Ontogeny and ecology of snapper (*Pagrus auratus*) in an estuary, the Mahurangi Harbour

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Abstract

This thesis examined the use of an estuary by the sparid *Pagrus auratus*, commonly known as snapper. The density and distribution of snapper (juveniles through to adults) was quantified over multiple spatial and temporal scales and associated with habitat.

Juveniles enter or are spawned within the Mahurangi Harbour over the warmer months, with densities highest in March. Ontogenetic shifts in fine-scale habitat occurred. Fine-scale analysis from the beam trawl showed juvenile snapper (< 10 cm) were mostly associated with horse mussels. Larger juveniles (> 4 cm) were also associated with bare areas. The 0+ fish (from the DUV) occupied fine-scale habitat comprised of muddy to sand substrata with structure of sponges and horse mussels with and without epifauna. The remaining year-classes occupied a coarser substratum, with shell hash the major secondary structure. An artificial reef experiment showed juvenile snapper were attracted to artificial horse mussels with and without epifauna rather than bare areas or controls. The 1+ year-class increased their habitat range, occupying areas with more uniform substrata. A growth shift through to the 2+ year-class was not observed, and this may be due to increasing mortality, (natural or predation), or emigration out of the harbour. Densities of the larger year-classes decreased over the cooler months but not all snapper leave permanently, with tagging showing up to 80% of fish to be resident.

Ontogenetic shifts occurred in diet with growth. Juveniles < 2 cm consumed planktonic copepods, with > 2 cm consuming benthic copepods, mysid and caridean shrimps and polychaetes. Snapper > 10 cm consumed brachyuran crabs, caridean shrimps, bivalves, polychaetes and hermit crabs, with > 30 cm fish able to consume harder shelled molluscs and bivalves. The *a priori* habitats were equally productive in terms of prey, and this may be advantageous for juveniles who can then select a habitat for other qualities, i.e. protection from predation. Despite the potential of snapper to utilise any sort of structure as cover or for rest, most structure within the Mahurangi are biogenic and susceptible to anthropogenic effects, especially sedimentation. The loss or decline of these biogenic species may therefore have a significant impact on the way snapper utilise the Mahurangi. Overall, understanding the ontogeny of snapper within estuaries will contribute to better management strategies for snapper in general.

Dedication

This thesis is dedicated to the memory of my Dad, Peter Usmar, who lost his battle with bone marrow cancer in the first year of this study.

It was from you I developed a love of the sea and fishing. You taught me many things, especially that I could do anything!

I miss you every day.

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Now for that job....

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CHAPTER ONE

General Introduction

Many marine organisms undergo major habitat or resource shifts over their life, due to factors such as changes in habitat use, resource utilisation abilities, predation risk or susceptibility to physical factors (Werner and Gilliam 1984). Ontogeny relates to the origin and development of an individual, while ontogenetic shifts occur in response to different life stages (e.g. Werner and Gilliam 1984; Dahlgren and Eggleston 2000). The ontogenetic shifts observed depend on the scale or scales at which observations are made at (Anderson 1994; Gillanders et al. 2003; McDermott and Shima 2006). Studies may occur for instance at a large scale, i.e. between estuaries and coastal areas (Gillanders et al. 2003), at a more intermediate scale such as within an estuary or lagoon (Sheaves et al. 2006; Burke et al. 2009) or at a fine-scale such as within the same kelp plant (Anderson 1994) or some combination of these. Examining ontogenetic shifts at varying scales can lead to a better understanding of the species under study, which is important for assessment and management (Sheaves 2006).

For a mobile species, many of which may regularly use more than one habitat type, an investigative approach that incorporates multiple habitat types may be the most appropriate for understanding ontogenetic complexity (Pittman et al. 2004). Various authors (reviewed by Pittman and McAlpine (2003)), have discussed fish and decapod crustaceans which over their lifetimes shift through a 'critical chain' of habitat types while using inshore areas, leading to the hypothesis that the composition and spatial arrangement of habitat types, including their proximity to one another is important in meeting the requirements of ontogenetic change. For example, for coral reef fishes, sheltered back-reef areas and lagoons often support small juvenile fish, while adults move out to adjacent deeper reefs; however; the use of distinct juvenile habitats can vary greatly amongst species (Doherty and Williams 1988; Nagelkerken et al. 2001; Gillanders et al. 2003). Utilisation of varied juvenile habitats may be possible for species with highly generalised diets or habitat types, while specialists may be constrained to one or two habitats (Nagelkerken et al. 2001; Nagelkerken and van der Velde 2004). If food resources are restricted, juveniles may settle directly into habitats

occupied by adult conspecifics (Jones 1987). For instance, different butterflyfish species (Family Chaetodontidae) exhibit different settlement strategies; including settling in preferential habitats or micro-habitats with adults, settling indiscriminately; but having higher survivorship in more complex habitats, or having juvenile habitats distinct from adults (Pratchett et al. 2008). Out of ten species studied, seven were found within the same habitat as large adults, and these seven species also had a strong reliance on particular corals, reflecting specific dietary requirements (Pratchett et al. 2008).

Highly mobile fish species in temperate coastal waters typically have a tri-phasic life history strategy, with three key phases (Pittman and McAlpine 2003). The first phase is the planktonic movement of eggs and larvae, the second phase that of juvenile use of shallow water areas, and the final phase that of an increase in home range related to both increasing body size and changing food requirements (Bond 1996; Pittman and McAlpine 2003). Many studies have sampled juvenile habitats and assumed that once juveniles are no longer found, they have moved to adult habitats (Gillanders et al. 2003). Although this may be true, without strong evidence relating to growth and movement over multiple scales, it is difficult to discount the alternative hypothesis that these individuals died, either naturally or through being preyed upon (Sheaves 2001; Gillanders et al. 2003). However, understanding the distribution of a range of year-classes among different habitats may provide some evidence for movement. For instance, Gillanders (1997b) showed that the density of blue groper juveniles (*Achoerodus viridis*) proportionally decreased from estuaries to open coastal reefs while the adults showed the reverse pattern. No differences in growth rates between estuaries and open coastal reefs were found, leading to the conclusion that fish undergo habitat shifts with increasing size (Gillanders 1997a).

Estuaries

Estuaries are transition zones, where fresh water from land drainage mixes with seawater creating some of the most biologically productive areas on Earth (Kennish 2002). They typically contain a mosaic of habitats that may include mangrove forests, seagrass meadows, salt-marsh, bivalve reefs and bare soft sediments. The main environmental parameters known to affect the spatial organisation of estuarine communities are salinity, dissolved oxygen, temperature, depth, turbidity, current

regime and substratum type, all of which can vary over a range of temporal and spatial scales (Kennish 1990). Research has suggested that up to 90% of the United States commercial catch and 70% of the Gulf of Mexico's recreational catches come from fish and invertebrates dependent on estuaries for completion of some critical life history stage (Caddy 2007). However, estuaries are among the most heavily impacted aquatic systems as they are sites of intense human activity, with a projected figure of six billion people utilising coastal areas by 2025 (Kennish 2002). As a result, estuaries are therefore highly vulnerable to anthropogenic impacts such as urbanisation, sedimentation, and agricultural run-off, which may reduce their ability to support productive and healthy populations of fish, shellfish and invertebrates, with habitat loss considered the biggest threat to biodiversity (Gray 1997; Lotze et al. 2006; Airoldi and Beck 2007).

Estuaries receive natural sediment inputs, which perform a number of important functions such as nutrient supply, burial of contaminated sediments, and buffering of coastal erosion (Thrush et al. 2004). However, environmental problems occur when the rate at which sediments deposit to these regions is greatly increased through human activities. Highly turbid waters can restrict light transmission, and directly affects suspension feeders by clogging feeding structures and interfering with particle selection (Thrush et al. 2004; Coen and Grizzle 2007). Human impacts as measured across twelve estuarine and coastal areas in North America, Europe and Australia resulted in the depletion of *c.* 90% of formerly important species (including biogenic habitat formers such as oyster reefs, sponges and corals), destroyed 65% of seagrass and wetland habitat, degraded water quality, and accelerated species invasions (Lotze et al. 2006).

Fish ecology

Reaching adulthood requires successful recruitment, growth and survival both within juvenile habitats, and during subsequent migration to adult habitats (Minello et al. 2003). The shallow and protected waters of estuaries and harbours contain fish species that range from truly estuarine to those that have a broad range extending beyond estuaries (Lenanton and Potter 1987; Potter et al. 1990; Robertson and Duke 1990). A number of factors may determine the assemblage structure of fishes in estuaries, including species interactions, biological processes and physical variation. Post-

recruitment processes are thought to have a significant influence on assemblages and may include factors such as predation, with other fish often being the most common predator (Werner et al. 1983; Connell and Kingsford 1998; Hindell et al. 2000; Baker and Sheaves 2005). It is not uncommon for 99% of a cohort's mortality to occur during the first 100 days of life through natural mortality or predation, with mortality rates negatively correlated with size (Potter et al. 1990). Fish that are potential prey have been known to perceive their level of predation risk through the interception of physical or environmental cues and reduce their level of risk by seeking out conditions or environmental regimes that may reduce a predator's efficiency (Clark et al. 2003). Turbid waters for example are also thought to provide refuge from predation (Blaber and Blaber 1980), but some piscivorous fish show little reduction in feeding under turbid conditions due to their ability to use non-visual senses (Sheaves 2001). A number of environmental factors may also play an important part in determining assemblage structure (Potter et al. 1990). For instance, within the Peel-Harvey estuary in Australia, the number of species, density and biomass of fish in the shallows were more highly correlated with distance from the estuary mouth and temperature, rather than salinity (Loneragan et al. 1986). Variability in water temperature, salinity and dissolved oxygen were found to contribute more to the early growth of juvenile sciaenid's than did the variability in diet and habitat structure in a Louisiana saltmarsh (Baltz et al. 1998).

The ability to forage efficiently can affect an individual's growth rate, which may in turn affect its vulnerability to predators and its ability to exploit certain food resources (Werner et al. 1983; Francis 1994). Size-specific shifts in diet have been well documented (e.g. Grossman et al. 1980; Robertson 1980; Szedlmayer and Lee 2004), with these shifts often associated with, or caused by, shifts in habitat (Werner and Gilliam 1984; Sudo and Azeta 2001; Szedlmayer and Lee 2004). Habitats can vary spatially and temporally in foraging profitability, and the added risk of predation means animals must balance the gains and risks as a consequence (Werner et al. 1983; Lineham et al. 2001). A study looking at the variability of King George whiting (*Sillaginodes punctata*) in relation to predators showed a trade-off, where fish preferred to forage in vegetated areas that provided refuge from predation regardless of the higher levels of food in nearby unvegetated habitat (Hindell et al. 2002).

Habitats and structural complexity

In the general ecological literature 'habitat' is the place where a population of a particular species lives at any particular time (e.g. Kramer et al. 1997). There have however been many discussions in the literature as to what actually constitutes habitat. Pittman and McAlpine (2003) developed a new interpretation; 'the habitat (or environment) of an animal is the interacting biotic and abiotic patterns and processes that an animal responds to in course of its life-cycle trajectory'. Being able to identify and describe habitat distributions at broad spatial scales enables an understanding of patterns in communities (Andrew and Mapstone 1987; Underwood et al. 2000). Often only one sampling method is employed, which may mean that only a small component of the population and environment can be studied (Rountree and Able 1997; Nagelkerken et al. 2001). Limiting studies to a singular habitat type or classification has allowed the simplification of what otherwise may be complex spatial patterns (Pittman and McAlpine 2003). This means linkages between habitats at different scales may not be properly understood, at the expense of understanding the species under study. For instance, a comprehensive survey across multiple habitats and locations within the lagoon of the Bay of La Parguera, Puerto Rico, revealed adult grunts (Family Haemulidae) associated with coral reefs during the day, but migrated to surrounding soft-bottom areas at night to feed primarily on benthic invertebrates (Burke et al. 2009). Therefore, a more comprehensive approach to assess habitat preferences of fish would include sampling across a range of habitats and analysing patterns of fish abundance, age/size structure, diet, species richness and composition (Gillanders 1997b).

Structural complexity can create micro-habitats that may allow the coexistence of predators and prey (Crowder and Cooper 1982). Habitat types are usually defined as a unit of dominant vegetation, such as kelp forests or seagrass beds (e.g. Shears et al. 2004; Coen and Grizzle 2007). These species can modify their environment and facilitate conditions for other members of the community by reducing stress or by increasing the flow of resources (Norkko et al. 2001). On rocky reefs, seaweeds support diverse and productive assemblages of small mobile invertebrates that contribute approximately 80% of energy flow and materials through rocky reef animal communities (Taylor 1998). Sedimentation onto reef areas reduces water clarity and can affect seaweeds directly, reducing primary production (Duarte 2002; Airoldi and Beck

2007). Within estuaries and sheltered coastal embayments, seagrass declines have been linked to anthropogenic influences such as eutrophication and sedimentation (Duarte 2002). Shellfish particularly bivalves, are now also recognised as important habitats, providing structural complexity in the form of reefs (e.g. oysters), aggregations (e.g. clams or horse mussels), or shell hash after they die (Coen and Grizzle 2007).

These areas provide habitat for many organisms, including fishes and are considered to be an important component of nurseries in many estuaries and sheltered coastal embayments (Beck et al. 2001; Gillanders et al. 2003; Heck et al. 2003; Coen and Grizzle 2007). Much of the literature focuses on the importance of structural complexity for fish, especially juveniles, and it is assumed more complex habitats provide protection from predation, and/or increased resources (Dahlgren and Eggleston 2000; Diaz et al. 2003). However, the underlying mechanisms are rarely tested (Sheaves 2005; McDermott and Shima 2006). For instance, until recently it was assumed that juvenile snapper using soft-sediment habitats lived within a relatively simple environment. However, more recent studies at finer spatial scales have shown these habitats are relatively complex, containing small-scale biogenic or physical features (Thrush et al. 2002). Across the many species of flatfish, traditional sampling has included environmental variables and sediment characteristics (usually mean grain size) that have shown the importance of relatively uniform, soft-sediments to this species group (Gibson 1994; Gibson and Robb 2000; Stoner and Abookire 2002). However, recent studies utilising cameras have found that variables such as surface bed form, structural complexity and the presence of worm tubes are also important in defining flatfish habitat (Stoner and Titgen 2003; Stoner et al. 2007).

It is commonly assumed that an association with a particular habitat or structural habitat type is a result of preference for that habitat (Crowe and Underwood 1998). Many habitat features are correlated in nature however, so the habitat variables that may seem to be the most important may not necessarily be important to the species under study (Kramer et al. 1997; Crowe and Underwood 1998). Well-planned descriptive studies are a necessary pre-cursor to experimental tests of hypotheses; however, experimental studies can be used to elucidate patterns, answer ecological questions and discriminate among hypotheses (Underwood et al. 2000). Multivariate analyses have been shown to help partition out patterns of ecological complexity (Clarke and Ainsworth 1993;

Anderson and Millar 2004), but experimentation is necessary to determine the variables that provide cues for fish (Kramer et al. 1997).

Snapper

The subject of this research is the sparid *Pagrus auratus* (Bloch and Schneider, 1801), commonly known as snapper. This species ranges across most of the temperate to subtropical Western Pacific, and into the tropical waters of the Northern Hemisphere (Paulin 1990). It supports large commercial and recreational fisheries around the world, including Australia (Fowler and Jennings 2003; Moran et al. 2003), Japan (Sudo et al. 1983; Sudo and Azeta 2001) and the east and west coasts of northern New Zealand (Francis 1993; Maunder and Starr 2001; Sullivan et al. 2005). Within New Zealand waters, snapper occur across the continental shelf from estuarine habitats to depths down to 200 m, but are most common in depths less than 50 m (Paul 1976; Francis 1993). They are generalist predators that take primarily invertebrate prey from soft sediments (Colman 1972) and rocky reefs (Choat and Kingett 1982). Snapper start reproducing at between three to five years of age (20–29 cm fork length), at which time around half the population change sex from female to male (Francis and Pankhurst 1988). Snapper are serial spawners and can spawn for up to five months over September–March, with peak activity in November-January (Crossland 1977; Crossland 1981; Scott and Pankhurst 1992; Francis 1994).

The management of snapper in New Zealand is divided spatially into six areas (stocks), with the SNA1 area on the east coast of the North Island being the most productive (Sullivan et al. 2005). All snapper stocks are considered fully exploited (Sullivan et al. 2005), so the effective management of the snapper resource, and protection of continuing juvenile recruitment, is considered necessary for its on-going existence. The importance of this species has also made it one of the most studied in New Zealand. A substantial amount of work has been carried out on coastal snapper populations. Colman (1972) gives details of studies from as far back as 1892, with more recent studies encompassing diet (Godfriaux 1969), growth and reproduction (Crossland 1977; Scott and Pankhurst 1992; Francis 1994; Francis 1997; Zeldis and Francis 1998), general ecology (Kingett and Choat 1981; Francis 1995), movement (Crossland 1976; Hartill et al. 2003; Parsons et al. 2003; Egli and Babcock 2004), marine reserve protection (Willis

et al. 2003; Denny et al. 2004; Willis and Millar 2005), habitat (Thrush et al. 2002; Ross et al. 2007), and behaviour (Morrison and Carbines 2006).

New Zealand estuaries and the contribution of this study

New Zealand's estuaries are distinct from other temperate estuaries in south-western Australia and southern Africa, in having no uniquely estuarine fish species and a high proportion of diadromous species (i.e. freshwater fish that spends an obligatory phase of their life-cycle at sea) (Potter et al. 1990; Jellyman et al. 1997). Seventeen out of the 27 indigenous freshwater fish species in New Zealand are diadromous, which illustrates the essential role that estuaries play in providing a pathway for these species (Jellyman et al. 1997).

Recent examples show the importance of New Zealand estuaries for some marine fish species. A broad-scale survey of 30 estuaries in northern New Zealand quantified assemblages of small-fish species and related these to numerous predictor variables (Francis et al. 2005). At least a third of the species sampled were juveniles that utilise open coasts as adults. However, sampling biases meant that relatively few species were caught, and diversity would probably increase if a number of different sampling methods were used (Francis et al. 2005). Otolith chemistry work from the west coast of the North Island's snapper fishery (SNA 8) strongly suggested that this population comes largely from one harbour, the Kaipara (Morrison et al. in review). Within this harbour, juvenile snapper were associated with nursery habitat composed of subtidal seagrass meadows and horse mussel beds (*Atrina zelandica*). Horse mussels are an important suspension feeder found in sandy to muddy soft sediments around New Zealand (Cummings et al. 1998). This species can grow up to 30 cm long and adds three-dimensional structure to soft-sediment habitats, providing refuge from predation for small fish and invertebrates, hard surfaces for the settlement of encrusting fauna and modifying flow (Cummings et al. 1998; Green et al. 1998; Cummings et al. 2001). Horse mussels are highly sensitive to elevated suspended sediment concentrations, which can depress their feeding rates and negatively affect physiological condition (Ellis et al. 2002; Hewitt and Pilditch 2004; Lohrer et al. 2006a).

The importance of estuaries and shallow embayments as fish nursery habitats is now widely acknowledged (Lenanton and Potter 1987; Potter et al. 1990; Morrison et al. in review). Estuaries and protected coastal embayments have been found to provide habitats important for the settlement of larval snapper from the plankton, acting as juvenile nurseries for snapper in the first few years of life (Gillanders 2002; Thrush et al. 2002; Morrison et al. in review). Adult snapper may also utilise estuaries and sheltered coastal embayments on a seasonal basis, moving between these and deeper coastal habitats (Hartill et al. 2003; Parsons et al. 2003; Willis et al. 2003). A better understanding is required of the resources used by snapper at different life stages and how important different habitats are in maintaining populations.

Most traditional work has involved extractive sampling techniques which only give a snapshot of how many fish are found in a particular habitat at a given time (Hartill et al. 2003). Habitat preferences can also vary with tidal and diel movements, as some species may utilise specific sites during the day, then migrate to adjacent areas at night to forage or to shelter and rest (Kramer et al. 1997; Rountree and Able 1997; Morrison et al. 2002). Repeated sampling over spatial and temporal scales enables a picture to be constructed of habitat use relative to time and size or age (Morrison et al. 2002). Ideally, multiple sampling methods would be used together to obtain more accurate population estimates and reduce sampling biases (Rozas and Minello 1997; Morrison and Carbines 2006). In New Zealand, estuarine snapper populations have only recently been investigated (Morrison et al. 2002; Hartill et al. 2003; Francis et al. 2005), with estuaries now acknowledged as important nursery grounds (Morrison et al. in review). However, we have no knowledge of how snapper may utilise these areas over time, or the habitats that may be important to different life stages. Connectivity between estuaries and the open coast at various life stages is also poorly understood (Morrison et al. in review).

Thesis overview and aims

The major objective of this thesis was to examine the ecology of snapper in an estuary, the Mahurangi Harbour, a drowned river valley considered representative of many northern New Zealand estuaries. Particular focus was directed at the habitat usage of

life stages from juveniles through to adults, at multiple spatial and temporal scales. The study site is described in detail first, and then the thesis chapter aims are outlined.

Study site

The Mahurangi Harbour is a sheltered estuary (24.5 km^2), on the north-eastern coast of New Zealand, approximately 50 km north of Auckland ($36^o30'S$, $174^o45'E$) (Figure 1). This estuary was formed by the 'drowning' of a river valley during the last post-glacial rise in sea level (Feeney and Challis 1984). The narrow entrance faces north-east creating a sheltered environment. The Mahurangi River provides the largest freshwater input, draining 45% (5445 hectares) of the total catchment area and contributing about 51% of the catchment's freshwater to the estuary (Feeney and Challis 1984). The harbour becomes steadily deeper towards the entrance, with mudflats more confined to the upper reaches of bays and inlets as the level of wave energy in the harbour increases (Feeney and Challis 1984). The tidal range is around 2 metres with extensive mudflats being exposed at low tide, and water clarity increasing towards the entrance. Soil eroded from the Mahurangi catchment is deposited into the harbour via the Mahurangi river, and from the smaller sub-catchments along the sides of the harbour between the river and the entrance (Gibbs 2006). The major sources of sediment are pasture (catchment area 70%), native forest (catchment area 20%) and exotic pine forest (catchment area 8%) (Gibbs 2006). Based on modelling estimates, pine forest contributes higher than expected sediment loads, with a high concentration in the upper harbour. However, most of the sediment load comes from pasture, and to a lesser extent native forest in the small sub-catchments along the sides of the harbour. Most of the sediment delivered to the harbour is washed off during storms (Gibbs 2006).

The organisation of the thesis is as follows:

Chapter Two: Density and distribution of juvenile snapper is quantified over multiple spatial and temporal scales and associated with habitat structure. Environmental data is used to identify specific factors correlated with areas of high abundance. An experiment is run in the field to separate the effect of habitat structure on the recruitment of juvenile snapper from other potential variables.

Chapter Three: The abundance and distribution of all sizes of snapper are quantified across a range of spatial and temporal scales using night-time video sampling. Habitat associations are examined at multiple scales to understand how snapper may utilise these habitats and if shifts in habitat use occurred with growth/increasing size. A tagging study is undertaken to quantify fish movement within and out of the harbour.

Chapter Four: The diet of snapper is examined with respect to fish size, and how this relates to the known habitats within the harbour on a seasonal basis. The results are then compared to published information on diets of snapper from coastal areas.

Figure 1: The Mahurangi Harbour, looking north to the where the river enters the harbour, from the mouth (upper left). The north-eastern arm can be seen to the far right of the picture.

CHAPTER TWO

Spatial and temporal patterns in juvenile snapper (*Pagrus auratus*: Sparidae) within an estuary

Introduction

Estuaries are utilised by a wide range of fish species at various life stages for spawning, feeding and migration. These are particularly important areas for juvenile fish, offering suitable conditions for growth and survival (Blaber and Blaber 1980; Robertson and Duke 1987; Gillanders 1997b; Morrison et al. 2002; Able et al. 2006; Morrison et al. 2008). This is seen in the very large numbers of juvenile fish found in many estuaries (Lenanton and Potter 1987; Potter et al. 1990). Estuaries are also highly vulnerable to habitat degradation from anthropogenic impacts such as urbanisation, sedimentation, and agricultural run-off, which may reduce their ability to support productive and healthy fish populations (Kennish 2002; Morrison et al. 2008). Since many of the larger marine species that use estuaries as nursery areas are of commercial and recreational importance, much emphasis has been placed on the need to preserve these areas in order to ensure the survival of important fisheries (Potter et al. 1990).

Within the marine environment, documenting temporal and spatial patterns in organism abundance is important for identifying and understanding possible causative processes (Underwood et al. 2000). Fish are not distributed randomly and their use of habitats can be complex. The value of estuaries as settlement areas for fish has been attributed to their lower predation risk, higher productivity, shelter from waves and storms, and structural complexity, which may enhance the abundance of juveniles and optimise their growth (Blaber and Blaber 1980; Potter et al. 1990; Sogard 1992; Gibson 1994; Le Pape et al. 2003; Baker and Sheaves 2005; Morrison et al. 2008). Differential larval supply may also affect the overall community structure with initial settlement patterns influencing the distribution of fish, especially if post-settlement movement is limited; therefore, it is important to make evaluations over multiple spatial and temporal scales (Francis 1995; Shima 2001; Laurel et al. 2003).

Structurally complex habitats may influence the population dynamics of a fish species and are thought to be most important for juvenile life stages, typically reducing predation-mediated mortality (Hixon and Beets 1993; Gibson 1994; Thrush et al. 2002). Alteration of habitat structure in these areas may have serious effects on survival and recruitment through the physical alteration of the substratum, with potential effects on settlement and food supply (Gibson 1994). In a comprehensive experimental study testing the hypotheses of structural heterogeneity, predation risk and food availability in both the field and laboratory, mangroves were found to provide structure at an intermediate scale in which the capture of invertebrate food prey by juvenile fish appeared optimal compared to the risk of predation (Laegdsgaard and Johnson 2001). At a particular size, fish became less vulnerable to predation and moved to open habitats to feed (Laegdsgaard and Johnson 2001). However, other reasons for utilising areas of structural complexity cannot be ruled out, therefore not all complex habitats may be valued equally (Laurel et al. 2007). Variability in water temperature, salinity and dissolved oxygen for instance, contributed more to the early growth of juvenile sciaenid's than did variability in diet and habitat structure in a Louisiana salt marsh (Baltz et al. 1998). Pacific cod (*Gadhus macrocephalus*) have a preference for Laminaria beds (large brown kelps), while saffron cod (*Eleginus gracilis*) seem to prefer eelgrass, and although these areas may have been chosen as a means of reducing predation, environmental covariates influencing this preference could not be discounted (Laurel et al. 2007). Many habitat features are correlated in nature, so the habitat variables that may seem to be the most important may not necessarily be the features important to the species under study (Kramer et al. 1997).

Snapper utilise a wide variety of habitats, including rocky reefs, estuaries and soft sediments, to depths of 200 m, but are most abundant over mud and sand at depths of less than 50 m (Paul 1976; Francis 1993). On reefs, abundances of 0+ snapper are lower over winter than summer, with fish found on sedimentary flats next to rocky reefs and kelp forests and associated with coralline turf (Kingett and Choat 1981). No relationship with topographic complexity was found in that study, rather the distributions were attributed to quality and quantity of food (Kingett and Choat 1981). A later study in the same area found the greatest densities of 0+ snapper along the reef-sand interface and this suggested a trade-off between the shelter provided by complex on-reef habitats and the food available in adjacent soft-sediments (Ross et al. 2007). In laboratory habitat-

choice experiments, juvenile snapper increased their use of a structurally complex habitat when a predator was present (Ross et al. 2007). Studies on juvenile snapper in soft sediments over large spatial scales have demonstrated small scale (< 1 km) spatial variability over several years (Francis 1995). The variability was attributed to differences in micro-habitat type, with snapper thought to prefer a muddy substratum over a muddy sand-shell hash mix (Francis 1995), although this could not be adequately tested due to the insufficient spatial resolution of the trawl used (Thrush et al. 2002). Distributions of 1+ and 2+ snapper in a soft sediment embayment were related to small-scale biogenic features such as burrows, shells, boulders, cobbles, depressions and sand waves that were nested within sand and mud (Thrush et al. 2002). These results emphasised the importance of habitat structure to juvenile snapper and refined the results of Francis (1995). No evidence was found for a relationship between potential food and the abundance of juvenile snapper with the conclusion that the association was driven by refuge from predation (Thrush et al. 2002).

Large-scale studies are often conducted for mobile fish species and may examine fish distribution in the context of physical processes, larval supply or predator distribution, but they often lack an experimental framework in which to measure the mechanisms that contribute to the observed distribution patterns (Laurel et al. 2003; McDermott and Shima 2006). Recent work has demonstrated that estuaries provide important habitats for the settlement of larval snapper from the plankton, and subsequently act as juvenile nurseries for snapper in the first one to two years of life (Gillanders 2002; Thrush et al. 2002; Sumpton and Jackson 2005; Morrison et al. in review). Evidence from the west coast of New Zealand has established that the coastal snapper stock (SNA 8) is largely derived from the estuaries adjacent to this coastal area (mainly the Kaipara harbour), with densities of 0+ snapper strongly correlated with seagrass (*Zostera mulleri*) and horse mussel beds (*Atrina zelandica*) (Morrison et al. in review). Very recently, large-scale field experiments using artificial seagrass units to assess the role of patch size and seagrass blade density in driving habitat usage by small fishes including have been conducted in the Whangapoua estuary in Coromandel. Higher numbers of small fish including juvenile snapper were found in association with the experimental units as compared to the surrounding bare sediment (M. Morrison, pers. comm.). Well-planned descriptive studies are a necessary pre-cursor to experimental tests of hypotheses,

however, experiments are often needed to elucidate patterns, answer ecological questions and discriminate among hypotheses (Underwood 2000).

The aim of this study was to quantify the density and distribution of juvenile snapper within an estuary and describe any relationship with habitat structure. Areas and habitat types within the Mahurangi Harbour were defined *a priori* using an existing habitat map (Morrison et al. 2000). Sampling was conducted every three months (i.e. the beginning of each season) over two years to ascertain if any ontogenetic shifts occurred within or between habitats over spatial and temporal scales. Environmental data was collected to identify specific factors correlated with areas of high juvenile snapper abundance. An artificial reef experiment was run in the field to separate the effect of habitat structure on the recruitment of juvenile snapper from other potential variables.

Methods

Study area

This study was carried out in the Mahurangi Harbour from December 2005 to September 2007. The harbour was divided into five arbitrary areas (upper, mid and lower parts of the central harbour and the two main arms), and broad-scale habitat types within these areas were also distinguished using detailed habitat and bathymetric data (Morrison et al. 2000) to enable consistent spatial sampling (Figure 2.1). The broad-scale habitats were defined as follows: "Horse mussels" – large areas of subtidal horse mussel beds; "sand" – large area of coarse to fine sand in the lower part of the harbour; "subtidal mud" – large tracts of uniform soft sediment, mainly in the subtidal channel areas; "shell hash" – area of large dead shell matter made up of mainly dead horse mussel and scallop shells; "intertidal" – area of mainly uniform soft sediment exposed at low tide.

Broad-scale sampling

A previous comparison of sampling gears, both passive and area-swept, found that dropped underwater video (DUV) was the most effective at capturing a wide range of snapper sizes, and returned numbers that appeared to represent near absolute densities (Morrison and Carbines 2006). However, for snapper < 50 mm the DUV was not as

effective as the beam trawl, which was the most effective sampling gear for snapper in the size range 10–80 mm (Morrison and Carbines 2006). Therefore, for this study, a beam trawl was used to sample small juvenile snapper every three months from December 2005 to September 2007 (December being the start of each settlement season for a year-class). All sampling was conducted from mid to high tide during the middle of the day. The trawl consisted of a 4 m wide beam from which was suspended a 3 m wide trawl net, with a 6 m deep cod-end composed of 9 mm mesh (Figure 2.2). A net spread of 3 m was assumed for estimating the area swept. Five areas were assigned throughout the harbour across known habitats of horse mussels, shell hash, sand and subtidal mud. Not all of the habitat types occurred in each area (Table 2.1). Initially, intertidal habitats were also sampled in areas 1, 4 and 5, but as very few fish were caught and it was a difficult area to work in, this habitat was discontinued for the beam trawling. Within each habitat type in each area, 4 haphazardly located shots were completed, with the positioning of the tows being wind and current dependent, although along the depth contours if possible. Each shot was ~ 200 m long from the time the gear made contact with the sea floor and the warp came up hard. A 5:1 warp to depth ratio was used with a tow speed between 1.5 and 2 knots. A total of 9 habitat types x 4 shots totalled 36 shots per season, over 8 seasons. All trawling was done from the Leigh Marine Laboratory's vessel R.V. Hawere. The catch from each shot was sorted quickly. All fish were identified (see Appendix 2.1 and 2.2) counted and measured to the nearest mm and then released alive. The exceptions were gobies and triplefins, which were counted but not measured due to their high numbers, and juvenile snapper, which were anaesthetised using MS222 then placed in 10% formalin in seawater. Snapper lengths and weights were measured at the end of the day back at the Leigh Marine Laboratory. All invertebrates and pieces of structure that came up in the trawl were identified, counted and/or noted. Depth, time and water temperature were recorded for every shot, while salinity (ppt) and secchi dish measurements in meters (i.e. measure of water clarity) were taken and recorded on every second shot.

Experimental test of the effect of structure

An artificial reef experiment was designed to determine if the addition of structure to a bare area within the harbour influenced the recruitment of small snapper, thus removing the effects of potential covariates at sites with natural structure. Artificial reef units

(ARU's) were designed, built and deployed over the summer of 2007–08. The results of this chapter and Chapter Three indicated that horse mussels were an important structural component utilised by juvenile snapper. The ARU's were designed to mimic a dense patch of horse mussels and the recruitment of fish to each patch was monitored over a six month period. Each unit was made of a 1 m^2 steel frame over which shade cloth was stretched to form a base that artificial horse mussels could be attached to. Ten individual horse mussels were collected and a silicon mould was taken off each one. Resin was poured into the mould to the volume of a third of the horse mussel and swirled around to form an outside coating over the whole horse mussel. Once set, foam was poured into the resin casing to make the horse mussel solid. A groove was ground into the top to resemble an open, living natural animal and twenty artificial horse mussels were attached to each frame with resin at haphazard positions. The experimental design was a balanced, randomised block design, of four levels with five replicates, making a total of 20 units. The levels were; plain horse mussels, horse mussels with epifauna, controls and bare areas. Horse mussels with epifauna had extra items added to them to mimic horse mussels in the field that have a large amount of invertebrate growth attached in the form of sponges, tunicates, soft corals etc. (Figure 2.3). Plain horse mussels were used directly out of the mould with no additions, while controls consisted of frames with shade cloth only, and bare areas were bare sediment. Frames were randomly assigned a number and deployed into the field mid-December 2007 in rows, with each unit 10 m apart. When the replicate was a bare area, it was marked by a rope and sub-surface float and the bare sediment was sampled to the right of the float. Each row of four replicates was connected by rope, and rope was connected across the top and bottom of the grid to enable divers to navigate around the grid easily in visibility that ranged from 0.5 to 2 m. The experiment was located in area three, sub-tidal mud habitat (Figure 2.3).

Visual surveys by the author and one other diver were completed approximately monthly, at the end of January, beginning of March and end of March-beginning of April. Counts were made of fish on each experimental unit and out to 1 m and a visual estimate was made of snapper size. At the end of April, the experiment was retrieved from the water. An enclosing net made of shade cloth (0.5 mm mesh) was attached to an aluminium frame designed to drop down into a slot on the steel frame of each ARU to ensure no fish escaped from around the edges. Before retrieval, a diver attached a

locator buoy to each frame to enable the collector net to be dropped down directly onto the ARU to minimise disturbance to fish. Once the collector net was sealed to the ARU, it was pulled to the surface, rinsed with fresh water and all fish and invertebrates retained were placed on ice. Each section of shade cloth with horse mussels attached was removed from the frame and place in a sealed bag to enable details of invertebrate growth onto the artificial horse mussels to be quantified. For the bare replicates, a 1 m^2 enclosing bag net made with 0.5 mm mesh, with lead weight around the base was placed down onto the sediment, and drawn closed. The weight around the edge enabled the bag to be closed without the edges of the net losing contact with the sediment, capturing all fish and invertebrates within that area; the bag was then lifted to the surface.

Data Analysis

Snapper density (standardised to number of fish per 100 m^2) and environmental data were shown graphically within the spatial (areas and habitat types) and temporal (seasons) sampling design for the harbour. As the sampling design contained missing cells (i.e. not all habitats occurred in all areas) these factors could not be tested using ANOVA. As the habitat types were assigned based on the initial areas (i.e. not randomly), pooling the data by area or habitat and testing these separately was not considered appropriate. Therefore, only seasonal differences were tested with ANOVA. Data were tested for homogeneity of variance using Cochran's C-test with an α level of 0.05. Where Cochran's tests were significant the data were transformed to meet the assumption of homogeneity (Quinn and Keough 2002). When significant differences were detected by ANOVA, Tukey's tests were used to determine where the differences lay (Quinn and Keough 2002).

Although the broad-scale habitat types were chosen *a priori*, the subtidal mud and sand areas that were assumed to be mostly devoid of structure may in fact contain structure that could influence the distribution of fish, and broad-scale sampling methods such as trawling may not capture this information (Thrush et al. 2002). Therefore, each tow was also assigned a structure class based on the major structural component of the catch. If only invertebrates, fish and shell grit were in the net, it was assumed the trawl was over 'bare' sediment. If horse mussels were also part of the catch it was assumed the tow was

over ‘horse mussel’ habitat and all other structure was assigned as ‘other structure’, which comprised mainly soft corals, large shell fragments and sponges. Differences between season and structure class were tested using a two-way factorial ANOVA. As there were multiple differences between seasons the differences between the structure classes within each season were also tested using ANOVA.

For size classes of fish, an index of relative importance (IRI) was constructed following Laurel et al. (2007). The habitat IRI was defined as the relative proportion of fish standardised to number of individual snapper per 100 m^2 in each 10 mm size class, sampled from a given habitat relative to all contributing habitats (n = 4). The IRI removes variation in the densities of snapper at each size, to find correlations between growth and potential habitat use. Therefore, an IRI score more or less than 0.25 indicates a possible preference for or underuse of that particular habitat. The same IRI was constructed for the structure class data (n = 3), with the null IRI score as 0.33. Regression analysis was used to determine if there were significant size related changes in habitat use or association with structure class. For example, a significant positive slope indicates a greater preference for a habitat with growth, while a negative slope indicates an underuse of that habitat. For the artificial reef experiment, differences between months and experimental units were tested with a two-factor ANOVA. Data were tested for homogeneity of variances using Cochran’s C-test with an α level of 0.05. All univariate analyses were performed using the statistical program STATISTICA 6.0 (StatSoft Inc.).

Principal components analysis (PCA) (PRIMER 6.0) based on Euclidean distance were conducted on the environmental variables of temperature, salinity, visibility and depth. The data were pooled at the transect level and examined using draftsman’s plots to locate any skewness in the data. If appropriate, the data were log-transformed to correct the skewness. The data were then normalised by PRIMER to account for the differences in measurement scales between the variables (Clarke and Warwick 2001). Classification and regression trees analysis (CART, Pro v.6, Salford Systems Inc.), was used to examine the relationship between juvenile snapper densities and the physical variables of season, area, habitat, depth and the environmental variables of temperature, salinity and visibility. For this data, seasons were combined across years: summer (December 05/06), autumn (March 06/07), winter (June 06/07) and spring (September 06/07). Trees

are used to explain variation of a single response variable by one or more explanatory variables with the objective of partitioning the response into homogeneous groups, while keeping the tree reasonably small (De'ath and Fabricius 2000). For simplicity, I used the smallest tree within 1 standard error (SE) of the tree that minimised the cross-validation error (De'ath and Fabricius 2000).

Results

Density and distribution of snapper

A total of 818 juvenile snapper ranging in size from 10–100 mm were captured. Areas within the harbour differed in their constituent habitat types and depths (Table 2.1). The majority of snapper were captured in depths of less than 10 m (Figure 2.4). There were clear differences in size and capture rates between seasons and across the harbour as a whole (Figure 2.5). A bimodal size distribution was apparent in December 2005 but not December 2006, due to a lack of smaller fish, and was apparent during March both years. Densities were highest at the beginning of March (autumn) for both years, with more than twice as many juveniles caught in March 2007 relative to 2006 (Figure 2.5 and 2.6). Capture rates in June 2006 and 2007 (winter) were lower, but a wide range of fish sizes was present, while fewer fish were captured during September of both years, with the juveniles being larger than in other seasons (Figure 2.5). Seasons differed significantly in fish densities ($p = < 0.001$), with Tukey's HSD test showing March 2006 and 2007 were different from all other seasons (Table 2.2). Harbour-wide population estimates were 115,661 juvenile snapper for March 2006, and 321,461 for March 2007. This changed seasonally and as this study sampled by habitats, a population estimate scaled by the proportion each habitat covered within the harbour could be calculated (Table 2.3).

During March of both years, fish were found throughout the harbour across all areas and habitats (Figure 2.6). However, highest densities were in the sand habitat, with few fish in the sand over other seasons (Figure 2.6 and 2.7A). Population density estimates scaled for the area of subtidal habitat, showed the abundance of snapper within the sand to be twice that of the horse mussels and more than 10-fold higher than the shell hash (Figure 2.7B). When split into 10 mm size classes, the density of juvenile snapper was

highest within the sand for the 20–50 mm size range (Figure 2.8A). Sizes ranged from 20–100 mm for snapper in the horse mussel, subtidal mud and shell hash. The index of relative importance (IRI) showed 10–50 mm snapper were positively associated with sand, with the 10–20 mm fish having a positive association with horse mussels. Fish > 50 mm were never caught over sand, but were proportionally more numerous within the horse mussels, subtidal mud and to a lesser extent shell hash. Regression analysis showed the density decrease over the sand to be significant ($r^2 = 0.45$, $p < 0.05$), as were the increases in densities with horse mussels ($r^2 = 0.89$, $p < 0.0001$) and subtidal mud ($r^2 = 0.79$, $p < 0.0001$). An increasing use of shell hash with size was also significant ($r^2 = 0.52$, $p < 0.05$).

Fine scale variation within habitats

Juvenile snapper were mainly associated with either patches of horse mussels or other structure (Figure 2.9). The exception was in March 2007, a strong recruitment year with twice the number of fish relative to 2006, with many more fish associated with bare areas than in previous seasons (Figure 2.9). A factorial 2-way ANOVA testing the effects of season and structure class showed significant differences for both (Table 2.4). Post-hoc Tukey's test showed numerous differences between seasons, and as there was a significant interaction between season and structure class, each season was analysed separately using a one-way ANOVA (Table 2.5). In December 2005, snapper were 10 times more likely to be associated with horse mussels and 7.5 times more likely to be in bare areas as compared to areas with other structures ($p < 0.001$). In March 2006, snapper were 4 times more abundant in areas with horse mussels as compared to bare areas ($p < 0.01$). Snapper densities in areas with horse mussels for both June 2006 and 2007 were significantly higher (10–12 times) than in areas with other structure ($p < 0.01$). In March 2007, juvenile snapper densities were higher from bare areas (1.6 and 1.2 times greater than horse mussels and areas with other structure respectively). This difference was not significant, and therefore indicated that as the densities were greater than previous seasons; snapper were more evenly spread through the harbour.

The comparison of structural classes with the *a priori* habitat types revealed some interesting patterns. Overall, snapper densities were highest in sand from both the March 2006 and 2007 surveys. Many of these tows contained horse mussels and other

structure (mostly sponges and soft corals) (Figure 2.10). Tows within the horse mussel habitat generally contained both horse mussels and other structure. The subtidal mud habitat tows contained small patches of horse mussels and shell hash, while the shell hash habitat had patches of large dead shell, with some patches of horse mussels (Figure 2.10). The IRI for the different size classes pooled over seasons indicated that the association with the structure class of horse mussels was above 0.33 for all sizes of juvenile snapper, except the 90–100 mm class (Figure 2.11B). Regression analysis was therefore not significant ($r^2 = 0.30$, $p > 0.05$). The decrease in the association of the other structure class with an increase in the size of fish was also not significant ($r^2 = 0.58$, $p > 0.05$), due to fish in the 70-80 mm range showing an affinity for 'other structure'. An increase in the positive association of bare areas for juveniles was evident as they increased in size to 50-60 mm, however the regression was also not significant ($r^2 = 0.54$, $p > 0.05$).

Environmental factors and snapper abundances

There was seasonal variation within the environmental data. Pooled sea surface temperatures fluctuated seasonally, with temperatures reaching 22^{o}C in summer and dropping to around 14^{o}C in winter (Figure 2.12). From December 2005 to March 2006, the average temperature in the harbour was 20^{o}C, while on the coast the temperature was 18^{o}C. In December 2006, the average temperature was 17^{o}C in the harbour and 16^{o}C around the coast, 4^{o}C cooler than the previous year. By March 2007, the temperature within the harbour was 22^{o}C, 2^{o}C warmer than the coast and having risen 5^{o}C since December. Temperatures were generally quite similar across the areas and habitats sampled (Appendix 2.4). Salinity fluctuated between 32 and 35 ppt, and also followed a seasonal pattern (Figure 2.12). Lowest salinities occurred during the cooler months, while higher salinities were evident over the warmer months. Across the areas and habitats sampled, salinity showed similar patterns with some fluctuations between areas (Appendix 2.5). The upper part of the harbour often had slightly lower salinities than other areas. During September 2006, horse mussels in area 3 and subtidal mud in area 5 had the lowest overall salinities (Appendix 2.5). Visibility in the harbour also fluctuated over time and showed some correlation with total rainfall recorded from the previous month (Figure 2.12). The lowest overall visibility occurred during September and December 2006, with rainfall for these months ~ 60–100 mm. Visibility was

highest during 2007, which correlated with low rainfall through the year to September 2007. The high amount of rain for September 2007 had some influence on the visibility, although the overall mean was higher than might be expected. Most of the rain fell around 4 days before this sampling period and when we look at the visibility readings across the different areas and habitats, we can see that this high rainfall had influenced the upper part of the harbour (areas 1 and 2) but the lower part (areas 3 and 4) was up to 1–2 m clearer, except for area 5 (the lower north eastern arm) (Appendix 2.6). Overall, the water was clearer within the main channel from area 2 through to area 3, the mid to lower part of the harbour.

Bubble plots of snapper densities from principal components analysis (PCA) were examined to find associations with temperature, salinity, visibility, and depth over time (Figure 2.13). The first two PC axes explained 79.4% of the total variability. The higher snapper densities were associated with salinity and temperature, towards the left of the plot over the warmer months, especially March 2007. There was some influence of depth and visibility within areas 2 and 3 (shell/sand) towards the top of the plot. The rest of the bubbles radiate along axis 1 towards the right, and if compared with the habitat plot we can see this relates to the horse mussel and subtidal mud habitats for the cooler seasons. Examination by season showed an initial split of warmer months (to the left) from cooler months, driven by salinity and temperature (Figure 2.13B). Within the warmer months, March 2007 was the most different to March 2006, December 2006 and 2007. Visibility and depth had less influence overall. By areas in the harbour, the PCA split area 3 and some of area 2 away from the other areas (towards the top) (Figure 2.13C). The variables depth and visibility have a strong correlation with these areas. By habitat type, the pattern is very similar with sand and shell hash towards the top, influenced by depth and visibility, and as area 3 contained the habitats sand and shell and these areas were the deepest sites, this is not surprising (Figure 2.13D).

Classification and regression tree analysis (CART) was used to relate densities of juvenile snapper to the explanatory variables of season, area, habitat, salinity, visibility and depth. The PCA showed temperature was tightly coupled with season, so temperature was removed from the CART analysis. This did not change the results significantly, but decreased the relative error surrounding the regression. Cross validation using the 1-SE rule selected a 6-leaf regression tree, which explained 51% of

the variation seen (CART 1998). At the first split, highest mean abundances of snapper (8.1) were related to the area with highest salinity (> 34.82 ppt) which also related to the March 2007 survey (Figure 2.14). Salinity was evenly high across the whole harbour in March 2007; therefore the leaf terminates at this point. The next highest mean abundance (3.2) of snapper relates to season, in particular autumn, for both March 2006 and 2007. This is further split by habitat, with the highest mean abundances (4.7) within the sand and horse mussel habitats. Depth < 7.32 m defined the next leaf, with mean abundance of 0.98 fish. Seasons then became separated into spring and summer vs. winter, with winter having a higher mean abundance (1.4) of fish than spring.

Experimental test of the effect of structure

The artificial reef experiment was run over four and a half months. Juvenile snapper were present during March (n = 6) and April 2008 (n = 9) and were associated with experimental units of plain horse mussels or horse mussels with added epifauna (Figure 2.15). There was one exception; a large snapper (150 mm) was resting in a hollow next to a control unit. Snapper were generally around the edges of experimental units, although in April 2008, two fish were seen above a unit (pers. obs.). There were no significant differences between months, but there were significant differences between experimental units (Table 2.6). Post-hoc Tukey's tests showed the difference to be between horse mussels with epifauna and bare areas, and horse mussels with epifauna and controls ($p < 0.05$). The snapper within the experiment were mainly 30–50 mm long, i.e. post-settlement size (Figure 2.16). No real differences in size were apparent for either month; however by April 2008 there were more fish in the size range 40–50 mm. When the experiment was retrieved, no snapper were present in the collectors. However, several snapper were seen by the author when marking each frame with floats. Being disturbed by the retrieval net may have meant these fish escaped capture. It was assumed fish would flee into the shelter when disturbed; although this occurred for other species (Appendix 2.3), it did not appear to have been the case for snapper.

Discussion

This study was the first to analyse spatial and temporal patterns of habitat use by juvenile snapper less than 100 mm in size, within a New Zealand estuary. The two years

of data presented here have shown how variable this can be, with temporal differences driving spatial variability. Densities of snapper were highest during March of both years, with densities in 2007 twice that of 2006, and as a result, fish were spread throughout all areas and across all habitat types. Snapper are serial spawners and can spawn for up to five months over September-March with peak activity in November-January (Crossland 1977; Crossland 1981; Scott and Pankhurst 1992; Francis 1994). December 2005 had a bimodal size distribution, with new recruits likely to have been spawned around October 2005, while December 2006 had no new recruits. Both March surveys also showed evidence of bimodality. The higher densities of snapper in March 2007 indicating spawning occurred later; around December 2006–January 2007. It is thought that multiple spawning may increase survival, by spreading reproductive effort over time, so that a species may increase the probability of matching the correct biotic and abiotic conditions for enhanced survival (Szedlmayer and Conti 1998). The harbour-scaled abundance estimate of 115,661 juvenile snapper for March 2006 is similar to the 105,000 obtained by Morrison and Carbines (2006) from the same time of year in 2004. Their study sampled randomly across the subtidal component harbour, whereas this study sampled by *a priori* habitat types across the harbour. The much higher densities from March 2007 gave a population estimate of 321,461 juvenile snapper, indicating 2007 may be an unusually high recruitment year.

Importance of structure

The importance of structure to fish species has been well studied (Sale et al. 1984; Ruiz et al. 1993; Pickett and Cadenasso 1995; Irlandi and Crawford 1997; Nagelkerken et al. 2001; Sheaves and Molony 2001; Thrush et al. 2002; Scharf et al. 2006; Caddy 2007; Ross et al. 2007). The fine-scale structure class data from March 2007 showed fish were more associated with bare areas than in previous seasons, indicating fish were widespread around the harbour. This was likely due to the much higher recruitment for this year, indicating fish may be limited by the lack of preferential habitats and therefore more likely to be in areas without structure (Connell and Jones 1991). Areas of structural complexity may provide refuge by limiting a predator's ability to move and have also been hypothesised to support a greater number of prey items (Laegdsgaard and Johnson 2001; Stoner and Titgen 2003). Studies on juvenile snapper from Japan indicate settling snapper actively seek habitats (mainly sand with seagrass) that provide

optimal feeding conditions, and when year class strength is high, late settling snapper are excluded from optimal sites and displaced into marginal habitats (Azeta et al. 1980; Sudo et al. 1983).

As snapper densities decreased, fish were mainly associated with either areas with horse mussels or other structure. Horse mussel habitat selected *a priori*, and the structure class horse mussels were both correlated with nearly all size classes of fish. The IRI for the fine-scale structure class data showed all the size classes of snapper (except 90-100 mm) were above the 0.33% threshold, indicating a preference for this type of habitat. The regression analysis was not significant, meaning that although the existence of any ontogenetic shift in habitat use with size was weak, the association with the structure class item, i.e. horse mussels was quite strong. Horse mussels form complex habitats throughout the harbour, encompassing 12% of the available seafloor (Morrison et al. 2000). The snapper associated with the subtidal mud habitat were mainly > 40 mm, and although there was less structure within this habitat, there were patches of sponges, shell hash and horse mussels throughout. Variability in post-settlement growth and mortality and the level to which post-settlement processes influence patterns of larval settlement can be a function of habitat structure (Petrik et al. 1999). Survivorship of juvenile Atlantic cod (*Gadus morhua*) has been shown to be positively related to habitat complexity and this may partly explain the slow recovery of this stock after its collapse as fishing gear had destroyed much of the habitat structure (Gotceitas and Brown 1993; Lineham et al. 2001). Studies characterising habitat of red snapper (*Lutjanus campechanus*) found juveniles were not randomly distributed, but attracted to complex habitats such as low-profile reefs or coarse shell hash (Szedlmayer and Conti 1998).

