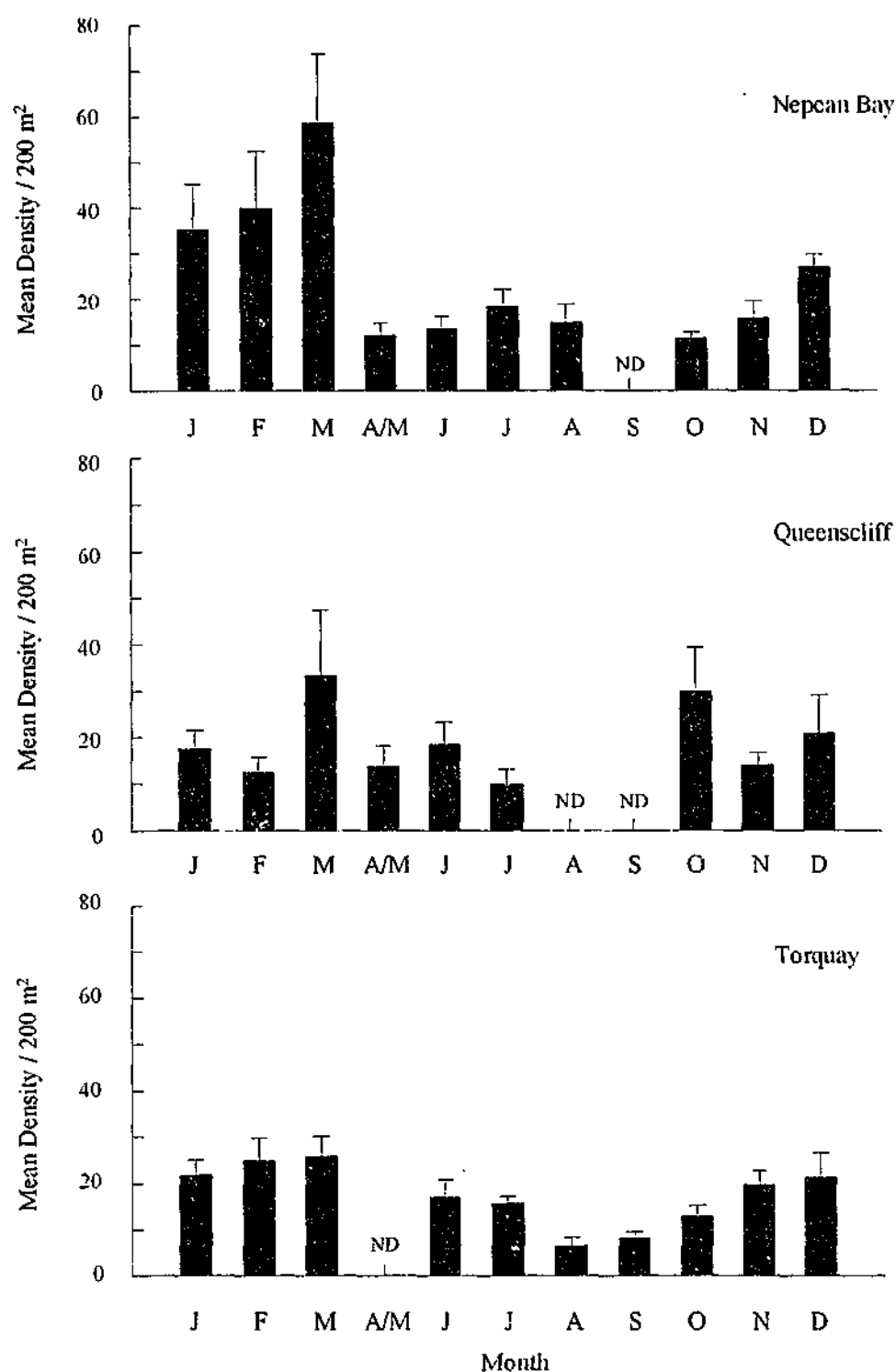


Figure 3.9: Total density of fishes (mean \pm SE; $n = 5$) recorded monthly at Torquay, Queenscliff and Nepean Bay from January - December 1996. ND = no data.

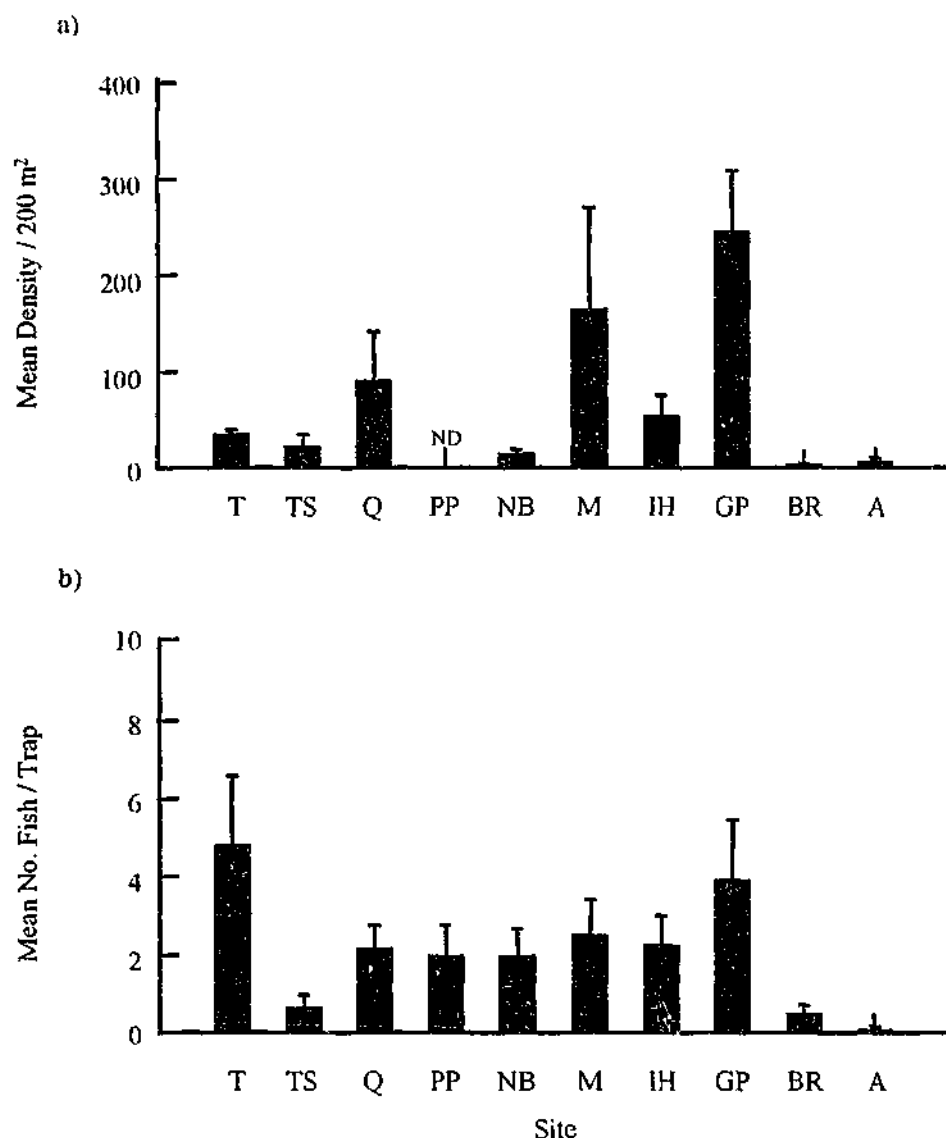


Figure 3.10: Total number of fishes (mean \pm SE) recorded from all sites using a) visual transects ($n = 5$) and b) fish traps ($n = 12$ at all sites except PP where $n = 6$). Sites were surveyed once only between December 1997 – April 1998. T = Torquay, TS = The Springs, Q = Queenscliff, PP = Pilot's Pier, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona. ND = no data. Note: maximum Y-value differs between survey methods.

Density of Notolabrus tetricus

Densities of bluelthroat wrasse, *Notolabrus tetricus*, varied significantly between the three sites (Fig. 3.11; Table 3.7). Densities of *N. tetricus* were significantly greater at Torquay than at Nepean Bay and Queenscliff (Fig. 3.11). Although mean *N. tetricus* density showed temporal variability (Fig. 3.11), this variation was not significant (Table 3.7).

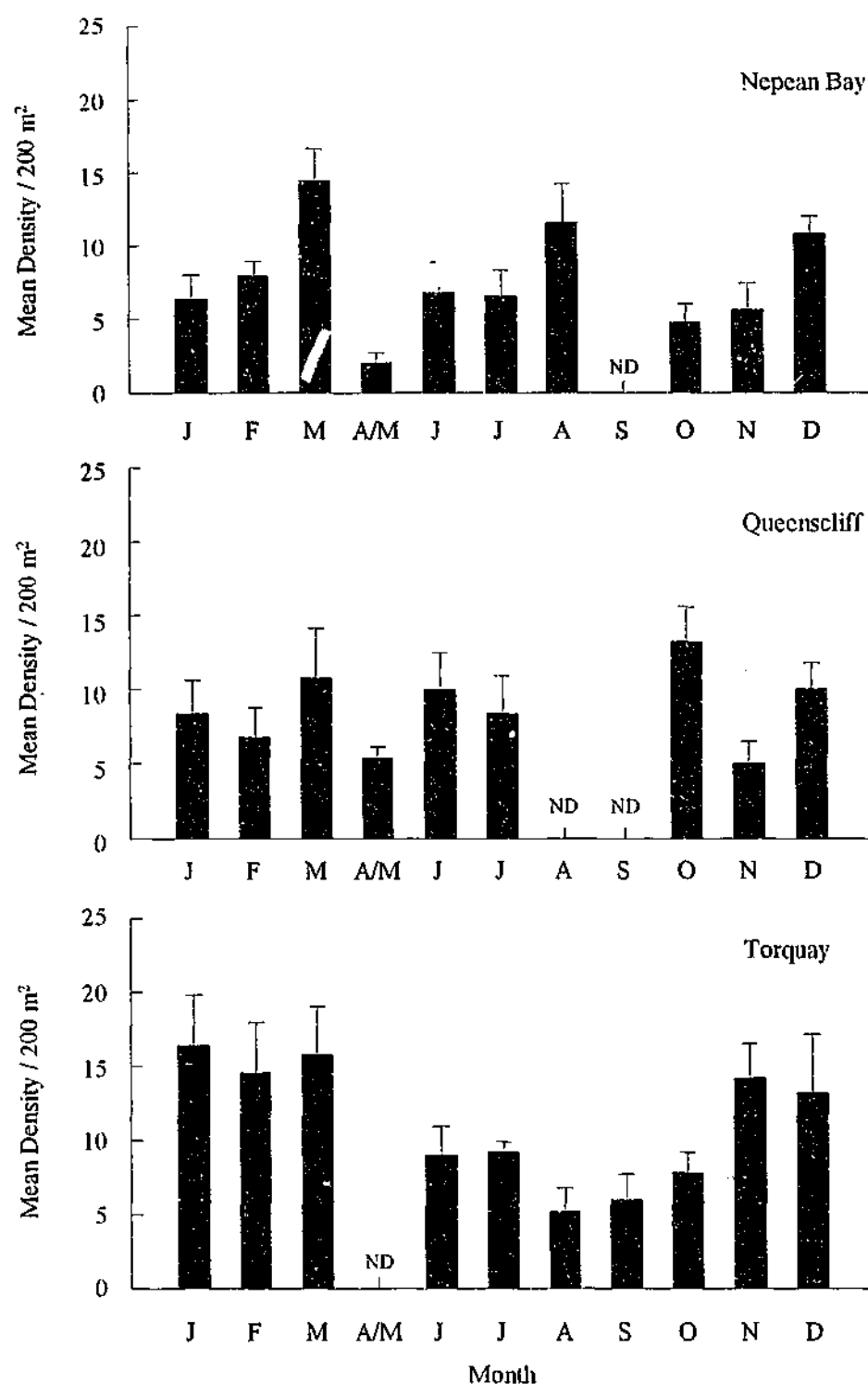


Figure 3.11: Density of *Notolabrus tetricus* (mean \pm SE; $n = 5$) recorded monthly at Torquay, Queenscliff and Nepean Bay from January – December 1996. ND = no data.

Densities of *N. tetricus* differed considerably across all nine sites visually surveyed, and analysis revealed a significant site effect (Fig. 3.12a; Table 3.8). *N. tetricus* densities were significantly greater at Torquay than all other sites (Fig. 3.12a). Densities of *N.*

tetricus also varied between the ten sites surveyed using fish traps, with most individuals recorded at Torquay, although catch rates were extremely variable between traps (Fig. 3.12b). *N. tetricus* were recorded in higher numbers and at more sites when surveyed visually than with fish traps (Figs. 3.12a and b).

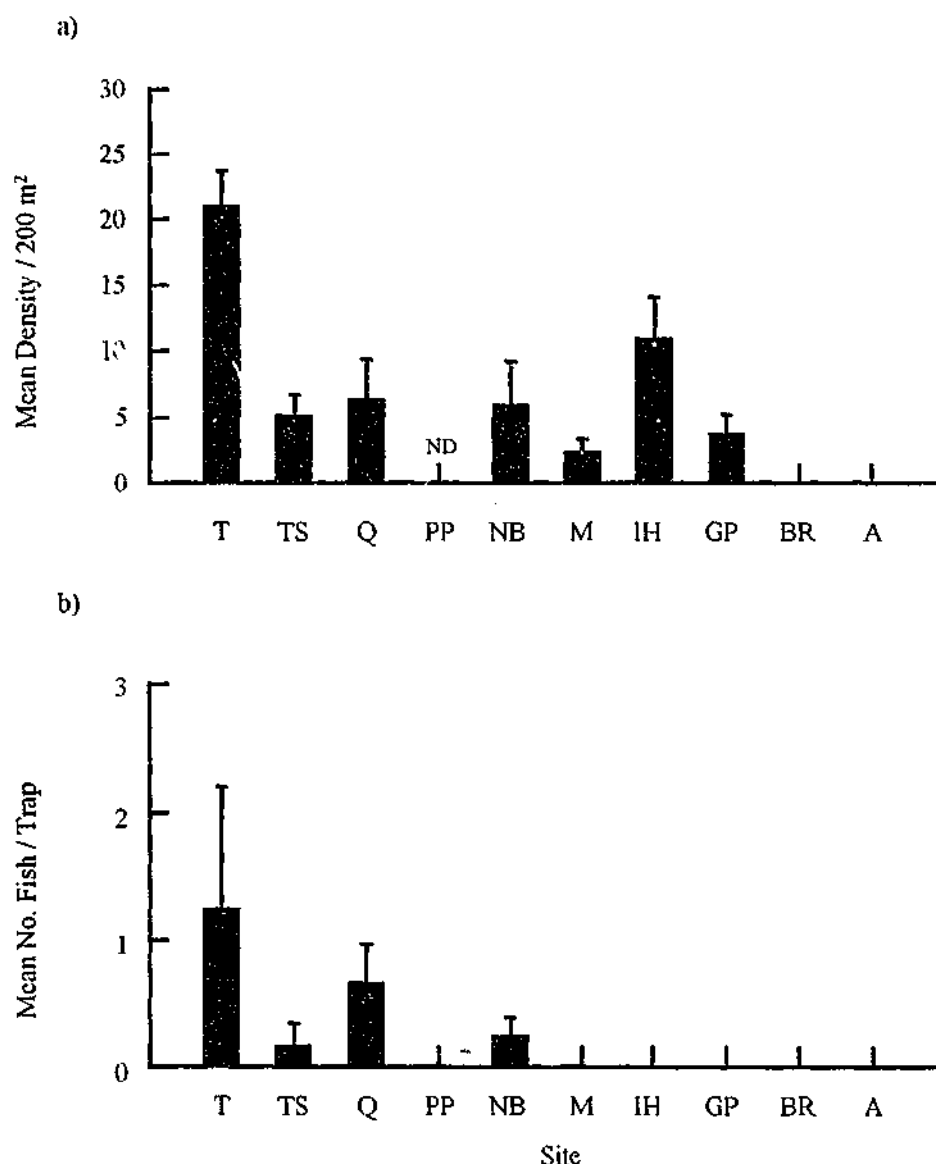


Figure 3.12: Number of *Notolabrus tetricus* (mean \pm SE) recorded from all sites using a) visual transects (n = 5) and b) fish traps (n = 12 at all sites except PP where n = 6). Sites were surveyed once only between December 1997 – April 1998. T = Torquay, TS = The Springs, Q = Queenscliff, PP = Pilot's Pier, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona. ND = no data. Note: maximum Y-value differs between survey methods.

Densities of Meuschenia freycineti, Meuschenia hippocrepis and Meuschenia flavolineata

Over the broad spatial scale, three leatherjacket species were consistently recorded, albeit in low numbers (Fig. 3.13). *Meuschenia freycineti* was rarely recorded visually, but when fish traps were used, this species was recorded at all sites except Black Rock (Figs. 3.13a and b). Numbers of *M. freycineti* caught in fish traps varied between sites, with significantly more fish at Indented Head and Pilot's Pier than at Black Rock (Fig. 3.13b; Table 3.8). Although ANOVAs could not be used due to low numbers, *Meuschenia hippocrepis* showed no distinct patterns between the sites or survey methods, while *Meuschenia flavolineata* was most common at Torquay, and more effectively surveyed visually than with fish traps (Figs. 3.13a and b).

Density of Odax cyanomelas

Although ANOVAs could not be used due to numerous zero values, densities of herring gale, *Odax cyanomelas*, showed a very distinct pattern. Over the broad spatial scale *O. cyanomelas* was visually recorded only at Torquay, The Springs and Nepean Bay, and densities at Nepean Bay were much higher than at the other sites (Fig. 3.14). No *O. cyanomelas* were caught in the fish traps.

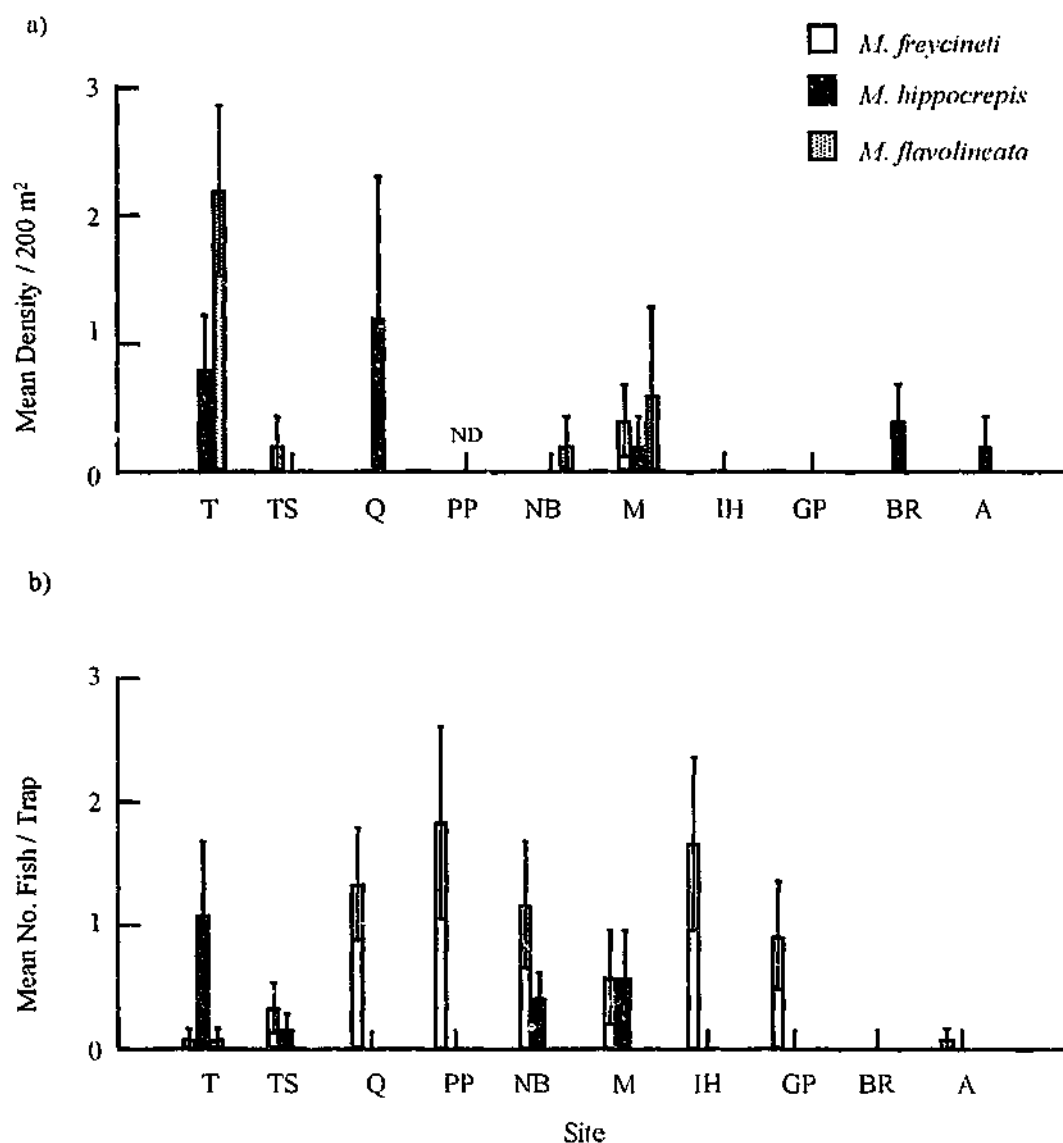


Figure 3.13: Number of *Meuschenia freycineti*, *Meuschenia hippocrepis* and *Meuschenia flavolineata* (mean \pm SE) recorded from all sites using a) visual transects ($n = 5$) and b) fish traps ($n = 12$ at all sites except PP where $n = 6$). Sites were surveyed once only between December 1997 – April 1998.

T = Torquay, TS = The Springs, Q = Queenscliff, PP = Pilot's Pier, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona. ND = no data.

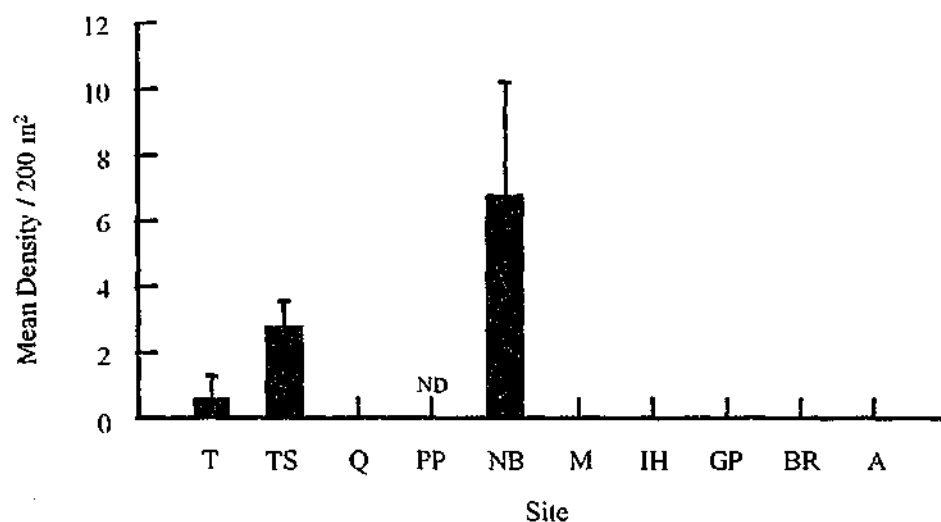


Figure 3.14: Number of *Odax cyanomelas* (mean \pm SE) recorded from all sites using visual transects ($n = 5$). Sites were surveyed once only between December 1997 – April 1998. T = Torquay, TS = The Springs, Q = Queenscliff, PP = Pilot's Pier, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona. ND = no data.

Macroalgal Surveys

In this study 22 macroalgal taxa were recorded: 1 Rhodophyte, 12 Phaeophyta and 9 Chlorophyta. Two seagrass taxa, *Amphibolus antarctica* and *Heterozostera tasmanica*, were also recorded (Table 3.9).

Table 3.9: Mean percentage cover of macroalgal taxa recorded at all nine sites surveyed in and around Port Phillip Bay (December 1997 - April 1998). T = Torquay, TS = The Springs, Q = Queenscliff, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona.

Taxon	Site								
	T	TS	Q	NB	M	IH	GP	BR	A
Rhodophyta									
<i>Laurencia</i> sp.	0	0	0	0	1.3	0	0	0	0
Phaeophyta									
<i>Acrocarpia paniculata</i>	15.8	0.5	0	0	0	0	0	0	0
<i>Caulocystis uvifera</i>	0	0	0.1	0	22.3	18.5	0	0	0
<i>Cystophora</i> sp.	19.3	2.6	8.6	10.0	27.4	19.5	7.9	1.9	0
<i>Dictyopteris muelleri</i>	0	0	0	0.1	0	0	0	0.8	0
<i>Ecklonia radiata</i>	0.4	43.3	19.5	11.8	11.5	7.8	1.3	8.2	14.3
<i>Lobospira bicuspidata</i>	6.1	1.4	0.1	0	0	0	0	0	0
<i>Perithalia caudata</i>	3.0	0	0	0	0	0	0	0	0
<i>Phyllospora comosa</i>	0	14.5	0	45.3	0	0	0	0	0
<i>Sargassum</i> sp.	4.3	2.8	6.5	1.4	14.3	9.3	29.3	14.6	13.4
<i>Seirococcus axillaris</i>	12.5	11.9	0	1.1	0	0	0	0	0
<i>Xiphophora chondrophylla</i>	0	0	0.9	0	0	0	0	0	0
<i>Zonaria</i> sp.	3.3	0.3	0.5	0	2.0	0	0.3	5.4	0
Chlorophyta									
<i>Caulerpa brownii</i>	0	0	1.9	0.3	0	5.9	0	1.5	0
<i>Caulerpa cactoides</i>	0	0	0.5	0	0	0	0	0	0
<i>Caulerpa flexilis</i>	0	0	0.3	0.3	0	0	0	0	0
<i>Caulerpa longifolia</i>	0	0	1.6	0	0	0	1.6	1.8	0
<i>Caulerpa remotifolia</i>	0	0	0	0	0	2.6	7.8	1.0	1.9
<i>Caulerpa</i> sp.	0	0	0	0	0.9	0	2.8	9.0	0
<i>Cladophora</i> sp.	0	1.9	15.6	0.8	0	0	5.8	0	0
<i>Codium fragile</i>	0	0	0.3	0.3	0	0	0	0	0
<i>Ulva</i> sp.	0	0	0.3	0	0.1	0	0	8.4	36.3
Seagrasses									
<i>Amphibolus antarctica</i>	20.0	0	26.5	0.1	0	0	0	0	0
<i>Heterozostera tasmanica</i>	0	0	0	0.9	0	0.5	0	0	0
Total number of taxa	9	9	15	12	8	7	8	10	4

See Appendix 3.2 for species authorities

The number of macroalgal taxa varied between the nine sites and was significantly lower at Nepean Bay than all sites except Altona (Fig. 3.15a; Table 3.10). The percentage cover of the kelp *Ecklonia radiata* was extremely spatially variable, with *E. radiata* cover significantly greater at The Springs than all other sites (Fig. 3.15b; Table 3.10). There were also significant differences between sites in the percentage cover of *Sargassum* sp., with greater cover at Grassy Point than all other sites (Fig. 3.15c; Table 3.10).

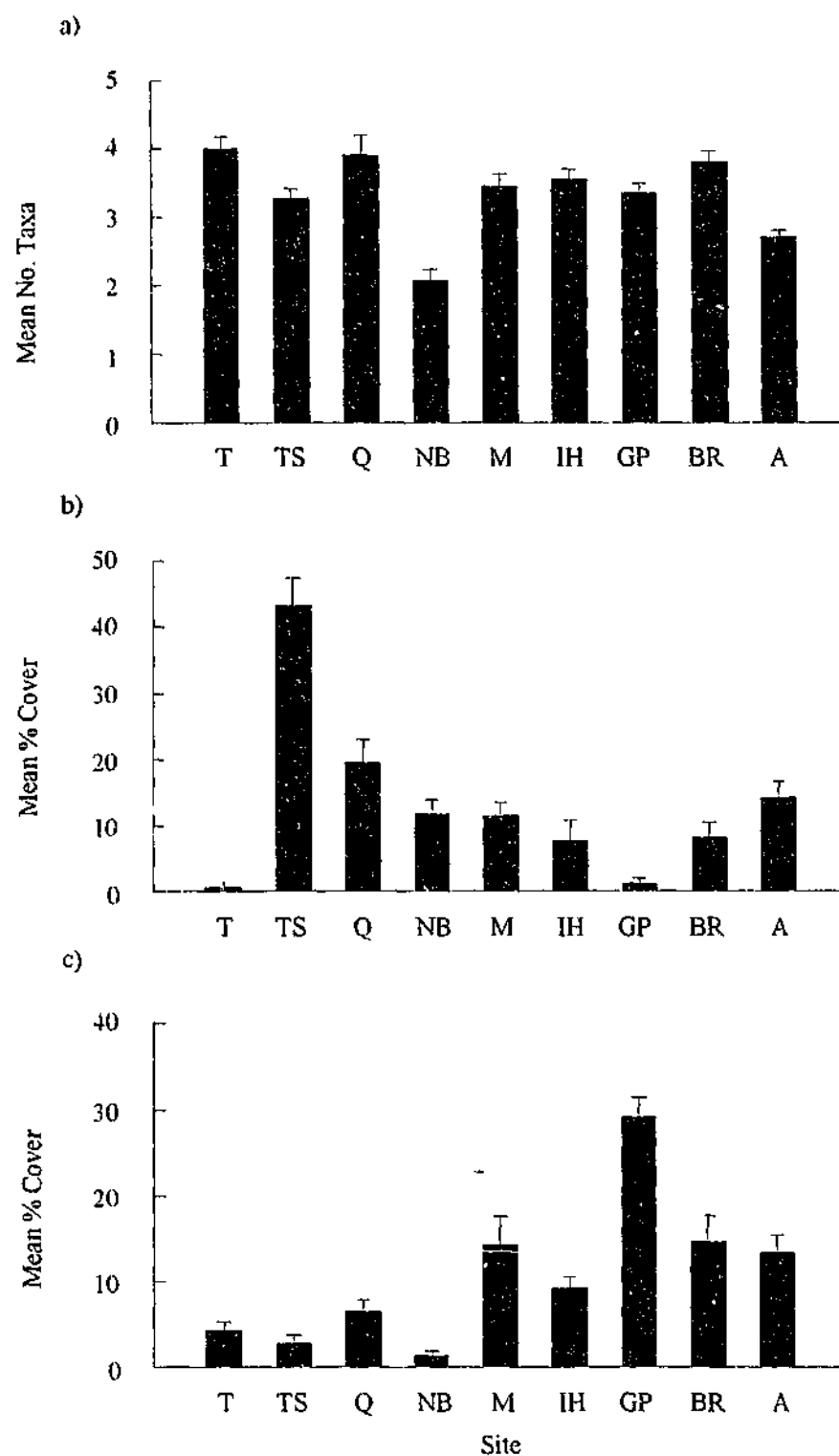


Figure 3.15: Mean (\pm SE; $n = 40$) a) number of macroalgal taxa, and percentage cover of b) *Ecklonia radiata* and c) *Sargassum* sp. recorded from all sites except Pilot's Pier. Sites were surveyed once only between December 1997 – April 1998. T = Torquay, TS = The Springs, Q = Queenscliff, NB = Nepean Bay, M = Mornington, IH = Indented Head, GP = Grassy Point, BR = Black Rock and A = Altona.

Table 3.10: One-factor ANOVAs comparing number of macroalgal taxa, and percentage cover of *Ecklonia radiata* and *Sargassum* sp., across all nine sites surveyed once between December 1997 - April 1998.

Source	MS	df	F	P
No. of Taxa^u				
Site	15.155	8	12.485	<0.001
Error	1.214	351		
<i>Ecklonia radiata</i>^l				
Site	8.389	8	26.163	<0.001
Error	0.321	351		
<i>Sargassum</i> sp.^l				
Site	6.158	8	23.165	<0.001
Error	0.266	351		

^u = untransformed data, ^l = $\log_{10}(x+1)$ transformed data

Comparison of the dissimilarity matrices of the mean fish assemblage and mean macroalgal assemblage data revealed no relationship between fish and macroalgal assemblages (Global RHO = 0.074, $P = 0.331$). There was also no relationship between the total density of fishes and the percentage cover of algae ($r = -0.246$, $df = 7$, $P > 0.05$). There were, however, significant correlations between the density of herringcale, *Odax cyanomelas*, and the brown alga, *Phyllospora comosa* ($r = 0.993$, $df = 7$, $P < 0.05$) and between the density of bridled leatherjackets, *Acanthaluteres spilomelanurus*, and the brown alga, *Sargassum* sp. ($r = 0.811$, $df = 7$, $P < 0.05$).

A comparison of the fish assemblage and site distance similarity matrices revealed a significant relationship, with closer sites being more similar in their fish assemblages than sites that were further apart (Global RHO = 0.542, $P = 0.006$).

Discussion

Fish assemblages in this study varied significantly through time. In general, fewer species and individuals were recorded in the winter-spring months (June-November). Seasonal peaks in abundance have been recorded for various fish species on temperate reefs in California (Stephens and Zerba, 1981), although most of these species were schooling or migratory species and were not considered reef residents (Stephens and Zerba, 1981). In contrast, most species recorded in this study were considered reef residents, and the main schooling species, the southern hulafish, *Trachinops*

caudimaculatus, occurs almost exclusively on reefs, hovering under rocky ledges (Gomon *et al.*, 1994; pers. obs.).

Seasonal differences in fish abundance may relate to water turbulence or temperature. Abundances of olive rockfish, *Sebastes serranoides*, decrease over winter, possibly as the fish seek shelter and/or move off the reef into deeper water in response to increasing water turbulence (Love, 1980). Seasonal differences in the densities of two rockfish species in California were also related to wave surge, which increased in the winter-spring months, and at these times fish sought shelter in crevices, making them difficult to detect (Larson, 1980). Fish abundance may also vary with water temperature (Stephens *et al.*, 1984; Choat *et al.*, 1988; Parker, 1990). Although large seasonal changes in water temperature (e.g. 6 to 28°C) can result in offshore movements (Parker, 1990), fish remained resident on reefs in Tasmania where temperatures ranged from 8 to 18°C (Barrett, 1995a). Water temperatures in this study ranged from approximately 11 to 20°C and it is unlikely that this temperature difference resulted in offshore movement. Fish may, however, become inactive and/or seek shelter when water temperatures drop, making them more difficult to observe (Buxton and Smale, 1989; Fowler, 1990). It is possible that both increased wave action and decreased water temperatures were responsible for the temporal patterns in species richness and total density of fishes recorded in this study.

Temporal variations in the abundance of reef fish have also been linked to seasonal patterns in recruitment (Kingett and Choat, 1981; Fowler, 1990). For example, seasonal differences in the abundance of *Chrysophrys auratus* were attributed to the influx of new recruits, as older individuals showed no temporal trends in abundance (Kingett and Choat, 1981). The most common species recorded in this study was the bluethroat wrasse, *Notolabrus tetricus*. However, very few *N. tetricus* recruits were observed. In general, visual transects do not adequately sample small cryptic individuals (Brock, 1982), and recruits often tend to hide in crevices, under rock ledges, or amongst algal fronds, making observation difficult (Stephens and Zerba, 1981). Over the temporal scale of this study (i.e. months), factors including water temperature, wave action, fish behaviour and recruitment may influence patterns of species richness and abundance. Ideally, studies need to be conducted at larger temporal scales (i.e. greater than the life span of the fishes) to fully examine the variation in reef fish assemblages through time.

Spatial variation in reef fish assemblages is often attributed to spatial variation in physical and/or biological characteristics such as reef topography (Connell and Jones, 1991), algal cover (Ebeling *et al.*, 1980) and water depth (McCormick, 1989). Both the number of species and total density of fishes differed significantly over the spatial scale of this study, and were significantly lower at sites in the northern end of Port Phillip Bay. Jenkins *et al.* (1996) also revealed consistently fewer fish species and individuals through time at sites in the northern end of Port Phillip Bay. In addition, there was a significant relationship between the fish assemblages and the distance between the sites, with closer sites having more similar fish assemblages (i.e. reefs in the north, centre and south of the bay grouped together). Reasons for these patterns are not clear, but sites closer together are probably exposed to similar environmental conditions. For example, sites close to the entrance into Port Phillip Bay are much more exposed to wave surge and tidal movement than sites further into the bay. These patterns may also relate to topographic complexity. High relief reefs tend to provide increased shelter in the form of ledges and/or crevices (Connell and Jones, 1991), and a greater diversity and abundance of food items (Buxton and Smale, 1989). Although topographic complexity was not formally measured in this study, observations suggested that reefs at the southern end of Port Phillip Bay were more rugose than reefs at the northern end.

Over a broad spatial scale, relationships between fish and macroalgal assemblages were not detected. There was also no relationship between the total density of fishes and the percentage cover of macroalgae. Macroalgae can form a conspicuous habitat on many temperate reefs and provides fish with a variety of resources, including food and shelter (Jones, 1984c; Ebeling and Laur, 1985; Holbrook *et al.*, 1990b). Macroalgal abundance can vary both spatially and temporally (Dayton *et al.*, 1984; Schiel and Foster, 1986), which may also significantly affect the associated fish assemblages (Bodkin, 1988; Carr, 1989; Schnitt and Holbrook, 1990a). However, studies that link spatial variation in fish assemblages with macroalgal cover have tended to sample very different habitats at each site, such as *Macrocystis pyrifera* canopies versus rocky bottom assemblages (Ebeling *et al.*, 1980), and macroalgal reefs versus coralline reef flats (Choat and Ayling, 1987; Holbrook *et al.*, 1990b). Temperate reefs around Port Phillip Bay are not characterised by the dense 10 m tall stands of *Macrocystis pyrifera* interspersed with coralline urchin barrens that are often reported from California (Ebeling *et al.*, 1980; Bodkin, 1988) and New Zealand (Choat and Ayling, 1987). Most reefs in this study

were covered by a variety of smaller canopy-forming and turfing macroalgal species and appeared structurally quite similar.

Variations in the population densities of many fish species may be explained by variation in the cover of particular macroalgal taxa (Bodkin, 1988; Holbrook *et al.*, 1990b; Anderson, 1994). The cover of many dominant macroalgal taxa in this study varied significantly between sites. *Odax cyanomelas* was common on the southernmost reefs in this study, in particular at Nepean Bay, and there was a significant correlation between the density of *O. cyanomelas* and the percentage cover of *Phyllospora comosa*. *O. cyanomelas* is an herbivorous species common on exposed rocky reefs (Gomon *et al.*, 1994), and feeds on *Ecklonia radiata* (Jones and Andrew, 1990; Jones, 1992). *O. cyanomelas* may also feed on *P. comosa*, but *E. radiata* was also very common at Nepean Bay, just below the water surface at depths shallower than those surveyed (pers. obs.). There was also a significant correlation between the densities of *Acanthaluteres spilomelanurus* and the cover of *Sargassum* sp.. *A. spilomelanurus* feeds on a variety of small invertebrates and it is possible, although unlikely, that these invertebrates are only associated with *Sargassum* sp.. Other researchers have related the densities of particular fish species to macroalgal taxa. Reefs with high densities of laminarian and fucoid algae support large numbers of labrids (Choat and Ayling, 1987). Striped surfperch, *Embiotoca lateralis*, feed on invertebrates associated with foliose red algae and consequently show a positive correlation with foliose red algal cover (Holbrook *et al.*, 1990b). Macroalgal assemblages on temperate reefs invariably change through time and fish and algal assemblages should ideally be sampled simultaneously over a number of years to determine whether a relationship exists between particular fish and macroalgal taxa.

Recent evidence has suggested that recruitment is an important process structuring reef fish assemblages (see review by Doherty and Williams, 1988). As very few recruits were recorded in this study, it was not possible to assess this hypothesis, but recruitment may still explain some of the spatial patterns observed. In general, fish larvae are patchily distributed through space, but sites closer together may be expected to receive similar larval supplies. Sites with high recruitment rates tend to support high densities of fish, while sites with low recruitment support fewer fishes (Fowler, 1990). Sites in northern Port Phillip Bay may experience either low rates of recruitment, or

environmental conditions at these sites (e.g. low topographic complexity) may be unsuitable for juvenile reef fish survival. Bell and Westoby (1986b) developed a model to explain how larval fish settle into seagrass beds, and it is quite possible that a similar process occurs on temperate rocky reefs. They proposed that competent fish larvae are patchily distributed through space before settlement, and rather than discriminating between seagrass beds at the time of settlement, they redistribute themselves within a seagrass bed after settlement to find microhabitats beneficial to survival (Bell and Westoby, 1986b). One consequence of this model is that correlations between the abundances of juvenile fish and seagrass complexity are unlikely over a large spatial scale. There was also no relationship between fish densities and macroalgal cover over a broad spatial scale in this study. Fish larvae in Port Phillip Bay are likely to be patchily distributed and settle to a variety of shallow water habitats (Jenkins *et al.*, 1996). Thus, it is possible that the broad scale spatial differences recorded in the fish assemblages in this study are related to both recruitment patterns and environmental conditions that influence post-settlement survival.

In studies of reef fish assemblages, it is important to consider not only spatial and temporal variation in the assemblages, but also the survey methods used to record these patterns. Commercial fishing statistics from methods, such as gill nets and fish traps, are often relied upon to provide an index of fish abundance for stock assessments and fisheries management. However, these methods are rarely compared with fisheries-independent techniques, such as underwater visual surveys. Despite recording fewer species and fewer fish (total density) in traps than on visual transects at all sites in this study, there was a significant relationship between the fish assemblages surveyed using the two methods. In contrast, previous studies have shown very little similarity between the fish assemblages recorded by visual surveys and those caught using fish traps (Ferry and Kohler, 1987; Miller and Hunte, 1987) or gill nets (Hickford and Schiel, 1995; Connell *et al.*, 1998). This lack of similarity is largely due to the size selectivity of fish traps (Ferry and Kohler, 1987) and gill nets (Hickford and Schiel, 1995). Fish traps tend to target large species and/or individuals, and are unlikely to catch small fish (e.g. *Trachinops caudimaculatus* and *Siphaemia cephalotes*), or juveniles, despite their abundance. Resident fishes such as labrids and pomacentrids are more often recorded visually than in fish traps (Ferry and Kohler, 1987; Miller and Hunte, 1987). Although labrids and pomacentrids were caught within fish traps in this study, most individuals

were recorded by visual survey (e.g. *Notolabrus tetricus*). The similarity in fish assemblages recorded using fish traps and visual surveys may relate to the time allocated for sampling. In general, visual surveys take a short term or instantaneous measurement of abundance whereas gill nets and fish traps are set over much longer time periods (e.g. several hours for gill nets and several days for fish traps). In this study, however, fish traps were set over a relatively short time period (1 hr), which was very similar to the time taken to complete the visual surveys (50 mins).

