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# **The composition and resilience of rockpool fish assemblages on the Central Hawke's Bay coast, New Zealand**

A thesis presented in partial  
fulfillment of the requirements  
for the degree of  
Master of Science in Ecology

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New Zealand

**Nathan John Glassey**

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## Errata Sheet

- 1) Misspelled word

“*Bellapiscus medius*” should read “*Bellapiscis medius*”

- 2) Cited literature omitted from Chapter 6:

Jones.G.P., Symes.C. (1998). Disturbance, habitat structure and the ecology of fishes on coral reefs. Australian Journal of Ecology. 23. 287 – 197.

## Abstract

Fish assemblages in rockpools on two intertidal platforms on the Central Hawke's Bay coast of New Zealand were studied from June 2000 to March 2001. Twenty-four species belonging to 14 families were collected from 226 rockpool censuses. The Tripterygiidae were the most speciose family, represented by 7 species. Fifty-seven percent of the total number of fish captured ( $n = 6133$ ) belonged to a single species, the robust triplefin *Grahamina capito*. Common subtidal species contributed significantly to the taxocene, indicating that much of the rockpool fish fauna is an extension of that in the shallow subtidal fringe. However, two specialist intertidal species (*Acanthoclinus fuscus* and *Bellapiscus medius*) were relatively abundant in the collections.

Significant relationships between rockpool fish assemblage structure, and rockpool habitat structure were discovered. Richness, abundance and biomass were generally greater in large pools with lots of shelter, located close to the low-tide mark. Further analysis revealed that assemblages in these pools contained many partial residents that were uncommon or absent from rockpools higher on the shore. Seasonality in the structure of rockpool fish assemblages was related primarily to recruitment events. During late spring and early summer, the abundance and density of resident species increased markedly as the result of an influx of settling larvae. However, species richness remained stable over the sampling period, probably because transient subtidal species (with the exception of the labrid, *Notolabrus celidotus*) did not contribute significantly to the rockpool fish community.

The rockpool fish community appeared to be resilient: taxocene structure re-established between collection events. However, the level and rate of resilience appeared to be lower than described in other studies, as the effects of sampling were still measurable after 3-months. The recovery of richness, abundance and biomass of fish was seasonally dependent, being slow in winter and spring, but rapid during summer. Specialist intertidal species were generally the best recolonisers, whereas partial resident species were poor recolonisers, and relied mainly on larval recruitment to colonise rockpools.



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## Chapter 1: General Introduction

### 1.1) Community ecology in the rocky intertidal zone

The rocky intertidal zone has been an important study system in the development of ecological theory. There are a large range of easily accessible sessile organisms that has made it a favourable habitat for conducting experiments and indeed the majority of ecological studies in the rocky intertidal zone have concentrated on slow-moving and sessile taxa, especially on emergent substrata (e.g. Dayton 1971; Sousa 1979, 1984; Underwood 1980; Paine & Levin 1981; Deither 1984; Farrell 1991; Menge 1991; Coates 1998; Dye 1998; Keough & Quinn 1998). The importance of biotic factors such as herbivory, predation and competition in the spatial structuring of these communities is well documented (Menge 1976; Petraitis 1990; Wootin 1992; Dye 1995). Likewise, the role that recruitment and settlement variability (Lewis 1976; Caffey 1985; Raimondi 1988; Dye 1990), physical disturbance (Dayton 1971; Paine & Levin 1981; Deither 1984; Sousa 1984, 1979), and environmental heterogeneity (Menge 1976; Menge & Lubchenco 1981; Menge *et al.* 1985) play in rocky intertidal community organisation has been described in a number of studies.

The upper limits of species distributions on emergent substrata are mostly determined by tolerance of long periods of desiccation or freezing associated with the tidal cycle (Metaxas & Scheibling 1993). Where space is limiting, physical disturbance (e.g. impact of drifting logs or the shearing force of large waves) maintains species diversity by creating open space that is spatially and temporally variable (Dayton 1971; Paine 1994). Holes and crevices in rock provide refuge from desiccation, physical disturbance and predation (Menge 1976; Menge *et al.* 1985), and heterogenous rock surfaces have been shown to promote diversity of sessile organisms (Menge & Lubchenco 1981). These factors set the framework and define the limits over which the various life stages of a particular species can exist, but patterns of local distribution are modified by a complex series of biological interactions (Knox 2001). Intra- and interspecific competition for food and space can have negative effects on growth and survival (Branch 1975; Underwood 1979; Choat 1977; Underwood *et al.* 1983); predation can prevent the establishment or persistence of populations (Luckens 1970; 1976) or

promote coexistence by the removal of competitive dominant individuals (Connell 1961); grazing can decrease or promote algal biomass and diversity depending on intensity (Branch *et al.* 1992). Research has also determined that the availability and/or settlement of planktonic larvae and algal propagules usually varies in space and time and that this may effect the type of interactions that develop post-settlement as well as the abundance and distribution of adult populations (Gaines & Roughgarden 1985; Lewin 1986; Caley *et al.* 1996).