A comprehensive review by Heck et al. (2003) looked at whether published studies that had evaluated seagrass beds as nurseries were justified in doing so under the nursery role hypothesis. This was defined by Beck (2001) as ‘a habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur’. Their review showed that overall survival was greatest within seagrass as compared to unvegetated areas, however there was little difference between seagrass and other structurally complex habitats in terms of protection, therefore it was the simple effect of structure and not some property of the

seagrass itself driving the association (Heck et al. 2003). The influence of structure on snapper recruitment was tested with an artificial reef experiment. There were significant differences between the densities of snapper on the artificial horse mussel units with epifauna, as compared to the bare areas and controls. Juvenile snapper were only associated with horse mussels with or without epifauna, except one larger snapper that was next to a control unit. Although the overall counts of snapper were small (n = 15), effectively only 10 m^2 of structure was added to the overall experimental area (~ 2000 m^2 in size). Mean densities were therefore ~ 40–120 (± 30) snapper per 100 m^2, while the highest mean density seen over the entire study from the beam trawling was only 4.7 (± 3) per 100 m^2 within the sand habitat. This equates to a 10–30-fold increase in snapper densities by adding the artificial reef to this area. This must be interpreted with some caution however, as this assumes recruitment to be uniform across an area. This would need to be tested using experimental units of larger sizes and in multiple areas.

Although juvenile snapper were seen around the units, they were never captured by the drop net process on retrieval of the experiment. A recent large-scale artificial seagrass experiment in the Whangapoua estuary, Coromandel, testing the effects of patch size in 2007 and blade density in 2009 and the role they play for small and juvenile fish and habitat usage also found drop nets over the artificial seagrass units in 2007 to be ineffective at catching juvenile snapper. The method was refined for the subsequent experiment in 2009 and an enclosing purse seine net that sampled the area adjacent as well as above the units was found to be much more effective by at least 10–20 times at capturing the small snapper that were associated with the artificial seagrass units (M. Morrison, pers. comm.). Overall, the addition of structure to an area that was previously simple and uniform, greatly enhanced densities of snapper and other fish seen within the artificial units. This indicates that the presence of structure was the driving factor in fish recruitment to this area, rather than some other factor of the environment or of the horse mussels themselves.

Densities of juvenile snapper from the Mahurangi were much higher than are found in west coast estuaries (Table 2.7). The density estimates from the west coast were obtained in a one-off study in 2003 (Morrison et al. in review). The west coast stock is considered a discrete population and much smaller than east coast stocks (Annala et al. 2004; Morrison et al. in review). Therefore, the population estimate difference may be

due to the differences between coasts. Very little work has been done on snapper densities within estuaries on the east coast. Limited trawls (n = 8) have been undertaken within subtidal seagrass in the Rangaunu estuary, approximately 250 km north of the Mahurangi. Rangaunu is considered relatively pristine, with extensive subtidal seagrass beds and high densities of snapper (mean 87 per 100 m^2 ± SE 19.6) (M. Morrison, unpublished data). As sampling was limited and only within one habitat type, the scaled-up population estimate is likely to be an overestimate making it difficult to compare with the Mahurangi densities (Table 2.3). Without further habitat sampling and comparisons to other east coast estuaries, it is not possible to really calculate how productive the Mahurangi Harbour is in comparison to other estuaries. Differences in densities between habitats within estuaries and harbours are likely to be quite variable. This can be seen between the two east coast estuaries, with the Mahurangi having little subtidal seagrass, therefore comparisons of densities between habitats and estuaries become more difficult. This highlights the need for further work on snapper distribution and abundance patterns within other estuaries, especially along the east coast.

Environmental factors

Water temperature and salinity were found to be correlated with higher snapper abundance in the Mahurangi, with mean salinity highest during March 2007. This was also correlated with the low rainfall from the months preceding the sampling (< 20 mm total). Summer both years had very different sea surface temperatures, with December 2005 4^oC warmer than 2006 and this difference may have contributed to the lack of new recruits for December 2006. By March 2007 however, the temperature was 2^oC higher than March 2006, so from an initial colder start, summer 2007 had a ~5^oC increase in temperature. The growth of juvenile marine fish is known to be enhanced by the higher temperatures within estuaries that occur over spring and summer (Potter et al. 1990; Francis 1994; Szedlmayer and Conti 1998). The rapid increase in growth may mean juveniles become less susceptible to predation (Kennish 1990; Stunz et al. 2002). In Texas, a decade of nearly uninterrupted warm winters has allowed the gray snapper (*Lutjanus griseus*) to flourish, with much higher densities, faster growth and fish being captured in estuaries where they have not previously been recorded (Tolan and Fisher 2009). Water temperature has a strong positive correlation with year-class strength in snapper in New Zealand (Francis 1993), but in Australia, the relationship with water

temperature is not considered a simple one, with variation in recruitment determined by survivorship of larvae and juveniles (Fowler and Jennings 2003).

Temporal patterns

From the March data, although fish were well spread though the harbour, highest densities of fish were found within the sand habitat. Over the remaining seasons however, few fish were captured over the sand by the beam trawl. Conditions within the harbour over winter 2007 (June) were very good with low rainfall from the previous month, high salinity, higher visibility yet densities of snapper were less than 2006. The densities of fish each September were lower than most other seasons also. The possible reasons for this may include higher predation rates driven by weaker association with structural protection, clearer water making fish more visible to predators or fish becoming less vulnerable to the beam trawl. The sand and shell hash habitats are in the lower part of the harbour and are the deepest sites (10–20 m), being part of the main channel. Current speed in this part of the harbour can be up to 0.7 ms^{-1} (Harris 1993). The majority of fish were caught in < 10 m of water, with the regression tree analysis suggesting depth changed seasonally. A number of predators have been caught in these areas (Morrison and Carbines 2006), therefore if not taken by predators, juvenile snapper may move off the deeper sand habitat where the largest recruitment occurs, to a shallower, less current driven environment that requires less energy to inhabit, with patches of structure for protection from predators. In Japan, 0+ snapper prefer fine sand and soft sediments that contain *Zostera* sp. or the alga *Sargassum* sp. in 10 m of water or less, and few fish are found near the mouth of estuaries where tidal currents are strongest (Azeta et al. 1980; Sudo et al. 1983).

The population estimate for September 2006 was higher than for 2007 (31,900 vs. 8,100), although fish were ~10 mm larger in 2007. Population estimates from the dropped underwater video work (DUV) (Chapter Three) however, indicated that numbers sampled by the beam trawl for September each year were low, with the DUV capturing larger 0+ snapper that the beam trawl did not sample. The DUV also showed there were 0+ juvenile snapper over the sand habitat after June each year (albeit in low densities, except for September 2006), which the beam trawl also did not capture. The beam trawl did not sample the fish the DUV did, and it was initially thought the

significant decline of juvenile snapper from over the sand habitat across the other seasons, and size classes from the IRI data may have been due to mortality or movement. The fine-scale habitat analysis, however, revealed high numbers of horse mussels and other structure in the sand habitat, so lack of structure that may protect fish from predators was thought not be the cause of the decline in abundance.

The apparent declines therefore were likely to be sampling artefacts of the beam trawl; either size selectivity, where the larger fish now out-run the trawl (i.e. September survey) or structural interference, with fish able to find refuge within structure that was not captured by the trawl (i.e. in sand habitat). The beam trawl is most effective for sampling snapper 1–80 mm long, while the DUV is most effective for snapper greater than 50 mm (Morrison and Carbines 2006). Therefore, size selectivity between the two methods probably accounts for the population differences seen for June to September (see General Discussion for elaboration). The higher temperatures over summer 2007 may have also contributed by enabling the snapper recruited from 2007 to become much larger and out-run the trawl. This confirms the importance of using a sampling method suitable for the hypothesis under study or to use a combination of methods to generate a robust data set.

Conclusions

From the habitat data, there was a significant use of habitats containing structure, particularly horse mussels. The influence of horse mussel structure was tested experimentally, with all juvenile snapper found on or close to the artificial horse mussels, particularly those with added epifauna. Overall, the Mahurangi Harbour has higher densities of juvenile snapper as compared with some west coast estuaries. Comparisons with the limited data from one east coast estuary showed that densities may differ significantly between harbours depending on the habitat, however, data is lacking. Time of year was the strongest predictor of juvenile snapper abundance, correlated with temperature and salinity, and these factors were linked. Recruitment of juvenile snapper was highest over the warmer months, however multi-modal distributions occurred. Snapper were well-spread throughout the harbour over the initial recruitment period, but by June, numbers had decreased significantly and snapper were mainly caught within horse mussel and subtidal mud areas. This was thought to be due

to natural mortality, predation or size-selective sampling by the beam trawl. The Mahurangi Harbour is susceptible to the impacts of soil erosion due to its catchment morphology and land use, with large quantities of sedimentation delivered to the estuary during floods (Gibbs 2006). Horse mussels are a large suspension-feeding bivalve that are vulnerable to increased sediment loads (Ellis et al. 2002). Therefore, loss of the horse mussel beds would mean a loss of a significant proportion of structural area that is utilised for juvenile snapper, probably as a predation refuge, and this may influence the overall survival of the recruits. This has important implications for the management of the Mahurangi Harbour as an area of habitat for juvenile snapper.

Table 2.1 Sampling details of habitat types selected *a priori*, and the areas they were sampled in and details of depth range and the average number of horse mussels (HM) per 100 m^2.

Habitat class	Areas	Tows per season	Min. Depth	Ave. Depth	Max. Depth	Ave. HM per 100 m^2
Horse mussels (HM)	1,2,3,4	16	2.00	4.64	9.00	0.93
Sand (Sa)	3	4	5.30	8.80	18.50	0.20
Subtidal mud (SG)	1,2,5	12	2.00	4.45	12.70	0.20
Shell hash (Sh)	3	4	5.00	12.88	16.30	0.23

Table 2.2 Summary of Tukey's HSD pairwise tests comparing catch rates of juvenile snapper per 100 m^2 for the factor season.

Season	Tukey's HSD test
March 2006	All other seasons except Mar 07
June 2006	Dec 06, Sep 07
September 2006	Dec 06, Sep 07
March 2007	All other seasons except Mar 06

Table 2.3 Population estimates of juvenile snapper (< 100 mm) based on the mean densities of juvenile snapper per 100 m^2 (± SE) scaled by the proportion of each *a priori* habitat type within the Mahurangi Harbour. Total area = 24.5 km^2, HM-horse mussels = 12%, sand = 15%, SG-subtidal mud = 21% and SH-shell hash = 2%.

	Mean number of snapper per 100 m^2 in each habitat				Population estimate for each habitat				
Season	HM	Sand	SG	SH	HM	Sand	SG	SH	Harbour total
Dec-05	0.24 (± 0.07)	0.08 (± 0.04)	0.14 (± 0.04)	0	7,044	3,063	7,146	0	17,253
Mar-06	1.07 (± 0.20)	1.54 (± 0.90)	0.51 (± 0.13)	0.21 (± 0.08)	31,544	56,656	26,440	1,021	115,661
Jun-06	0.47 (± 0.09)	0.04 (± 0.01)	0.35 (± 0.09)	0	13,781	1,531	17,865	0	33,177
Sep-06	0.33 (± 0.10)	0	0.26 (± 0.09)	0.17 (± 0.06)	9,800	0	13,577	817	24,194
Dec-06	0.13 (± 0.04)	0	0.08 (± 0.05)	0	3,675	0	4,287	0	7,962
Mar-07	1.32 (± 0.35)	4.75 (± 1.43)	2.06 (± 0.35)	0.46 (± 0.10)	38,894	174,563	105,758	2,246	321,461
Jun-07	0.27 (± 0.09)	0	0.24 (± 0.09)	0	7,963	0	12,148	0	20,111
Sep-07	0.08 (± 0.04)	0	0.03 (± 0.01)	0.17 (± 0.09)	2,450	0	1,429	817	4,696

Table 2.4 Results of the 2-factor main effects ANOVA comparing catch rates of juvenile snapper per 100 m^2 between seasons and three structure class variables: bare areas, horse mussels and other structure. Analyses were done on 4th root transformed data.

Effect	**SS**	**df**	**MS**	**F**	***p*-value**
Season	214.6	8	26.85	80.26	**< 0.001**
Structure class	3.46	2	1.73	5.17	**< 0.010**
Season*Structure class	8.77	14	0.63	1.87	**0.030**
Error	88.24	264	0.33		

Table 2.5 Results of one-way ANOVA's for each season comparing catch rates of juvenile snapper per 100 m^2 between season and three structure class variables: bare areas, horse mussels and other structure. For significant differences, Tukey's HSD test was completed, with highest abundance in bold. Analyses were done on 4th root transformed data.

Season	**Structure class**	**Tukey's HSD test**
Dec-05	< 0.001	**HM**-S, **B**-S
Mar-06	<0.01	**HM**-B
Jun-06	< 0.001	**HM**-S
Sep-06	NS	
Dec-06	NS	
Mar-07	NS	
Jun-07	< 0.05	**HM**-S
Sep-07	NS	

Table 2.6 Results of factorial ANOVA for the artificial reef experiment comparing snapper counts between two sampling months, and for each experimental unit (bare, control, horse mussel plain and structured). Significant result is in bold.

Effect	**SS**	**df**	**MS**	**F**	***p*-value**
Month	0.23	1	0.23	0.44	0.52
Exp unit	5.07	3	1.69	3.32	**< 0.05**
Month*Exp unit	0.88	3	0.29	0.57	0.64
Residual	16.8	33	0.51		

Table 2.7 Population estimates for juvenile (0+) snapper from the Mahurangi Harbour as compared with densities obtained for one other east coast harbour, marked with ** (M.Morrison pers. comm.) and seven west coast harbours (from Morrison et al. in review).

Harbour	Subtidal area (km^2)	Density per km^2	Population estimate for each harbour
Mahurangi**	12.5	9,253	115,661
Rangaunu**	54	870,000	46,980,000
Whangape	3.3	1,091	36,013
Hokianga	28.6	434	124,099
Kaipara	431.6	257	1,107,699
Manukau	139.7	179	249,577
Raglan	9.9	1399	13,853
Aotea	8.3	339	2,812
Kawhia	17.9	233	4,175

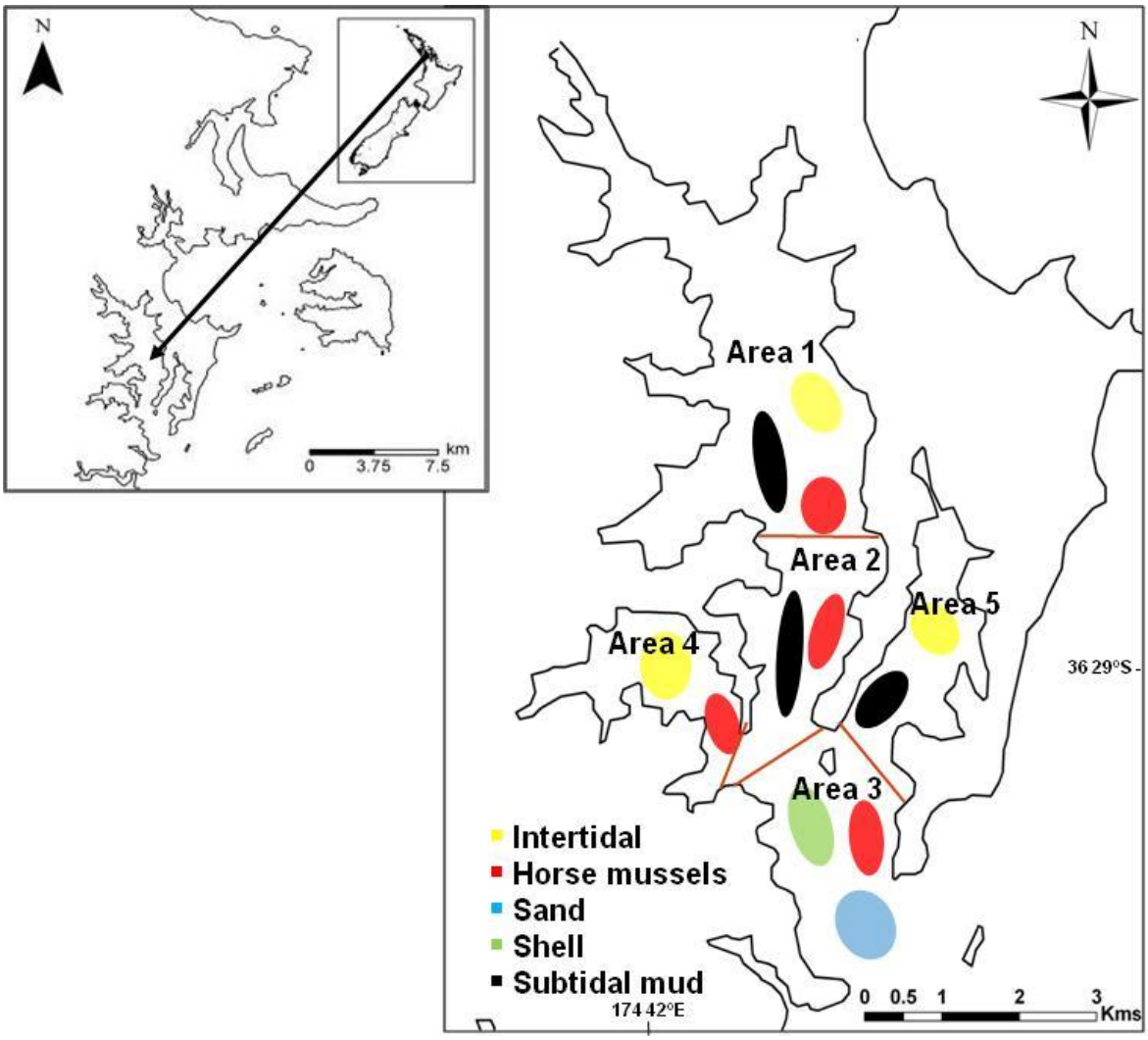


Figure 2.1 Location of the Mahurangi Harbour on the north-east coast of New Zealand, the areas the harbour was divided into, habitats sampled and their locations.

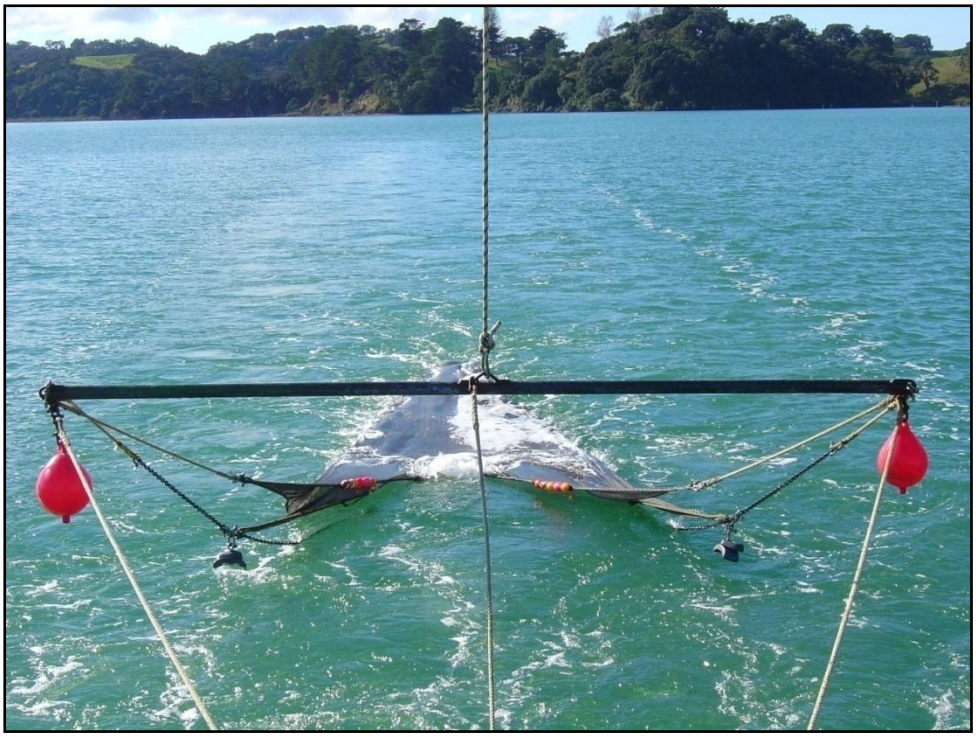


Figure 2.2 Beam trawl being towed on the surface behind the vessel R.V. Hawere.

A

B

C

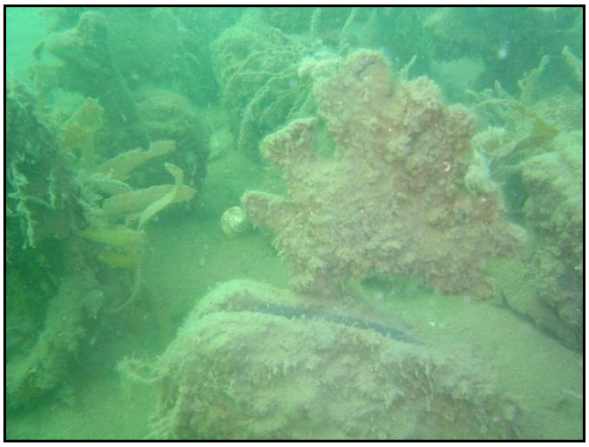


Figure 2.3 Artificial reef experimental design: A) Five replicates of plain horse mussels (left) and horse mussels with epifauna (right), B) underwater photo of plain horse mussels after 3 months, C) horse mussels with added epifauna after same period.

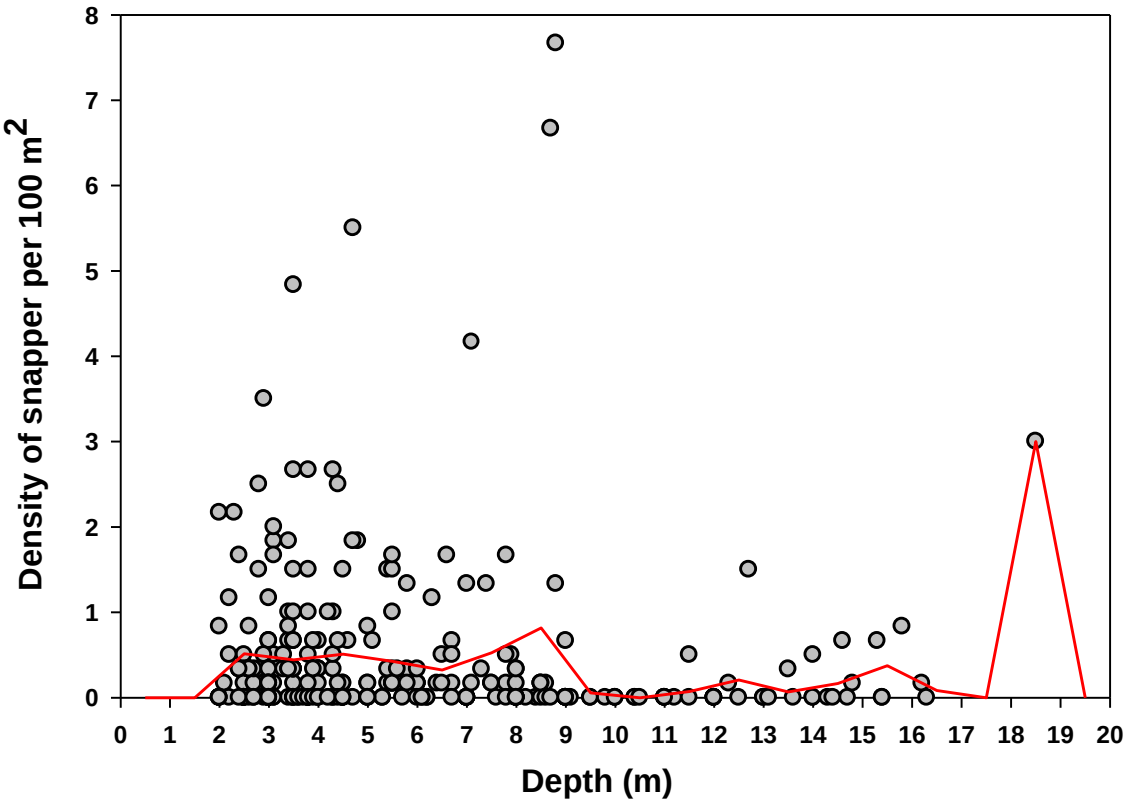


Figure 2.4 Snapper density versus depth across all sites and seasons. Red line represents average density per 1 m depth interval.

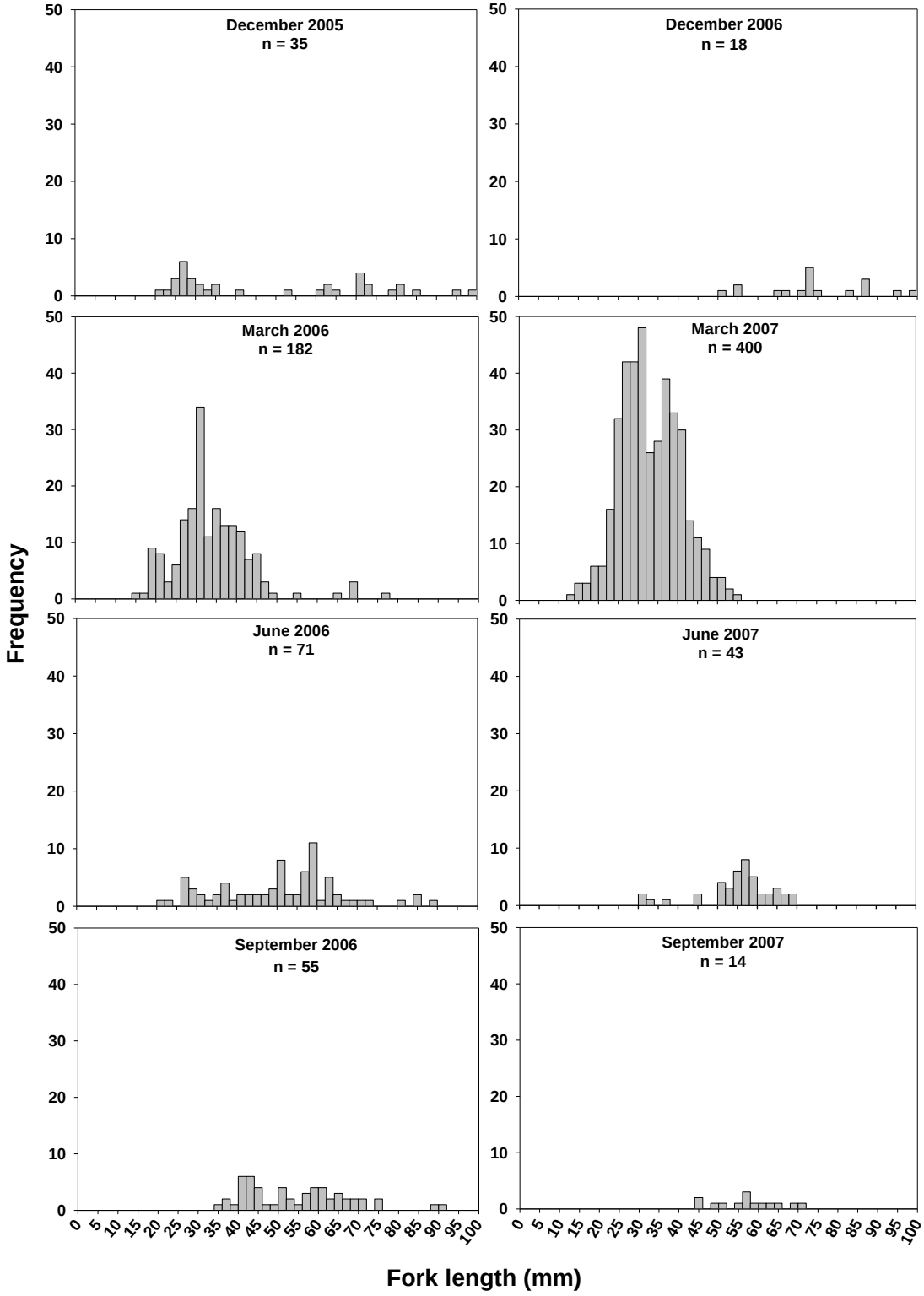


Figure 2.5 Size frequency distributions of juvenile snapper captured by the beam trawl each sampling season. n = number of fish caught in total for the sampling period.

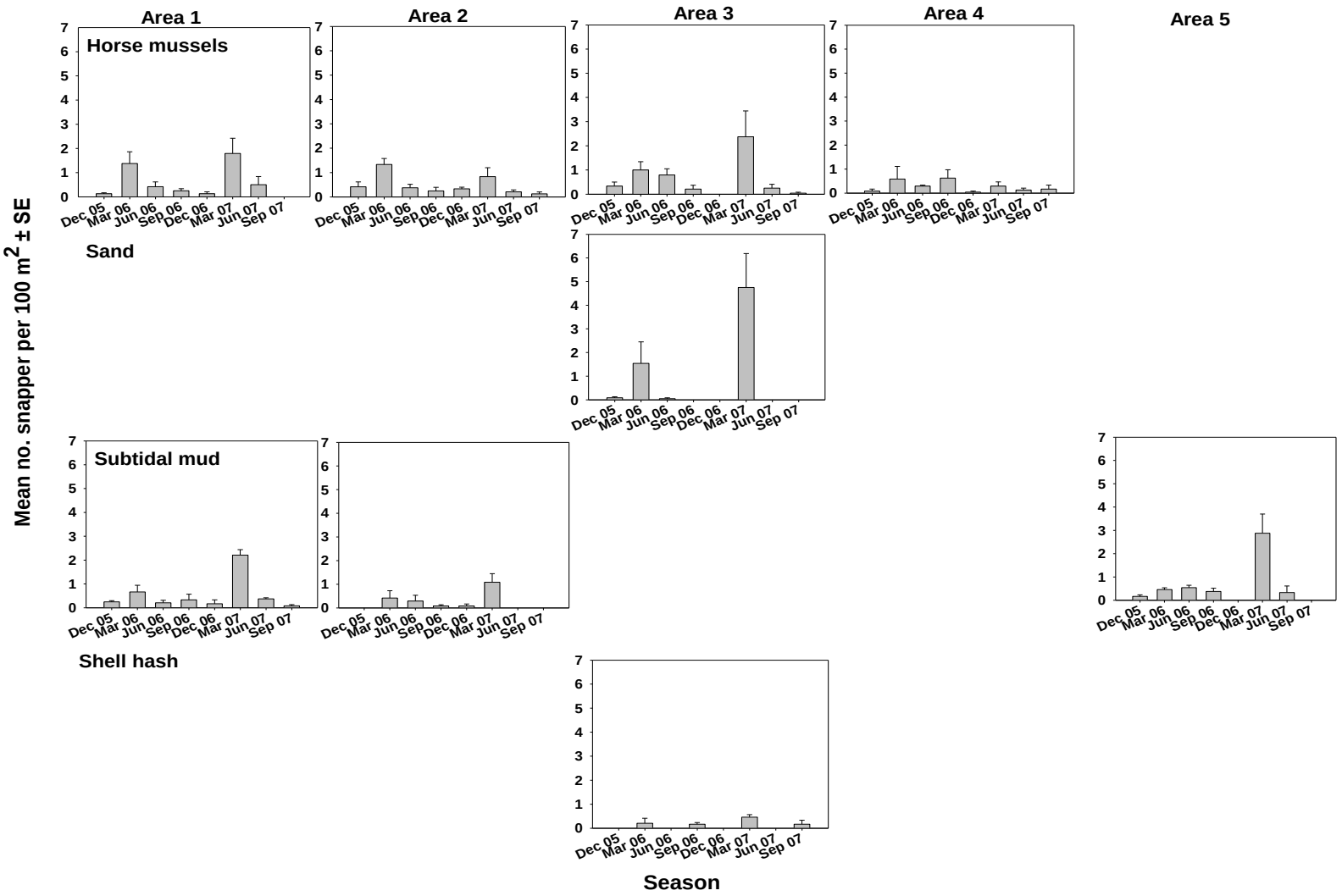


Figure 2.6 Mean number of snapper caught per 100 m^2 each season by areas (across top) and habitat (down side).

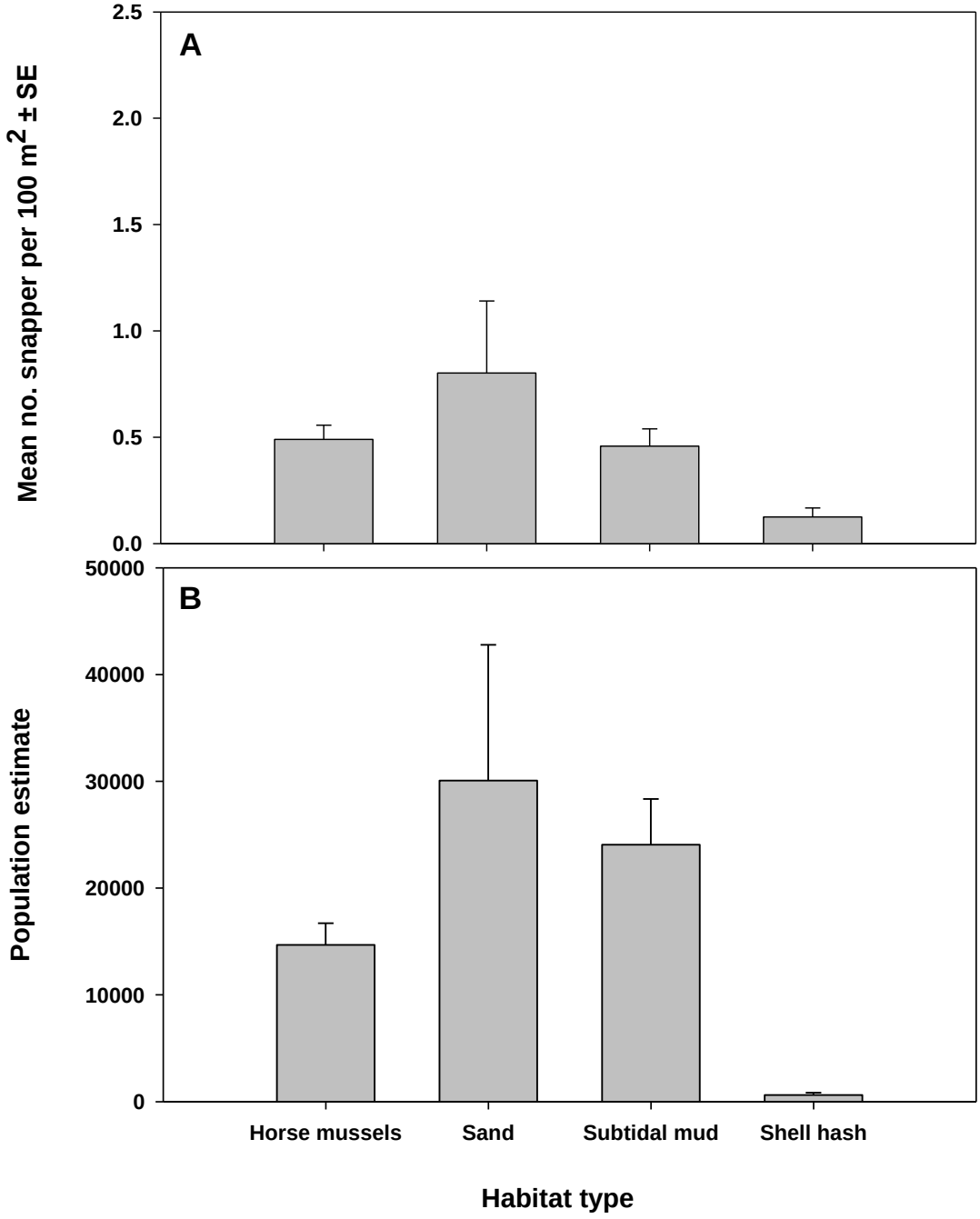


Figure 2.7 A) Mean number of juvenile snapper per 100 m^2 within the *a priori* habitat types and, B) population estimate scaled up to the area of the harbour (24.5 km^2) by the approximate percentage each habitat encompasses (horse mussels = 12%, sand = 15%, subtidal mud = 21% and shell hash = 2%).

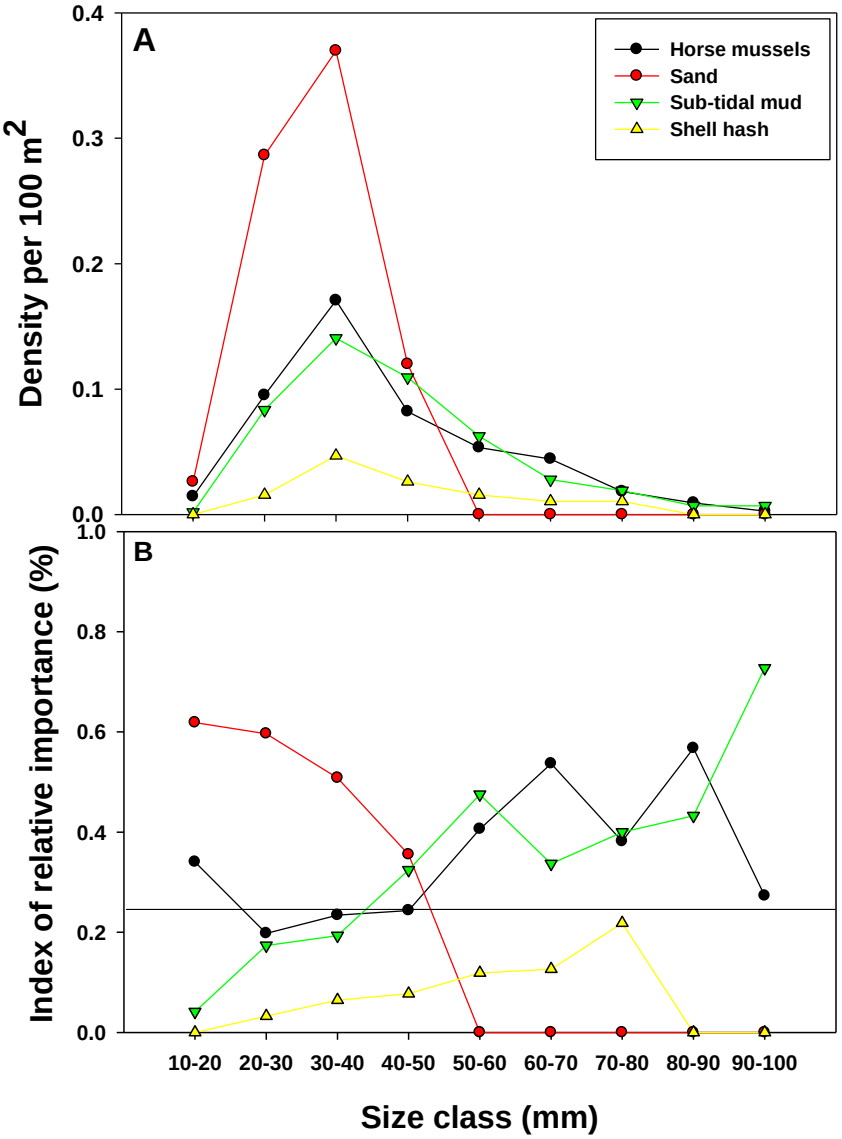


Figure 2.8 A) Density of juvenile snapper per 100 m^2 and, B) index of relative importance (IRI) split into 10 mm size classes over the *a priori* habitat types, pooled across seasons. The IRI is calculated as the proportion of each size class within each habitat type (n = 4), with values above the line representing a positive association with that habitat for that size class, and values below the line representing underuse.

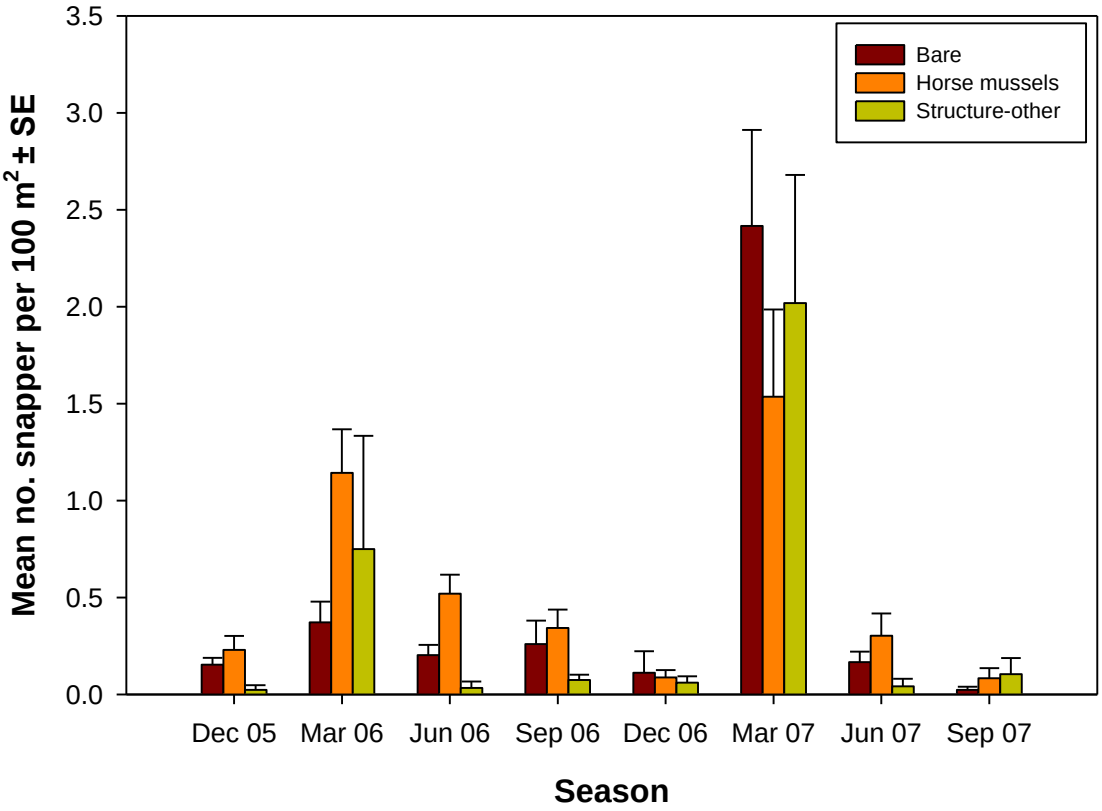


Figure 2.9 Mean density of juvenile snapper over each season and the association with structure class defined as bare, horse mussels or other structure.

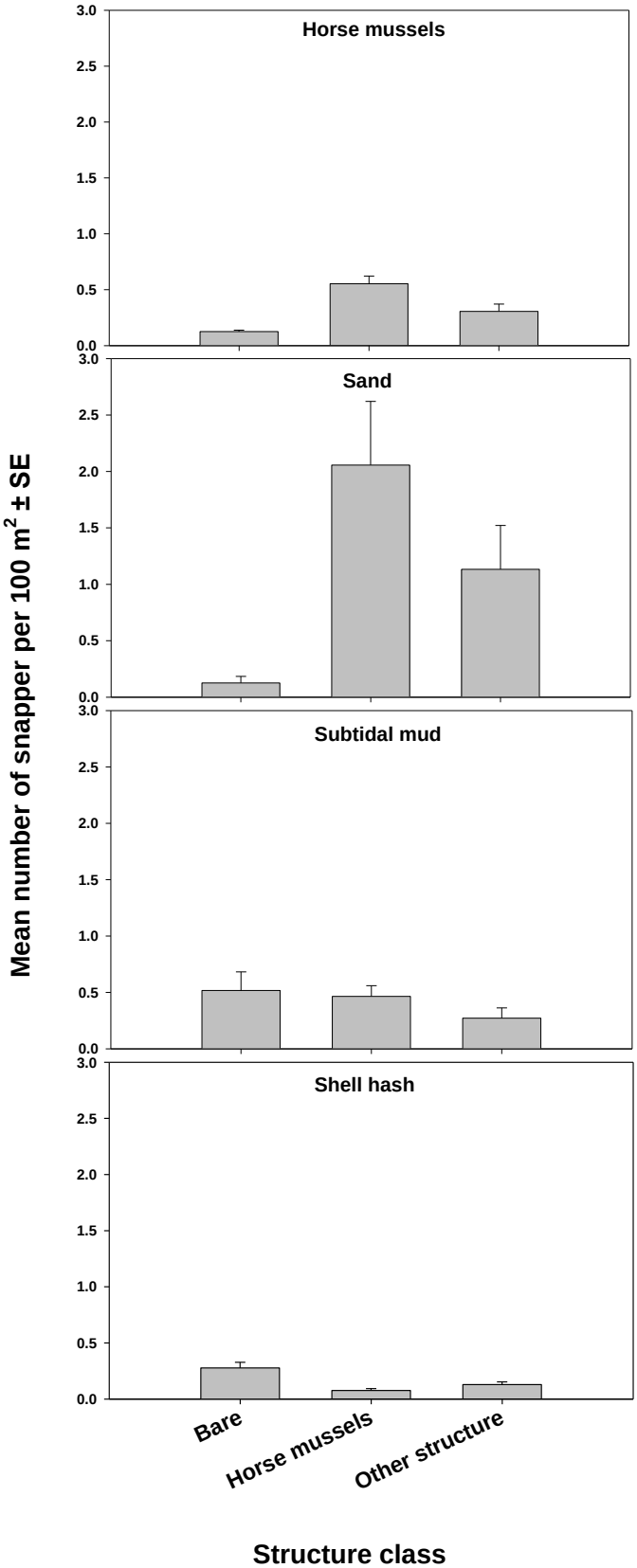


Figure 2.10 Mean number of juvenile snapper per 100 m^2 within each habitat type by structure class from each beam trawl tow.

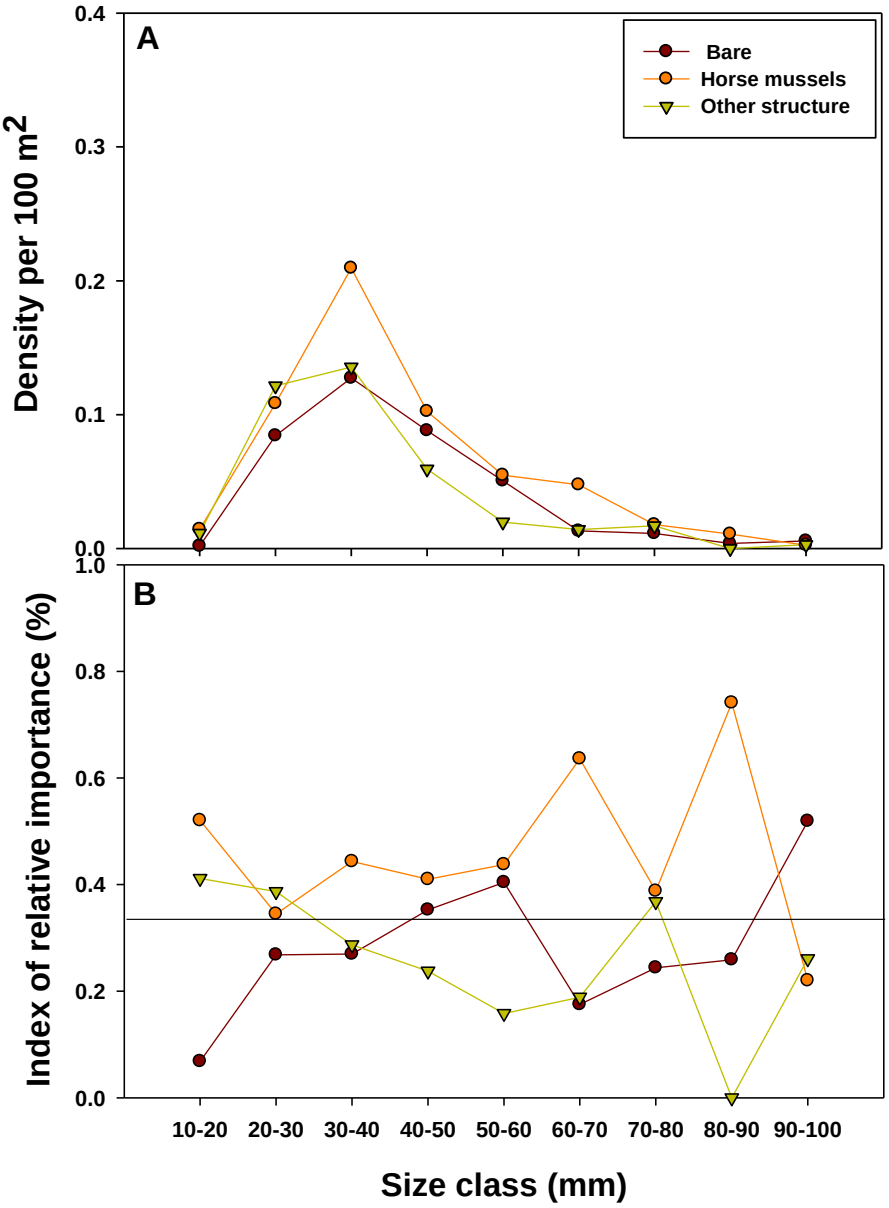


Figure 2.11 A) Density of juvenile snapper per 100 m^2 and, B) index of relative importance (IRI) split into 10 mm size classes by structure class from tows pooled across seasons. The IRI is calculated as the proportion of each size class within each structure class (n = 3) with values above the line representing a positive association with that structure class for that size class, and values below the line representing underuse.

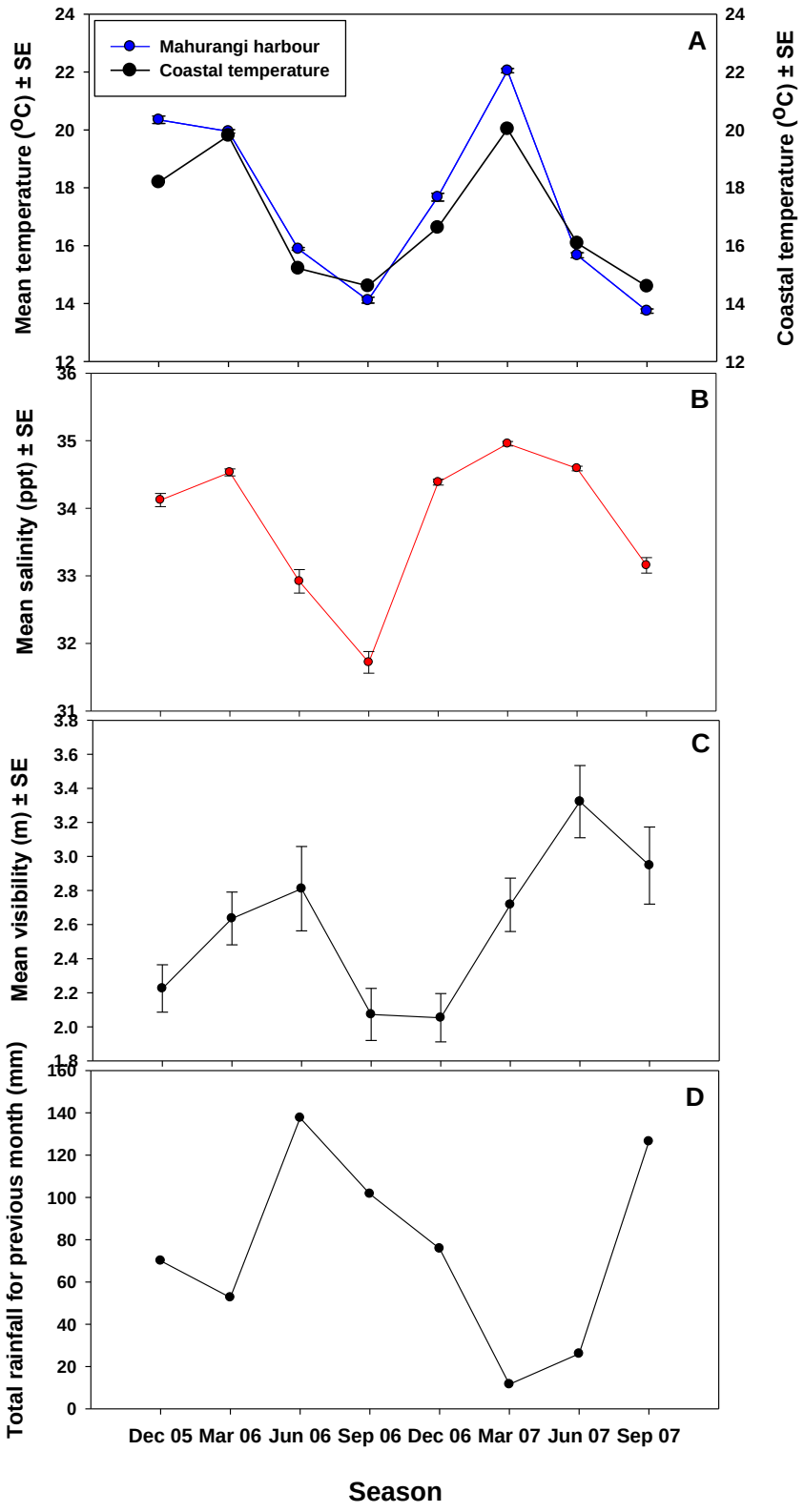


Figure 2.12 Environmental data collected at the time of each beam trawl sampling. A) Mean sea surface temperature from the Mahurangi Harbour compared with coastal sea surface temperature collected at Leigh Marine Laboratory, B) mean salinity pooled by season, C) mean visibility pooled by season and, D) total rainfall for the local area for the month before the beam trawl sampling months.