Although estimates of abundance of most species were higher by visual survey than fish traps, there were some notable exceptions. In particular, the sixspine leatherjacket, *Meuschenia freycineti*, was regularly caught in fish traps, but only rarely observed visually. Monacanthids tend to be secretive fish, and many species change colour to mimic their background, thus making them difficult to observe (Ferry and Kohler, 1987). *M. freycineti*, and to a lesser extent *Meuschenia hippocrepis*, often seek shelter under rock ledges or in rocky crevices (Gomon *et al.*, 1994) and are thus less likely to be observed visually. In contrast, most *Meuschenia flavolineata* were recorded visually, and this species tends to be less cryptic with individuals readily observed hovering in pairs above the reef (Gomon *et al.*, 1994). Monacanthids, particularly *M. freycineti* and *M. hippocrepis*, are increasingly being targeted by commercial trap fishers in and around Port Phillip Bay, and their susceptibility to fish traps may have important management implications. *M. freycineti* and *M. hippocrepis* also appear to be permanent residents on these reefs (see Chapter 5), which may further increase their vulnerability to overfishing.

This study showed that within Port Phillip Bay, closer reefs had more similar fish assemblages than reefs that were further apart, and that this similarity was not simply related to the macroalgal assemblages. The densities of some fish species did, however, appear to vary with the cover of particular macroalgal taxa. Factors such as water temperature, wave action and topographic complexity may all be important in structuring these fish assemblages, and should be considered in future studies that examine the spatial and temporal variation in temperate reef fish assemblages. Although there was a significant relationship between the fish assemblages surveyed using the two methods (visual surveys and fish traps), the number of species and abundance of fishes recorded were higher on the visual surveys. Any technique used to

survey reef fish assemblages will have its own set of advantages and disadvantages. In practice, a variety of assessment techniques may be necessary to accurately survey reef fish assemblages, although the most appropriate method will depend on the objectives of the study and the species of interest. Particularly in shallow reef areas accessible to SCUBA diving, a combination of trapping and *in situ* visual surveys may give more comprehensive information than either method alone (Miller and Hunte, 1987).

Summary

This study revealed both spatial and temporal variation in species richness and total densities of fishes on rocky reefs in and around Port Phillip Bay. Fewer species and individuals were recorded over winter, and this may be in response to decreased water temperatures and/or increased wave surge, with individuals becoming inactive and seeking shelter at this time. Fewer species and individuals were recorded from sites in the north of Port Phillip Bay, and there was a significant relationship between fish assemblages and the distance between sites, with closer sites having more similar fish assemblages. Reasons for these patterns are undoubtedly complex, but sites closer together are likely to experience more similar conditions, such as wave action and tidal movement.

Although there was no relationship between fish and macroalgal assemblages, population densities of many fish species varied with the cover of particular macroalgal taxa (e.g. *Acanthaluteres spilomelanurus* and *Sargassum* sp.). Macroalgal cover will invariably change through time, and ideally both fish densities and macroalgal cover should be surveyed simultaneously over a number of years to determine any relationship between particular fish species and macroalgal taxa.

Despite recording consistently fewer fish species and individuals using fish traps, results from this study suggest that fish traps may be an effective method of surveying some temperate reef fishes, particularly in areas not accessible to other techniques due to water depth or habitat complexity. In areas such as shallow rocky reefs, a combination of fish trapping and visual surveys may give more comprehensive information on the fish assemblages present than either method alone.

Appendix 3.1: Authorities for fish species recorded throughout this thesis.

Species	Authority	Species	Authority
Parascyllidae		Chironemidae	
<i>Parascyllium variolatum</i>	Duméril	<i>Chironemus marmoratus</i>	Günther
Rhinobatidae		<i>Threpterus maculosus</i>	Richardson
<i>Trygonorrhina guaneri</i>	Whitley	Aplodactylidae	
Urolophidae		<i>Aplodactylus arcidens</i>	Richardson
<i>Urolophus gigas</i>	Scott	Cheilodactylidae	
Syngnathidae		<i>Cheilodactylus nigripes</i>	Richardson
<i>Phyllopteryx taeniolatus</i>	Lacepède	<i>Dactylophora nigricans</i>	Richardson
<i>Stigmatopora argus</i>	Richardson	Latrididae	
<i>Stigmatopora nigra</i>	Kaup	<i>Latridopsis forsteri</i>	Castelnau
<i>Urocampus carinirostris</i>	Castelnau	Pomacentridae	
Scorpaenidae		<i>Parma victoriae</i>	Günther
<i>Gymnapistes marmoratus</i>	Cuvier	Labridae	
Aploactinidae		<i>Notolabrus fucicola</i>	Richardson
<i>Aploactisoma milesii</i>	Richardson	<i>Notolabrus tetricus</i>	Richardson
Platycephalidae		<i>Pictilabrus laticlavus</i>	Richardson
<i>Platycephalus laevigatus</i>	Cuvier	Odacidae	
Serranidae		<i>Haletta semifasciata</i>	Valenciennes
<i>Caesioperca rasor</i>	Richardson	<i>Neodax balteatus</i>	Valenciennes
Plesiopidae		<i>Odax acroptilus</i>	Richardson
<i>Trachinops caudimaculatus</i>	McCoy	<i>Odax cyanomelas</i>	Richardson
Apogonidae		<i>Siphonognathus beddomei</i>	Johnston
<i>Siphaemia cephalotes</i>	Castelnau	Blenniidae	
<i>Vincentia conspersa</i>	Klunzinger	<i>Parablemmius tasmanianus</i>	Richardson
Dinolestidae		Clinidae	
<i>Dinolestes lewini</i>	Griffith	<i>Heteroclinus wilsoni</i>	Lucas
Sillaginidae		Callionymidae	
<i>Sillaginodes punctata</i>	Cuvier	<i>Eocallionymus papilio</i>	Günther
Gerreidae		<i>Foetorepus calauropontus</i>	Richardson
<i>Parequula melbournensis</i>	Castelnau	Monacanthidae	
Sparidae		<i>Acanthaluteres spilomelanurus</i>	Quoy and Gaimard
<i>Chrysophrys auratus</i>	Bloch and Schneider	<i>Acanthaluteres vittiger</i>	Castelnau
Mullidae		<i>Brachaluteres jacksonianus</i>	Quoy and Gaimard
<i>Upeneichthys vlamingii</i>	Cuvier	<i>Eubalichthys gunnii</i>	Günther
Pempherididae		<i>Meuschenia australis</i>	Donovan
<i>Pempheris multiradiata</i>	Klunzinger	<i>Meuschenia flavolineata</i>	Hutchins
Girellidae		<i>Meuschenia freycineti</i>	Quoy and Gaimard
<i>Girella zebra</i>	Richardson	<i>Meuschenia galii</i>	Waite
Scorpididae		<i>Meuschenia hippocrepis</i>	Quoy and Gaimard
<i>Scorpius aequipinnis</i>	Richardson	<i>Meuschenia trachylepis</i>	Günther
<i>Tilodon sexfasciatus</i>	Richardson	<i>Scobinichthys granulatus</i>	Shaw
Enoplosidae		Aracnidae	
<i>Enoplosus armatus</i>	White	<i>Aracana aurita</i>	Shaw
Pentacerotidae		Tetraodontidae	
<i>Pentaceropsis recurvirostris</i>	Richardson	<i>Contusus brevicaudus</i>	Hardy
		<i>Tetractenos glaber</i>	Fremerville
		Diodontidae	
		<i>Diodon nictemerus</i>	Cuvier

Appendix 3.2: Authorities for species recorded in the macroalgal surveys

Species	Authority
Phaeophyta	
<i>Acrocarpia paniculata</i>	(Turner) Areschoug
<i>Caulocystis uvifera</i>	(C. Agardh) Areschoug
<i>Dictyopteris muelleri</i>	(Sonder) Reinbold
<i>Ecklonia radiata</i>	(C. Agardh) J. Agardh
<i>Lobospora bicuspidata</i>	Areschoug
<i>Perithalia caudata</i>	(Labillardière) Womersley
<i>Phyllospora comosa</i>	(Labillardière) C. Agardh
<i>Seirococcus axillaris</i>	(R. Brown ex Turner) Greville
<i>Xiphophora chondrophylla</i>	(R. Brown ex Turner) Montagne
Chlorophyta	
<i>Caulerpa brownii</i>	(C. Agardh) Endlicher, Lucas
<i>Caulerpa cactoides</i>	(Turner) C. Agardh, Harvey
<i>Caulerpa flexilis</i>	Lamouroux
<i>Caulerpa longifolia</i>	C. Agardh, Lucas
<i>Caulerpa remotifolia</i>	Sonder, Harvey
<i>Codium fragile</i>	(Suringar) Hariot, Lucas
Seagrasses	
<i>Amphibolus antarctica</i>	(Labillardière) Sonder & Ascherson ex Ascherson
<i>Heterozostera tasmanica</i>	(Martens ex Ascherson) den Hartog

Chapter 4

Distribution, Abundance and Size Structure of *Menschenia freycineti* and *Menschenia hippocrepis* Populations

Introduction

One of the major aims of ecological studies is to describe and explain the distribution and abundance of organisms. In order to achieve this aim we need to examine individuals over their entire life span as different life history stages will be influenced by different factors, particularly if an organism is found in different habitats as a recruit/juvenile and as an adult (Ebenman, 1992). Reef fish studies, both tropical and temperate, have tended to focus on species that recruit directly onto the reef (Jones, 1984b; Victor, 1987, Fowler *et al.*, 1992), with fewer studies examining the distribution and abundance of species whose recruits settle to a different, often spatially separate, habitat from that of the adults (Jones and Andrew, 1993; Gillanders, 1997a).

Numerous tropical and temperate reef fish species show spatial separation in the habitats used by recruits/juveniles and adults, indicating ontogenetic shifts in habitat use. These differences in distribution range from changes in depth within a reef (Jones, 1984a; McCormick, 1989) through to the changing use of spatially discrete habitats, such as seagrass beds and reefs (e.g. Love *et al.*, 1991; Eggleston, 1995). Estuaries and their associated seagrass habitats are considered important nursery areas for many fish species whose adults occur on reefs (Bell and Pollard, 1989; Parrish, 1989), and the links between these habitats are thought to be important for sustaining many reef fish populations (Bell and Worthington, 1993).

The most common patterns of movement between seagrass and reef habitats appear to involve the dispersal of larvae inshore from reefs to seagrass beds (Victor, 1987; Lough and Bolz, 1989), followed by the movement of juveniles and/or sub-adults back to reefs at a later stage (Love *et al.*, 1991; Bell and Worthington, 1993). It is not known whether these ontogenetic shifts in habitat use are obligatory or just preferred, but for many species, seagrass beds may offer advantages in terms of reduced predation on small

recruits and juveniles (Werner and Hall, 1988; Parrish, 1989; Grant and Brown, 1998). In turn, fishes may benefit from a change in resources with increasing size (Werner and Gilliam, 1984). Size-specific shifts in food preferences occur for many fish species and are often associated with shifts in habitat use (Livingston, 1982; Werner and Gilliam, 1984).

Leatherjackets (Family: Monacanthidae) are some of the most easily recognised fish in southern Australian waters due to their prominent dorsal spine and modified scales that form a tough leathery skin. Two monacanthid species common along the Victorian coast are the sixspine leatherjacket, *Meuschenia freycineti*, and the horseshoe leatherjacket, *Meuschenia hippocrepis*. *M. freycineti* is distributed along the Australian coast from northern New South Wales to southern Western Australia, including Tasmania (Gomon *et al.*, 1994). *M. hippocrepis* is not as widespread and is distributed from Wilson's Promontory in Victoria to the Houtman Abrolhas in Western Australia, including the northern coast of Tasmania (Gomon *et al.*, 1994). Both species are susceptible to fish traps (see Chapter 3) and are commonly taken by recreational and commercial fishers (Hannan and Williams, 1998). However, despite their abundance in southern Australian coastal waters, and their potential for being overfished, very few studies have examined the ecology of *M. freycineti* and *M. hippocrepis*.

Recruits and juveniles of several monacanthid species, including *M. freycineti*, are found in seagrass beds within estuaries, while adult individuals occur primarily on coastal rocky reefs (Bell *et al.*, 1978). *M. freycineti* larvae appear to settle to shallow seagrass beds (e.g. *Zostera capricorni* and *Heterozostera tasmanica*), and remain there for approximately 12 months before migrating offshore to coastal reefs (Bell and Worthington, 1993), often via other habitats such as *Posidonia* seagrass beds (Middleton *et al.*, 1984; Jordan *et al.*, 1998). Adults are also occasionally recorded in seagrass beds and on rocky reefs within estuaries (Bell and Worthington, 1993). Few studies have examined the distribution of *M. hippocrepis*, but in contrast to *M. freycineti*, there is no evidence to suggest that *M. hippocrepis* individuals recruit to seagrass beds (Jenkins *et al.*, 1993, 1996).

Southeastern Australia is characterised by large stretches of coastal reefs interspersed with sheltered bays and estuaries that possess both seagrass beds and rocky reefs, and

provide ample opportunity for movement between seagrass and reef habitats (Bell and Worthington, 1993). The main aim of this study was to compare the size structure of *M. freycineti* and *M. hippocrepis* between inshore seagrass beds and offshore rocky reefs in Port Phillip Bay. It was necessary to confirm differences in size frequency distributions between these two habitats before further studies that aimed to test hypotheses relating to the recruitment and movement patterns of *M. freycineti* and *M. hippocrepis*, could be done (see Chapter 6). An additional aim was to determine the best time of year to survey recruits/small juveniles of *M. freycineti*. To fully examine the size structure of these species and the habitat preferences of settling larvae (Chapter 6), it was necessary to know the time of year that recruits and small juveniles were abundant. To do this adult populations of *M. freycineti* were sampled to determine the spawning time (i.e. estimate the approximate recruitment period) of *M. freycineti* within Port Phillip Bay.

Methods

Study Sites

Ten sites within Port Phillip Bay (five reef and five seagrass) were surveyed to compare the size structure and abundance of *Meuschenia freycineti* and *Meuschenia hippocrepis* in seagrass beds and on rocky reefs (Fig. 4.1). Where possible, reef sites (Grassy Point, Indented Head, Pilot's Pier, Queenscliff and Nepean Bay) were selected on the basis of reasonable catch rates of *M. freycineti* (see Chapter 3). Preliminary trapping revealed consistently low and variable catch rates of *M. hippocrepis* at all reef sites except Nepean Bay, however, no other reefs previously surveyed within Port Phillip Bay revealed reasonable catch rates of *M. hippocrepis* (see Chapter 3). Seagrass sites (Grand Scenic, Grassy Point, Indented Head, St Leonards and Blairgowrie) were chosen to be as close as possible to these reefs. Two sites (Grassy Point and Indented Head) were characterised by both inshore seagrass beds and offshore rocky reefs. Sampling of *M. freycineti* was done at The Springs (Fig. 4.1) to determine the spawning time and thus estimate the approximate recruitment period of this species. As this part of the study involved the removal of fish for gonad analysis, it was necessary to select a site that did not interfere with the examination of movement patterns and growth of *M. freycineti* (Chapter 5).

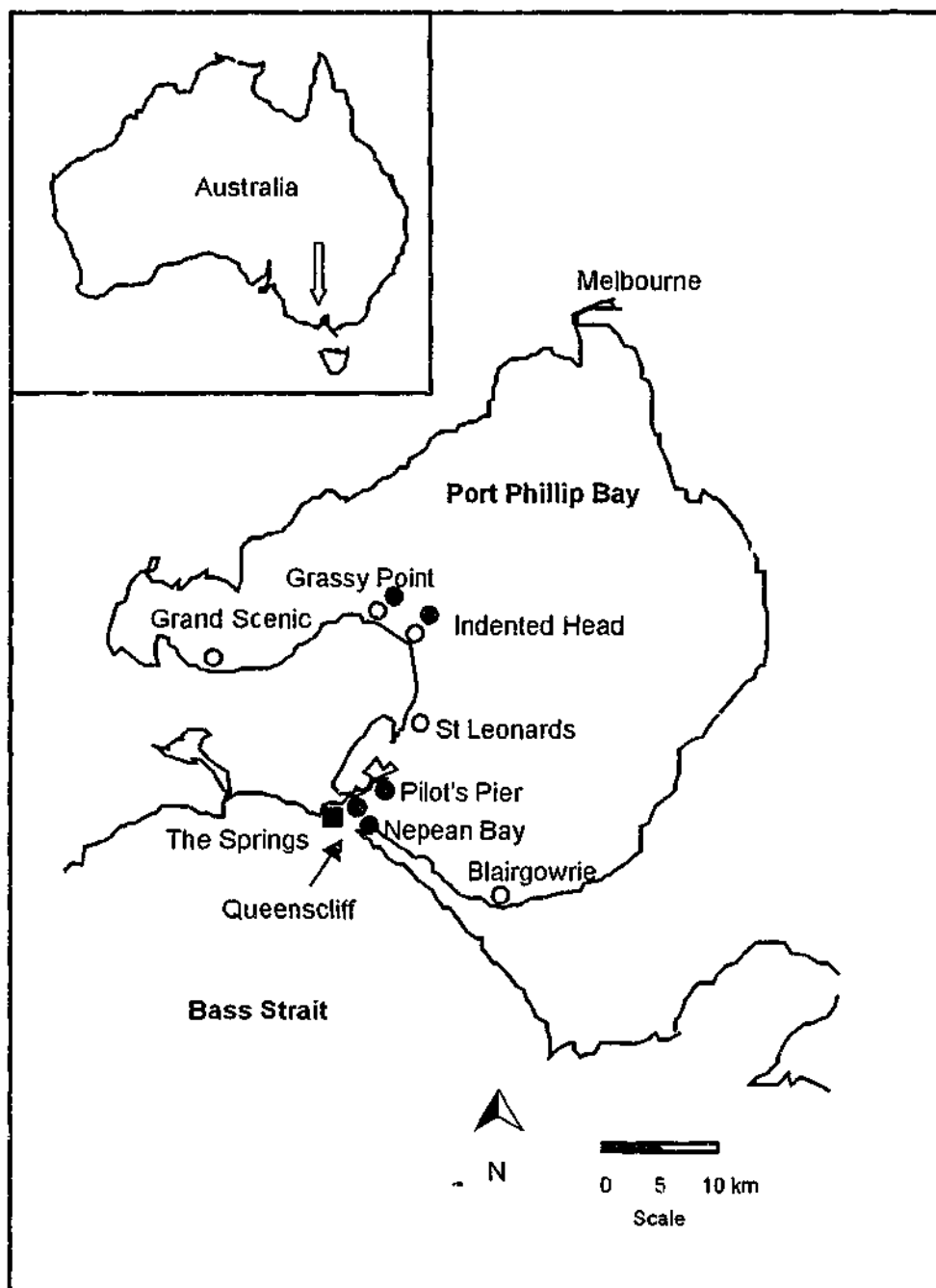


Figure 4.1: Location of study sites in Port Phillip Bay. Sites surveyed for the examination of abundance and size structure of *M. freycineti* and *M. hippocrepis* populations are marked with circles (open = seagrass; closed = reef). Specimens for gonad analyses were collected from the reef at The Springs (closed square). Inset: location of Port Phillip Bay on the Australian coast.

Spawning Season of Meuschenia freycineti

Meuschenia freycineti individuals were collected monthly from February 1996 to January 1997 from the reef at The Springs (Fig. 4.1) to determine the spawning season

of this species. Specimens were collected using eight baited fish traps that were haphazardly set on the reef. After a soak time of approximately 4 hrs, all fish traps were retrieved and emptied. All *M. freycineti* individuals caught were recorded and approximately 20 individuals (half male/half female) were kept each month. Any remaining fish were subsequently released. Fish were placed into a plastic bin with 50 l of fresh seawater, to which a lethal dose (1 g/10 l) of fish anaesthetic (benzocaine) was added. Gonosomatic indices were then calculated for each individual (gonad weight/body weight less gonad weight $\times 100$). Gonads were preserved in Bouin's fixative for 48 h and then transferred to 70% ethanol. Following fixation gonads were embedded in paraffin, sectioned transversely and stained with Mayer's haematoxylin and eosin. Although previous studies have fixed fish gonads for histological analysis, using Bouin's fixative, for periods of only 24-48 h (e.g. Gillanders 1995c); gonads from the first few months of sampling were not preserved. Despite increasing the fixation period to 2-3 weeks, and cutting the gonads into small sections before fixation, histological analyses were not possible due to poor fixation.

At this time attempts were also made to examine the age structure and diet of *M. freycineti*. The removal of otoliths was not straightforward due to the thickness of the skull and the very small size of the otoliths, and after numerous unsuccessful attempts to remove otoliths from adult individuals, an examination of the age structure of *M. freycineti* was abandoned. Gut samples were taken at the time of gonad removal and preserved in 4% formalin in seawater. However, dietary analyses could not be done due to poor preservation and contamination of the samples.

Abundance and Size Structure of Meuschenia freycineti and Meuschenia hippocrepis in Seagrass

Monthly surveys of *Heterozostera tasmanica* seagrass beds were done over the recruitment period (November – May; refer to the results section entitled Spawning Season of *Meuschenia freycineti*). Monthly surveys were conducted from November 1996 to May 1997 at Grand Scenic, St Leonards and Blairgowrie, and from November 1998 to May 1999 at Grassy Point and Indented Head (Fig. 4.1). Sampling could not be conducted in some months due to poor weather conditions.

Fish were sampled with a beach seine net. In general, six replicate non-overlapping hauls were taken at each site per month (refer to figures for the exact number of hauls). Analyses examining spatial and temporal variation in *M. freycineti* and *M. hippocrepis* abundances were based on six hauls per month where possible, but size frequency distributions include all replicate hauls pooled over months. Seagrass sampling was conducted fortnightly in 1996/1997 compared to monthly in 1998/1999, so when more than six hauls per month were taken (i.e. more than one day per month was sampled), data were averaged over days to give a mean catch rate per month. All fish caught in the seine net were identified and recorded and the total length (TL) of all *M. freycineti* and *M. hippocrepis* was also recorded. All fish were released as soon as possible after counting and/or measuring. Although individuals were not tagged to avoid re-sampling, it is very unlikely that fish in seagrass were recaptured due to the technique used and the patchiness of fishes within seagrass beds. Refer to Chapter 2 for a detailed description of the seine net methodology.

Abundance and Size Structure of Meuschenia freycineti and Meuschenia hippocrepis on Reefs

Surveys were conducted approximately monthly from February 1997 to June 1999 at Indented Head, Pilot's Pier and Nepean Bay (Fig. 4.1) to examine the size structure and temporal variation in the abundance of *Meuschenia freycineti* and *Meuschenia hippocrepis* on reefs. Adverse weather prevented trapping in some months, particularly at Indented Head. The reef at Indented Head was quite shallow (2-3 m) and conditions were often too rough for trapping (i.e. waves breaking on the reef).

Six baited fish traps were haphazardly set on the reef at each site, although the number of traps set varied in some months (refer to figures for exact trap numbers). Analyses comparing the numbers of *M. freycineti* and *M. hippocrepis* over time were based on six traps/month where possible, but the size frequency distributions include all replicate traps set each month. Additional fish trapping was conducted in some months as part of a study examining the movement patterns and growth of *M. freycineti* and *M. hippocrepis* on reefs (Chapter 5). When more than six traps per month were set (i.e. more than one day per month was sampled), data were averaged over days to give a mean catch rate per month. After a soak time of approximately 1 hr, all fish traps were retrieved and emptied.

Captured fish were identified, and the number and size (TL) of *M. freycineti* and *M. hippocrepis* individuals were recorded. *M. freycineti* and *M. hippocrepis* were tagged to avoid re-sampling. All fish were subsequently released. For a detailed description of the trapping methodology refer to Chapter 2.

Statistical Analyses

Trap catches at the Grassy Point and Queenscliff reefs revealed low and variable catch rates of *Meuschenia freycineti*, so Analyses of Variance (ANOVAs) examining temporal variation in abundance of *M. freycineti* could only be done for data from Indented Head, Pilot's Pier and Nepean Bay. As the months surveyed varied between reef sites, separate ANOVAs examining temporal variation in abundance of *M. freycineti* and *Meuschenia hippocrepis* were done for each site. Spatial and temporal variation in the abundance of *M. freycineti* and *M. hippocrepis* in seagrass beds were examined using two-factor ANOVAs for each species. The first ANOVA compared abundance at Grand Scenic, St Leonards and Blairgowrie from December 1996 to April 1997 (hereafter referred to as 1996/1997), and the second compared abundance at Grassy Point and Indented Head from November 1998 to May 1999 (hereafter referred to as 1998/1999).

A difference in the ratio of male to female *M. freycineti* at The Springs was examined using a chi-squared test.

Results

Spawning Season of Meuschenia freycineti

From the total number of fish caught (225), female *Meuschenia freycineti* constituted 54.67 % and males 45.33 % of the individuals sampled at The Springs, indicating that the sex ratio of the population was not significantly different from 50:50 ($\chi^2 = 1.977$, $P > 0.05$). Female *M. freycineti* dominated the small size classes ranging from 220-369 mm TL, and males dominated the large size classes (245-418 mm TL). On average, female *M. freycineti* were approximately 40 mm smaller than males (Fig. 4.2).

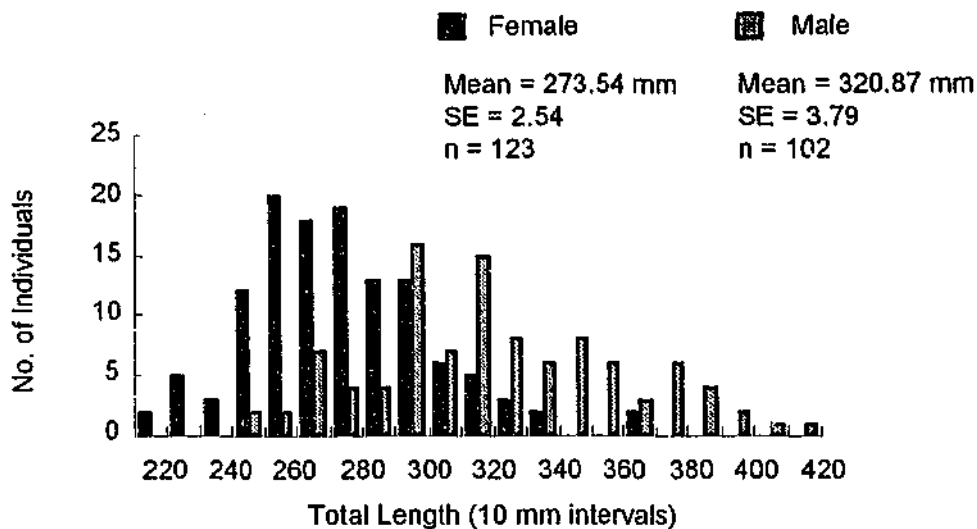


Figure 4.2: Size frequency distribution of *M. freycineti* individuals trapped on the reef at The Springs from February 1996 – January 1997 for gonad analyses.

Gonosomatic indices (GSI) for female *M. freycineti* were high in February and March 1996 and again from October 1996 through to January 1997 (Fig. 4.3a). Values for male *M. freycineti* were more variable but appeared high in February 1996, dropped in March 1996, and increased again around September 1996 (Fig. 4.3b). These monthly GSI values suggest that spawning in *M. freycineti* within Port Phillip Bay occurs over an extended period from spring through summer. The presence of *M. freycineti* recruits and small juveniles between 15-50 mm TL in seagrass beds between November and May (Fig. 4.4) also suggests that spawning probably commenced in September and continued for a period of several months.

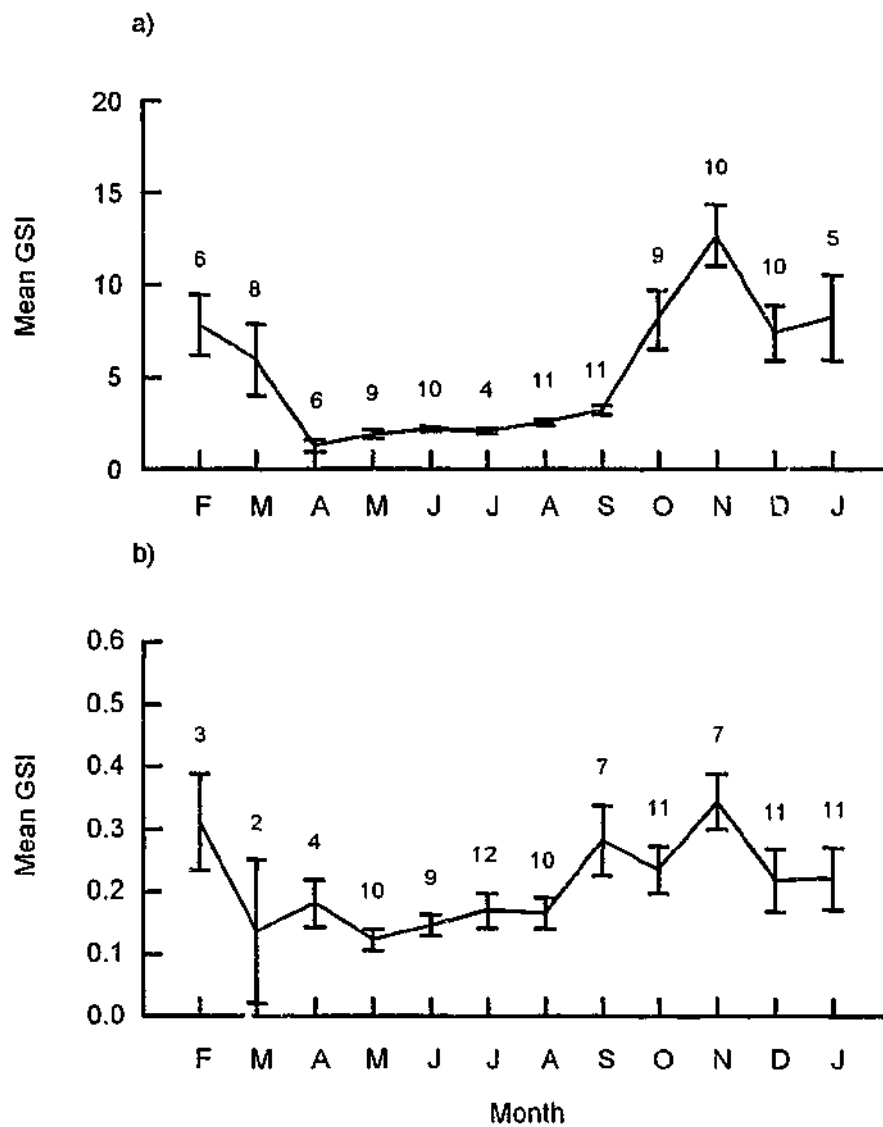


Figure 4.3: Mean (\pm SE) gonosomatic indices (GSI) for a) female and b) male *M. freycineti* trapped on the reef at The Springs from February 1996 – January 1997. Numbers above each point refer to the number of fish sampled each month. Note: maximum Y-value differs between the sexes.

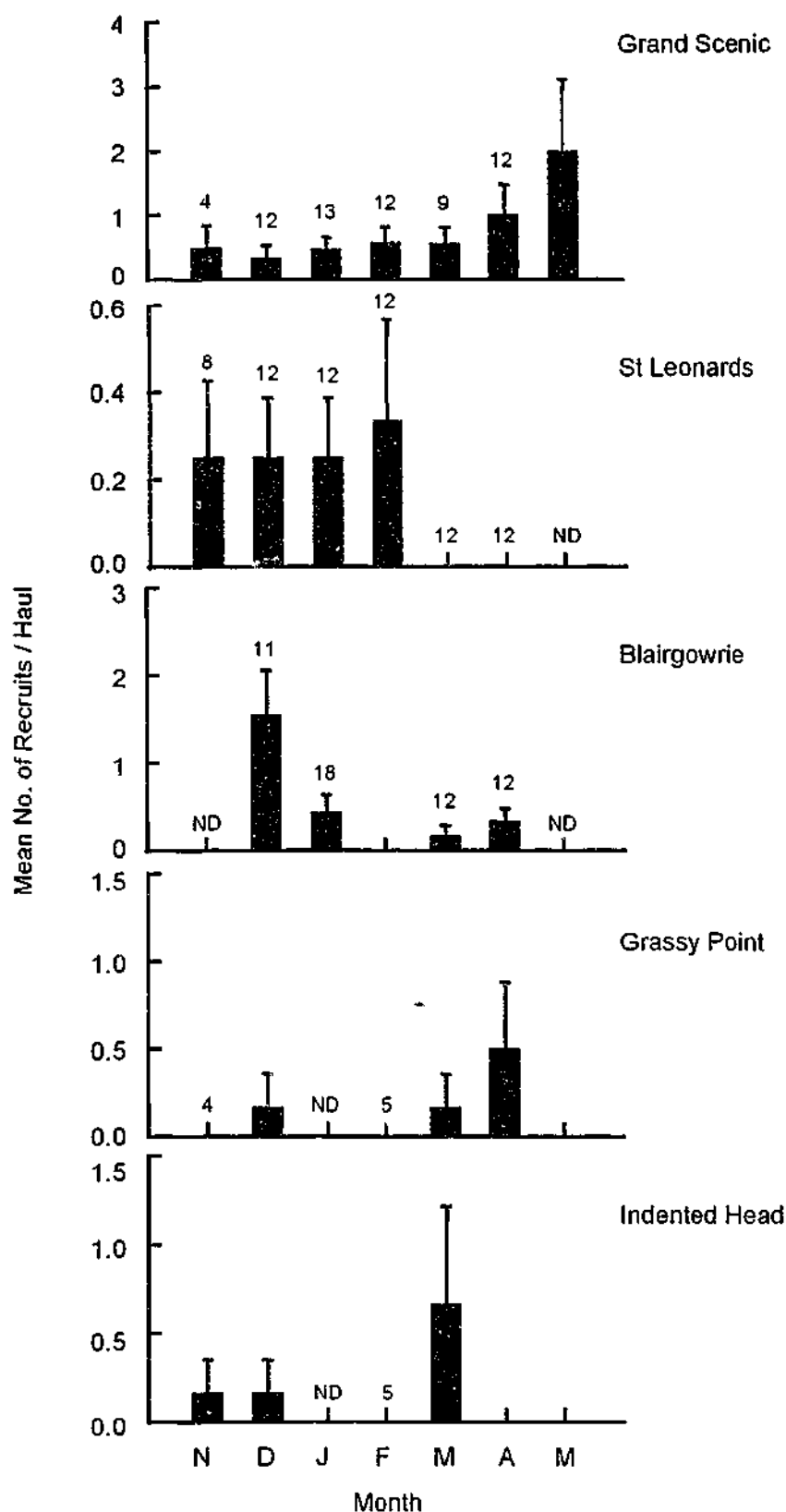


Figure 4.4: Mean number (\pm SE) of *M. freycineti* recruits in seagrass beds at Grand Scenic, St Leonards and Blairgowrie (November 1996 – May 1997), and Grassy Point and Indented Head (November 1998 – May 1999). $n = 6$ except where indicated above the bar. ND = no data. Note: maximum Y-value differs between sites.

*Spatial and Temporal Variation in the Abundance of Meuschenia freycineti
and Meuschenia hippocrepis in Seagrass*

Meuschenia hippocrepis individuals were not recorded in seagrass beds over the period of this study. Abundance of *Meuschenia freycineti* varied significantly between seagrass sites sampled in 1996/1997, but not over time (Figs. 4.5a, b and c; Table 4.1).

Abundance of *M. freycineti* was significantly greater at Grand Scenic and Blairgowrie than at St Leonards (Figs. 4.5a, b and c). This pattern was consistent when all replicate hauls were included (Figs. 4.5d, e and f). In 1998/1999, abundance of *M. freycineti* was very low and variable and there was no significant difference between sites or months (Fig. 4.6; Table 4.1).

Table 4.1: Two-factor ANOVAs comparing abundance of *M. freycineti* over time within seagrass beds in 1996/1997 (December 1996 – April 1997; Grand Scenic, St Leonards and Blairgowrie) and 1998/1999 (November 1998 – May 1999, excluding January; Grassy Point and Indented Head).

Source	MS	df	F	P
1996/1997¹				
Month	0.029	4	0.646	0.632
Site	0.715	2	16.087	<0.001
Month*Site	0.042	8	0.947	0.484
Error	0.044	75		
1998/1999¹				
Month	0.042	5	1.991	0.094
Site	0.007	1	0.325	0.571
Month*Site	0.017	5	0.821	0.540
Error	0.021	56		

¹ = $\log_{10}(x+1)$ transformed data

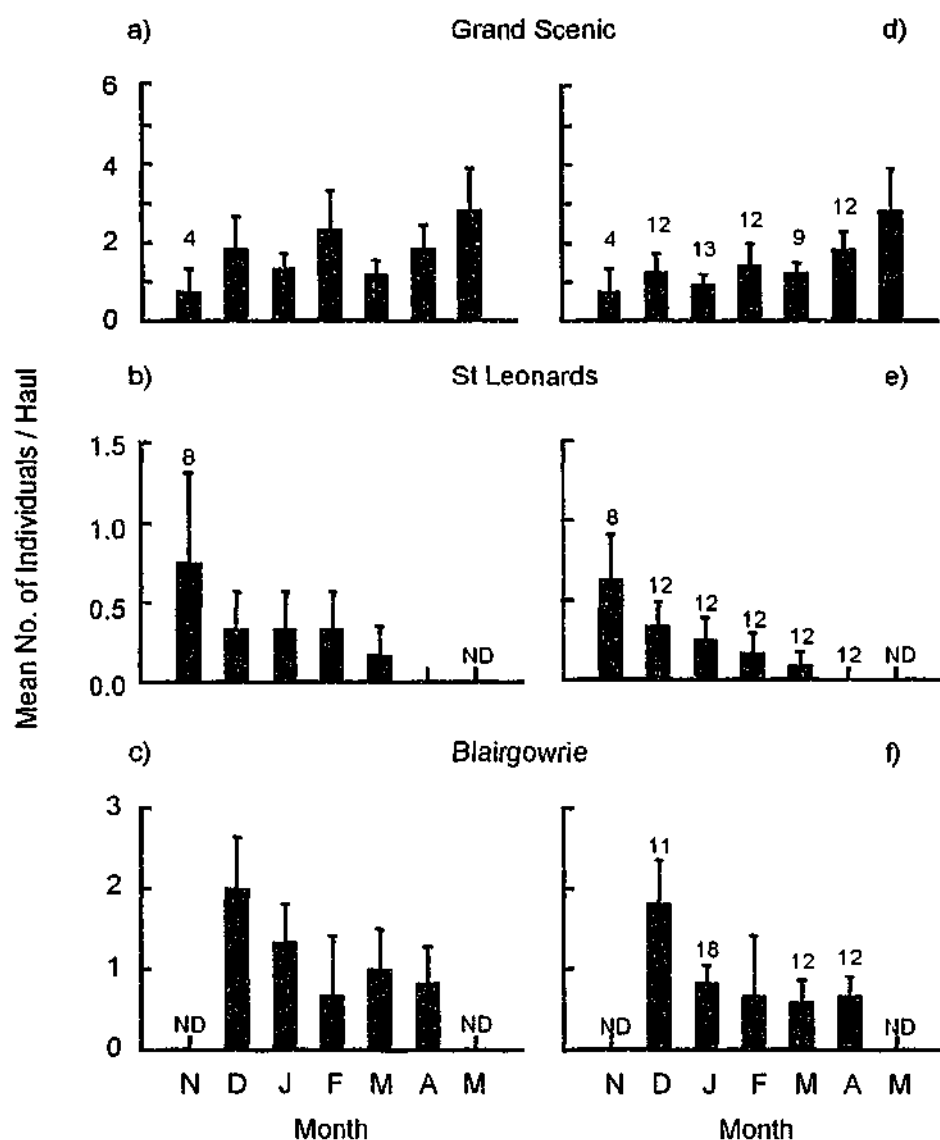


Figure 4.5: Mean number (\pm SE) of *M. freycineti* in seagrass beds at Grand Scenic, St Leonards and Blairgowrie (November 1996 – May 1997). Figs. a), b) and c) include only the standard six hauls/month (used for analyses). Figs. d), e) and f) include all replicate hauls (used for size frequency distributions). $n = 6$ except where indicated above the bar. ND = no data. Note: maximum Y-value differs between sites.

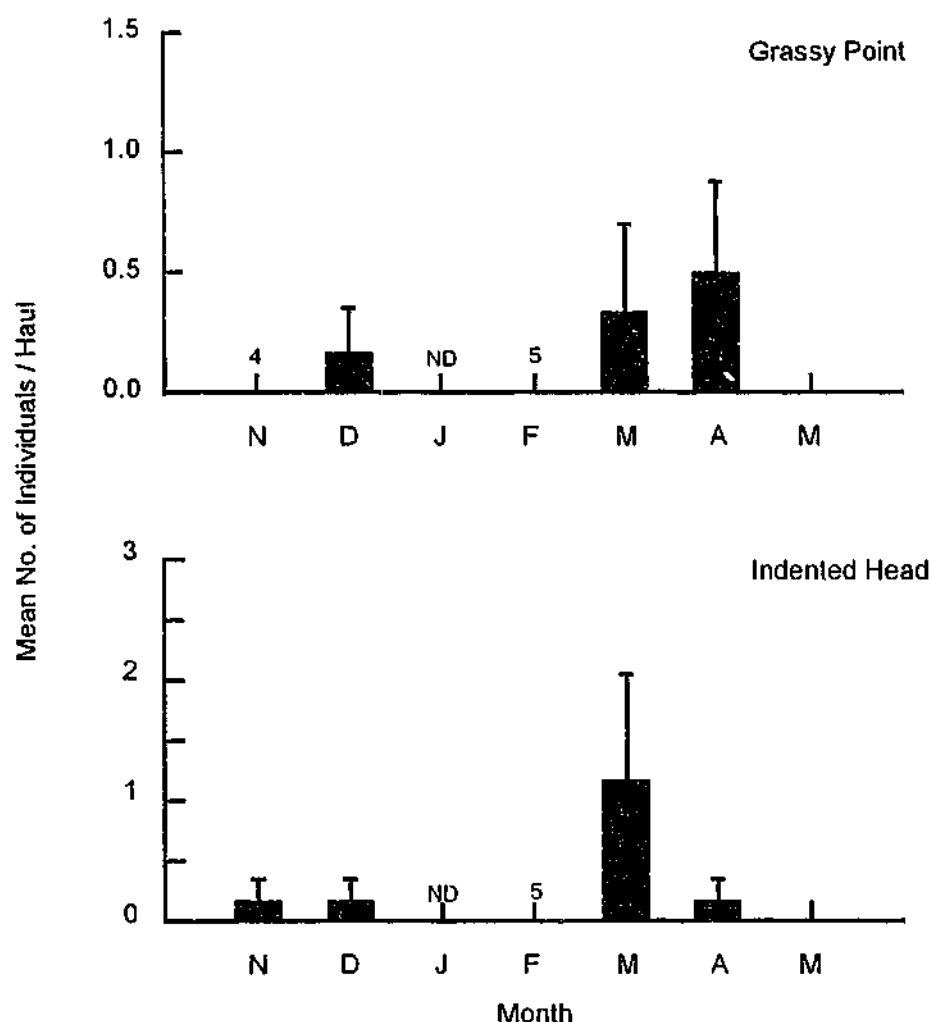


Figure 4.6: Mean number (\pm SE) of *M. freycineti* in seagrass beds at Grassy Point and Indented Head (November 1998 – May 1999). $n = 6$ except where indicated above the bar. ND = no data. Note: maximum Y-value differs between sites.