Intertidal rockpools are a conspicuous part of rocky shores world-wide but in the ecological literature, the biota of these pools has received far less attention than the biota on emergent substrata (Mextaxas & Scheibling 1993). Underwood (1981) even suggested that rockpools do not represent an intertidal habitat since the biota inhabiting pools are not emersed during low tide. However, rockpools do not confer the relative stability of the subtidal environment and during the ebb tide, environmental conditions can vary considerably. Insolation, freshwater (rain or streams), and extreme cold can alter rockpool temperature, salinity, pH, and dissolved oxygen. These changes are influenced by the tidal position of a pool (which determines the length of emergence) and also by physical factors including surface area, depth, volume and shading (Daniel & Boyden 1975; Morris & Taylor 1983; Huggett & Griffiths 1986). Consequently, physicochemical change during low tide is more pronounced in small, high-shore pools.

Because the environmental conditions of rockpools depend on physical factors such as pool size as well as pool tidal position, the spatial distribution of organisms in rockpools are to some extent 'azonal' (Zander *et al.* 1999). However, a number of studies have described patterns of zonation of rockpool algae and invertebrates along intertidal height gradients, including a decrease in biomass and diversity in pools with increasing height above low water (Goss-Custard *et al.* 1979; Femino & Mathieson 1980; Sze 1980; Huggetts & Griffiths 1986). Other studies have shown that rockpool community structure is correlated with physical factors of pools including wave exposure, surface area, depth and volume (Sze 1980; Dethier 1984; Fairweather & Underwood 1991; Mgaya 1992; Metaxas *et al.* 1994). In general though, the variability in community structure among rockpools is larger than that on emergent substrata, with pools at the same height on the shore showing large variability in species composition and abundance (Knox 2001).



The few studies that have examined seasonality of community structure in rockpools have concentrated mainly on algae and fish. Seasonal change in the abundance of different algal taxa appears to be species-specific (Femino & Mathieson 1980; Deither 1982; Underwood & Jernakoff 1984) while the abundance of fish in rockpools appears to be inversely related to temperature (Thompson & Lehner 1976; Grossman 1982).

As on emergent substrata, biological interactions modify local distribution patterns determined by the physical factors mentioned above. However, rockpools are patchily distributed on rocky shores and within the limited space in pools, interactions are generally more intense than on emergent substrata (Metaxas & Scheibling 1993). Competitive dominance in rockpool algal assemblages has been documented (Lubchenco 1982; Chapman 1990; Chapman & Johnson 1990), although grazing by littorinids, limpets and echinoderms has been found to limit algal distribution, diversity and abundance (Paine & Vadas 1969; Lubchenco 1978; Underwood & Jernakoff 1984; Chapman 1990; Chapman & Johnson 1990). Other studies have shown that predation by whelks, crabs and fish may control the population size of rockpool littorinids, limpets, barnacles, tubeworms and copepods (Lubchenco 1978; Dethier 1980; Fairweather 1987). Information on the influence of recruitment variability in rockpools is sparse, but Dethier (1980) attributed part of the variability in recovery of a rockpool community (post-disturbance) to the irregularity of planktonic recruitment. Likewise, there is little information on the effect of physical disturbance in organising rockpool communities. Deither (1984) found that the rate of recovery from disturbance of surfgrass and some invertebrate species depended upon the magnitude of disturbance and varied among species. Moring (1996) observed a decrease in mussel, fish and algal abundance in 3 rockpools following two hurricanes but determined that the effects were relatively short-term.

Intertidal rockpools may be useful systems to develop and test ecological models and theories because they have well-defined boundaries, they can be easily manipulated and they are of manageable size (Metaxas & Schiebling 1993). In particular, they provide ideal habitat to examine island biogeography theory (MacArthur & Wilson 1967), metapopulation dynamics (Bengtsson 1993; Bengtsson & Ebert 1998) and habitat segregation (Davis 2000).



## 1.2) Rocky intertidal fish

Factors regulating the taxonomic and numerical composition of fish in marine habitats have received increasing attention (Gibson 1969; Bennett & Griffiths 1984; Choat & Ayling 1987; Choat *et al.* 1988; Carr 1991; Connell & Jones 1991; Prochazka & Griffiths 1992; Mahon & Mahon 1994; Chabanet *et al.* 1997; Ault & Johnson 1998; Davis 2000; Silberschneider & Booth 2001) but there is no firm evidence on the relative importance of different mechanisms (e.g. competition, predation, habitat complexity) likely to shape rocky intertidal fish communities (Faria & Almada 2001). Studies have focused on the role of competition and habitat partitioning in these communities (Mayr & Berger 1992; Davis 2000), others have looked at patterns of community stability and resilience (Thomson & Lehner 1976; Grossman 1982, 1986; Willis & Roberts 1996), while others have examined spatial patterns of community organisation in relation to habitat variables including height above low water (Gibson 1972; Yoshiyama 1981), shelter availability and habitat complexity (Bennett & Griffiths 1984; Behrens 1987; Prochazka & Griffiths 1992).