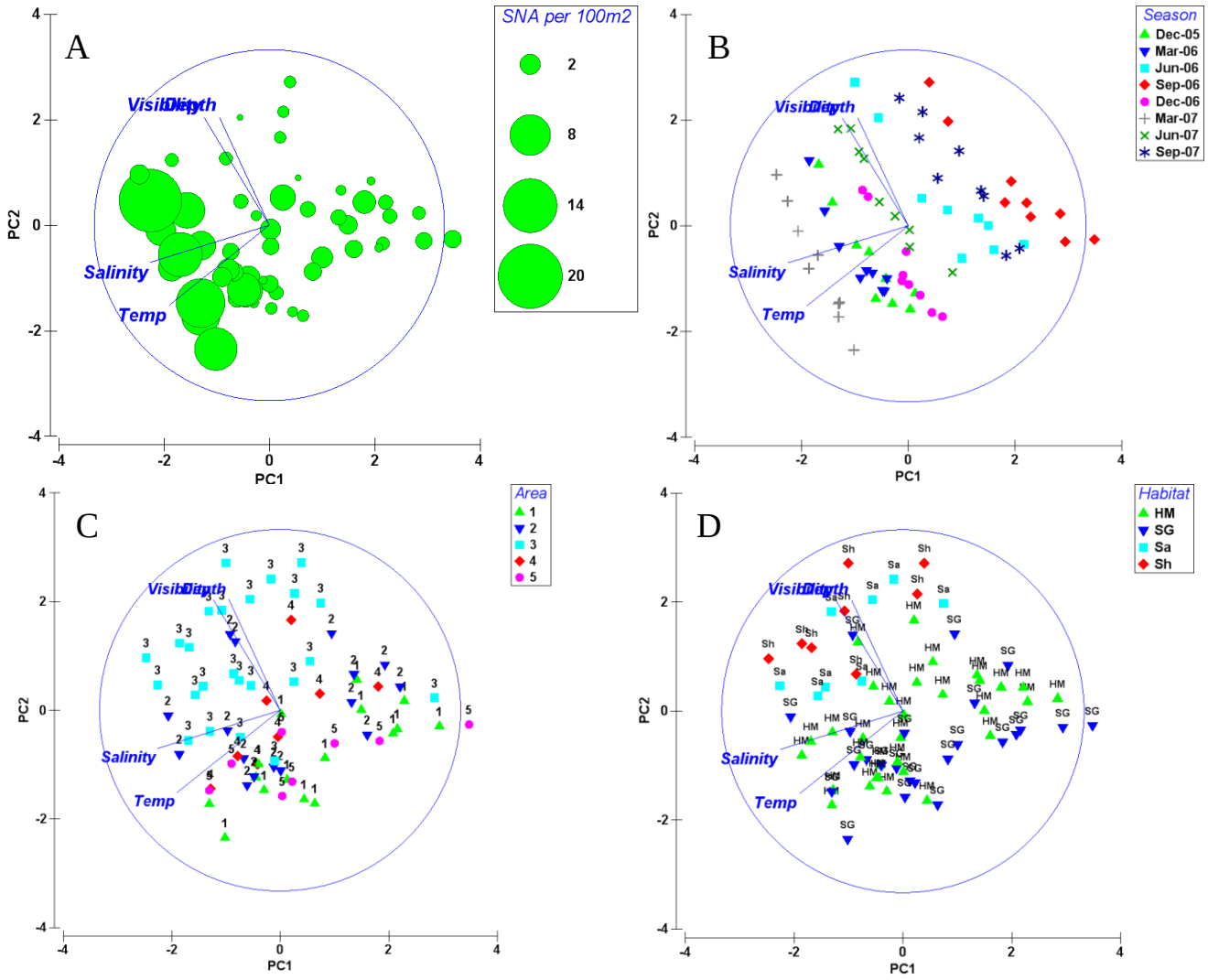


Figure 2.13 PCA plots of environmental and depth data displayed against A) the mean number of juvenile snapper per 100 m^2, B) seasons, C) areas in the harbour, and D) habitats sampled. Habitat type – HM = horse mussels, SG = subtidal mud, Sa = sand and Sh = shell hash. PCA axis 1 = 44.3%, axis 2 = 35.1%. Note: Visibility and depth are superimposed on each plot.

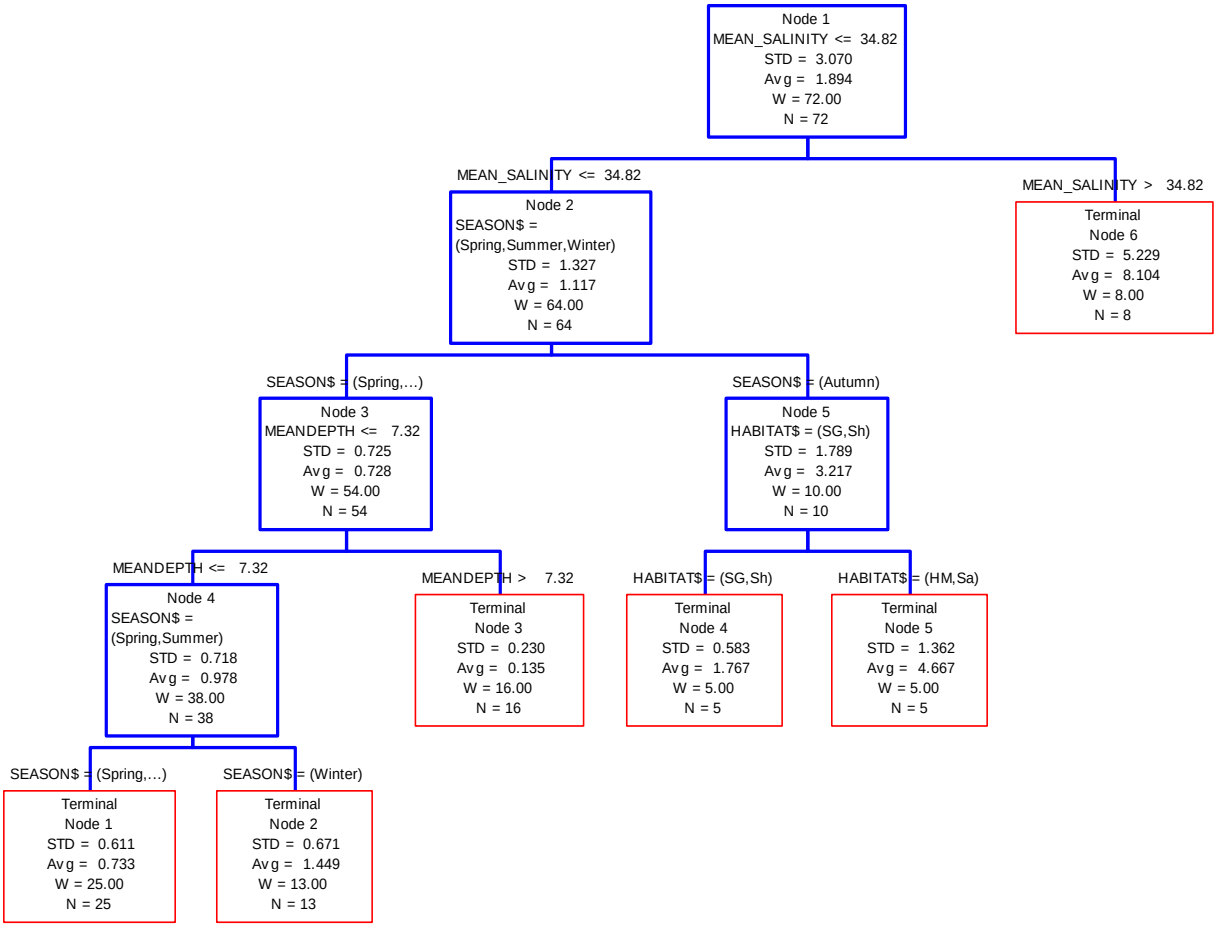


Figure 2.14 Regression tree relating the abundance of juvenile snapper per 100 m^2 to the explanatory variables of season (n = 8, summer = Dec 05, 06; autumn = Mar 06, 07; winter = Jun 06, 07; spring = Sep 06, 07), area (1-5), habitat type HM = horse mussels, Sa = sand, SG = subtidal mud and Sh = shell hash), salinity (ppt) and visibility (m). The 6-leaf tree, chosen from the cross-validation plot under the 1 SE rule explained 51% of the variance.

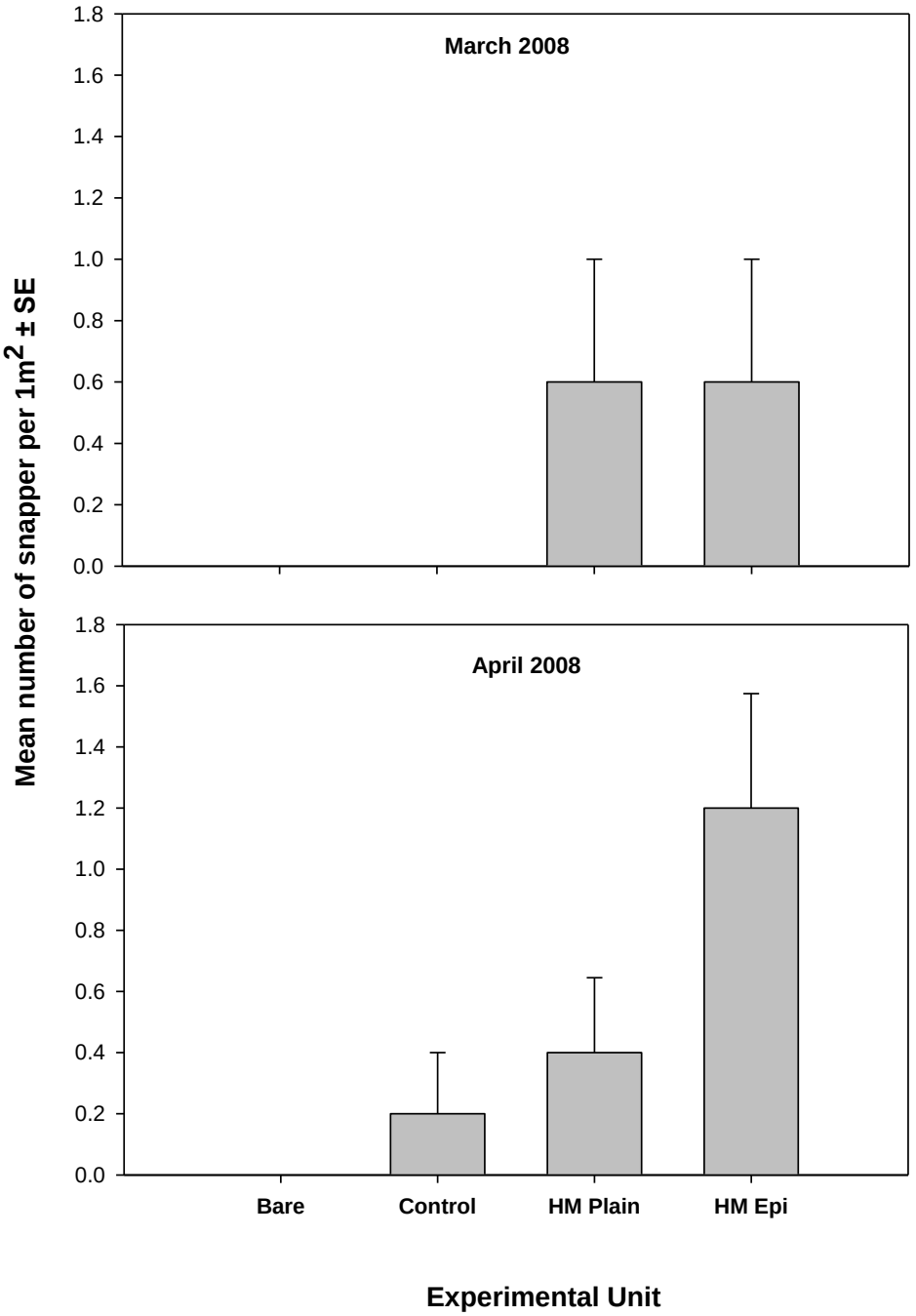


Figure 2.15 Mean number of snapper per $1m^2$ over 5 replicates of each artificial reef experimental unit type over the two months snapper were present (start of March and end March-start of April). Bare = bare sediment, control = frame with mesh only, HM plain = frames with plain horse mussels, HM Epi = frames with horse mussels with added epifauna.

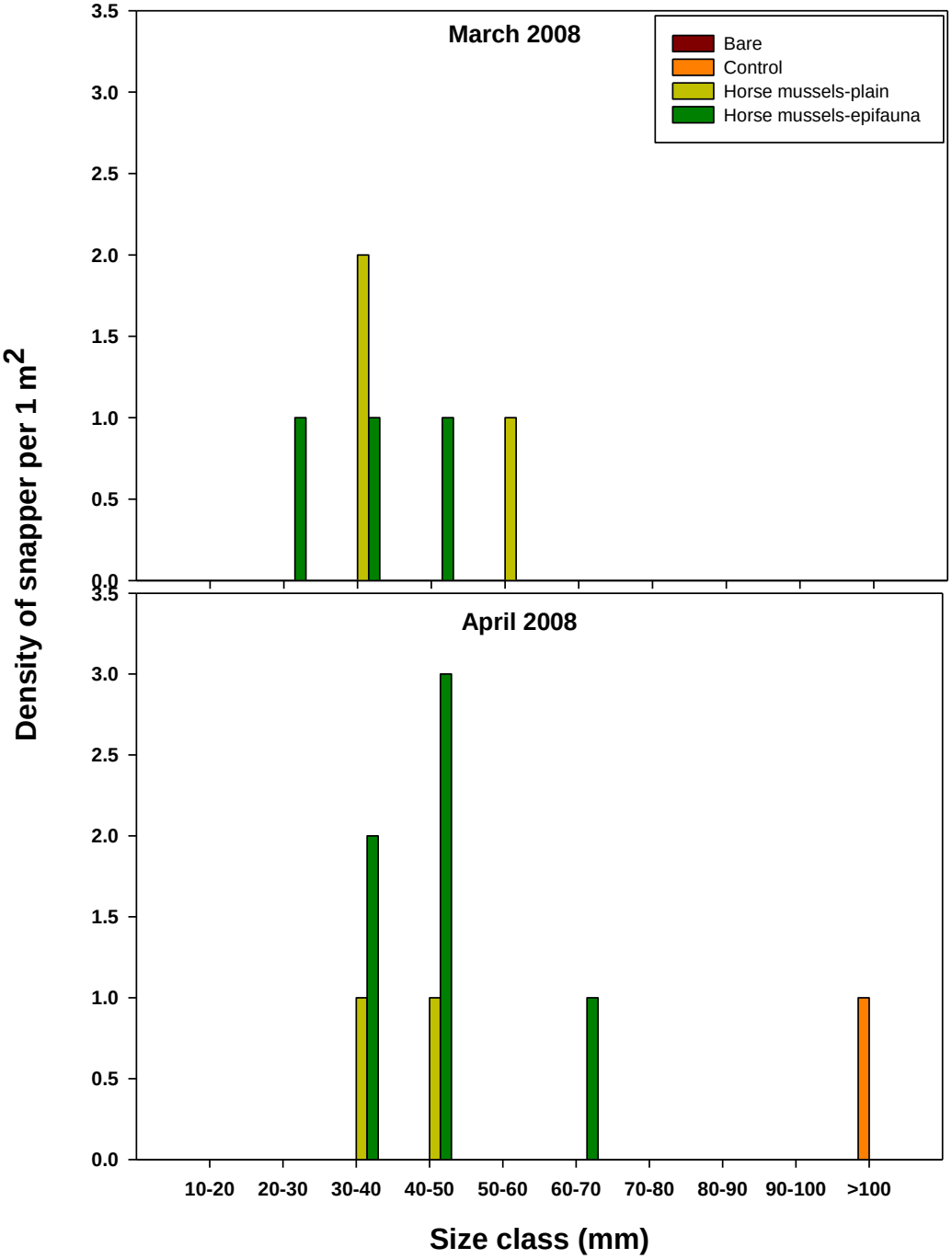


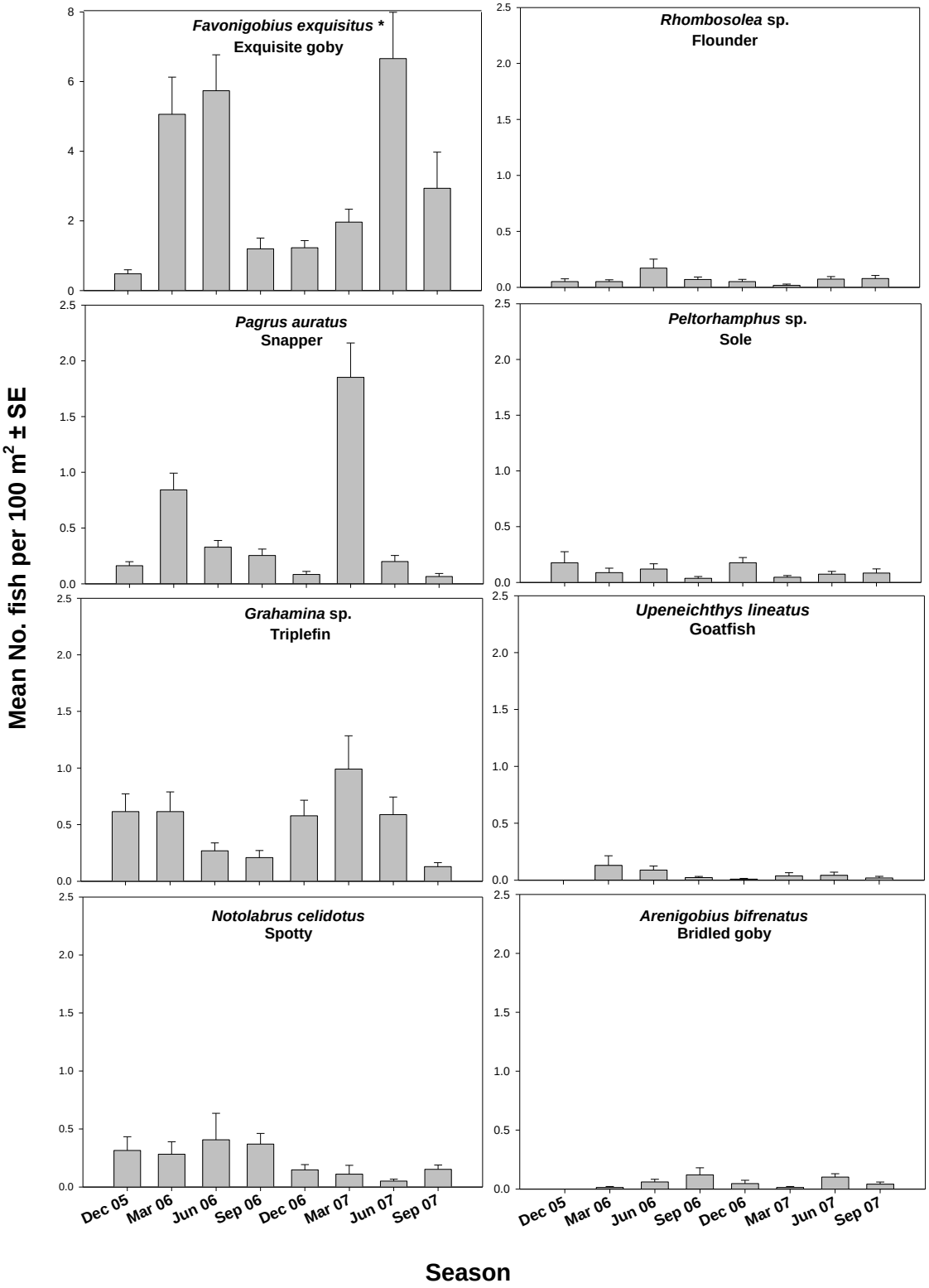
Figure 2.16 Density of snapper per 1 m^2 each month by size class on the artificial reef experimental units.

Appendices

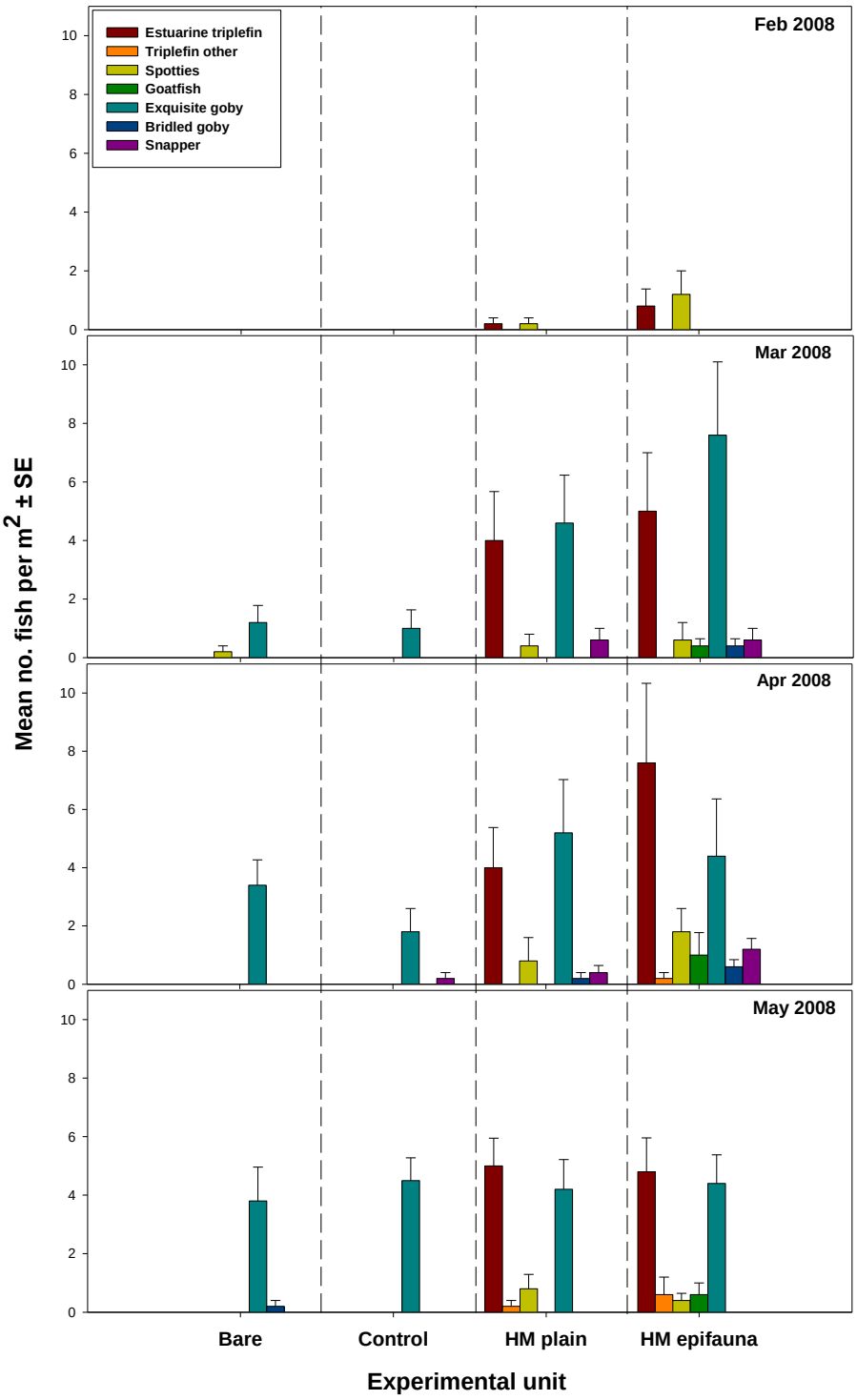
Appendix 2.1 List of all the fish species captured by the beam trawl each season as raw counts.

Common name	Scientific name	Dec-05	Mar-06	Jun-06	Sep-06	Dec-06	Mar-07	Jun-07	Sep-07	Total
Snapper	*Pagrus auratus*	35	182	71	55	18	400	43	14	818
Flounder	*Rhombosolea sp.*	11	11	37	15	11	4	16	17	122
Spotties	*Notolabrus celidotus*	68	61	88	80	32	24	11	33	397
Exquisite goby	*Favonigobius exquisitus*	104	1093	1239	258	265	424	1439	634	5456
Sand goby	*Favonigobius lentiginosus*	3	26	5	0	3	0	7	0	44
Bridled goby	*Arenigobius bifrenatus*	0	3	13	26	10	3	22	9	86
Triplefin	*Grahamina sp.*	133	133	58	45	125	214	127	28	863
Sole	*Peltorhamphus latus*	38	19	26	8	38	10	16	18	173
Northern bastard cod	*Pseudophycis breviuscula*	7	1	0	0	0	0	0	0	8
Rock cod	*Lotella rhacinus*	0	11	0	0	0	2	1	3	17
Goatfish	*Upeneichthys lineatus*	0	28	19	5	2	8	9	4	75
John dory	*Zeus faber*	0	0	1	0	1	0	0	0	2
Jack mackeral	*Trachurus novaezelandiae*	0	0	0	1	0	0	0	0	1
Yellow-eyed mullet	*Aldrichetta forsteri*	5	0	0	0	0	4	0	0	9
Anchovy	*Engraulis australis*	0	89	0	0	0	0	0	0	89

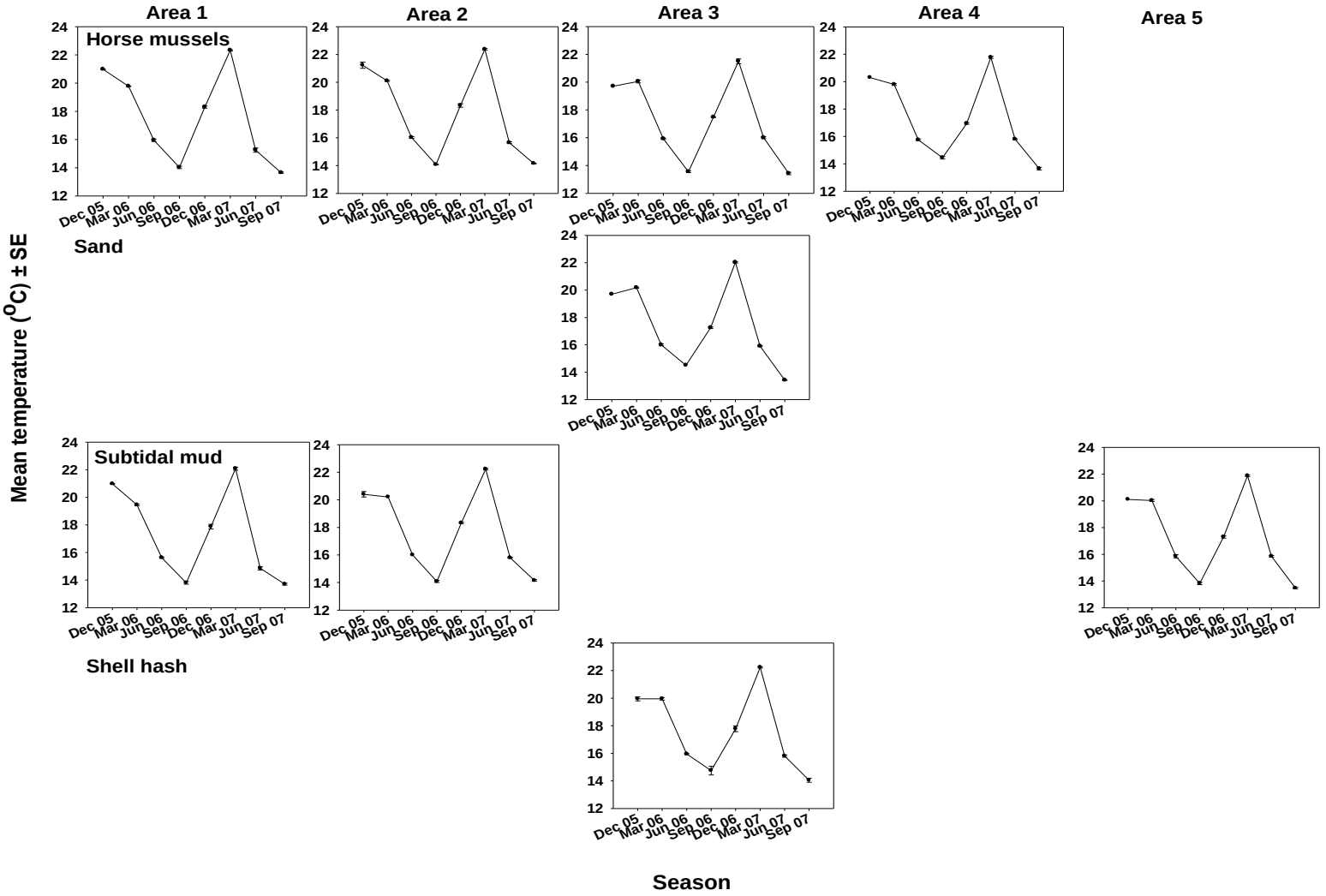
Appendix 2.2 Density per 100 m^2 of the top eight fish species captured each season by beam trawl. Note different Y axis scale for exquisite goby.



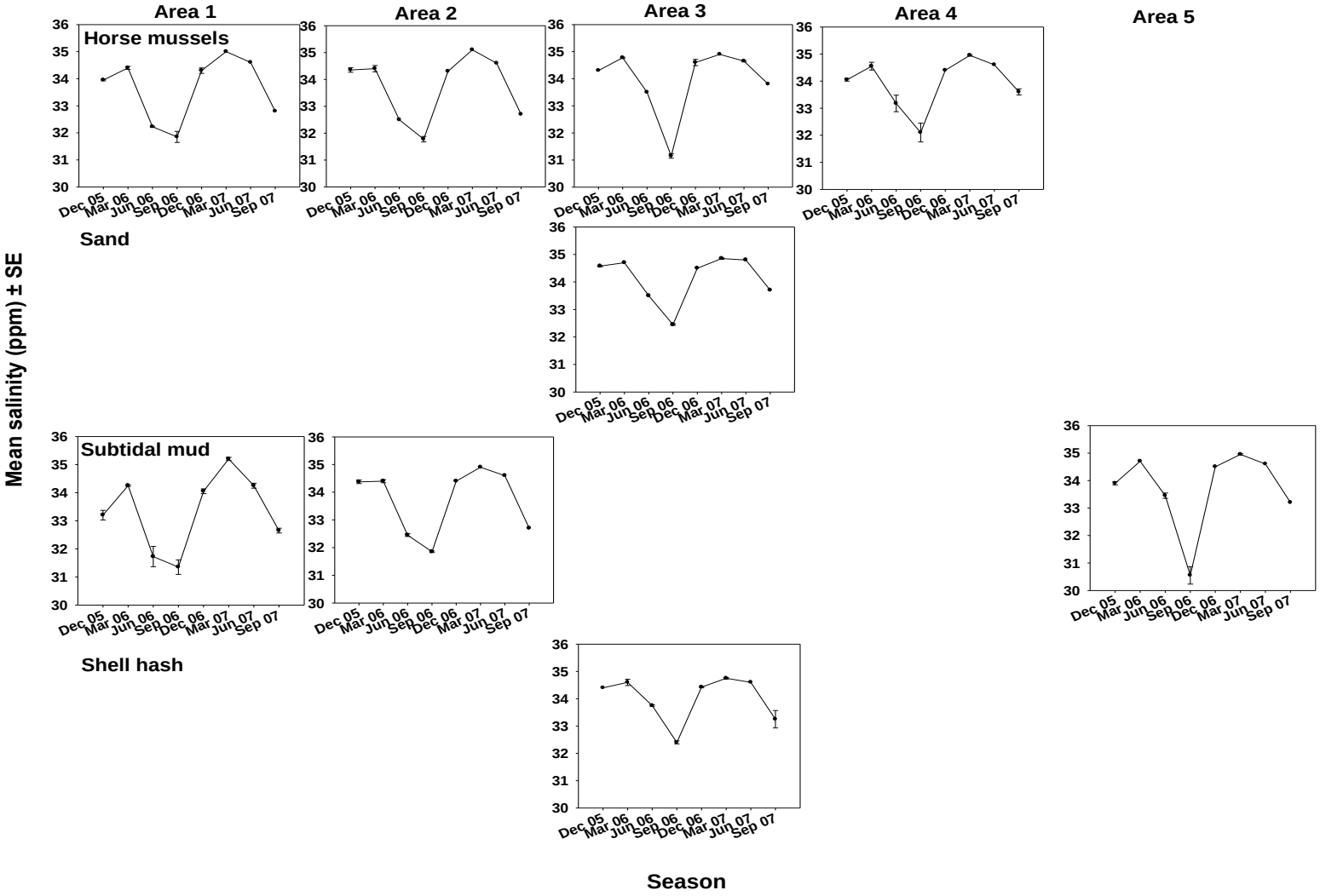
Appendix 2.3 Density per m^2 of all fish species from the artificial reef experiment on each experimental treatment: Bare, control, plain horse mussels and horse mussels with epifauna.



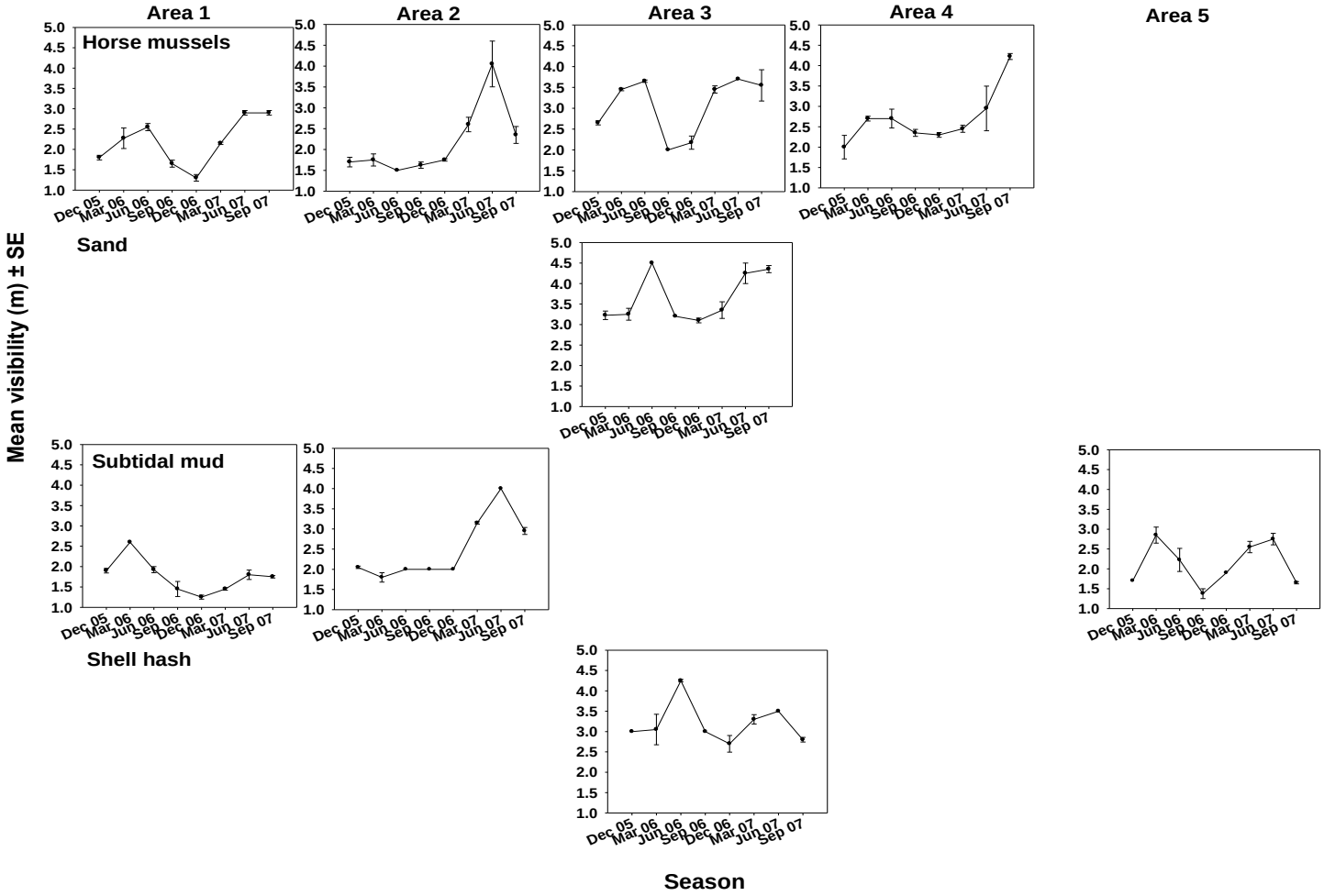
Appendix 2.4 Mean temperatures over each sampling season within each area (1-5) and habitat type.



Appendix 2.5 Mean salinities over each sampling season within each area (1-5) and habitat type.



Appendix 2.6 Mean visibility over each sampling season by secchi disk reading in meters for each area (1-5) and habitat type.



CHAPTER THREE

Ontogenetic shifts of snapper (*Pagrus auratus*: Sparidae) and movement patterns within an estuary

Introduction

It is well established that fish associate with complex habitats to reduce predation, increase food availability and/or obtain physical shelter (Crowder and Cooper 1982; Sale et al. 1984; Gibson 1994; Diaz et al. 2003; Laurel et al. 2003; Carbines et al. 2004; Mumby et al. 2004; Nagelkerken and van der Velde 2004; Rooker et al. 2004; Platell et al. 2007; O'Donnell 2008). Fish are not distributed randomly and their use of habitats can be complex, with the habitat selection process taking place at numerous times as species undergo extensive ontogenetic shifts (Werner and Gilliam 1984; Dahlgren and Eggleston 2000). Information on why organisms exhibit ontogenetic shifts is important for understanding the dynamics of a population (Dahlgren and Eggleston 2000). For mobile animals such as fish, spatial heterogeneity at many different scales may mean that the selection of habitat is a hierarchical process in which a general region is selected first, then a major habitat type, followed by successively finer-scale decisions about the local habitat features it encounters (Kramer et al. 1997). Ontogenetic shifts by juvenile Nassau grouper *Epinephelus striatus* for instance, support the hypothesis that habitat shifts are made to minimise the ratio of mortality risk to growth rate (Dahlgren and Eggleston 2000).

Benthic habitat complexities are known to influence fish abundance (Jones 1988a; Stoner et al. 2007; Carbines and Cole 2009) with patterns potentially altering along depth gradients, which may be related to the available habitat (Jones 1984; Gillanders 1997b). Grunts (*Haemulon* sp.), for instance, have been found to utilise the shallow biotopes of the lagoon Bay of La Parguera as juveniles and then migrate offshore to adult habitats in the form of increasingly deep reefs (Burke et al. 2009). New Zealand snapper, among other species, may use estuaries or other sheltered habitats during recruitment, with subsequent shifts to deeper, more exposed habitats as adults (Blaber

and Blaber 1980; Morrison 1990; Potter et al. 1990; Gillanders and Kingsford 2000; Morrison et al. 2002; Platell et al. 2007; Morrison et al. in review). Complex habitats within estuaries may be made up of biogenic structures (e.g. sponges, seagrass etc.), which are vulnerable environmental degradation (Caddy 2007; Morrison et al. in review). Movement of fish and how much time they spend in particular areas are also important measures of habitat use (Gillanders et al. 2003; Able 2005; Hindell 2007). A wide array of tagging studies have been undertaken on snapper including conventional external tag and recapture e.g. (Paul 1967; Crossland 1976; Crossland 1982; Gilbert and McKenzie 1999), visible implant fluorescent elastomer tags (Willis et al. 2003) and acoustic monitoring (Hartill et al. 2003; Parsons et al. 2003; Egli 2008). These studies have shown a variety of movement patterns, which has led to snapper being termed 'resident' or 'migratory' (Paul 1967; Crossland 1976; Paul 1976; Crossland 1977). The majority of tag and recapture studies in New Zealand have recaptured snapper within ~ 20 km of the tagging location, however some fish have been known to travel great distances (e.g. 418 km) (Paul 1967; Crossland 1976; Crossland 1982; Gilbert and McKenzie 1999). More recent work has demonstrated that some snapper have long-term site fidelity and may only move on the scale of hundreds of meters (Willis et al. 2001; Hartill et al. 2003; Parsons et al. 2003; Egli 2008). Evidence from Shark Bay, Australia suggests snapper (also *P. auratus*) also behave in a similar manner and although there are resident snapper within Shark Bay there is also an annual spawning migration from oceanic waters into the inner bay, which then acts as a snapper nursery (Moran et al. 2003).

Various methods are used to quantify fish distributions and abundances (Rozas and Minello 1997; Willis and Babcock 2000; Spencer et al. 2005; Morrison and Carbines 2006; Laurel et al. 2007). Snapper in New Zealand have traditionally been sampled using methods such as trawl surveys, mark and recapture, visual census, baited underwater video (BUV) and hook and line (Paul 1976; Kingett and Choat 1981; Crossland 1982; Francis 1995; Willis et al. 2000; Ross 2003; Gilbert et al. 2006; Ross et al. 2007), with these methods usually undertaken during the day. Recently a camera system (dropped underwater camera or 'DUV') has been developed to estimate the abundances and population length frequencies of benthic fish, with the added advantage of being able to simultaneously get detailed habitat and sediment structure information (Morrison and Carbines 2006; Carbines and Cole 2009). This method is effective at

quantifying snapper distributions and abundances, providing estimates of near absolute abundance of inactive fish 'sleeping' on the seafloor at night and reliably measuring fish greater than 5 cm (Morrison and Carbines 2006). By the time snapper are disturbed by the DUV lights or boat noise they have usually already been captured by the video. Day/night sampling of Mediterranean fish found significant differences between assemblages with more species visible during the day; however, the large sparids were more visible at night as they rested on the bottom and were very easy to approach (Azzurro et al. 2007). Night time sampling of fish within the Little Egg Harbour estuary in New Jersey revealed adult stages and fish beyond their first year, which had previously been underestimated and underappreciated due to daytime sampling bias and gear avoidance (Rountree and Able 1997). It was therefore suspected that the importance of estuaries to later juvenile and adult stages has been overlooked in many studies worldwide, with future research likely to reveal that these stages are an important component of estuarine ichthyofauna (Rountree and Able 1997).

The Mahurangi Harbour is a productive environment for snapper, particularly juveniles (Morrison and Carbines 2006). However, just how snapper utilise estuaries over their lifetime is poorly understood in New Zealand. The aim of this chapter was to quantify abundances and distributions of all sizes of snapper through time within the Mahurangi Harbour. Habitat associations were examined at multiple scales to understand how snapper may utilise these habitats and if shifts in habitat use occurred with growth. The DUV sampling was undertaken at night to obtain near absolute abundance estimates of snapper (Morrison and Carbines 2006). This provided a unique insight into how snapper behave at night as most other sampling of snapper has occurred during the day. A tagging study was also undertaken to better understand potential movement of fish within and out of the harbour to provide a more accurate picture of habitat use.

Methods

Dropped underwater video (DUV)

Surveys were undertaken with the DUV every three months from March 2006 to December 2007, with two extra summer surveys in February 2006 and January 2007

(see Figure 2.1 for location map in Chapter Two, Figure 3.1 for transect examples). The winter survey in June 2007 had to be abandoned due to persistent bad weather.

The DUV consisted of a 13.5 kg bulb keel and tail fin, which steadied and orientated a forward and downward facing (~ 30^{o}) frame fitted with a light sensitive Sony 470 low-light security camera and two parallel scaling lasers (10 mW) located 21 cm apart (Figure 3.2A and B). Light was provided by four white LCD torches. The scaling lasers were used to measure the width of each transect and fish length. The distance between the laser dots provided a constant scaling regardless of distance, but for measuring fish, as the angle of rotation from horizontal increases, the accuracy of the measurement decreases. A rotation of greater than 70 degrees from horizontal has been shown to increase the measurement error above 10% of the body length (Harvey et al. 2002). When analysing the tapes, frames of each snapper to be measured were stepped forward until the fish was in the same field of view as the lasers, with each fish measured along the body from nose to tail. If the snapper was high in the frame and could not be positioned, or the nose and tail were not visible, it was not measured.

The theoretical birth date of all snapper is conventionally defined as January 1^{st} as it is near the November-December peak of spawning and is a convenient origin for each year class (Paul 1976; Scott and Pankhurst 1992; Francis 1994). Length-frequency modes have been shown to correspond to age classes (Paul 1976; Francis 1994). Size frequency graphs were plotted for each season, with size (initially in 1 cm size class bins) to enable the central modal point to be calculated as per Paul (1976) for each season. From this snapper were assigned to a year-class of 0+, 1+, 2+, 3+ and > 3+ (Figure 3.3). For the Hauraki Gulf, growth curves based on otoliths and scale ages are available from Paul (1976) and Francis (1994). The size ranges for each year-class were then compared with these growth curves and were found to be very similar. Modes coalesced above 3+, so fish > 3+ were lumped. Although no aging from otoliths was completed in this study, it has been assumed that the year-classes defined are as accurate as possible, as the sizes within each year class fall within the definitions of Paul (1976) and Francis (1994) (Figure 3.4). It is possible that snapper at the boundaries of each year-class may be misclassified; however this bias would be expected to be consistent across all the year-classes and is not likely to affect the overall result.

The DUV was suspended by a rope and a live-feed coaxial cable directly below the vessel and sent digital video footage directly to a recording device (Sony Video Walkman GV-D900E PAL) on the vessel under power (~ 1.5–2 knots). The live-feed enabled the operator to monitor the DUV and to 'fly' it over structural items in its path by lifting the camera via the rope. Global Positioning System (GPS) location, date, time and depth were all burned in real time onto the recorded footage using a Video Titler (Horita GPT-50) integrated with the vessel's depth sounder and GPS (Figure 3.2C). Sampling was undertaken at night at least an hour after dark to give the fish a chance to settle. Due to visibility constraints, filming commenced approximately 2.5 hours before high tide and continued for around the same time after high tide. Weather conditions over each sampling period were reasonably consistent, as to fly the camera effectively the conditions needed to be settled, with little wind or swell. Up to four transects (visibility, weather change or equipment failure meant this number was at times less) per habitat type (n = 5) were completed at night over the 9 sampling seasons. Each transect was approximately 7 minutes long, equating to an area surveyed of approximately 300–600 m^2 depending on the visibility, which affected the transect width (Table 3.1).

Video analysis

All video footage was processed by the author, and details of the data collected are in Appendix 3.1. Each transect was considered at a number of scales. Data for the overall transect was collected using the date and time stamps and GPS co-ordinates. The total area sampled by each transect was back-calculated as the average within-transect width (multiple estimates taken over transect to correct for height variability) multiplied by the transect length as measured by GPS.

Within each transect, habitat breaks were recorded. If the substratum type or secondary structure was different for more than 30 seconds, it was recorded as a within-transect habitat break (Appendix 3.1). This made it possible to quantify transects at a finer spatial scale. As each fish was encountered, the position was recorded; it was identified to species level and measured for length. The area all around the fish was then quantified 10 m^2 around the fish, giving snapper quadrat data. The nearest item of structure to the fish was identified, (e.g., a horse mussel) and that distance estimated.

All items alive or dead around the fish were counted or estimated as percent cover. The major habitat and secondary structure types within this 10 m^2 quadrat were also recorded (see Appendix 3.1B for definitions). Within each transect, a number of randomly positioned habitat quadrats were also analysed. Random GPS points within each transect ('random habitat point') were assigned, a 10 m^2 quadrat was put around each point and quadrats were quantified in exactly the same way as the snapper quadrats. This enabled a comparison of the snapper data to areas without fish. For transects that had an overall uniform substratum type, i.e. no within-transect breaks, five random habitat quadrats were assigned. Along a transect that had multiple within-habitat breaks, three random habitat quadrats were assigned per break. On the odd occasion that the random quadrat included a fish somewhere in it, it was noted only. This gave me data at three spatial scales for each transect; 1) overall transect, 2) habitat breaks within-transect and 3) a quadrat around each individual fish species or random habitat quadrat.

Tagging

Tagging was undertaken on the 30/31 October 2006, 15 December 2006 and 9 February 2007, with a total of 354 snapper tagged. Snapper were caught using a 200-hook commercial longline set across the lower part of the harbour (area 3) in approximately 8–15 m depth, from the Leigh Marine Lab's RV Hawere, using pilchards and squid for bait. The soak time for each longline was approximately 45 minutes to an hour. Fish were held in a 500 l tank with flow-through seawater system on board the vessel. Snapper were retrieved from the tank for tagging using a plastic scoop to minimise any handling and white cotton gloves were used so as not to transfer bacteria to the fish. Each fish was measured to fork length and a ~ 10 cm yellow dart tag (Hallprint Australia) was inserted under the scales and anchored onto the dorsal fin rays (Figure 3.5A). Snapper were retrieved off the bottom slowly to minimise swim bladder inflation. However, if required, air was released by way of insertion of a hypodermic needle into the swim bladder. Once tagged, fish were placed back into the flow-through seawater tank and recovery was monitored for several minutes. Fish were then released back into the harbour, within the area of tagging (Figure 3.5B).

Statistical analyses

Transects varied in length or width, so all data were standardised to number of fish per 100 m^2. As the sampling design contained missing cells (i.e. not all habitats occurred in all areas) these factors could not be analysed using ANOVA. The habitats were initially assigned based on areas from habitat maps, therefore pooling the data by area or habitat and testing these separately was not considered appropriate. As the data was unbalanced (i.e. varying numbers of transects were completed each season), a non-parametric multivariate analysis of variance by permutation (PERMANOVA) using Bray-Curtis similarities (Anderson et al. 2008) was used to investigate differences in abundance over seasons. Season was a fixed factor and the data were square-root transformed to reduce the Poisson skew in the data (Quinn and Keough 2002). To determine the relationship between year-class of snapper and the factors season, area and *a priori* habitat type, the data were examined using non-metric multi dimensional scaling (MDS) with Bray-Curtis similarities (Clarke 1993). The data were square-root transformed and pooled at the transect level. Eigen-vectors for each year-class were overlaid to indicate the direction of importance for each year-class and their relationship to each other. Mean abundance of each year-class per 100 m^2 were overlaid as bubble plots to indicate the areas and habitats within the harbour each year-class was associated with.

To investigate how well the fine-scale habitat variables related to the *a priori* habitat types a principal components analysis (PCA) (Clarke 1993) was run on the major substrata, secondary structure and mean counts of structural items defined from the DUV transects. The data were pooled at the transect level and square-root transformed to reduce the right-skew after perusal of draftsman scatter plots. As depth was not skewed, it was left untransformed. Eigen-vectors < 0.2 were not plotted for clarity. Canonical analysis of principal coordinates (CAP) (Anderson et al. 2008) was used to test the validity of the assigned habitat types as well as the classification success. This technique performs a constrained ordination on a specific *a priori* hypothesis (i.e. no difference between the habitat types), or finds the strongest correlation with some set of variables and chooses the axes that best separate the designated habitat types in multivariate space, carrying out a permutation test for differences between the groups. CAP carries out a leave-one-out allocation of observations to habitat types to obtain misclassification errors which indicate the success of the classification system (Anderson et al. 2008). The analysis was run using Bray-Curtis similarities on square-

root transformed data. The procedure BEST (Bio-Env + stepwise) was undertaken to find the best 'match' between the multivariate among-sample pattern for snapper and the fine-scale habitat variables associated with them, by searching for high-rank correlations (Spearman rank). The extent to which these two patterns match reflects the degree to which the chosen environmental data helps 'explain' the biotic pattern. Both matrices were based on Bray Curtis similarities as both sets of data were based on counts. All analyses were run using PRIMER 6.0 and PERMANOVA + for PRIMER 6.0 (PRIMER-E 2008).

To examine the relationship of snapper with fine-scale habitat, snapper counts for each size class were converted to a density estimate per 100 m^2 that takes into account the random habitat quadrats as well as the snapper quadrats. This was done as the snapper quadrats were not taken randomly from within each transect, rather all snapper were included so as not to lose the valuable data this information provided. Therefore, it was important to quantify the habitat variables where snapper *were not* and add them to the snapper data to remove the bias of non-randomness. This was done using the following equation:

$$D_{substratum} = \frac{N}{A \times (S/T)} \times 100$$

$D_{substratum}$ = Snapper density (per 100 m^2) associated with each major substratum or secondary structure (see Appendix 3.1B for definitions)

N = Total number of individual snapper split into size classes, associated with each of the defined major substrata or major secondary structure

A = Total area surveyed

S = Total number of individual random habitat points associated with each of the defined major substrata or major secondary structure

T = Total number of random habitat points surveyed

Therefore, the number of individual snapper recorded in a particular habitat was divided by the area occupied by that habitat to get an estimate of density across each of the defined major substrata or major secondary structure habitat by size class. As the estimates calculated are not means, no error could be calculated. To test for differences

in fine-scale habitat use by each size class of snapper, a PCA (Clarke 1993) was run on the major substrata and structural variables using size-class as a factor.