Temporal Variation in the Abundance of Meuschenia freycineti and Meuschenia hippocrepis on Reefs

Abundance of *Meuschenia freycineti* varied significantly over time at all three reefs (Figs. 4.7a, 4.8a and 4.9a; Table 4.2). At Pilot's Pier (Figs. 4.7a and b) and Nepean Bay (Figs. 4.8a and b), these patterns were consistent when all replicate traps were included. However, at Indented Head the pattern was consistent for all months except April 1997, when the number of fish decreased considerably when all replicate traps were included (Figs. 4.9a and b). At both Pilot's Pier (Fig. 4.7) and Nepean Bay (Fig. 4.8) catch rates were variable, and there were no apparent seasonal patterns in abundance. At Indented

Head, *M. freycineti* abundance decreased after April 1997 and was low for the remainder of the study, with only slight increases in both January 1998 and January 1999 (Fig. 4.9).

Table 4.2: One-factor ANOVAs comparing abundance of *M. freycineti* over time on reefs sampled between February 1997 - June 1999. Note: months sampled at each site vary. Indented Head: 1997 - Mar, Apr, May, Sep, Dec; 1998 - Jan, Mar, Apr, May, Jul, Aug, Sep, Oct; 1999 - Jan, Mar, Apr, Jun. Pilot's Pier: 1997 - Mar, Apr, May, Aug, Sep, Oct, Nov, Dec; 1998: Jan, Feb, Apr, Jul, Aug, Sep, Oct; 1999: Jan, Feb, Apr, May. Nepean Bay: 1997 - Apr, May, Sep, Oct, Nov, Dec; 1998 - Jan, Feb, Apr, Jun, Jul, Aug, Sep, Oct, Nov; 1999 - Jan, Feb, Mar, Apr, May, Jun.

Source	MS	df	F	P
Indented Head¹				
Month	0.368	16	6.680	<0.001
Error	0.055	84		
Pilot's Pier¹				
Month	0.150	18	3.780	<0.001
Error	0.040	99		
Nepean Bay¹				
Month	0.125	20	2.289	0.003
Error	0.055	117		

¹ = $\log_{10}(x+1)$ transformed data

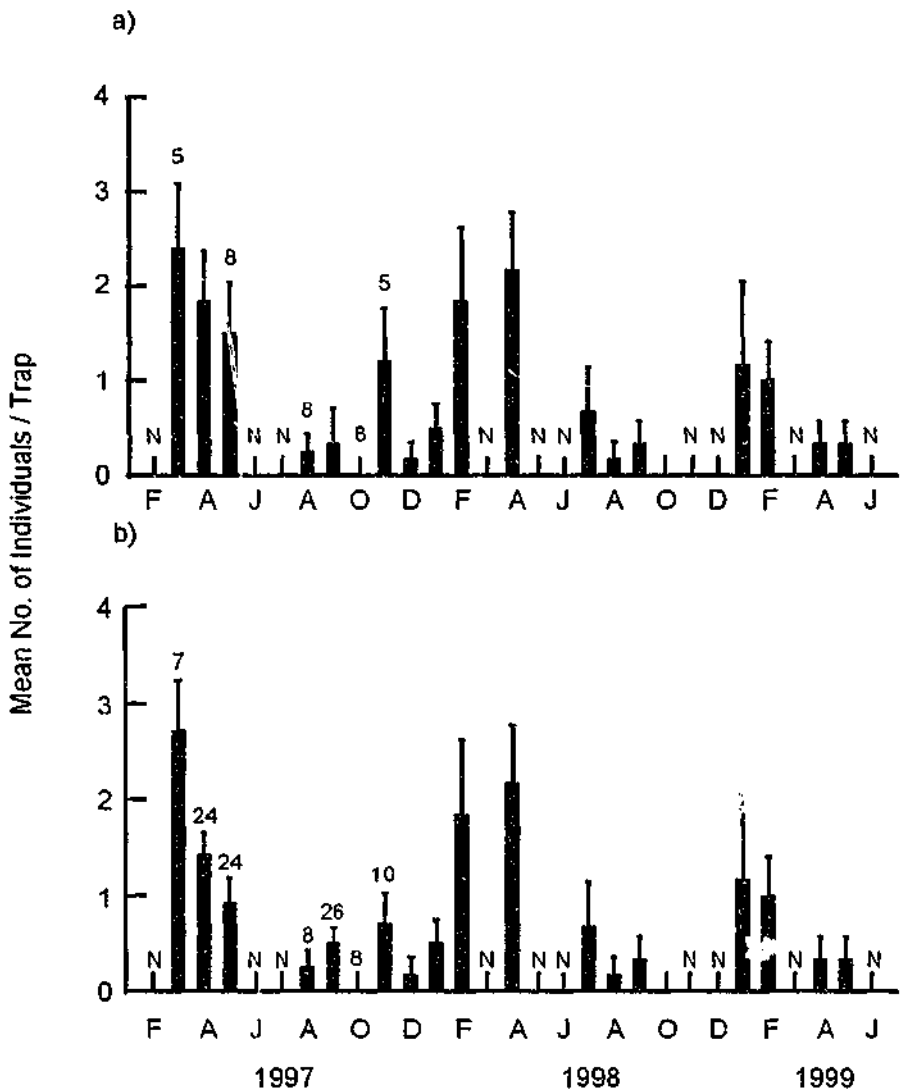


Figure 4.7: Mean number (\pm SE) of *M. freycineti* on the reef at Pilot's Pier, a) including only the standard six traps/month (used for analyses), and b) including all traps set each month (used for size frequency distributions). $n = 6$ except where indicated above the bar. N = no data.

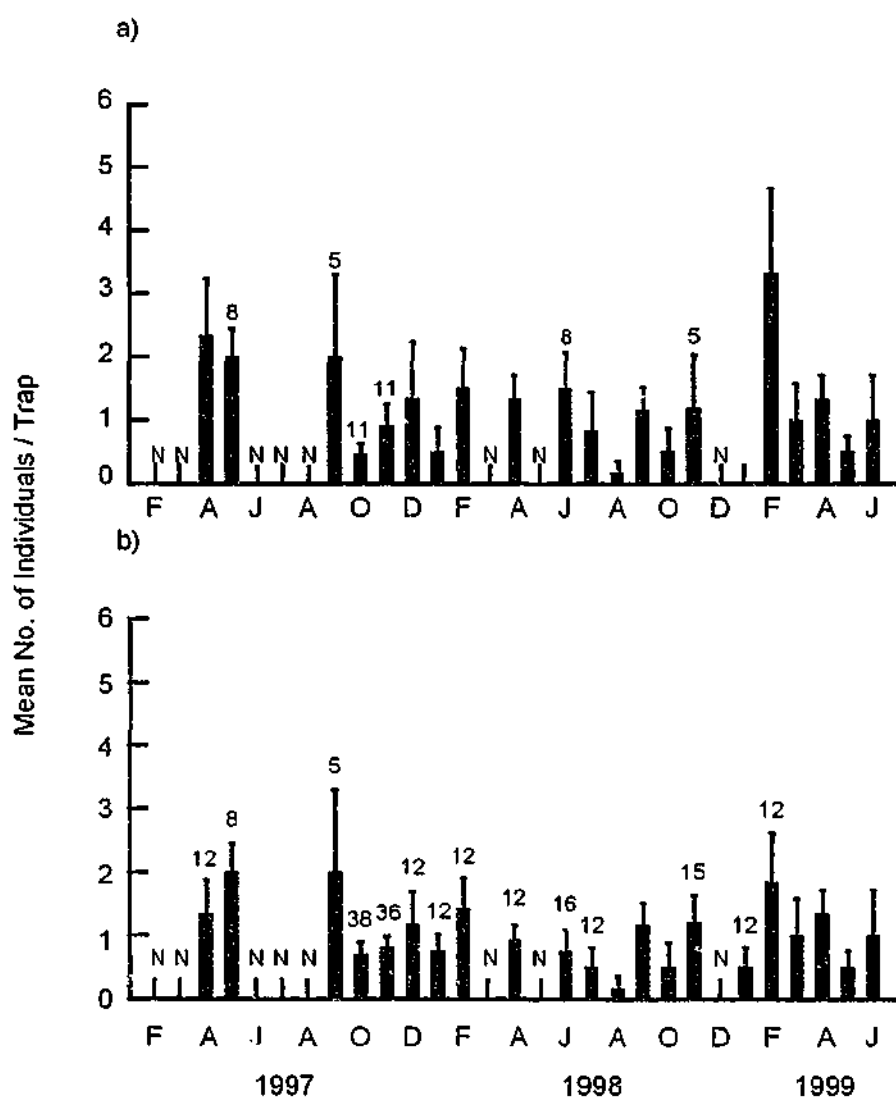


Figure 4.8: Mean number (\pm SE) of *M. freycineti* on the reef at Nepean Bay, a) including only the standard six traps/month (used for analyses), and b) including all traps set each month (used for size frequency distributions). $n = 6$ except where indicated above the bar. N = no data.

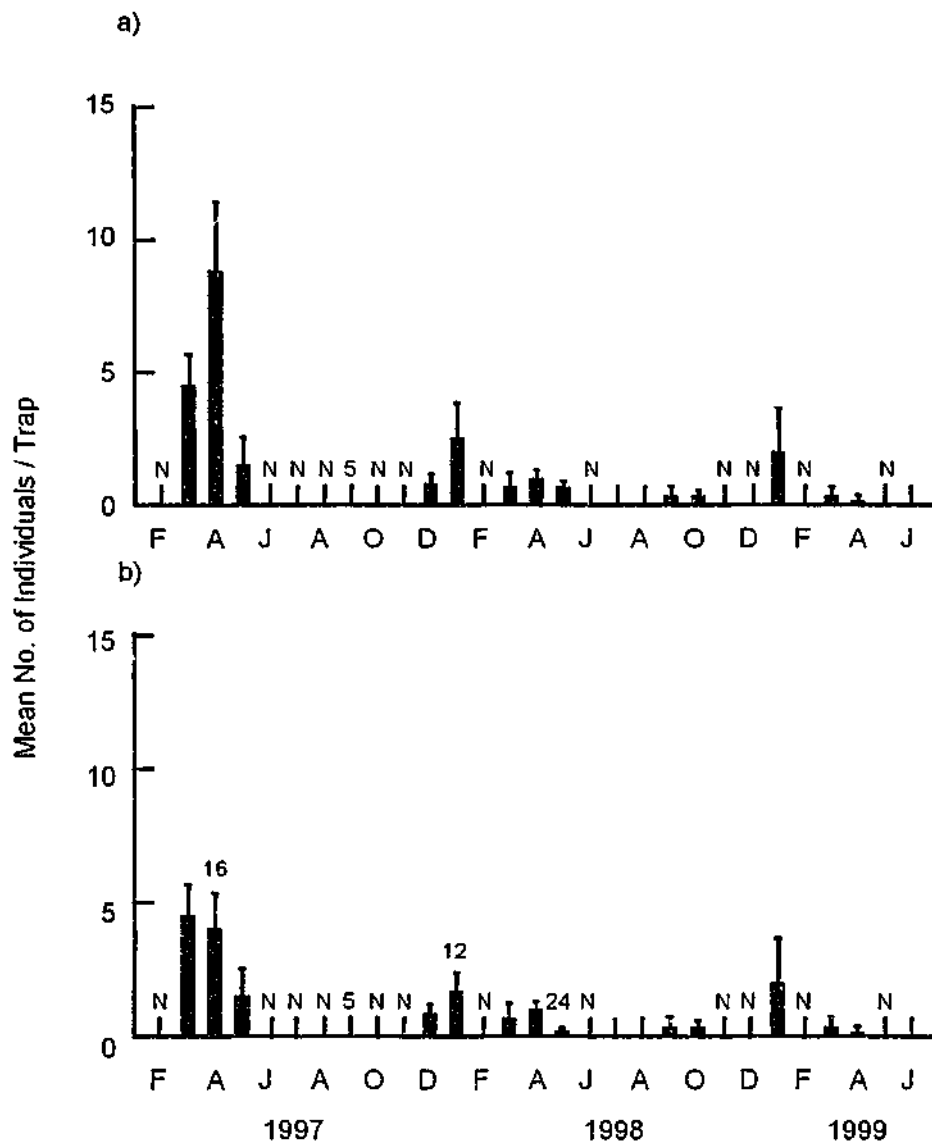


Figure 4.9: Mean number (\pm SE) of *M. freycineti* on the reef at Indented Head, a) including only the standard six traps/month (used for analyses), and b) including all traps set each month (used for size frequency distributions). $n = 6$ except where indicated above the bar. N = no data.

No *Meuschenia hippocrepis* were trapped at Pilot's Pier, and numbers of individuals at Indented Head were so low and variable that an ANOVA was not possible (Fig. 4.10). However, abundance of *M. hippocrepis* did vary significantly over time at Nepean Bay (Fig. 4.11a; Table 4.3). Patterns were consistent when all replicate traps were included (Figs. 4.11a and b), although no seasonality was evident.

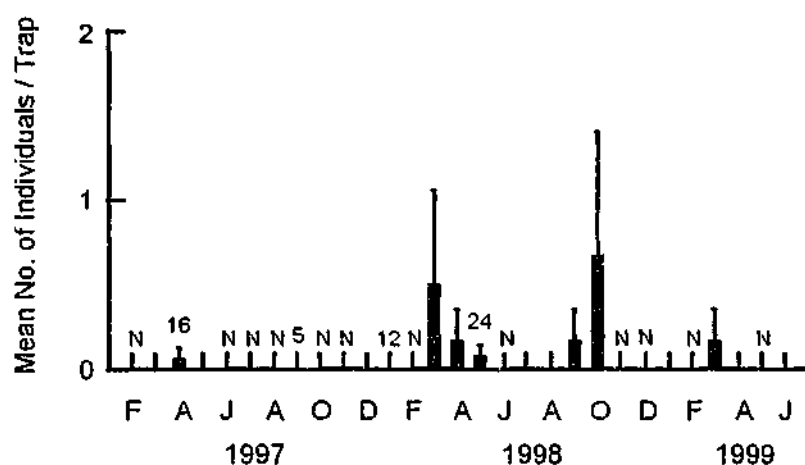


Figure 4.10: Mean number (\pm SE) of *M. hippocrepis* on the reef at Indented Head (includes all traps set each month). $n = 6$ except where indicated above the bar. Surveys were conducted from February 1997 – June 1999. N = no data.

Table 4.3: One-factor ANOVA comparing abundance of *M. hippocrepis* over time on the reef at Nepean Bay (1997 – Apr, May, Sep, Oct, Nov, Dec; 1998 – Jan, Feb, Apr, Jun, Jul, Aug, Sep, Oct, Nov; 1999 – Jan, Feb, Mar, Apr, May, Jun).

Source	MS	df	F	P
Nepean Bay ¹				
Month	0.147	20	1.922	0.017
Error	0.077	117		

¹ = $\log_{10}(x+1)$ transformed data

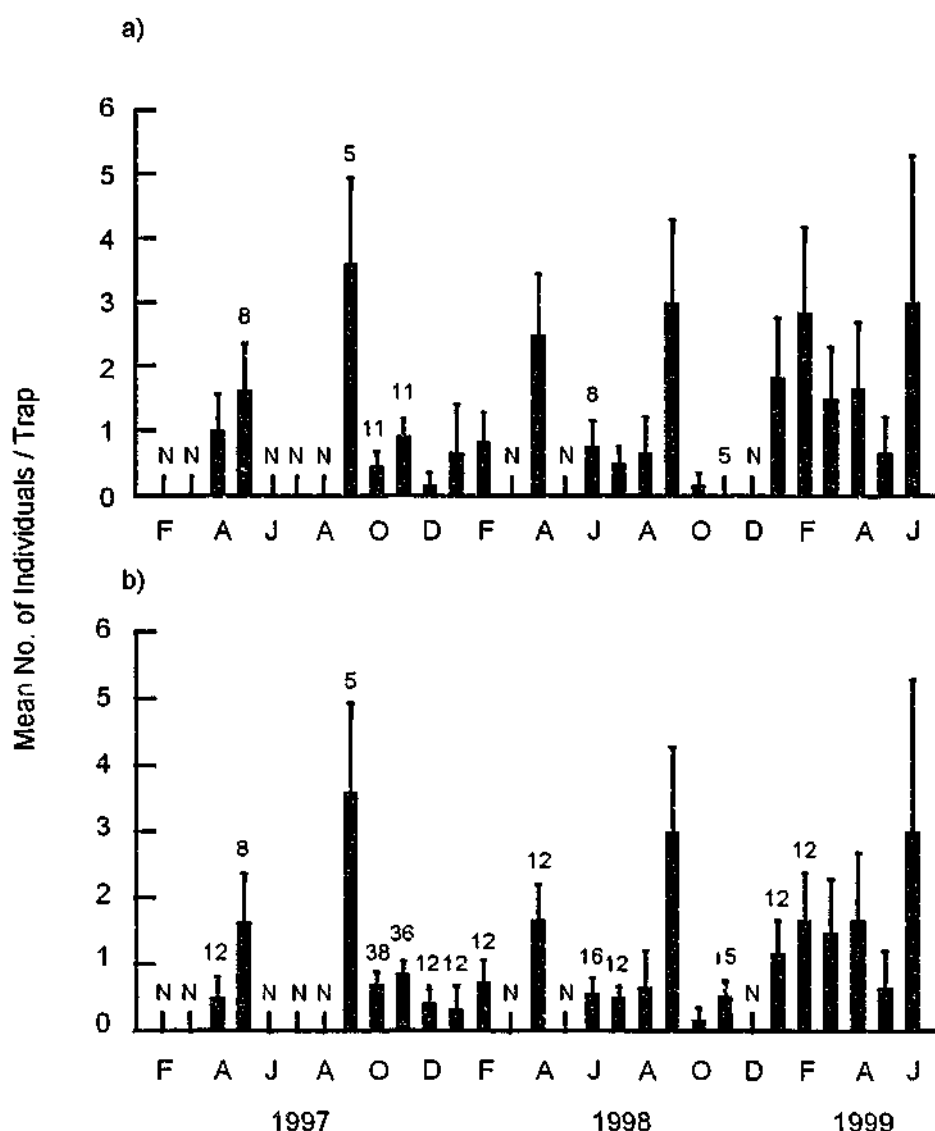


Figure 4.11: Mean number (\pm SE) of *M. hippocrepis* on the reef at Nepean Bay, a) including only the standard six traps/month (used for analyses), and b) including all traps set each month (used for size frequency distributions). $n = 6$ except where indicated above the bar. N = no data.

Size Structure of *Meuschenia freycineti* Populations

Size frequency distributions of *Meuschenia freycineti* pooled over site and sampling months for both seagrass and reef habitats clearly revealed smaller individuals in seagrass beds compared to rocky reefs (Fig. 4.12). *M. freycineti* in seagrass were on average 200 mm smaller than individuals on rocky reefs (Fig. 4.12). This pattern was consistent across all sites (Fig. 4.13). At Grassy Point and Indented Head, the two locations with both inshore seagrass and offshore reefs, most large individuals were recorded on the reefs, although a few large fish were recorded in seagrass, particularly at Indented Head

(Fig. 4.13). At the remaining seagrass and reef sites individuals were consistently smaller in the seagrass, with only a slight overlap in sizes between habitats (Fig. 4.13).

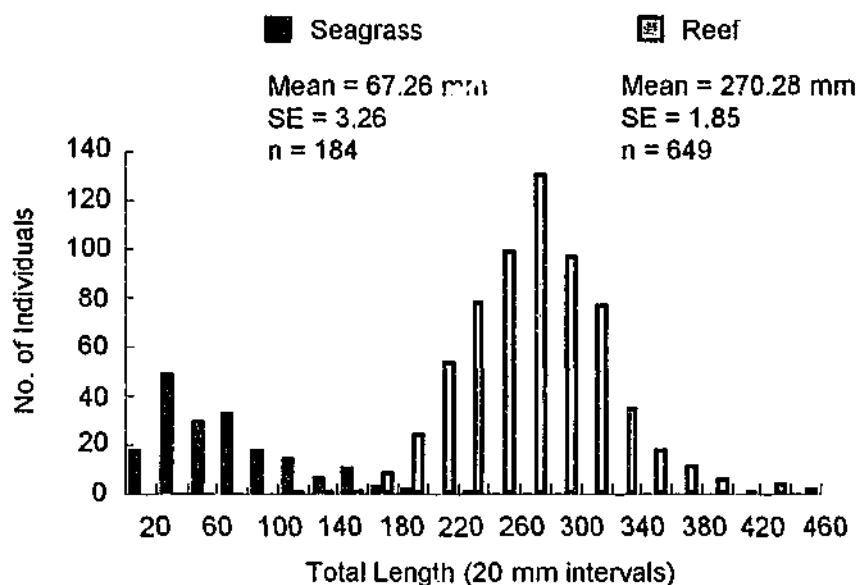


Figure 4.12: Size frequency distributions of *M. freycineti* from seagrass beds and reefs. Data from seagrass beds were pooled over sites and sampling months, as were data from reef sites (seagrass – November 1996 – May 1997 and November 1998 – May 1999; reef – February 1997 – June 1999).

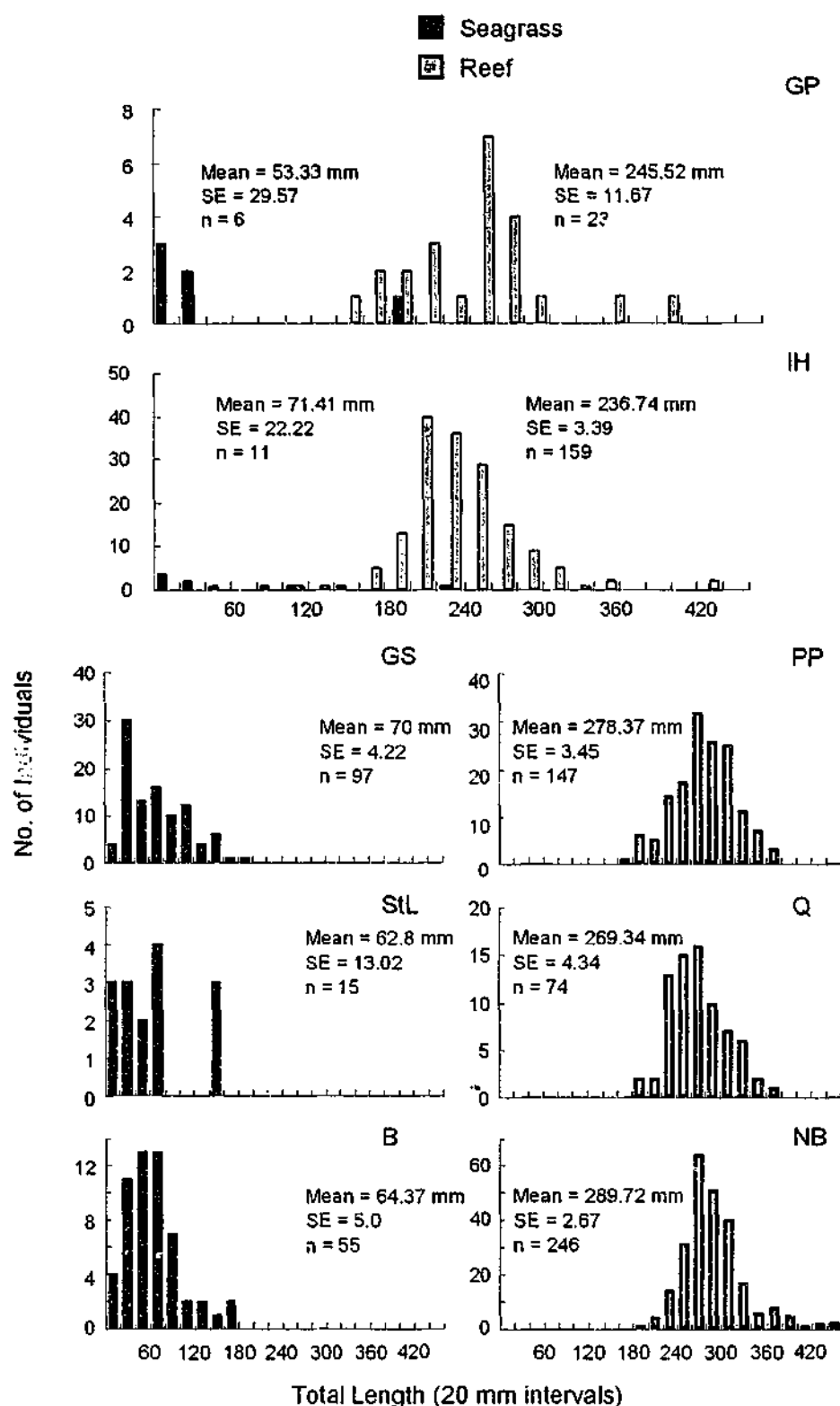


Figure 4.13: Size frequency distributions of *M. freycineti* from seagrass beds and reefs. Data were pooled across sampling months (seagrass – GP and IH; November 1998 – May 1999 and GS, StL and B; November 1996 – May 1997; reef – February 1997 – June 1999). GP = Grassy Point, IH = Indented Head, GS = Grand Scenic, PP = Pilot's Pier, StL = St Leonards, Q = Queenscliff, B = Blairgowrie, NB = Nepean Bay. Note: maximum Y-value differs between sites.

Size Structure of Meuschenia hippocrepis Populations

Meuschenia hippocrepis individuals were not observed in seagrass, and were only recorded at three of the reef sites, mostly at Nepean Bay. The average size of *M. hippocrepis* on rocky reefs was considerably smaller than the mean size of the reef-based *Meuschenia freycineti* (Figs. 4.12 and 4.14). The size range of *M. hippocrepis* individuals varied between sites, with larger individuals recorded near the entrance to Port Phillip Bay (Fig. 4.15).

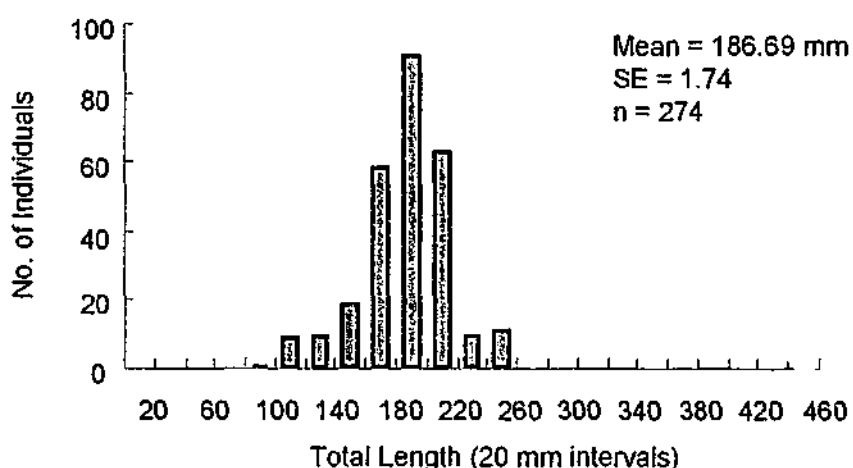


Figure 4.14: Size frequency distributions of *M. hippocrepis* from reefs. Data were pooled over sites and sampling months (February 1997 – June 1999).

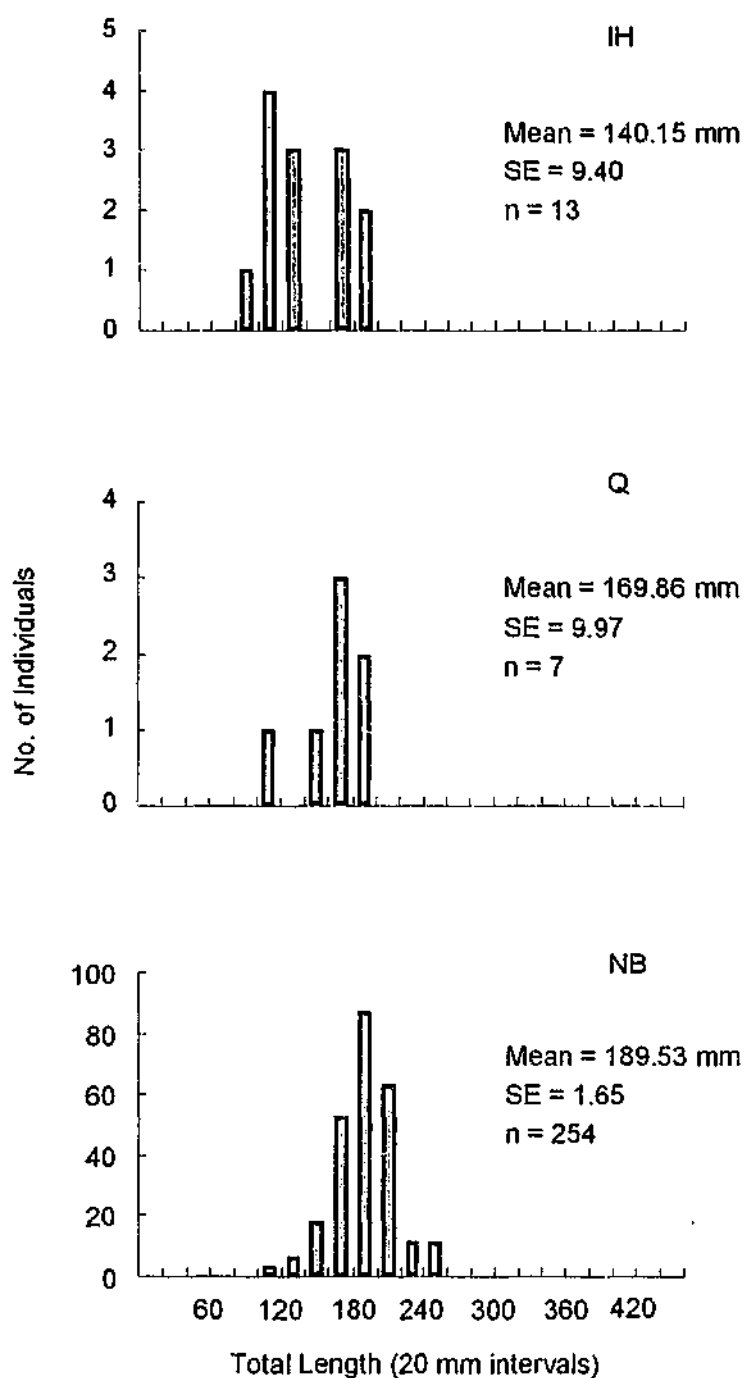


Figure 4.15: Size frequency distributions of *M. hippocrepis* from reefs. Data were pooled across sampling months (February 1997 – June 1999). IH = Indented Head, Q = Queenscliff, NB = Nepean Bay. Note: maximum Y-value differs between sites.

Discussion

Gonosomatic indices suggested that spawning in *M. freycineti* began in September/October (spring) and continued for a period of several months. In temperate waters, the reproductive period of many marine fishes is characterised by a single protracted spawning season (Warner, 1975; Jones, 1980; Wilk *et al.*, 1990; Gillanders, 1995c). This often occurs over spring/summer and may relate to increased water temperatures and productivity at this time (Barrett, 1995b). Access to abundant food supplies may be critical for larval survival, and by spawning over a period of several months, fish increase the probability that some offspring encounter productive conditions. Settlement from late spring through to autumn also coincides with increased growth and productivity of seagrass beds and associated invertebrates (Bird and Jenkins, 1999). Settlement of *M. freycineti* observed in this and previous studies is indicative of an extended spawning period. *M. freycineti* larvae appear to settle out of the water column at approximately 10-15 mm TL, and recruits and small juveniles have been recorded in seagrass beds in Port Phillip Bay (Jenkins *et al.*, 1993) and in Western Port Bay (Edgar and Shaw, 1995) from late spring through to autumn (November – May), and in estuaries in New South Wales from early spring to summer (September – December) (Bell *et al.*, 1978; Middleton *et al.*, 1984; Hannan and Williams, 1998). Although the spawning season of *Meuschenia hippocrepis* was not determined in this study, anecdotal evidence (i.e. the presence of juveniles) suggests that recruitment occurs over a similar time period (spring-summer) to that of *M. freycineti*. However, until studies examining the reproductive biology and recruitment patterns of *M. hippocrepis* are done, we can only speculate on the timing of the spawning season of this species.

Distinct differences were recorded in the size structure of *M. freycineti* and *M. hippocrepis* populations. *M. hippocrepis* were only recorded from reef habitats, and tended to be smaller than *M. freycineti* occurring on reefs. In contrast, *M. freycineti* showed distinct differences in size structures between seagrass and reef habitats. Recruits and juveniles of *M. freycineti* were only recorded in seagrass beds, while most large individuals (>200 mm TL) were recorded on reefs, with only a few large individuals observed in seagrass beds. Surveys of seagrass beds using a large mesh seine net also caught very few large individuals of *M. freycineti* (J. Hindell pers. comm. 1999). These

patterns were consistent over the period of the study at all the seagrass and reef sites surveyed. It is important to note that although the majority of *M. freycineti* caught in the seagrass beds were recruits/juveniles, larger individuals were caught on occasion, suggesting that seagrass beds may serve more than just a nursery function (Edgar and Shaw, 1995).

Differences in the population size structure between different depths and/or habitats are generally believed to arise through the movement of juveniles and/or sub-adults to deeper waters, or from seagrass to reef habitats (Bell and Worthington, 1993).

Numerous studies have demonstrated ontogenetic shifts in habitat by both tropical and temperate reef fishes (see reviews by Parrish, 1989, Bell and Worthington, 1993). For example, Gillanders (1997a) found large numbers of small *Achoerodus viridis* in seagrass beds and on shallow estuarine reefs, while most large individuals were found on exposed coastal reefs. Juvenile rockfish tend to recruit to shallower depths than those occupied by conspecific adults, and often move to deeper waters as they age (Love *et al.*, 1991). Although the abundance and size structure of *M. freycineti* populations in Port Phillip Bay supports a model of ontogenetic movement between inshore seagrass beds and offshore reefs, individuals were not tagged and movement is only one of many factors that may generate these patterns. Other factors that may be important in generating spatial differences in the size structure of *M. freycineti* include differential recruitment, mortality, growth, sampling methodology and habitat selection (Gillanders, 1997a). The importance of habitat selection by settling larvae in generating the distribution patterns observed is examined in Chapter 6.

Many studies show correlations between the distribution and abundance of recruits and adults (Victor, 1986b; Doherty and Fowler, 1994). Although no *M. hippocrepis* recruits were recorded in this study, the distribution of juvenile *M. hippocrepis* reflected adult distribution patterns. In contrast, *M. freycineti* recruits were found only in seagrass beds, and there was no evidence to suggest that *M. freycineti* recruit directly onto reefs. Juvenile *M. freycineti* were also abundant in seagrass beds, reflecting recruitment patterns, but the distribution of adult *M. freycineti* was very different to that of the recruits and juveniles, with most adults observed on reefs. Thus, unlike *M. hippocrepis*, recruitment does not appear to explain the distribution patterns of adult *M. freycineti*.

Differences in the size structure of *M. freycineti* populations between seagrass and reef habitats provide indirect evidence for ontogenetic movements between these habitats. In addition, very few large *M. freycineti* were recorded within seagrass beds, lending further support to a model of ontogenetic movement.

Differential mortality of *M. freycineti* recruits and small juveniles between seagrass beds and reefs may also explain the size frequency distribution and abundance patterns observed in this study. Shallow water habitats such as seagrass beds and mangroves are often considered important nursery areas for many fish species, due to the protection they provide (Parrish, 1989). It is possible that *M. freycineti* settle to both seagrass and reef habitats, but that small recruits/juveniles on the reefs experience greater mortality. Mortality patterns for large mobile reef fish, such as *M. freycineti*, are largely unknown due to the difficulties associated with distinguishing mortality from movement (Jones, 1991). However, until we have some indication of the mortality rates experienced by *M. freycineti* in different habitats, the importance of differential mortality in generating these distribution patterns cannot be discounted.

The size structure of fish populations may be influenced by differential patterns of growth. That is, *M. freycineti* in seagrass may be small and old, while similar sized individuals on reefs may be considerably younger. Monthly size compositions of *M. freycineti* in seagrass were plotted (data not presented) in an attempt to resolve initial growth patterns; however, too few individuals were recorded to yield any information on the variation in growth in recruits/juveniles. It seems unlikely, however, that individuals experience reduced growth in seagrass, as seagrass beds are considered to be important nursery areas due, in part, to the abundant food supply they provide (Bell and Pollard, 1989). Gillanders (1997b) showed that although most small *Achoerodus viridis* occurred within seagrass beds and shallow estuarine reefs, and large individuals were more common on coastal reefs, the differences were not due to differential growth rates between the habitats. Juvenile rockfish also show higher growth rates in shallow water than deep water habitats (Love *et al.*, 1991). Barrett (1995b) examined the influence of habitat on growth in the monacanthid, *Meuschenia australis*, and found that habitat-related factors were not sufficient to influence growth rates in this species. Although growth rates for *M. freycineti* are largely unknown (but see Chapter 5), individuals in

seagrass beds would not be expected to exhibit slow growth, and it is unlikely that differential growth would account for the differences in size of *M. freycineti* recorded in the two habitats.

Sampling methodology is an important consideration in any study examining the distribution and abundance of fishes, particularly when studies encompass more than one life history stage or habitat type. Every survey technique has its own biases, and it is often necessary to use different methods to accurately survey fish at different life history stages or in different habitats. In this study, small *M. freycineti* recruits and juveniles were only recorded in seagrass. However, seagrass beds were sampled with a fine-mesh seine net, which is unlikely to catch large fishes effectively. In contrast, reefs were surveyed using fish traps, which due to their large mesh size (25 mm) will not accurately sample small recruits. Sporadic fish trap surveys of the seagrass beds were conducted during the study, but only one large male *M. freycineti* (230 mm TL) was caught at Grassy Point. Although it was not possible to survey the reefs using a fine-mesh seine net, no recruits/juveniles of *M. freycineti* were recorded during 12 months of visual surveys of fishes on reefs in and around Port Phillip Bay (Chapter 3). Juvenile fish were rare on the visual surveys and almost totally absent from fish trap surveys, with only one juvenile *M. hippocrepis*, measuring 64 mm TL, caught in the fish traps over three years of trapping. In an attempt to survey recruits in seagrass beds and on reefs using the same methodology, small mesh (1 mm) bait traps were trialed in both habitats, which unfortunately failed to capture any fish in either habitat. Although the effects of sampling bias cannot be discounted, the generality of these patterns (see Parrish, 1989; Bell and Worthington, 1993) suggests that size structure differences between habitats were not sampling artefacts.

The distribution and abundance patterns of *M. freycineti* recruits and juveniles in seagrass beds and *M. hippocrepis* juveniles on rocky reefs may reflect habitat or depth selection by settling larvae. Monacanthid larvae may spend several weeks in the water column (Kingsford and Milicich, 1987), moving over various habitats before selecting one for settlement. Non-random habitat selection by settling larvae can occur in response to prey abundance (Levin, 1994), competition (Jones, 1987a, b) or predation (Jones, 1991). Thus *M. freycineti* may actively choose to settle to inshore seagrass beds

while *M. hippocrepis* larvae choose to settle directly onto deeper reefs. It is also possible that settlement is random, but *M. freycineti* and *M. hippocrepis* recruits survive better in seagrass beds and on rocky reefs, respectively. A previous study surveying shallow water habitats in Port Phillip Bay recorded *M. freycineti* recruits and small juveniles in seagrass beds and rubble reefs, but no *M. hippocrepis* individuals in the same inshore habitats (Jenkins and Wheatley, 1998). Although habitat selection by settling larvae may explain the distribution of *M. hippocrepis*, it does not explain why *M. freycineti* adults occur mainly on reefs.

Despite the possibility that the patterns observed in this study may be generated to some degree by habitat selection, movement and/or differential recruitment, growth and mortality, the importance of movement cannot be discounted. If fish do move between seagrass beds and rocky reefs, these movements, which may cover considerable distances (Bell and Worthington, 1993), must involve substantial advantages. Larvae may choose to settle in seagrass beds to avoid the greater competition and predation thought to occur on reefs (Parrish, 1989). Recruits may then move offshore to reefs as resources, such as food and shelter, become inadequate within seagrass beds (Gillanders and Kingsford, 1998). The diet of monacanthids is very diverse and includes a range of both invertebrate and algal taxa (Bell *et al.*, 1978), and *M. freycineti* individuals undergo a shift in feeding with growth. Recruits and juveniles tend to feed on invertebrates, such as harpacticoid copepods and gammarid amphipods, which are common in seagrass, while adults feed on a diverse array of reef-based invertebrates and algal taxa (M. Wheatley, unpubl. data). Feeding shifts are often associated with shifts in habitat use (McCormick, 1998), but it is not known whether changes in feeding habits cause individuals to move between habitats. With increasing size, individuals of *M. freycineti* may also outgrow the shelter provided by seagrass beds. Adults of *M. freycineti* are often observed under ledges or in crevices on rocky reefs (M. Wheatley, pers. obs.), and individuals may undergo ontogenetic shifts from seagrass beds to reefs when seagrass no longer provides adequate food or shelter.