Fishes that occupy the marine intertidal zone have proven to be difficult to classify in terms of their use of this habitat (Gibson 1982; Horn *et al.* 1999). Some species live there for almost all their lives, others enter to forage during the high-tide, and others may use the intertidal zone to complete only part of their life-history (Gibson & Yoshiyama 1999). Several attempts have been made to classify intertidal fish based on the duration of their occupancy (Gibson 1969; Thomson & Lehner 1976; Grossman 1982; Mahon & Mahon 1994). They all make a distinction between permanent inhabitants and others that are present for varying lengths of time. *True* (Gibson 1969), *typical* (Breder 1948), or *primary* (Thompson & Lehner 1976) *residents* are small, cryptic forms that show morphological, physiological, and behavioural adaptations to intertidal life and are rarely found below low water. They settle intertidally as larvae and grow, reproduce and die there (Gibson & Yoshiyama 1999). *Partial* (Gibson 1969) or *secondary* (Thompson & Lehner 1976) *residents* include species whose main distribution is subtidal but may occur intertidally, particularly as juveniles (Mahon & Mahon 1994). The term '*transient*' has sometimes been used to describe this group (Potts 1980) but is more commonly associated with pelagic fish that visit the intertidal zone during high-tide (Thompson & Lehner 1976), usually to feed (tidal visitors;

Gibson 1969). *Accidental species* (Gibson & Yoshiyama 1999) are rarely found and usually represent pelagic fish stranded on the falling tide.

As well as variation in the use of intertidal habitat, intertidal fish diverge in body shape and behaviour due to their different dependence on the benthic environment (Zander *et al.* 1999). For resident species, adaptations are required because the intertidal zone is typically turbulent and undergoes marked fluctuations in environmental conditions associated with the tidal cycle (Gibson 1982; Horn *et al.* 1999). Resident fish are generally small, negatively buoyant, and thigmotactic (Gibson 1969, 1982; Paulin & Roberts 1992; Willis & Roberts 1996; Kotrschal 1999), remaining close to the substrate and utilizing rock crevices. Behavioural adaptations such as homing ability (Gibson 1967; Green 1971a; Berger & Mayr 1992; Yoshiyama *et al.* 1992) allow resident fish to respond to changes in their physical environment, particularly during the ebbing tide, by moving to a rockpool refuge. For fish remaining in rockpools during the low tide, changes in environmental conditions can be large, and physiological tolerance to these changes have been described for a number of intertidal species (Nakamura 1976a,b; Horn & Riegle 1981; Graham *et al.* 1985; Brix *et al.* 1999; Zander *et al.* 1999; Fangué *et al.* 2001).

Intertidal fish communities around the world are composed of resident fish and typically subtidal species (Thompson & Lehner 1976; Christensen & Winterbottom 1981; Grossman 1982; Varas & Ojeda 1990; Mahon & Mahon 1994; Willis & Roberts 1996). The relative importance of each group varies between locations (Gibson & Yoshiyama 1999) but comparisons are difficult because community composition varies seasonally (Beckley 1985a,b, 2001; Bennett 1987; Willis & Roberts 1996) and depends on the type of intertidal habitat sampled. Within localities, low shore and large rockpools are more diverse and typically harbour more partial residents and transient species (Bennett & Griffiths 1984; Prochazka & Griffiths 1992; Mahon & Mahon 1994), testimony to the relative stability and similarity to the subtidal of environmental conditions in large, low-shore pools. Fish inhabiting smaller pools will generally be subject to larger environmental fluctuations, and may be more vulnerable to predation and physical agitation by currents and waves (Neider 1993; Mahon & Mahon 1994). Rockpool complexity and the amount of shelter available have also been found to be positively correlated with diversity and abundance of fish (Marsh *et al.* 1978; Bennett & Griffiths

1984; Prochazka & Griffiths 1992; Neider 1993). In addition, a number of studies have demonstrated intra- and interspecific habitat partitioning in rockpool fish assemblages whereby different age classes or species occupy pools of different sizes, tidal positions, habitat complexity, and substrate types (Nakamura 1976a,b; Mayr & Berger 1992; Davis 2000; Faria & Almada 2001). Few studies have directly examined the role of biotic interactions in the organisation of these communities. The impact of predation from within the community is generally considered to be insignificant (Gibson & Yoshiyama 1999), although Bennett & Griffiths (1984) suggested that predation from fish foraging at high tide and birds during the low tide might be sufficient for cryptic behaviour to be advantageous in evolutionary terms. There is more uncertainty about the role of competition. Nakamura (1976b), Mayr & Berger (1992) and Davis (2000) suggested that microhabitat partitioning in rockpool fish assemblages was a mechanism that reduced competition. However, Faria & Almada (2001) suggested that microhabitat partitioning could also be achieved from niche divergence related to differences in life history and, in addition, agonistic behaviour (usually related to access to shelter) has been demonstrated in a number of rockpool fish assemblages (Marsh *et al.* 1978; Mayr & Berger 1992; Faria *et al.* 1998).