Results

Broad-scale associations of snapper with habitat

Over the 9 sampling seasons, 389 transects were completed over the five areas and five *a priori* habitat types, encompassing ~ 121,000 m^2 within the Mahurangi Harbour. Snapper of all sizes were found across all areas and habitat types over time, with on average, 1–1.5 snapper per 100 m^2 (Figure 3.6, Appendix 3.2–3.6). This scaled up to the population level of the harbour gave an overall number of ~ 145,000–300,000 snapper at any given time (these values differ for each year-class Table 3.2 and across habitats, Appendix 3.7). On average, the highest densities of snapper were found in area 3 (lower harbour, 1.8 per 100 m^2), followed by area 2 (mid harbour, 1.5 per 100 m^2), then area 1 (upper harbour 0.98 per 100 m^2) (Figure 3.6). Averages of snapper per 100 m^2 over the *a priori* habitat types were highest in the shell hash (2.3 per 100 m^2), then sand (1.5 per 100 m^2) and horse mussel habitat (1.48 per 100 m^2) (Figure 3.6).

There were significant differences in the numbers of snapper overall across all seasons (Table 3.3). Pairwise tests indicated December 2006 had on average, fewer fish than any other season. The 0+, 1+ and 2+ year-classes showed significant differences in densities over the seasons (Table 3.3). Pairwise tests for the sizes 0+ and 1+ distinguished January to June from the later seasons of September to December each year, while the higher densities in March 2006 for the 2+ fish were distinguished from most other seasons. Within the 0+ year-class, fish ranged in size from 0–11 cm. As the DUV is unreliable for detecting fish < 5 cm (Morrison and Carbines 2006), the smaller sizes in this year-class were under-represented. This can be seen over time, with higher densities of 0+ fish towards the mid to end of each year (Figure 3.7, Table 3.2). The density of 0+ snapper over the sand in September 2006 was high in comparison to all other seasons (Appendix 3.2 and 3.7). A growth shift was observed for the 0+ to 1+ and 2+ to 3+ year-classes across seasons, with higher abundances at the start of each year, but the same shift was not seen for the 1+ to 2+ snapper (Figure 3.7, Appendix 3.2–3.6).

Plots of individual snapper by year-class (pooled across all seasons) show a clear pattern of decreasing densities with growth. Individuals become more concentrated around the main body of the harbour, with the 1+ fish more widespread than all other year-classes (Figure 3.8). The GPS location was plotted to summarise distribution patterns across each year-class. However, there was very little difference between the year-classes in terms of average location (Figure 3.9A). The average GPS location was then examined by seasons pooled over the two years of sampling for each year-class. From mid-summer through to the start of the following summer, snapper appeared to follow a similar trend of movement (except for the 1+); however the distance between the points was not large, indicating little seasonal difference (Figure 3.9B–F).

Multi-dimensional scaling (MDS) plots of all the snapper year-classes indicated fish were more closely associated with the *a priori* habitat types of horse mussels, sand and shell hash across the mid to lower parts of the main section of the harbour (areas 2 and 3) and to some extent the subtidal mud and horse mussels within the upper part of the harbour (area 1) (Figure 3.10A). Year-class eigen-vectors were overlaid on the plot to examine any differences. The MDS plot separated the 0+ (towards the bottom of the plot) and 1+ year-class (towards the left of the plot). Densities (bubble plots) of snapper were layered over the MDS plot to look for differences. The abundance of 0+ snapper was slightly less than 1+, with the 1+ fish more widespread through the harbour, with increased densities towards the top of the MDS plot in intertidal and subtidal mud habitats around the harbour (Figure 3.10B and C). Abundance per 100 m^2 decreased with an increase in size, and snapper in general were found within the mid to lower part of the harbour (Figure 3.10D–F). These areas were also the deeper part of the harbour, ranging from 9–20 m through the main channel, encompassing sand and shell hash in area 3 and subtidal mud in area 2. The horse mussel beds in these areas are shallower than the sand and shell hash habitats (~ 4–8 m). Each individual snapper was plotted by the depth it was found at, however no clear relationship was observed (Figure 3.11). Means densities of snapper per 100 m^2 by year-classes over average transect depth were also plotted, but again, no relationship was seen with depth.

The year-classes also differed across the *a priori* habitat types, with highest densities of snapper in the shell hash and lower densities in the intertidal habitat (Figure 3.12). Average densities of the 0+ fish were 2-fold higher in the shell hash, sand and horse

mussels as compared to the subtidal mud and intertidal habitats. Densities of the 1+ fish were about 25% higher in the shell hash compared to the other habitats and over twice as abundant compared to the intertidal areas. Densities of the 2+ fish were 2 to 5–fold higher in the shell hash than other habitats. The 3+ abundance was highest in the shell hash and sand habitats, and the fish larger than 3+ were 2–fold more abundant in the shell hash compared to other habitats (Figure 3.12, Appendix 3.2 –3.6).

Fine-scale habitat associations with broad scale habitat

The DUV transect analysis not only provided information at a broad-scale transect level, but also allowed data to be collected in the form of major habitat breaks within transects and at the level of fish and random habitat quadrats. Within the broad-scale *a priori* habitat types, major substrata and major secondary structure were identified (see Appendix 3.1 for full list). Shell hash varied in percent coverage so was defined as either major substrata or secondary structure. If more than 60% of the substratum was shell hash it was defined as major substrata. If percent cover was less than this, it was defined as major secondary structure (Appendix 3.1). The sand and shell hash habitats were the most complex, with the major substrata more coarse than the other three *a priori* habitat types, i.e., the substrata was comprised of muddy sand through to shell hash (Figure 3.13). The least complex habitat was the intertidal with a mostly muddy substratum with some patches of shell pieces. Within the horse mussel habitat, horse mussels were often patchy, interspersed with areas of mud, while the subtidal mud habitat had patches of complexity in places, including one small area of shell hash within area 2 (Figure 3.13). The major substrata and secondary structure data were subjected to a PCA analysis, which clearly separated the *a priori* habitat types by the fine-scale variables (Figure 3.14A). The sand and shell habitats separated by PC1 to the right were characterised by shell grit/sand, broken topography, rippled bedform and depth. To the left are the shallower, muddier sites of horse mussels, intertidal and subtidal mud, characterised by dimpled topography and burrows with coverage of 21–30%. Substrata with no structure (bare) and areas with structure in the form of horse mussels and horse mussels with sponges were split by PC2. Several subtidal mud points were pulled towards the middle of the plot driven by some small sections of shell hash seen within this habitat.

The constrained analysis (CAP) closely matched the PCA plot and found significant differences between the habitat types (p = 0.001) (Figure 3.14B). This analysis was run to reveal the potential classification success of the broad scale *a priori* habitats by the fine-scale habitat variables recorded within them. The classification success was high (82.5%, misclassification error = 17.5%) across all the habitat types, with classification success for intertidal (100%), horse mussels (86.1%), sand (77.8%), subtidal mud (69.2%) and shell hash (66.7%) habitats. The four principal coordinate axes used for the CAP analysis explained 96.9% of the variability in the original dissimilarity matrix, indicating the strength of the association between the multivariate data cloud and the hypothesis of the group differences (Anderson 2002). Misclassification occurred between horse mussels and subtidal mud due to large patches of horse mussel habitat that were devoid of horse mussels and subtidal mud that contained some patches of horse mussels. Some subtidal mud sites were classified as intertidal and some as shell hash. Several sand and shell hash sites were misclassified as each other due to their similar substratum types and the occurrence of similar secondary structure in the form of sponges and some horse mussels with sponges. This can be seen in the CAP and MDS plot with the cross-over of some of the habitat points (Figure 3.13 and 3.13).

Snapper associations with habitat

The fine-scale PCA of the mean counts of major structural items from the snapper and random habitat quadrats clearly separated the variables along PC1 (Figure 3.15). All the intertidal and most of the subtidal mud sites were strongly pulled towards the left of the plot by no structure, while PC2 separated the remaining data by the major habitats shell hash, sand and horse mussels, which had particular structural items associated with them (Figure 3.15). Scallops, shell pieces, macroalgae and sponge eigen-vectors were separated by PC2 towards the shell hash and sand habitats, while plain horse mussels and horse mussels with epifauna, soft corals and hydroid eigen-vectors were pulled down by PC2 towards the horse mussel and some subtidal mud habitats. The eigen-vectors for worm tubes and pits tended to be drawn between the two groups indicating they were found across most habitat types (Figure 3.15).

The distance from each snapper within fish quadrats and from the middle of each random habitat quadrat to the closest item of structure was measured and the distances

compared among year-classes (Figure 3.16A). The ratios of snapper quadrats to random habitat quadrats were always above 1, meaning each year-class of snapper were more likely to be associated with an item of structure within 5 m than a randomly chosen habitat quadrats (Figure 3.16B). Most fish were within 50 cm of some sort of structure, however for the smaller year-classes (0+, 1+, 2+), this ratio was highest at 40 cm. Interestingly, the larger fish (3+, > 3+) had ratios of 1.5–2.5 at zero distance, indicating these larger fish were often leaning against an item of structure (Figure 3.16B).

To connect the fine-scale habitat variables to snapper, abundance was converted to densities per 100 m^2 as a proportion of the associated random habitat quadrats over the total area (m^2) sampled. The association of areas containing structure with bare areas for year-classes of snapper was obviously different (Figure 3.17A). The ratio of structure to bare areas was much greater than 1 for all year-classes, indicating a preference of all year-classes for areas with structure. This association strengthened with the larger year-classes of fish, culminating in > 3+ fish having a ratio of 10:1 in favour of structure (Figure 3.17B). Snapper were associated with 9 different categories of major substrata. Abundances for 1+ fish and larger were more associated with coarse substrata than fine sands and mud, particularly shell armouring and large shell hash (Figure 3.18). Densities of 1+ fish were also higher in the mud to fine sand groups than the 2+, 3+ and > 3+ snapper. 0+ snapper differed from the other year-classes in being less associated with coarse substrata and more associated with the finer substrata (Figure 3.18). Fish > 3+ were more strongly associated with shell hash than other substratum. Principal components analysis (PCA) confirmed a split between the year-classes associated with major substrata (Figure 3.19). The smaller year-classes (0+, 1+), were separated along PC1, from the larger year-classes. 0+ and 1+ fish were further split along PC2, by the major substratum variables. 0+ upwards and to the right, driven by finer sands and mud, and down towards 1+ fish, which was driven by higher densities related to more coarse substrata (Figure 3.19).

The relationship between snapper and the major secondary structure followed a similar pattern to the major substrata across the year-classes. The 1+ fish and larger were associated with shell, sponges, horse mussel with epifauna, and plain horse mussels in descending order of importance (Figure 3.20). The 0+ fish differed by being more associated with sponges, horse mussels with epifauna and other structure (mostly worm

tubes, macroalgae, pits and scallops) (Figure 3.20). PCA of the association of year-classes with major secondary structure again separated the smaller year-classes from the larger along PC1, with the 0+ and 1+ fish also split by PC2 (Figure 3.21). 0+ snapper were more associated with sponges, horse mussels with epifauna and other towards the top right of the plot, while a stronger association with bare areas and shell drew 1+ fish downwards to the right (Figure 3.21). Biota and/or environmental matching (BEST) analysis for all snapper and the substratum characteristics (consisting of the major substrata, secondary structure, topography and bedform variables, plus presence of burrows, see Appendix 3.1B for details), revealed a correlation of 0.45 with the variables shell hash, shell grit/sand, horse mussels, worm tubes and sponges.

Movement

A total of 354 snapper were tagged from November 2006 to February 2007 (Table 3. 4). All tagging was completed within area 3, the lower part of the harbour, across a depth range of 8–15 m (Figure 3.22). The recapture rate was 9.9 % (35/354) over 886 days. Of these recaptures, 80% came from within the Mahurangi Harbour (Figure 3.22). Recaptures were mostly made over the summer months (Figure 3.23). However, no fishing effort was recorded over the tagging programme, so this could not be corrected for. The smallest distance moved for recaptures was on the order of 100's of meters, while the greatest distance travelled was to Whangarei Harbour ~ 100 km north (Figure 3.22 and Figure 3.24). Recaptures within the harbour were within 2 km of the original tagging area, while outside the distance travelled from the tagging area ranged from 2–100 km. The first tag return was made within 11 days and the last 886 days after release (Figure 3.23 and 3.21). Minimum distance travelled was not correlated with either days at liberty (Figure 3.24) or fish size (Figure 3.25).

Discussion

The aim of this study was to estimate densities of snapper of all year-classes, and define within the Mahurangi Harbour the areas and habitats important to snapper over time. Tagging was undertaken to determine the scale of movement among snapper. The DUV enabled data to be collected at both broad and fine-scale levels. These were at the level

of the overall *a priori* habitat type, at the level of each transect and around each individual fish.

Temporal differences

The one-off sampling population estimate of 166,000 snapper found by Morrison and Carbines (2006) was similar to the overall estimates found from this study of ~ 145,000-300,000. However, sampling over multiple spatial and temporal scales, enabled a more accurate population estimate to be calculated within habitats as well as across the harbour as a whole. Snapper abundance within the harbour fluctuated seasonally, and was significantly lower in December 2006 than other months. The highest population estimate ~ 300,000 was from September 2006, but by December 2006 this had dropped to 138,000. This was driven by a significant increase in 0+ snapper over the sand in September 2006, which was unusually large in comparison to all other seasons, but by December 2006 densities over sand were much lower (100–fold less) and this was the main contributor to the overall population estimate drop. There was also a substantial decrease in the number of 1+ and 2+ snapper from September to December 2006 (1+ 93,000 to 36,000, 2+ 44,000 to 17,000). Some of the decrease can be attributed to a growth shift through to the next year-class; however, the 1+ fish decrease did not follow the same pattern, with no corresponding large year-class shift seen moving through to the 2+ year-class at the beginning of 2007.

A number of possibilities may contribute to these decreases for the 0+ and 1+ fish, including mortality, predation, emigration or non-capture by the DUV. For the 0+ fish at the beginning of the year, some of the decrease would be due to the size selectivity of the DUV. However the high increase in the 1+ density indicates that some of the decrease is due to a growth shift through to the 1+ year-class. Environmental data (Chapter Two) showed high rainfall (~ 140 and 100 mm) from June to September 2006 and increased turbidity from September to December 2006, especially in the upper part of the harbour. Increased densities of 1+ fish moved into the subtidal mud and intertidal areas within the upper reaches of the harbour that had higher turbidity and this may have resulted in increased mortality. Although the 0+ were not as wide-spread as the 1+ fish, they were generally within more fine sand to muddier habitats within the horse mussels, subtidal mud and some intertidal areas, therefore may have been also subjected

to increased turbidity. High concentrations of suspended sediments negatively affect 0+ juvenile snapper by increasing respiration, decreasing activity including feeding, and eventual increased mortalities (M. Lowe, unpublished data). The higher turbidity may also mean less snapper were seen by the DUV. The 1+ fish may have also emigrated from the harbour to adjacent coastal embayments and reefs as other work has shown estuaries act as juvenile nurseries for snapper in the first one to two years of life (Gillanders 2002; Gillanders 2002; Thrush et al. 2002; Morrison et al. in review). However, without movement data for this size class this remains speculative.

June 2006 also had lower numbers of fish than other months, although this was not statistically significant. Size frequency analysis indicated the lower densities were partly due to the lack of larger snapper (3+ and > 3+) within the harbour. September 2007 was also significantly different to other months with very few > 3+ snapper in the harbour. Studies undertaken on rocky reefs in marine reserves around north-eastern New Zealand revealed a strong seasonal pattern in snapper abundance, with snapper densities in autumn nearly double those in spring (Willis et al. 2003; Denny et al. 2004). Larger adult snapper are thought to follow a seasonal migration from deeper to shallow coastal waters over summer, which may be related to water temperature changes and/or the formation of spawning aggregations (Crossland 1976; Paul 1976; Sumpton et al. 2003). Although September 2006 had higher population estimates than 2007 for both 3+ and > 3+ fish, both spring densities were much lower than both autumn estimates (March), indicating a similar pattern may be occurring within the estuary (Appendix 3.7).

Effects of growth on detectability

The inability of the DUV to reliably detect snapper < 5 cm in length could be clearly seen in the difference between densities of 0+ fish at the beginning-mid part of the year and later in the year, with 0+ snapper densities being significantly greater (2–4 fold) towards the end of each year (September to December). This was in direct contrast to the beam trawl sampling (Chapter Two) where abundances of 0+ fish decreased over the year. This was good confirmation that above about 7–8 cm snapper are able to out-swim the trawl and the DUV becomes a more reliable sampling method. This also highlights the importance of using methods appropriate for the hypothesis being tested or using a combination of methods rather than one in isolation.

Habitat classification

Habitat types are classified by physical and/or biological factors (e.g. Shears et al. 2004). Spatial variability differed with location, with the main body of the harbour having higher snapper densities than the arms of the harbour. Within the main body of the harbour, the mid and lower areas contained more fish overall and these areas also had more complex habitats of shell hash, sand and horse mussels (in descending order of complexity). The high classification success for the *a priori* habitat types based on the major substrata and secondary structure defined from the DUV analysis revealed the original habitat types chosen from the habitat map were meaningful and could be used to reliably categorise the Mahurangi at a broad-scale level. However, the DUV also gave the ability to refine the original classification, especially for the more complex habitat types. The lower classification success for the structurally more complex shell hash and sand habitats indicated that these areas could be defined differently, with for instance, 'sponges' as a category similar to horse mussels. The areas with sponges were often quite extensive, forming very complex structural areas, with fish often on top of, amongst or leaning against them. Some subtidal mud areas were misclassified due to their similarity to some intertidal sites and because of patches of structure. The subtidal mud habitat within area 2 (in the middle of the harbour) had some large patches of structural complexity in the form of a large patch of shell hash similar to the *a priori* shell hash defined from area 3 and some patches of horse mussels. These patches also often had secondary structure in the form of sponges, hydroids and soft corals and potentially this habitat could be subdivided into two, indicating the importance of being able to define more fine-scale patches for habitat classification.

Depth often affects the distribution of fish (Blaber and Blaber 1980; Gillanders 1997b; Francis et al. 2002; Stoner et al. 2007). Past studies on snapper have found that depth distributions vary, suggesting that water depth may not influence snapper abundance per se; rather the presence of favourable habitat and other factors are likely to be more influential (Sumpton and Jackson 2005). Within the Mahurangi Harbour, depths ranged from 1.7 m in the intertidal to 20 m out on the sand near the mouth of the harbour. Beam trawl data analysis (Chapter Two) showed higher densities of 0+ snapper were found in less than 10 m, however, DUV analysis showed no pattern with depth over any of the year-classes. For the 0+ fish, this may be a size selective sampling artefact of the beam trawl, which under-samples fish > 7–8 cm (Morrison and Carbines 2006).

Fine-scale habitat associations

The DUV data analysis also allowed a detailed analysis of habitat around each snapper. As data were collected at night, it revealed a pattern of habitat use by snapper rarely seen before. Rountree and Able (1997) found by sampling at night that previous studies in the Little Egg harbour in New Jersey had underestimated an important component of the fish fauna, namely large fishes that appeared to utilise the shallow bays, shoals and marsh creek habitats during the night. Large snapper are known to be mobile during the day (Hartill et al. 2003; Parsons et al. 2003; Egli and Babcock 2004), with little chance of seeing them with the DUV during the day (author's unpublished data). However, night sampling revealed patterns that were quite different to what was expected. The ratio of snapper association to structure vs. bare areas for each year-class was significant as snapper increased in size. This was unexpected, and due mostly to larger fish utilising areas of structure as a place to rest.

Areas containing patches of structure such as horse mussels can provide protection for organisms from wave forces and alter current flows, reducing velocity and hydrodynamic forces (Green et al. 1998; O'Donnell 2008). The shell hash was the major substratum that snapper aged 1+ and older seemed to associate with. In particular, > 3+ fish were proportionally more abundant (47%) in this habitat than nearly all other substrata combined. Observations from the video were that many of the larger snapper settled amongst the shell hash, which may give them some stability to rest and protection from currents. Snapper were often leaning against other items of structure also, such as sponges, horse mussels or within pits, suggesting these habitats are also providing a more stable place to rest. The ratio of distance to the nearest item of structure reflects this for all ages, but especially 3+ and older. The 0+, 1+ and 2+ snapper had higher numbers 40–50 cm away from structure and these smaller fish may be using the cover of darkness to feed (Muller 1998), but remaining close enough to cover if it is required to escape predators. The cover of darkness may also mean that the association with structure need not be so strong to avoid predators. Observations from the video gave the impression that these smaller fish were more active than the larger fish at night (pers. obs.). A similar pattern in other fish has been seen. For instance, observations of juvenile French grunts (*Haemulon flavolineatum*) found fish in close association during the day with mangrove prop roots, but at night these areas were

deserted as the juveniles moved out to the adjacent soft-bottom habitat to feed (Burke et al. 2009).

0+ snapper from the beam trawl sampling (Chapter Two) were mostly associated with horse mussels based on the structure that came up with the fish in the trawl as a crude analysis of habitat association; however the DUV allowed a more complex picture to be drawn. Fine-scale analysis revealed the major substrata and secondary structure that snapper were most associated with at night. This could then be compared to the random habitat quadrats where snapper were not found to determine associations between snapper and habitat variables. Data from the *a priori* habitats indicated that 0+ densities were higher amongst the shell hash, similar to the other year-classes. However, fine-scale associations from the DUV showed 0+ fish differed from other year-classes, with higher densities of snapper on sandy to muddier sediments, rather than the shell hash. These fish were also associated with sponges and horse mussels with epifauna as secondary structure than the other sizes. Overall, from the horse mussel data (both with and without epifauna) the association with horse mussels was the same as with sponges. The 'other' category included worm tubes, algae, pits and scallops and the association of 0+ fish with this category was higher than the other year-classes, indicating that any structure per se may be utilised by 0+ snapper. Juvenile snapper (3–10 cm) sampled from estuaries along the west coast of New Zealand were strongly associated with horse mussels and subtidal seagrass (particularly in the Kaipara harbour), and terrestrial debris such as logs and branches in the Whangape estuary (Morrison et al. in review). Snapper of this size were rare on the open coast (Morrison et al. in review). 0+ red snapper (*Lutjanus campechanus*) appeared to select relic shell beds at first settlement (Szedlmayer and Conti 1998), but choose any small relief structure over flat substratum (Workman and Foster 1994).

Older year-classes showed a similar pattern that differed from the 0+ fish. These snapper were more common within the coarse substrata, especially shell hash. They were also more associated with major secondary structure of shell hash, horse mussels and then sponges in descending order of importance. 1+ snapper also had higher numbers in the less complex habitats of subtidal mud and intertidal areas, indicating this year-class was more widely distributed throughout the harbour. The lower ratio of the association of fish with structure to bare areas confirmed that 1+ fish were more

associated with bare areas than the other year-classes, but as the ratio was 2.5:1, structure was still more important. It would appear that the 0+ fish are therefore avoiding the shell hash habitat so highly favoured by the larger fish, especially the > 3+ year-class. This pattern was only revealed through analysis of the more fine-scale habitat surrounding each individual fish, rather than from data at the more broad-scale *a priori* habitat level. Overall, at a broad-scale, ontogenetic shifts were not obvious amongst the various year-classes across the *a priori* habitat types. However, snapper showed ontogenetic shifts in habitat use within the harbour, at a more fine-scale habitat level.

The smaller 0+ snapper were more prevalent in the sandy to muddy sediments that contain large patches of horse mussels and sponges. This may be a way of avoiding the larger fish which may potentially pose a threat to them. 0+ snapper within a rocky reef environment generally occupied the interface between reef and adjacent soft sediment, which was hypothesised to give them the greatest chance of avoiding multiple predators by using the reef as cover from pelagic predators, and the soft sediment and turfing algae as better foraging areas, but also to keep a safe distance from reef-associated predators (Ross et al. 2007). Both 1+ and 2+ snapper over soft sediments were found by Thrush et al. (2002) to be most abundant in areas with structural features such as depressions, burrows, shells, boulders, cobbles and sand waves. When compared with this study, the structural items differ, but snapper still remain associated with structure of one form or another. The main items of structure within the Mahurangi Harbour are also largely biogenic or the remains of biogenic structure (e.g. scallop and horse mussel shells) and therefore vulnerable to habitat degradation from anthropogenic activities around the harbour. Long-term monitoring over 11 years within the Mahurangi harbour has seen a change in the ecology of the estuary consistent with increased sediment loading, with decreases in intertidal bivalves, and in some areas a decline in subtidal horse mussels (Cummings et al. 2005).

Movement

The snapper tagged as part of this study appeared to be mostly resident, or at least returning to the Mahurangi if they leave, with 80% of the fish recaptures coming from within the harbour. Exact tagging GPS locations were not recorded; rather fish were

released within one area. Therefore, within the harbour exact distances could not be calculated, rather estimates of minimum distance moved were made, with snapper moving between 100's meters up to 2 km. Of the 20% of fish that moved out of the harbour 11.4% were recaptured within < 20 km, while the remaining 8.6% were recaptured up to 100 km away. Recaptures within the harbour were mostly over the summer. This could indicate the fishing pressure on the harbour was quite seasonal or the fish were less catchable over winter.

The recaptured fish were all tagged within the Mahurangi originally. None of the ~ 10,000 snapper simultaneously tagged outside the harbour at various locations within the Hauraki Gulf as part of the wider tagging study (M. Morrison and D. Parsons unpublished data) were recaptured within the Mahurangi. The reasons for this are unclear, but may indicate that snapper within the Mahurangi remain within, or close to, the harbour possibly because this was where they settled as juveniles, while juveniles that settle elsewhere have no such association with this area. In some parts of Australia, snapper stocks exhibit different migratory behaviour patterns suited to the local environments of the various stocks (Moran et al. 2003). For example, adult and sub-adult snapper from the oceanic and two inner-gulf regions of Shark Bay Western Australia do not leave their home body of water, from which it was concluded that distinct stocks can coexist in close geographic proximity (Moran et al. 2003).

The disadvantage of this type of tag and recapture study is that nothing is known about the movement of the fish while at liberty, so the distance the fish may have moved before recapture is unknown. However, of the 35 fish recaptured in the harbour, 13 were at liberty for more than 12–24 months and 8 were at liberty more than 24 months, which would seem to be a clear indication that if fish leave the harbour they are returning at least once and most likely are resident. A previous tagging study using acoustic tags on snapper within the Mahurangi Harbour followed 20 fish for up to 70 days, with the majority of individuals remaining within the harbour (Hartill et al. 2003). Two of the larger fish (> 3+) moved in and out of the harbour on a regular basis, however the majority moved on the scale of 100's–1000's meters, with a diurnal movement rhythm. Detections were also lower at night and it was hypothesised that tagged fish had moved away at night or their ability to be detected was reduced by resting in areas of high structural heterogeneity (Hartill et al. 2003). Data from this study would suggest that the

latter is probable. A larger acoustic tag study that included receivers further along the coast would be needed to accurately assess if snapper do make daily excursions out of the harbour, where and how far they go. It is unknown at this stage how the larvae enter the harbour; however it is possible that resident, larger fish may spawn close to the harbour entrance contributing to the population on a local scale.

Conclusions

Ontogenetic shifts were not obvious over the broad scale *a priori* habitat types, however at the fine-scale habitat level the 0+ fish utilised different habitat to the rest of the year-classes. The 0+ year-class was associated with sandy to muddy substrata containing structure comprised of horse mussels and sponges. With an increase in size (except for the 1+ fish) abundances decreased either due to mortality, predation or emigration. The 1+ year-class was also widely distributed within the harbour, utilising bare areas of intertidal and subtidal mud more than the other year-classes. The rest of the year-classes were found amongst more coarse substrata, mostly sandy with shell grit and large shell hash as structure, although sponges and horse mussels were also used to a lesser degree. Interestingly, with an increase in size/age came an increase in the night-time use of structure relative to bare areas, with > 3+ fish having a ratio of 10:1 in this regard. It was shown that at zero distances from structure, the larger sizes had a higher ratio as they utilised structure as a place to rest against or in, in the case of large pits. The small year-classes had higher ratios up to 40 cm away from structure and appeared more active, which may mean they are using the cover of darkness to feed, yet remaining close to structure in case it is required for shelter. However, this also may be because structure is not needed as much at night for protection. Previous acoustic tagging found snapper were largely resident within the harbour, moving on scales of 100–1000's of meters, however two larger fish regularly moved in and out of the harbour, leaving early in the morning and returning late afternoon. Tagging from this study also indicated that snapper are largely resident, with only 20% of the recaptures coming from outside the Mahurangi. It is likely that larger snapper may utilise the harbour seasonally, however there are some fish that remain year-round, or return after emigrating, as 80% of recaptures were close to the release site. As snapper are mobile, they may be using the harbour at night as a place to rest and making daily excursions out, or remain in the harbour within established home ranges. The majority of structure within the Mahurangi

is biogenic and has been shown to be susceptible to anthropogenic impacts, the loss of which may have a detrimental effect on the way snapper use the Mahurangi Harbour.

Table 3.1 Number of DUV transects completed each season, by area and *a priori* habitat type within the Mahurangi Harbour. HM = horse mussels, I = intertidal, SG = subtidal mud, Sa = sand and Sh = shell hash.

Season	Area	Habitat type	No. transects per habitat
Feb-06	1	HM, I, SG	4, 3, 3
Feb-06	2	HM, SG	3, 3
Feb-06	3	HM, Sa, Sh	4, 4, 3
Feb-06	4	HM, I	3, 4
Feb-06	5	I, SG	2, 4
Mar-06	1	HM, I, SG	4, 4, 4
Mar-06	2	HM, SG	4, 4
Mar-06	3	HM, Sa, Sh	4, 4, 3
Mar-06	4	HM, I	4, 4
Mar-06	5	I, SG	4, 4
Jun-06	1	HM, I, SG	4, 4, 4
Jun-06	2	HM, SG	4, 4
Jun-06	3	HM, Sa, Sh	4, 4, 4
Jun-06	4	HM, I	4, 4
Jun-06	5	I, SG	4, 3
Sep-06	1	HM, I, SG	1, 4, 4
Sep-06	2	HM, SG	3, 4
Sep-06	3	HM, Sa, Sh	2, 3, 4
Sep-06	4	HM, I	3, 3
Sep-06	5	I, SG	3, 4
Dec-06	1	HM, I, SG	4, 4, 4
Dec-06	2	HM, SG	4, 3
Dec-06	3	HM, Sa, Sh	4, 4, 4
Dec-06	4	HM, I	4, 4
Dec-06	5	I, SG	4, 4
Jan-07	1	HM, I, SG	4, 4, 3
Jan-07	2	HM, SG	4, 4
Jan-07	3	HM, Sa, Sh	4, 4, 4
Jan-07	4	HM, I	4, 4
Jan-07	5	I, SG	4, 4
Mar-07	1	HM, I, SG	4, 4, 4
Mar-07	2	HM, SG	4, 4
Mar-07	3	HM, Sa, Sh	4, 4, 4
Mar-07	4	HM, I	4, 4
Mar-07	5	I, SG	4, 4
Sep-07	1	HM, I, SG	4, 3, 4
Sep-07	2	HM, SG	4, 4
Sep-07	3	HM, Sa, Sh	4, 4, 4
Sep-07	4	HM, I	4, 0
Sep-07	5	I, SG	0, 0
Dec-07	1	HM, I, SG	4, 0, 4
Dec-07	2	HM, SG	4, 4
Dec-07	3	HM, Sa, Sh	4, 4, 4
Dec-07	4	HM, I	4, 4
Dec-07	5	I, SG	0, 4

Table 3.2 Population estimates (E.P.) of snapper over the sampling seasons, based on the mean densities of each year-class per 100 m^2 scaled by the proportion of each *a priori* habitat type within the Mahurangi Harbour (see Appendix 3.7 for SE and densities within each *a priori* habitat).

Season	0+	1+	2+	3+	> 3+	Total E.P.
Feb-06	42,720	93,385	37,885	20,128	3,400	197,518
Mar-06	41,822	96,731	85,453	33,391	12,014	269,411
Jun-06	82,111	42,760	21,344	9,377	3,834	159,426
Sep-06	140,199	92,605	44,479	16,175	9,358	302,816
Dec-06	59,274	36,239	17,322	19,502	6,080	138,417
Jan-07	4,343	126,160	24,200	32,764	9,592	197,059
Mar-07	14,422	94,702	25,845	25,365	14,961	175,295
Sep-07	89,767	23,750	46,498	15,929	411	176,355
Dec-07	100,854	31,928	26,257	14,011	8,860	181,910

Table 3.3 Results of one-way non parametric analysis of variance (PERMANOVA) on abundance data (per 100 m^2) for year-classes of snapper over seasons. Data were square root transformed and Bray Curtis similarities used. Significant results are in bold.

Year-class	df	SS	MS	Pseudo-F	*P* (perm)	Unique permutations
All snapper	8	23428	2928	3.06	**0.001**	999
0+	8	2.07E+05	25905	12.43	**0.001**	998
1+	8	1.45E+05	18127	9.14	**0.001**	999
2+	8	77126	9641	4.05	**0.001**	999
3+	8	28985	3623	1.72	0.093	997
> 3+	8	17108	2139	1.59	0.126	999

Table 3. 4 Details of tagged snapper from the Mahurangi Harbour and recapture information. MH = Mahurangi Harbour, OUT = recaptured outside the harbour. All fish were tagged within area 3 (see Figure 3.22) across a depth range of 8-15 m.

Tag No.	Date tagged	Date recaptured	Length at tagging (cm)	Length at recapture (cm)	Growth (cm)	Location captured	Depth (m)	Days at liberty
A074	30/10/2006	10/11/2006	29.0	30	1.0	MH - entrance	6	11
A232	31/10/2006	17/12/2006	33.6	32	-1.6	OUT - Inner Channel	10	47
A163	31/10/2006	16/12/2006	36.5	42	5.5	OUT - Gannet Rock Hauraki Gulf	56	46
A331	15/12/2006	3/01/2007	28.0	31	3.0	MH - off Scotts Landing	10	49
A214	31/10/2006	13/01/2007	36.0	35	-1.0	MH - entrance	15	74
A016	30/10/2006	2/01/2007	20.7	24	3.3	MH – mouth of Pukapuka Inlet	6	64
A048	30/10/2006	4/02/2007	22.8	25	2.2	OUT - Inner Whangarei Hbr	3	97
A243	31/10/2006	12/02/2007	24.6	28	3.4	MH – near entrance	2.4	104
A205	31/10/2006	17/02/2007	22.6	24	1.4	MH - out from Sullivans Bay	6	109
A134	31/10/2006	31/01/2007	31.1	33	1.9	OUT - Off Wenderholm beach	18	92
A037	30/10/2006	25/03/2007	40.1	48	7.9	MH – mid channel off Scott's Landing	15	146
A259	31/10/2006	7/04/2007	22.0	28	6.0	MH - entrance	11	158
A247	31/10/2006	25/04/2007	30.9	30	-0.9	MH - Opahi Bay	1	176
A085	31/10/2006	8/05/2007	24.6	27	2.4	MH - entrance	9	189
A172	31/10/2006	14/06/2007	47.4	50	2.6	OUT - 1.5m North Flat Rock	45	226
A380	9/02/2007	29/07/2007	44.5	47	2.5	MH, west of Casnell Is.	4	170
A112	31/10/2006	13/01/2008	26.5	29	2.5	MH	10	439
A364	9/02/2007	27/01/2008	33.5	37	3.5	MH - near Scotts Landing	8	352
A338	15/12/2006	30/01/2008	25.3	25	-0.3	MH - off Casnell Is.	4.5	441
A061	30/10/2006	6/02/2008	25.0	28	3.0	MH	8	464
A158	31/10/2006	2/02/2008	25.7	28	2.3	MH - off Otarawao Bay	5	459
A231	31/10/2006	25/01/2008	26.1	29	2.9	MH – off Scotts Landing,	8	451
A228	31/10/2006	15/02/2008	35.6	43	7.4	MH - upper	6	472
A124	31/10/2006	30/03/2008	27.5	27	-0.5	MH - entrance	12	516
A277	31/10/2006	26/04/2008	26.4	28	1.6	Mahurangi Hbr, Scotts Landing	6	543
A213	31/10/2006	31/10/2008	32.2	37	4.8	MH - Grants Island,	2	731
A200	31/10/2006	15/11/2008	25.6	40	14.4	OUT - off Moturoa and Kawau Island	20	746
A173	31/10/2006	13/12/2008	30.6	30	-0.6	MH	10	774
A375	9/02/2007	5/01/2009	24.5	30	5.5	MH - Jamesons bay	6	696
A299	15/12/2006	29/01/2009	27.3	28	0.7	MH	9	806
A236	31/10/2006	26/01/2009	33.7	34	0.3	MH - entrance - Saddle Rock	14	818
A135	31/10/2006	1/03/2009	27.5	30	2.5	MH - entrance	10	852
A068	9/02/2007	30/03/2009	32.4	35.5	3.1	OUT - Between channel Is & Cape Barrier	45	882
A279	15/12/2006	8/04/2009	32	36.0	4.0	MH - entrance	19	886
A096	30/10/2006	8/04/2009	33	36.0	3.0	MH – off rocks Mahurangi Regional Park	5-8	886

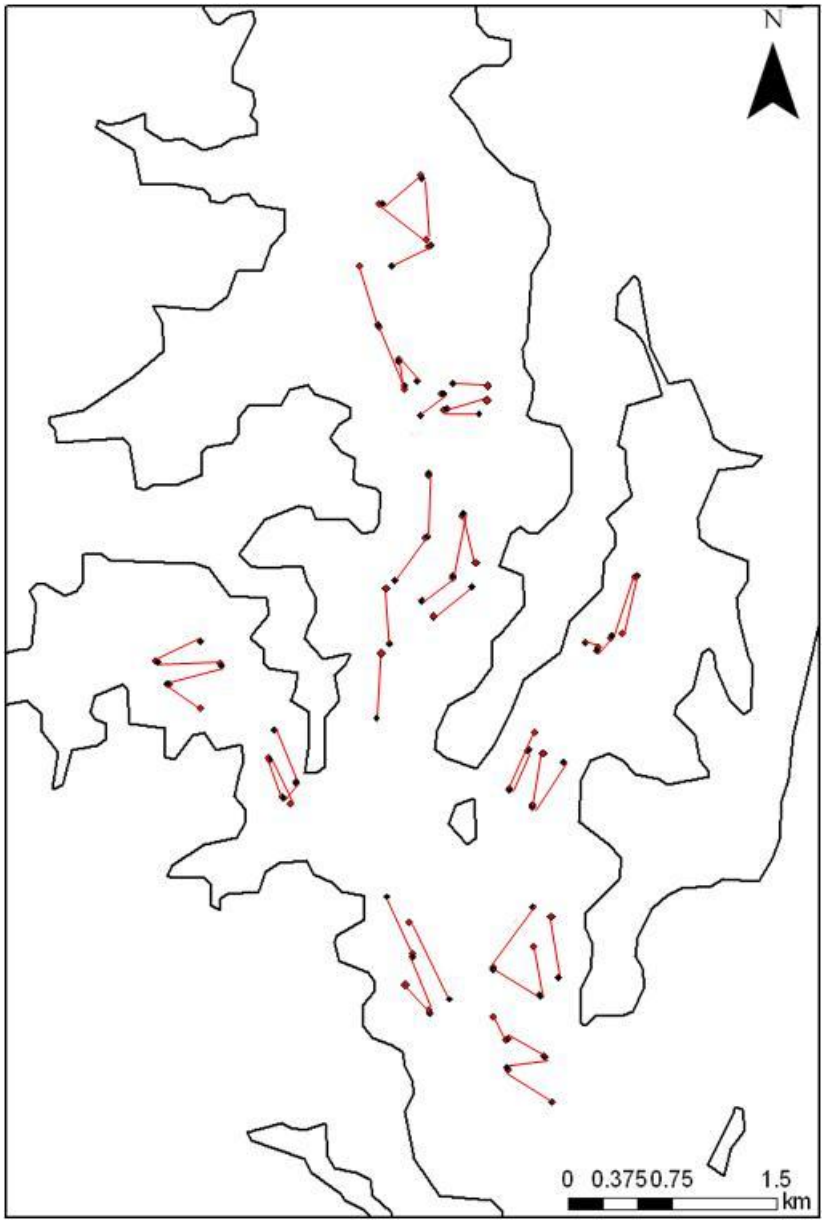


Figure 3.1 Example of DUV transects and locations within the Mahurangi Harbour.

A)

B)

C)

Figure 3.2 Dropped underwater video (DUV), A) side view of DUV, B) front view of DUV, C) example of DUV output with snapper in the frame.

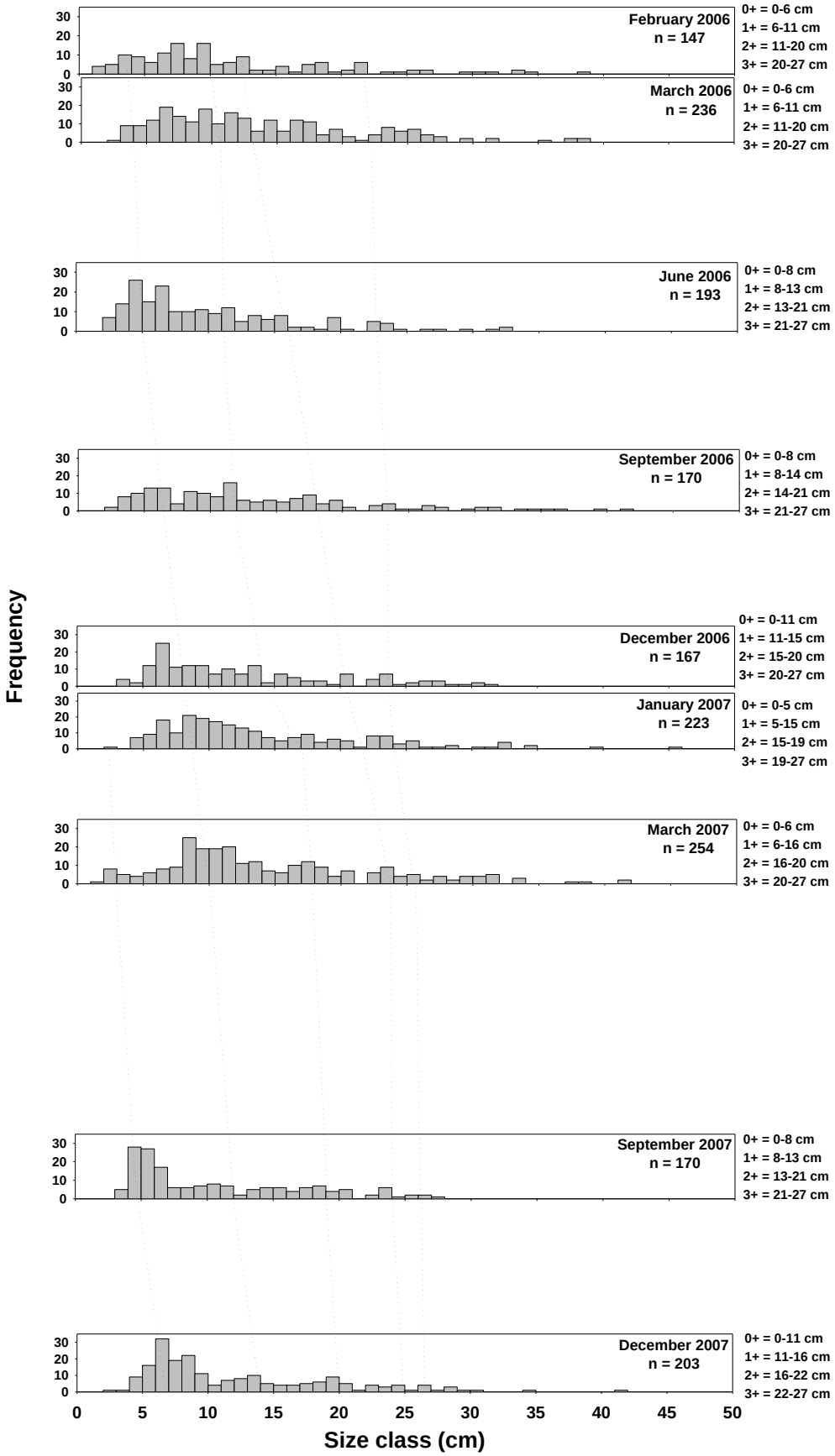


Figure 3.3 Length-frequency distributions for snapper sampled in the Mahurangi Harbour; n = sample size. Dotted lines indicate central modal point for each season.

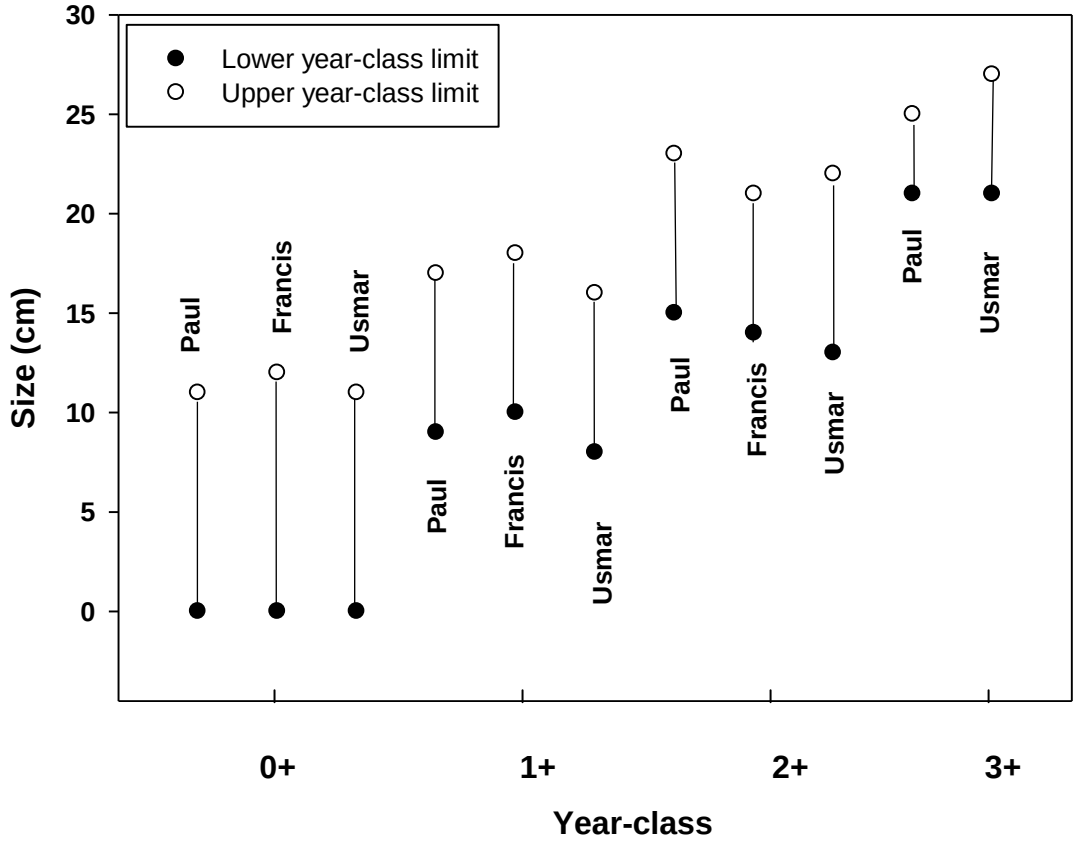


Figure 3.4 Comparison of year-classes from Paul (1976) and Francis (1994) with year-class ranges calculated from length frequency distributions for this thesis.

A)

B)

Figure 3.5 A) Example of tag, and tag position on snapper, B) a released, newly tagged snapper.

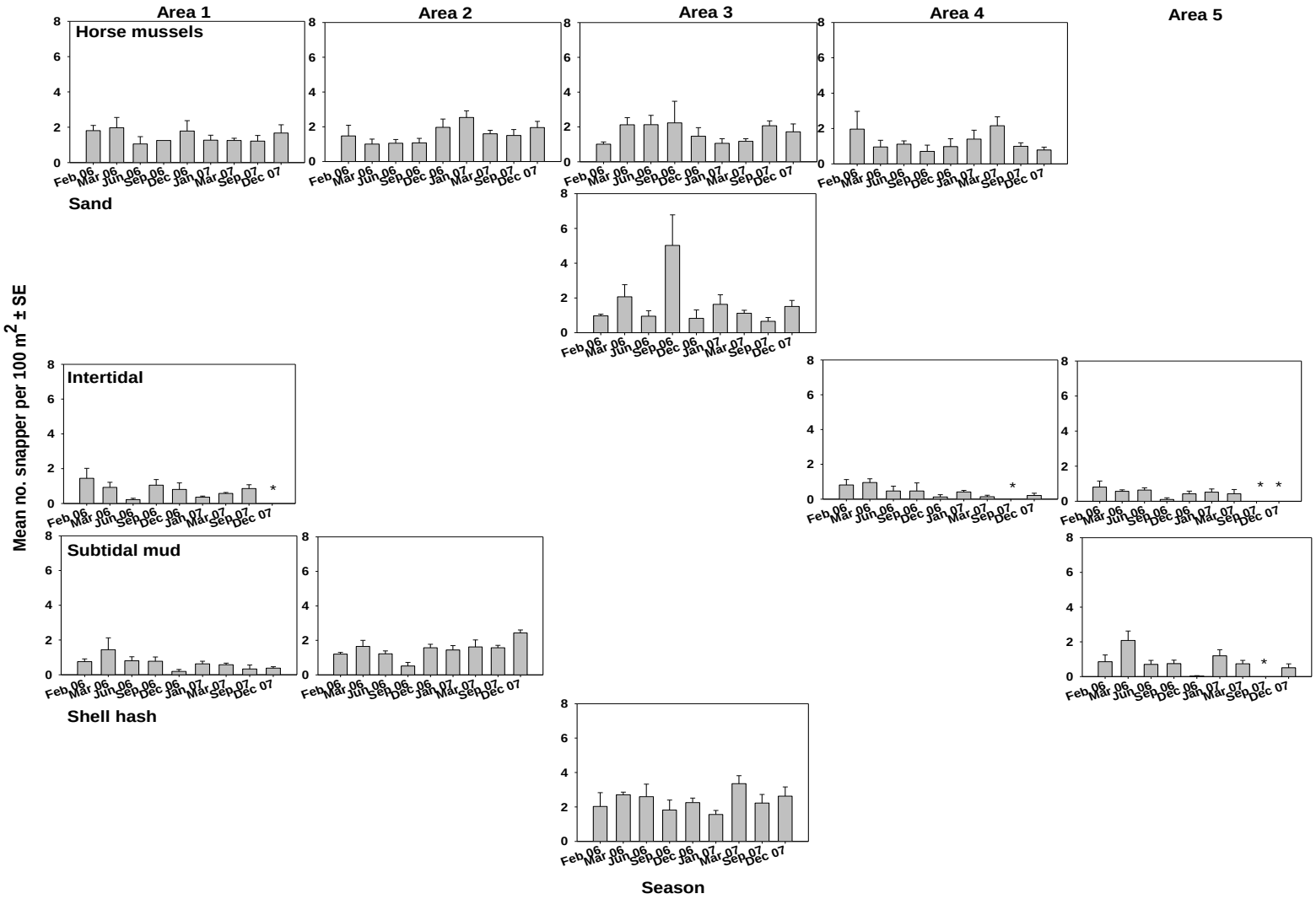


Figure 3.6 Mean numbers of snapper over 9 sampling seasons, by area and *a priori* habitat type. Asterisks indicate no sampling completed.