The links, in terms of fish movements, between seagrass beds and rocky reefs are not well understood, and many questions remain unanswered, including what factors drive movements between these habitats, are these movements necessary for survival (Bell and

Worthington, 1993), at what size/age do individuals migrate, and do they utilise other available habitats (e.g. unvegetated sand). Some species, such as *Achoerodus viridis*, which settle to inner estuarine habitats before moving to offshore coastal reefs, also settle directly to offshore reefs (Gillanders and Kingsford, 1993). That is, many *A. viridis* individuals appear to successfully complete their life cycle without using shallow estuarine habitats (Gillanders and Kingsford, 1993), suggesting that the use of inner estuarine habitats is not critical to survival. In the case of *M. freycineti*, however, there is no evidence to suggest that individuals recruit directly onto offshore reefs, and our current knowledge suggests that, shallow water habitats (e.g. seagrass beds and rubble reefs) are very important for the successful recruitment of this species.

M. freycineti and *M. hippocrepis* abundances on reefs were extremely variable over the temporal scale of this study, but no seasonal patterns in abundance were detected (cf. Chapter 3). Monthly size frequency distributions were plotted in an attempt to determine what time of year *M. freycineti* individuals migrate from seagrass beds to reefs. These plots, however, did not provide any insight into the timing of movement between the habitats (data not presented). According to Bell and Worthington (1993) *M. freycineti* in New South Wales settle to seagrass beds and remain there for approximately 12 months before moving offshore to coastal reefs. Consistent monthly surveys of *M. freycineti* in seagrass beds and on reefs, over consecutive years, would be required to determine the timing of movement of individuals between these habitats in Port Phillip Bay.

Although this study has shown that recruits/juveniles of *M. freycineti* occur in seagrass beds and that adults are largely found on reefs, previous studies have recorded large *M. freycineti* in alternative habitats, such as deep *Posidonia* seagrass beds (Middleton *et al.*, 1984; Jordan *et al.*, 1998) and inner shelf unvegetated habitats (Gray and Otway, 1994). Middleton *et al.* (1984) proposed that *M. freycineti* use *Posidonia* beds as an intermediate habitat as they migrate between inshore seagrass beds and offshore reefs, and this is supported by the presence of intermediate sized individuals in *Posidonia* beds. In contrast, the presence of large *M. freycineti* on inner shelf unvegetated habitats may occur either through direct migration from inshore seagrass beds, or from seasonal

movements off reefs, to these areas. Extensive surveys are required to determine which of these hypotheses holds for *M. freycineti*.

The distinct difference in the distribution of recruits/juveniles of *M. freycineti* and *M. hippocrepis* recorded in seagrass beds and on reefs, respectively, may reflect habitat selection by settling larvae. As seagrass beds tend to occur in shallower waters than reefs these patterns may reflect either habitat or water depth preferences by settling larvae. Experimental seagrass and reef units were set up at both water depths in an attempt to determine the relative importance of habitat and depth in structuring *M. freycineti* and *M. hippocrepis* populations (see Chapter 6).

Summary

Despite the widespread distribution and abundance of monacanthids on temperate reefs in southern Australia, very few studies have examined their population structure. This study provides the first detailed description of the distribution, abundance and size structure of *Meuschenia freycineti* and *Meuschenia hippocrepis* populations. *M. hippocrepis* individuals were only recorded on reefs and do not appear to utilise inshore seagrass beds. In contrast, the proportion of small *M. freycineti* individuals (recruits and juveniles) decreased from seagrass to reef habitats, while the number of adult *M. freycineti* increased. Although seagrass beds appear to stock reef populations of adult *M. freycineti*, direct information on the fate of individuals within seagrass beds is still required. Although a range of processes including recruitment, mortality, growth and habitat selection may explain these different distribution patterns, the most likely explanation for the different size frequency distributions of *M. freycineti* in the different habitats is movement of individuals between seagrass beds and reefs. This chapter highlights the need for experimental studies that examine the relative importance of these different processes in structuring *M. hippocrepis* and *M. freycineti* populations (see Chapter 6).

Chapter 5

Movement Patterns and Growth of *Meuschenia freycineti* and *Meuschenia hippocrepis* on Reefs

Introduction

Studies examining assemblages of temperate reef fishes have shown that the distribution and abundance of the component species can vary considerably (see Chapters 3 and references therein). Growth and movement are two important demographic parameters that have the potential to significantly affect the distribution and abundance of reef fish populations. Growth rates determine how long it will take for an organism to reach a given size, and consequently, its vulnerability to predation and ability to exploit, and compete effectively for, necessary resources (Francis, 1994). Growth rates may be affected by different environmental factors, for example, food supply and water temperature (Jones, 1986; Francis, 1994), and can directly influence population size, time to maturation and reproductive output, as these traits are usually more dependent on body size than age (Jones, 1984b).

Fish are generally considered to be highly mobile organisms. Movement can bring fish in contact with their basic needs such as food, shelter and reproduction, and can also remove them from detrimental and potentially fatal situations including unfavourable environmental conditions, predation and fishing pressure. Fish movements can occur over a broad range of spatial and temporal scales that may change depending on the life-history stage of the fish, and the purpose of the movement. For example, fish movements may include local and daily movements within a home range for feeding (Norman and Jones, 1984), seasonal and large spatial scale migrations of adults to spawning sites (Crossland, 1976; Shimada and Kimura, 1994; Beentjes and Francis, 1999), and obligatory/preferential movements by juveniles or sub-adults between nursery and adult habitats (see Chapter 4; also Gillanders and Kingsford, 1993; Hyndes *et al.*, 1996; Gillanders, 1997a). Despite their potential for extensive movement, many tropical and temperate reef fishes are quite sedentary and site-attached, often spending their entire life associated with a small area of reef (Davis and Anderson, 1989; Sale,

1991). Familiarity with a small patch of reef may offer advantages including knowledge of good feeding and shelter sites (Barrett, 1995a).

In any study of fish movement, it is important to consider the influence of habitat. Irrespective of spatial and temporal scale, many movements are accompanied by a shift in habitat (e.g. ontogenetic movements between seagrass beds and reefs). Alternatively, different habitats can act as a possible barrier to movement. Information about movement patterns and barriers is important for developing appropriate fisheries management strategies (Hilborn, 1990). Potential barriers include thermoclines, changes in water velocity and salinity, and interruptions to continuous habitats (e.g. rocky reefs separated by extensive sand patches). Boundaries of open sand are known to be effective deterrents to the emigration of labrids and monacanthids (Barrett, 1995a). Love's (1980) study revealed restricted movement of olive rockfish, possibly due to the isolation of the study reef by the barren sandy habitat surrounding the reef. Large expanses of bare sand may restrict movement by many reef fishes as they provide very limited shelter.

The mark-release-recapture method has been widely used in both tropical and temperate marine systems to analyse the growth and movement patterns of fishes, to estimate population size, and to examine exploitation and mortality rates (e.g. Parker, 1990; Heinisch and Fable, 1999; Young *et al.*, 1999). Tagging is commonly used in studies that examine fish growth and movement as these aspects can be addressed simultaneously and include fewer assumptions than studies estimating population parameters such as mortality (Murray, 1990). However, numerous problems are inherent with the use of conventional tags (see Kearney, 1988). In particular, the details of any movements between release and recapture are unknown, and movement can only be inferred from the tagging/release and recapture locations of the fish (Sheaves, 1993). Tagging studies examining growth and movement also assume that the tag itself does not interfere with the 'normal' growth and movement patterns of the tagged fish. Despite these limitations, tagging is still a very important tool for investigating the movement patterns and growth of temperate reef fish.

While monacanthids are very abundant on temperate reefs in southern Australia, very few studies have examined their growth rates and/or movement patterns (but see Barrett, 1995a, b), and no information is available on these life history parameters for

species occurring on coastal reefs in Victoria. The major aim of the present study was to use mark-release-recapture techniques to describe the long-term movement patterns, site fidelity and growth rates of two monacanthid species, *Meuschenia freycineti* and *Meuschenia hippocrepsis*, on temperate rocky reefs within Port Phillip Bay, Victoria. A second aim was to examine the potential for movement by these species across large open sand patches adjacent to reefs that are a potential barrier to fish movement. An understanding of the growth and movement patterns of these fish, and how these factors vary spatially and temporally, will help us to examine their importance in determining the distribution and abundance of *M. freycineti* and *M. hippocrepsis*.

Methods

Movement Patterns and Growth of Meuschenia freycineti and Meuschenia hippocrepsis on Reefs

The movement patterns and growth of *Meuschenia freycineti* and *Meuschenia hippocrepsis* were examined using mark-release-recapture techniques. *M. freycineti* individuals were tagged over 24 months from March 1997 to February 1999, at three reefs within Port Phillip Bay: Indented Head, Pilot's Pier and Nepean Bay (Fig. 5.1). Tagging of *M. hippocrepsis* individuals was conducted over 9 months from June 1998 to February 1999 at Nepean Bay only (Fig. 5.1). All three reefs were covered by a variety of small canopy-forming and turfing macroalgal taxa (see Chapter 3). For a detailed description of the study sites refer to Chapter 2.

Individuals for tagging were captured using wire-mesh fish traps. In general, six baited traps were haphazardly set on the reef at each site. Trapping was conducted approximately monthly, although adverse weather prevented trapping in some months, while good conditions permitted additional trap runs in other months. Traps were left for approximately 1 hr and upon retrieval, all *M. freycineti* and *M. hippocrepsis* individuals were measured to the nearest millimetre (total length (TL)) and tagged before release. For a more detailed description of the trapping methodology refer to Chapter 2. Only fish with a total length >150 mm were tagged, as the use of conventional tags on small fish is believed to contribute to increased mortality rates (Moring, 1990). Fish were tagged using small (40 mm) terracotta-coloured plastic dart tags (Hallprint). Individually numbered tags were inserted just below the dorsal fin on

the left-hand side of each fish. All fish were released immediately after tagging and as close as possible to their capture location. Fish were not double-tagged due to concerns about the possibility of increased tag-induced mortality. In an attempt to evaluate tag loss and mortality due to tagging, *M. freycineti* were tagged ($n = 10$) in the laboratory in September 1996 and held in a flow-through seawater aquarium until November 1996 (50 days). There was no mortality due to tagging, and rates of tag loss were low (10%).

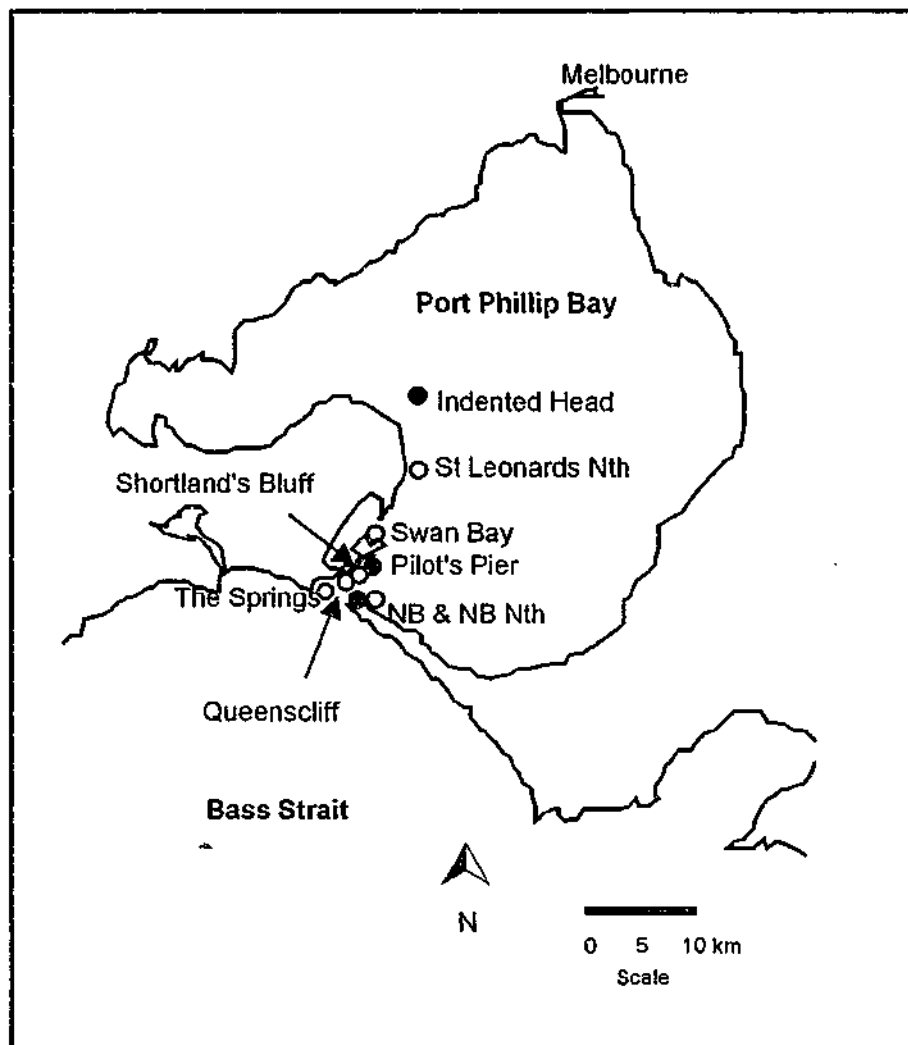


Figure 5.1: Location of study sites in Port Phillip Bay (closed circles = tagging reefs; open circles = reefs sporadically surveyed for recaptures. NB = Nepean Bay and NB Nth = Nepean Bay Nth).

Attempts to recapture tagged individuals continued until June 1999, although one tagged *M. hippocrepis* was recaptured in September 1999 as part of an unrelated

project. To determine whether movement occurred between sites, six additional reefs (Nepean Bay Nth, Shortland's Bluff, Swan Bay, Queenscliff, The Springs and St Leonards Nth) were also sampled opportunistically over the period of the study for tagged individuals (Fig. 5.1). Reef fidelity was defined as the recapture of tagged individuals at their site of release, and the number of times tagged individuals were captured at their release site was used as an indication of the duration of occupancy.

Mark-release-recapture data examining movement and growth were collected in conjunction with studies on the distribution, abundance and size structure of *M. freycineti* and *M. hippocrepis* populations within Port Phillip Bay (see Chapter 4).

The tag number, site, date and size (TL) of each recaptured fish were recorded. Recapture rate (not including multiple recaptures) is expressed as a percentage, and was calculated by dividing the total number of fish tagged and released by the number of fish recaptured. Growth rates were calculated as the increase in length during time at liberty (i.e. time between tagging and recapture) and were expressed in millimetres per day (mmd^{-1}). Only fish at liberty for >30 days were used for calculations of growth rate (Young *et al.*, 1999). To determine whether all sizes of tagged *M. freycineti* and *M. hippocrepis* were vulnerable to recapture, the size frequency distributions of tagged fish were compared with the size frequency distributions of the tagged length of recaptured fish using chi-squared exact randomisation tests (SPSS). Exact significance tests were used because the expected values for some cells were very low. Separate analyses were conducted for each species and each site. Growth rates were compared between the sexes for *M. freycineti* at each site using one-factor analyses of variance (ANOVAs). It was not possible to run a two-factor ANOVA comparing growth rates between sites and sexes due to the low numbers of female *M. freycineti* recorded at Indented Head and Pilot's Pier. An attempt was made to fit a von Bertalanffy growth curve to the tag-recapture data using Fabens' (1965) method. Unfortunately, the low number of fish tagged and then recaptured, the small size range of the fish that were tagged and the short time periods that most individuals were at liberty meant that this procedure did not produce meaningful growth curves (Terry Walker, pers. comm. 2001).

*Potential Movement of Meuschenia freycineti and Meuschenia hippocreps
Across Sand*

Experiments to examine the potential movement of *Meuschenia freycineti* and *Meuschenia hippocreps* from a rocky reef over sand (a potential barrier to movement) were conducted at Nepean Bay in October 1997 (Fig. 5.1). Nepean Bay was selected for these experiments because a large patch of sand occurs adjacent to the reef, and because trap catches of both *M. freycineti* and *M. hippocreps* were relatively consistent at this site.

Baited traps were set on the reef, and on the sand 5 m and 10 m from the reef. Eleven baited traps were haphazardly assigned to each location. As only a limited number of traps were available, the experiment was conducted 12 times, to increase replication and to ensure an equal number of replicate traps in each location. Traps were hauled after a soak time of 1 hr, and all fish were identified, counted, measured (TL) and released.

To analyse the potential movement of *M. freycineti* and *M. hippocreps* over sand, the numbers of fish caught in the different locations on each sampling trip (time) were compared using two-factor ANOVAs. Planned comparisons compared the numbers of fish between reef and sand locations, and also between both sand locations.

Results

*Movement Patterns of Meuschenia freycineti and Meuschenia hippocreps on
Reefs*

Over the sampling period, 271 *Meuschenia freycineti* and 36 *Meuschenia hippocreps* were tagged and released within Port Phillip Bay, and 74 (27.3%) *M. freycineti* and 11 (30.6%) *M. hippocreps* individuals were recaptured (Table 5.1). Only 36 *M. hippocreps* individuals were tagged as the majority of *M. hippocreps* caught at Nepean Bay measured <150 mm TL, the minimum size for tagging (Moring, 1990). Both species showed a high degree of site fidelity as all individuals were recaptured at their tagging/release site. Surveys of nearby reefs revealed no tagged individuals of either species. There was no apparent short-term mortality associated with either trapping or tagging as all individuals swam away rapidly upon release, and very few recaptured fish showed any signs of infection around the tag insertion point, and most tag wounds

appeared to have healed externally. In addition, very few tags appeared damaged by biting and/or scraping, although most tags were covered relatively quickly (within approx. 30 days) by epiphytic algae.

Table 5.1: Summary data of the long-term movements of *M. freycineti* and *M. hippocrepis* within Port Phillip Bay. Data derived over 28 months for *M. freycineti* (March 1997 – June 1999), and over 16 months for *M. hippocrepis* (June 1998 – September 1999).

Species	No. of fish tagged	No. of recaptures (including multiples)	No. of recaptures (excluding multiples)	Recapture rate (%)	Mean recaptures per individual	Highest recaptures per individual
<i>M. freycineti</i>						
Indented Head	59	5	5	8.5	1	1
Pilot's Pier	84	41	22	26.2	1.8	5
Nepean Bay	128	95	47	36.7	1.7	7
Overall total	271	141	74	27.3		
<i>M. hippocrepis</i>						
Nepean Bay	36	14	11	30.6	1.3	3

Meuschenia freycineti

The numbers of *Meuschenia freycineti* tagged and recaptured varied considerably between the sites (Table 5.1). Recapture rates were comparatively high at both Pilot's Pier (26.2%) and Nepean Bay (36.7%), but considerably lower at Indented Head (8.5%). Multiple recaptures of the same individual were not considered in the overall percentage of recaptures for each site. Although most individuals were only recaptured once, multiple recaptures were recorded at both Pilot's Pier and Nepean Bay, with one individual recaptured seven times (Fig. 5.2).

Size frequency distributions of tagged *M. freycineti*, and the lengths at tagging of recaptured *M. freycineti*, are presented in Figure 5.3. The size frequency distributions were not significantly different, indicating that all sizes of tagged fish were vulnerable to recapture. This result was consistent across all three sites: Indented Head ($\chi^2 = 7.481$, $df = 7$, $P = 0.323$), Pilot's Pier ($\chi^2 = 6.592$, $df = 9$, $P = 0.705$), and Nepean Bay ($\chi^2 = 8.058$, $df = 13$, $P = 0.880$). The average size of *M. freycineti* individuals tagged did, however, increase toward the southern end of Port Phillip Bay (Fig. 5.3).

Most recaptures of tagged *M. freycineti* occurred over a short time period (i.e. <100 days): Indented Head (80%), Pilot's Pier (69.6%) and Nepean Bay (63.8%) (Fig. 5.4).

At Indented Head, only one individual was at liberty for >100 days (250 days), while at Pilot's Pier and Nepean Bay 95.7% and 95.5%, respectively, of recaptured individuals were recaptured within one year (Fig. 5.4). The maximum period at liberty was 530 days for an individual tagged and recaptured at Nepean Bay (Fig. 5.4).

Despite the short time periods between tagging and recapture, and the fact that most fish were only recaptured once, the recapture histories of *M. freycineti* indicate that most individuals were recaptured at their site of release between 6-12 months after tagging (Tables 5.2, 5.3 and 5.4; also see Appendices 5.1, 5.2 and 5.3). These data coupled with the lack of recaptures at nearby reefs provide good evidence for the long-term residency of *M. freycineti* on these reefs, particularly Nepean Bay (Table 5.4).

No seasonal patterns in the recapture of tagged *M. freycineti* were apparent at Indented Head, although very few individuals were actually recaptured at this site (Fig. 5.5). At Pilot's Pier, most recaptures occurred in April and May 1997, not long after tagging was initiated, while at Nepean Bay, recapture numbers were greatest in October and November 1997 (Fig. 5.5). Untagged *M. freycineti* were continually caught at all three sites throughout the study period (Fig. 5.5).

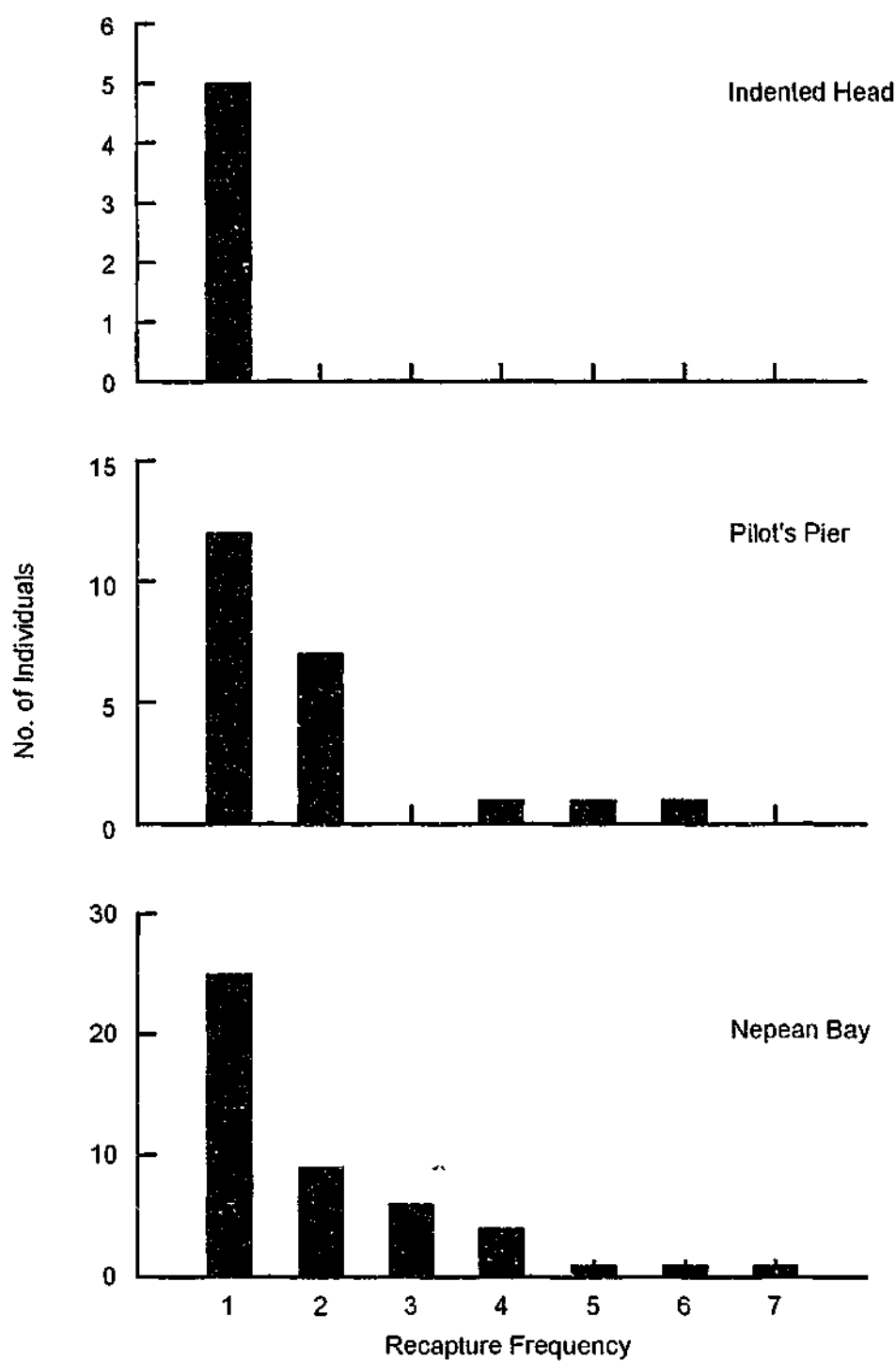


Figure 5.2: Recapture frequency of tagged *M. freycineti* within Port Phillip Bay. Note: maximum Y-value differs between sites.

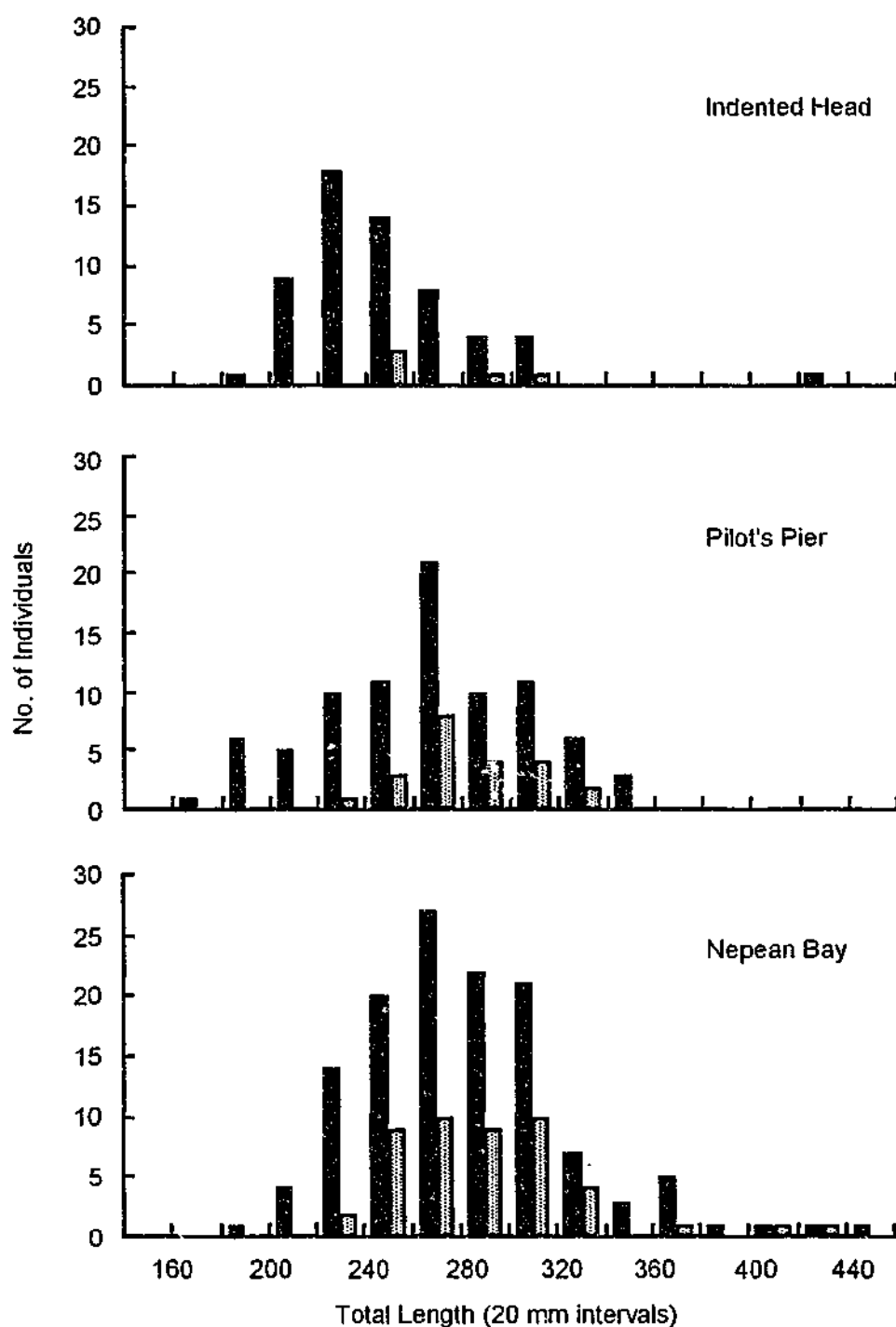


Figure 5.3: Size frequency distributions of *M. freycineti* at tagging (dark bars), and the lengths at tagging of recaptured *M. freycineti* (light bars) at Indented Head, Pilot's Pier and Nepean Bay.

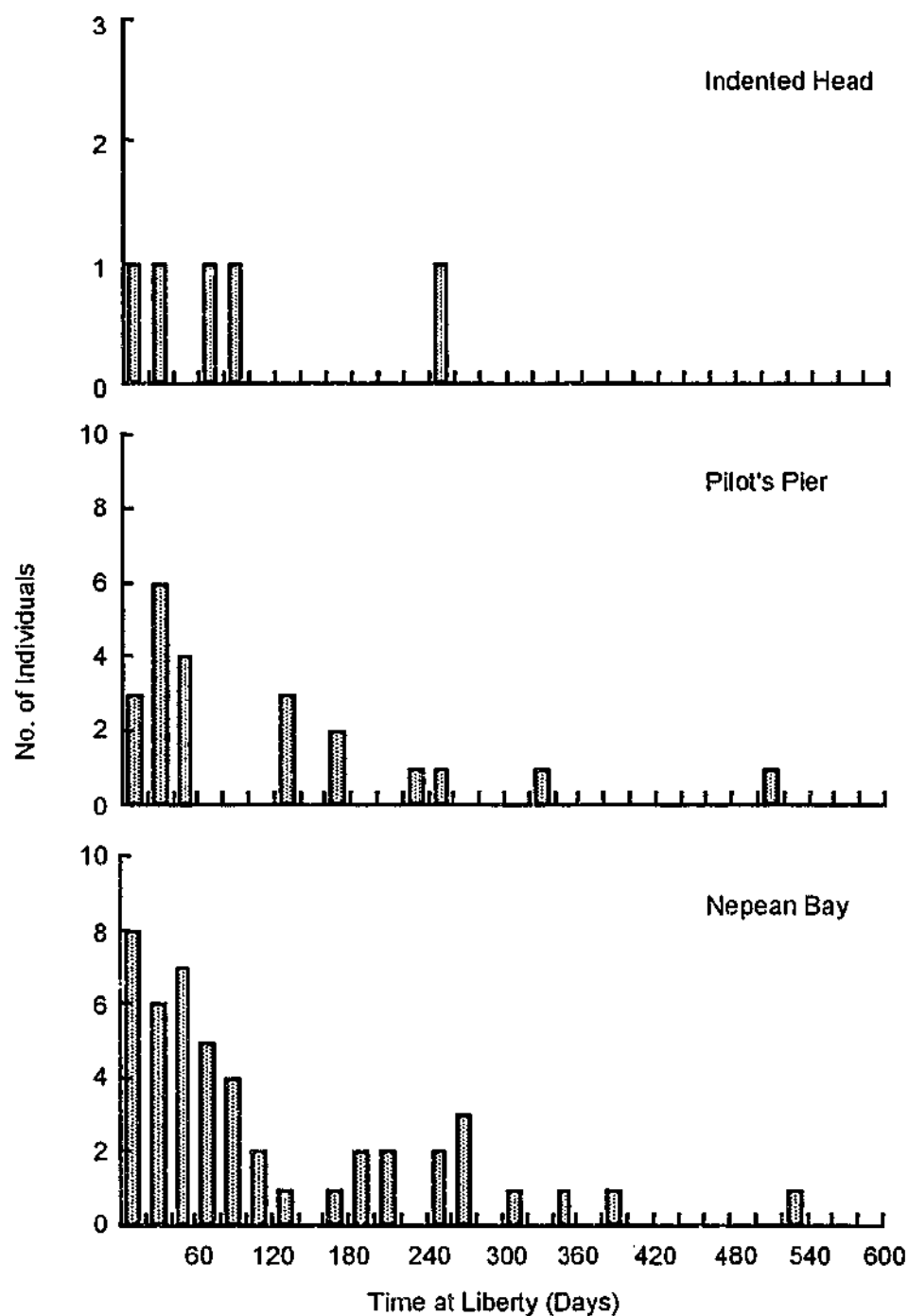


Figure 5.4: Time at liberty for *M. freycineti* tagged and recaptured at Indented Head, Pilot's Pier and Nepean Bay. Note: maximum Y-value differs between sites.

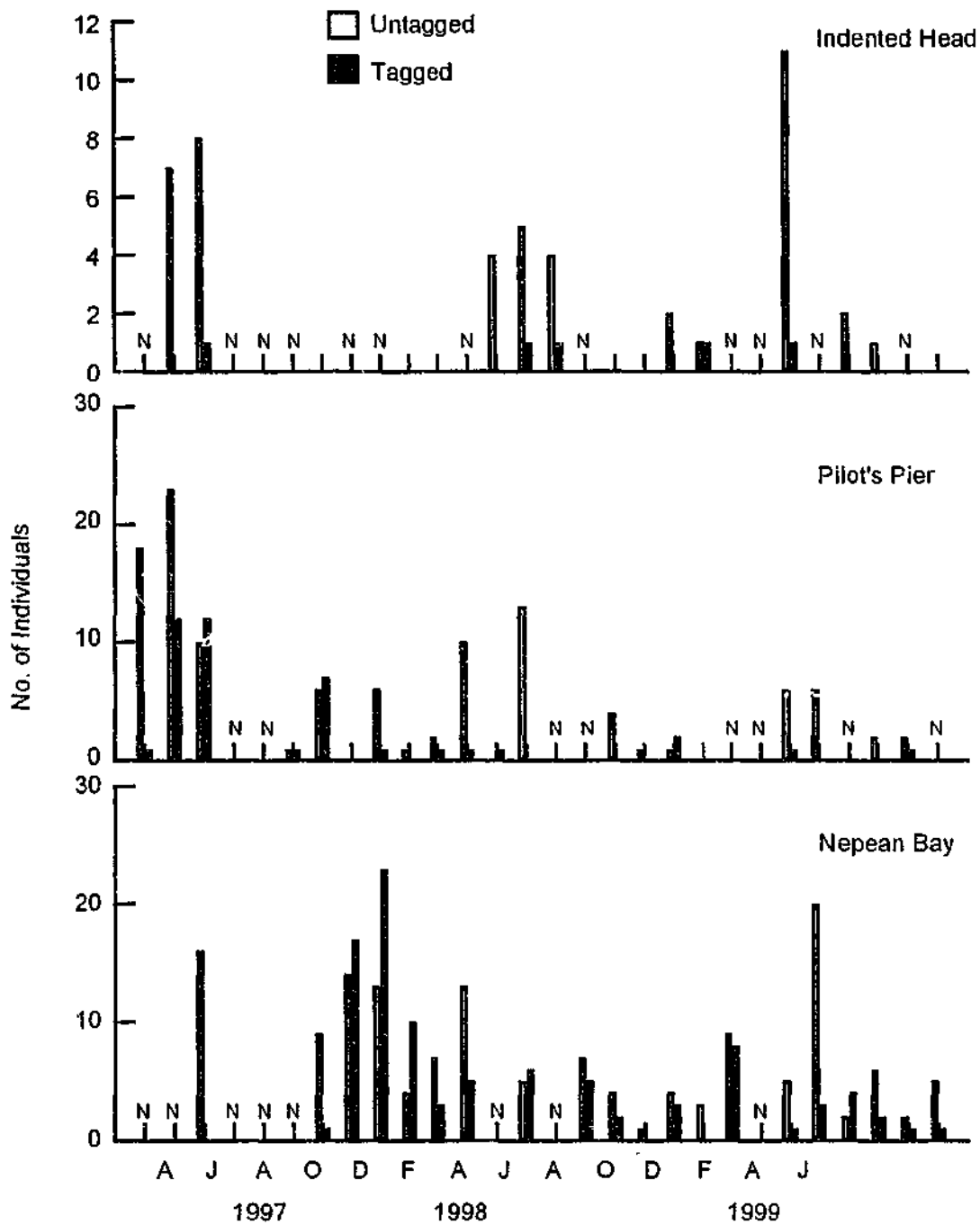


Figure 5.5: Total number of untagged and tagged *M. freycineti* individuals (including multiple recaptures) trapped at Indented Head, Pilot's Pier and Nepean Bay over the study period. N = no data. Note: maximum Y-value differs between sites.

Table 5.3: cont.[illegible]

Table 5.4: Summary of the number of captures and subsequent recaptures of *M. freycineti* at Nepean Bay between May 1997 and June 1999. The numbers in the diagonal line indicate the number of individuals caught on the date indicated. Subsequent numbers across each row indicate the number of tagged fish recaptured on each date.

[illegible]

Table 5.4: cont.[illegible]

Table 5.4: cont.

Date Tagged	Date recaptured		
	15.4.99	6.5.99	8.6.99
24.5.97	0	0	0
17.9.97	0	0	0
9.10.97	0	0	0
23.10.97	0	0	0
29.10.97	0	0	0
7.11.97	0	0	0
13.11.97	0	0	0
9.12.97	0	0	0
5.2.98	0	0	0
22.4.98	1	0	0
17.6.98	0	0	0
24.7.98	0	0	0
18.8.98	0	0	0
11.9.98	0	0	0
22.10.98	0	0	0
6.11.98	0	0	0
17.11.98	0	0	0
5.1.99	0	0	0
5.2.99	0	0	0
22.2.99	1	1	1

Meuschenia hippocrepis

Meuschenia hippocrepis were tagged and recaptured over 12 months at Nepean Bay only. Thirty-six *M. hippocrepis* were tagged, and 11 (30.6%) tagged individuals were recaptured (Table 5.1). Multiple recaptures of the same individual were not considered in the calculation of recapture rate (Table 5.1). Only two *M. hippocrepis* individuals were recaptured on multiple occasions, with one individual recaptured twice and a second individual recaptured three times.

Size frequency distributions of tagged *M. hippocrepis*, and the lengths at tagging of recaptured *M. hippocrepis*, are presented in Figure 5.6. The size frequency distributions were not significantly different, indicating that tagged fish of all sizes were equally vulnerable to recapture ($\chi^2 = 1.557$, $df = 4$, $P = 0.894$).

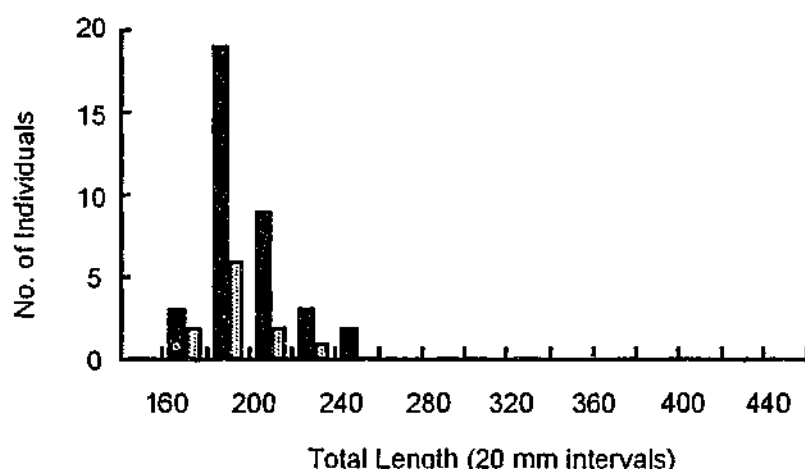


Figure 5.6: Size frequency distributions of *M. hippocrepis* at tagging (dark bars), and the lengths at tagging of recaptured *M. hippocrepis* (light bars) at Nepean Bay.

The recapture period for *M. hippocrepis* individuals was short (approx. 12 months). Most *M. hippocrepis* individuals were recaptured in <100 days, with only one individual caught after this period at 192 days (Fig. 5.7).

Despite the short time periods between tagging and recapture, and the fact that most fish were only recaptured once, the recapture history of *M. hippocrepis* at Nepean Bay indicates that most individuals were recaptured at their site of release approximately 3

months, and for one individual approximately 6 months, after tagging (Tables 5.5; also see Appendix 5.4). These data coupled with the lack of recaptures at nearby reefs provide evidence for the long-term residency of *M. hippocrepis* on the reef at Nepean Bay.

There were no seasonal patterns in the recaptures of tagged *M. hippocrepis*. Untagged *M. hippocrepis* individuals were continually caught throughout the study (Fig. 5.8), although most recaptures occurred in September and November, 1998, only a few months after tagging was initiated (Fig. 5.8).

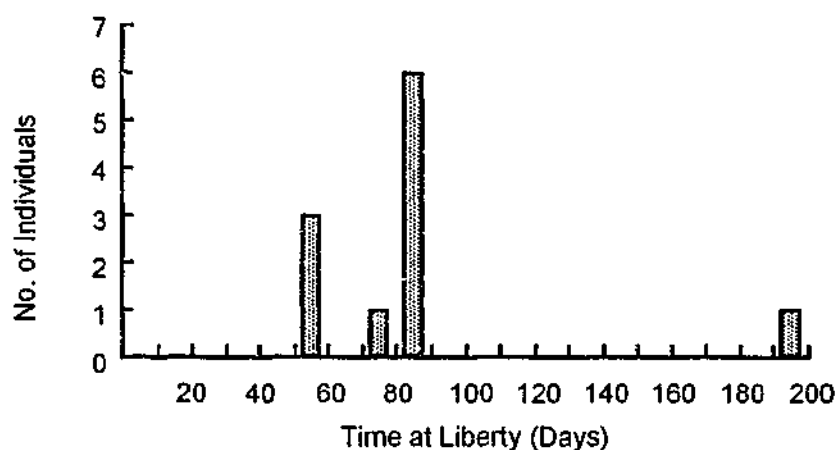


Figure 5.7: Time at liberty for *M. hippocrepis* tagged and recaptured at Nepean Bay.

Table 5.5: Summary of the number of captures and subsequent recaptures of *M. hippocrepis* at Nepean Bay between June 1998 and September 1999. The numbers in the diagonal line indicate the number of individuals caught on the date indicated. Subsequent numbers across each row indicate the number of tagged fish recaptured on each date.