As well as being spatially variable, studies have shown that there is a large temporal component to the structure of intertidal fish communities. On a short time-scale, the structure of these communities changes with the influx of subtidal fish during the flood tide (Thompson & Lehner 1976; Black & Miller 1991). Seasonal change in community structure is pronounced, and in most communities is related to an influx of larval fish following breeding seasons (Moring 1986; Bennett 1987; Willis & Roberts 1996) and the presence or recruitment of more transient and partial resident species during summer months (Ali & Hussein 1990; Beckley 2000). The influence of transient species on community structure is illustrated by Prochazka (1996), who noted that because of their year round absence from an intertidal community on the west coast of South Africa there was no seasonal variation in species diversity and density. The limited number of studies that focus on longer time scales tend to suggest that intertidal fish are a persistent part of the intertidal biota, in that community structure is similar from year to year despite slight fluctuations in species abundances and ranks (Grossman 1982, 1986; Collette 1986; Lardner *et al.* 1993) that reflect variable spawning or recruitment success (e.g. Yoshiyama *et al.* 1986). Related to the topic of persistence of community structure

is that of stability and resilience (Gibson & Yoshiyama 1999). Resilience refers to the ability of a community to return to its original composition following a disturbance, and a high level of resilience confers stability to an ecological community (Dayton *et al.* 1984). It is not known how often rockpools are disturbed, but the mobility of fish relative to other components of the intertidal zone allows communities to recover by movement of fish from unaffected areas. Intertidal fish communities have been shown to recover from natural disturbances (Thompson & Lehner 1976; Moring 1996) and periodic defaunation (sampling) (Grossman 1982; Willis & Roberts 1996) so appear to be resilient to perturbations to community structure. Fish start recolonising defaunated pools within 1 tidal cycle, but full recovery is generally considered to take up to 3 months (Collette 1986; Willis & Roberts 1996; Polivka & Chotkowski 1998). Few studies have focused on seasonal variability in the rate of recovery but Beckley (1985b) and Willis & Roberts (1996) showed that communities were generally slower to recover during winter. Fewer studies still have focused on spatial scales of disturbance but communities may take longer to recover following large-scale perturbations (Barber *et al.* 1995).

### 1.3) New Zealand intertidal fish

In New Zealand, no fish is restricted to the intertidal zone (Paulin & Roberts 1992) although Paulin & Roberts (1993) identified 3 species that occur primarily in pools and could therefore be considered true residents. Most population and community-level studies of fish that do occur in New Zealand rockpools have been conducted in subtidal habitats (Thompson 1979; Jones 1984a,b; Choat & Ayling 1987; Duffy 1988; Kingsford *et al.* 1989) where most taxa are probably more abundant. Other studies of New Zealand rockpool fish have focused on taxonomy (Fricke 1994; Clements *et al.* 2000), geographical distribution patterns (Paulin & Roberts 1993; Francis 1996), physiology (Davison 1984; Innes & Wells 1985; Hill *et al.* 1996; Brix *et al.* 1999) or interactions between a small number of species (Berger & Mayr 1992; Mayr & Berger 1992). Community-level studies in rockpools have proved difficult due to the cryptic nature of intertidal fish assemblages and taxonomic difficulties (Willis & Roberts 1996) and in general, the community-level dynamics of fish in New Zealand rockpools are largely unknown.

On the Hawke's Bay coast (North Island, New Zealand) most of the information that exists on rockpool fish communities is qualitative (Creswell & Warren 1990; Duffy 1992; Roberts & Stewart 1992) and included only in species inventories. The Hawke's Bay rockpool fish fauna, and that of New Zealand in general is dominated by the family Tripterygiidae, whereas in overseas locations different families dominate (South Africa – Clinidae, North America – Cottidae, Atlantic and Mediterranean – Blenniidae, Gobiidae) (Gibson & Yoshiyama 1999). As most ecological studies of rockpool fish are from non-New Zealand locations, it would be interesting to see if the community dynamics of a fauna dominated by the Tripterygiidae conform to patterns described elsewhere. However, without quantitative information, it is difficult to examine the relative importance of different mechanisms likely to shape these rocky intertidal fish communities. The present study proposes to address the lack of information on New Zealand rockpool fish communities by:

1. describing the rockpool fish fauna on two intertidal reefs in Central Hawke's Bay, New Zealand (Chapter 2);
2. determining the nature of the relationship between rockpool fish assemblage structure and physical characteristics of rockpools (Chapter 3);
3. examining seasonality in community structure (Chapter 3) and;
4. examining the response of rockpool fish to disturbance (removal) to determine the resilience and stability of assemblage structure (Chapter 4).<sup>1</sup>

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<sup>1</sup> In this study, a rockpool is a crack or depression in the intertidal platform that is isolated from the open ocean during low tide. This does not include surge guts, channels and pools that are constantly flushed with water from the sea swell.