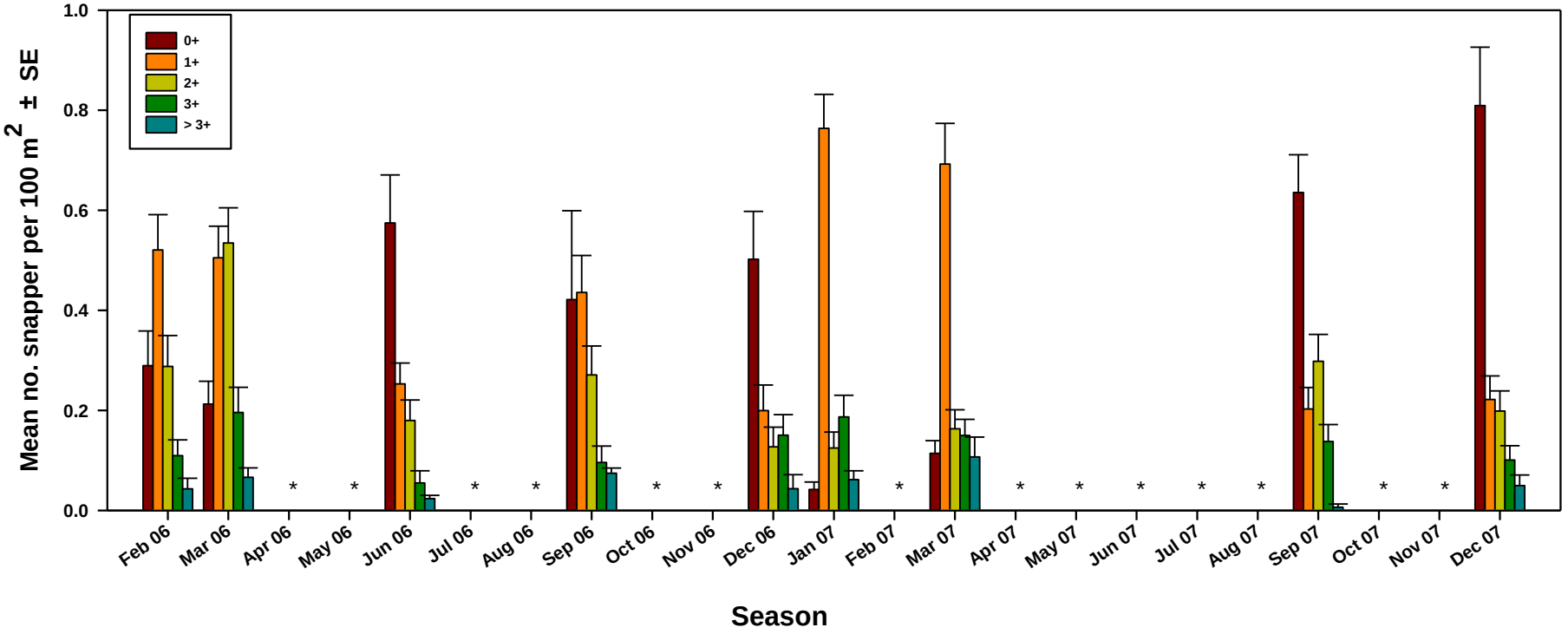


Figure 3.7 Mean numbers of snapper per 100 m^2, by year-class over time. Asterisks indicate no sampling completed.

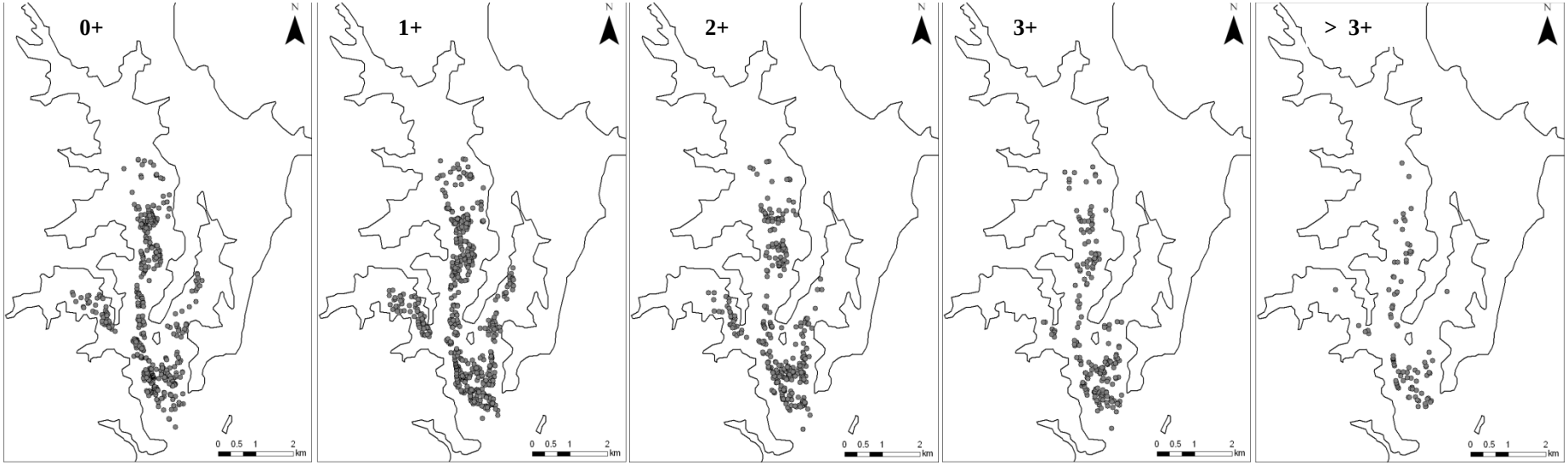


Figure 3.8 Location of individual fish seen by the DUV within each year-class, pooled by season within the Mahurangi Harbour.

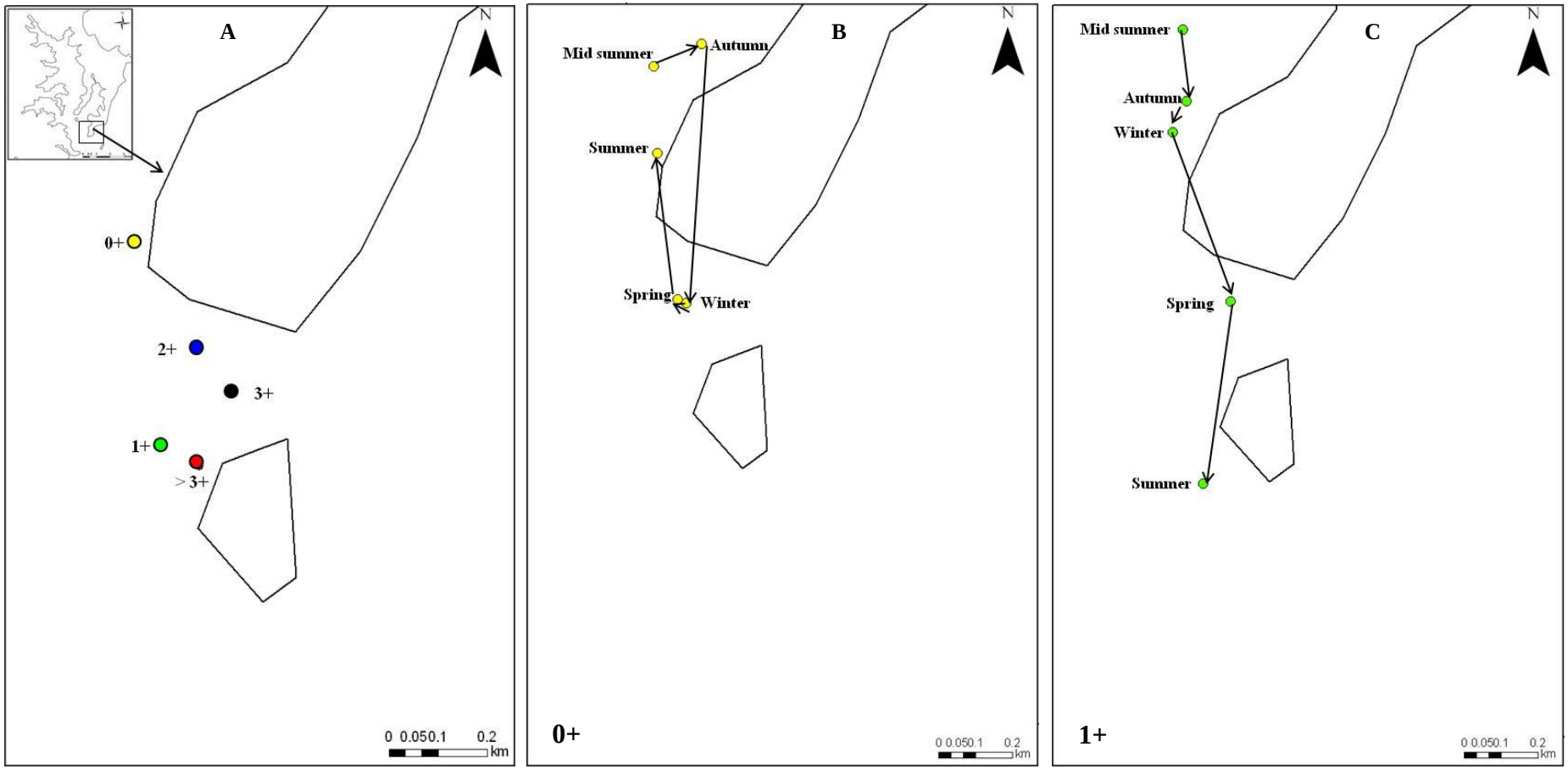


Figure 3.9 Average GPS location for A) all year-classes of snapper over all seasons and habitats, B–F) average GPS location indicating movement of each year-class over each season pooled over the two years, by areas and *a priori* habitat types within the Mahurangi Harbour.

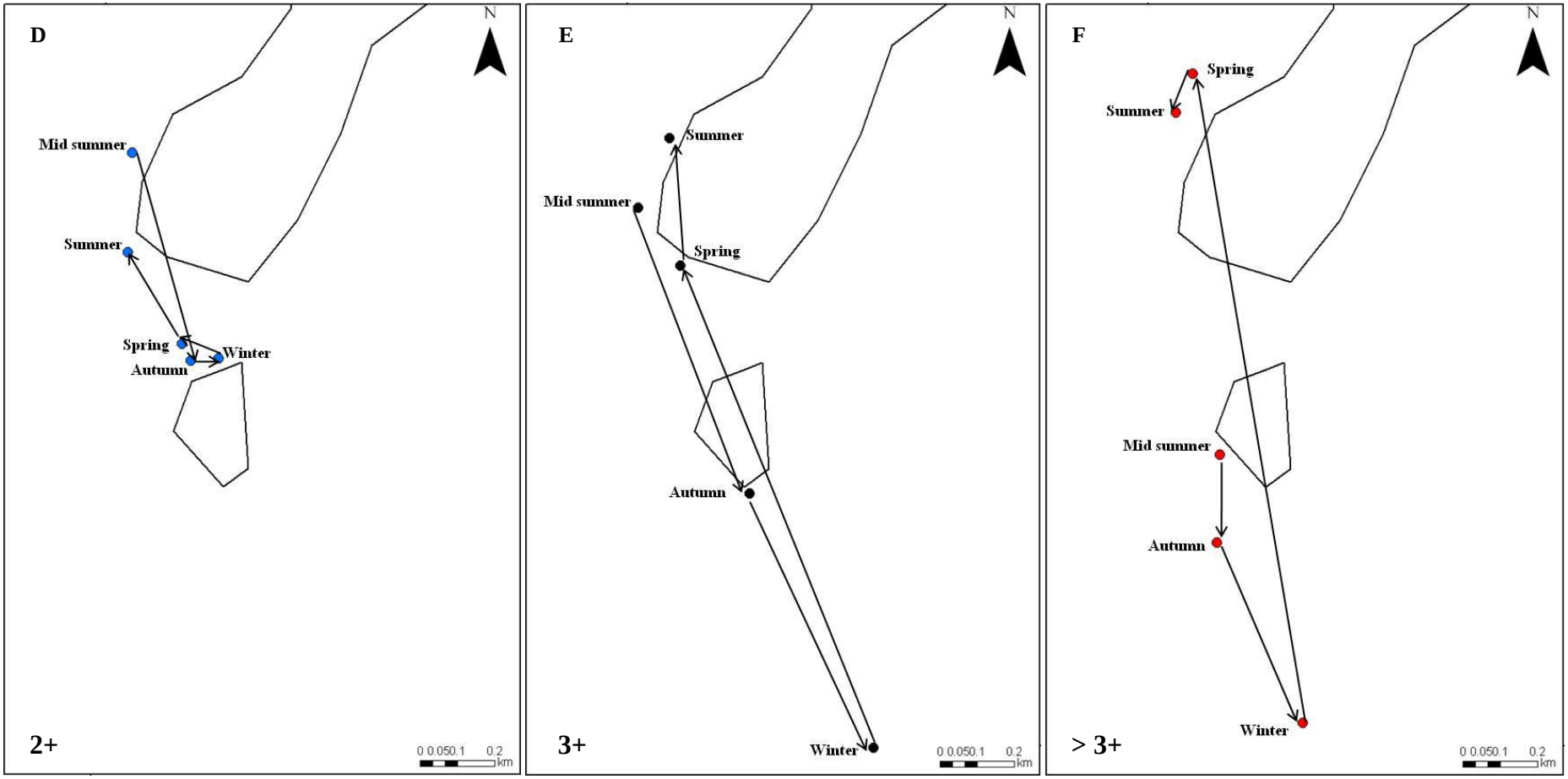


Figure 3.8 cont.

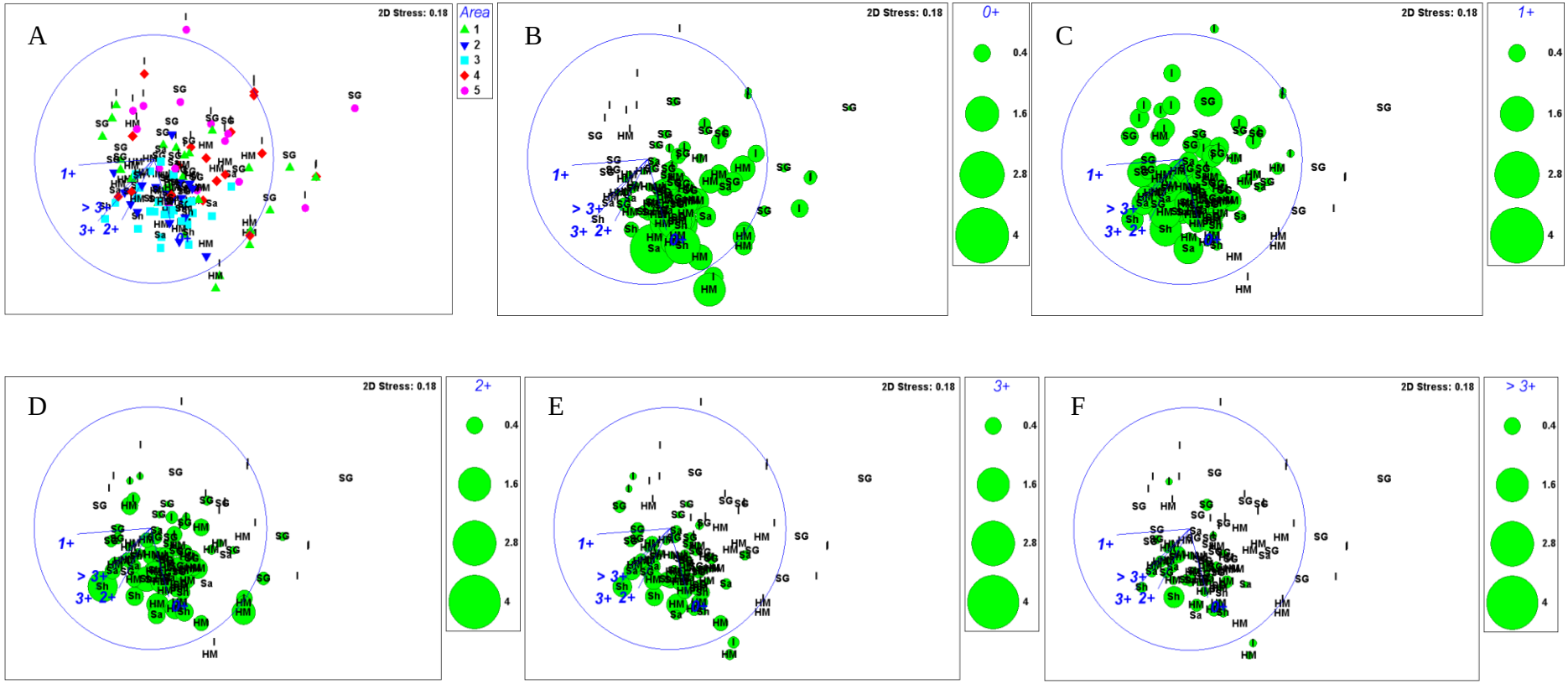


Figure 3.10 Multi-dimensional scaling (MDS) plots of A) mean number of snapper per 100 m^2 seasonally against area (1–5) and *a priori* habitat types (HM = horse mussels, I = intertidal, SG = subtidal mud, Sa = sand, Sh = shell hash). Year-class vectors were overlaid to indicate the direction of year-class influence, B–F) abundance of snapper overlaid as bubble plots for each year-class. Data was pooled at the transect level, square-root transformed and Bray Curtis similarities were used.

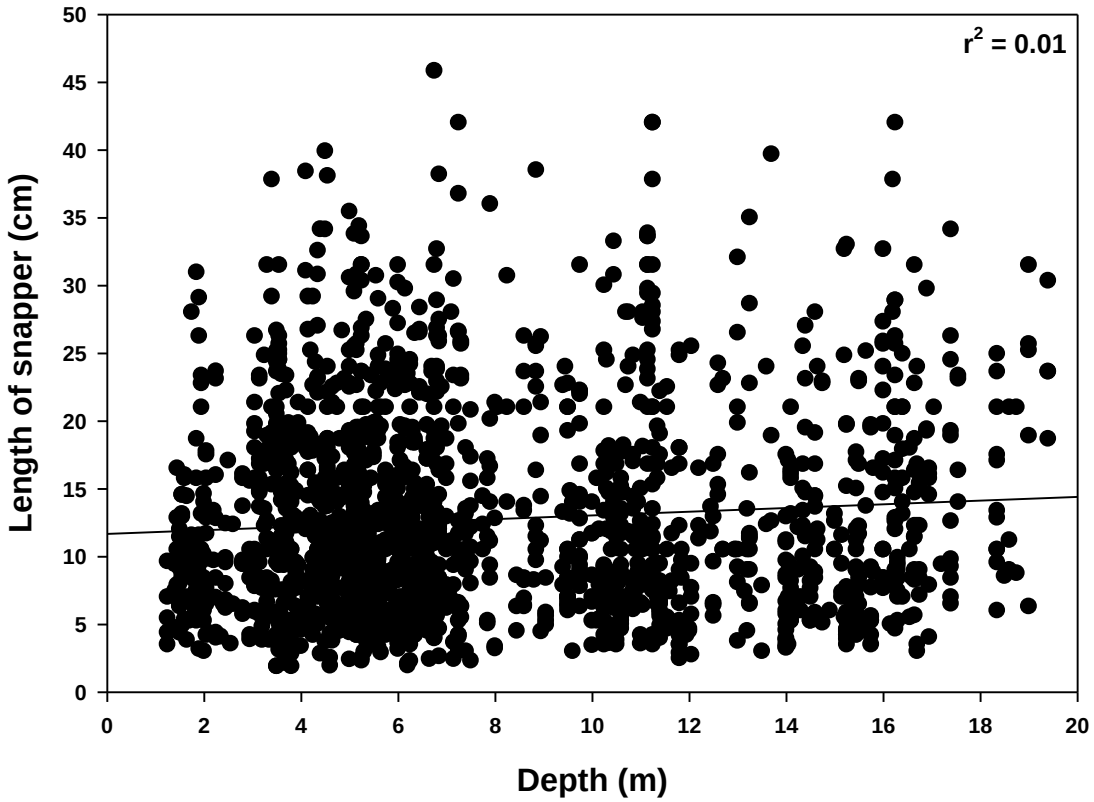


Figure 3.11 Length (fork length) of each individual snapper (cm) by the depth (m) it was recorded at.

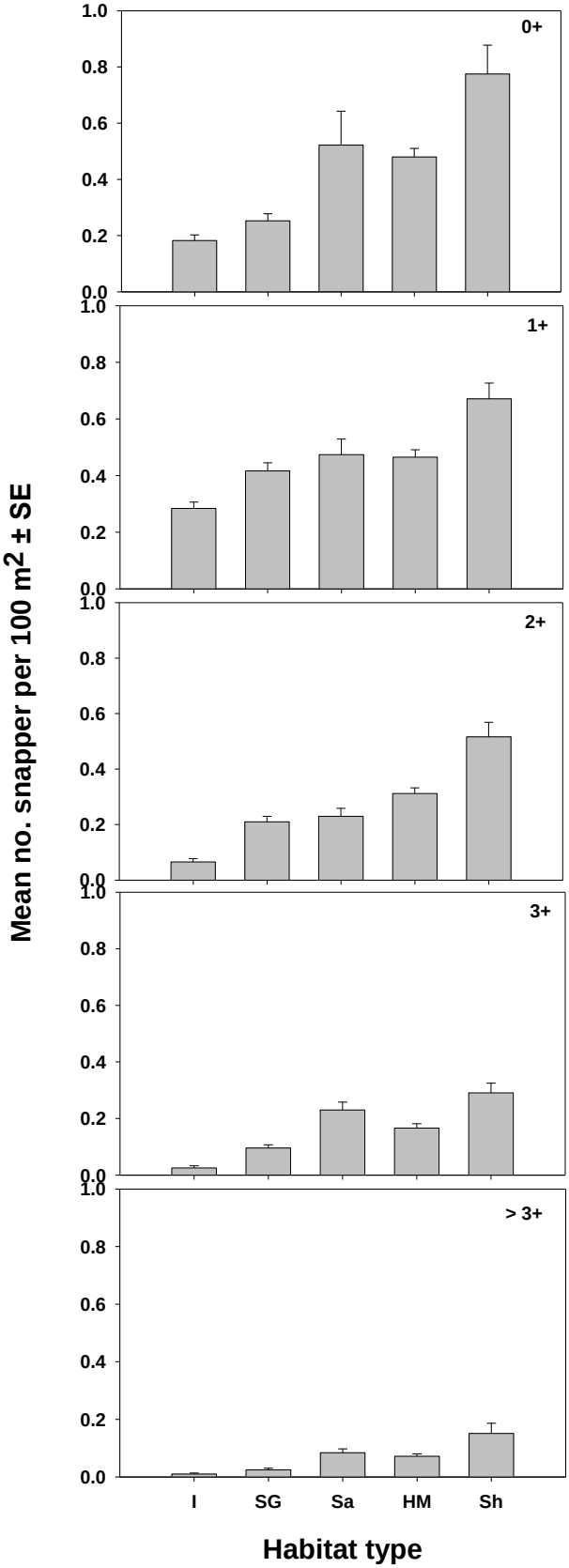


Figure 3.12 Mean numbers of snapper per 100 m^2 within each *a priori* habitat type, split into year-classes. I = intertidal, SG = subtidal mud, Sa = sand, HM = horse mussels and Sh = shell hash.

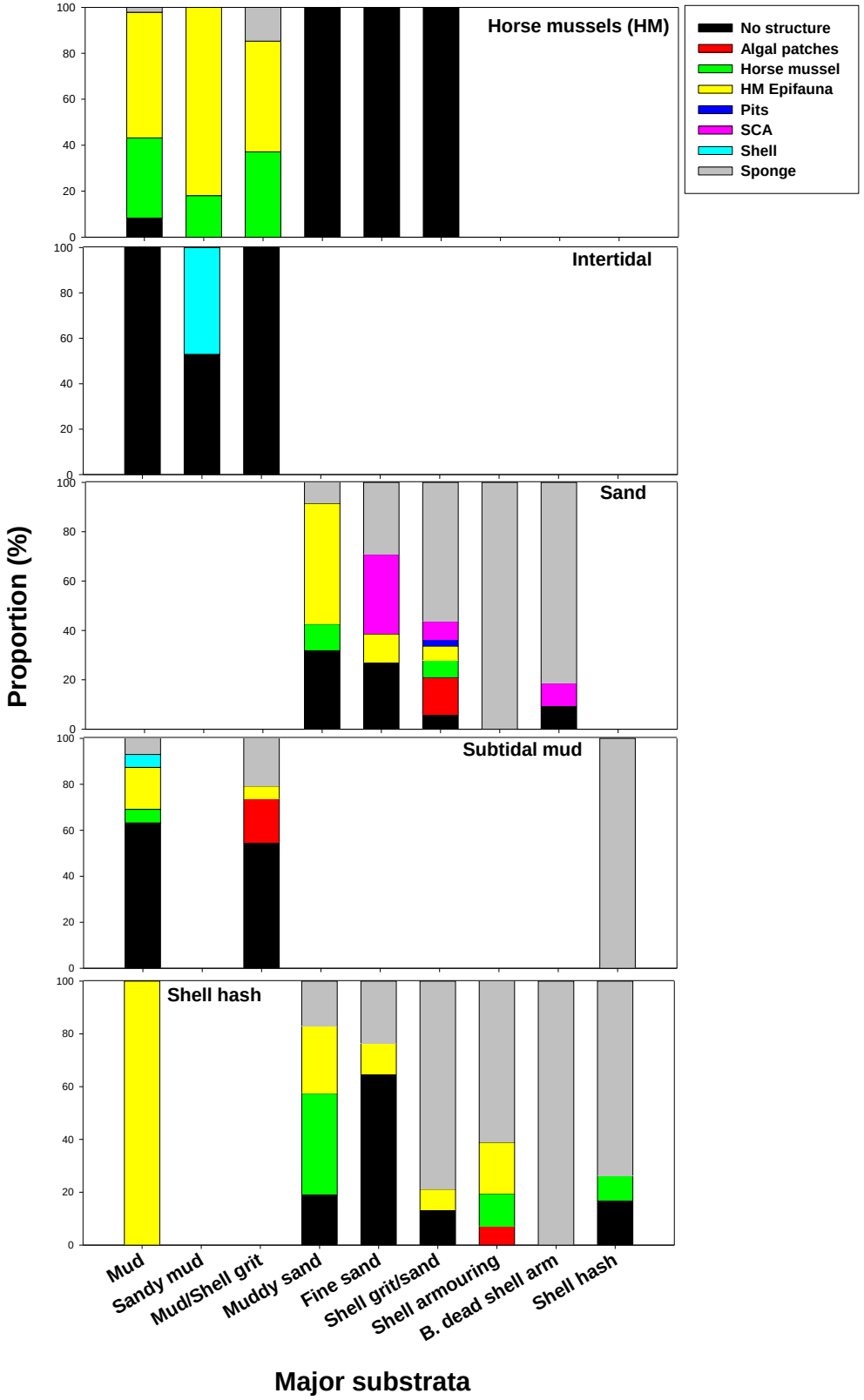


Figure 3.13 Summary of the major substrata and major secondary structure contained within the *a priori* habitat types. Data are counts taken from the major DUV fish and random habitat quadrats within transects and converted to a proportion. Scale of substratum from left to right is fine to coarse. Note: SCA = scallops and B.dead shell arm = buried dead shell armouring.

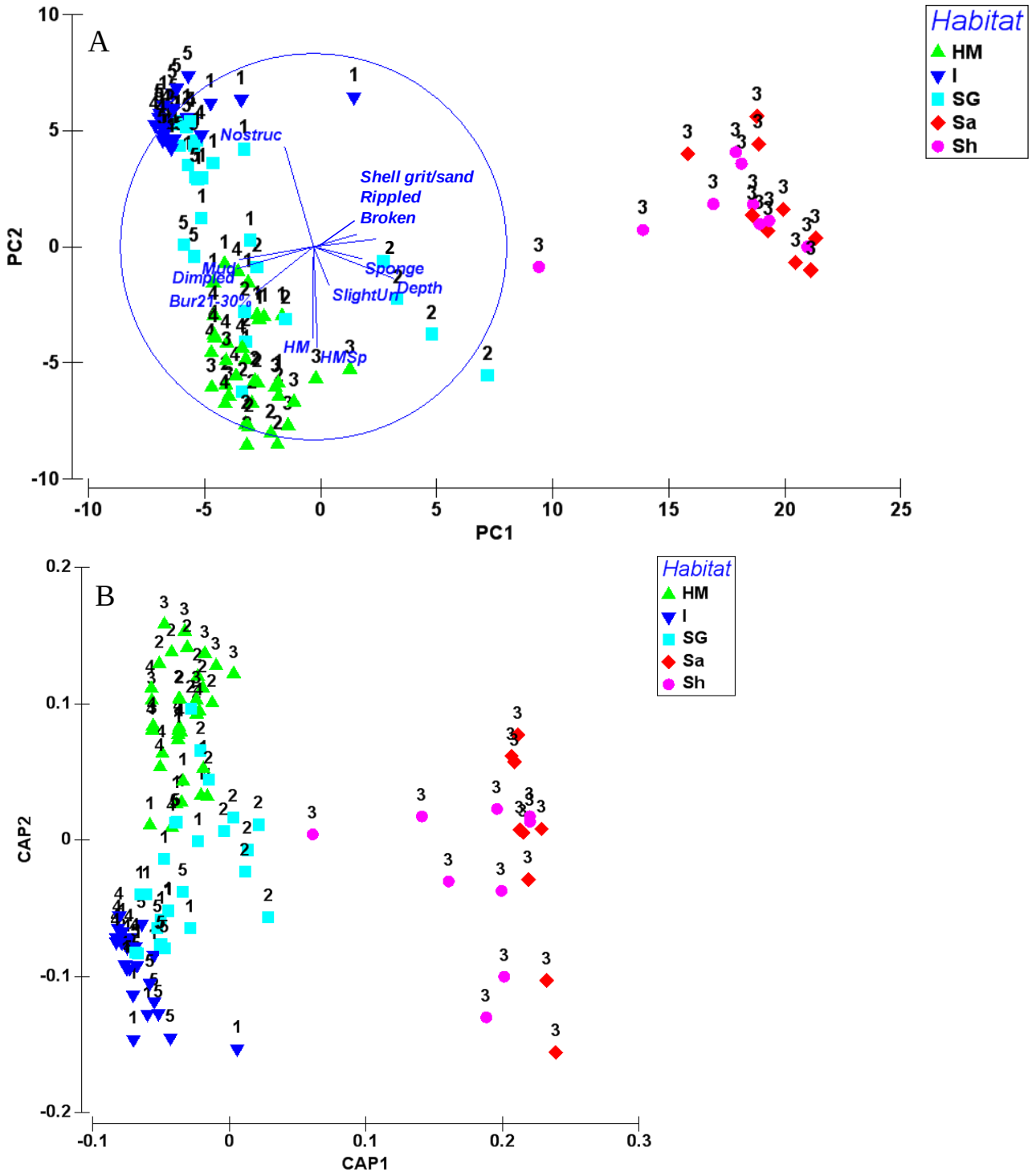


Figure 3.14 A) Principal coordinates analysis (PCA) of major substrata and secondary structure (Nostruc = bare, Bur = burrows, HMSp = horse mussels with sponges, Slightun = slightly undulating). Eigen-vectors < 0.2 were not plotted for clarity. B) Canonical analysis of principal coordinates (CAP) (constrained) based on Bray-Curtis similarities. Labels are *a priori* habitat types (HM = horse mussels, I = intertidal, SG = subtidal mud, Sa = sand, Sh = shell hash) and areas (1–5). PCA1 = 49.7%, 2 = 14.3%.

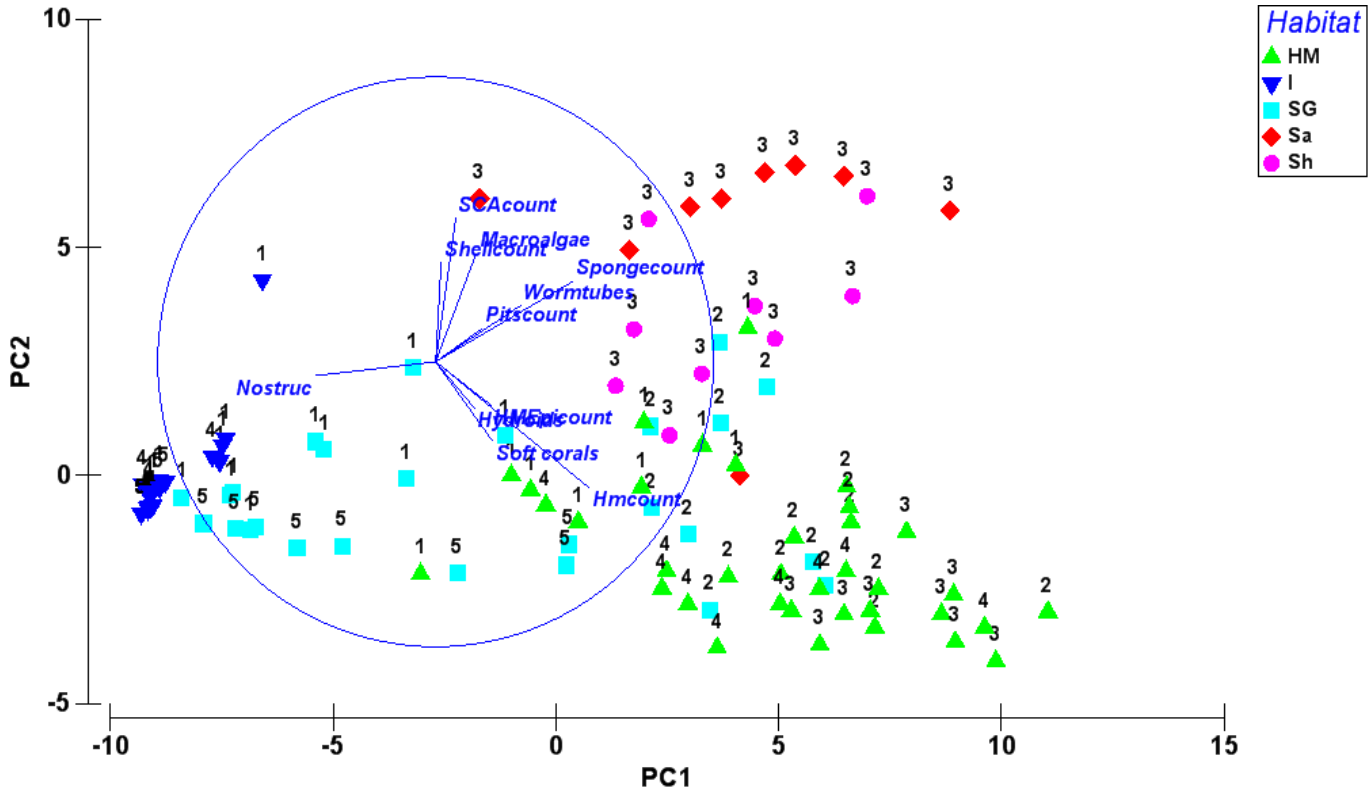


Figure 3.15 Principal coordinates analysis (PCA) of mean counts of structural items and number of bare areas associated with snapper from snapper and random habitat quadrats. Areas (1-5) and *a priori* habitat types (HM = horse mussels, I = intertidal, SG = subtidal mud, Sa = sand, Sh = shell hash) within the Mahurangi Harbour. Eigen-vectors < 0.2 were not plotted for clarity. Nostruc = bare, SCAcount = scallops, HMEpicount = horse mussels with epifauna attached, Hmcount = horse mussels. PC1 = 67.6%, 2 = 12.1%.

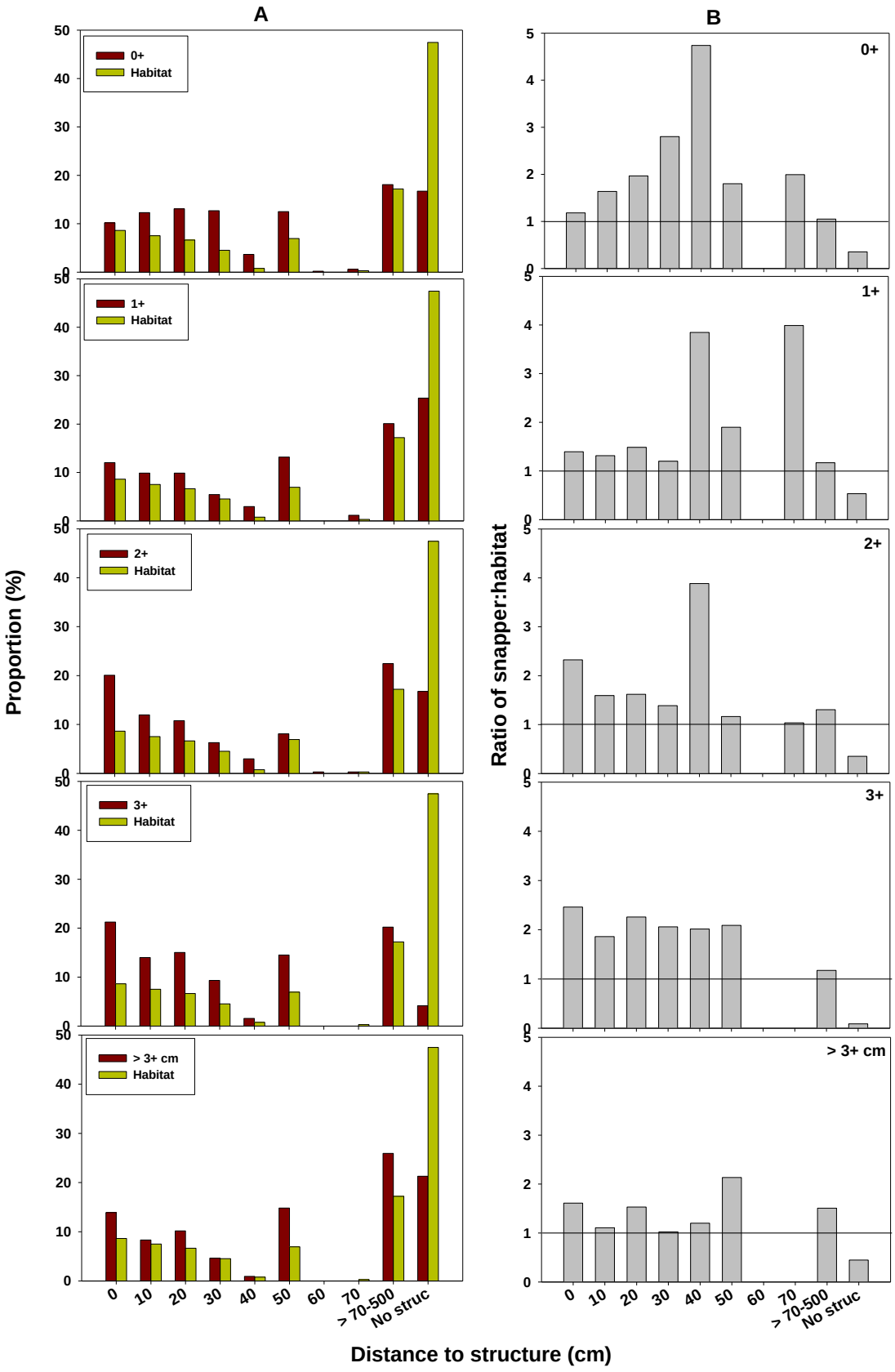
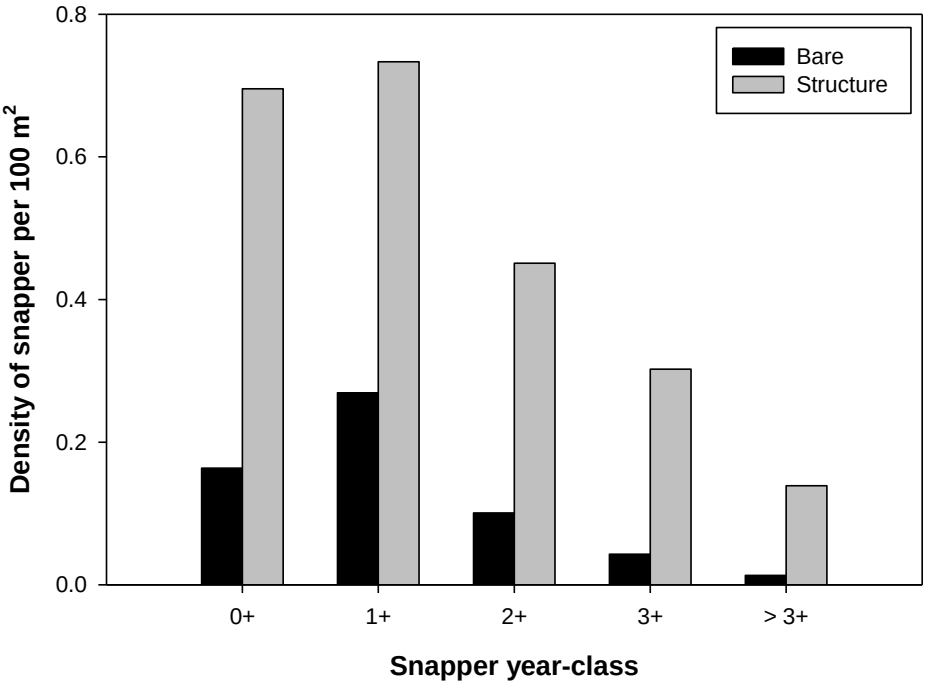


Figure 3.16 A) Distance (cm) to the nearest structural item from snapper and random habitat quadrats (i.e. 0 = snapper leaning on structure, no struc = no structural item in quadrat), B) ratio of snapper to random habitat quadrats at each distance. Counts were converted to proportions of the overall totals.

A)



B)

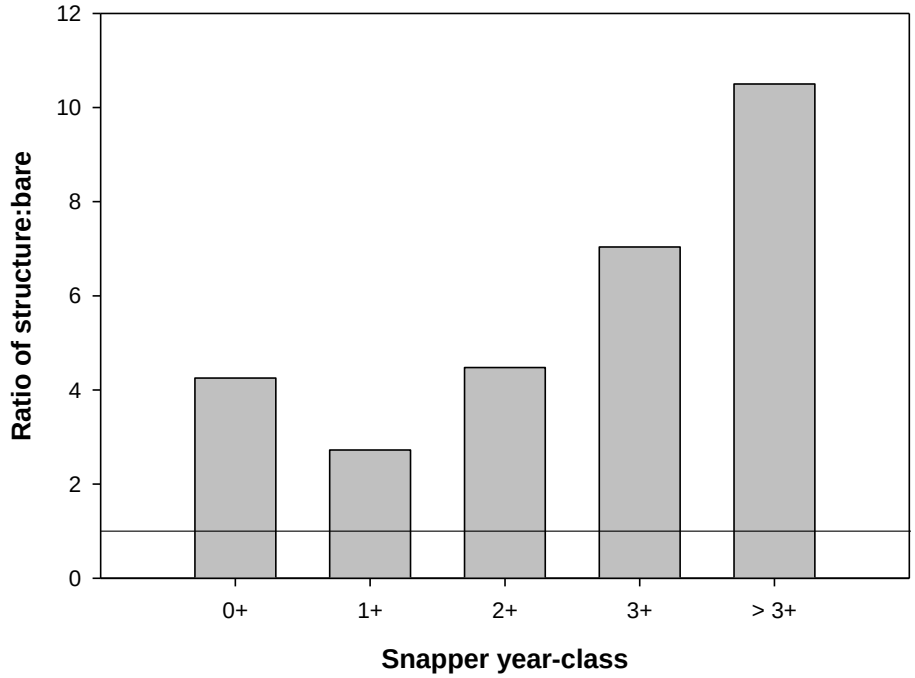


Figure 3.17 A) Relationship of snapper with areas that are bare, or contain structure, density of snapper per 100 m^2 was calculated as a proportion of all snapper and random habitat quadrats across all transects by year-class; B) ratio of structure to bare areas by year-class.

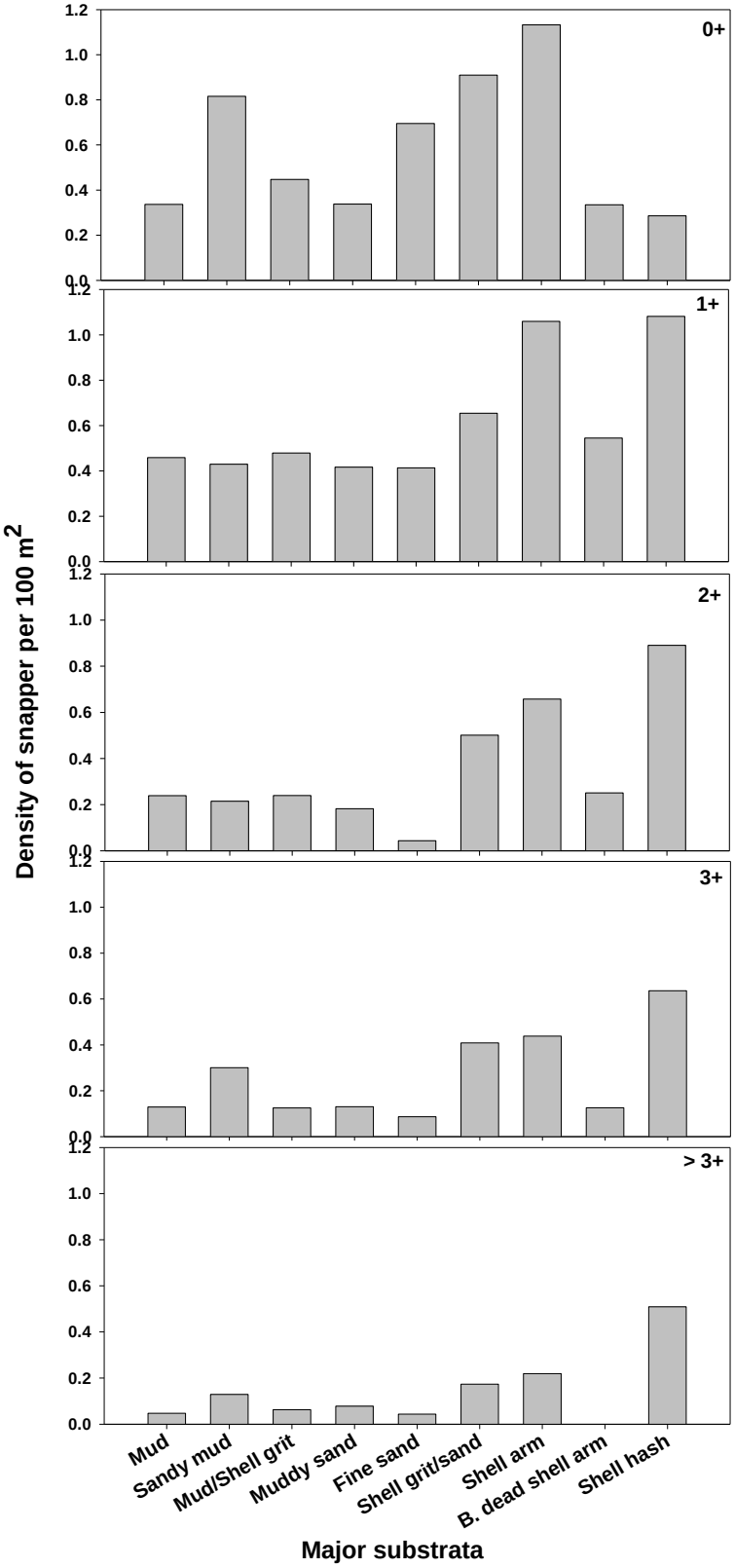


Figure 3.18 Relationship of snapper by year-class with major substrata defined from dropped underwater video (DUV) transects. Density of snapper per 100 m^2 was calculated as a proportion of random habitat quadrats by transect area divided by counts of snapper within each of the major substrata. ("Shell arm" = shell armouring and "B. Dead shell arm" = buried dead shell armouring).

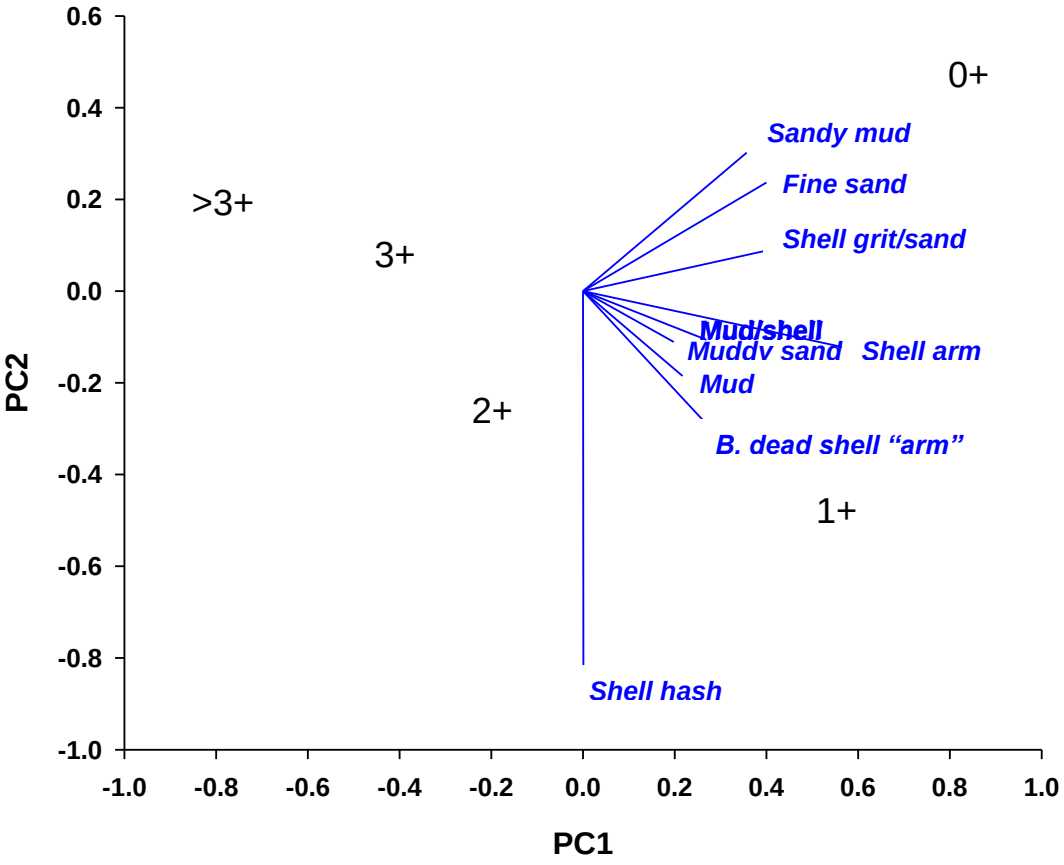


Figure 3.19 Principal coordinates analysis (PCA) of snapper densities per 100 m^2 by year-class and their association with major substrata defined from the dropped underwater video (DUV) transects. ("Shell arm" = shell armouring and "B. Dead shell arm" = buried dead shell armouring). PC1 = 75.4%, PC2 = 12.4%

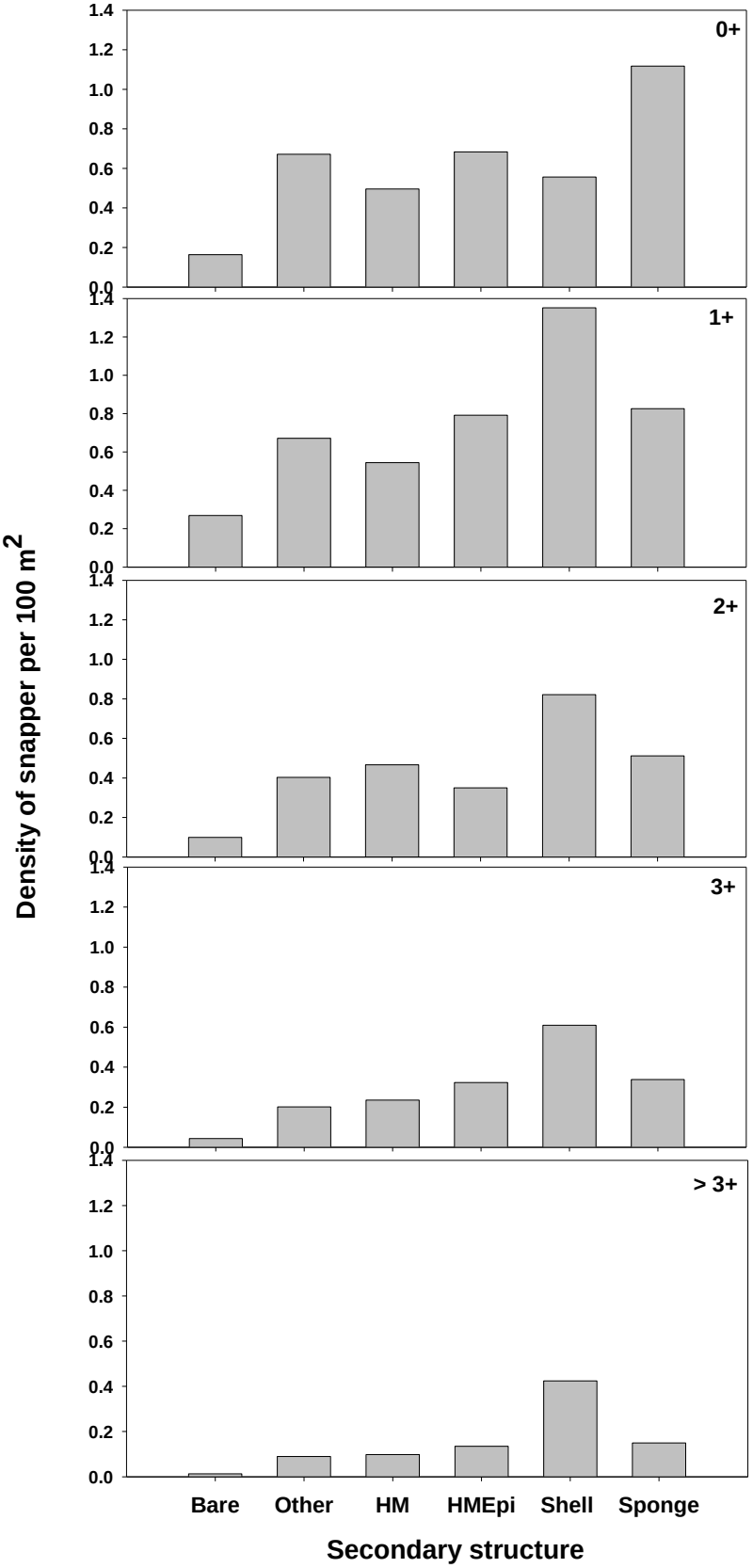


Figure 3.20 Relationship of snapper by year-class with major secondary structure across dropped underwater video (DUV) transects. Density of snapper per 100 m^2 was calculated as a proportion of all snapper and random habitat quadrats across all transects by year-class. (HM = horse mussels, HMEpi = horse mussels with epifauna.