Date Tagged	Date recaptured									
	17.6.98	24.7.98	18.8.98	11.9.98	6.11.98	5.2.99	22.2.99	23.3.99	8.6.99	2.9.99
17.6.98	8	0	1	6	0	0	0	0	0	0
24.7.98		5	0	0	0	0	0	0	0	0
18.8.98			2	0	1	0	0	0	0	0
11.9.98				9	3	0	0	0	0	0
6.11.98					6	0	0	0	0	0
5.2.99						2	0	0	0	0
22.2.99							4	1	1	1

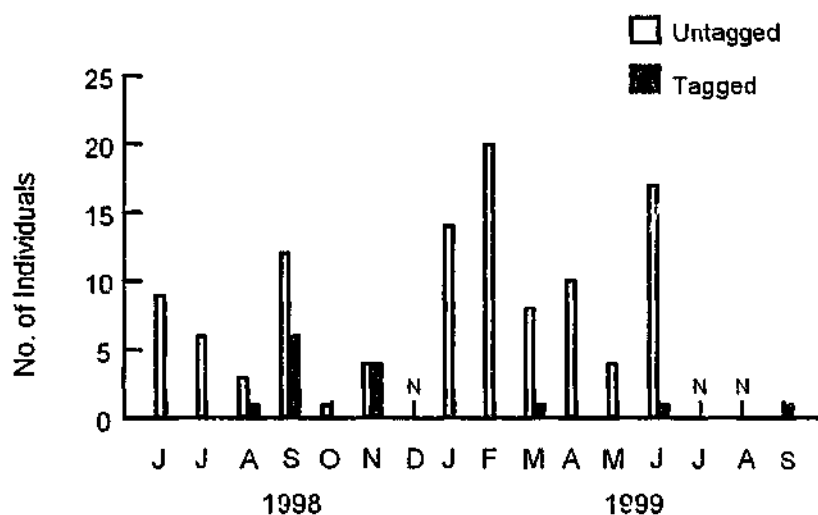


Figure 5.8: Total number of untagged and tagged *M. hippocrepis* individuals (including multiple recaptures) trapped at Nepean Bay over the study period. N = no data.

Potential Movement of Meuschenia freycineti and Meuschenia hippocrepis Across Sand

Numbers of both *Meuschenia freycineti* and *Meuschenia hippocrepis* varied significantly between the three locations: reef and sand 5 m and 10 m from the reef (Fig. 5.9). Although some *M. freycineti* individuals were trapped over sand, significantly more were recorded on the reef than at either sand location (Fig. 5.9a; Table 5.6). Additionally, there was no significant difference in the number of *M. freycineti* individuals recorded on sand 5 m and 10 m from the reef (Fig. 5.9a; Table 5.6). All *M. hippocrepis* individuals were recorded on the reef (Fig. 5.9b).

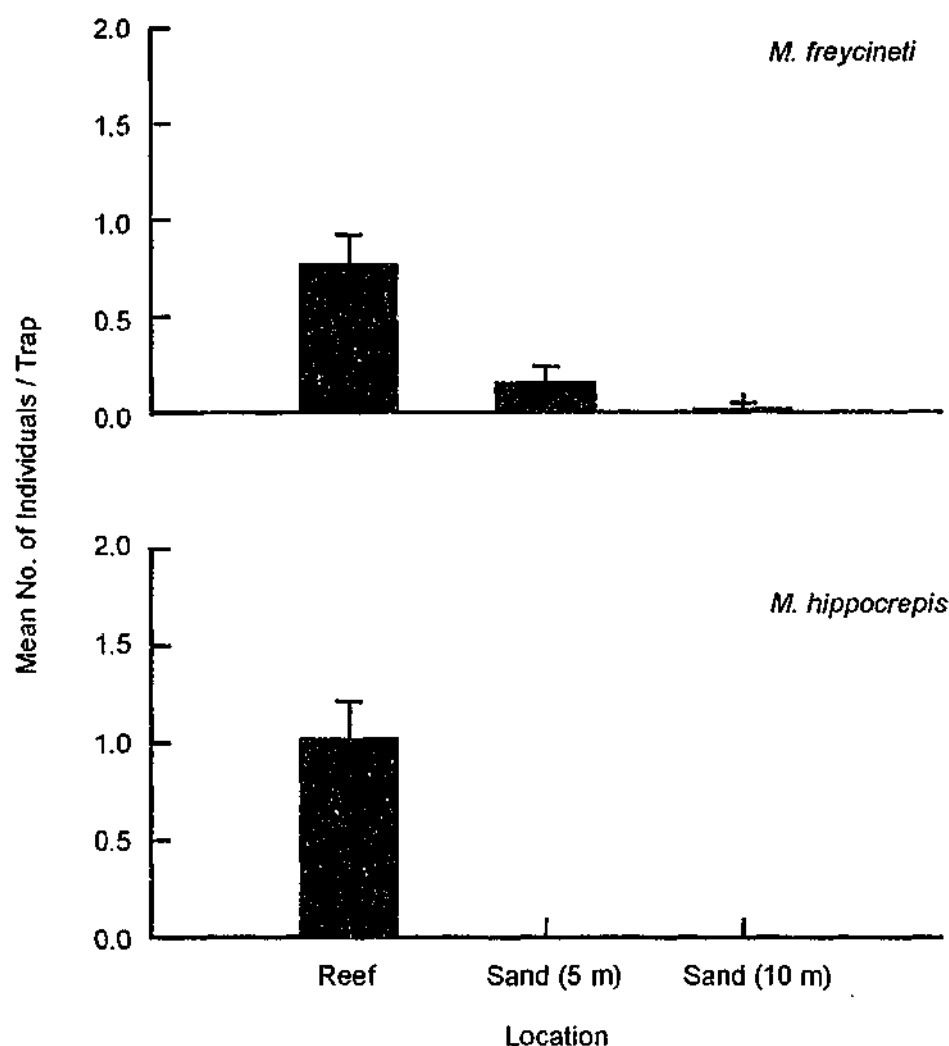


Figure 5.9: Number (mean \pm SE; $n = 44$) of *M. freycineti* and *M. hippocrepis* on the reef and on the sand 5 m and 10 m from the reef, at Nepean Bay (October 1997).

Table 5.6: Two-factor ANOVA comparing the numbers of *M. freycineti* between locations (reef, and sand 5 m and 10 m from the reef), and over time; and single-degree-of-freedom planned comparisons between reef and sand locations and between both sand locations.

Source	MS	df	F	P
Location	0.453	2	20.085	<0.001
Time	0.022	11	0.976	0.474
Location*Time	0.018	22	0.810	0.706
Error	0.023	96		
Reef vs Sand	0.879	1	38.961	<0.001
Sand (5 m) vs Sand (10 m)	0.027	1	1.209	0.274

Growth of Meuschenia freycineti and Meuschenia hippocrepis on Reefs

Meuschenia freycineti

The mean overall growth rate of *Meuschenia freycineti* was higher at Indented Head than at Pilot's Pier or Nepean Bay (Fig. 5.10). However, individual growth rates at all three sites were extremely variable (Appendices 5.1, 5.2 and 5.3). As only one female *M. freycineti* was recaptured at Indented Head it was not possible to examine any differences in growth rates between the sexes for this site (Appendix 5.1). At Pilot's Pier there were no significant differences in growth rates between the sexes (Fig. 5.10; $F_{(1,12)} = 3.019$, $P = 0.108$), while at Nepean Bay males had significantly higher growth rates than females (Fig. 5.10; $F_{(1,32)} = 21.459$, $P = <0.001$). It was not possible to determine any seasonal patterns in the growth of *M. freycineti* as individuals tended to be recaptured on one occasion either: (i) very shortly after tagging, making estimates of growth unreliable; or (ii) after an extended period covering two or three seasons, and as such, the growth rate could not be divided into seasonal components.

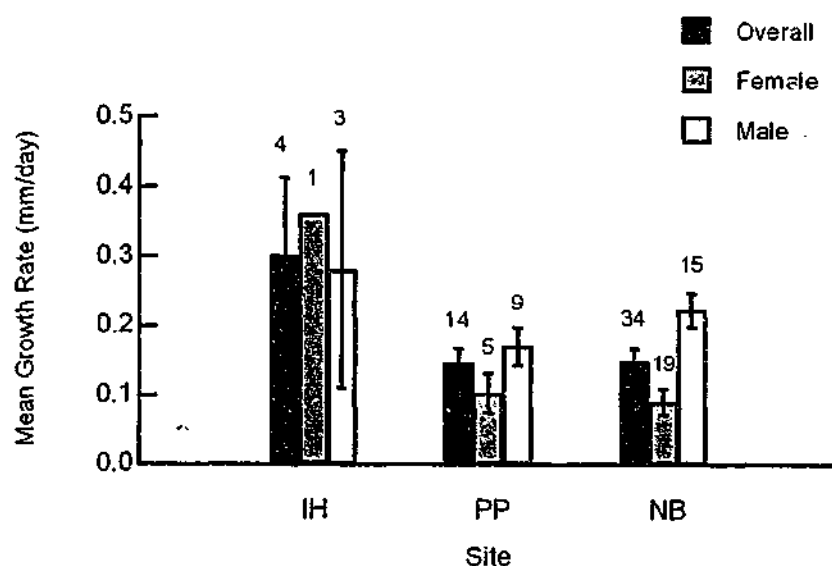


Figure 5.10: Mean (\pm SE) overall growth rate of recaptured *M. freycineti*, and of female and male *M. freycineti*, at Indented Head (IH), Pilot's Pier (PP) and Nepean Bay (NB). Numbers above the bars refer to the number of fish.

Meuschenia hippocrepis

Meuschenia hippocrepis had a mean \pm SE growth rate of 0.12 ± 0.02 mmd^{-1} . This is much lower than that recorded for *Meuschenia freycineti* (see Fig. 5.10). As with *M. freycineti*, growth rates of *M. hippocrepis* varied considerably between individuals, ranging from 0-0.25 mmd^{-1} (Appendix 5.4). Individual *M. hippocrepis* were not sexed, as they are not obviously sexually dichromatic, so it was not possible to examine any differences in growth rates between the sexes. Recaptured *M. hippocrepis* were only at liberty for a short period of time, which was not adequate to determine any seasonal patterns in growth.

Discussion*Analysis of Fish Movement*

Recapture rates for *Meuschenia hippocrepis* and for *Meuschenia freycineti* at both Pilot's Pier and Nepean Bay were comparable to Barrett's (1995a) study examining monacanthid movement on a rocky reef in Tasmania. High recapture rates of these species at their tagging/release sites, coupled with a lack of evidence revealing any movement between reefs, suggest that *M. freycineti* and *M. hippocrepis* may be permanent residents on these reefs. Mark-release-recapture studies have revealed limited movements for a variety of reef fishes, with most individuals being recaptured at or very near their release site (e.g. Parker, 1990; Szedlmayer and Shipp, 1994). Barrett (1995a) also demonstrated that the monacanthids, *Meuschenia australis* and *Penicipelta* (= *Acanthaluteres*) *vittiger*, were permanent residents of a temperate rocky reef in Tasmania, and both species appeared to possess large overlapping home ranges. Behavioural investigations of *M. freycineti* and *M. hippocrepis* were not conducted as part of this study as both species, *M. freycineti* in particular, were not readily observed visually (see Chapter 3). Further research, ideally utilising acoustic tags, may determine whether *M. freycineti* and *M. hippocrepis* patrol home ranges, and if so, the size of these areas.

Reasons for the low recapture rate of *M. freycineti* at Indented Head are not clear. Catch rates of *M. freycineti* decreased dramatically at this site over the period of this study (see Chapter 4), possibly in response to intensive commercial and recreational fishing pressure. It is also possible that *M. freycineti* individuals use the reef at Indented

Head as an intermediate habitat as they migrate between nursery and adult habitats. The reef at Indented Head is close to some of the nursery areas (seagrass beds) used by this species (see Chapter 4) and is located at an intermediate water depth. *M. freycineti* at Indented Head were also smaller than conspecifics at Pilot's Pier and Nepean Bay.

Despite reasonable recapture rates for both *M. freycineti* and *M. hippocrepis*, many tagged fish were not recaptured. When tagged fish are not recaptured, it is generally assumed that they have moved or died. However, the number of fish recaptured can also depend on tag loss and fish behaviour (Sheaves, 1993). Although tag loss was not measured in the field, results from the laboratory study revealed low rates of tag loss (10%) for *M. freycineti*. Despite this, individuals showing evidence of tag loss (i.e. scars) were occasionally caught in the field. Tag loss can occur as a result of the tagging process, particularly in small fish (Ogden and Buckman, 1973), and also through the behaviour of the fish themselves (e.g. scraping their sides along the reef: Ogden and Buckman, 1973; Matthews and Reavis, 1990). No small fish (<150 mm TL) were tagged in this study and all tagged *M. freycineti* swam away rapidly after release. Tagged *M. freycineti* held in the laboratory were provided with concrete blocks for shelter, and none were observed attempting to remove their tags on the blocks. *M. freycineti* individuals were often observed under rock ledges, in crevices or amongst kelp fronds (M. Wheatley pers. obs.), which may reduce their vulnerability to fish traps and recapture. Fish may also become trap shy, leading to reduced recapture rates (Barrett, 1995b). Evidence from recaptures of tagged individuals suggests that adults of *M. freycineti* and *M. hippocrepis* undergo only limited movements. However, many tagged fish were not recaptured, and it was not possible to determine the relative importance of movement, tag loss and fish behaviour in accounting for their whereabouts.

Although there was no evidence to suggest movement by *M. freycineti* and *M. hippocrepis* individuals between reefs, untagged individuals were continually caught at the tagging/release sites throughout the study. There are two possible explanations for this: first, that both *M. freycineti* and *M. hippocrepis* were continually moving between reefs and spending only a short period of time at any particular reef; and second, that not all individuals on these reefs were tagged. Although fish traps set on nearby reefs did not capture any tagged *M. freycineti* or *M. hippocrepis*, trapping on these reefs was

sporadic and catch rates were extremely variable. More consistent trapping on nearby reefs is necessary to fully discount the possibility of movement between reefs, but evidence from a related species, *Meuschenia australis* (Barrett 1995a), suggests that *M. freycineti* and *M. hippocrepis* are unlikely to have home ranges large enough to encompass the different reefs surveyed in this study. Due to the great variability in catch rates, it is quite likely that many *M. freycineti* and *M. hippocrepis* individuals remained untagged at each site. At Nepean Bay, 164 fish were tagged (Table 5.1), which is approximately half the number of leatherjackets tagged in Barrett's (1995a) study on a similar sized reef. Fewer individuals were tagged in this study as tagging effort was divided between three reefs, compared to weekly trapping at one reef in Barrett's (1995a) study. Thus, highly variable catch rates and reduced tagging effort are the most likely explanations for the continual capture of untagged individuals at these reefs, and not movement by *M. freycineti* and *M. hippocrepis* individuals between reefs.

This study revealed no evidence of seasonal movement by either *M. freycineti* or *M. hippocrepis*. Tagged fish were captured throughout the year, and gave no indication of movement away from the reefs. Higher rates of recapture in some months simply reflect increased trapping effort in those months (see Chapter 4). A major drawback in the use of conventional external tags is that there is no measure of movement between tagging and recapture, so recapture at the site of release may result from either limited movement or from homing behaviour (Hilborn, 1990). However, the lack of evidence for seasonal movement, coupled with multiple recaptures of individuals at their release site after varying periods at liberty, further supports the idea that both *M. freycineti* and *M. hippocrepis* are permanent residents on temperate reefs, at least within Port Phillip Bay.

The validity of studies using conventional external tags also relies on the assumption that the recapture of tagged individuals is not influenced by fish size (Kearney, 1988). Fish size can influence recapture success in a number of ways. Tagging can lead to increased mortality in small fish (Ogden and Buckman, 1973), so that only large fish are recaptured. Large fish within traps may also prevent the entry of smaller fish through antagonistic interactions. However, small fish were not tagged as part of this study and all sizes of *M. freycineti* and *M. hippocrepis* tagged were vulnerable to recapture. In addition, most traps containing *M. freycineti* and *M. hippocrepis* held individuals over a

range of sizes, and there was no evidence to suggest that larger individuals prevented entry into the traps of smaller fish.

The large sand patch adjacent to the reef at Nepean Bay did appear to severely restrict the movement of both *M. freycineti* and *M. hippocrepis*, and this result emphasises the importance of taking into account fish-habitat associations when examining fish movement patterns. Both species were continually caught on the reef at Nepean Bay. No *M. hippocrepis*, and only very few *M. freycineti* were trapped on sand only short distances from the reef. Previous studies have also shown that extensive patches of open sand are an effective boundary to movement for many temperate reef fishes (Love, 1980; Jones and Andrew, 1993; Barrett, 1995a). Limited movement over exposed sandy areas has been shown by the monacanthid *Penicipelta* (= *Acanthaluteres*) *vittiger*, but these movements appeared to be restricted to a small number of individuals within the population (Barrett, 1995a). This contrasts with the results of Chapter 4, which suggested that juveniles/sub-adults of *M. freycineti* undertake extensive migrations over bare sand as they move between inshore seagrass beds and offshore reefs. The effectiveness of extensive areas of sand as a barrier to movement may depend on the life history stage of the fishes.

Restricted movement over considerable time periods can have important implications not only for the distribution and abundance of *M. freycineti* and *M. hippocrepis* populations, but also for the management of these species. Given their limited movements and susceptibility to traps (Chapter 3), there is a real potential for local populations of *M. freycineti* and *M. hippocrepis* to be severely depleted by intense fishing pressure. Marine Protected Areas are increasingly being considered as a viable fisheries management option when other methods such as catch restrictions, closed seasons and size limits are not effective. Reefs surrounded by open sand boundaries should be considered in the design and location of Marine Protected Areas, particularly if the area set aside for these parks is quite small, as these boundaries can naturally restrict movements of fish and thus protect them from overfishing (Barrett, 1995a).

Analysis of Growth

Growth rates varied between the two species, with a mean growth rate of 0.12 mmd^{-1} recorded for *M. hippocrepis* and between $0.18\text{--}0.30 \text{ mmd}^{-1}$ for *M. freycineti* at the

different sites. The growth rates of *M. freycineti* at Indented Head (0.30 mmd^{-1}) and *M. hippocrepis* at Nepean Bay (0.12 mmd^{-1}) were calculated from only a small number of individuals, most of which were at liberty for a short period of time, and therefore, must be interpreted with caution. The values recorded for *M. freycineti* at Pilot's Pier and Nepean Bay (0.19 mmd^{-1} and 0.18 mmd^{-1} , respectively) are very similar to the average growth rate recorded for a related species, *Menschenia australis* on a temperate reef in Tasmania (N. Barrett, pers. comm. 2000).

Individual growth rates for both species were highly variable. Growth rates of *M. freycineti* varied between individuals both within and between reefs. Variable growth has been reported for fish at a number of spatial scales, ranging from different sites and/or habitats (Victor and Brothers, 1982; Pitcher, 1992; Sogard, 1992), down to variation within a site or habitat (Beckman *et al.*, 1991; Pitcher, 1992). Differences in growth rates among habitats may arise through variation in important biological or physical parameters such as water temperature, food availability and shelter, which can have a direct or indirect effect on growth rates (Sogard, 1992). In contrast, variations within a location or habitat have been reported to arise from genetic and/or social factors (Chevassus, 1982). The size of a fish at tagging, and the month in which it is tagged, can also influence growth rate (Heinisch and Fable, 1999). Barrett's (1995b) study attributed variable growth rates in monacanthids to habitat variation, genetics, and social interactions. A suitable habitat may be critical for growth in terms of providing adequate food and shelter from predation, and is likely to be particularly important for species that are territorial or that possess small home ranges, encompassing only a single habitat type (Barrett, 1995b). Although there was no evidence to suggest that *M. freycineti* or *M. hippocrepis* move between reefs, observations indicate that they are wide-ranging over the area of a single reef, and as a result, small-scale habitat variation is unlikely to influence growth rates. Genetic and social factors may, however, become important at and around the time of maturity and over subsequent reproductive periods. Growth in monacanthids appears to be very rapid for the first few years, after which it slows appreciably (Barrett, 1995b). This slowing in growth rates may coincide with the onset of maturity. At the time of sexual maturity it is supposed that energy will be diverted from somatic growth to reproduction. Social interactions, particularly during the breeding season (e.g. courting and territory defence), may also impact on the time available for feeding and result in reduced growth. It is possible that the variable

growth rates of *M. freycineti* and *M. hippocrepis* resulted from the tagging of fish at different ages, with younger individuals growing faster than older ones. Length-at-age curves were not calculated for either species, as the removal of individuals for aging would have interfered with the study of movement patterns. In addition, time constraints and problems encountered when attempting to remove otoliths from *M. freycineti* meant that the otoliths were not removed from fishes taken from the Springs for gonad analysis (Chapter 4).

Growth rates may also differ between the sexes. It was not possible to sex *M. hippocrepis* individuals in the field, as they are not obviously dichromatic (Kuitert, 1993). *M. freycineti* was readily sexed in the field, and growth rates were significantly different at Nepean Bay, with females showing slower growth. A similar result was recorded for *Meuschenia australis* in Tasmania (Barrett, 1995b). Although there was no significant difference in growth rates between male and female *M. freycineti* at Pilot's Pier, this analysis was only done with a small number of fish. It is important to note that any difference in growth rates between the sexes may have been confounded with seasonal differences in growth rates. It was not possible to examine seasonal differences in growth, but previous studies have revealed a strong seasonal component to growth, with growth rates tending to decrease over winter, possibly due to decreased water temperatures (Sogard, 1992; Francis, 1994).

It is important in any study of growth based on tagging that the tags do not interfere with growth. Potentially, growth of tagged fish may be reduced by various factors including infection at the point of tag entry (Barrett, 1995b). Although the growth of tagged and untagged *M. freycineti* and *M. hippocrepis* could not be compared using length-at-age data, as aging was not conducted as part of this study, very few recaptured *M. freycineti* or *M. hippocrepis* showed any sign of infection around the tag insertion point. Previous studies demonstrate that the effects of tagging on fish growth rates can vary between species. Tagging did not appear to affect growth rates of gag, *Mycteroperca microlepis*, as there were no physiological effects of tags, and while individual growth rates varied considerably, the rates recorded matched previous studies using length-at-age data (Heinisch and Fable, 1999). In contrast, external tags increased mortality and reduced growth by up to 25% in female sablefish, *Anoplopoma fimbria* between 2-9 years of age, although the growth rates of male fish were unaffected

(McFarlane and Beamish, 1990). Whether the growth of tagged fish is representative of the population will depend on the species, size and sex of fish tagged, and the type of tag used. The potential impact of tags must be acknowledged, and results from studies that utilise conventional tags, should be interpreted with caution. Ideally, information on growth rates collected from tagging should be interpreted in combination with information gained from an analysis of length-at-age data.

Conclusion

Few studies have examined the movement patterns and growth of temperate reef fish, possibly due to the difficulties of sampling during regularly inclement weather and in cold water that frequently has limited visibility. Despite their limitations (see Chapter 2), fish traps are increasingly being used in temperate reef fish studies as they can sample in conditions that are unsuitable for other techniques such as visual surveys (e.g. deep water, low visibility). Traps can be positioned to target specific areas, and allow the movements of fish to be described in considerable detail (Sheaves, 1993; Barret 1995a, b). Further research into the movement patterns and growth of *M. freycineti* and *M. hippocrepis* is necessary, particularly with respect to the age of individuals on reefs and to their home range size. Nevertheless, these results provide some insight into the scale of movements and growth of *M. freycineti* and *M. hippocrepis* on rocky reefs within Port Phillip Bay. It is important to note that because only larger individuals (i.e. >150 mm TL) were tagged, the high degree of reef residency described in this chapter relates only to fish within this size range, and movement patterns of smaller individuals appear to be substantially different (see Chapter 4). This highlights the need for future studies to consider the movement patterns of individuals over their entire lifespan.

Summary

Movement and growth have the potential to significantly affect the distribution and abundance of temperate reef fishes. This study revealed considerable variation in the growth rates of both *M. freycineti* and *M. hippocrepis* individuals. Differences were also recorded in the growth rates of *M. freycineti* between the sites. There was no evidence to suggest any movement by individuals between reefs, and both *M. freycineti* and *M. hippocrepis* appeared to be permanent reef residents. However, this pattern of

limited movement refers only to larger individuals, and smaller recruits and/or juveniles appear to undergo more substantial movements (see Chapter 4).

Detailed studies of movement are also important for fisheries management. The limited movements of both *M. freycineti* and *M. hippocrepis* observed in this study can have important management implications in terms of the rapid depletion of local populations, particularly as these species are readily caught by fish traps. Movements of *M. freycineti* and *M. hippocrepis* appeared to be limited in part by the natural sand barrier present at Nepean Bay. This result has important implications for management, particularly with respect to Marine Protected Areas. Sand barriers need to be considered in the establishment of Marine Protected Areas as the areas of reef set aside for these parks are often quite small. By restricting fishing even on small reefs isolated by sand boundaries, we may more effectively protect many temperate fish populations from overfishing.

Appendix 5.1: Growth rate information obtained from recaptures of tagged *M. freycineti* released and recaptured at Indented Head. Tag number, sex, date tagged (T), total length at tagging TL (T), recapture number, date recaptured (R), total length at recapture TL (R), length change and growth rate are provided. All lengths are in mm. N/A refers to individuals that were at liberty <30 days, or to errors in measurement.

Tag no.	Sex	Date (T)	TL (T)	Recap. no.	Date (R)	TL (R)	Length change	Growth rate
130	F	29.1.98	255	1	16.4.98	282	27	0.36 mm d^{-1}
48	M	30.4.97	247	1	14.5.97	246	-1	N/A
131	M	29.1.98	255	1	7.5.98	300	45	0.46 mm d^{-1}
241	M	24.9.98	316	1	28.10.98	328	12	0.35 mm d^{-1}
289	M	7.5.97	289	1	12.1.99	296	7	0.03 mm d^{-1}

Appendix 5.2: Growth rate information obtained from recaptures of tagged *M. freycineti* released and recaptured at Pilot's Pier. Tag number, sex, date tagged (T), total length at tagging TL (T), recapture number, date recaptured (R), total length at recapture TL (R), length change and growth rate are provided. All lengths are in mm. N/A refers to individuals that were at liberty <30 days, or to errors in measurement.

Tag no.	Sex	Date (T)	TL (T)	Recap. no.	Date (R)	TL (R)	Length change	Growth rate
3	F	3.9.97	242	1	10.9.97	242	0	N/A
				2	30.9.97	241	-1	N/A
4	F	3.9.97	242	1	30.9.97	245	3	N/A
46	F	13.5.97	262	1	20.5.97	261	-1	N/A
52	F	28.4.97	263	1	20.5.97	277	14	N/A
60	F	4.4.97	280	1	13.5.97	287	7	0.18 mm d^{-1}
67	F	4.4.97	289	1	13.5.97	290	1	0.03 mm d^{-1}
			290	2	30.9.97	303	13	0.09 mm d^{-1}
69	F	22.4.97	307	1	13.5.97	311	4	N/A
				2	21.9.98	340	29	0.06 mm d^{-1}
71	F	10.4.97	275	1	28.4.97	275	0	N/A
				2	21.11.97	306	31	0.15 mm d^{-1}
78	F	24.3.97	293	1	4.4.97	292	-1	N/A
				2	28.4.97	295	3	0.13 mm d^{-1}
				3	9.5.97	302	7	N/A
				4	20.5.97	296	1	0.27 mm d^{-1}
92	F	24.3.97	276	1	4.4.97	280	4	N/A
44	M	13.5.97	262	1	9.1.98	310	48	0.20 mm d^{-1}
59	M	4.4.97	305	1	20.5.97	317	12	0.26 mm d^{-1}
			317	2	30.9.97	335	18	0.14 mm d^{-1}
72	M	10.4.97	318	1	20.5.97	326	8	0.20 mm d^{-1}
81	M	24.3.97	301	1	4.4.97	313	12	N/A
				2	10.4.97	305	4	N/A
				3	22.4.97	305	0	N/A
				4	28.4.97	305	0	0.00 mm d^{-1}
				5	13.5.97	314	9	N/A
				6	20.5.97	313	-1	N/A
82	M	24.3.97	273	1	20.2.98	300	27	0.08 mm d^{-1}
83	M	24.3.97	265	1	4.4.97	266	1	N/A
84	M	24.3.97	255	1	22.4.97	261	6	N/A
				2	28.4.97	264	3	0.50 mm d^{-1}

Appendix 5.2: cont.

Tag no.	Sex	Date (T)	TL (T)	Recap. no.	Date (R)	TL (R)	Length change	Growth rate
				3	29.8.97	283	19	0.21 mm d^{-1}
				4	3.9.97	281	-2	N/A
				5	10.9.97	285	4	0.57 mm d^{-1}
99	M	21.3.97	334	1	10.4.97	340	6	N/A
112	M	20.2.98	293	1	16.3.98	300	7	N/A
202	M	15.1.99	298	1	27.5.99	335	37	0.28 mm d^{-1}
255	M	18.8.98	323	1	15.1.99	327	4	0.03 mm d^{-1}
259	M	24.7.98	232	1	11.9.98	239	7	0.14 mm d^{-1}

Appendix 5.3: Growth rate information obtained from recaptures of tagged *M. freycineti* released and recaptured at Nepean Bay. Tag number, sex, date tagged (T), total length at tagging TL (T), recapture number, date recaptured (R), total length at recapture TL (R), length change and growth rate are provided. All lengths are in mm. N/A refers to individuals that were at liberty <30 days, or to errors in measurement.

Tag no.	Sex	Date (T)	TL (T)	Recap. no.	Date (R)	TL (R)	Length change	Growth rate
11	F	24.5.97	245	1	29.10.97	259	14	0.09 mm d^{-1}
				2	7.11.97	262	3	0.33 mm d^{-1}
				3	13.11.97	264	2	0.33 mm d^{-1}
17	F	24.5.97	283	1	17.9.97	284	1	0.01 mm d^{-1}
				2	23.10.97	285	1	0.03 mm d^{-1}
				3	29.10.97	285	0	0.00 mm d^{-1}
				4	13.11.97	290	5	0.33 mm d^{-1}
				5	24.7.98	306	16	0.06 mm d^{-1}
				6	6.11.98	310	4	0.04 mm d^{-1}
21	F	24.5.97	279	1	5.2.98	291	12	0.05 mm d^{-1}
119	F	5.2.98	288	1	17.6.98	304	16	0.12 mm d^{-1}
				2	6.11.98	309	5	0.04 mm d^{-1}
				3	22.2.99	310	1	0.13 mm d^{-1}
122	F	5.2.98	250	1	6.11.98	279	29	0.11 mm d^{-1}
125	F	5.2.98	232	1	20.2.98	250	18	N/A
164	F	13.11.97	290	1	5.2.98	286	-4	N/A
				2	22.4.98	296	10	0.13 mm d^{-1}
				3	17.6.98	303	7	0.13 mm d^{-1}
166	F	13.11.97	300	1	9.12.97	298	-2	N/A
173	F	7.11.97	260	1	9.12.97	265	5	0.16 mm d^{-1}
				2	5.2.98	266	1	0.02 mm d^{-1}
				3	11.9.98	288	22	0.10 mm d^{-1}
175	F	7.11.97	295	1	13.11.97	293	-2	N/A
177	F	29.10.97	241	1	7.11.97	242	1	N/A
178	F	29.10.97	276	1	13.11.97	275	-1	N/A
				2	9.12.97	275	0	0.00 mm d^{-1}
181	F	29.10.97	308	1	7.11.97	311	3	N/A
				2	13.11.97	311	0	N/A
186	F	23.10.97	320	1	29.10.97	315	-5	N/A
				2	7.11.97	315	0	N/A
				3	13.11.97	314	-1	N/A
				4	9.12.97	317	3	0.12 mm d^{-1}
187	F	23.10.97	281	1	29.10.97	286	5	N/A
				2	7.11.97	281	-5	N/A

Appendix 5.3: cont.

Tag no.	Sex	Date (T)	TL (T)	Recap. no.	Date (R)	TL (R)	Length change	Growth rate
190	F	9.10.97	270	1	23.10.97	265	-5	N/A
				2	29.10.97	272	2	N/A
				3	13.11.97	268	-4	N/A
194	F	17.9.97	304	1	9.10.97	305	1	N/A
				2	29.10.97	302	-3	N/A
				3	7.11.97	303	1	0.11 mm d ⁻¹
195	F	17.9.97	272	4	22.4.98	304	1	0.01 mm d ⁻¹
				1	23.10.97	277	5	0.14 mm d ⁻¹
				2	29.10.97	276	-1	N/A
				3	7.11.97	281	5	0.56 mm d ⁻¹
				4	13.11.97	286	5	0.83 mm d ⁻¹
196	F	17.9.97	262	5	22.4.98	344	58	0.36 mm d ⁻¹
				6	17.6.98	360	16	0.29 mm d ⁻¹
				1	9.12.97	265	3	0.04 mm d ⁻¹
197	F	17.9.97	236	1	23.10.97	242	6	0.17 mm d ⁻¹
198	F	17.9.97	280	1	9.10.97	287	7	N/A
				2	23.10.97	284	-3	N/A
				3	13.11.97	286	2	0.10 mm d ⁻¹
				4	9.12.97	286	0	0.00 mm d ⁻¹
200	F	17.9.97	278	1	7.11.97	278	0	0.00 mm d ⁻¹
252	F	11.9.98	258	1	17.11.98	263	5	0.07 mm d ⁻¹
				2	22.2.99	260	-3	N/A
				3	25.3.99	278	18	0.58 mm d ⁻¹
277	F	17.6.98	277	1	22.2.99	295	18	0.07 mm d ⁻¹
284	F	17.6.98	315	1	11.9.98	317	2	0.02 mm d ⁻¹
295	F	22.4.98	246	1	17.6.98	251	5	0.09 mm d ⁻¹
313	F	22.2.99	260	1	25.3.99	266	6	0.19 mm d ⁻¹
				2	15.4.99	272	6	0.29 mm d ⁻¹
329	F	22.2.99	280	1	8.6.99	286	6	0.06 mm d ⁻¹
20	M	24.5.97	340	1	9.12.97	395	55	0.28 mm d ⁻¹
121	M	5.2.98	251	1	22.4.98	276	25	0.33 mm d ⁻¹
				2	6.11.98	308	32	0.16 mm d ⁻¹
123	M	5.2.98	405	1	22.4.98	430	25	0.33 mm d ⁻¹
152	M	9.12.97	317	1	5.2.98	323	6	0.10 mm d ⁻¹
153	M	9.12.97	263	1	22.4.98	306	43	0.32 mm d ⁻¹
167	M	7.11.97	310	1	9.1.98	318	8	0.13 mm d ⁻¹
184	M	29.10.97	296	1	23.1.98	318	22	0.25 mm d ⁻¹
185	M	23.10.97	284	1	29.10.97	285	1	N/A
				2	7.11.97	283	-2	N/A
				3	13.11.97	285	2	N/A
				4	9.12.97	290	5	0.19 mm d ⁻¹
189	M	23.10.97	321	1	29.10.97	324	3	N/A
				2	7.11.97	321	-3	N/A
				3	13.11.97	321	0	N/A
				4	9.12.97	331	10	0.38 mm d ⁻¹
				5	7.1.98	340	9	0.31 mm d ⁻¹
193	M	17.9.97	283	1	23.10.97	287	4	0.11 mm d ⁻¹
218	M	5.1.99	430	1	25.3.99	460	30	0.38 mm d ⁻¹
238	M	22.10.98	318	1	17.11.98	324	6	N/A
239	M	22.10.98	327	1	6.11.98	333	6	N/A
				2	17.11.98	336	3	N/A
254	M	11.9.98	324	1	5.1.99	350	26	0.22 mm d ⁻¹
282	M	17.6.98	372	1	24.7.98	378	6	0.16 mm d ⁻¹
291	M	22.4.98	310	1	17.6.98	326	16	0.29 mm d ⁻¹
				2	15.4.99	367	41	0.14 mm d ⁻¹
315	M	22.2.99	260	1	25.3.99	272	12	0.39 mm d ⁻¹
				2	6.5.99	282	10	0.24 mm d ⁻¹

Appendix 5.4: Growth rate information obtained from recaptures of tagged *M. hippocrepis* released and recaptured at Nepean Bay. Tag number, sex, date tagged (T), total length at tagging TL (T), recapture number, date recaptured (R), total length at recapture TL (R), length change and growth rate are provided. All lengths are in mm. N/A refers to individuals that were at liberty <30 days, or to errors in measurement.

Tag no.	Date (T)	TL (T)	Recap. no.	Date (R)	TL (R)	Length change	Growth rate
171	11.9.98	192	1	6.11.98	205	13	0.23 mm d ⁻¹
245	11.9.98	191	1	6.11.98	205	14	0.25 mm d ⁻¹
246	11.9.98	161	1	6.11.98	170	9	0.16 mm d ⁻¹
256	18.8.98	175	1	6.11.98	185	10	0.13 mm d ⁻¹
270	24.7.98	210	1	11.9.98	210	0	0.00 mm d ⁻¹
272	17.6.98	191	1	11.9.98	197	6	0.07 mm d ⁻¹
278	17.6.98	238	1	11.9.98	244	6	0.07 mm d ⁻¹
281	17.6.98	209	1	18.8.98	213	4	0.06 mm d ⁻¹
			2	11.9.98	214	1	0.04 mm d ⁻¹
283	17.6.98	193	1	11.9.98	201	8	0.09 mm d ⁻¹
285	17.6.98	200	1	11.9.98	213	13	0.15 mm d ⁻¹
326	22.2.99	193	1	25.3.99	199	6	0.19 mm d ⁻¹
			2	8.6.99	208	9	0.12 mm d ⁻¹
			3	2.9.99	212	4	0.05 mm d ⁻¹

Chapter 6

The Influence of Habitat and Water Depth on the Distribution and Size Structure of Temperate Fish Assemblages

Introduction

The life cycles of many reef fishes are characterised by a dispersive (planktonic) larval stage followed by a relatively sedentary (benthic) adult stage. Variation in the abundance of adult fish populations will be affected by the survivorship of individuals at all stages throughout this life cycle (Robertson *et al.*, 1993; Doherty and Fowler, 1994; Carr and Hixon, 1995). The transition from the water column to the benthos is considered to be a critical period in development (Steiner *et al.*, 1982), and settlement by larvae to particular habitats may increase their chances of survival. Habitat selection by settling fish larvae has been widely demonstrated for both tropical (Shulman, 1985; Doherty, 1991) and temperate reef fish species (Carr, 1991; Lincoln Smith *et al.*, 1991), and may occur in response to food and shelter availability (Levin, 1994), competition (Jones, 1987a) and/or predation (Jones, 1991).

The role of shallow water seagrass beds as important nursery areas for many reef fish species has been widely recognised (Bell and Pollard, 1989; Bell and Worthington, 1993). The use of seagrass beds by juveniles of some reef fish species is generally attributed to increased food availability and a reduced risk of predation (Orth *et al.*, 1984). However, juveniles of other reef fish species do not utilise seagrass beds, and instead their larvae appear to settle directly onto reefs. Evidence from Chapter 4 suggests that *Meuschenia freycineti* individuals settle to seagrass beds, but that *Meuschenia hippocrepis* recruits do not utilise these beds. Other evidence (i.e. the presence of small juveniles; M. Wheatley pers. obs.) suggests that *M. hippocrepis* recruits directly to reefs. As seagrass beds tend to occur in shallow waters and reefs in deeper waters, it is not known whether these settlement patterns reflect specific habitat or depth preferences. Many species also demonstrate strong size-specific partitioning in their distribution by depth irrespective of habitat, with juveniles tending to be more abundant in shallow waters (Jones, 1984a; Harmelin-Vivien *et al.*, 1995).

Changing habitat and/or depth requirements are evident during the development of many reef fishes (Jones, 1984a; McCormick, 1989; Love *et al.*, 1991; Eggleston, 1995). With increasing body size, some species migrate from seagrass beds to reefs (Chapter 4; Gillanders, 1997a), and may benefit from the associated changes in resources (Eggleston, 1995). Many fish undergo ontogenetic feeding shifts, which are often coupled with shifts in habitat use. For example, Gillanders (1995b) found that the diet of recruits/small juveniles of *Achoerodus viridis* in seagrass beds was dominated by benthic crustaceans (tanaids), while reef-based adults fed primarily on mussels and urchins. In addition, shelter requirements may change with growth, and the juvenile habitat (e.g. seagrass bed) may no longer provide adequate shelter for larger individuals. Fish may also become less vulnerable to predation as they grow, allowing them to exploit water depths or alternative habitats that are too risky for smaller individuals (Ruiz *et al.*, 1993). Patterns of increasing fish size with increasing water depth may also reflect migration to deeper waters, as individuals may benefit from extended lives due to a lower metabolism at lower water temperatures (i.e. greater water depths) (Macpherson and Duarte, 1991).

During earlier investigations I recorded distinct differences in the distribution and size structure of *M. freycineti* and *M. hippocrepis* populations in seagrass and reef habitats in Port Phillip Bay (Chapter 4). While individuals of *M. freycineti* settle to inshore seagrass beds before migrating to reefs at a later stage, indirect evidence suggests that larvae of *M. hippocrepis* settle directly to reefs. Extensive surveys of shallow water habitats (unvegetated sand, seagrass beds and rubble reefs) in Port Phillip Bay have revealed no evidence to suggest that *M. hippocrepis* recruit to shallow water habitats (Jenkins *et al.*, 1993), while recruits/juveniles of *M. freycineti* are not observed in deep water habitats (M. Wheatley pers. obs.). Both habitat type (seagrass and reef) and water depth are likely to influence the distribution, abundance and size structure of *M. freycineti* and *M. hippocrepis*. Very few studies have simultaneously examined the influence of habitat type and water depth in structuring fish populations (but see Lonzarich and Quinn, 1995).

The aim of this study was to determine the influence of water depth and habitat type (seagrass and reef) on the distribution and size structure of temperate fish assemblages and populations, and in particular, populations of *M. freycineti* and *M. hippocrepis*, in

Port Phillip Bay. A secondary aim was to further examine ontogenetic changes in the distribution of *M. freycineti* between seagrass and reef habitats. Artificial seagrass beds and artificial reefs were set up at two water depths to test the specific null hypotheses that: (i) there were no differences in the fish assemblages and abundances of individual species between habitats (seagrass and reef) and depths (shallow and deep); and (ii) there were no differences in the size frequency distributions of individual species, specifically *M. freycineti* and *M. hippocrepis*, between habitats (seagrass and reef) and depths (shallow and deep).