## **Chapter 2: Study area, methodology and description of the fish fauna**

### **Abstract**

The fish fauna in 96 intertidal rockpools on the Hawke's Bay coast, New Zealand was censused between June 2000 and March 2001 to determine the taxonomic and numerical composition of the community. Twenty-six of these rockpools were repeatedly censused to examine the resilience of the assemblages as part of Chapter 4. From a total of 226 census occasions, 6133 fish from 24 species and 13 families were collected. The triplefins (Tripterygiidae) were the dominant family (7 species, 70% of individuals and 64% of biomass). Other common families included the clingfish (Gobiesocidae), rockfish (Plesiopidae) and weedfish (Clinidae). Most of the species collected were small, cryptic resident fish but juveniles of common reef species were also collected. All species collected have been reported from subtidally fringing habitats in New Zealand suggesting there is a large subtidal component to the Central Hawke's Bay intertidal fish fauna. Recruitment events accounted for seasonality in abundance and biomass, but species richness did not change over the census period. The collections in the present study are compared to those made in previous studies in the Central Hawke's Bay, and the distributional affinities of the fauna are discussed. An assessment of the census technique is also presented.

### **2.1) Introduction**

#### **2.1.1) New Zealand rockpool fish fauna**

The New Zealand rockpool fish fauna is relatively speciose ( $n = 94$ ) and exhibits a high degree of endemism (61.7%) (Paulin & Roberts 1992, 1993). Most of the rockpool fish fauna is widely distributed in New Zealand waters (59.6%), with smaller northern (29.8%) and southern (10.6%) components (Paulin & Roberts 1993). Cook Strait is generally regarded as the region where northern and southern species overlap (Moreland

1959; Francis 1988; Paulin & Roberts 1992, 1993) rather than a distinct biogeographic boundary. A similar conclusion has been reached for reef fishes (Francis 1996), echinoderms (Pawson 1965), crabs (Dell 1968), and algae (Moore 1961) and reflects the mixing of warmer southerly flowing and cooler northerly flowing water masses on the central east coast of New Zealand (Heath 1985).

Paulin & Roberts (1992) distinguish between 2 groups of fish that occur in rockpools in New Zealand. Rockpool fishes per se are commonly found in pools as adults and comprise the typical intertidal fish fauna, including true and partial residents. Surge zone fishes are small subtidal fishes or juveniles of subtidal fish that are occasionally found in rockpools and subtidal channels. They are more typical of the coastal reef fauna and are not usually found as breeding adults in rockpools, except those that are open to the sea. Only 3 rockpool fish species (*Acanthoclinus fuscus*, *Bellapiscus medius* and *B. lesleyae*) are generally confined to the intertidal zone in New Zealand (Paulin & Roberts 1993), suggesting that the intertidal fauna comprises a large proportion of partial residents that carry out their adult life intertidally but whose main distribution may be subtidal.

The rockpool fish families with the most representatives include the triplefins (Tripterygiidae – 21 species), clingfish (Gobiesocidae – 9 species), blennies (Blenniidae – 5 species), pipefish and seahorses (Syngnathidae – 4 species), and rockfish (Plesopidae – 4 species) (Prochazka *et al.* 1999). The high level of endemism (61.7%) comparative to non-rockpool species (5.7% - Paulin & Roberts 1993) presumably reflects differences between typical intertidal fishes and their non-intertidal counterparts (Prochazka *et al.* 1999). Intertidal fishes are generally small, negatively buoyant (Zander *et al.* 1999), territorial (Gibson 1982), and short-lived (Paulin & Roberts 1992), traits that reduce vagility and increase the likelihood of speciation (see Rosenblatt 1963).

### **2.1.2) Central Hawke's Bay rockpool fish fauna**

An extensive intertidal platform averaging 50m in width borders most of the Hawke's Bay coast (Duffy 1992) and is characteristic of the New Zealand east coast from East

Cape to Kaikoura (Morton & Miller 1968; Department of Conservation 1994). The platform is scattered with rockpools of different shapes and sizes (Morton & Miller 1968; Department of Conservation 1994; pers. obs.) but the rockpool fish fauna is described mainly from collections made from surge guts and channels open to the sea, or from large rockpools close to low water (Duffy 1992; Roberts & Stewart 1992; Paulin & Roberts 1993; Department of Conservation 1994). Roberts & Stewart (1992) collected 74 species from intertidal, shallow subtidal and estuarine habitats between Hawke Bay and Porangahau. Presumably, Paulin & Roberts (1993) used those collections (among others) to describe 42 rockpool species from the Gisborne – Hawke's Bay region. Duffy (1992) collected 35 species from 5 large pools between Mangakuri and Blackhead Beach, and Creswell & Warren (1990) recorded five intertidal species from 8 Central Hawke's Bay localities. Te Angiangi Marine Reserve (Central Hawke's Bay) has 11 species listed as being found intertidally (Department of Conservation 1994).