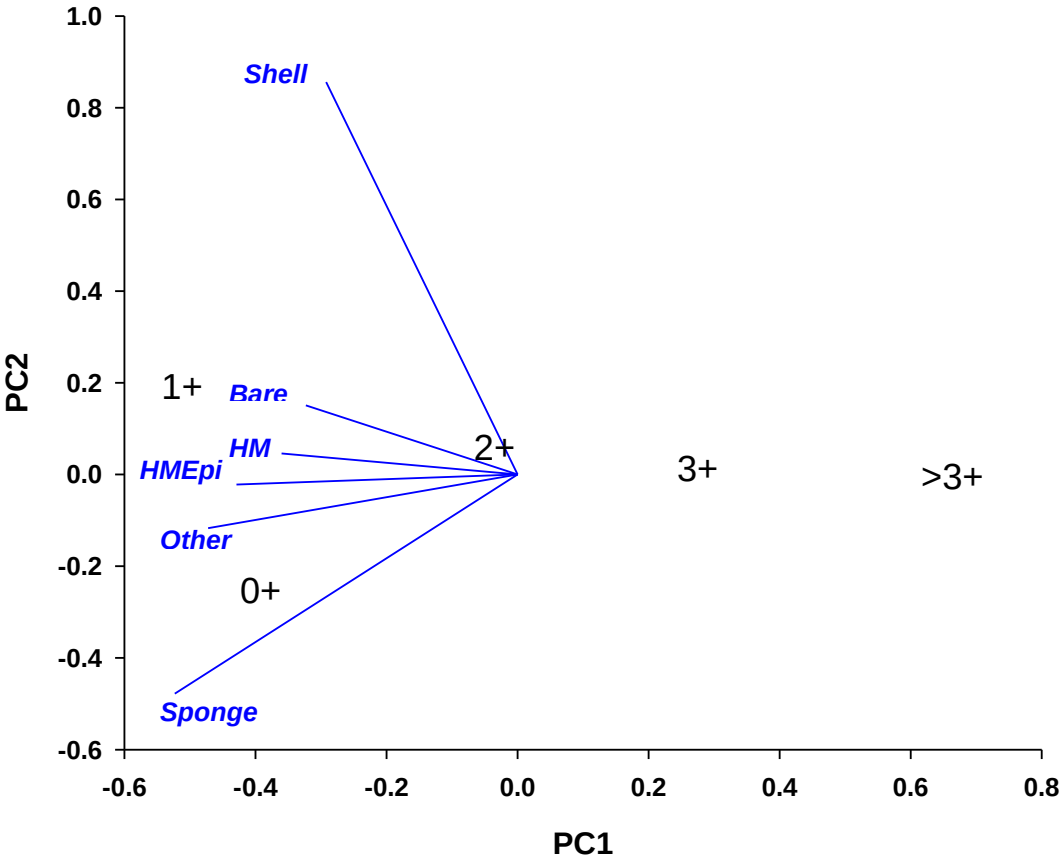


Figure 3.21 Principal coordinates analysis (PCA) of snapper densities per 100 m^2 by year-class and their association with major secondary structure defined from the dropped underwater video (DUV) transects. HM = horse mussels, HMEpi = horse mussels with attached epifauna. PC1 = 88.3%, PC2 = 9.9%.

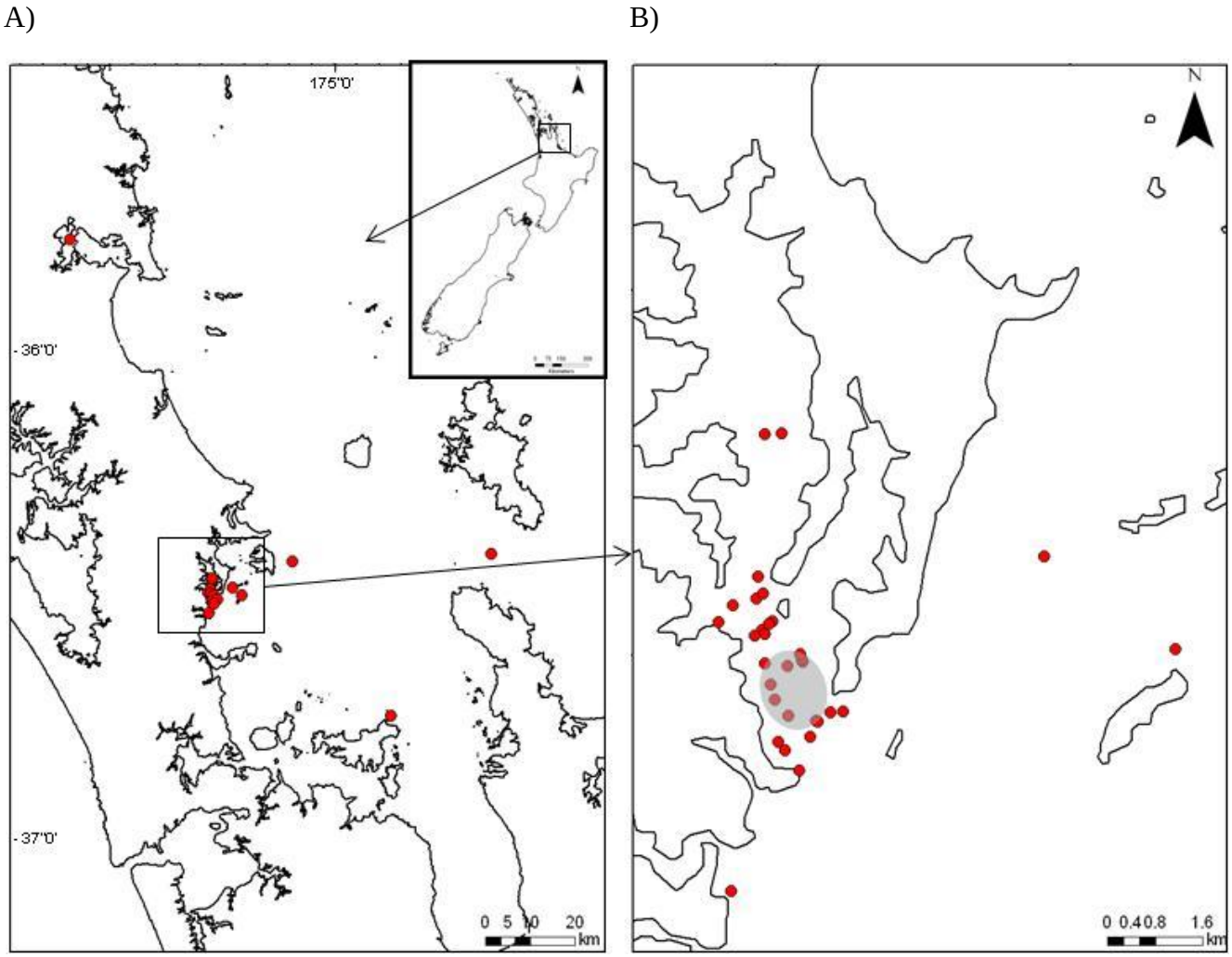


Figure 3.22 Movement of tagged snapper from the Mahurangi Harbour. A) Locations of recaptured snapper are indicated by red circles, B) expanded view, within and close to the harbour. Grey shaded area indicates the area snapper were tagged and released (n = 354).

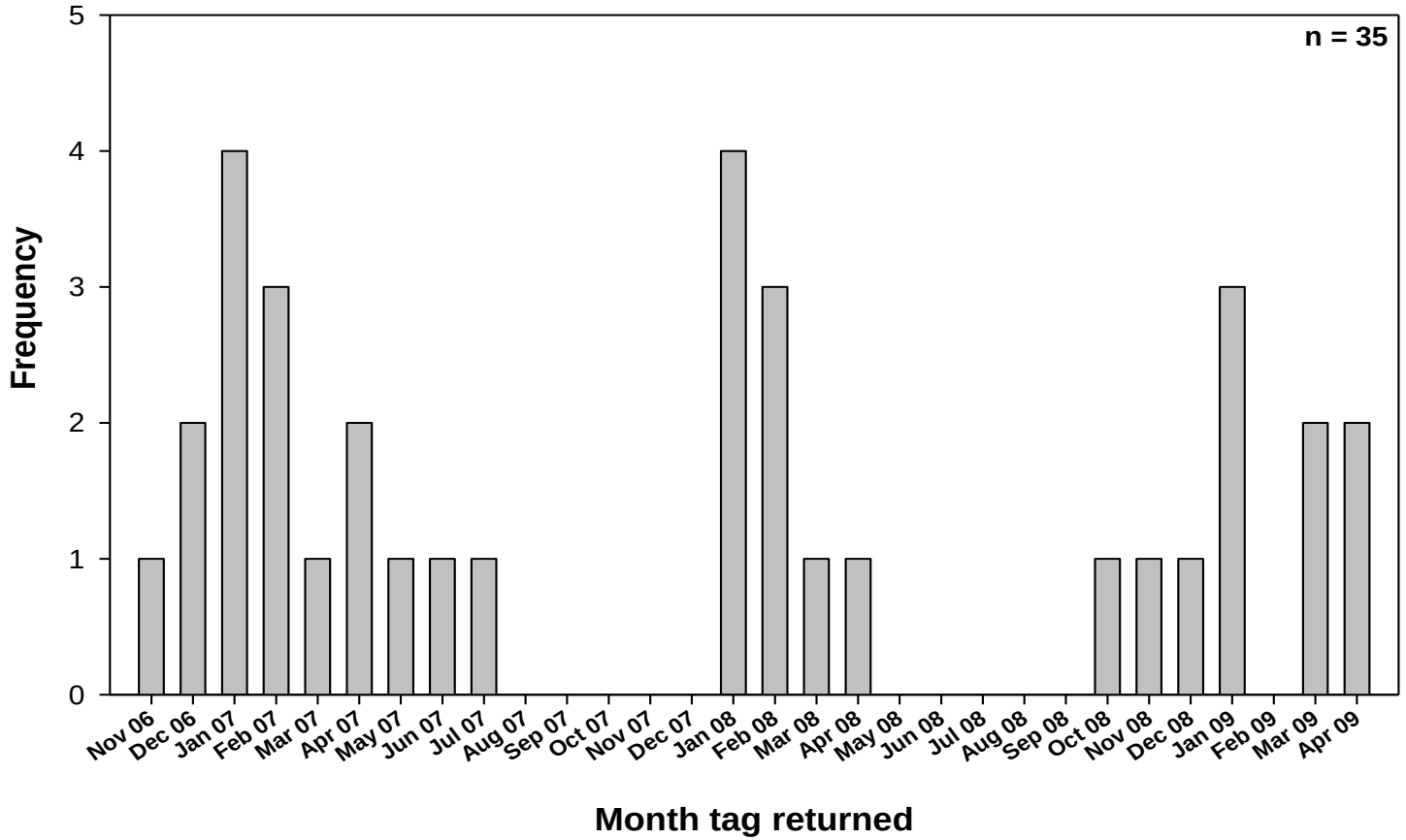


Figure 3.23 Frequency and month of tag return for snapper within the Mahurangi Harbour. All snapper were tagged between November 2006 – February 2007.

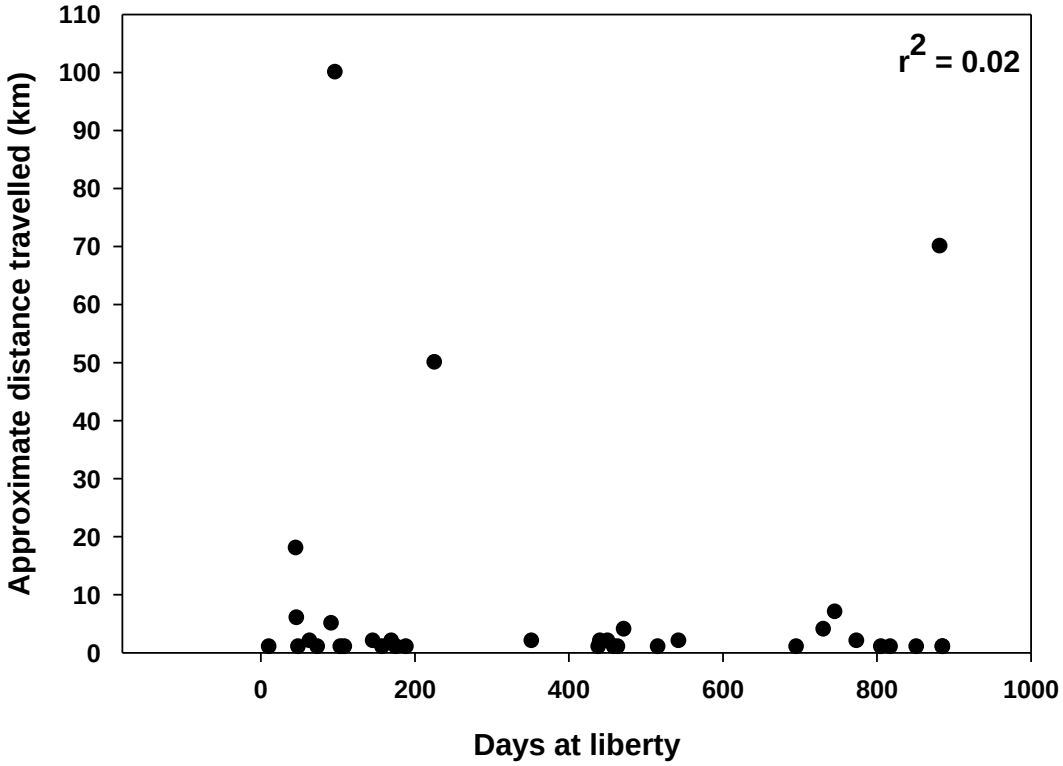


Figure 3.24 Number of day's snapper were at liberty and the approximate distance each fish covered in that time.

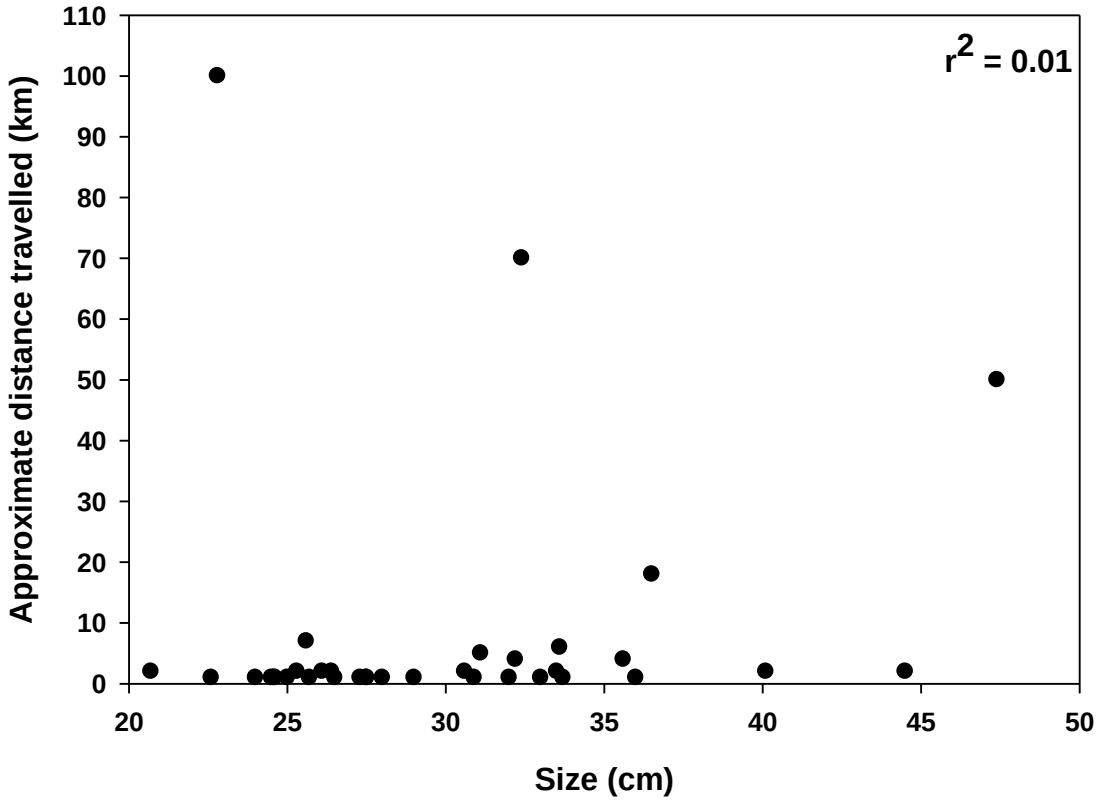


Figure 3.25 Size of snapper at tagging vs. the approximate distance travelled.

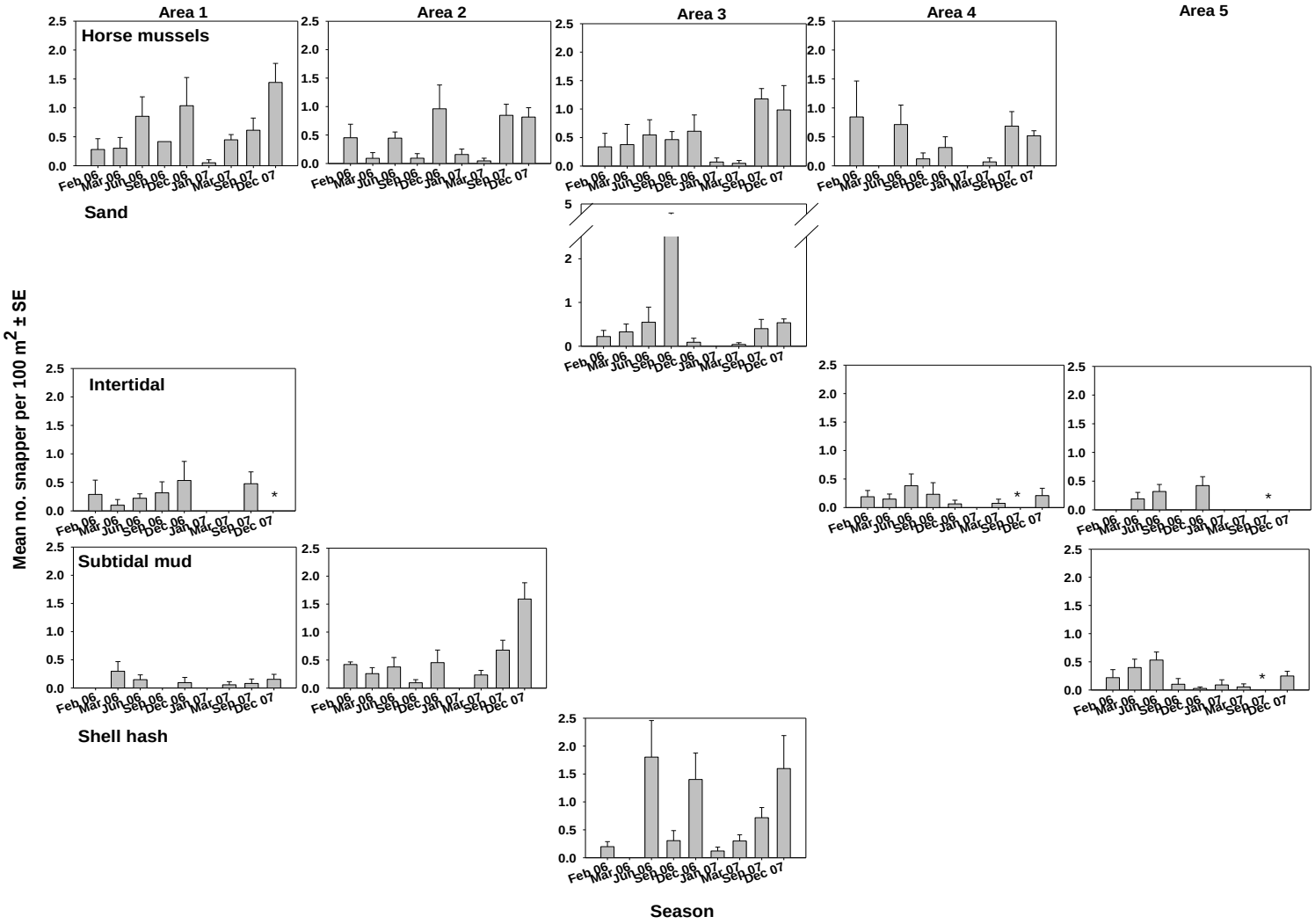
Appendices

Appendix 3.1 A) Data collected from the DUV transects at 3 levels: transect, breaks within transects and individual fish and habitat, B) definition of major substrata, secondary structure, topography and bedform.

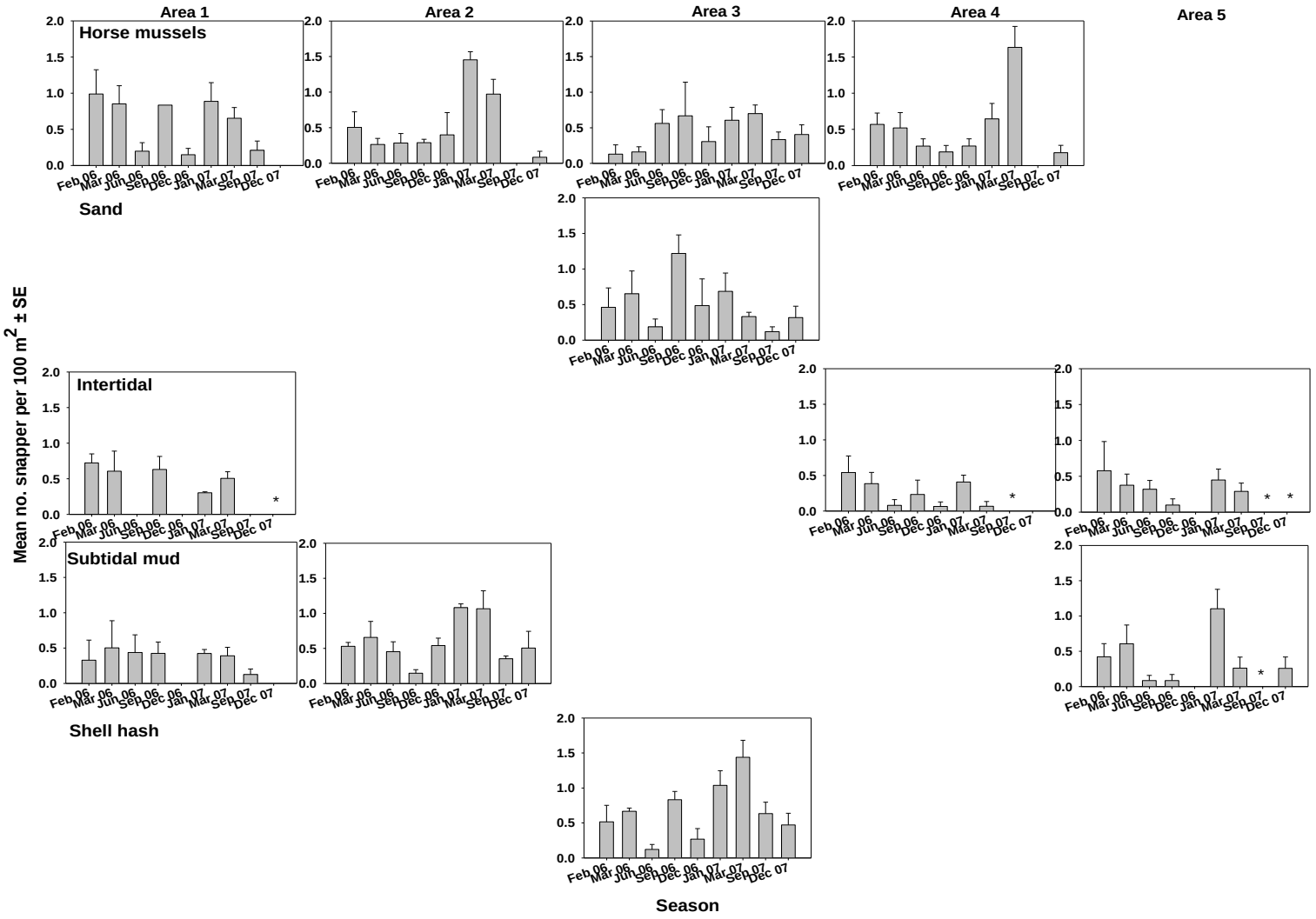
A) Transect level	**Habitat break level**	**Individual fish/habitat points level**
Season	Major substrata*	Picture Quality
Area	Secondary structure (% cover)*	Frame count
Habitat type*	Start Count	Frame latitude/long
Transect	Start latitude	Depth (m)
Date	Start longitude	Quadrat-Fish species or habitat
Start Time	Start Depth	Orientation
Start Count	End Count	Actual Length cm
Start latitude	End latitude	Proximity structure + distance
Start longitude	End longitude	Major substrata
Start Depth	End Depth	Secondary structure (% cover)
End Time	Transect break length	Topography*
End Count	Break Size (m^2)	Bedform*
End latitude		Burrows (% cover)
End longitude		Worm tubes (1-5, 5 = total cover)
End Depth		Pits (counts)
Transect size (m^2)		Shell (counts)
Total transect length (m)		Macroalgae (counts)
Transect width (m)		Horse mussels (counts)
Average width transect (m)		Horse mussels with epifauna (counts)
Total transect time (mins)		Horse mussels lying down (counts)
		Dead horse mussel shards (% cover)
		Scallops (counts)
		Scallops with epifauna (counts)
		Starfish-species (counts)
		Anemones stalked or wandering (counts)
		Ascidians (counts)
		Soft corals
		Sponge-species (counts)
		Hydroids (counts)
		Styella clava (counts)
		Sea cucumbers (counts)
		Rocks (count)
		Other species

B) Habitat types	**Major substrata**	**Secondary structure**	**Topography**	**Bedform**
Horse mussels (HM)	Mud	Bare	Flat	Flat
Sand (Sa)	Sandy mud	Horse mussels	Slightly undulating	Rippled
Intertidal (I)	Mud/Shell grit	Horse mussels epifauna	Moderately undulating	Dimpled
Subtidal mud (SG)	Muddy sand	Shell hash	Heavy undulation	Mounded
Shell hash (Sh)	Fine sand	Sponges		
	Shell grit/sand	Other		
	Shell armouring			
	Buried dead shell armouring			
	Shell hash			

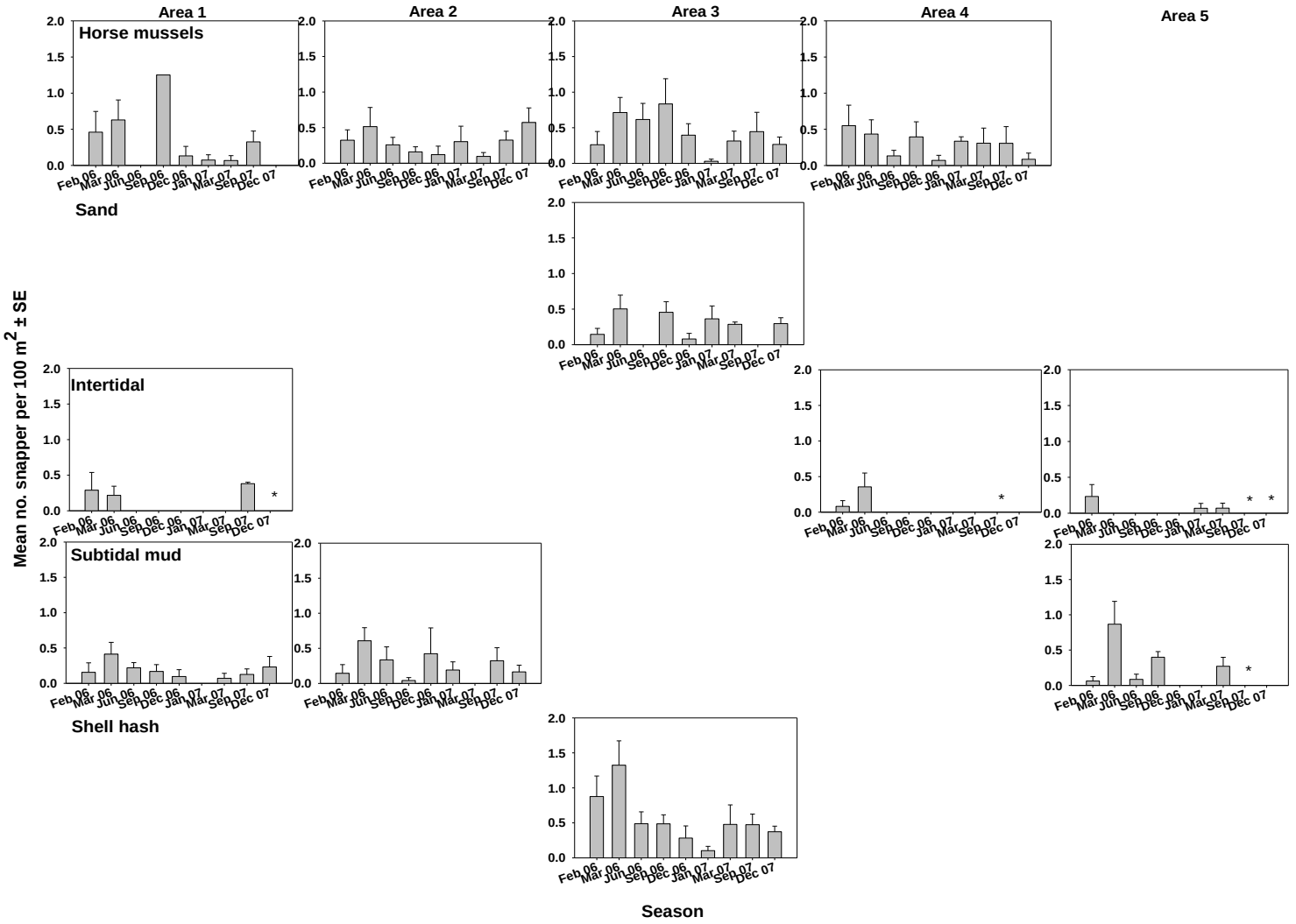
Appendix 3.2 Mean number of 0+ snapper per 100 m^2 over seasons, areas and habitat types. Asterisks indicate no sampling completed.



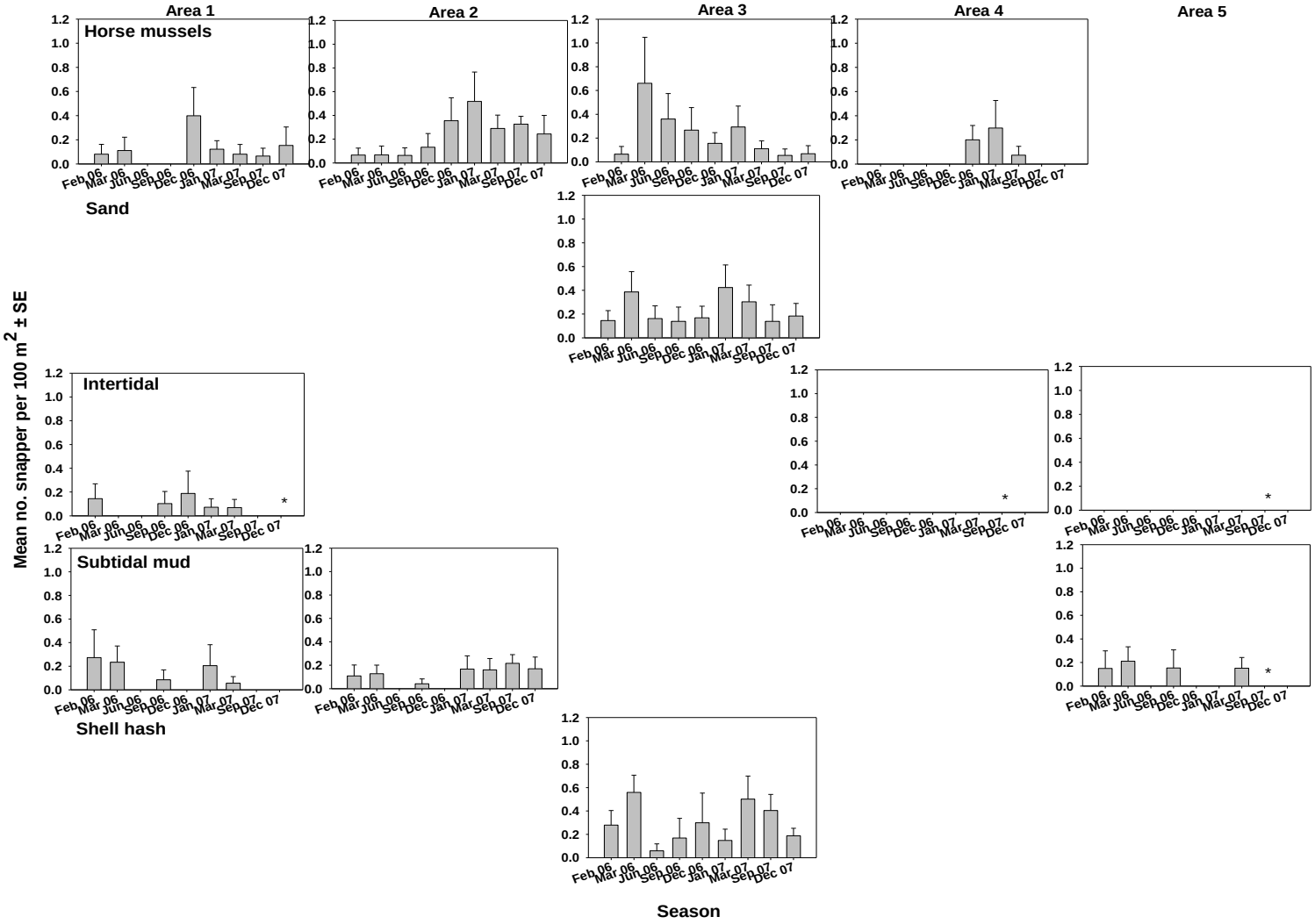
Appendix 3.3 Mean number of 1+ snapper per 100 m^2 over seasons, areas and habitat types. Asterisks indicate no sampling completed.



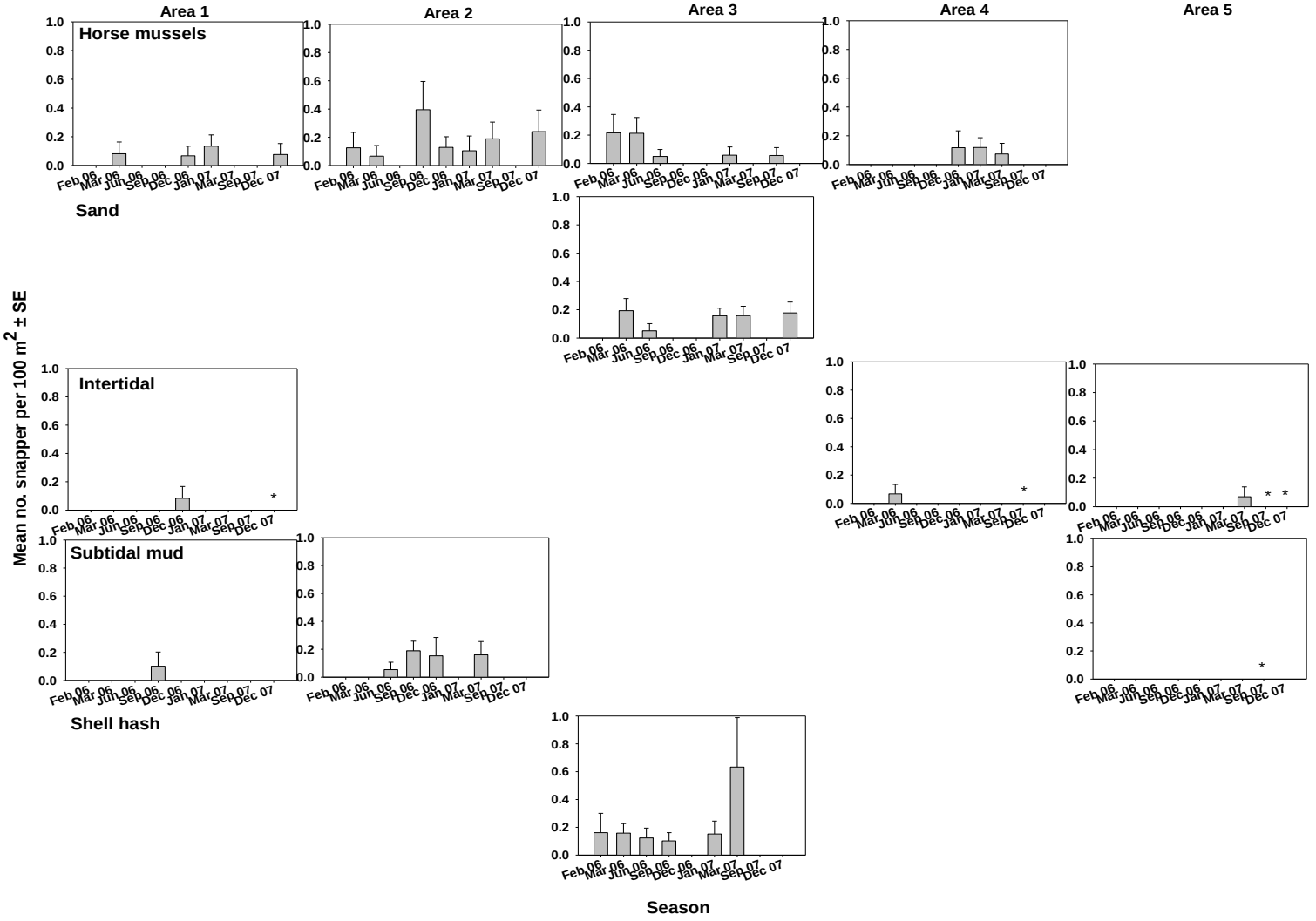
Appendix 3.4 Mean number of 2+ snapper per 100 m^2 over seasons, areas and habitat types. Asterisks indicate no sampling completed.



Appendix 3.5 Mean number of 3+ snapper per 100 m^2 over seasons, areas and habitat types. Asterisks indicate no sampling completed.



Appendix 3.6 Mean number of > 3+ snapper per 100 m^2 over seasons, areas and habitat types. Asterisks indicate no sampling completed.



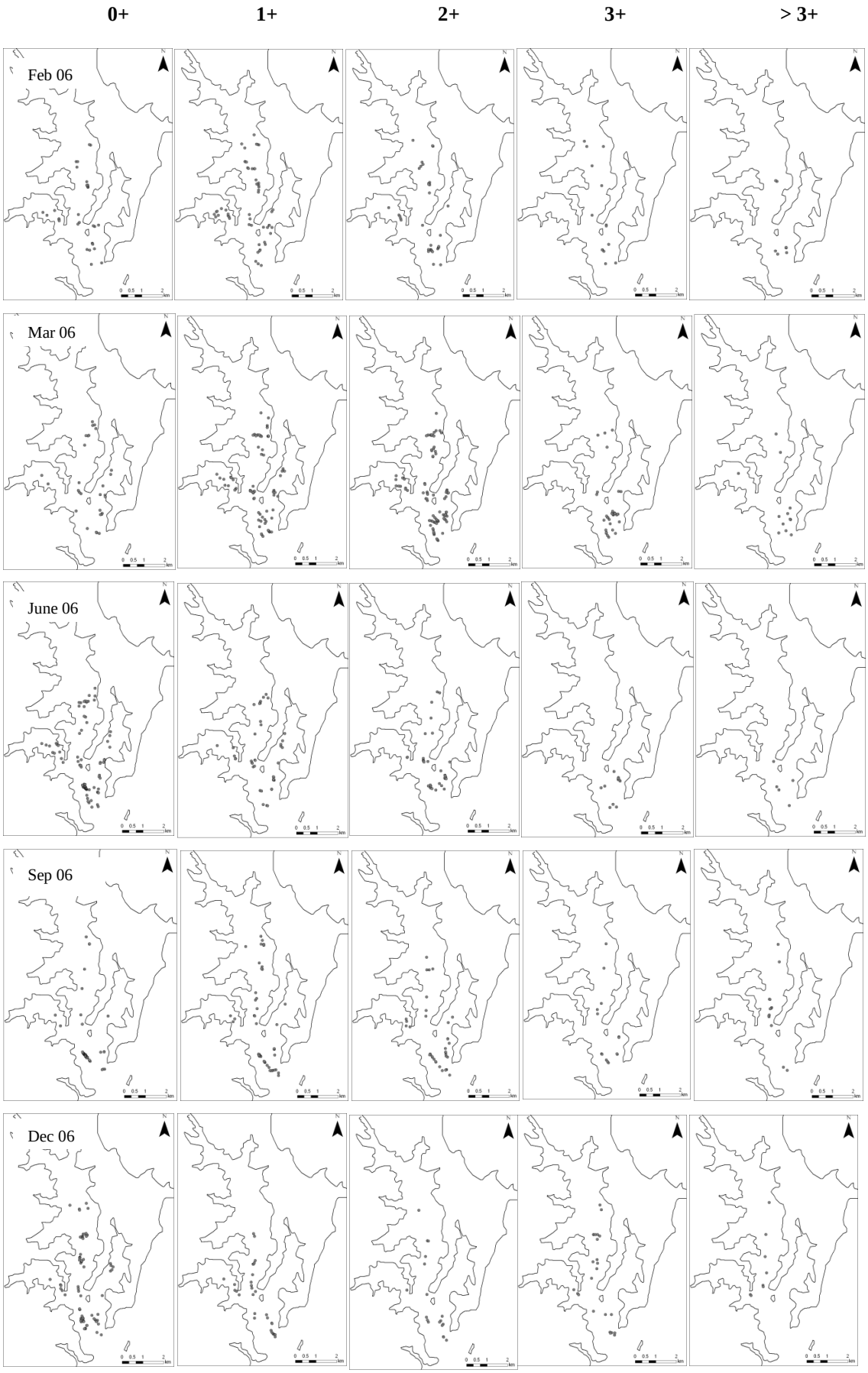
Appendix 3.7 Population estimates (E.P.) of snapper based on mean densities per 100 m^2 (± SE) scaled by the proportion of each *a priori* habitat type within the Mahurangi Harbour. Total area of harbour = 24.5 km^2, HM-horse mussels = 12%, I-Intertidal = 24%, Sa-sand = 15%, SG-subtidal mud = 21% and SH-shell hash = 2%.

	Mean number snapper per 100 m^2					Estimated population					
0+	**HM**	**I**	**Sa**	**SG**	**Sh**	**HM**	**I**	**Sa**	**SG**	**Sh**	**Total E.P.**
Feb-06	0.45 (± 0.09)	0.17 (± 0.04)	0.21 (± 0.04)	0.21 (± 0.03)	0.19 (± 0.03)	13,230	9,996	7,717	10,804	972	42,720
Mar-06	0.2 (± 0.06)	0.14 (± 0.03)	0.32 (± 0.05)	0.31 (± 0.04)	0	5,880	8,232	11,760	15,949	0	41,822
Jun-06	0.64 (± 0.07)	0.30 (± 0.04)	0.54 (± 0.10)	0.33 (± 0.04)	1.80 (± 0.19)	18,816	17,640	19,845	16,978	8,831	82,111
Sep-06	0.22 (± 0.04)	0.19 (± 0.05)	3.21 (± 0.43)	0.06 (± 0.02)	0.30 (± 0.06)	6,468	11,172	117,967	3,087	1,505	140,199
Dec-06	0.73 (± 0.10)	0.33 (± 0.06)	0.09 (± 0.02)	0.16 (± 0.04)	1.40 (± 0.14)	21,462	19,404	3,307	8,232	6,869	59,274
Jan-07	0.07 (± 0.02)	0	0	0.03 (± 0.01)	0.11 (± 0.02)	2,058	0	0	1,697	588	4,343
Mar-07	0.15 (± 0.03)	0.02 (± 0.01)	0.04 (± 0.01)	0.11 (± 0.02)	0.30 (± 0.01)	4,410	1,176	1,470	5,890	1,475	14,422
Sep-07	0.83 (± 0.07)	0.47 (± 0.07)	0.40 (± 0.07)	0.37 (± 0.07)	0.71 (± 0.06)	24,402	27,636	14,700	19,515	3,514	89,767
Dec-07	0.94 (± 0.09)	0.20 (± 0.04)	0.53 (± 0.03)	0.66 (± 0.12)	1.59 (± 0.18)	27,636	11,760	19,477	34,158	7,822	100,854
1+											
Feb-06	0.55 (± 0.08)	0.61 (± 0.06)	0.46 (± 0.08)	0.42 (± 0.06)	0.52 (± 0.07)	16,149	35,840	16,937	21,929	2,530	93,385
Mar-06	0.42 (± 0.06)	0.45 (± 0.06)	0.65 (± 0.09)	0.59 (± 0.08)	0.67 (± 0.01)	12,424	26,746	23,960	30,330	3,271	96,731
Jun-06	0.328 (± 0.04)	0.13 (± 0.03)	0.18 (± 0.03)	0.34 (± 0.05)	0.12 (± 0.02)	9,637	7,824	6,840	17,860	598	42,760
Sep-06	0.40 (± 0.07)	0.35 (± 0.06)	1.21 (± 0.08)	0.22 (± 0.04)	0.83 (± 0.04)	11,771	20,678	44,784	11,292	4,080	92,605
Dec-06	0.28 (± 0.05)	0.02 (± 0.01)	0.48 (± 0.11)	0.15 (± 0.04)	0.26 (± 0.04)	8,253	1,250	17,825	7,596	1,314	36,239
Jan-07	0.90 (± 0.07)	0.38 (± 0.03)	0.68 (± 0.07)	0.91 (± 0.06)	1.04 (± 0.06)	26,395	22,703	25,174	46,804	5,084	126,160
Mar-07	0.99 (± 0.07)	0.29 (± 0.04)	0.33 (± 0.01)	0.57 (± 0.07)	1.44 (± 0.07)	29,098	16,895	12,182	29,476	7,050	94,702
Sep-07	0.13 (± 0.03)	0	0.12 (± 0.02)	0.24 (± 0.03)	0.63 (± 0.05)	3,996	0	4,346	12,305	3,103	23,750
Dec-07	0.17 (± 0.04)	0	0.32 (± 0.05)	0.25 (± 0.06)	0.47 (± 0.05)	4,896	0	11,644	13,079	2,308	31,928
2+											
Feb-06	0.39 (± 0.06)	0.18 (± 0.05)	0.14 (± 0.02)	0.11 (± 0.03)	0.87 (± 0.09)	11,556	10821	5,334	5,883	4291	37,885
Mar-06	0.57 (± 0.06)	0.19 (± 0.04)	0.50 (± 0.06)	0.62 (± 0.06)	1.32 (± 0.10)	16,957	11198	18,468	32,344	6485	85,453
Jun-06	0.25 (± 0.05)	0	0	0.22 (± 0.04)	0.48 (± 0.05)	7,390	0	0	11,568	2386	21,344
Sep-06	0.51 (± 0.08)	0	0.45 (± 0.05)	0.20 (± 0.03)	0.48 (± 0.04)	14,970	0	16,690	10,437	2381	44,479
Dec-06	0.18 (± 0.04)	0	0.07 (± 0.02)	0.15 (± 0.06)	0.28 (± 0.05)	5,276	0	2,909	7,749	1387	17,322
Jan-07	0.18 (± 0.04)	0.02 (± 0.01)	0.36 (± 0.05)	0.07 (± 0.02)	0.10 (± 0.02)	5,455	1331	13,334	3,570	508	24,200
Mar-07	0.19 (± 0.04)	0.02 (± 0.01)	0.28 (± 0.03)	0.11 (± 0.03)	0.48 (± 0.08)	5,765	1356	10,529	5,851	2344	25,845
Sep-07	0.35 (± 0.06)	0.37 (± 0.01)	0	0.22 (± 0.05)	0.47 (± 0.05)	10,302	22343	0	11,536	2317	46,498
Dec-07	0.23 (± 0.05)	0	0.29 (± 0.03)	0.13 (± 0.03)	0.37 (± 0.03)	6,784	0	10,877	6,769	1826	26,257

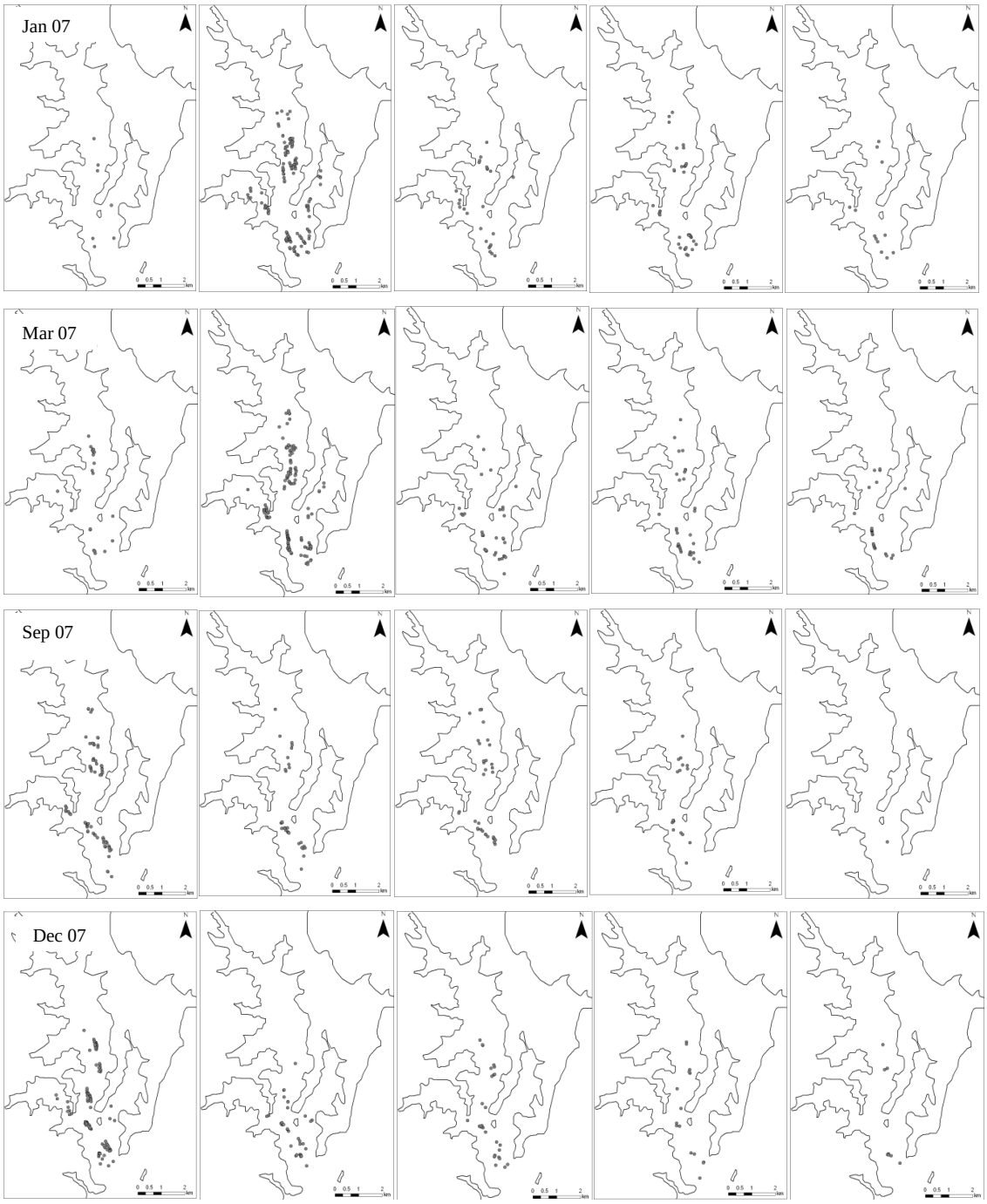
Appendix
3.7 cont.