Methods

Study Sites

This study was done at two sites within Port Phillip Bay: Grassy Point and Indented Head (Fig. 6.1). Both sites have inshore shallow seagrass (*Heterozostera tasmanica*) beds and offshore rocky reefs. These sites were surveyed in earlier investigations that examined spatial variation in fish assemblages on rocky reefs (Chapter 3), and the distribution, abundance and size structure of *Meuschenia freycineti* and *Meuschenia hippocrepis* in seagrass and reef habitats (Chapter 4). Refer to Chapter 2 for a detailed description of the study sites.

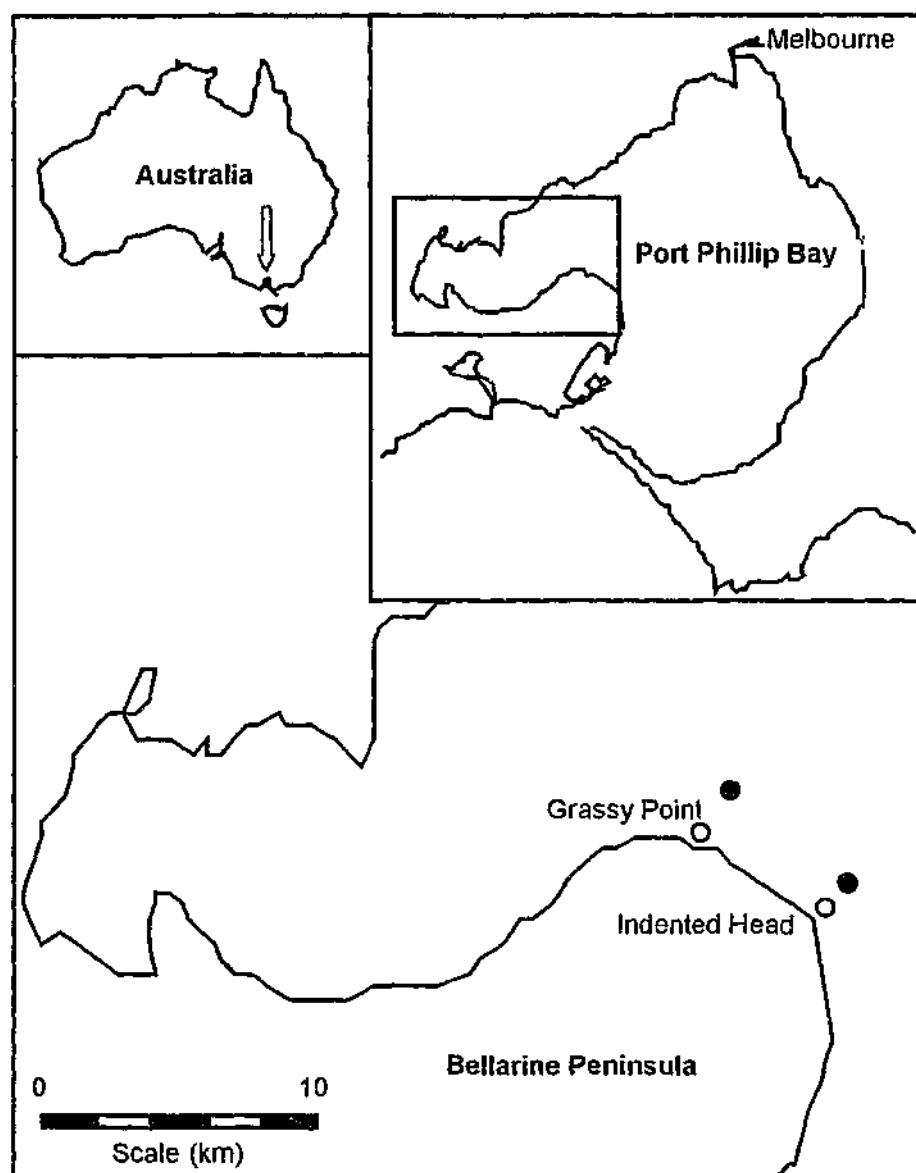


Figure 6.1: Location of the study sites within Port Phillip Bay. Insets are the location of the Bellarine Peninsula in Port Phillip Bay, and of Port Phillip Bay on the Australian coast. Open circles = shallow sites; closed circles = deep sites.

The Influence of Habitat and Water Depth on the Distribution and Size Structure of Fish Assemblages and Populations

A field experiment examined the influence of habitat type and water depth on the distribution and size structure of temperate fish assemblages and populations, in particular populations of *Meuschenia freycineti* and *Meuschenia hippocrepis*. At each site, artificial reefs and artificial seagrass beds were set up at two depths: shallow (approx. 0.5 m below mean low water spring at both sites) and deep (2-3 m at Indented Head and 5 m at Grassy Point). It was necessary to establish the experimental habitats

at different deep depths because the natural reefs at the two sites occurred at different depths (see Chapter 2). At each depth, there were five replicates of each habitat type (Fig. 6.2).

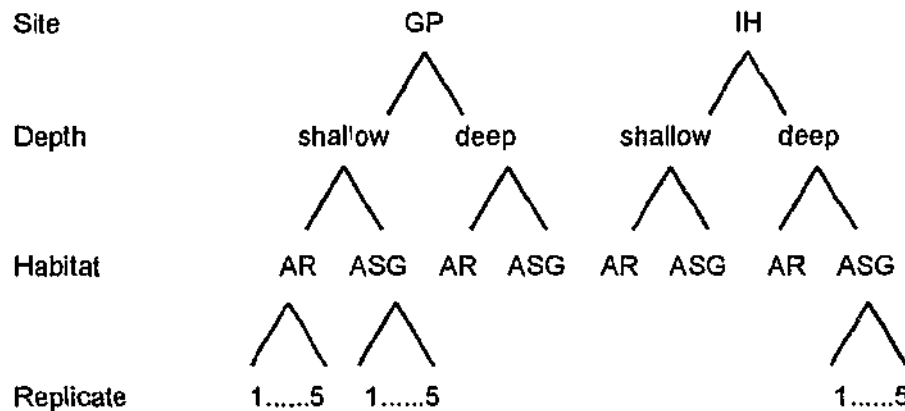


Figure 6.2: Outline of the design for the field experiment. GP = Grassy Point, IH = Indented Head, AR = artificial reef and ASG = artificial seagrass.

Artificial seagrass beds were constructed from galvanised steel mesh grids measuring 240 cm × 100 cm. The grid size was 10 cm × 5 cm, providing 480 cross-points for the attachment of artificial seagrass. Green polypropylene 'twirling' ribbon was used to simulate *Heterozostera tasmanica* blades. Eight strips of ribbon (width 0.5 cm and length 100 cm) were tied to each cross-point, forming individual bunches, each with 16 leaves approximately 45 cm long (Plate 6.1). These beds approximated the leaf morphology and density of natural *H. tasmanica* beds in the area (Jenkins and Sutherland, 1997).

Each artificial reef was built using 15 haphazardly arranged concrete blocks (Plate 6.2). Five blocks of three different sizes were used to construct each reef, providing a range of crevice sizes. All blocks measured 390 mm length × 190 mm width, but height and crevice size varied between the three block types: height = 190 mm, 140 mm and 90 mm, and crevice size = 130 mm × 150 mm, 90 mm × 150 mm and 40 mm × 150 mm, respectively. Each artificial reef covered approximately the same volume as an artificial seagrass bed.

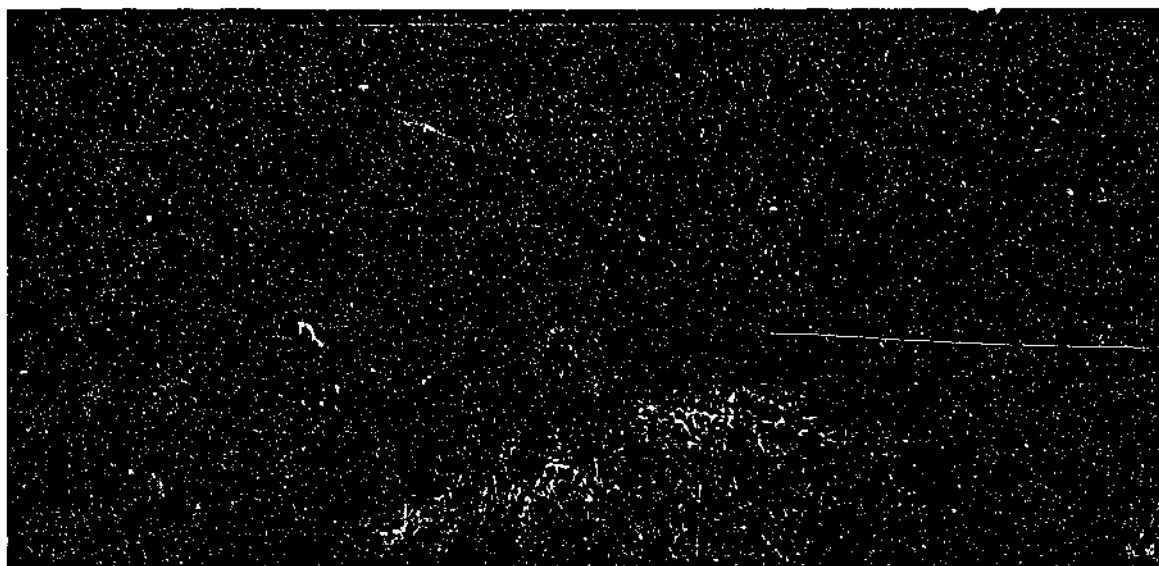


Plate 6.1: Artificial seagrass bed at the deep depth at Indented Head.

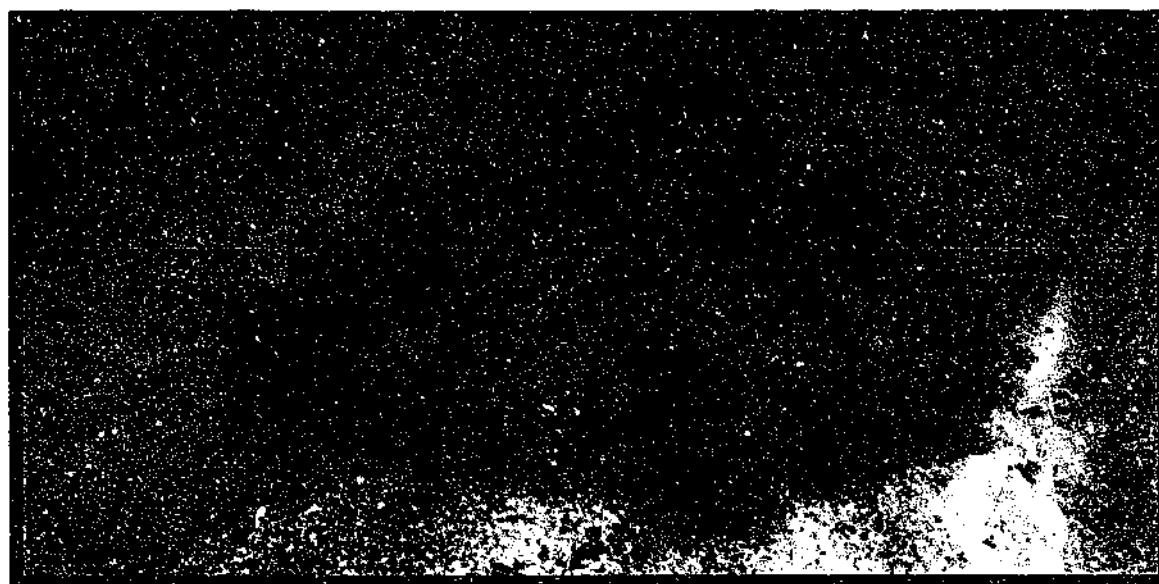


Plate 6.2: Artificial reef at the deep depth at Grassy Point.

Initially the experimental habitats were set up on unvegetated sand approximately 20 m from the nearest natural seagrass or reef habitat (water visibility rarely exceeded 5 m at these sites). Despite a successful pilot study trialing artificial reefs on sand at numerous sites including Indented Head and Grassy Point during the previous summer, artificial reefs at the shallow sites were buried by sand within days of setting up the current experiment. It was necessary to place the experimental habitats directly onto natural seagrass beds. This was possible at both depths at Indented Head, but only at the shallow depth at Grassy Point, as there was no natural *H. tasmanica* bed in the deep area at Grassy Point. Experimental reefs and seagrass beds were placed directly on to sand at the deep site at Grassy Point. Artificial reefs and artificial seagrass beds were haphazardly arranged and separated by at least 10 m.

Experimental habitats were sampled approximately fortnightly when possible from mid January to early May 1999. Over this period, the habitats at Indented Head were surveyed on seven occasions (3.2.99, 19.2.99, 1.3.99, 17.3.99, 30.3.99, 7.4.99 and 4.5.99), and at Grassy Point on six occasions (18.1.99, 19.2.99, 1.3.99, 30.3.99, 7.4.99 and 4.5.99). It was not possible to survey both artificial reefs and artificial seagrass beds using the same method. The experimental habitats were too small to survey using fish traps, and a pilot study trialing visual surveys of the artificial seagrass beds showed very limited success (<10% of the fish caught within a seine net were observed visually).

Artificial seagrass beds were sampled with a 6 m long seine net, with a 2.4 m drop and a mesh size of 1 mm. Short (1 m long) ropes were attached to each end of the seine net, and shallow artificial seagrass beds were sampled by encircling the habitat within the net and hauling the net over the bed. The net was then lifted into a plastic bin, walked into shore and sorted. All fish caught were recorded, and the total length (TL) of all individuals except pipefish (Family: Syngnathidae) was measured. Deep seagrass beds were sampled in a similar manner, except that two divers encircled the bed with the net and recorded all fish caught and measured the total length of all individuals except pipefish underwater. Pipefish were often extremely abundant and it is difficult to estimate their length in the field, particularly underwater. At both depths, all individuals were returned to the artificial seagrass bed as soon as possible after counting and/or measuring.

At both depths, each artificial reef was surveyed visually by a single SCUBA diver, using a five minute timed count (one diver haphazardly surveyed three reefs and the second diver the remaining two reefs). Each diver swam slowly around the entire reef, lifting blocks if necessary to observe any fish hidden within crevices or between blocks. Despite the cryptic nature of many species, five minutes was ample time to thoroughly search each reef. All fish were identified and their total length estimated and recorded.

Fish Surveys of Nearby Natural Seagrass and Reef Habitats

Surveys of natural seagrass beds and reefs at Indented Head and Grassy Point were done to determine whether the patterns observed on the experimental habitats were representative of natural habitats. Seagrass surveys were conducted approximately monthly over the period of the experiment, although surveys were not conducted in January 1999 due to adverse weather conditions and time constraints. Fine-mesh seine nets were used to sample both natural and experimental seagrass beds. Natural reefs were sampled only sporadically over the experimental period due to poor weather conditions and time constraints. It was not possible to survey both natural and experimental habitats on the same day, and suitable diving days over the study period were limited. In addition, although the field experiment was designed to examine the importance of habitat and depth in structuring fish assemblages as a whole, the main focus was on *Meuschenia* spp., which are more accurately surveyed using fish traps than visual surveys (see Chapter 3). Fish traps also have the advantage of being able to be set in conditions unsuitable for diving. Hence, the natural reefs were surveyed using fish traps and the experimental reefs were surveyed visually, as their small size precluded sampling using traps.

Surveys of the natural seagrass beds and reefs at Grassy Point and Indented Head also formed part of an investigation examining the distribution, abundance and size structure of *Meuschenia freycineti* and *Meuschenia hippocrepis* in seagrass beds and on rocky reefs in Port Phillip Bay (Chapter 4). Refer to Chapter 2 for a full description of the methods used to survey the natural habitats.

Statistical Analyses

Due to differences in the location of the experimental habitats between the sites (i.e. experimental habitats on natural seagrass at Indented Head, and natural seagrass and sand at Grassy Point), all analyses were done separately for each site.

Non-metric Multi-Dimensional Scaling (NMDS) was used to graphically represent differences in the fish assemblages between depths and habitats. Ordinations were plotted separately for each sampling time. Two-factor crossed Analyses of Similarity (ANOSIMs) were used to test the null hypothesis that there were no differences in fish assemblages between depths and between habitats at each sampling time for each site.

Repeated measures Analyses of Variance (ANOVAs) compared the number of species, total abundance of all fish, and the abundance of the most widespread species between habitats and depths, with time as the "within-subjects" factor (Winer *et al.*, 1991).

Results of the repeated measures ANOVAs were interpreted using Greenhouse-Geiser adjusted *P*-values. ANOVA tables of these results also present the Greenhouse-Geiser epsilon statistic, which is used to adjust the probability value when compound symmetry fails, thus increasing the reliability of the results (the closer the value to one, the more reliable the analysis). Analyses incorporating both depths and both habitat types were possible only for the number of species and the total abundance of all fish, as numbers of individual species were too small and variable, and thus violated ANOVA assumptions. Some species were, however, only recorded on one habitat type, and in such cases, repeated measures analyses were used to compare abundances between depths only. In cases where there was no significant interaction with time, but there was a significant depth x habitat interaction, the cause of the interaction was examined using simple main effects contrasts, comparing habitats for each depth separately.

Results

Fish Assemblages

There was considerable overlap in the species composition of the fish assemblages recorded on the experimental habitats at Grassy Point and Indented Head, although some species were only recorded at one site, albeit in small numbers (e.g. *Gymnapistes marmoratus* and *Trygonorrhina guanierius*) (Tables 6.1 and 6.2). However, the

abundance of many species differed markedly between sites. For example, *Stigmatopora argus* and *Vincentia conspersa* were more abundant at Grassy Point, while *Acanthaluteres spilomelanurus* was more abundant at Indented Head (Tables 6.1 and 6.2).

The NMDS plots and ANOSIMs comparing fish assemblages among depths and habitats revealed significant differences between depths and between habitat types on each sampling occasion at Grassy Point (Fig. 6.3; Table 6.3). The ordination plots do, however, show differences in the spread of experimental units between sampling times (Fig. 6.3). For example, plots of data from 19.2.99, 30.3.99 and 4.5.99 show distinct groupings of replicate units into each depth and habitat combination, while data from 1.3.99 show no clear pattern (Fig. 6.3). At Indented Head, significant differences in the fish assemblages between habitats were recorded on all but one occasion (1.3.99), and significant differences between water depths were recorded on 19.2.99, 1.3.99, 17.3.99 and 7.4.99 (Fig. 6.4; Table 6.3). As with Grassy Point, ordination plots for Indented Head reveal differences in the spread of replicate units between sampling times, showing clear clustering into habitats and depths on some occasions (e.g. 7.4.99), but not at other times (e.g. 1.3.99) (Fig. 6.4).

Table 6.1: Fish species recorded on the experimental habitats at Grassy Point (January – May 1999). Total number of fish recorded on each habitat type. Numbers in brackets refer to the mean number of fish per habitat unit. Data are pooled over sampling times. ASG = artificial seagrass and AR = artificial reef.

Taxa	Grassy Point			
	shallow ASG	AR	deep ASG	AR
Rhinobatidae				
<i>Trygonorrhina guaneri</i>	0	2(0.07)	0	0
Urolophidae				
<i>Urolophus gigas</i>	1(0.03)	0	0	0
Syngnathidae				
<i>Stigmatopora argus</i>	665(22.17)	0	0	0
<i>Stigmatopora nigra</i>	1(0.03)	0	0	0
<i>Urocampus carinirostris</i>	1(0.03)	0	0	0
Aploactinidae				
<i>Aploactisoma milesii</i>	0	0	1(0.03)	0
Platycephalidae				
<i>Platycephalus laevigatus</i>	0	0	1(0.03)	0
Apogonidae				
<i>Siphaenia cephalotes</i>	4(0.13)	0	2(0.07)	0
<i>Vincentia conspersa</i>	0	0	2(0.07)	80(2.76)
Mullidae				
<i>Upeneichthys vlamingii</i>	0	0	2(0.07)	4(0.14)
Enoplosidae				
<i>Enoplosus armatus</i>	14(0.47)	1(0.03)	6(0.2)	0
Odacidae				
<i>Neoodax balteatus</i>	6(0.2)	3(0.1)	38(1.27)	10(0.35)
Blenniidae				
<i>Parablennius tasmanianus</i>	0	38(1.27)	0	0
Clinidae				
Unidentified clinidae	18(0.6)	21(0.7)	17(0.57)	5(0.17)
Callionymidae				
<i>Eocallionymus papilio</i>	0	0	0	5(0.17)
Gobiidae				
Unid gobiidae	0	0	1(0.03)	1(0.03)
Monacanthidae				
<i>Acanthaluteres spilomelanurus</i>	18(0.6)	0	37(1.23)	1(0.03)
<i>Acanthaluteres vittiger</i>	1(0.03)	0	11(0.37)	0
<i>Brachaluteres jacksonianus</i>	12(0.4)	0	13(0.43)	7(0.24)
<i>Méuschenia freycineti</i>	6(0.2)	0	0	0
Diodontidae				
<i>Diodon nictemerus</i>	2(0.07)	1(0.03)	0	0
Unidentified fish	0	6(0.2)	0	1(0.03)
Total No. Taxa	13	6	12	8

See Appendix 1 in Chapter 3 for species authorities

Table 6.2: Fish species recorded on the experimental habitats at Indented Head (January – May 1999). Total number of fish recorded on each habitat type. Numbers in brackets refer to the mean number of fish per habitat unit. Data are pooled over sampling times. ASG = artificial seagrass and AR = artificial reef.

Taxa	Indented Head			
	shallow ASG	AR	deep ASG	AR
Syngnathidae				
<i>Stigmatopora argus</i>	48(2)	0	9(0.26)	0
Scorpaenidae				
<i>Gymnapistes marmoratus</i>	3(0.13)	1(0.03)	0	0
Apogonidae				
<i>Siphaemia cephalotes</i>	5(0.21)	0	52(1.49)	0
<i>Vincentia conspersa</i>	0	0	0	12(0.34)
Mullidae				
<i>Upeneichthys vlamingii</i>	0	0	2(0.06)	0
Enoplosidae				
<i>Enoplosus armatus</i>	31(1.29)	0	0	0
Cheilodactylidae				
<i>Dactylophora nigricans</i>	5(0.21)	0	1(0.03)	1(0.03)
Labridae				
<i>Notolabrus tetricus</i>	0	1(0.03)	0	3(0.09)
Odacidae				
<i>Neodax balteatus</i>	1(0.04)	0	7(0.2)	0
Blenniidae				
<i>Parablennius tasmanianus</i>	0	6(0.17)	0	39(1.11)
Clinidae				
Unidentified clinidae	10(0.42)	17(0.49)	5(0.14)	18(0.51)
Callionymidae				
<i>Eocallionymus papilio</i>	0	0	0	6(0.17)
Gobiidae				
Unid gobiidae	0	0	0	1(0.03)
Monacanthidae				
<i>Acanthaluteres spilomelanurus</i>	14(0.58)	0	100(2.86)	0
<i>Acanthaluteres vittiger</i>	0	0	12(0.34)	0
<i>Brachaluteres jacksonianus</i>	0	0	18(0.51)	3(0.09)
<i>Eubalichthys gunnii</i>	0	0	0	1(0.03)
<i>Meuschenia freycineti</i>	5(0.21)	6(0.17)	0	0
Tetraodontidae				
<i>Tetractenos glaber</i>	0	1(0.03)	0	0
Diodontidae				
<i>Diodon nictemerus</i>	0	1(0.03)	0	0
Unidentified fish	0	3(0.09)	0	3(0.09)
Total No. Taxa	9	7	9	9

See Appendix 1 in Chapter 3 for species authorities

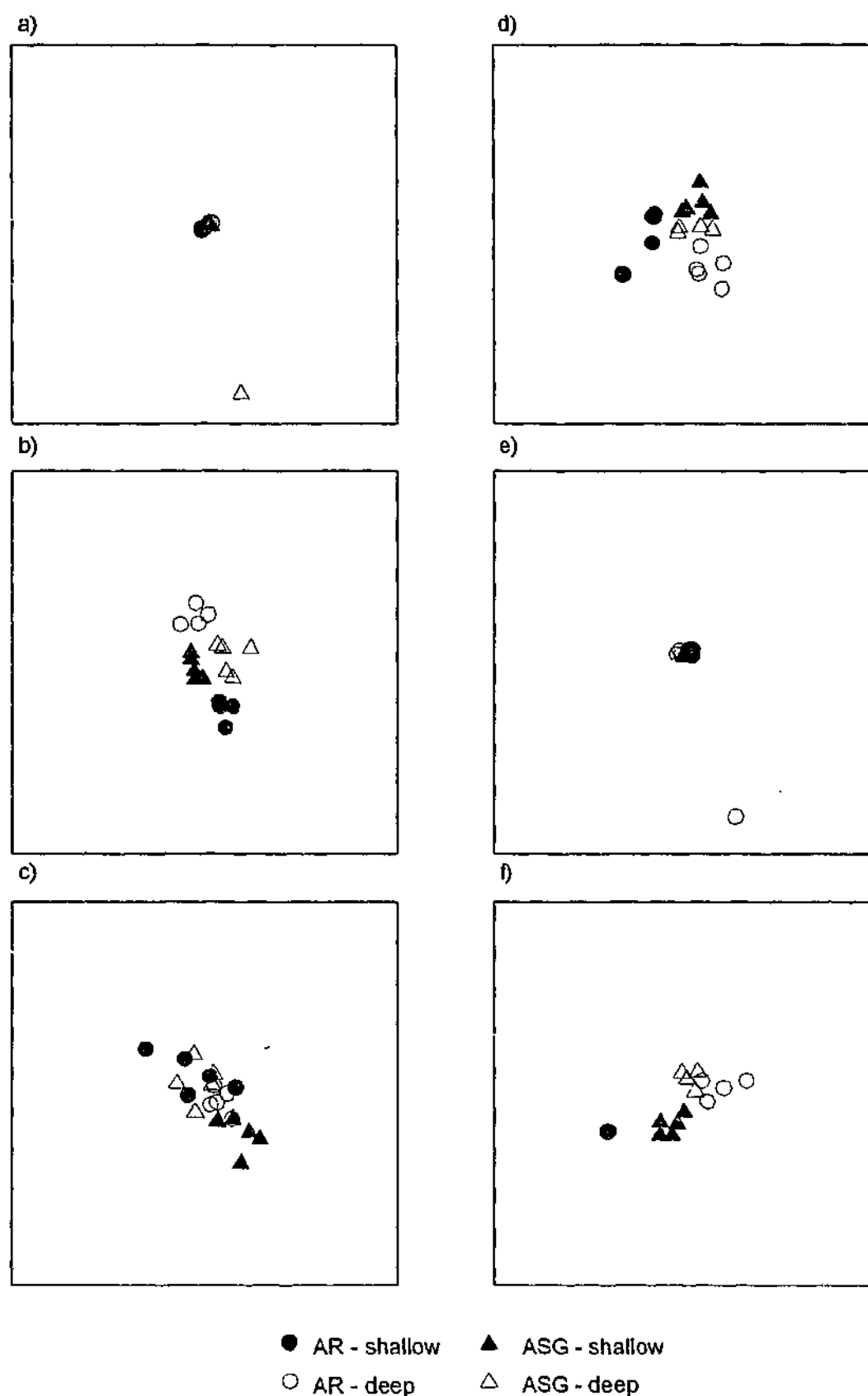


Figure 6.3: 2-D NMDS ordinations of the fish assemblages at Grassy Point, plotted separately for each sampling time. a) 18.1.99; stress = 0.01. b) 19.2.99; stress = 0.06, c) 1.3.99; stress = 0.12, d) 30.3.99; stress = 0.09, e) 7.4.99; stress = 0.01 and f) 4.5.99; stress = 0.05. Each point depicts a replicate habitat.

Table 6.3: Two-factor crossed ANOSIMs comparing fish assemblages between habitats (seagrass and reef) and depths (shallow and deep) for each sampling time at Grassy Point and Indented Head. Note: analysis not possible for data collected on 4.5.99 at Grassy Point as fish were only recorded on one shallow reef habitat.

Source	R	P	R	P
	Grassy Point		Indented Head	
18.1.99				
Depth	0.591	<0.001		
Habitat	0.572	0.010		
3.2.99				
Depth			0.361	0.090
Habitat			0.800	<0.001
19.2.99				
Depth	0.871	<0.001	0.696	0.010
Habitat	0.925	<0.001	0.708	0.020
1.3.99				
Depth	0.582	<0.001	0.109	0.030
Habitat	0.576	<0.001	0.453	0.070
17.3.99				
Depth			0.144	0.010
Habitat			0.187	0.010
30.3.99				
Depth	0.732	0.010	0.190	0.060
Habitat	0.843	<0.001	0.574	<0.001
7.4.99				
Depth	0.727	<0.001	0.834	0.010
Habitat	0.700	<0.001	0.734	0.030
4.5.99				
Depth			0.366	0.090
Habitat			0.695	0.030

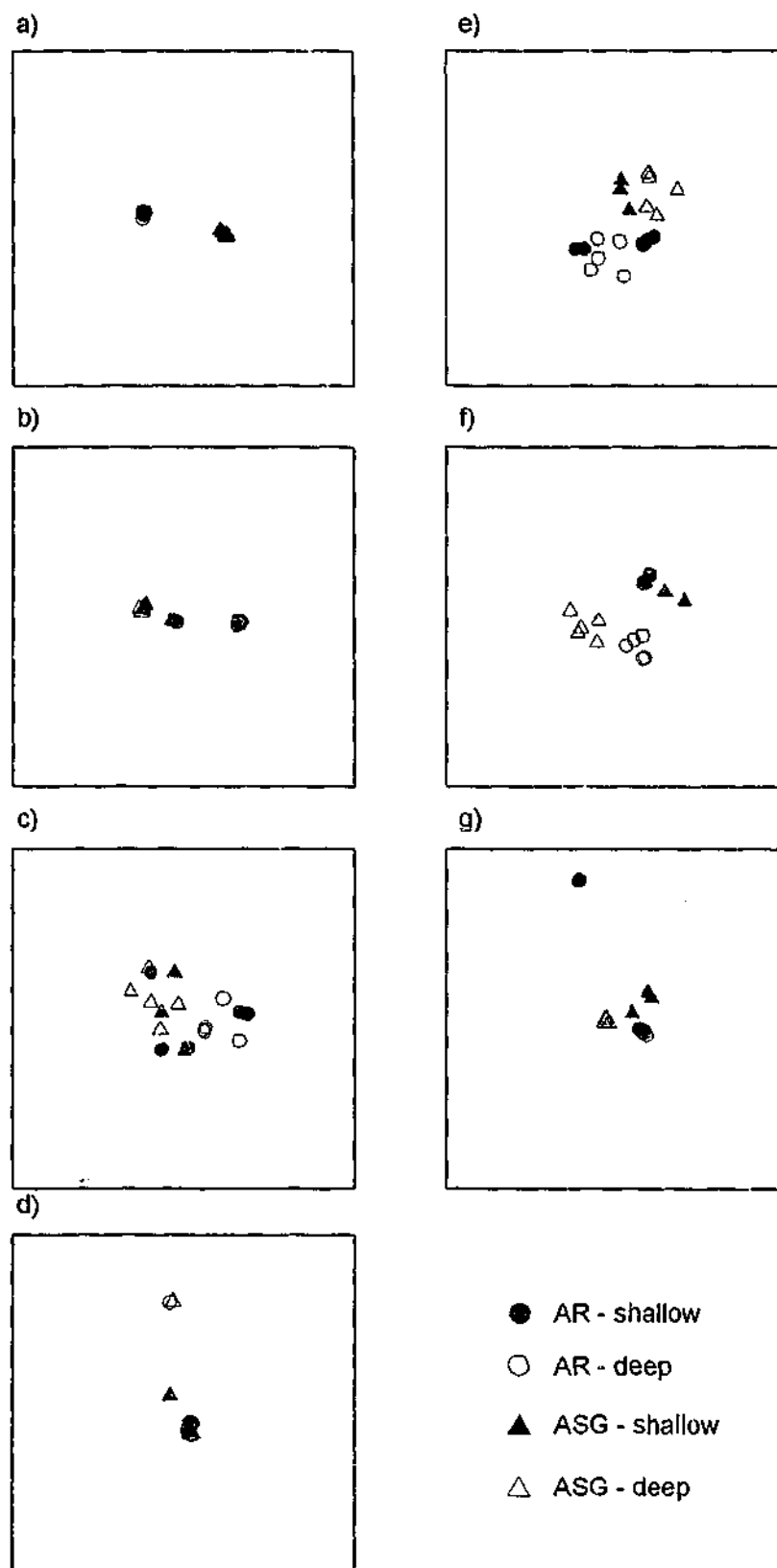


Figure 6.4: 2-D NMDS ordinations of the fish assemblages at Indented Head, plotted separately for each sampling time. a) 3.2.99; stress = 0.01, b) 19.2.99; stress = 0.01, c) 1.3.99; stress = 0.10, d) 17.3.99; stress = 0.01, e) 30.3.99; stress = 0.07, f) 7.4.99; stress = 0.01 and g) 4.5.99; stress = 0.01. Each point depicts a replicate habitat.

Number of Species and Total Abundance of All Fishes

Over the study period, 26 species were recorded on the experimental habitats at the two sites (Tables 6.1 and 6.2). At Grassy Point, there were no significant differences in the number of species recorded through time, or between the two depths (Fig. 6.5a; Table 6.4). There was, however, a significant effect of habitat, with consistently more species recorded in seagrass beds than on reefs (Fig. 6.5a; Table 6.4).

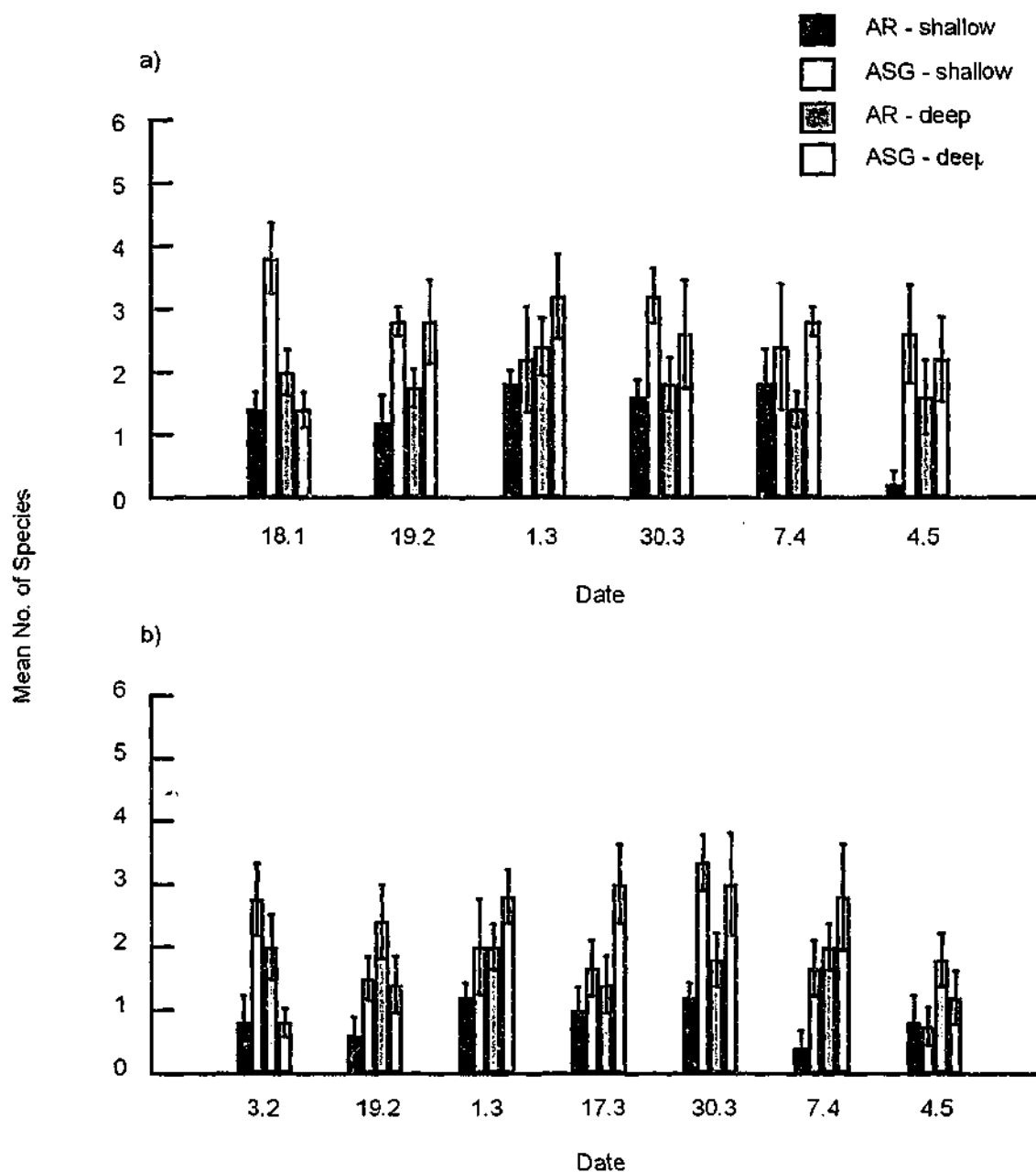


Figure 6.5: Mean (\pm SE) number of species recorded on the experimental habitats at a) Grassy Point and b) Indented Head ($n = 5$). AR = artificial reef and ASG = artificial seagrass.

Table 6.4: Repeated measures ANOVA comparing the number of species between habitats (seagrass and reef) and depths (shallow and deep) over six sampling dates at Grassy Point. Data were $\log_{10}(x+1)$ transformed. G-G = Greenhouse-Geiser adjusted *P*-values. Greenhouse-Geiser Epsilon = 0.7303.

Source	MS	df	F	P	G-G
Between Subjects					
Depth	0.008	1	0.215	0.650	
Habitat	0.698	1	19.222	0.001	
Depth*Habitat	0.101	1	2.790	0.116	
Error	0.036	15			
Within Subjects					
Time	0.065	5	2.596	0.032	0.051
Time*Depth	0.035	5	1.409	0.231	0.246
Time*Habitat	0.036	5	1.448	0.217	0.234
Time*Depth*Habitat	0.058	5	2.330	0.051	0.073
Error	0.025	75			

In contrast, at Indented Head the number of species recorded varied significantly over time, and there was also a significant interaction between depth and habitat (Fig. 6.5b; Table 6.5). However, comparisons of habitats at each depth revealed no significant differences between habitats at either depth (Fig. 6.5b; Table 6.5).

Table 6.5: Repeated measures ANOVA comparing the number of species between habitats (seagrass and reef) and depths (shallow and deep) over seven sampling dates at Indented Head. Data were $\log_{10}(x+1)$ transformed. G-G = Greenhouse-Geiser adjusted *P*-values. Greenhouse-Geiser Epsilon = 0.6489.

Source	MS	df	F	P	G-G
Between Subjects					
Depth	0.358	1	15.554	0.001	
Habitat	0.320	1	13.898	0.002	
Depth*Habitat	0.283	1	12.318	0.003	
Shallow					
Habitat	0.075	1	3.276	0.092	
Deep					
Habitat	0.000	1	0.004	0.951	
Error	0.023	14			
Within Subjects					
Time	0.078	6	3.423	0.005	0.015
Time*Depth	0.041	6	1.805	0.108	0.143
Time*Habitat	0.047	6	2.053	0.067	0.101
Time*Depth*Habitat	0.053	6	2.300	0.042	0.072
Error	0.023	84			

There was a significant interaction between time, depth and habitat for the total abundance of all fishes recorded at Grassy Point (Fig. 6.6a; Table 6.6). Separate analyses for each sampling time revealed a significant interaction between depth and habitat at five of the six sampling times (Table 6.7). On these dates, the total abundance

of fish was significantly different between habitats at the shallow depth only, with more fish recorded in seagrass beds than on reefs (Fig. 6.6a; Table 6.7). On 7.4.99, there was no effect of depth or habitat on the total abundance of fishes observed (Fig. 6.6a; Table 6.7).

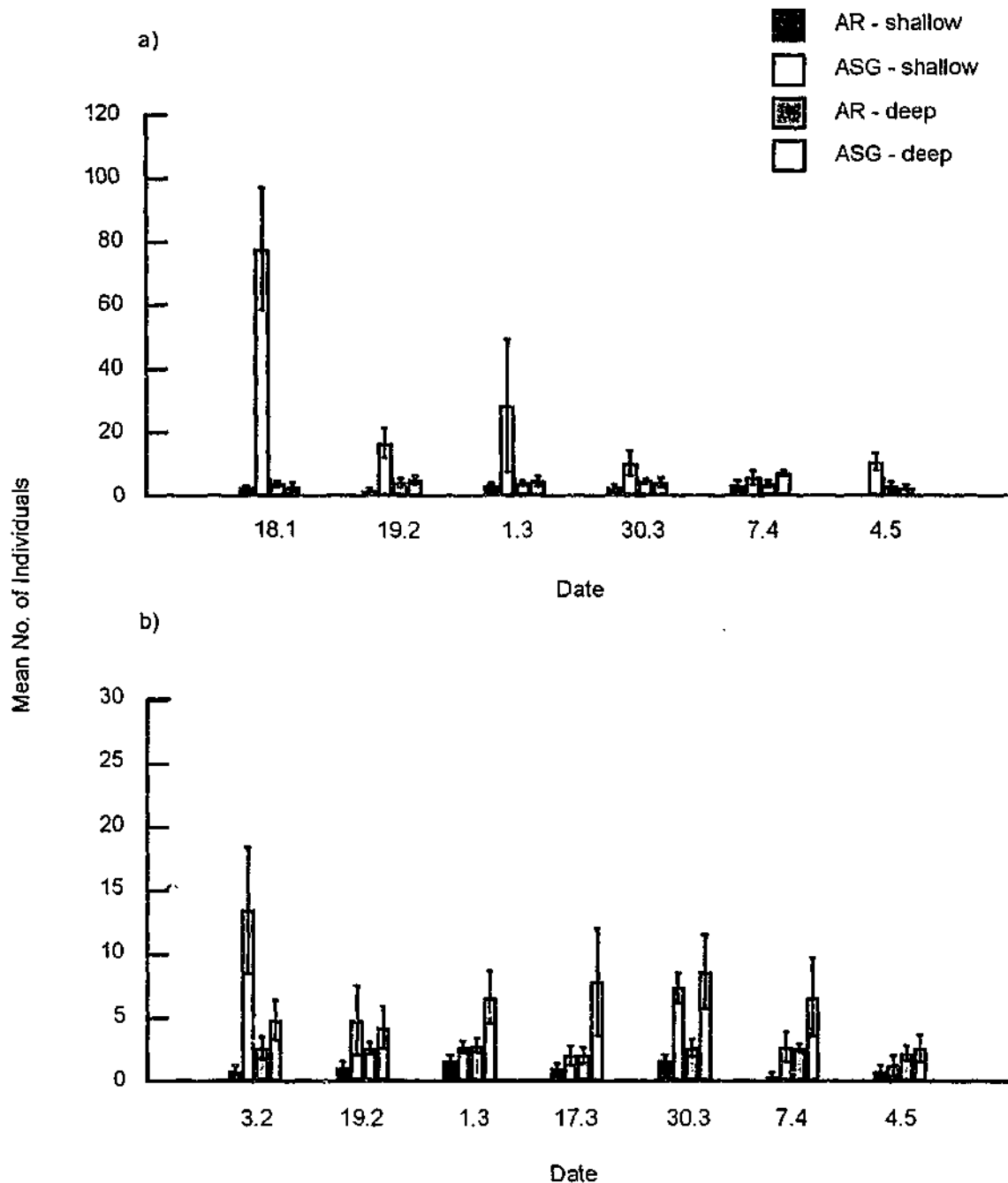


Figure 6.6: Mean (\pm SE) abundance of all fishes recorded on the experimental habitats at a) Grassy Point and b) Indented Head ($n = 5$). AR = artificial reef and ASG = artificial seagrass. Note: maximum Y-value differs between the sites.