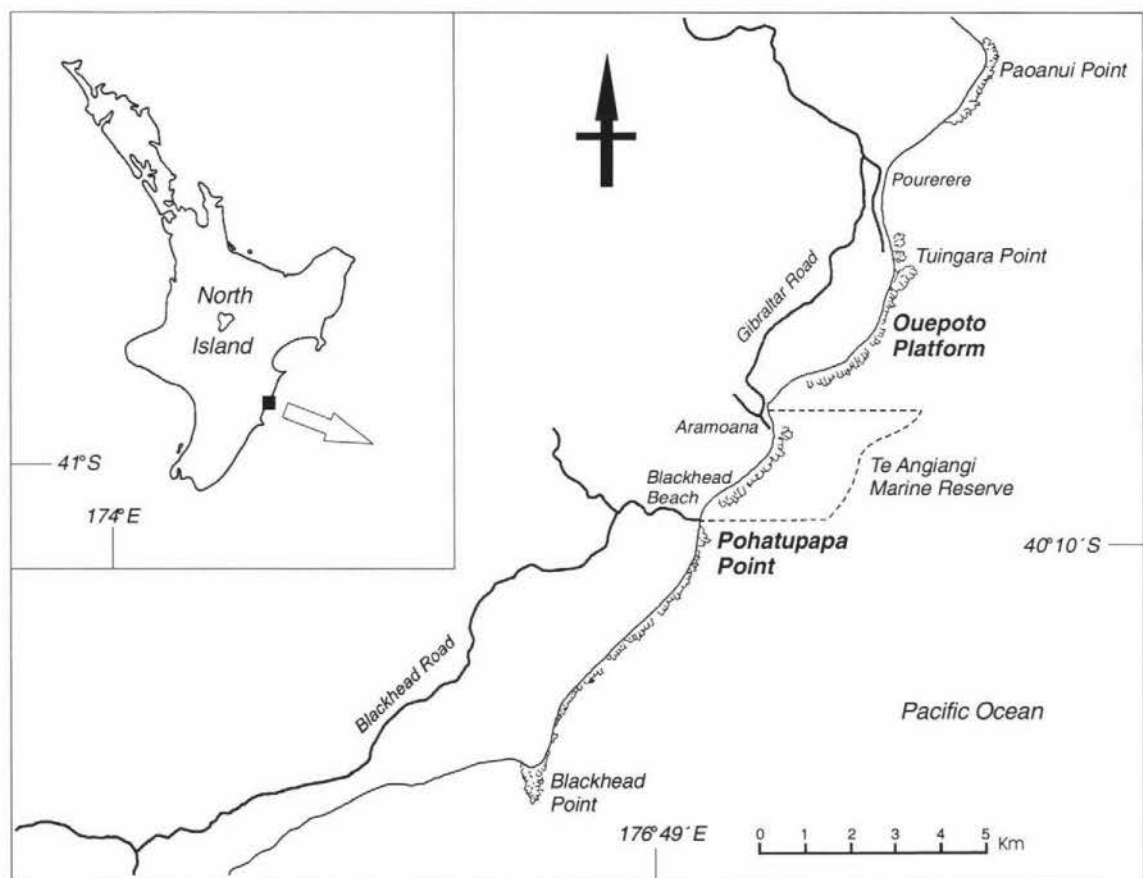
Surge guts and channels are generally thermally and chemically stable as they are constantly flushed by waves and swell. In contrast, rockpools typically experience extreme fluctuations in physical environment parameters when exposed at low water (Metaxas & Scheibling 1993). The larger and deeper a pool and the lower its position on the shore, the more it will correspond to a sublittoral (subtidal) habitat in terms of the stability of temperature, salinity and dissolved oxygen (Knox 2001). Low shore and large pools generally harbour large numbers of partial residents (Lardner *et al.* 1993; Mahon & Mahon 1994; Willis & Roberts 1996) and it is likely that collections restricted to this habitat will be skewed towards this part of the fish fauna. This is particularly relevant in New Zealand where populations of most rockpool fishes extend into the shallow subtidal (Thompson 1981; Duffy 1988; Paulin & Roberts 1992, 1993; Francis 2001). Without collections from rockpools at all shore heights it is difficult to distinguish between true resident rockpool species and partial and transient residents that take advantage of space in thermally and chemically stable pools and channels.

The aim of this chapter is to describe the rockpool fish fauna sampled on two Central Hawke's Bay intertidal platforms and compare it to previous studies of intertidal fishes in the region. Details of the study area and sampling methods are provided as background to the detailed studies reported in Chapters 3 and 4.



## 2.2) Study area

This study was conducted in Central Hawke's Bay, North Island, New Zealand (Fig. 1). The coastline is characterised by a series of broad wave-cut intertidal mudstone platforms, separated from each other by sand beaches (Creswell & Warren 1990; Plate 1). The intertidal platform between Tuingara Point and Ouepoto (hereafter referred to as the Ouepoto platform) ( $40^{\circ}08'S$   $176^{\circ}51'E$ ) is 3.5 km long and in most places extends about 115m to the subtidal fringe (Fig. 1). The intertidal platform at Pohatupapa Point ( $40^{\circ}10'S$   $176^{\circ}50'E$ ) is located 3 km south of the Ouepoto platform and is separated from it by two sand beaches and a 2 km long intertidal platform that is the landward boundary of Te Angiangi Marine Reserve (Fig. 1). The platform at Pohatupapa Point is



**Figure 1 Central Hawke's Bay sampling sites (in bold).**

about 115m wide but becomes narrow southwards where it runs along the base of steep mudstone cliffs for approximately 6.5 km. Above the high tide mark between Blackhead Beach and Tuingara Point is a sand beach and a small dune system covered with marram grass (*Ammophila arenaria*) and sand grass (*Spinifex hirtus*), backed by steep, extensively slumped hills of cretaceous and tertiary rock (Kamp 1992).