3+											
Feb-06	0.05 (± 0.02)	0.05 (± 0.03)	0.14 (± 0.03)	0.17 (± 0.05)	0.28 (± 0.04)	1,646	2,829	5,334	8,952	1,366	20128
Mar-06	0.22 (± 0.07)	0	0.38 (± 0.05)	0.19 (± 0.03)	0.56 (± 0.04)	6,671	0	14,186	9,797	2,737	33391
Jun-06	0.10 (± 0.04)	0	0.16 (± 0.03)	0	0.06 (± 0.02)	3,113	0	5,973	0	291	9377
Sep-06	0.10 (± 0.03)	0.04 (± 0.02)	0.13 (± 0.04)	0.09 (± 0.02)	0.17 (± 0.05)	3,046	2,411	5,104	4,787	826	16175
Dec-06	0.27 (± 0.05)	0.06 (± 0.03)	0.16 (± 0.03)	0	0.30 (± 0.07)	8,164	3,680	6,190	0	1,467	19502
Jan-07	0.30 (± 0.05)	0.02 (± 0.01)	0.42 (± 0.05)	0.11 (± 0.03)	0.15 (± 0.03)	9,048	1,410	15,572	6,005	726	32764
Mar-07	0.14 (± 0.03)	0.02 (± 0.01)	0.30 (± 0.04)	0.12 (± 0.02)	0.50 (± 0.06)	4,086	1,350	11,153	6,320	2,455	25365
Sep-07	0.11 (± 0.03)	0	0.13 (± 0.05)	0.10 (± 0.03)	0.40 (± 0.05)	3,279	0	5,110	5,563	1,978	15929
Dec-07	0.11 (± 0.04)	0	0.18 (± 0.04)	0.05 (± 0.02)	0.18 (± 0.02)	3,418	0	6,747	2,925	921	14011
27+											
Feb-06	0.07 (± 0.03)	0	0	0	0.16 (± 0.04)	2,610	0	0	0	789.3	3400
Mar-06	0.09 (± 0.02)	0.02 (± 0.01)	0.19 (± 0.02)	0	0.15 (± 0.02)	2,825	1,304	7,112	0	772.2	12014
Jun-06	0.01 (± 0.01)	0	0.05 (± 0.02)	0.01 (± 0.01)	0.12 (± 0.02)	363	0	1,867	1,000	603.2	3834
Sep-06	0.13 (± 0.05)	0	0	0.10 (± 0.02)	0.10 (± 0.02)	3,879	0	0	4,981	498	9358
Dec-06	0.07 (± 0.02)	0.03 (± 0.01)	0	0.04 (± 0.06)	0	2,307	1,631	0	2,142	0	6080
Jan-07	0.10 (± 0.02)	0	0.15 (± 0.01)	0	0.15 (± 0.03)	3,057	0	5,793	0	742	9592
Mar-07	0.06 (± 0.01)	0.02 (± 0.01)	0.16 (± 0.01)	0.05 (± 0.02)	0.63 (± 0.01)	1,932	1,356	5,834	2,737	3,102	14961
Sep-07	0.01 (± 0.01)	0	0	0	0	411	0	0	0	0	411
Dec-07	0.08 (± 0.03)	0	0.17 (± 0.02)	0	0	2,329	0	6,531	0	0	8860

Appendix 3.8 Location of individual snapper from DUV by season and year-class.



Appendix 3.8 cont.



CHAPTER FOUR

Ontogenetic diet shifts in snapper (*Pagrus auratus*: Sparidae) within an estuary

Introduction

The survival, growth and reproduction of fish depend on the quality and quantity of food taken in and the nutrients generated by feeding (Wootton 1990). As fish grow, their diet changes and ontogenetic shifts may occur to maximise the intake of energy and nutrients, which in turn increases growth rate and potentially decreases vulnerability to predation (Werner and Gilliam 1984; Stouder et al. 1994). Different sizes of fish have different energy requirements and this may be reflected in the prey consumed or the time spent foraging (Gillanders 1995). Size-specific shifts in diet are often associated with, or caused by, shifts in habitat (Jones 1984; Werner and Gilliam 1984; Sudo and Azeta 2001; Szedlmayer and Lee 2004). Differing habitats can vary spatially and temporally in foraging profitability and the added risk of predation means animals must balance the gains and risks as a consequence (Werner et al. 1983). There can be considerable differences in prey availability between habitats and seasons, which may be reflected in the diet of the animals being studied (Grossman 1980; Schafer et al. 2002). The ability to kill and consume prey can be affected by morphological differences in fish (Wootton 1990; Platell et al. 1998). Larger fish may have the ability to crush larger prey items, so as fish increase in size, the size of the prey and the proportion of hard-bodied prey may increase in their diet (Wainwright 1988; Gillanders 1995; Platell et al. 1998).

Estuaries are thought to provide shelter from predation and adverse physical conditions, and abundant food for adult and juvenile fish that may not be available, or is limited in offshore waters (Blaber and Blaber 1980; Beck et al. 2001; Laegdsgaard and Johnson 2001). Snapper are generalist predators that take primarily invertebrate prey from soft sediments (Godfriaux 1969; Colman 1972) and rocky reefs (Choat and Kingett 1982; Russell 1983). Previous studies on the diet of snapper are mostly from coastal areas and

have shown that snapper consume a wide variety of prey from a large variety of taxa (see Appendix 3). The earliest reports were compiled by New Zealand lighthouse keepers in the late 1800's, with shellfish, crustaceans, small fish, jellyfish, octopus and sea urchins the main components (Thomson 1891). Later studies showed similar results, with molluscs, crustaceans, echinoderms, teleost fish and salps listed as the major prey (Powell 1937; Graham 1939; McKenzie 1960). The ecological factors of size, seasons, habitats, depth, time of day and region were considered to have an impact on the diet of snapper in a complex study by Godfriaux (1969). Six thousand snapper stomachs were examined by Colman (1972) from the inner and outer Hauraki Gulf. There were few differences seasonally and some ontogenetic trends were noted, although little was known about the substratum the fish were caught over other than that it was either mud or silt (Colman 1972). The analysis of 50 species of fish from coastal rocky reefs found 44 species to be carnivorous, including snapper (Russell 1983). Overall, these studies showed how opportunistic a species the snapper is, feeding on a wide variety of species, over a variety of habitats and depths, which probably accounts for its success as a species in New Zealand waters (Godfriaux 1969; Godfriaux 1970; Colman 1972).

The aim of this chapter was to quantify the diet of snapper within an estuary, the Mahurangi Harbour, and examine if there were any ontogenetic shifts in feeding activity with increasing size and how this may relate to the known habitats within the harbour on a seasonal basis. The results were then compared to published information on diets of snapper from coastal areas.

Methods

Sampling

Three methods were used to capture snapper for dietary analysis. Beam trawling was used to sample juvenile snapper up to 100 mm long every three months from December 2005 to September 2007 (i.e. the beginning of each new season), across known habitats of horse mussel, shell hash, sand and subtidal mud habitats (see Chapter Two for location details and methodology). Initially, intertidal habitats were also sampled, but as there were very few fish caught and it was a hazardous area to work in, sampling this habitat was discontinued. Juvenile snapper (< 100 mm) from the beam trawl samples

were anesthetised using MS222 then placed in 10% formalin in seawater. Fish lengths and weights were measured at the end of the day. Snapper > 100 mm were caught using a combination of rod and reel with small jigging hooks and a recreational longline with 25 hooks per set using salted pilchards as bait, every three months from December 2005 to December 2006. As large snapper are mobile, the harbour was not stratified into habitats for these samplings. Longline sets were haphazardly placed depending on wind and current within the mid-lower region of the harbour (average depth 6–8 m), with rod fishing close by. Fish caught by longline and rod were killed, weighed, measured and gutted immediately. The stomach and intestine from the oesophagus to anal opening was removed and put into 10% formalin in seawater to fix the contents. All stomachs were opened and the contents identified within 3 days of being fixed.

It has been shown that differential digestion rates have caused errors in the estimation of dietary importance in other studies (Hyslop 1980). For example, a laboratory experiment by Beukers-Stewart and Jones (2004) showed fish were digested approximately four times faster than crustaceans, leading to a gross over-estimation of crustaceans in the diet. An initial pilot study from November 2005 of snapper caught by rod and longline, during mid-morning, mid-day, early evening and several hours after dark showed digestion in the snapper guts was minimal mid-morning and after dark. This correlates with the preferred feeding times of early morning and dusk for snapper (Godfriaux 1969). The study by Colman (1972) however, did not fully reflect this, with size of the snapper dictating stomach fullness. Stomachs of larger fish > 20cm were generally fuller in the morning than the evening and small fish were often full over the whole day indicating they fed continuously. Francis (1997) calculated the digesto-somatic index for 0+ snapper, which indicated they fed continuously throughout the day and ceased feeding at night. Therefore, the beam trawling for the small juvenile snapper was conducted throughout the day, and longline and rod sampling of large juvenile and adult snapper was undertaken during mid-morning to capture snapper with the fullest, least digested stomach contents.

To examine potential prey species of small juveniles, a Smith-McIntyre grab (area sampled = 0.1 m^2) was used to sample the sediment within each of the horse mussel, sand, large shell hash and subtidal mud habitats. Four grabs were taken from each of three haphazardly placed sites within each habitat. A sub-sample of each grab was taken

by hand-core (diameter 50 mm, length 100 mm) with a total volume of approximately 50 cm^3. The sample was washed over a 330 µm mesh sieve and inspected for benthic animals with the aid of a dissecting microscope. Measurements of copepods from the smallest snapper stomachs indicated a sieve mesh this size should retain the smallest animals eaten by juvenile snapper.

Analysis of stomach samples

All fish from the beam trawls were processed except for the two March samples where the fish were sub-sampled from tows for analysis due to high numbers. All fish caught on rod and longline were processed. All snapper stomach contents were analysed the same way regardless of size, with small fish stomach contents being examined under a dissecting microscope. The stomach of snapper is clearly definable and was separated from the intestine. Each stomach was weighed, opened and the fullness estimated on a scale of 0–10. The contents were placed in a Petri dish and given a rating of 1–5 for how digested the contents were (1 = no or very little digestion to 5 = mush). The empty stomach was then weighed and this was subtracted from the total weight to give a total weight for the contents. Stomach contents were identified to the lowest possible taxonomic level. Unidentifiable materials have the potential to bias results as they may contain more than one dietary category (Schafer et al. 2002), so they were excluded from all analyses.

There are a number of methods for analysing gut contents, each with different biases (Hyslop 1980; Cortes 1997; Marshall and Elliott 1997). No one method of stomach analysis gives a complete picture of dietary importance (Berg 1979; Cortes 1997) so four measurements were taken to get an accurate representation of the diet of snapper within an estuary. 1) Percent composition or relative volume identifies which prey type forms the bulk of the diet; 2) percent numerical frequency shows the most frequently consumed prey type; 3) percent frequency of occurrence provides a measure of constancy of a prey item in the diet (Hyslop 1980); and 4) the index of relative importance combines the three previous measures (Pinkas et al. 1971).

1) Percentage composition or relative volume (%C)

$$\%C = w_x/W_x \times 100$$

Where:

w = the estimated volume of a particular prey type in gut x

W = the total food volume in gut x

The percent composition of individual prey items was determined visually by area coverage over a 1 x 1 cm or 1 x 1 mm grid for very small prey items and expressed as a proportion of the total gut contents. Items that were broken into pieces but clearly definable were grouped, e.g. 'shrimp pieces'. Unidentifiable material was either too digested, or contained a number of taxa that could not be clearly distinguished. However, if the dietary items were a mix of crustaceans, they were identified as 'crustacean pieces' (see Appendix 4.1 and 4.2). Unidentifiable material was excluded from the analysis as it has the potential to bias results (Schafer et al. 2002).

2) Percentage numerical abundance (%N)

$$\%N = i_x/I_x \times 100$$

Where:

i = the number of individuals of a particular prey type that occurred in gut x

I = the total number of individuals of all prey types counted in gut x

Whole individuals of each prey type were counted. As many items were broken up, especially in larger fish, unique parts of the body that could be counted were defined for different species. For species with a head, this was counted as one individual. In bivalves the hinges were counted and for gastropods the opercula were counted.

3) Percentage frequency of occurrence (%O)

$$\%O = n/N \times 100$$

Where:

n = the number of fish in which a particular prey type or species occurred

N = the total number of fish in the sample

Estimates of volume can be influenced by the presence of a few large items and it is not always possible to get counts of individual prey species, so the frequency of occurrence of each prey type was recorded. Although this method does not give information on the

relative bulk of each dietary component, it does give a crude qualitative picture of the food spectrum and the constancy of a prey type within the stomach (Hyslop 1980).

4) Index of relative importance (%IRI)

$$\%IRI = (\%N + \%C) \times \%O/100$$

This index combines the first three measures and the rationale for it is that it downplays the biases of the individual components, with the aim of providing a more accurate description of dietary importance (Cortes 1997). However, using a single index such as the IRI for the description of the diet may allow some of the information that went into the calculation to be lost; therefore the components that make up the index must also be provided separately (Berg 1979).

Data Analysis

Snapper were separated into two size groups to examine any ontogenetic variation in the diet. Small juveniles (0–100 mm) from the beam trawls were kept separate from the larger juveniles and adult snapper (> 100 mm). This allowed analysis of the diet composition of the small juveniles at a finer resolution, i.e. 10 mm size classes vs. 50 mm size classes for the larger fish. The initial exploratory data analysis pooled species to major prey taxa (Family to Order level). For the fish < 100 mm, these were copepods, mysid shrimps, caridean shrimps, polychaetes, brachyuran crabs, crustacean larvae and amphipods. For the fish > 100 mm, these were brachyuran crabs, caridean shrimps, bivalves, polychaetes, pagurid crabs, gastropods, mysid shrimps, algae and teleost fish. The major taxa that contributed most to the diets were then examined at a lower taxonomic level if possible (thereafter called major prey items). Principal components analysis (PCA) on the IRI of the major prey taxa was performed for the size class and habitat data. The data was square-root transformed prevent the most abundant prey dominating the analysis (Quinn and Keough 2002). Analysis of similarity (ANOSIM) was used to test differences among factors. Both these procedures were completed in Plymouth Routines in Multivariate Ecological Research version 6 (PRIMER 6) (Clarke and Warwick 2001). To determine if there was any correlation between the invertebrates observed in the environment and the prey within the diet of small juvenile snapper, Spearman's rank order correlation was calculated. Spearman's rank was used

over Pearson's correlation as it is a more robust measure and the data showed evidence of non-normality even after transformation (Quinn and Keough 2002).

Results

Stomachs of the 351 snapper were analysed with fish ranging in size from 10.1 to 550 mm. Of the 263 juvenile snapper < 100 mm, none had an empty stomach. Of the larger snapper > 100 mm, 4 of the 92 fish had empty stomachs so they were excluded from the analysis. Stomach fullness differed between the two size groups. On average, the snapper < 100 mm scored 7 out of 10 for fullness, while the fish > 100 mm scored 4.5 out of 10 for fullness. The fish < 100 mm were always more full than the larger fish across all seasons, with both the September samplings having fish with the least amount of food in their stomachs (Figure 4.1). The mean fullness of the larger fish decreased from December 2005, to the lowest level in September 2006, following a similar pattern to the juvenile fish, but increased again in December 2006.

Diet showed clear shifts with size. The index of relative importance (IRI) showed a shift from almost 100% consumption of copepods in the smallest size class sampled (10–20 mm, post-settlement snapper), to a more diverse range of prey as snapper size increased (Figure 4.2A and B). Copepods continued to be taken up to 70 mm in size, but became less important after 40 mm, with fish adding mysid shrimps, caridean shrimps and polychaetes to their diet (Figure 4.2A). In the larger size classes (100–550 mm), brachyuran crabs and shrimps dominated; with the mysid shrimps being replaced by caridean shrimps from 150–350 mm (Figure 4.2B). Calanoid copepods comprised approximately 90% of the diet of 10–20 mm sized fish by occurrence, abundance and volume and were the major component of the copepod group (Figure 4.3). Small crustacean larvae were also taken by the smaller size classes. Mysid shrimps were consumed from 20–150 mm, with a sharp increase in consumption of mysids between 100–150 mm (Figure 4.3 and 4.4). Snapper also consumed different species of caridean shrimps. The species *Palaemon affinis* dominated the shrimps in fish 30 to 70 mm, with unidentified caridean shrimps becoming more important through the rest of the size classes. The gammaridean amphipod group split into 'others' and 'corophiid amphipods' with the former preferred by larger fish > 70 mm and the latter by fish < 40

mm. Brachyuran crabs were consumed by most size classes of fish but were more important in the diet of fish above 100 mm (Figure 4.2). Fish < 100 mm mostly consumed *Halicarcinus* sp. crabs, while diets of fish > 100 mm were dominated by a mixture of the brachyuran crabs *Macrophthalmus hirtipes*, *Helice crassa* and *Halicarcinus* sp. (Figure 4.4). Bivalves were consumed by snapper from 200 mm in length and were mostly *Austrovenus stutchburyi* (cockles), although some *Musculista stenhousia* (Asian data mussel) were also consumed (Figure 4.4). The pagurids (hermit crabs) were consumed by snapper from 250 mm (Figure 4.2 and 4.4). Polychaetes were consumed in small quantities across most size ranges and small amounts of gastropods, algae and small teleosts made up the rest of the stomach contents for fish > 100 mm (Figure 4.2, 4.3 and 4.4).

Principal components analysis (PCA) of the major prey taxa consumed by all sizes of snapper showed a shift in diet with size. PC1 accounted for 49.5% of the variability and PC2 23%; therefore the PCA was a good descriptor of the data in higher space (Clarke and Warwick 2001) (Figure 4.5). Fish length increased steadily along PC1, from right to left. Copepods, mysid shrimps, unidentified shrimps and the brachyuran crabs had the longest eigen-vectors, reflecting the importance of these prey items to the size class groups they related to (Figure 4.5). These were 10–20 mm for the copepods and 20–80 mm for the mysid shrimps. The unidentified shrimps were positioned in the middle of PC1, while the eigen-vector for brachyuran crabs sat between the 150–550 mm ranges, indicating their importance to a wide size range of snapper (Figure 4.5). Cockles (*Austrovenus stutchburyi*) and hermit crabs (Paguridae) were positioned towards PC2 amongst the largest sizes of fish that consumed these items as prey (Figure 4.5). These results were therefore consistent with the previous ones.

The major prey items consumed showed some seasonal patterns, however, it was difficult to determine for snapper < 100 mm whether these were driven by seasonal fluctuations in the environment or by the growth of snapper (Figure 4.6). Without seasonal data from prey abundances in the environment, this could not be determined; therefore it had to be assumed that size was the major factor driving dietary differences. ANOSIM found no significant differences in prey abundance over season (global R = 0.06, p = 0.15) for the fish < 100 mm. However, ANOSIM showed significant differences by season for the snapper > 100 mm (global R = 0.156, p = 0.02). Pairwise

tests identified December 2005 as the cause of the significant difference, being different to every other season, except June 2006. The diversity of species found in the stomach from December 2005 as compared to the other seasons was probably the contributing factor for this (Figure 4.6). As a general pattern, the species that appeared in the stomachs of snapper all year round were the mysid shrimps, caridean shrimps, brachyuran crabs and polychaetes (Figure 4.6).

Snapper < 100 mm were sampled across four habitat types: horse mussels, sand, subtidal mud and shell hash. The IRI from the data pooled over the 8 seasons for the four habitats showed few differences for the major prey taxa amongst habitat types (Figure 4.7). As with the seasonal data, it was difficult to separate the influence of the size of the fish from habitat. Fish from the sand habitat had consumed slightly higher amounts of calanoid copepods (Figure 4.8). However, the largest fish caught over the sand habitat was < 50 mm, and as nearly all the fish in this size range consumed copepods, size rather than habitat type was probably the driver. Mysid shrimps were numerically abundant in the diet of fish from horse mussels and subtidal mud, but the volume was higher within the shell hash where they formed the bulk of the diet along with the calanoid copepods and amphipods (Figure 4.8). Gammaridean amphipods were only found in the stomachs of fish caught across sand and shell hash (Figure 4.7 and Figure 4.8). PCA of the habitat data (PC1 59%, PC2 26.5%) on the major prey items showed the gammaridean amphipods had the longest eigen-vectors indicating a strong influence on the data (Figure 4.9). These were comprised of 'corophiidae' and 'other' and were split between the shell and sand respectively. However ANOSIM conducted on the habitat data was not significant (global R = 0.07, p = 0.85), therefore the null hypothesis of no difference in prey species across different habitats was not rejected.

Abundance of prey in sediment vs. diet

As the sediment samples were collected only once during winter 2007, the abundance of prey found within the samples could only be compared with the occurrence of species in the diet of the fish taken in the same season, to avoid temporal confounding in the data. Overall, the species observed in the diet showed no significant correlation with the prey observed in the wild (Spearman rank, p = 0.45). Significantly more calanoid copepods, caridean shrimps, mysid shrimps and crustacean larvae were observed in the diet of

small juvenile snapper than in the environment, indicating snapper were actively selecting these prey. From the invertebrates taken by grab samples within the harbour, ostracods dominated, but were rarely seen in the diet of small snapper (Figure 4.10).

Discussion

Snapper are capable of eating a wide variety of prey and can adapt their feeding preferences to what is available in the environment (Godfriaux 1969; Godfriaux 1970; Colman 1972; Russell 1983). Fish that can adapt in this way and grow satisfactorily on a wide range of food items would be unlikely to be disadvantaged by competition with other species, or food shortages (Weatherly 1963; Godfriaux 1970). Previous work on snapper diet from the Hauraki Gulf have recorded up to 100 prey taxa, comprised of up to 10 major taxa (Godfriaux 1969; Colman 1972) (see Appendix 4.1 and 4.2). This lack of dietary specialisation has been suggested as the reason why snapper are so successful within the Hauraki Gulf (Godfriaux 1969; Godfriaux 1970), and most likely in all areas they are found around the New Zealand coast. The data collected here has demonstrated snapper within the Mahurangi Harbour also eat a wide variety of prey. The total number of major prey items for snapper < 100 mm was 36, with 7 major taxa, while 39 major prey items and 9 major taxa were recorded for snapper > 100 mm. The large numbers of snapper examined by Godfriaux (1969) (1194 fish) and Colman (1972) (6000 fish) from the inner and outer Hauraki Gulf and a detailed analysis of prey may have contributed to the large number of taxa recorded from these studies. A lesser number of prey species in the Mahurangi Harbour or higher numbers of preferential prey, both may have contributed to a lesser number of species seen from this study. For instance, the previous work of Godfriaux (1969) and Colman (1972) listed Echinodermata as being an important prey item, with the brittle star *Amphiura* sp. and the heart urchin *Echinocardium cordatum* dominating. From the fish examined here, only one fish had these items in its stomach, however both these species are abundant in the harbour (authors unpublished data), and were an important component of the diets of > 300 mm snapper taken from the Mahurangi Harbour by Coleman (1972).

Many studies on ontogenetic shifts in diet have considered a wide size range of fish (Jones 1984; Xue et al. 2005; Platell et al. 2007; Wells et al. 2008), but they have not always analysed diet over a narrow range of size increments. Of the previous work on

snapper diet, only the studies by Godfriaux (1969) and Colman (1972) considered size and the corresponding ontogenetic shifts in diet, but not at increments smaller than 50 mm for the juveniles. For this study, fish < 100 mm were grouped into size classes of 10 mm so a more detailed analysis of where the largest ontogenetic shifts take place was possible. The fish > 100 mm were grouped into 50 mm size classes. No fish were taken under 10 mm. This may be because they had not settled out of the plankton or had gone through the mesh of the beam trawl.

Clear ontogenetic dietary shifts occurred. The fish in the 10–20 mm range had a diet of almost exclusively copepods, with a few bivalve and crustacean larvae. However, only 7 snapper sized 10-20 mm were captured from March both years, so this should be interpreted with caution. The copepods were dominated by planktonic calanoids (~90%), planktonic and benthic cyclopoids, with a few benthic harpacticoid copepods taken by fish closer to 20 mm in size. Above 20 mm, the diet became more diverse, with mysid and caridean shrimps (such as *Palaemon affinis*), and polychaetes being consumed, indicating more benthic feeding. At around 60 mm, brachyuran crabs such as *Halicarcinus* sp. and *Helice crassa* and amphipods were consumed. The 10–20 mm snapper from this study were therefore consuming prey from the plankton and became more benthic orientated above this as evidenced by the increase in shrimps, polychaetes and crabs. Fish in Australian seagrass meadows also consumed copepods to approximately 7 mm in length then switched to amphipods and isopods (Edgar and Shaw 1995). Crustaceans dominated diets of juvenile snapper in the Rangaunu and Manukau harbours on the east and west coast of northern New Zealand (M. Lowe, pers. comm.). Planktonic calanoid copepods dominated the diet of small fish (20–60 mm) from the Rangaunu harbour, with a switch to brachyuran crabs, caridean shrimps and bivalves at 80–100 mm. Mysid shrimps dominated in the west coast harbour (Manakau), with shrimps, brachyurans, polychaetes, amphipods and copepods occurring but not as important (M. Lowe, pers. comm.). Interestingly, in the majority of other snapper diet studies that considered size of snapper in their analyses (particularly Godfriaux (1969) and Colman (1972)), copepods are not mentioned as part of the diet at all. Godfriaux (1969) listed mysids, megalopae and polychaetes as being important for small snapper < 120 mm, and Colman (1972) listed mysids, polychaetes, amphipods and shrimps as the most important prey items for small snapper < 100 mm. Both these studies were done in the Hauraki Gulf and included fish samples taken from the

Mahurangi Harbour. Copepods may have become part of the category ‘other crustaceans’, were not identified, or were not available in the environment at the time, or more preferential prey was available.

The comparison of dietary prey with prey abundance in the environment indicated that ostracods were the most prolific crustacean available, yet they were rarely taken by small snapper. Bivalves were also high in numbers in the environment but rarely targeted. The most common species were *Theora lubrica, Corbula zelandica* and *Arthritica bifurca*, yet *Austrovenus stutchburyi* were eaten most by larger snapper. Bivalves were eaten by snapper > 200 mm, whose jaws and mouth are probably are better adapted for removing bivalves from the sediment than those of small snapper. Polychaetes within the environment and the stomachs seemed to be at similar levels. However, by Family, snapper were taking maldanid, pectinerid, hesionid, orbinid, nereid and cirritulid polychaetes, while in the cores, exogonids, ophelids, and capitellids dominated. In particular, cirritulids and the bivalve *Theora lubrica* are increasing across two subtidal sites within the harbour (Cummings et al. 2005) where the small snapper and cores were taken. The prey most strongly selected by fish < 100 mm however, were the calanoid copepods, caridean and mysid shrimps and crustacean larvae as these appeared in significantly higher proportions in the diet than in the environment. This would then suggest that snapper < 100 mm target particular prey, but have the ability to utilise alternative prey items if needed.

Benthic grab samples of prey over 4 mm, processed by Williams (2009), have shown little correlation with the contents of the large juvenile to adult snapper stomachs from this study. Overall, bivalves dominated numerically, particularly *Corbula zelandica*, which was not seen in any large snapper stomachs. Brittle stars, polychaetes, heart urchins, shrimps and crabs were also abundant, however only a few stomachs contained any of the particular prey species from the grabs. The grab samples, however, may have been biased in the collection of species such as brachyuran crabs (e.g. *Macrophthalmus hirtipes*) that were shown to be important in the diet of large snapper.

Overall, for the snapper > 100 mm, brachyuran crabs dominated the diet. From size 100–300 mm, the IRI showed brachyurans comprised over 50% of the diet. The predominant species were *Macrophthalmus hirtipes, Helice crassa* the mud crab,

Halicarcinus sp, *Petrolisthes novaezelandiae* (the red false crab) and *Nectocarcinus antarcticus* in decreasing order of importance. Crabs were an important component of previous snapper diet work (Thomson 1891; Powell 1937; Graham 1939; McKenzie 1960). Godfriaux (1969) listed 11 species of crab and Colman (1972) listed at least 4. From my study, *Macrophthalmus hirtipes, Nectocarcinus antarcticus* and *Petrolisthes novaezelandiae* and *Halicarcinus* sp. were consumed by snapper and were the only crabs in common with previous studies. *Helice crassa* have become an important brachyuran prey item in the diet of snapper from the Mahurangi Harbour. This crab is predominantly found in the intertidal and large snapper have been seen within a number of the intertidal sites in the Mahurangi (pers. obs., Chapter Three). These results were similar to those of Godfriaux (1969), who took snapper from two places in the Mahurangi. Colman (1972), however, examined fish taken from near the entrance of the Mahurangi each month over a year and found polychaetes and ophiuroids were important to fish over 200 mm in length, which differs to this study. The study of Coleman (1972) however, took fish from over 20 m in depth which may be the reason there were differences in the dominant prey items. These results show how opportunistic larger snapper can be when selecting species in the larger size ranges, while the juvenile fish appeared to be more specific.

For snapper in the size range 100–150 mm, mysid shrimps were the second most abundant dietary item. From 80–100 mm mysids appeared to decrease, however, only 8 snapper were caught in this size range. Snapper within 100–150 mm had consumed large mysid shrimps (in comparison to what the previous size classes had consumed) as part of their diet. Although prey size was not measured, it was observed that in the majority of cases, as snapper grew, the prey size generally became larger. It is well known that prey size generally increases with fish growth (Wootton 1990; Edgar and Shaw 1995; Platell et al. 1998; Schafer et al. 2002) and that larger individuals can consume larger and heavier prey (Xue et al. 2005). This is consistent with the optimal foraging theory, which states that larger predators tend to consume larger prey to maximise the energetic gain relative to capture effort (Wootton 1990). In the snapper stomachs, the same species were often taken at differing sizes, e.g. the crab *Halicarcinus* sp. was important across a range of snapper sizes, and as prey, became steadily bigger as larger size classes of fish consumed them (pers. obs.).

For fish of the size 150–250 mm, caridean shrimps were second behind the brachyuran crabs in abundance. Most shrimps were unable to be identified to species due to being in pieces or partially digested. However, the presence of claws of the snapping shrimp in the intestinal tracts of many of the fish, point to a number of the shrimps being *Alpheus* sp. Above 250 mm in size the snapper diet became more varied. Bivalves, hermit crabs, polychaetes, gastropods and teleost fish were consumed in higher numbers. The majority of the bivalves consumed were the cockle *Austrovenus stutchburyi*. In a number of fish this was all they had in their stomachs, with cockles being crushed into many pieces. Environmental monitoring of the Mahurangi Harbour over the last 12 years has shown a decline in cockles in the upper reaches of the harbour, with an increase in numbers in the mid harbour area (area 2 of this study) and closer to the mouth (area 3 this study) (Cummings et al. 2005). The majority of large snapper were caught from these two areas and the increasing populations of cockles appear to be an important prey item for these fish.

The Asian date mussel *Musculista stenhousia* and the green lipped mussel *Perna caniliculus* occurred in two fish that were captured further up the harbour, near the mangroves where the fish probably picked these species off the mangrove trunks. Snapper larger than 250 mm consumed hermit crabs, Colman (1972) also recorded a similar result. The ability to consume hermit crabs would require a strong bite to break open the shell to access the crab. In previous snapper diet studies, molluscs were an important component for fish over 300 mm, which is probably the size required to consume hard shelled prey (Godfriaux 1969; Godfriaux 1970; Colman 1972). In the examination of four other species of fish, *Pseudocaranx lutescens* (trevally) of a similar size were only able to eat bivalves with a shell less than 1 mm thick. This would limit their competition with snapper, which can access shells such as *Austrovenus stutchburyi* and *Dosinia* sp. that have shells much thicker than 1 mm (Godfriaux 1970). Feeding ability in three species of labrid was predicted best by crushing strength (Wainwright 1988). Fish switched from soft bodied prey to harder bodied prey when their jaws reached a certain crushing strength, despite differences in size of fish or gape size (Wainwright 1988). Snapper have a strong jaw with sharp canine-like teeth and a double row of smooth grinding teeth capable of crushing hard bodied prey, and can crush large gastropods such as paua, large crabs, chitons and bivalves (Doak 1972; Russell 1983; Francis 1988).

Temporal patterns were difficult to identify without having comprehensively sampled the prey in the environment at the same time to gain an understanding of the seasonal fluctuations. Some size ranges of snapper were caught in fewer numbers seasonally, which meant that fewer fish were available for analysis. For instance, only 10 snapper were caught overall in the 100-150 mm size range. The benthic grabs and subsequent cores were limited in that they only sampled what was available in the benthos and not in the water column. The sampling was also only completed once during winter 2007. Therefore, any seasonal patterns seen may also be related to the ontogenetic shift of prey species as snapper increased in size, as well as potential seasonal fluctuations in prey. Seasonal variations in prey in the environment for small yellow croaker *Pseudosciaena polyactis* had previously been studied, but it was also acknowledged that size of the fish could also affect the diet composition (Xue et al. 2005). Overall however, for snapper < 100 mm, no significant seasonal differences in diet were detected. For the snapper > 100 mm, there were significant differences between the seasons sampled. Pairwise tests partitioned out December 2005 as different to all other seasons except June 2006, due to the higher diversity of animals within the stomachs. The diversity of species was highest over the warmer seasons, however, no two seasons were similar, indicating that as snapper age they may take a wider variety of prey. The lack of larger fish (300-400 mm) caught may also have contributed to this difference.

Stomach fullness varied over each season for both small juveniles and large juvenile-adult snapper. Generally, for both size groups, stomachs were fuller over the warmer months and declined in fullness towards winter. The mean fullness rating over each season showed snapper < 100 mm had stomachs that were always more than half-full, with an overall average of 7 out of 10. Small fish are likely to eat as much as possible to grow at a faster rate which would confer advantages to the fish (Werner and Gilliam 1984; Gillanders 1995). Stomach fullness over September 2006 and 2007 was much lower for both size groups than other seasons. The fish > 100 mm averaged a fullness of 4.5 out of 10 and was always less than for the small snapper. It has been shown that as fish increase in size, the percentage of empty or less full stomachs also increases due to less frequent feeding (Colman 1972; Jones 1984). Increased feeding over warmer months is thought to be due an increased metabolic rate and somatic growth, which means increased demands for energy (Godfriaux 1969; Colman 1972). This is thought to slow down as snapper increase in size and with lower water temperatures (Godfriaux

1969; Colman 1972; Francis 1997) and explains why fullness of the gut was also less for snapper > 100 mm in size over the cooler months. Fish may also feed more in summer and autumn in preparation to lay down fat deposits and for reproduction (Wootton 1990; Xue et al. 2005). Both small and large fish had less full stomachs in September, the end of winter, which supports these theories.

Size-specific shifts in diet are often associated with, or caused by shifts in habitat (Werner and Gilliam 1984; Sudo and Azeta 2001; Szedlmayer and Lee 2004). Diet was examined for any potential ontogenetic shifts across the *a priori* habitat types within the Mahurangi Harbour. Overall, there were no apparent habitat-specific feeding differences in small juvenile snapper. All major prey groups were found within stomachs of fish taken from across all the different habitats types, with the exception of amphipods. Gammaridean amphipods were more abundant in the stomachs of fish taken from the shell hash and sand habitats. As amphipods were found in the diet of snapper across the size range of 20–100 mm, they could not be considered a potential reason for a size-related habitat shift. March samples caught fish mostly in the post-settlement size range of 15–40 mm, across most habitats. It would appear therefore that all the *a priori* habitats within the Mahurangi Harbour have similar prey items and fish < 100 mm may utilise these specific habitats types for other reasons such as protection from predation. Red snapper (*Lutjanus campechanus*) are also found to be opportunistic feeders and in a study over two years in the northern Gulf of Mexico, were found to undergo ontogenetic feeding shifts (Wells et al. 2008). Snapper primarily consumed prey associated with sand and mud substrata, despite fish being found amongst sand, shell and reef habitats, suggesting the structural importance of shell and natural reef habitats may be more important for snapper survival than additional prey resources (Wells et al. 2008).

Overall, within the Mahurangi Harbour all the *a priori* habitat types had similar prey items as evidenced by the stomach contents. Stomach fullness indicated that the small fish were eating more intensively than the larger fish and this pattern may be consistent with temporal changes. Larger snapper were well supported by the variety of prey phyla; very few stomachs were empty, therefore the harbour is capable of supporting a wide range of snapper size classes.

Conclusions

Snapper consume a wide variety of prey items. When compared with previous studies, fewer species were found in the diet but the prey items consumed are similar taxa, with different species taken depending on the availability of prey. Ontogenetic dietary shifts in juvenile snapper (< 100 mm) within the Mahurangi Harbour occurred with growth, rather than over space or time. For these small fish, there was a clear shift from the consumption of planktonic copepods to a more varied benthic diet of benthic copepods, mysid and caridean shrimps and polychaetes as fish grew. However, previous work from the Hauraki Gulf did not identify copepods as being important to small post-settlement snapper. When compared to the benthic core samples, small snapper tended to strongly select calanoid copepods, mysid shrimps, caridean shrimps and crustacean larvae. Snapper > 100 mm consumed a wide variety of prey, dominated by brachyuran crabs, caridean shrimps, bivalves, polychaetes and hermit crabs. There were significant seasonal differences for these fish driven by one season, however prey consumed each season was different, showing how opportunistic snapper are. The habitat types studied within Mahurangi Harbour appear to be equally productive for the major prey taxa utilised by small juvenile snapper and this may be advantageous for small snapper, which can then select a particular habitat for other qualities, i.e. protection from predation.

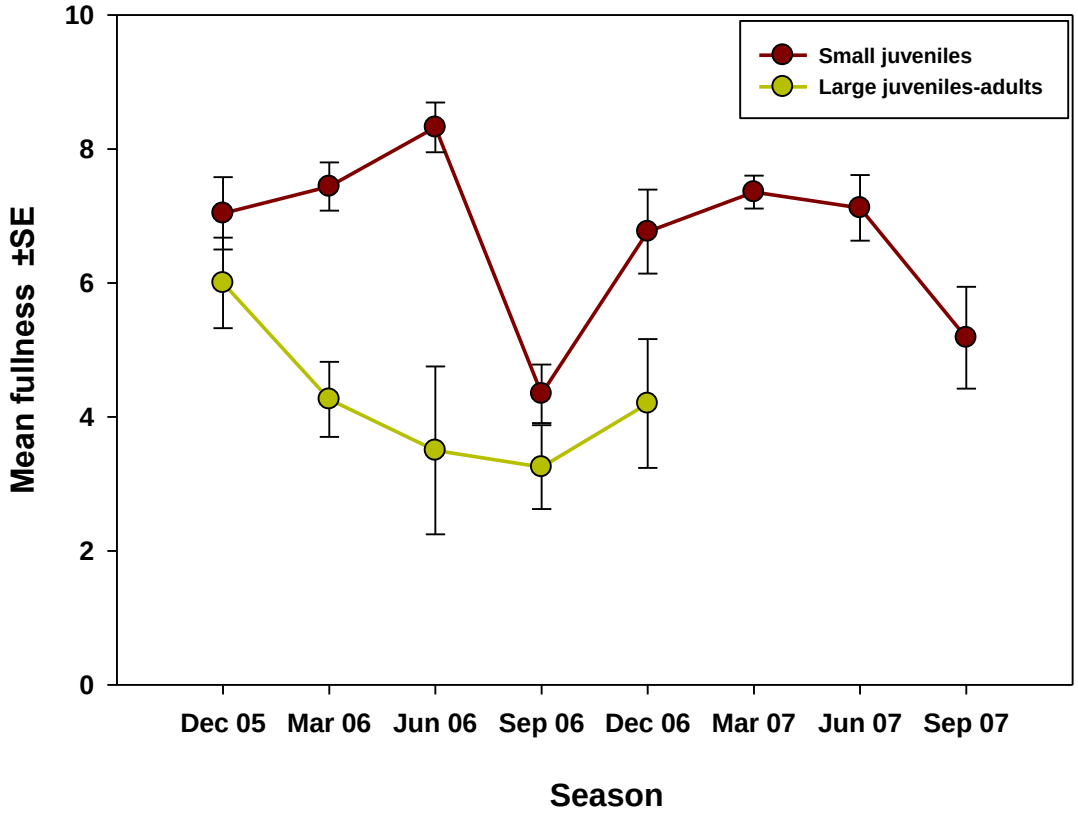


Figure 4.1 Stomach fullness over each sampling season for both the small juvenile snapper (0–100 mm), and large juvenile-adult snapper (100–550 mm). Note only 5 seasons of sampling were completed for the large juvenile-adult snapper.

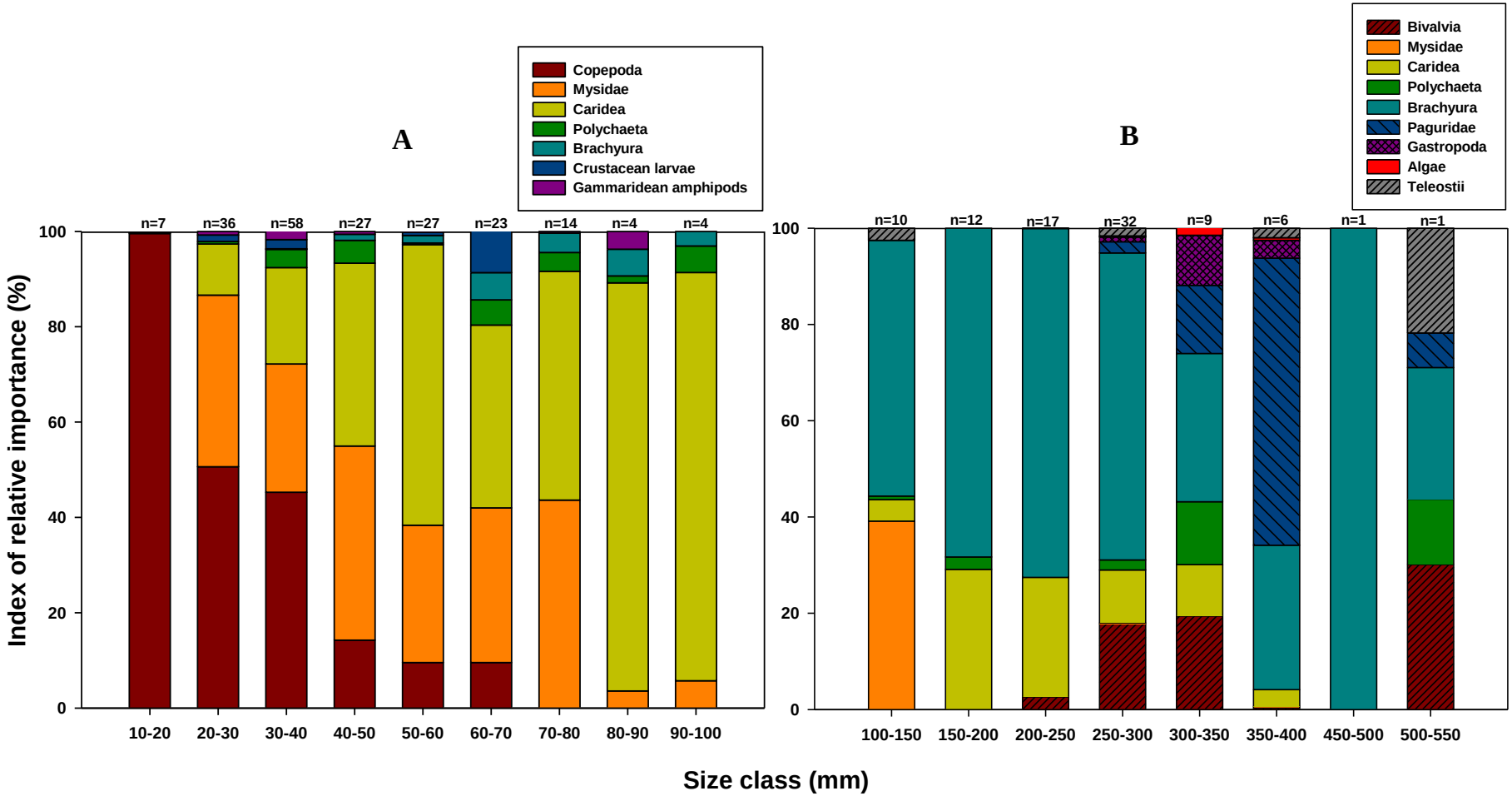


Figure 4.2 Index of relative importance of the major prey taxa found within the stomachs of: A) small juvenile snapper 0–100 mm in length, B) large juvenile-adult snapper 100–550 mm. Number of fish (n) for each size class is denoted above each size class bar.

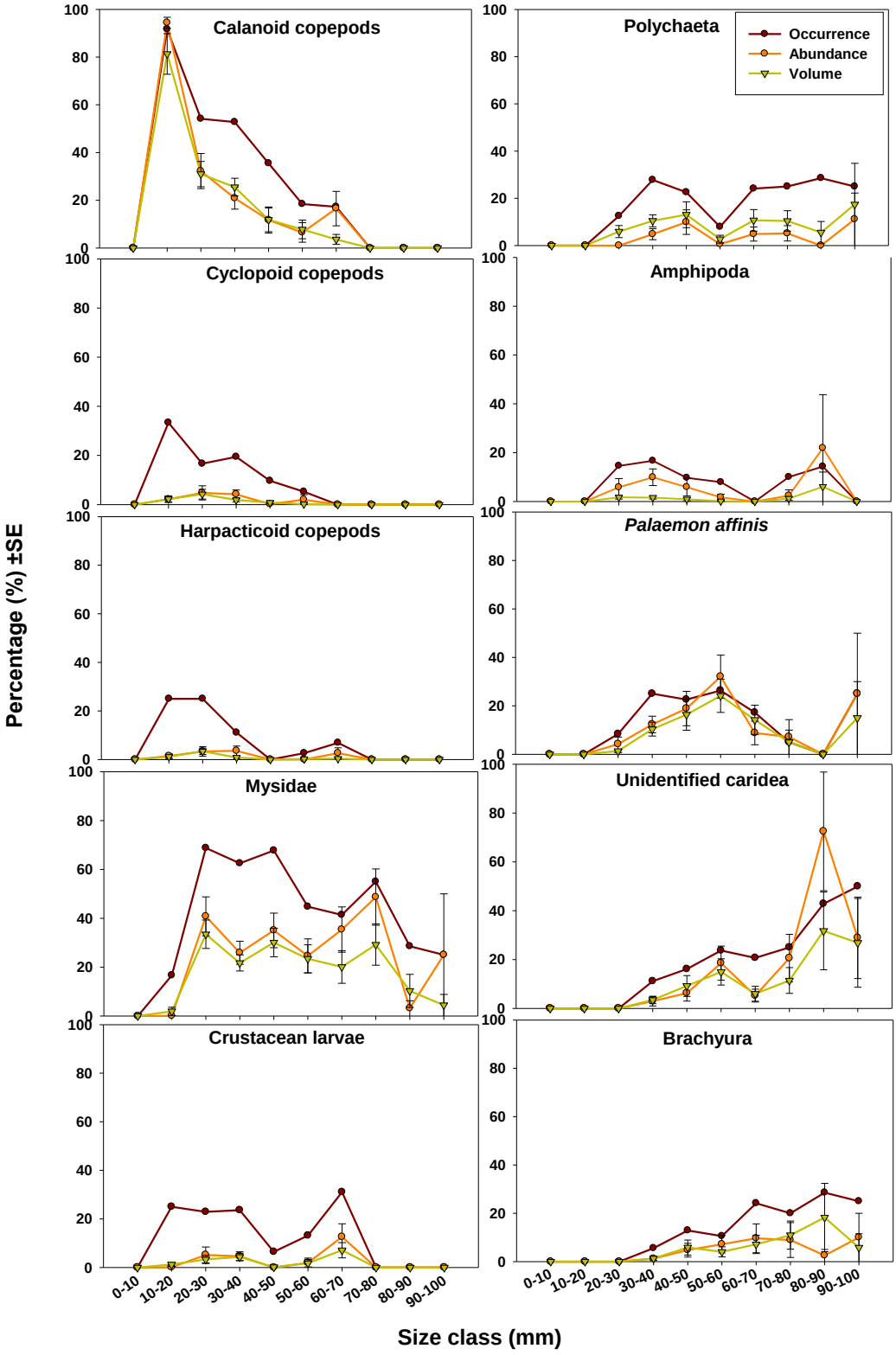


Figure 4.3 Percent frequency of occurrence, numerical abundance and volume, of the major prey items found in stomachs of small juvenile snapper in 10 mm size classes.

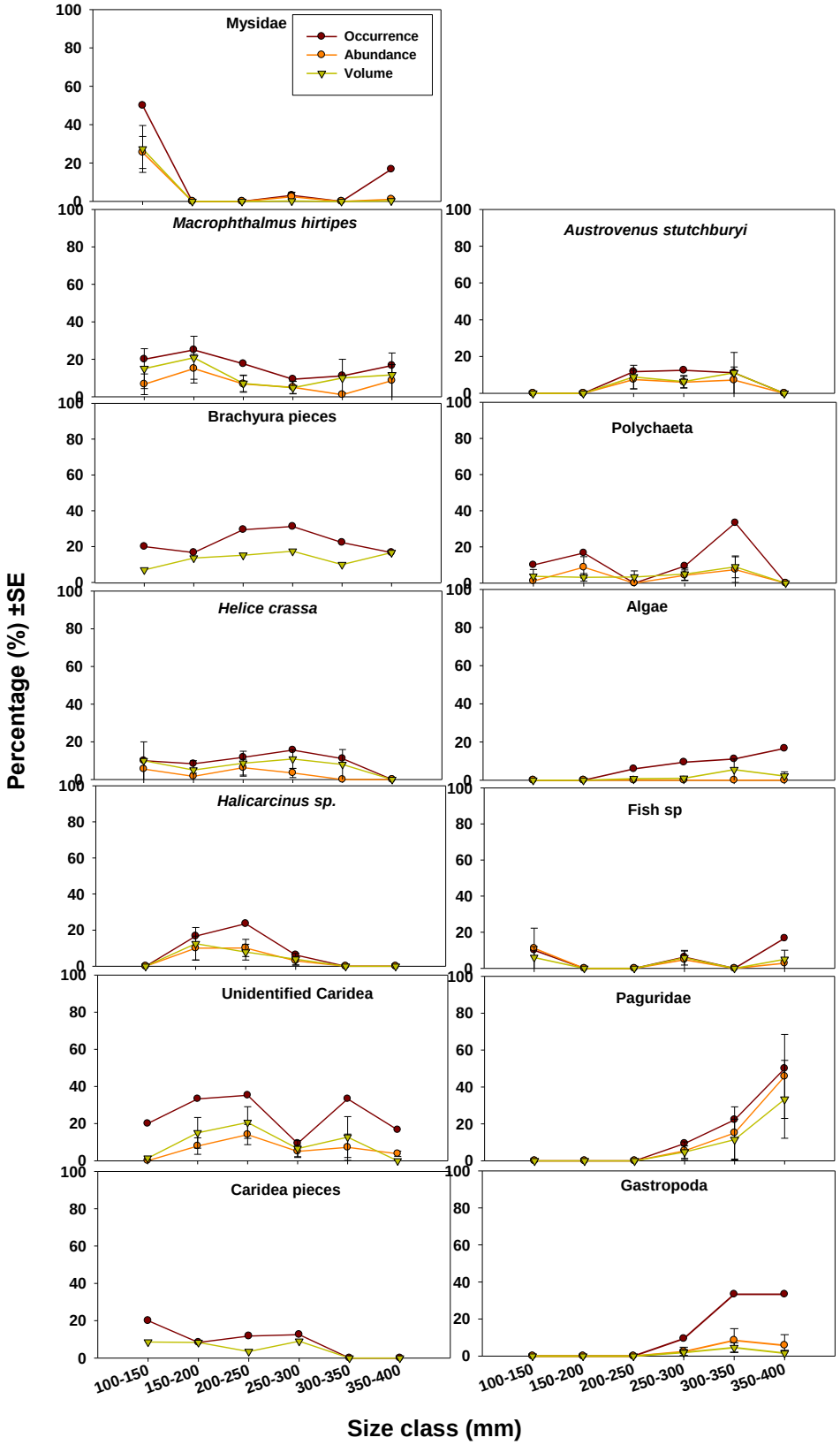


Figure 4.4 Percent frequency of occurrence, numerical abundance and volume of the major prey items found in stomachs of large juvenile-adult (100–550 mm) snapper over each size class. (Note: no fish 400–450, only 1 fish each for sizes 450–500, 500–550, so these were not included).

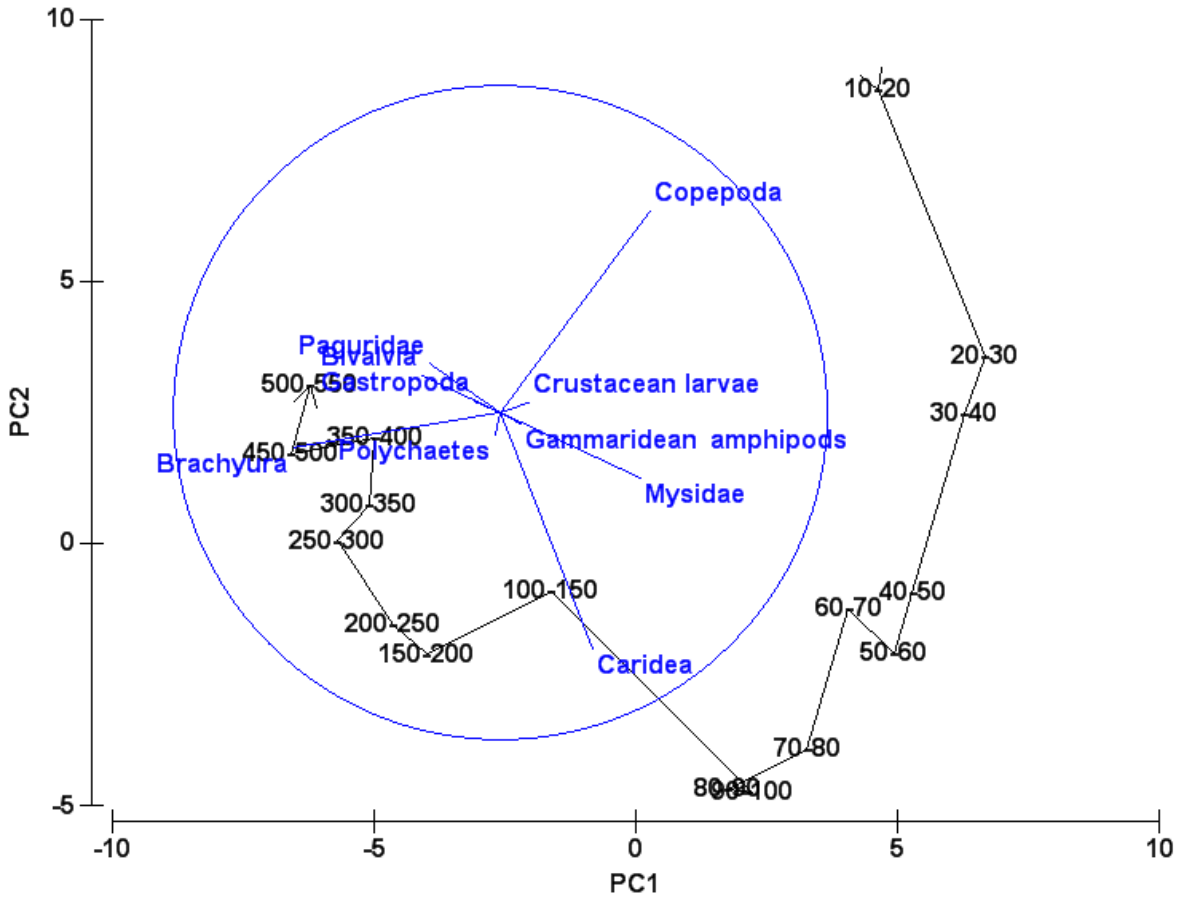


Figure 4.5 Principal components analysis of the major prey taxa consumed by small juvenile to adult snapper (0–550 mm), pooled over time. Analysis is based on square-root transformed data. PC1 = 49.5%, PC2 = 23%.