Table 6.6: Repeated measures ANOVA comparing total abundance of all fishes between habitats (seagrass and reef) and depths (shallow and deep) over six sampling dates at Grassy Point. Data were $\log_{10}(x+1)$ transformed. G-G = Greenhouse-Geiser adjusted *P*-values. Greenhouse-Geiser Epsilon = 0.6991.

Source	MS	df	F	P	G-G
Between Subjects					
Depth	0.658	1	8.937	0.009	
Habitat	3.400	1	46.158	<0.001	
Depth*Habitat	3.349	1	45.475	<0.001	
Error	0.074	15			
Within Subjects					
Time	0.316	5	4.610	0.001	0.004
Time*Depth	0.266	5	3.885	0.003	0.010
Time*Habitat	0.115	5	1.680	0.150	0.175
Time*Depth*Habitat	0.326	5	4.762	0.001	0.003
Error	0.069	75			

Table 6.7: Two-factor ANOVAs comparing total abundance of all fishes between habitats (seagrass and reef) and depths (shallow and deep) separately over each sampling date at Grassy Point. It was necessary to conduct separate ANOVAs for each time as there was a significant Time*Depth*Habitat interaction (see Table 6.6). Data were $\log_{10}(x+1)$ transformed.

Source	MS	df	F	P
18.1.99				
Depth	1.816	1	41.994	<0.001
Habitat	1.502	1	34.730	<0.001
Depth*Habitat	2.557	1	59.110	<0.001
<u>Shallow</u>				
Habitat	3.989	1	92.775	<0.001
<u>Deep</u>				
Habitat	0.070	1	1.621	0.221
Error	0.043	16		
19.2.99				
Depth	0.037	1	0.706	0.414
Habitat	0.850	1	16.234	0.001
Depth*Habitat	0.688	1	13.142	0.002
<u>Shallow</u>				
Habitat	1.629	1	31.322	<0.001
<u>Deep</u>				
Habitat	0.004	1	0.078	0.784
Error	0.052	15		
1.3.99				
Depth	0.237	1	3.032	0.101
Habitat	0.488	1	6.246	0.024
Depth*Habitat	0.477	1	6.105	0.025
<u>Shallow</u>				
Habitat	0.964	1	12.364	0.003
<u>Deep</u>				
Habitat	<0.001	1	<0.001	0.984
Error	0.078	16		

Table 6.7: cont.

Source	MS	df	F	P
30.3.99				
Depth	0.026	1	0.353	0.561
Habitat	0.106	1	1.462	0.244
Depth*Habitat	0.331	1	4.578	0.048
<u>Shallow</u>				
Habitat	0.406	1	5.639	0.030
<u>Deep</u>				
Habitat	0.031	1	0.435	0.519
Error	0.072	16		
7.4.99				
Depth	0.090	1	1.106	0.309
Habitat	0.164	1	2.017	0.175
Depth*Habitat	0.023	1	0.278	0.605
Error	0.081	16		
4.5.99				
Depth	0.020	1	0.274	0.608
Habitat	1.073	1	14.650	0.001
Depth*Habitat	1.136	1	15.509	0.001
<u>Shallow</u>				
Habitat	2.209	1	30.265	<0.001
<u>Deep</u>				
Habitat	<0.001	1	0.006	0.939
Error	0.073	16		

At Indented Head, there were significant differences in the total abundance of all fishes recorded between habitats, depths and sampling times (Fig. 6.6b; Table 6.8).

Significantly more fishes were recorded on seagrass than reef habitats, and on deep than shallow units (Fig. 6.6b).

Table 6.8: Repeated measures ANOVA comparing total abundance of all fishes between habitats (seagrass and reef) and depths (shallow and deep) over seven sampling dates at Indented Head. Data were $\log_{10}(x+1)$ transformed. G-G = Greenhouse-Geiser adjusted *P*-values. Greenhouse-Geiser Epsilon = 0.6343.

Source	MS	df	F	P	G-G
Between Subjects					
Depth	0.972	1	10.581	0.006	
Habitat	2.210	1	24.068	<0.001	
Depth*Habitat	0.165	1	1.799	0.201	
Error	0.092	14			
Within Subjects					
Time	0.183	6	3.629	0.003	0.012
Time*Depth	0.060	6	1.177	0.326	0.331
Time*Habitat	0.099	6	1.959	0.081	0.117
Time*Depth*Habitat	0.070	6	1.386	0.230	0.253
Error	0.051	84			

*Abundance and Size Structure of Individual Taxa Recorded on the
Experimental Habitats*

Meuschenia freycineti and *Meuschenia hippocrepis*

Despite recording reasonable numbers of both *Meuschenia hippocrepis* and *Meuschenia freycineti* on artificial habitats in a pilot study over the summer of 1997/1998, and on natural habitats in recent summers (Jenkins *et al.*, 1993, 1996; Jenkins and Wheatley, 1998), no *M. hippocrepis* and very few *M. freycineti* were recorded on the experimental habitats in the current study. Although abundances of *M. freycineti* were too low and variable for ANOVAs, graphical representations of the data show a distinct pattern with respect to habitat and water depth (Figs. 6.7a and b). At both sites, *M. freycineti* was only recorded on shallow water habitats (Figs. 6.7a and b). At Grassy Point, individuals were recorded on artificial seagrass beds on the first two sampling dates only (Fig. 6.7a), while at Indented Head most individuals of *M. freycineti* were observed on the reef habitats, although individuals were also present in seagrass beds on the first two sampling dates (Fig. 6.7b).

Abundances of *M. hippocrepis* were extremely low on the natural reefs over the period of the experiment, with very few individuals at Indented Head, and none at Grassy Point (see Chapter 4). Numbers of *M. freycineti* on natural seagrass beds and reefs at Indented Head (see Chapter 4) and Grassy Point (see Chapter 4 and only two fish on the reef) were also very low.

Size frequency distributions of *M. freycineti* recorded on the experimental habitats revealed that although individuals in seagrass beds spanned a large size range from 15 – 200 mm TL, small recruits/juveniles were only recorded in seagrass beds, particularly at Grassy Point (Fig. 6.8a). In contrast, *M. freycineti* on the artificial reefs at Indented Head tended to be larger, ranging from 100–200 mm TL (Fig. 6.8b).

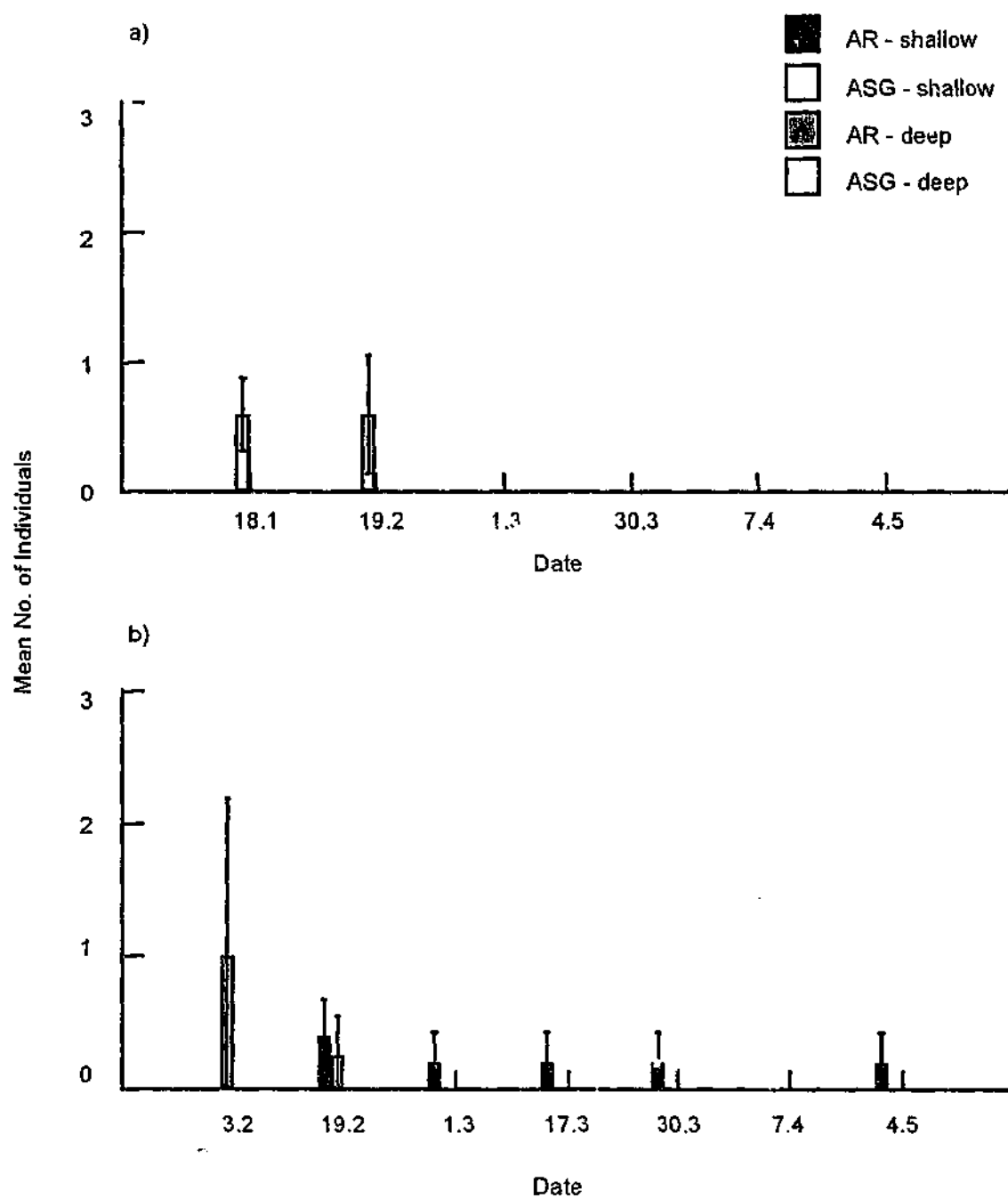


Figure 6.7: Mean (\pm SE) number of individuals of *M. freycineti* recorded on the experimental habitats at a) Grassy Point and b) Indented Head ($n = 5$). AR = artificial reef and ASG = artificial seagrass.

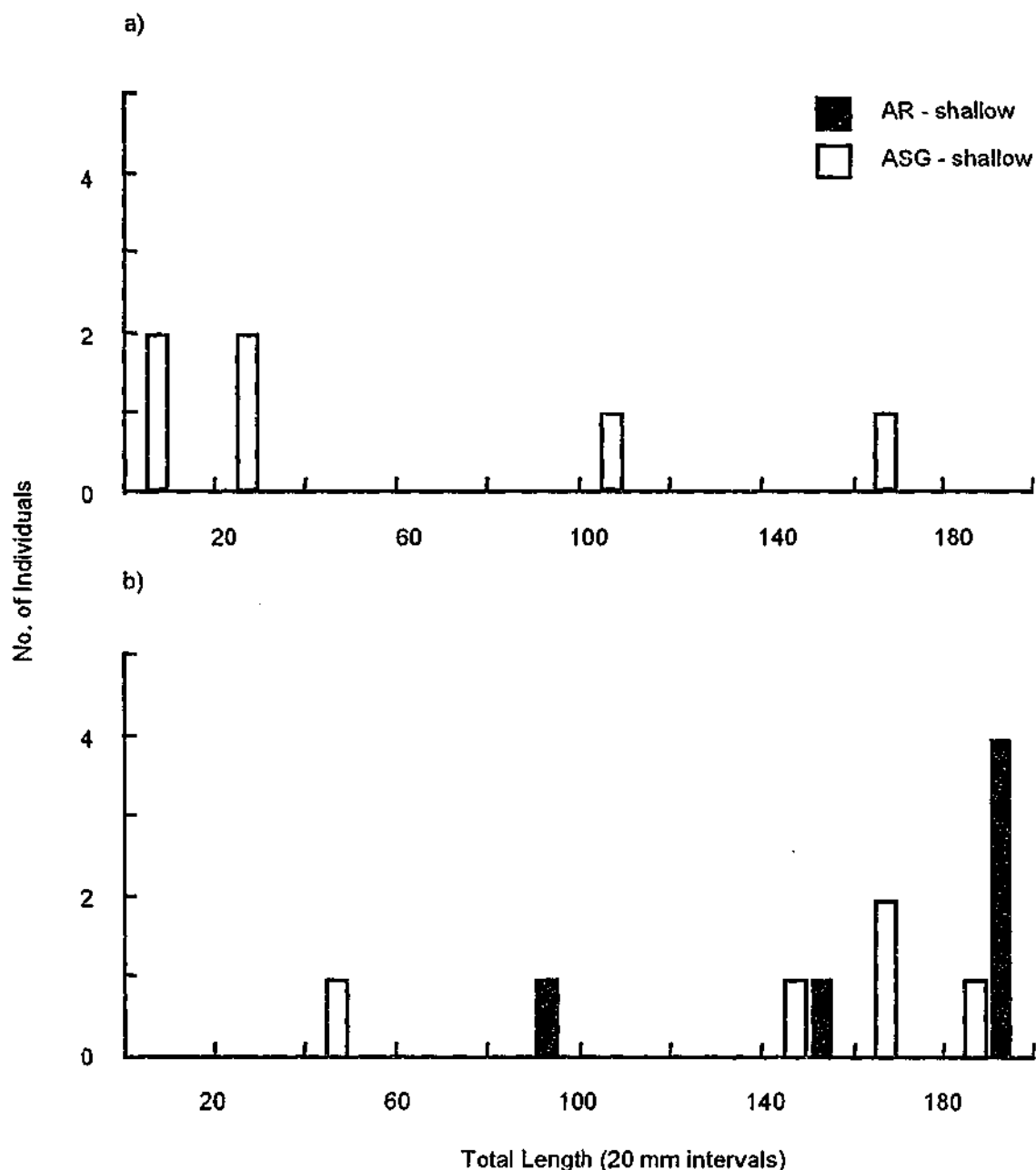


Figure 6.8: Size frequency distributions of *M. freycineti* recorded on the shallow experimental units at a) Grassy Point and b) Indented Head. Data are pooled over sampling times. AR = artificial reef and ASG = artificial seagrass.

Bridled Leatherjacket, Acanthaluteres spilomelanurus

Bridled leatherjackets, *Acanthaluteres spilomelanurus*, occurred almost exclusively on artificial seagrass beds at Grassy Point (Fig. 6.9a), and were only recorded on artificial seagrass beds at Indented Head (Fig. 6.9b). Analyses comparing abundances of *A. spilomelanurus* between depths over time within seagrass habitats revealed a significant

effect of time, but no effect of depth, at Grassy Point (Table 6.9). At Indented Head, there was no significant difference in the abundance of *A. spilomelanurus* between depths or over time, but variation between replicate habitat units may have masked a trend for increased abundances on deeper seagrass beds (Fig. 6.9b; Table 6.9).

Numbers of *A. spilomelanurus* on the shallow artificial seagrass beds were comparable with abundances recorded on shallow natural seagrass over the period of the study, although individuals were only recorded on one occasion in the natural seagrass beds (Fig. 6.9). The deep natural seagrass bed at Indented Head was not sampled during the study due to time constraints, so it is not possible to compare abundances on deep natural and artificial seagrass beds. No individuals of *A. spilomelanurus* were trapped on the natural reefs over the period of the experiment.

The size structure of *A. spilomelanurus* was very similar between depths at both sites, particularly at Indented Head (Fig. 6.10). The majority of individuals present on the experimental habitats were small recruits/juveniles (i.e. <40 mm TL), although a few larger individuals were recorded in the shallow seagrass beds at Grassy Point (Fig. 6.10).

Table 6.9: Repeated measures ANOVAs comparing the number of *A. spilomelanurus*, between depths (shallow and deep) on experimental seagrass habitats over four sampling times at Grassy Point, and five sampling times at Indented Head. Artificial reefs and sampling dates (7.4.99 and 4.5.99) were excluded due to low numbers of *A. spilomelanurus*. Data were $\log_{10}(x+1)$ transformed. G-G = Greenhouse-Geiser adjusted *P*-values. Greenhouse-Geiser Epsilon = 0.6343.

Source	MS	df	F	P	G-G
<u>Grassy Point</u>					
Between Subjects					
Depth	<0.001	1	0.003	0.954	
Error	0.112	8			
Within Subjects					
Time	0.235	3	7.420	0.001	0.006
Time*Depth	0.025	3	0.781	0.516	0.470
Error	0.032	24			
<u>Indented Head</u>					
Between Subjects					
Depth	1.246	1	4.823	0.070	
Error	0.258	6			
Within Subjects					
Time	0.031	4	0.496	0.739	0.605
Time*Depth	0.099	4	1.566	0.216	0.251
Error	0.063	24			

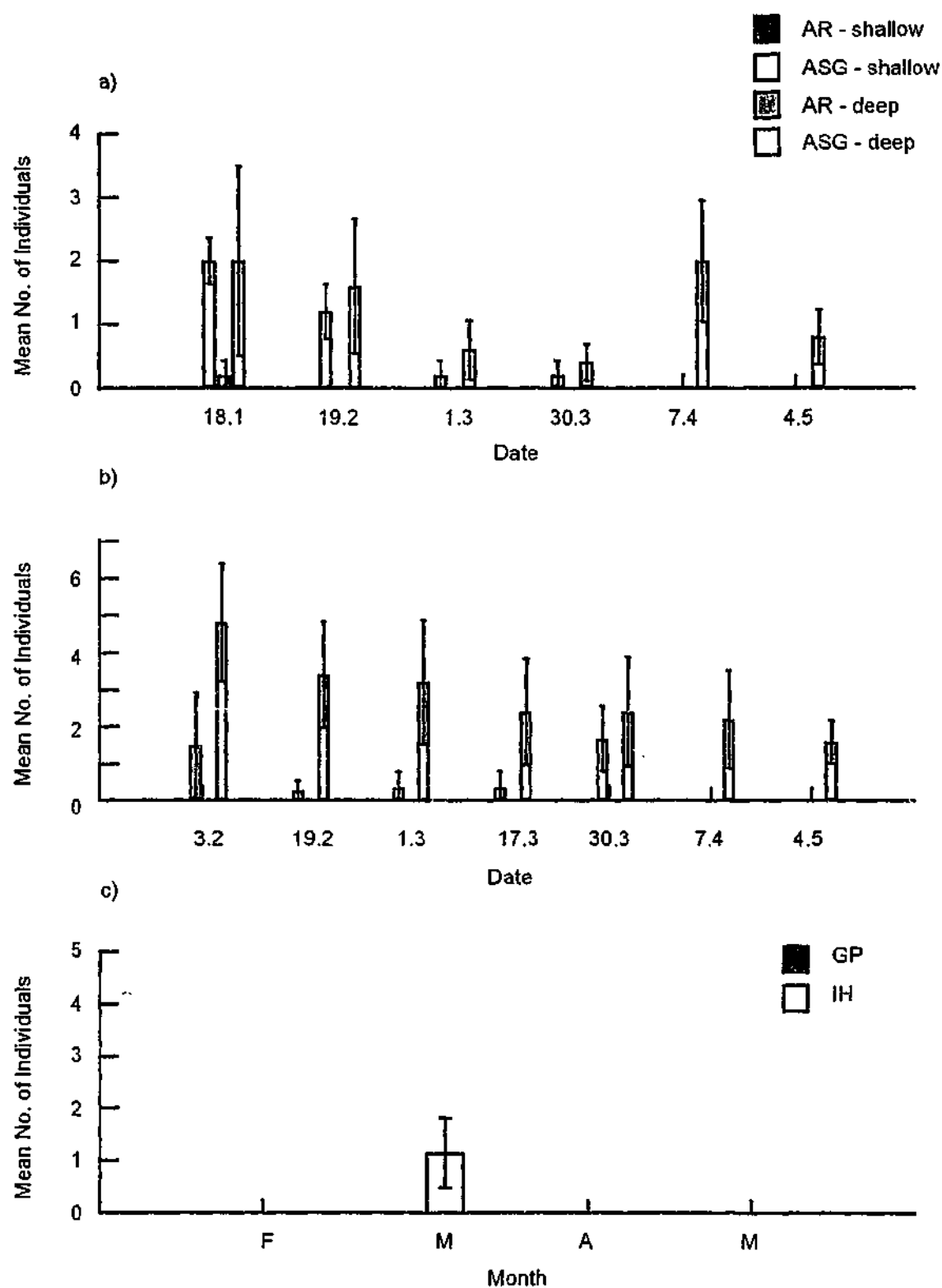


Figure 6.9: Mean (\pm SE) number of *A. spilomelanurus* recorded on the experimental habitats at a) Grassy Point and b) Indented Head ($n = 5$); AR = artificial reef and ASG = artificial seagrass. c) Mean (\pm SE) number of *A. spilomelanurus* recorded on natural seagrass beds at Grassy Point (GP) and Indented Head (IH) ($n = 6$ in all months except February when $n = 5$). Note: maximum Y-values differ between the graphs.

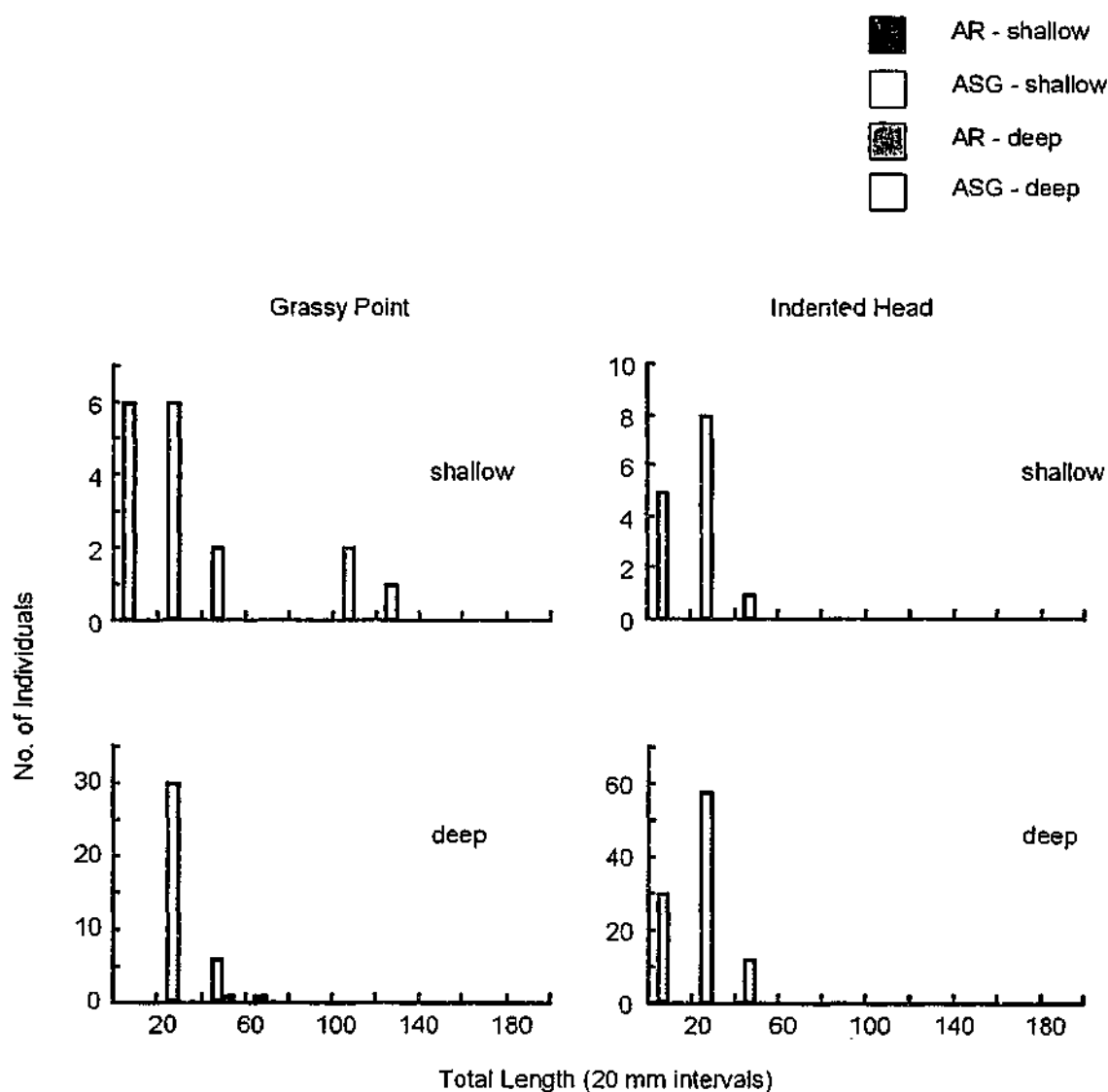


Figure 6.10: Size frequency distributions of *A. spilomelanurus* recorded on the experimental habitats at Grassy Point and Indented Head. Data are pooled over sampling times. AR = artificial reef and ASG = artificial seagrass. Note: maximum Y-value differs between sites and depths.

Spotted Pipefish, Stigmatopora argus

Spotted pipefish, *Stigmatopora argus*, showed a very distinct pattern with respect to habitat type (Fig. 6.11). At Grassy Point, analyses were not necessary as individuals of *S. argus* were only recorded on the shallow artificial seagrass beds (Fig. 6.11a). At Indented Head, analyses were not possible due to the presence of numerous zero values, however, individuals of *S. argus* were observed only on artificial seagrass beds, but occurred at both depths (Fig. 6.11b). Abundances of *S. argus* were much lower at Indented Head than at Grassy Point (Figs. 6.11a and b).

Abundances of *S. argus* were comparable between the shallow artificial and natural seagrass beds (Fig. 6.11).

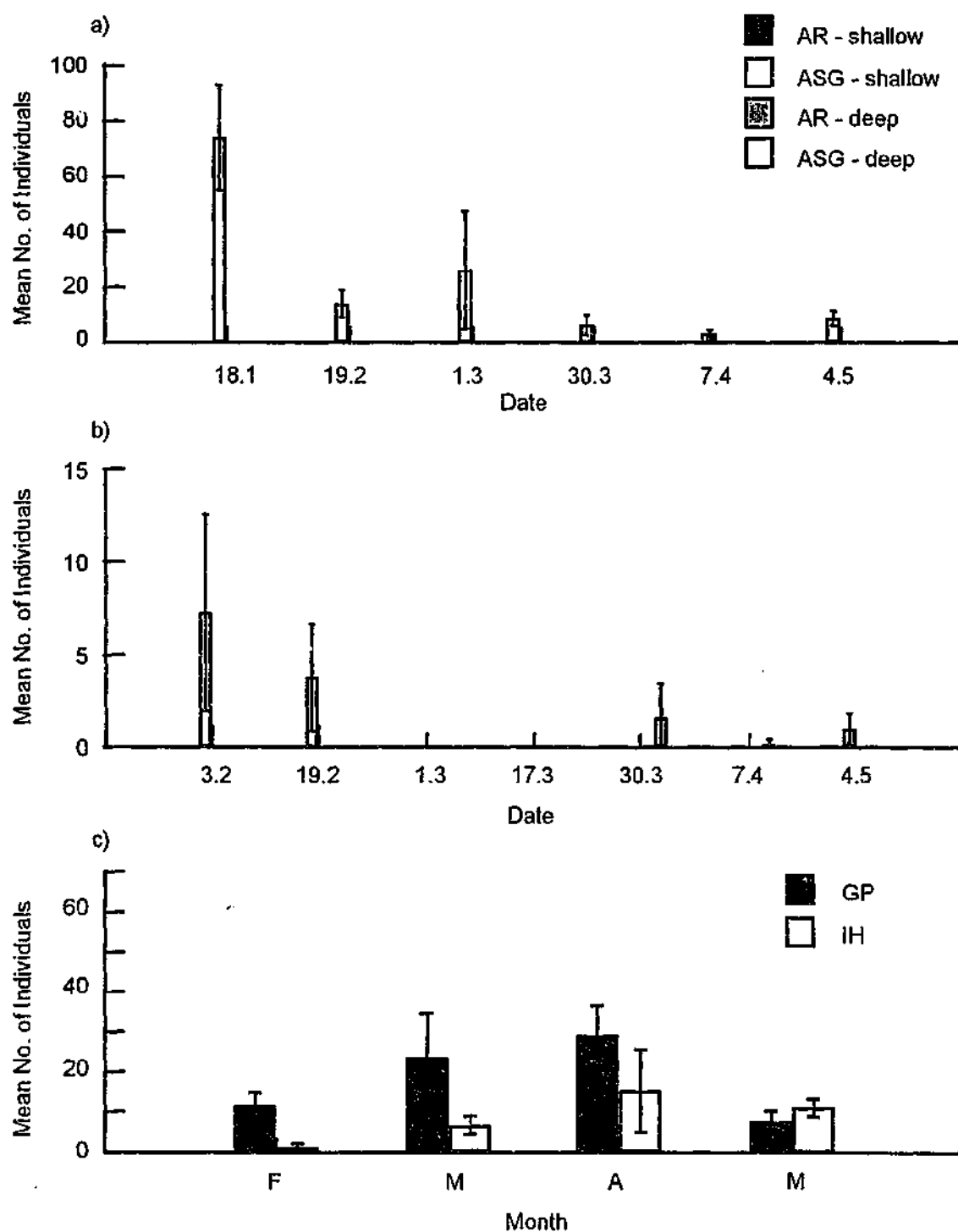


Figure 6.11: Mean (\pm SE) number of *S. argus* recorded on the experimental habitats at a) Grassy Point and b) Indented head ($n = 5$); AR = artificial reef and ASG = artificial seagrass. c) Mean (\pm SE) number of *S. argus* recorded on natural seagrass beds at Grassy Point (GP) and Indented Head (IH) ($n = 6$ in all months except February when $n = 5$). Note: maximum Y-value differs between graphs.

Tasmanian Blenny, Parablennius tasmanianus

The distribution of the Tasmanian blenny, *Parablennius tasmanianus*, showed a distinct pattern with respect to habitat type and water depth (Fig. 6.12). *P. tasmanianus* was only recorded on artificial reefs, but the depth distribution clearly differed between the sites (Fig. 6.12). At Grassy Point, analyses were not necessary as all individuals of *P. tasmanianus* were recorded on shallow reefs (Fig. 6.12a). In contrast at Indented Head, individuals occurred at both water depths, and although analyses were not possible due to the presence of numerous zero values, *P. tasmanianus* appeared to be more abundant on the deep artificial reefs (Fig. 6.12b).

No individuals of *P. tasmanianus* were recorded on the natural reefs or seagrass beds over the period of the experiment. The fish traps used in this study were unlikely to sample small fish such as blennies due to their large mesh size, so it is not known whether *P. tasmanianus* abundances recorded on the experimental reefs are comparable with natural reefs.

The size structure of *P. tasmanianus* was very similar at Grassy Point and Indented Head, and between depths at Indented Head (Fig. 6.13). The majority of individuals present on the experimental reefs ranged from 20–80 mm TL (Fig. 6.13).

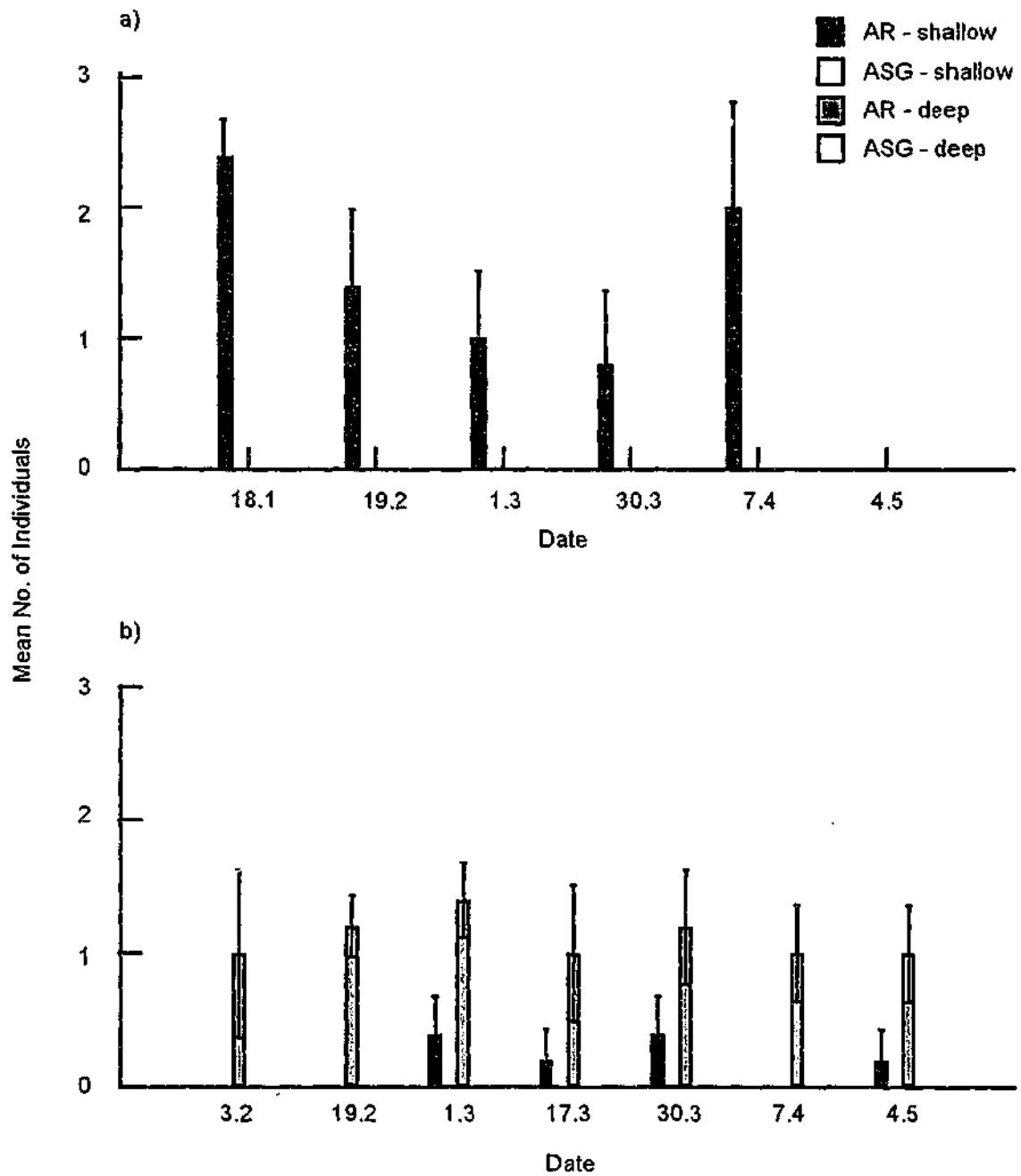


Figure 6.12: Mean (\pm SE) number of *P. tasmanianus* recorded on the experimental habitats at a) Grassy Point and b) Indented Head ($n = 5$); AR = artificial reef and ASG = artificial seagrass.

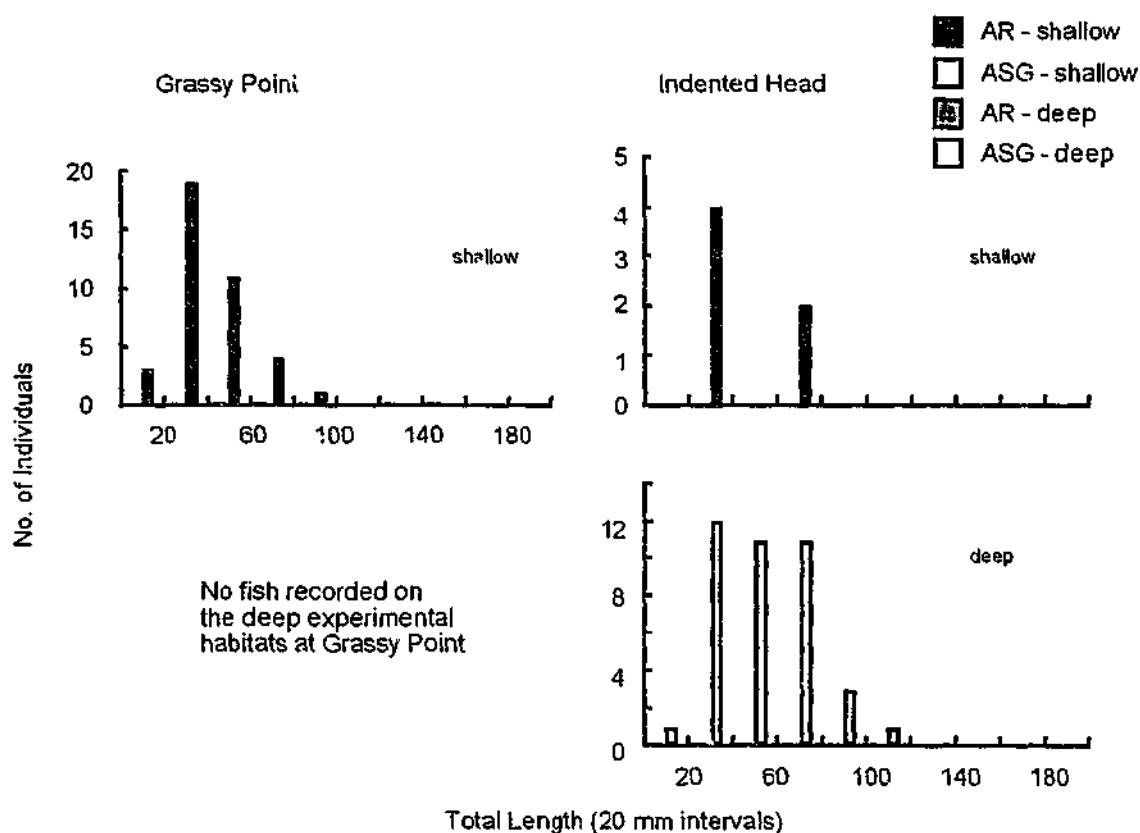


Figure 6.13: Size frequency distributions of *P. tasmanianus* recorded on the experimental habitats at Grassy Point and Indented Head. Data are pooled over sampling times. AR = artificial reef and ASG = artificial seagrass. Note: maximum Y-value differs between sites, and between depths at Indented Head.

Southern Cardinal Fish, Vincentia conspersa

Southern cardinal fish, *Vincentia conspersa*, showed a distinct difference in distribution between habitat types and water depths (Fig. 6.14). At Grassy Point, analyses were not possible due to the presence of numerous zero values, however, *V. conspersa* were recorded only on the deep artificial habitats, and most individuals were observed on the deep reefs, although on two sampling occasions, individuals were recorded on deep seagrass beds (Fig. 6.14a). Although not as abundant at Indented Head *V. conspersa* were only observed on the deep artificial reefs (Fig. 6.14b).

No individuals of *V. conspersa* were recorded on the natural habitats over the study period.

There were no obvious differences in the size frequency distributions of individuals of *V. conspersa* between sites (Fig 6.15), or between habitat types at Grassy Point (Fig.

6.15a). The majority of individuals observed on the experimental habitats ranged in size from 20–60 mm TL (Fig. 6.15).