**Plate 1 Aerial view of the intertidal platform at Te Angiangi Marine Reserve and Pohatupapa Point (towards the top of the picture).**

The intertidal algae and macroinvertebrates at both sites are representative of Central Hawke's Bay intertidal platforms (Creswell & Warren 1990; Haddon & Anderlini 1993). These platforms are typically of low elevation and vertical relief, and are dominated by *Corallina officinalis* and *Hormosira banksii* flats, interrupted by beds of seagrass (*Zostera muelleri*) (Creswell & Warren 1990). Cracks and depressions in the bedrock become pools during low water. The dominant algae in these rockpools are coralline turfs (*C. officinalis*, *Halimtilon roseum* and *Jania micarthyrodia*) and *H. banksii*. Closer to the subtidal fringe the phaeophytes *Cystophora torulosa*, *Cystophora retroflexa*, *Carpophyllum maschalocarpum*, *Carpophyllum plumosum*, *Glossophora kunthii* and *Zonaria* spp are common. Common gastropod species in the rockpools



include the catseye *Turbo smaragdus*, common topshell *Melagraphia aethiops*, southern creeper *Zeacumantus subcarinatus*, spotted whelk *Cominella maculosa*, mud whelk *Cominella glandiformes* and dark rock shell *Haustorium haustorium* (Creswell & Warren 1990).

The principle features of oceanic circulation influencing the Central Hawke's Bay coast are the Wairarapa Coastal Current and the East Cape Current (Heath 1985; Chiswell 2000). The cooler Wairarapa Coastal Current (syn. Southland Current) is generally considered to flow north over the continental shelf, whereas the warmer East Cape Current is thought to flow south as a series of eddies along the outer edge of the shelf (Barnes 1985; Heath 1985; Chiswell 2000). The bulk of both currents is probably deflected south-east somewhere near Cape Turnagain, and the relative strength of each varies seasonally (Heath 1985). The presence of warm and cold oceanic currents means this coast is of general interest to marine biogeographers (Knox 1960, 1963; Morton & Miller 1968).

### 2.3) Methods

The resilience of the rockpool fish community to disturbance was examined at two timescales; (i) recovery after 1 month, and (ii) recovery after 3 months. Previous research in New Zealand (Willis & Roberts 1996) and elsewhere (Grossman 1982; Collette 1986; Polivka & Chotkowski 1998) suggests that three months would allow sufficient time for the fish community to completely recover from sampling disturbance. Twenty-six pools were sampled at Pohatupapa Point (Fig. 1). These covered a representative range of pool sizes, distance from low water and habitat characteristics. Destructive censuses of the fish assemblages in each pool were taken one month apart in winter (June, July 2000), spring (October, November 2000) and summer (February, March 2001) (Table 1). The repeatedly sampled pools are referred to as the 'experimental pools'. Fourteen control (i.e. previously unsampled) rockpools were sampled each time the experimental pools were resampled (Table 1). Control pools were located on the Ouepoto platform and were as similar as possible to the experimental pools. A separate control site was chosen so that harvesting pressure was not concentrated in one area. The position of experimental and control pools was

recorded using digital photographs and a hand-held GPS to aid relocation and ensure control pools were not resampled accidentally (Appendix 1). Multi-Response Permutation Procedure (MRPP; McCune & Mefford PCORD Version 4 1999) was used to test for differences in habitat characteristics between the experimental and control pools.

**Table 1 Sampling regime for 26 rockpools on Pohatupapa Point (experimental) and 70 rockpools on the Ouepoto platform (control).**

Pool number	Pool type	Month sampled					
		June 2000	July 2000	Oct 2000	Nov 2000	Feb 2001	Mar 2001
1 – 26	Experimental	√	√	√	√	√	√
27 – 40	Control		√				
41 – 54	Control			√			
55 – 68	Control				√		
69 – 82	Control					√	
83 – 96	Control						√

To simulate a catastrophic disturbance, rockpools were sampled using the ichthyocide rotenone. Rotenone powder containing 7% rotenone by weight was mixed to a thin paste with seawater and biodegradable detergent. The paste was spread throughout the pool from a plastic squirt bottle that made it easy to access small holes and crevices, and hand mixing until the water was uniformly milky but clear enough to see the bottom. Fish were collected with small hand nets as they swam towards the surface of the pool. When this activity ceased the bottom of the pool, crevices and algae were thoroughly searched using a mask and snorkel. The pool was then periodically checked for fish while subsequent pools were being sampled. Searching ceased when the entire pool had been examined and no more fish were found. In March 2001, fish captured on the surface of 40 pools were kept separate from those found on the bottom of the pools. These samples were then compared to determine if species composition differed between the methods. All fish were placed in labelled plastic bags and stored at -20°C.