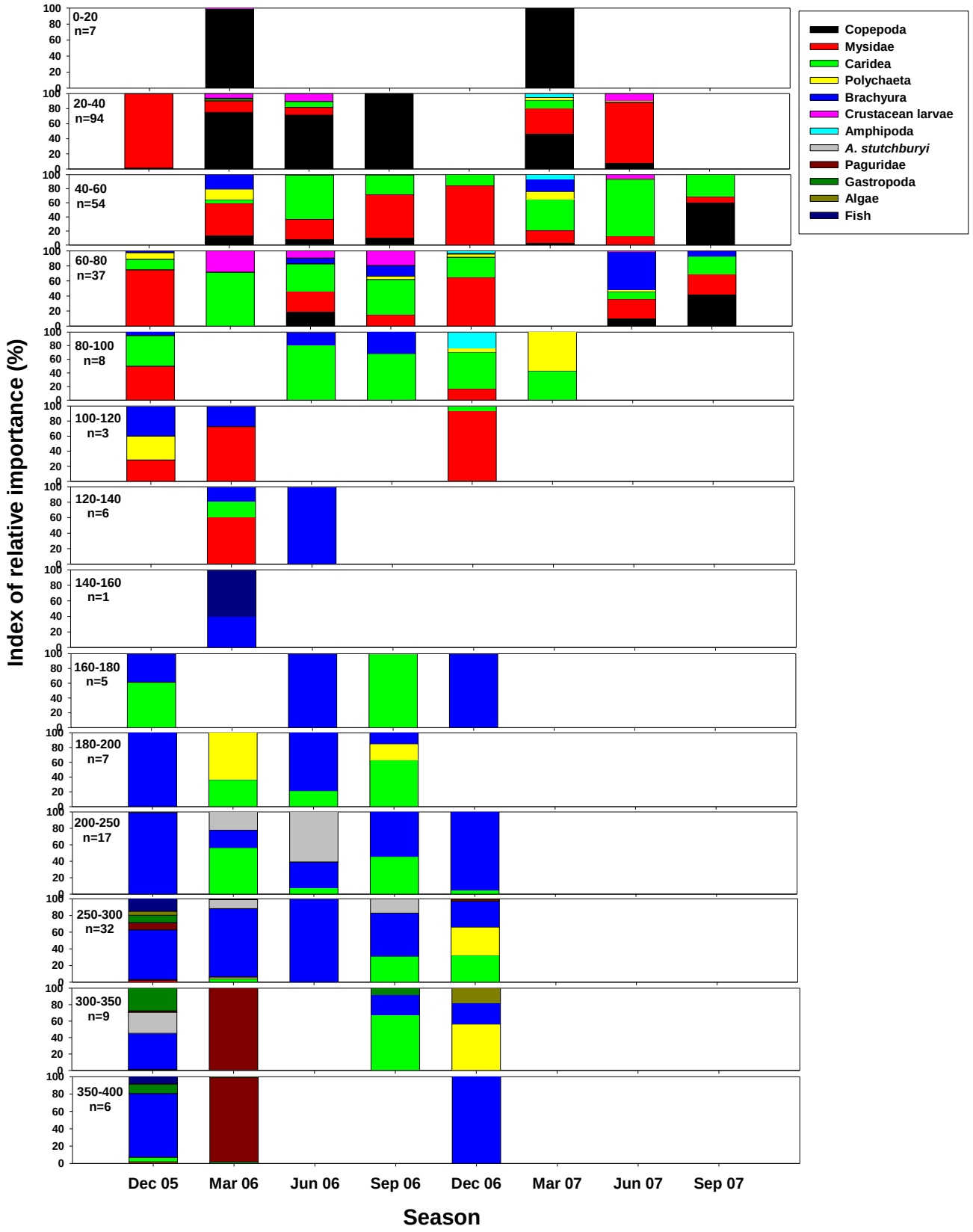


Figure 4.6 Index of relative importance of the major prey items consumed by all sizes of snapper over 8 seasons for fish 10–100 mm, and 5 seasons for fish 100–400 mm. n = number of fish contributing to each size class. Note: Between 400–550 mm only two fish were caught so they are excluded from this summary.

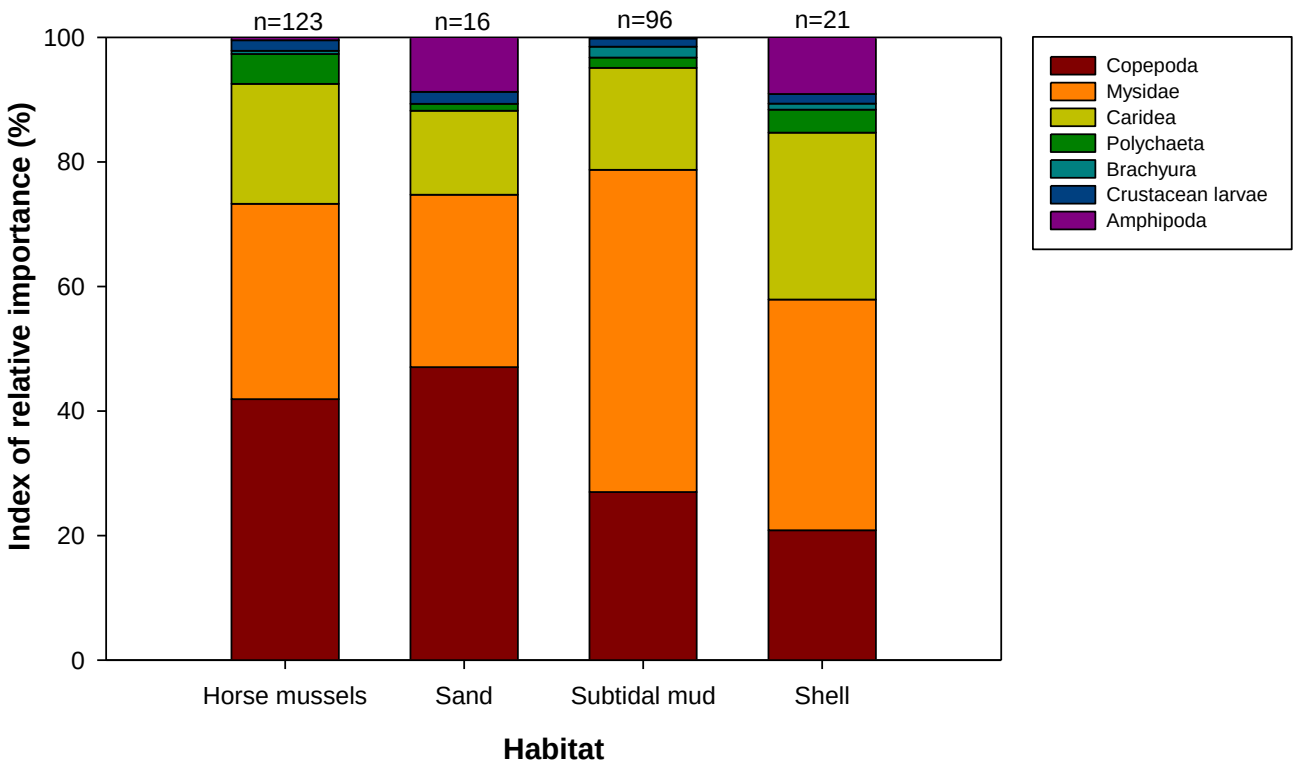


Figure 4.7 Index of relative importance of the major prey phyla found in snapper < 100 mm across four habitat types pooled over time. Number of fish (n) of each habitat sampled is denoted above each size class bar.

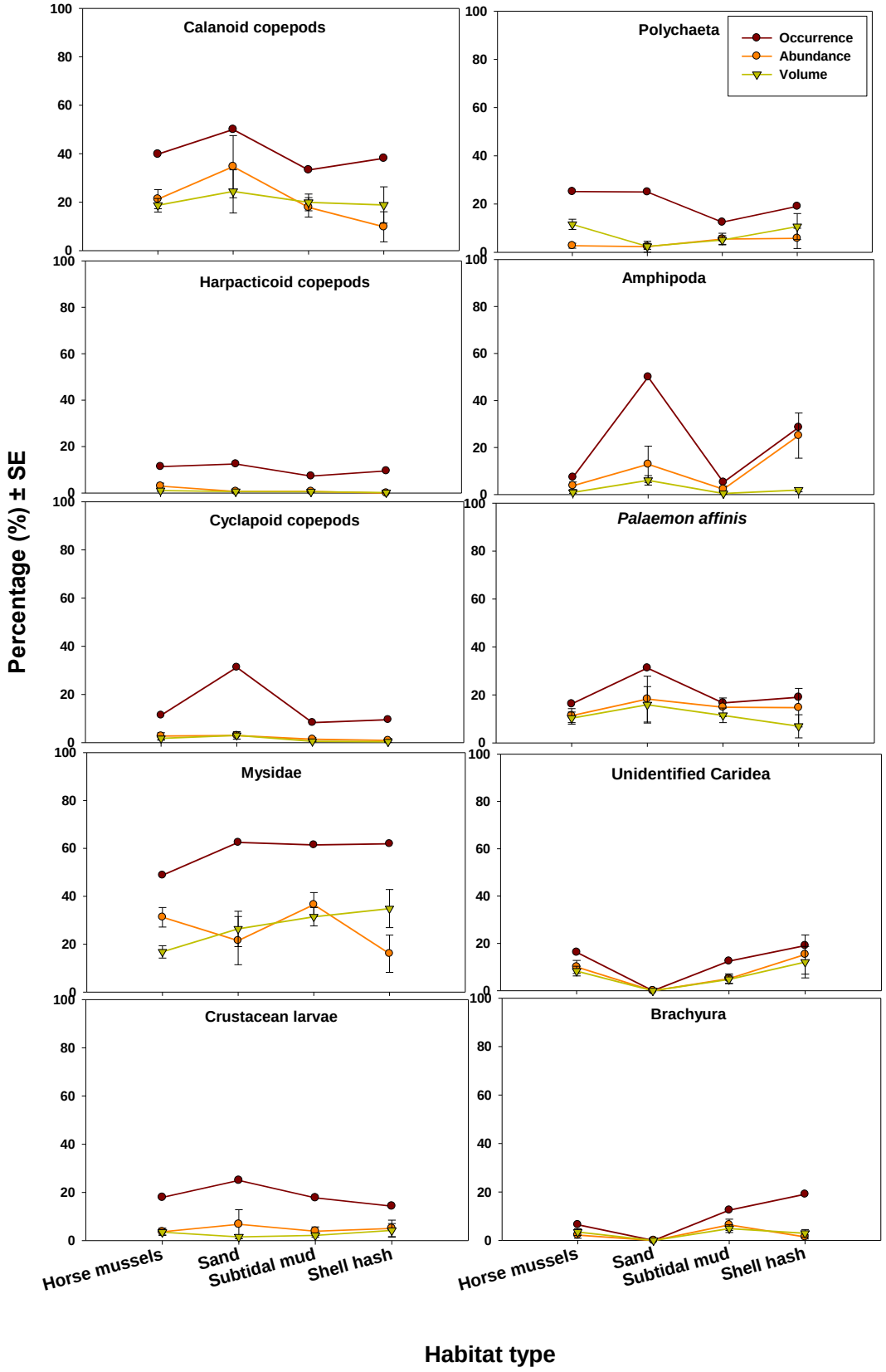


Figure 4.8 Percent frequency of occurrence, numerical abundance and volume, of the major prey phyla found in stomachs of snapper < 100 mm from different habitat types.

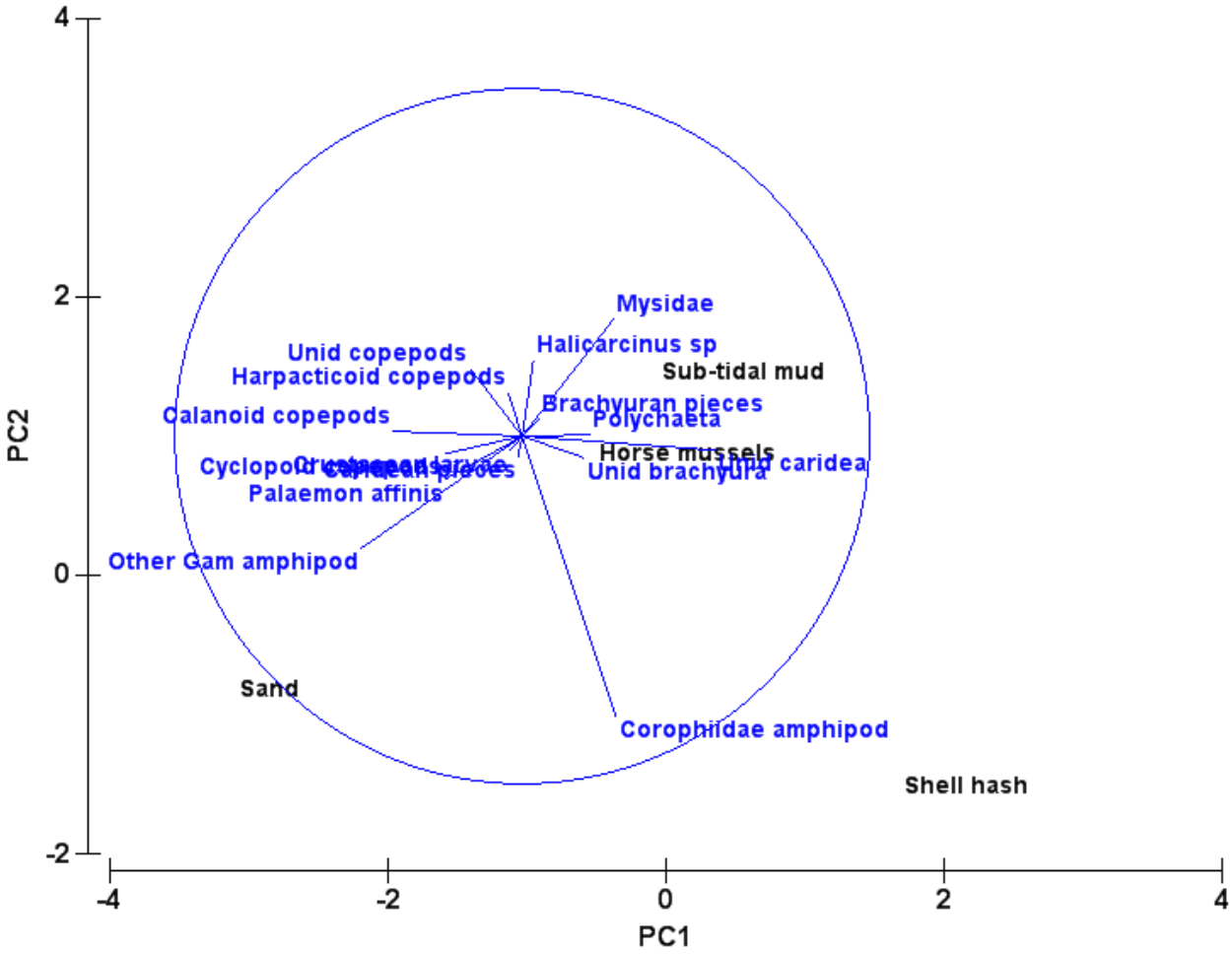


Figure 4.9 Principal components analysis of the major prey items consumed by snapper < 100 mm, over eight seasons, by habitat type. Analysis is based on square-root transformed data.

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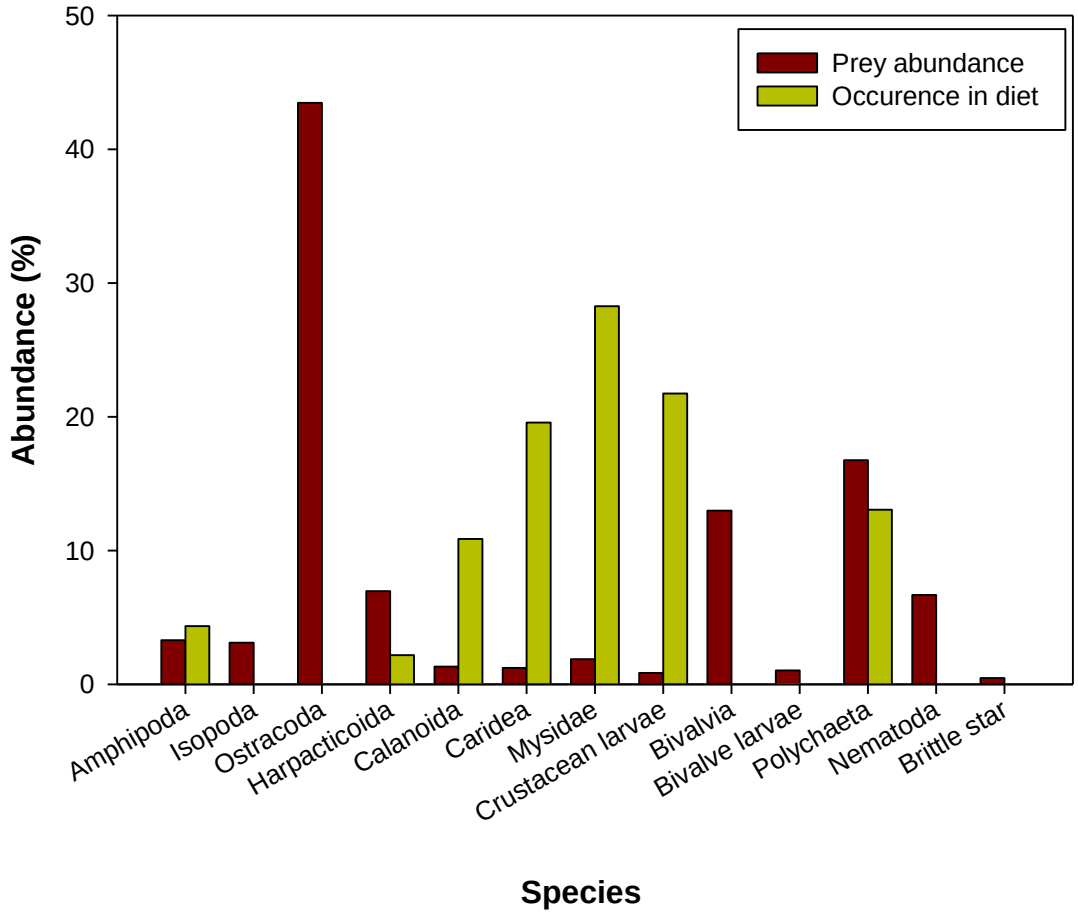

Figure 4.10 Comparison of percent abundance of prey in the Mahurangi Harbour and in the diet of snapper < 100 mm for June 2007. Abundance of prey in the environment was based on mean numbers per 200 cm^3; occurrence in diet was percent mean frequency of occurrence.

Appendices

Appendix 4.1 Percent occurrence, abundance and composition of the major prey items in the diet of small juvenile snapper 0-100 mm in size.

Prey Item	% Occurrence	% Numerical abundance	% Composition
Mysidae	55.513	31.259	24.224
Copepoda			
Unidentified copepoda	12.548	3.194	4.756
Calanoidia	37.262	19.240	19.253
Cyclopaedia	11.787	2.417	1.522
Harpacticoidia	9.886	1.969	0.967
Caridea			
Palaemon affinis	17.490	12.996	10.673
Unidentified shrimps	14.829	8.151	6.999
Caridean pieces	3.802		2.399
Brachyura			
Halicarcinus sp.	3.422	2.627	1.352
Helice crassa	0.760	0.239	0.268
Unidentified crabs	4.183	1.118	1.171
Brachyuran pieces	2.662		1.211
Crustacean pieces	6.084		3.697
Crustacean larvae	17.871	3.920	2.897
Amphipoda			
Gammaridaen	4.943	1.155	0.499
Corophidaea	6.464	4.200	0.626
Isopoda	1.141	0.746	0.037
Ostracoda	0.760	0.677	0.016
Bivalvia			
Bivalve veliger	3.422	0.845	0.113
Polychaeta			
Unidentified polychaeta	17.871	2.769	7.523
Cirritulidae	0.380	0.049	0.130
Glycerid sp.	0.380	0.062	0.045
Hesionidae	0.380	0.271	0.140
Maldanidae	0.380	0.062	0.199
Nereid sp.	0.760	0.443	0.060
Orbinid sp.	0.380	0.045	0.098
Pectineriad sp.	0.760	0.284	0.204
Chaetopterous sp.	0.760		0.330
Telostii	0.760	0.657	0.293
Algal sp.	0.380		0.152
Unidentified zooplankton	0.380		0.133
Anemone	0.380		0.306
Ascidiacea	0.760		0.023
Ophiuroidea	0.380		0.106
Acari	0.380		0.380
Eggs	3.422		2.242
Digested material	12.167		5.143
Sand	0.380		0.030

Appendix 4.2 Percent occurrence, abundance and composition of the major prey items in the diet of large juvenile-adult snapper 10-55 cm in size.

Prey Item	% Occurrence	% Numerical abundance	% Composition
Brachyura			
Macrophthalmus hirtipes	17.045	15.186	10.242
Nectocarcinus antarcticus	2.273	1.584	1.295
Hemigrapsus sp	1.136	0.168	0.168
Halicarcinus sp	9.091	8.562	4.635
Petrolisthes novaezelandiae	2.273	1.894	1.380
Helice crassa	11.364	6.448	8.239
Crab pieces	26.136		14.482
Paguridae	10.227	7.221	5.249
Mysidae	7.955	8.608	3.181
Stomatapoda	2.273	1.584	1.313
Caridea			
Unidentified shrimp	21.591	12.394	9.885
Shrimp pieces	10.227		6.066
Crustacean pieces (%)	1.136		0.487
Bivalvia			
Austrovenus stutchburyi	9.091	8.730	5.345
Venericardia purpurata	1.136	0.216	0.122
Nucula sp	4.545	4.903	2.631
Perna sp	1.136	0.152	0.055
Musculista sp	2.273	2.879	2.218
Unidentified bivalvia	1.136		0.053
Bivalve siphons	3.409	1.094	0.726
Gastropoda			
Zeaculmanthus sp	1.136	0.244	0.025
Cominella sp	1.136	0.027	0.013
Unidentified gastropoda	9.091	4.102	1.459
Ostracoda	1.136		0.076
Echinodermata			
Echinocardium sp.	1.136	0.069	0.005
Ophiuroids	3.409		0.613
Telostii	5.682	3.409	3.534
Platyhelminthes	1.136	1.515	0.090
Oligachaeta	2.273		1.479
Polychaeta			
Unidentified polychaeta	9.091	4.776	3.028
Orbinidae	1.136	1.515	0.236
Cossuridae	1.136	1.212	0.439
Green algae	4.545		0.901
Red algae	1.136		0.189
Algae mixed	1.136		0.148
Nematoda	1.136	1.371	0.045
Ascidiacea	3.409	0.138	0.424
Shell pieces	5.682		0.612
Digested material	11.364		4.196

Appendix 4.3 Summary of previous snapper diet studies within New Zealand.

Author	Year	Journal	Area	Depth	No. Snapper	Size	Major prey groups	% Occurrence/Volume	Composition of major prey groups
Thomson, M	1891	Trans & Proc Royal Soc NZ	NE NZ	NR	510	NR	Mollusca Crustacea Teleostii Hippocampus Sea-eggs		Mussels, barnacles, octopus Crayfish, crabs, shrimps
Powell, A.W.B	1937	Trans & Proc Royal Soc NZ	Hauraki Gulf	NR	3515	NR	Crustacea Mollusca Echinodermata Teleostii Salps	37.5 17.9 17.5 15	*Tawera sp., Glycymeris sp.*
Graham, D.H	1939	Trans & Proc Royal Soc NZ	Otago	NR	NR	NR	Crustacea Mollusca Teleostii		*Sardinops neopilchardus*
McKenzie, M.K	1960	Proc. NZ Ecol. Soc	Hauraki Gulf	NR	NR	NR	Crustacea Mollusca Echinodermata Polychaeta Salps		Hermit crabs Bivlaves, squid Brittle stars
Godfriaux, B.L	1969	NZJMFR	Hauraki Gulf	10-55m	1194	All	Crustacea Polychaeta Echinodermata Mollusca Mysidae Teleostii Gastropoda Urochordata	43.8 11.2 9.6 7.6 5.1 4.2 0.7 1.8	Brachyuran crabs, Hermit crabs, Shrimps, Amphipods Brittle stars, Heart urchins Bivalves, squid, octopus Ascidians, Salps
						by size < 12cm	Mysidae Megalopa Polychaeta		*Tenagomysis macropsis*
						12-30cm	Brachyura Echinodermata Natant decapods Amphipoda Anomura Other crustacea		*Hemiplax hirtipes, Hombronia depressa, Notomithrax minor* Brittle stars, Heart urchins Crangonidae, Pandalidae, *Palaemon affinis, Alpheus sp.* *Pagurus sp* (hermit crabs) Isopods, stomatopods, cumaceans, remains unid, barnacles
						30+	Mollusca Teleostii Echiuroidea Brachyura Thalassinidea		28 sp. bivalve, but major sp. *Dosinia zelandica, Anomie watery* *Sardinops neopilchardus, Engraulis australis, Trachurus novaezelandiae, Cupola antae,* eels *Hemiplax hirtipes, Hombronia depressa, Notomithrax minor* *Upogebia sp.*

Appendix 4.3 cont.									
			Mahurangi Hbr	9m	42	12-48cm	Natant decapods Urochordata Crustacea Mollusca Polychaeta Echinodermata Teleostii	 23.2 4.7 2.8 0.7 0.2	Crangonidae, Pandalidae, *Palaemon affinis, Alpheus sp.* Ascidians, Salps
Coleman, J.A	1972	NZJMFR	Hauraki Gulf	19-90m	154	5-10cm	Crustacea Polychaeta Ophiuroidea Echinodermata Other food	72.5 21 3.5 1.5 1.5	Mysidae (31%), Amphipoda (16%), Natant decapoda (10%), other (9%), Paguridae (1.5%), Brachyura (5%)
					360	10-15cm	Crustacea Polychaeta Ophiuroidea Echinodermata Other food Teleostii	68 21 5.5 1.5 1.5 1.5	Mysidae (30%), Amphipoda (15%), Natant decapoda (5%), other (10%), Brachyura (9%)
					585	15-20cm	Crustacea Polychaeta Ophiuroidea Echinodermata Other food Teleostii Mollusca Echiuroidea	45 18 13.5 3 3 2 2 13.5	Mysidae (12%), Amphipoda (13.5%), Natant decapoda (4%), other (5%), Paguridae (1.5%), Brachyura (9%)
					826	20-25cm	Crustacea Polychaeta Ophiuroidea Echinodermata Other food Teleostii Mollusca Echiuroidea	40 25 18 4.5 4 3 4 1.5	Mysidae (4%), Amphipoda (12%), Natant decapoda (5%), other (5.5%), Paguridae (1.5%), Brachyura (12%)
					1714	25-30cm	Crustacea Polychaeta Ophiuroidea Echinodermata Other food Teleostii Mollusca Echiuroidea	42.5 20 18 3 5 4.5 5.5 1.5	Mysidae (4%), Amphipoda (8%), Natant decapoda (4%), other (6%), Paguridae (4.5%), Brachyura (16%)
					1494	30-35cm	Crustacea	37	Mysidae (2.5%), Amphipoda (5%), Natant decapoda (3%), other (4%), Paguridae (4.5%), Brachyura (18%)

Appendix 4.3 cont.									
							Polychaeta	18	
							Ophiuroidea	15	
							Echinodermata	3	
							Other food	7	
							Teleostii	5	
							Mollusca	12	
							Echiuroidea	3	
					708	35-40cm	Crustacea	34	Mysidae (2.5%), Amphipoda (3%), Natant decapoda (3%), other (6%), Paguridae (5.5%), Brachyura (14%)
							Polychaeta	14	
							Ophiuroidea	10	
							Echinodermata	3	
							Other food	6	
							Teleostii	13.5	
							Mollusca	14.5	
							Echiuroidea	5	
					311	40+cm	Crustacea	28	Mysidae (1.5%), Amphipoda (1.5%), Natant decapoda (2%), other (6%), Paguridae (5.5%), Brachyura (11.5%)
							Polychaeta	10	
							Ophiuroidea	5	
							Echinodermata	1.5	
							Other food	15	
							Teleostii	17	
							Mollusca	21	
							Echiuroidea	2.5	
Russell, B.C	**1983**	**NJMFR**	**NE NZ**	**< 20m**	**23**	**26-56cm**	**Polychaeta**	**83.3/2.7**	***Aphrodite sp***
							Crabs	**66.7/30.9**	***Plagusia chabrus***
							Echinoids	**61.1/28.3**	***Evechinus chloriticus***
							Gastropoda	**22.2/16.9**	***Cookia sulcata, Haliotis virginea***
							Bivalvia	**16.7/10.7**	***Gari stangeri, Trichomusculus barbatus***
							Fishes	**16.7/3.3**	
							Hermit crabs	**11.1/0.8**	
							Chitons	**11.1/3.0**	***Eudoxochiton nobilis, Ornithochiton neglectus***
							Ophiuroidea	**5.6/2.6**	
							Euchiuroids	**5.6/0.6**	***Urechis novaezelandiae***
Lowe, M	**2008**	**Unpublished PhD thesis**	**Rangaunu Hbr**			**20-60mm**	**Copepoda**		**Calanoid copepods**
						80-100mm	**Crustacea**		**Brachyuran crabs, *Aora typica* (amphipod), *Palaemon affinis* (shrimp), Bivalves**
			Manukau Hbr			**40-100mm**	**Mysidae**		
							Crustacea		***Palaemon affinis, Pontophilus* (shrimp), *Halicarcinus sp.* (Brachyuran crab)**
							Polychaeta		
							Amphipoda		**Parakalliope, Caprellidae**
							Copepoda		***Paracalanus sp***
									Paracalanus sp, Temora turbinata, Corycacus auckandicies,*(pelagic), *Euterpra acutifrons
			Mahurangi Hbr			**< 100mm**	**Copepoda**		
							Mysidae		
							Polychaeta		

CHAPTER FIVE

General Discussion

This is the first New Zealand study to examine snapper habitat usage in an estuary over multiple spatial and temporal scales, from newly settled recruits through to large adults. Ontogenetic shifts in diet and habitat use were examined and related to potential environmental drivers and movement.

Ontogenetic shifts

Use of structure and habitat

Ontogenetic habitat shifts are common for mobile species such as fish, whose post-larvae settle from the water column to benthic habitats (Dahlgren and Eggleston 2000). Fish show differences between species in terms of ontogeny, with most fish generally fitting into one of four ontogenetic patterns associated with habitat; 1) no change in habitat associations between juveniles and adults; 2) a decrease in the number of habitats used by adults compared to juveniles; 3) an increase in the number of habitats used by adults; and 4) use of nursery areas by juveniles followed by movement to an entirely different adult habitat (Gillanders et al. 2003; Mellin et al. 2007; Lecchini and Poignonec 2009). Data from this study would suggest ontogenetic shifts by post-settlement snapper within the Mahurangi Harbour fit three of these four patterns at different scales. At the broadest spatial scale of the estuary, 1 would apply. At the intermediate spatial scale of the *a priori* habitat types, 2 would apply. At the finest scale of individual habitats, 2 would also apply. From the tagging study results, some adults also show movement to entirely different habitats outside of the harbour – therefore 4 would also apply. Ontogeny can occur at numerous scales, and therefore the scale being examined needs to be defined, especially for mobile fish. Here we are specifically discussing snapper in estuaries; ontogeny in reef habitats and other coastal environments may be very different.

The beam trawl and DUV revealed that 0+ snapper occupied different fine-scale habitats relative to other year-classes. Although only coarse structure class information

was obtained from the beam trawl, the information obtained from the DUV was similar, but more detailed. The major substrata they occupied (as determined from the DUV) were muddy to sandy habitats, containing structure in the form of sponges and horse mussels, both with and without epifauna. Fish 1+ and older were associated with a coarser substratum, which was sandy with shell grit, and with secondary structure in the form of large shell hash, then horse mussels and sponges in descending order of importance. None of the year-classes differed significantly in abundance with depth, with snapper of all sizes being found from 1 m to 20 m water depth. Smaller 0+ juveniles therefore occupied different fine-scale habitats within the harbour to the other year-classes. Horse mussels and other structure may afford shelter from predators and provide protection from currents for these smaller fish.

The > 3+ fish had the highest ratio of 10:1 in night-time use of structure relative to bare areas. These larger sized snapper often rested against the structure or within it in the case of large pits. The ratio of usage of structure to bare areas for the younger year-classes (0+ to 2+) was highest at ~ 40 cm away from the structural element. These fish appeared more active, which may mean they are using the cover of darkness to feed, yet remaining close to structure in case it is required for shelter. It is also possible that the cover of darkness means structure is not as important to these small fish as predators may be less active. For instance, 0+ Atlantic cod utilised habitat complexity less at night than day in the presence of a predator (Anderson et al. 2007). The older snapper year-classes therefore utilised areas of structure more than the smaller year-classes did, which was unexpected. However, the mechanisms of usage were likely different, with the smaller fish potentially trying to avoid predators, while the larger fish used structure as objects to physically sleep against. This pattern would not have been revealed by any other sampling method (except maybe by divers, however the cost and logistics of working in this environment would be much higher than the DUV) or by sampling during the day, as snapper were never seen/captured by the DUV in daytime sampling (Morrison and Carbines 2006, pers. obs.). This supports the argument of Rountree and Able (1997) that sampling in estuaries during the day only may underestimate an important component of the fish fauna.

An artificial reef experiment was run in the field to separate the effect of habitat structure on the recruitment of juvenile snapper from other potential variables. The

artificial units were constructed from moulds of real horse mussels with the aim of determining whether it was structure attracting juvenile snapper rather than some other factor of the environment or the explicit identity of the horse mussels themselves. Juvenile snapper were more associated with artificial horse mussels (with and without epifauna) as compared to adjacent bare areas and controls. Although the numbers of snapper recorded were low in comparison to other species, densities of snapper per unit area of artificial structure were 10 to 30-fold higher than the densities found elsewhere in the harbour over the study period. This would suggest that the structure of the horse mussels is likely to be the component utilised by juvenile snapper, rather than some other co-variable of habitat structure. A large-scale habitat manipulation on two juvenile cod species (*Gadus morhua* and *Gadus ogac*) showed abundances of both species to increase at sites enhanced with artificial eelgrass, and decrease at sites where eelgrass was removed. This result was shown in years of both high and low abundance, suggesting that these species were capable of selecting the preferred complex habitat while still in the pelagic phase, as opposed to larval supply and hydrodynamics driving habitat usage (Laurel et al. 2003).

Diet

The ability to forage efficiently can affect an individual's growth rate, which may have an impact on its vulnerability to predators and its ability to exploit certain food resources (Werner et al. 1983; Francis 1994). Estuaries that are highly productive may offer fitness-enhancing foraging opportunities, however animals often face trade-offs between foraging and avoiding predators (Dahlgren and Eggleston 2000). Dietary analysis of juvenile snapper < 10 cm showed ontogenetic shifts in diet. Snapper 1–2 cm long ate copepods almost exclusively, with a few bivalve and crustacean larvae. Snapper larger than 2 cm consumed a more diverse prey of small mysid and caridean shrimps (such as *Palaemon affinis*) and polychaetes, as copepods declined. Brachyuran crabs such as *Halicarcinus* sp. and *Helice crassa* and amphipods were taken by the larger juveniles (~ 6 cm).

Stomach analysis of juveniles < 10 cm showed snapper had similar prey items in their guts across all *a priori* habitat types. Therefore, all *a priori* habitat types were considered similar in terms of the prey items important to juveniles. This also suggested

that the structure of these habitats, rather than the prey assemblages they supported, was the most likely factor affecting densities of small snapper. Snapper larger than 25 cm (3+ and greater) consumed a wide variety of prey, dominated by brachyuran crabs, caridean shrimps and polychaetes, bivalves and hermit crabs. Although hermit crabs were taken by snapper larger than 25 cm, they were the dominant prey item in the diet of snapper 350–400 mm. For snapper > 10 cm, there were significant seasonal differences driven by a greater diversity of prey consumed over the warmer months. No two seasons were similar, however, indicating that as snapper grow; they become more opportunistic feeders, taking a wider variety of prey.

There were no seasonal differences in the prey species that juvenile snapper (1–10 cm) consumed. Fullness of the gut however did differ seasonally, with approximately two-thirds less in the stomachs of juvenile snapper in spring (September) each year. Increased feeding over warmer months is thought to be due to increased metabolic rate and somatic growth, which means increased demands for energy (Godfriaux 1969; Colman 1972). This demand for energy is thought to slow down as snapper increase in size and with lower water temperatures (Godfriaux 1969; Colman 1972; Francis 1997) and may explain why gut fullness was also less for snapper > 10 cm in size over the cooler months.

Spatial and temporal differences

Temporal variations in abundance were apparent over most year-classes, particularly for the 0+, 1+ and > 3+ year-classes, with the two years of sampling showing very different patterns. Snapper are serial spawners, which can lead to multi-modal recruitment (Crossland 1977; Crossland 1981; Scott and Pankhurst 1992; Francis 1994) as observed in this study. Strong annual and inter-annual variability in juvenile recruitment within Japan, Australia and New Zealand has consequently influenced variability in year-class strength, which has a flow-on affect on the fishery (Azeta et al. 1980; Francis 1993; Fowler et al. 2005). Highest densities of juveniles sampled by the beam trawl were recorded in March of both years, with the average density of 0+ fish in 2007 being twice that of 2006. Similar temporal patterns were found for the > 3+ snapper (using DUV), with higher abundances of this year-class over the warmer months, especially March 2007, and lower abundances over winter. It is thought that snapper seasonally migrate

from deeper to shallow coastal waters over summer due to water temperature changes and/or the formation of spawning aggregations (Crossland 1976; Paul 1976; Francis 1993; Sumpton et al. 2003). Strong seasonal patterns in abundances of adult snapper have been observed around reefs in north-eastern New Zealand, with densities in autumn nearly double those in spring (Willis et al. 2003; Denny et al. 2004). It is therefore possible that the higher numbers of > 3+ snapper within the Mahurangi over the summer of 2006–2007 were spawning within the lower harbour and may have contributed to the doubling of the numbers of new recruits by March 2007.

Growth shifts through to the next year-class could be seen from the DUV data, especially for the 0+ and 1+ year-classes. The 1+ fish were more widely spread throughout the harbour, moving out into the subtidal mud and intertidal habitats and becoming less strongly associated with structure than the other year-classes. However, the ratio of association of structure to bare areas was still 2.5:1 indicating that even in these muddy, less structured habitats, small snapper were still finding and utilising small patches of structure. This shift into less structured habitats by the 1+ year-class may be indicative of increasing their home range with growth and in doing so, increasing their foraging opportunities**.** Snapper between the sizes of 10–15 cm (1+ year-class) also switched to a diet consisting of brachyuran crabs (*Macrophthalmus hirtipes* and *Helice crassa*) and large mysid shrimps.

No obviously high numbers could be seen moving through to the 2+ year-class from the 1+ year-class. It is possible that many of these fish died, were preyed upon, emigrated, or were not captured by the DUV. However, 0+ snapper densities were higher at this time from the DUV, and so it is thought that not being detected by DUV was unlikely, given the numbers of smaller fish being detected. High rainfall occurred from June to September 2006, with a corresponding increase in turbidity from September to December 2006, especially in the upper part of the harbour. The increased abundance of 1+ fish in subtidal mud and intertidal areas included these upper reaches, fish in the more turbid water may have died. Higher levels of suspended sediments can negatively affect juvenile snapper by increasing respiration, decreasing activity including feeding, reducing condition, and eventually increasing mortality (M. Lowe, unpublished data). Emigration from the harbour is also a possibility, as previous work has shown that at around 2+, snapper move away from nursery areas and out onto the coast (Gillanders

2002; Morrison et al. in review). Tagging studies and otolith research from south Australia have found snapper moved from nursery areas at around 3 years of age and redistributed themselves throughout various State waters (Fowler et al. 2005). From the age of six it was thought these fish then become resident in the regions to which they had moved (Fowler et al. 2005). Tropical snapper (*Lutjanus russelli*) are known to utilise estuaries as juveniles (defined as fish with immature gonads, up to 21 cm), then move offshore as they get older (Sheaves 1995a). Snapper from the year-class 2+ and greater are found within the inner and outer Hauraki Gulf areas at < 50 m depth, but have been captured at depths > 50 m (Colman 1972; Paul 1976; Francis 1995). These snapper are either moving into the Hauraki Gulf from more sheltered areas or are recruiting to these areas from the plankton and surviving. However, these types of movement patterns from estuaries and sheltered coastal bays to the outer coast are not well understood for snapper in New Zealand.

Movement

Tagging studies from Australia and New Zealand have shown that a large proportion of tagged snapper are recaptured close to their release point, with only a small proportion of fish moving greater distances (Crossland 1976; Parsons et al. 2003; Sumpton et al. 2003; Egli and Babcock 2004). This has been interpreted as implying either that a large proportion of the snapper population is resident within a location or that annual spawning migrations offshore to onshore occur with a fairly high degree of fidelity to spawning grounds from year to the next (Moran et al. 2003). As snapper are a mobile species, some individuals may be using the harbour at night as a place to rest and making daily excursions out, while others may remain in the harbour within established home ranges.

Results from the tagging component of this study support this theory, with 80% of the snapper recaptured within the harbour from 100's of metres to up to 2 km from the original tagging location. Of the 20% recaptured outside the harbour only 8.6% (3 fish) moved up to 100 km away. Snapper may make daily movements out of the harbour and use the harbour at night as a place to rest. The higher numbers of > 3+ snapper utilising areas of structure support this theory, with the surrounding structure potentially providing protection for snapper from wave movement as they rest. In a previous study,

tagging of snapper using acoustic transponders within the Mahurangi revealed 20 of the 28 fish tagged were detected for up to 70 days within the array of receivers, with daily movements suggesting a relatively restricted home range (Hartill et al. 2003). This methodology is limited to larger animals and to the distance of the array, yet provides an important tool for improving our understanding of fish habitat usage (Hartill et al. 2003). Telemetry technology is advancing rapidly and may soon become a viable alternative for very small animals (Gillanders et al. 2003). New approaches will be required to enable us to gain a better understanding of actual movements around and out of the harbour and out to the open coast.

Potential anthropogenic effects and their impact for fish

Anthropogenic impacts can affect estuarine environments by altering habitats and contributing to changes in community structure and dynamics (Kennish 2002; Caddy 2007). In many regions of New Zealand, estuaries are vulnerable to sedimentation, in particular from land-based activities such as agriculture, forestry and increased development (Morrison et al. 2008). Long-term monitoring (11.5 years) within the Mahurangi harbour has seen a change in the ecology of the estuary consistent with increased sediment loading (Cummings et al. 2005). At a number of sites in the Mahurangi, densities of the cockle, an intertidal bivalve (*Austrovenus stutchburyi*) have decreased. Cockles were a large component of the diet for snapper > 25 cm and were consumed proportionally more than a number of other potential bivalve prey items. However, in the last few years, peaks of recruitment-sized individuals of intertidal bivalves (cockles) have been found at some sites, which emphasises the potential for recovery (Cummings et al. 2005). Horse mussels and sponges comprise biogenic structure and exist in numerous areas of the harbour providing structural complexity. They can provide refuges from predation, modify boundary flow and act as substrata for settlement of epifauna (Cummings et al. 1998). These areas of structure have been shown to be utilised by all sizes of snapper, but particularly juveniles in the 0+ year-class. Both horse mussels and sponges are sensitive to increased sedimentation (Ellis et al. 2002; Hewitt and Pilditch 2004; Lohrer et al. 2006a). At subtidal sites there has been no increase in horse mussel densities, with existing populations showing slow growth (Cummings et al. 2005). Therefore, further increases in sedimentation to this estuary may adversely affect these biogenic structures, which may in turn result in a loss of

habitat utilised by snapper. Increasing sedimentation to the harbour from the surrounding catchment has been recognised as an issue by various stakeholders. As a result, the Auckland Regional Council (ARC), in conjunction with Rodney District Council (RDC), launched in 2004 a community based project called the Mahurangi Action Plan to help reduce erosion and the amount of sediment entering the harbour (Auckland Regional Council 2004).

Size selectivity of the different methods

It is widely acknowledged that the estimation of fish abundances and associated population size structures is almost impossible to achieve without some form of bias or variability across methods (Andrew and Mapstone 1987; Rozas and Minello 1997; Underwood et al. 2000). A previous study in the Mahurangi Harbour examined a number of different sampling methods, and the two best suited to sampling snapper were the beam trawl and the dropped underwater video (DUV) (Morrison and Carbines 2006). The beam trawl was most effective for juvenile snapper in the range 1–8 cm (0+ year-class) and the DUV was most effective for snapper greater than 5 cm. Therefore, in my study the two methods were used in combination to provide a more complete picture of snapper distribution and abundance.

Because two methods were used, each best suited to different sized snapper, and because sampling was done at different times (day vs. night), the first two chapters of this thesis were divided according to method. 0+ snapper abundance decreased over the year and by the end of the calendar year, snapper were at the upper end of the 0+ year-class size range (~ 8–11 cm) and were more likely to evade the beam trawl. Within the *a priori* habitat types, the highest juvenile snapper densities occurred over sand in March, but after March very few fish were caught there. The DUV data shows, however, that there were 0+ snapper over the sand after March, with September 2006 in particular having densities similar to March 2006. For smaller fish, there is the potential to hide within or around structure, which may not be able to be sampled by the beam trawl, adding another potential bias to the sampling.

The corresponding analysis of the DUV data for the 0+ year-class showed the opposite trend, with abundance increasing over the year (Figure 1). The sampling by Morrison

and Carbines (2006) was over one season (autumn 2004), so it was unclear how the abundance from both methods might change over time. Combining both abundance estimates from the beam trawl and DUV over each sampling season, however, confirmed the argument of Morrison and Carbines (2006) that the DUV under-samples snapper less than 5 cm (Figure 1). Therefore, to get the best understanding of densities and abundance of small juvenile snapper less than 5–7 cm, the beam trawl is the most appropriate method to use, although only broad-scale information about corresponding habitat associations can be obtained, given the integrating nature of the tow. In contrast, the DUV can provide much finer-scale habitat information, but the potentially cryptic nature of small snapper less than 5 cm means that their densities will be significantly underestimated. Both methods therefore, have their corresponding advantages and disadvantages when sampling 0+ snapper. The DUV becomes an increasingly more effective tool for this year-class as the fish grows, and is most suited for use over the winter (June) through to the end of each year. This highlights the importance of selecting an appropriate sampling methodology or using a combination of methods based on the hypothesis being posed.

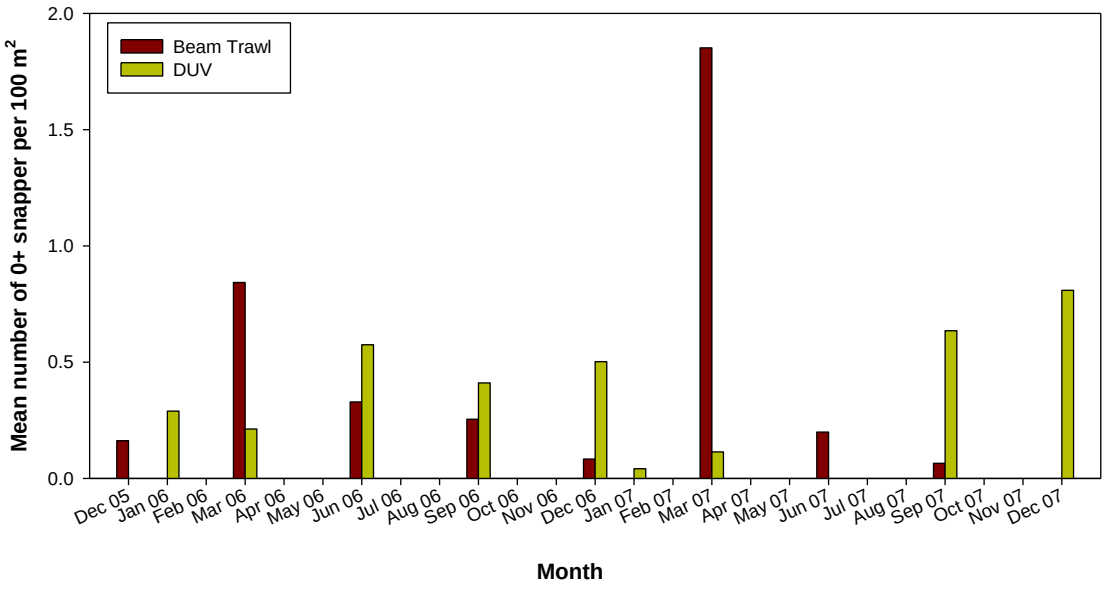

Figure 1. Mean number of snapper per 100 m^2 in the 0+ year-class (1–11 cm) from the beam trawl and DUV sampling over the two years of data collection. Months with only one bar are where only one sampling methodology was used, months with no bars shows months when no sampling was completed by either method.

Conclusions

The Mahurangi Harbour is utilised by all year-classes of snapper, from 1 to 60 cm. High densities of juveniles enter or are spawned within the harbour and settle over the warmer months. Ontogenetic shifts in fine-scale habitat and diet occurred between year-classes. The fine-scale habitat the 0+ fish occupied was different from the larger snapper, with muddy to sand substrata, and structure consisting of sponges and horse mussels. The older year-classes tended to occupy a coarser substratum with shell hash as the major secondary structure. An experiment utilising artificial horse mussels showed that densities of small snapper were higher on the experimental units with structure, than on bare areas or control plots. Therefore, it is likely to be the actual structure of the horse mussels that is important, rather than some other factor of the environment or the live horse mussels themselves.

The 1+ year-class increased their habitat range, occupying more subtidal mud and intertidal areas. A growth shift through to the 2+ year-class was not clear, and this may be due to increasing mortality, either natural or through predation, or emigration out of the harbour. Turbidity in the harbour may have an impact on the natural mortality rate of juvenile snapper. Densities of the larger year-classes (3+ and greater) decrease over the cooler months but not all these fish leave permanently, with tagging showing up to 80% of fish to be resident. Snapper may make daily movements out of the harbour and use the harbour at night as a place to rest. The higher numbers of > 3+ snapper utilising areas of structure support this theory, with the surrounding structure potentially providing protection from currents for snapper as they rest.

There was a clear shift from the consumption of planktonic copepods (< 2 cm) to a more varied diet of benthic copepods, mysid and caridean shrimps and polychaetes as fish grew (2–10 cm). Snapper > 100 mm consumed a wide variety of prey, dominated by brachyuran crabs, caridean shrimps, bivalves, polychaetes and hermit crabs, with the larger fish (> 30 cm) able to consume harder-shelled molluscs and bivalves. The habitat types studied within Mahurangi Harbour had similar prey taxa that were utilised by small juvenile snapper, and this may be advantageous for small snapper who can then select a particular habitat for other qualities, i.e. protection from predation. The large

snapper > 10 cm showed differences in diet seasonally, but all seasons differed in prey composition showing how opportunistic snapper are as a species.

Despite the ability of snapper to utilise any sort of existing structure as cover or for sleeping against, the major forms of structure utilised within the Mahurangi are biogenic and therefore susceptible to anthropogenic effects, especially increased sedimentation. Sedimentation has been found to impact the Mahurangi Harbour, particularly bivalves, although some recovery has been seen in cockle populations. The loss or decline of these biogenic structural species may therefore have a significant impact on the way snapper utilise the Mahurangi Harbour. The juveniles in the year-class 0+ in particular could lose an important component of habitat that may protect them from predators, and increased mortality could have a flow-on effect to the harbour as a whole, and in turn potentially the surrounding snapper fishery. This component is unknown, and could serve as the basis for future research.

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