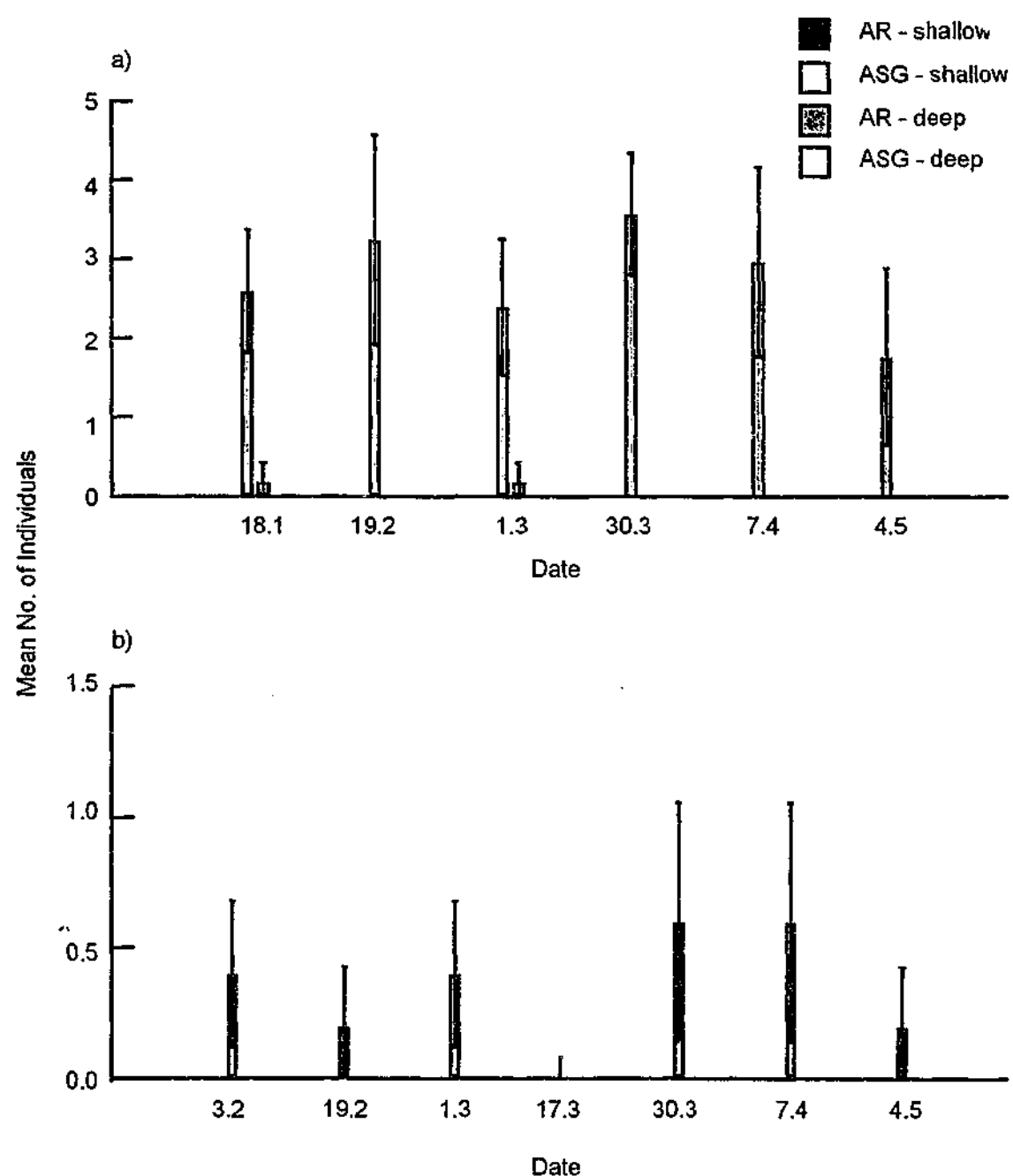


Figure 6.14: Mean (\pm SE) number of *V. conspersa* recorded on the experimental habitats at a) Grassy Point and b) Indented Head ($n = 5$). AR = artificial reef and ASG = artificial seagrass. Note: maximum Y-value differs between the sites.

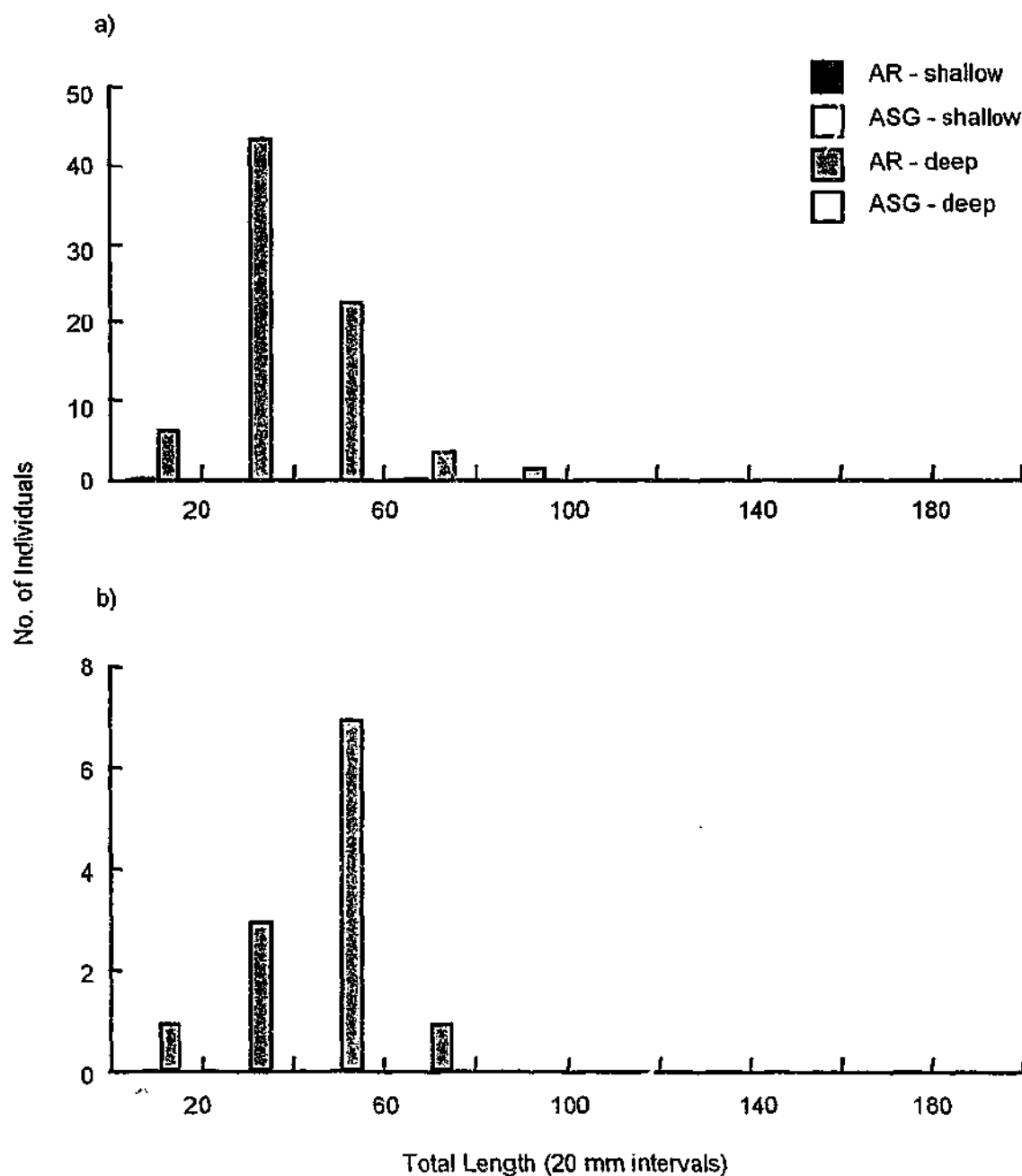


Figure 6.15: Size frequency distributions of *V. conspersa* recorded on the deep experimental habitats at a) Grassy Point and b) Indented Head. Data are pooled over sampling times. AR = artificial reef and ASG = artificial seagrass. Note: maximum Y-value differs between the sites

Unidentified Weedfish (Family: Clinidae)

Weedfish were consistently recorded on the experimental habitats, albeit in small numbers, over the period of the experiment. Analyses were not possible due to low numbers of fish and extreme variability between replicate habitats, but in contrast to most species, weedfish did not show any distinct habitat or water depth preferences at either site (Fig. 6.16).

Abundances of weedfish on artificial seagrass beds were comparable with numbers recorded on natural seagrass beds (Fig. 6.16). No weedfish were recorded on the natural reefs, although the fish traps used in this study do not adequately sample small species such as weedfish due to their large mesh size.

There were no obvious differences in the size structure of weedfish between habitat types or water depths at either site (Fig. 6.17). Weedfish spanned a large size range on seagrass beds and reefs at both depths, although the largest individuals recorded (>150 mm TL) were found only on artificial seagrass beds (Fig. 6.17).

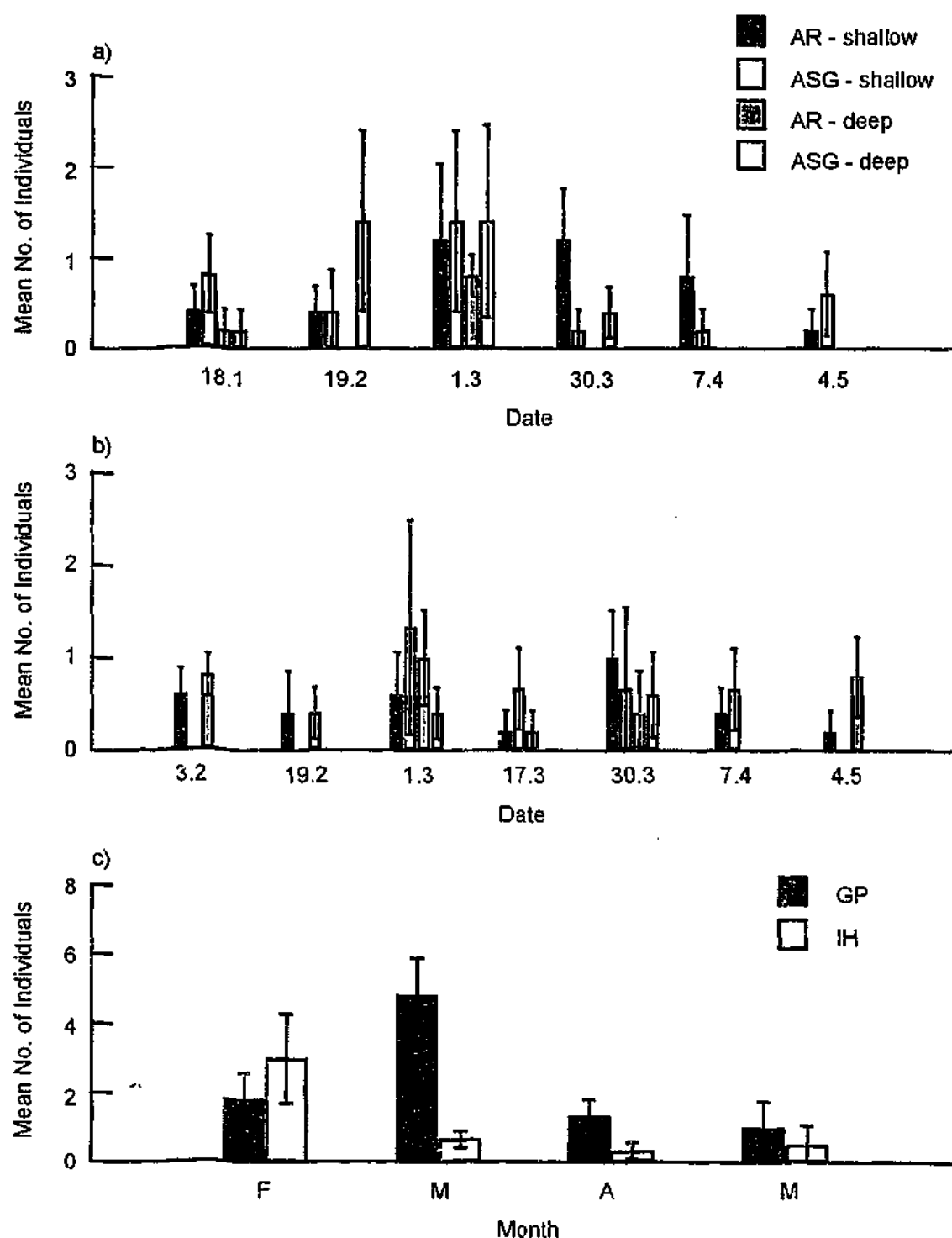


Figure 6.16: Mean (\pm SE) number of weedfish recorded on the experimental habitats at a) Grassy Point and b) Indented head ($n = 5$); AR = artificial reef and ASG = artificial seagrass. c) Mean (\pm SE) number of weedfish recorded on natural seagrass beds at Grassy Point (GP) and Indented Head (IH) ($n = 6$ in all months except February when $n = 5$). Note: maximum Y-value differs between graphs.

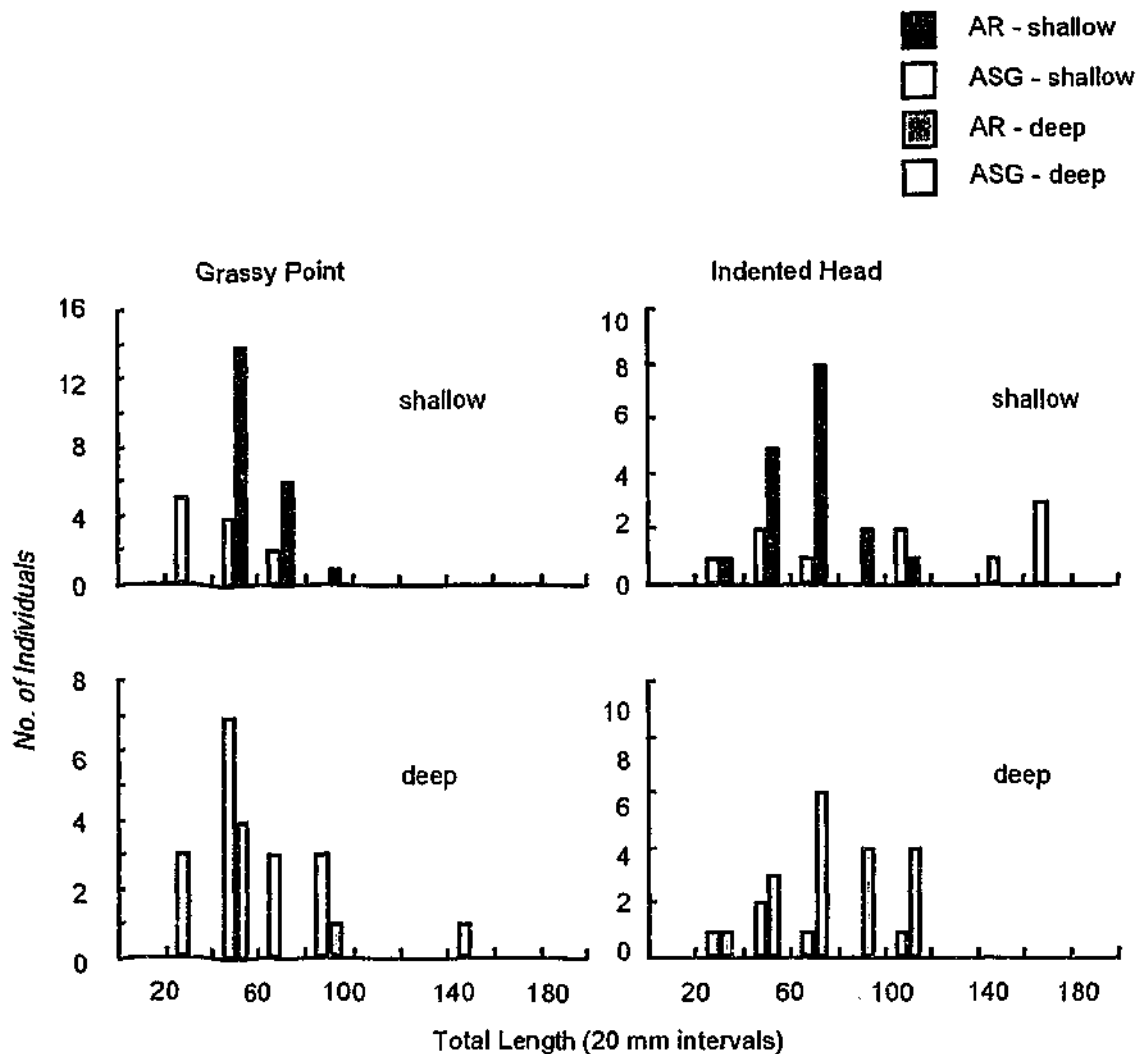


Figure 6.17: Size frequency distributions of weedfish recorded on the experimental habitats at Grassy Point and Indented Head. Data are pooled over sampling times. AR = artificial reef and ASG = artificial seagrass. Note: maximum Y-value differs between sites, and between depths at Grassy Point.

Discussion

Both *Meuschenia hippocrepis* and *Meuschenia freycineti* were recorded on artificial habitats at Grassy Point and Indented Head in a pilot study during the previous summer (1997/1998). During the pilot study *M. hippocrepis* had been consistently observed on artificial reefs, particularly at the deep site at Indented Head, while *M. freycineti* were observed on both artificial reefs and seagrass beds at both sites. A previous study utilising artificial seagrass beds in this area of Port Phillip Bay also reported recruits/juveniles of *M. freycineti* on artificial seagrass beds (Jenkins and Sutherland, 1997). However, in the current study no individuals of *M. hippocrepis*, and very few *M. freycineti*, were recorded on the experimental habitats.

Concurrent sampling of nearby natural reefs and seagrass beds over the same period also revealed low numbers of *M. freycineti* and *M. hippocrepis* compared to previous years. Grassy Point was specifically chosen for this experiment not only because of its shallow water seagrass beds and offshore reefs, but also because *M. freycineti* recruits were consistently recorded in natural seagrass beds at this site during the previous summer (Jeremy Hindell unpubl. data). Reasonable numbers of *M. freycineti* (2-3 individuals/artificial bed) were also consistently recorded on artificial seagrass beds at Grassy Point in the summer after this experiment was conducted (Greg Jenkins unpubl. data). Thus, evidence suggests that *M. freycineti* and *M. hippocrepis* do utilise artificial habitats, that both species are generally quite common on natural and artificial habitats at Grassy Point and Indented Head, and that the current study unfortunately coincided with a year of low recruitment for these species.

Reasons for the poor recruitment of *M. freycineti* and *M. hippocrepis* observed over the period of this study are undoubtedly complex, but may relate to large-scale weather patterns. Port Phillip Bay experienced unusually consistent and strong easterly winds over the study period (M Wheatley pers. obs.), and poor recruitment was also recorded for other species such as King George whiting, *Sillaginodes punctata* (Greg Jenkins unpubl. data). It is also possible that the experimental habitats used in this study were too small to be located by settling larvae. However, this explanation seems unlikely as small artificial seagrass beds and artificial (concrete block) reefs have been used successfully in previous studies (Gascon and Miller, 1982; Jenkins and Sutherland, 1997). In addition, the experimental units were set up on natural seagrass beds, allowing colonisation not only by settling larvae, but also by individuals moving onto the habitats from the surrounding seagrass beds, and numerous other fish species (both recruits and adults) were recorded on the experimental habitats.

Habitat complexity is believed to play an important role in structuring both seagrass and reef fish assemblages (Bell and Westoby, 1986a; Holbrook *et al.*, 1993; Anderson, 1994; Jenkins and Wheatley, 1998). Both habitat type and water depth influenced the distribution, and to a lesser extent the size structure, of fish assemblages in this study, although the relative importance of the two factors varied between the sites. At Indented Head, there was a significant interaction between habitat and depth with respect to the number of species recorded, with more species present on seagrass than

reef habitats, and more species on deep than shallow habitats. In contrast, at Grassy Point there was only a significant effect of habitat, with more species recorded on seagrass than on reef. Seagrass beds are considered important nursery areas for many fish species (Pollard, 1984), and numerous species recorded on the seagrass beds were present as juveniles (e.g. *Acanthaluteres spilomelanurus* and *Enoplosus armatus*). In addition, many species were found almost exclusively on seagrass beds, and appear to be well adapted to this habitat. For example, spotted pipefish, *Stigmatopora argus*, were extremely abundant on the shallow seagrass habitats, particularly at Grassy Point. In terms of the total abundance of fishes, there was a significant interaction between habitat and depth at Grassy Point, with greater numbers of fishes recorded in the shallow seagrass habitats. This result is most likely driven by the high numbers of *S. argus* recorded on the shallow artificial seagrass beds.

In general, habitat type appeared to be more important than water depth in determining the distribution of fishes. Differences in the distribution and abundance of fishes between habitats may relate to different food and shelter requirements. Both *Parablennius tasmanianus* and *Vincentia conspersa* showed a strong preference for reef over seagrass habitats. Individuals of these species spend most of their time sheltering within rocky caves and crevices (Gomon *et al.*, 1994) and may not obtain appropriate shelter within seagrass beds. In contrast, *S. argus* and *A. spilomelanurus* showed a strong preference for seagrass beds. Previous studies have also shown that abundances of *Stigmatopora* spp. are much greater in seagrass beds compared to alternative habitats (e.g. reefs and unvegetated sand) (Ferrell and Bell, 1991; Jenkins and Wheatley, 1998). *S. argus* resemble seagrass blades in their body shape and colouration, and feed by holding onto a blade of seagrass with their tail and picking off mobile prey such as copepods and amphipods (Howard and Koehn, 1985). Jenkins and Sutherland (1997) reported a strong preference by juvenile *A. spilomelanurus* for seagrass beds, and suggested that this pattern reflected habitat selection by settling larvae, possibly in response to increased food availability and/or reduced predation within seagrass beds. Increased invertebrate numbers have been recorded in artificial seagrass beds compared to beds simulating macroalgae (Jenkins and Sutherland, 1997), and increased food supply may have influenced the distribution of juvenile *A. spilomelanurus*. Although food availability was not measured in this study, experimental seagrass beds and reefs were rapidly colonised by filamentous algae and a variety of invertebrate taxa, and it is

possible that prey type/abundance differed between the habitats accounting for the habitat preferences shown by fishes in this study.

Although there was considerable overlap in the species composition of the fish assemblages, abundances of some species varied substantially between the sites. For example, *S. argus* and *V. conspersa* were much more abundant at Grassy Point than at Indented Head. These patterns may relate to different environmental conditions at the two sites. Reefs and seagrass beds at Indented Head were more exposed to wave action and strong tidal currents than those at Grassy Point. Additionally, predatory fishes are more abundant at St Leonards (approx. 2 km from Indented Head) than at Grassy Point (J. Hindell unpubl. data).

The importance of different habitats and water depths in structuring fish populations may vary not only between species, but also with increasing size/age for a single species. Small recruits and juveniles of *M. freycineti* were only recorded in shallow seagrass beds, while larger individuals were found only on shallow reefs. Providing both habitat types (seagrass beds and reefs) at both water depths (shallow and deep) should have allowed me to determine the relative importance of habitat and water depth in explaining the different size frequency distributions recorded for *M. freycineti* (Chapter 4). Unfortunately the experiment coincided with a poor recruitment year, but these findings do highlight the importance of studying fishes at more than one stage in their life cycle.

The species composition of the fish assemblages recorded on the experimental seagrass beds resembled the assemblages occurring on nearby natural seagrass habitats. In contrast, the species recorded on the experimental reefs differed from those recorded on natural reefs, although this was possibly due to the different survey methods used (i.e. visual surveys and fish traps, respectively). As this chapter was designed to examine the influence of habitat and water depth on the distribution and size structure of temperate fish assemblages, specifically populations of *M. freycineti* and *M. hippocrepis*, natural reefs were surveyed using fish traps as these species are very susceptible to trapping (Chapter 3). However, most species observed on the experimental reefs were small and cryptic (e.g. blennies) and were not readily collected using fish traps. Although not possible due to time constraints, visual surveys of the natural reefs should also have been conducted as part of this study.

The results of this study must be considered in light of the different methods used to survey the two habitat types, and the potential biases of these methods. Seine nets have been effective in sampling many seagrass fishes, particularly species occurring within or above the seagrass canopy, such as *Stigmatopora* sp. and *A. spilomelanurus* (Connolly, 1994; Jenkins and Sutherland, 1997). However, seine nets are less effective in surveying small sediment-associated fishes within seagrass beds (e.g. weedfish) (Jenkins and Sutherland, 1997). Hence, finding that *S. argus* and *A. spilomelanurus* were very common in seagrass beds may in part reflect the method used to sample the seagrass beds. Obviously the survey methods used in a study such as this need to be as unbiased as possible, and ideally the same method should be used to survey both habitat types. However, the effectiveness of a particular method can also vary between habitats. Seine nets efficiently survey seagrass fishes, but do not adequately survey reef fishes due to the topographic complexity of reef habitats. In contrast, visual surveys are generally inadequate for sampling seagrass fishes due to the structure of seagrass beds, and the behaviour of the fishes within the beds. The methods used in this study were considered appropriate for surveying fish assemblages in seagrass and reef habitats, and because the experimental units were quite small it is likely that most fish on each replicate habitat were recorded, regardless of the method used.

It is now widely recognised that fish assemblages may be affected by a whole suite of pre- and post-settlement processes, and that these processes may affect the component species in different ways. Experiments like the one described in this chapter allow us to determine the relative importance of factors such as habitat structure and water depth in explaining the distribution, abundance and size structure of fish assemblages and populations. Habitat, and to a lesser extent water depth, were important factors explaining the distribution of most fish species. However, not all individuals were affected similarly, with many species demonstrating a strong preference for seagrass beds over reefs, while other species showed the reverse pattern. Generalisations about the importance of different processes in regulating fish assemblages may not be possible until we understand how factors such as habitat complexity affect individual species (Petrik *et al.*, 1999). Ultimately, defining the precise role that habitat and water depth play in determining the distribution and size structure of fish assemblages will lead to a better understanding of the particular requirements for successful recruitment, and will

thus increase our ability to effectively manage fish stocks by protecting the necessary habitats.

Summary

The influence of habitat and water depth on the distribution and size structure of fish assemblages has been well studied. However, most work has focussed on the effects of complexity within one habitat type (e.g. seagrass beds or rocky reefs). Additionally, studies tend to focus on only one life history stage of the associated fishes. In this chapter, the distribution, abundance and, to a lesser extent, the size structure of fish populations varied between habitats (seagrass and reef) and between water depths. Habitat type appeared to be more important than water depth, with most species showing a clear preference for seagrass beds (e.g. *Stigmatopora argus*) or reefs (e.g. *Vincentia conspersa*), although habitat preferences may change during a fish's life cycle (e.g. *Meuschenia freycineti*). The availability of food and shelter, and/or the densities of predators and competitors may determine these preferences. These results highlight the need for further studies examining habitat preferences of fishes, and how these preferences may change throughout ontogeny.

Chapter 7

General Discussion

The life cycles of most marine organisms, including reef fishes, can be divided into two distinct stages; a dispersive larval stage followed by a benthic adult stage. In general studies that examine the influence of different factors on the distribution and abundance of reef fishes have tended to focus either on factors affecting larvae in the water column (pre-settlement) or those influencing juveniles/adults on the reef (post-settlement). However, this division is arbitrary, as numerous processes acting before, during and after settlement will be important in determining the distribution and abundance of marine organisms. Moreover, the distribution and abundance of any one stage (i.e. egg, larva, juvenile and adult) will be influenced by events at all other stages of the life history (Jones, 1991).

To date, very few studies have examined the larval stages of reef fishes due to the inherently difficult nature of surveying very small fish in large bodies of water (but see Leis and Carson-Ewart, 1997, 1998). What is clear from studies examining settlement of reef fishes is that the number of larvae settling to a particular reef is highly variable in space and time (Doherty and Williams, 1988; Fowler *et al.*, 1992; Doherty and Fowler, 1994). This variability most likely results from variable mortality experienced by larvae in the water column and the oceanographic currents transporting the larvae (Leis, 1991).

Once larvae have settled to a reef, characteristics of the reef habitat such as water depth, topography and algal cover may have a profound influence on the distribution and abundance of reef fish species through a variety of mechanisms (Jones and Syms, 1998). Habitat characteristics can directly affect the size of reef fish populations if the availability of critical resources (e.g. food or shelter) influences rates of recruitment and mortality (Jones, 1988b). Settling reef fish larvae have been shown to distribute themselves non-randomly, which suggests habitat preferences by these larvae (Schmitt and Holbrook, 1996). However, it is important to note that differential mortality associated with different microhabitats within a reef may also be responsible for the non-random patterns observed (Gutierrez, 1998). Although reef fishes show a wide

range of habitat preferences at settlement (Marliave, 1977; Sweatman, 1983, 1988; Booth, 1992; Schmitt and Holbrook, 1996), and these preferences have the potential to significantly alter the distribution and abundance of reef fish populations and assemblages, the consequences of these habitat preferences are not well understood (Booth and Wellington, 1998).

Patterns of distribution and abundance established at settlement may also be modified by movements associated with the selection of particular habitats some time after settlement (Jones, 1991). It is common to observe spatial segregation in the distribution of reef fish recruits/juveniles and adults based on habitat (Chapter 4; Gillanders and Kingsford, 1993; Gillanders, 1997a). These distributions may result from settlement preferences by settling larvae and/or movements by recruits or juveniles redistributing themselves amongst microhabitats some time after settlement, followed by the eventual migration of juveniles to the adult habitat. Although in these species the habitat preferences of settling larvae may not directly influence the distribution patterns of adult fishes, the availability of suitable 'nursery' habitats may ultimately limit or determine adult abundance patterns (Booth and Wellington, 1998). Despite the potentially fundamental role that fish-habitat interactions may play in determining the distribution and abundance of reef fishes, habitat is often neglected in studies examining reef fish populations and assemblages as researchers tend to focus on particular processes (e.g. recruitment, predation and competition) without considering how these processes may be influenced by habitat (Jones and Syms, 1998).

The vast majority of reef fish studies have been conducted on tropical coral reefs, and while the factors influencing the distribution and abundance of coral reef fishes may also apply to temperate reef fishes, there are currently too few studies of temperate systems to assess the universality of the models generated from research on coral reef fishes. This thesis has examined the ecology of temperate reef fishes in southeastern Australia, specifically focussing on the influence of habitat, in terms of algal cover, water depth and type (seagrass vs reef), on the distribution and abundance of temperate fishes, and how habitat may affect factors such as movement. Very few studies have examined temperate reef fishes in Australia, and this study provides the first detailed examination of the ecology of reef fishes in Victorian coastal waters.

The influence of different factors, such as habitat, on the distribution and abundance of temperate reef fishes may vary depending on the species and life history stage examined, and the spatial and temporal scales at which a study is conducted (Jones, 1988a; Sale, 1998). The first part of this thesis provided a detailed account of the variation in temperate reef fish assemblages in and around Port Phillip Bay, and revealed significant differences between reef fish assemblages over both space and time. In general, fewer species and individuals were recorded over winter/spring, possibly as individuals become inactive and seek shelter in response to increased wave action and decreased water temperatures at this time (Larson, 1980; Buxton and Smale, 1989). Significantly fewer species and individuals were recorded at sites in the north of the bay (i.e. Altona and Black Rock), and sites closer together had more similar fish assemblages than sites further apart. These patterns are most likely due to nearby reefs experiencing more similar biotic and abiotic conditions (e.g. recruitment, wave action, tidal movement) than distant sites.

Over the spatial scale of this study (10-100's km), there was no relationship between fish and macroalgal assemblages. This result contrasts with previous studies showing that algal assemblages can vary substantially between reefs, consequently affecting the composition of fish species inhabiting the reefs (Bodkin, 1988; Carr, 1989; Schmitt and Holbrook, 1990a; Anderson, 1994). However, these studies have tended to focus on fish assemblages occurring in very distinct algal habitats such as *Marocystis pyrifera* canopies versus coralline covered rock flats, while all the reefs surveyed in this study were covered by similar small canopy-forming and turfing algal taxa. There was a significant relationship between the percentage cover of some algal taxa and the abundances of individual fish species (e.g. *Phyllospora comosa* and *Odax cyanomelas*). The cover of different algal taxa will invariably change through time, and fish numbers and algal cover need to be surveyed simultaneously over a number of years to thoroughly determine the relationships, if any, between particular fish and algal taxa.

Fish size is often ignored in studies examining reef fish populations, which tend to focus only on the total abundance of fishes. The work in Chapter 4 examined the distribution, abundance and size structure of two reef fish species commonly found in the coastal waters of southeastern Australia: the sixspine leatherjacket, *Meuschenia freycineti*, and the horseshoe leatherjacket, *Meuschenia hippocrepis*. Previous studies have shown that

individuals of *M. freycineti* recruit to shallow seagrass beds, while adults are more abundant on offshore reefs (Bell *et al.*, 1978; Bell and Worthington, 1993; Jenkins *et al.*, 1993). In contrast, very few studies have examined the distribution and abundance of *M. hippocrepis*, but there is no evidence to suggest that individuals of *M. hippocrepis* recruit to seagrass beds in Port Phillip Bay (Jenkins *et al.*, 1993, 1996). Distinct differences were recorded in the size structure of populations of *M. freycineti* and *M. hippocrepis* in this study. Individuals of *M. hippocrepis* were only recorded on reefs, and tended to be smaller than individuals of *M. freycineti* found on reefs. In contrast, *M. freycineti* were recorded on both seagrass beds and rocky reefs, and showed clear differences in size between these habitats. Recruits and juveniles of *M. freycineti* were only recorded in seagrass beds, while most large individuals (>200 mm TL) were recorded on reefs, with only a few large individuals present in seagrass. These differences in the size structure of populations of *M. freycineti* and *M. hippocrepis* between seagrass and reef habitats may be due to a range of factors including differential rates of recruitment and mortality between these habitats. The remainder of this thesis, however, focussed on the importance of habitat selection by settling larvae and ontogenetic movements in establishing the patterns observed.

Numerous species of temperate reef fish show spatial separation in the habitats utilised by recruits/juveniles and adults, indicating ontogenetic shifts in habitat use. Given this, the most likely explanation for the spatial separation in the distribution of recruits/juveniles and adults of *M. freycineti* recorded in this study is that individuals settle to inshore seagrass before migrating to reefs at a later stage. While the benefits of shallow water seagrass beds for juvenile fishes are well known (Orth *et al.*, 1984; Bell and Pollard, 1989), the motivation behind movements of juveniles back to reefs is less well understood. Ontogenetic changes in resource use have been recorded for many reef fish species (Shulman and Ogden, 1987; Lirman, 1994; Green, 1996), and adult fishes can have very different resource requirements compared to juveniles (e.g. food and shelter may become inadequate within seagrass beds). Studies are also required to determine whether these changes in habitat use by individuals of *M. freycineti* are obligatory. Evidence from another temperate reef fish, *Achoerodus viridis*, suggests that seagrass beds are used only preferentially, as individuals can successfully recruit directly to coastal reefs (Gillanders and Kingsford, 1993). Although differences in the size structure of individuals of *M. freycineti* between seagrass beds and rocky reefs is

compelling evidence for ontogenetic movements between these habitats, establishing a direct relationship between recruits/juveniles in seagrass beds and adults on reefs will not be easy. Novel, but expensive, approaches including micro-tags (Beukers *et al.*, 1995) and otolith microchemistry (Gillanders and Kingsford, 1996) will need to be employed due to the size and high rates of mortality experienced by recruits/small juveniles, and the considerable distances between many seagrass and reef habitats.

While evidence from Chapter 4 suggests that ontogenetic movements play a significant role in determining the distribution of *M. freycineti*, the relative importance of movement appears to vary between closely related species and also between life history stages within species. In contrast to *M. freycineti*, individuals of *M. hippocrepis* do not undergo ontogenetic movements between seagrass and reef habitats, and evidence (i.e. presence of juveniles) suggests that this species recruits directly to reefs.

Tagging/recapture data collected from adult *M. freycineti* and *M. hippocrepis* on reefs suggest that individuals of both species, at this stage of their life cycle, are resident to particular reefs and undergo only very limited movements within a reef (Chapter 5). In addition, while juvenile *M. freycineti* appear to undertake extensive migrations over unvegetated sand as they move from inshore seagrass beds to offshore reefs, a large sand patch adjacent to the reef at Nepean Bay severely restricted the movements of adult *M. freycineti* and *M. hippocrepis*. As *M. freycineti* and *M. hippocrepis* are often targeted by both commercial and recreational fishers, these limited movements may have important consequences for populations that are subject to intense fishing pressure. As movement by adult *M. freycineti* and *M. hippocrepis* between reefs appears unlikely, there is a real potential for local abundances of these fishes to be severely depleted, particularly as these species are very susceptible to trapping (Chapter 3). Although the occurrence of dispersive larvae may reduce the effects of overfishing, Marine Protected Areas may be a viable management option for protecting such reef-based fisheries (Barrett, 1995a). By establishing Marine Protected Areas on reefs surrounded by natural boundaries to movement (e.g. large patches of sand) these parks may help to protect adult fish stocks, while also providing a source of new recruits to adjacent fished areas.

One of the most striking patterns observed in this study related to the differences in the distribution of recruits/juveniles of *M. freycineti* and *M. hippocrepis* between seagrass

beds and rocky reefs. Although the patterns of distribution observed (i.e. recruits/juveniles of *M. freycineti* and *M. hippocrepis* in seagrass beds and on reefs, respectively) may have arisen through the interaction of numerous factors, the final part of this thesis was designed to examine the importance of habitat selection and movement in establishing these patterns. As the larvae of most reef fishes have the potential to disperse considerable distances away from the spawning site, larvae must be able to distinguish a suitable settling site from the myriad of habitats they might encounter (Sweatman, 1988). Seagrass beds are considered to be important nursery habitats for the juveniles of many reef fish species, due to a reduced risk of predation and increased food supply within the beds (Orth *et al.*, 1984; Parrish, 1989; Bell and Worthington, 1993). However, many reef fishes do not utilise seagrass beds and instead appear to settle directly onto reefs (e.g. *M. hippocrepis*). As seagrass beds tend to occur in shallow waters and reefs in deeper waters, if the distribution of *Meuschenia* spp. recruits/juveniles reflects habitat selection by settling larvae, are these choices driven by specific habitat or water depth preferences? By establishing artificial seagrass beds and artificial reefs in shallow and deep waters this study attempted to determine the influence of habitat type (seagrass vs reef) and water depth (shallow vs deep) on the distribution and size structure of temperate fish assemblages, specifically populations of *M. freycineti* and *M. hippocrepis*. Despite evidence from previous studies showing that both *M. freycineti* and *M. hippocrepis* utilise artificial habitats, and that both species are relatively common at the sites selected for the experiment, no *M. hippocrepis* and very few *M. freycineti* were recorded on the artificial habitats. Thus it appears that the experiment unfortunately coincided with a period of low recruitment for these species. As very few *M. freycineti* were recorded, it was possible only to speculate on the specific habitat and water depth preferences of this species. However, the distribution and size structure of individuals of *M. freycineti* did support the contention that larvae of *M. freycineti* settle to seagrass beds before moving to reefs at a later stage.

Although numbers of *Meuschenia* spp. were low during the experiment, numerous other species were recorded on the artificial habitats, and these species showed some interesting habitat and water depth preferences. Habitat type appeared to be more important than water depth in influencing the distribution and abundance of fishes, with most species showing distinct preferences for either seagrass (e.g. *Stigmatopora argus* and *Acanthaluteres spilomelanurus*) or reef (e.g. *Vincentia conspersa* and *Parablennius*

tasmanianus). The number of species tended to be greater in seagrass beds than on reefs, possibly because seagrass beds are important nursery areas, and many of the fishes recorded in seagrass were present only as juveniles (e.g. *Enoplosus armatus*). Generalisations about the relative importance of habitat in determining the distribution and abundance of fish may not be possible until we understand how different characteristics of the habitat affect the component species (Petrik *et al.*, 1999). More experimental studies manipulating habitat characteristics are required to determine how fish-habitat interactions influence processes such as recruitment, competition and predation. Only then will we understand how these processes interact with each other, and with the habitat, to produce the distribution and abundance patterns observed. Defining the precise role that habitat plays in structuring fish populations will ultimately lead to a better understanding of the particular requirements of different species, and thus increase our ability to effectively manage fish stocks by protecting appropriate and/or necessary habitats.

The distribution and abundance of temperate reef fishes varies not only between species and between individuals within a species at different life history stages, but also over space and time. These variations are in response to a whole range of different abiotic and biotic factors operating before, during, and after settlement. The work in this thesis highlights the importance of fish-habitat interactions, and how habitat may influence processes such as settlement and movement. Despite the emphasis throughout this study on the importance of inshore seagrass beds as nursery areas for juvenile *M. freycineti*, followed by their migration to offshore reefs at a later stage, previous studies have recorded *M. freycineti* in a range of habitats, including deep water *Posidonia* seagrass beds (Middleton *et al.*, 1994; Jordon *et al.*, 1998) and inner continental shelf waters (Gray and Otway, 1994). In addition, large *M. freycineti* have been recorded in shallow water seagrass beds, suggesting that seagrass may serve more than just a nursery role (Edgar and Shaw, 1995). Although *M. freycineti* appear to undergo ontogenetic movements between seagrass and reef habitats, many questions about these movements remain, not the least of which are to establish a link, in terms of movement, between individuals in seagrass and reef habitats, and to determine the links between these and other habitats, such as deep water *Posidonia* beds and inner shelf unvegetated habitats. Traditionally, temperate reefs have been viewed as closed systems, and very few studies have examined the links between these reefs and adjacent areas such as

seagrass beds, intertidal reefs and estuaries (Gillanders, 1995a). However, as studies are now revealing the potential for important links between temperate reefs and adjacent habitats (Chapter 4; Bell and Worthington, 1993; Gillanders, 1997a), with many reef fishes utilising adjacent habitats like inshore seagrass beds during the early stages of their life cycle, temperate reefs must now be considered more as open systems.

Future studies examining ontogenetic movements will also need to address questions relating to the necessity and spatial scale of these movements, and the relationship between the numbers of larvae leaving reefs and settling to seagrass beds and the numbers of juveniles migrating back to reefs (Bell and Worthington, 1993). The contribution that juvenile reef fish settling to seagrass beds make in sustaining adult populations on the reef is likely to vary between fish species, and may also depend on the proximity of the adjacent environments, and possibly the magnitude of recruitment (Gillanders, 1995a). What is clear from the work in this thesis is the need to consider the processes affecting the recruitment of juveniles to the adult population, as variation in juvenile recruitment has the potential to affect the abundance of adult fishes, at least as strongly as initial settlement of larvae (Robertson, 1998).

In a study such as this it is important to consider the influence of gear selectivity. Fine-mesh seine nets have been effective in sampling many seagrass fishes, particularly juveniles and species that occur within the seagrass canopy (Connolly, 1994; Jenkins and Sutherland, 1997). However, seine nets are less effective in surveying sediment-associated fishes and large individuals. In contrast fish traps, due to their large mesh size, are much more effective in surveying large fishes, and are generally inadequate for sampling juveniles (Whitelaw *et al.*, 1991). Visual surveys have been widely used to sample reef fishes accurately, but are unsuitable for seagrass fish surveys. The methods used in this study were considered appropriate for the habitats in which they were used, however, the potential biases of these methods must be taken into account.

While studies examining temperate reef fishes are increasing, integrated studies examining the relative importance of different factors, including habitat and movement, at multiple spatial and temporal scales are still required before we can determine the factors that are most important in determining the distribution and abundance of reef fishes. Although difficult to achieve, as many temperate reef fishes are long lived, studies incorporating all life history stages and exceeding the generation time of the

study species will provide the greatest insights (Hixon, 1998). We must also integrate studies conducted at different spatial scales; large-scale descriptive/correlative studies with small-scale experimental studies. Although the vast majority of reef fish studies are conducted in tropical waters owing to good working conditions and the opportunity to conduct experiments using patch reefs, this study has shown that temperate waters are also amenable to experimentation. Future studies of temperate reef fish will need to incorporate more manipulative experiments designed to illuminate the interactions between, and determine the relative importance of, the different processes that result in the distribution and abundance patterns we observe on these reefs.

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