In the laboratory fish were thawed and identified to species. Nomenclature follows Paulin & Roberts (1992), except for the Tripterygiidae, which follow Fricke (1994) and Clements *et al.* (2000). Each species was categorised as a resident (true or partial) or surge zone (transient) species. Surge zone species include those listed as surge zone species by Paulin & Roberts (1992). True residents include *Bellapiscus medius*, *B. lesleyae* and *Acanthoclinus fuscus* (see 2.1.1). Partial residents include those listed by Paulin & Roberts (1992) as 'rockpool fish' (excluding true residents). All fish were weighed to the nearest 0.01g using a Mettler-Toledo PB 3002 electronic balance. Total length (TL) was measured to the nearest mm using a small fish board constructed from a piece of half-pipe with metric rulers set on the inner walls. Large specimens were dissected, and examined to determine if they had consumed any fish during sampling. Only freshly ingested specimens were retrieved and included in the data set. Reference specimens of each species were deposited in the fish collection of the Museum of New Zealand Te Papa Tongarewa, and a small number of Tripterygiid specimens were provided to researchers from the University of Auckland for a study of Tripterygiid phylogeny and phylogeography (Clements *et al.* in prep).

Habitat variables known to influence the density and diversity of rockpool fishes include surface area, pool depth, pool volume, substrate composition, shelter from predators, physical complexity and height above low water (Green 1971c; Gibson 1972; Bennett & Griffiths 1984; Prochazka & Griffiths 1992; Macpherson 1994; Mahon & Mahon 1994). Each of these variables was measured or estimated for all pools sampled in this study.

- **Pool height** above low water was measured during spring-tide using a Laser Plane PX665 laser level. Both reefs are relatively uniform and the flood tide inundates pools sequentially based on their tidal height.
- **Pool surface area (m<sup>2</sup>)** was estimated by placing a gridded 1m<sup>2</sup> quadrat over each rockpool, and summing the number of 10cm<sup>2</sup> grids that fell over the surface of the water. The quadrat was flipped and the summation repeated until the entire surface area of the pool had been covered.

- **Mean depth (m)** was estimated by averaging a minimum of fifty random depth measurements from each pool.
- **Rockpool volume (l)** was estimated by multiplying pool surface area by mean depth.
- **Substrate composition** was estimated by recording the substrate category beneath a wooden pointer passed through a predetermined corner of at least 75 randomly selected grids. Substrate categories were: bare rock, sand, seagrass, rubble, coralline turf, *Hormosira banksii* and foliose algae. Using this point intercept method, a single point could record more than one category.
- **Shelter from predators** was estimated using two methods. The availability of rock shelter was estimated by summing the number of 10cm<sup>2</sup> grids covering a crevice or overhang (including those outside the pool surface perimeter), and dividing by the total number of grids (“crevice density”). Cover provided by algae and rocks was estimated subjectively using a scale of zero to five, with zero indicating no cover (Bennett & Griffiths 1984).
- **Physical complexity (rugosity)** was also estimated subjectively on a zero to five scale (Faria & Almada 2001). A pool containing little or no relief scored zero, while a pool with an irregularly shaped bottom scored higher (maximum of 5).

## 2.4) Results

### 2.4.1) Rockpools

A representative range of rockpools were sampled that included some very large pools although smaller pools were more common at both sites (Plate 2; Table 2). Rockpool height above low water ranged from 9cm to 104cm and size (surface area) ranged from 0.68m<sup>2</sup> to 19.10m<sup>2</sup>. Larger pools (surface area) had more shelter in the form of crevices ( $r = 0.505$ ,  $P < 0.001$ ) but crevice density was uncorrelated with pool size ( $r = 0.01$ ,  $P =$



0.426; regressions performed on  $\log_{10}(x+1)$  transformed data). Coralline turfs (*Corallina officianalis*, *Haliptilon roseum* and *Jania micarthrodia*) and bare rock were the most common substrate types although foliose algae was common in pools towards low water (Plate 2). The measured and estimated habitat variables for all pools are presented in Appendix 2. There was no significant difference between the experimental and control pools ( $T = 0.277$ ,  $P = 0.467$ ; MRPP conducted with  $\log_{10}(x+1)$  transformed habitat data). This is consistent with Haddon & Anderlini's (1993) findings that the intertidal platforms on this part of the Hawke's Bay coast were all very similar in terms of their biota and indicates that the Ouepoto platform is a valid control site.



**Plate 2** Top left – pool 13 (larger pool); top right – pool 15 (small pool with dense mat of coralline turf; bottom left – pool 9 (high-shore pool with bare rock substratum); bottom right – pool 12 (low-shore pool with dense cover of foliose algae). See Appendix 2 for rockpool dimensions.

**Table 2** Summary statistics for habitat variables measured from 26 rockpools on Pohatupapa Point and 70 rockpools on the Ouepoto platform.

Habitat variable		Experimental rockpools (n = 26)				Control rockpools (n = 70)			
		Minimum	Maximum	Mean	± 1SE	Minimum	Maximum	Mean	± 1SE
Position	Height (cm asl)	35	98	64.2	4.3	9	104	60.8	2.7
Size	Surface area m <sup>2</sup>	0.90	19.10	4.12	0.92	0.68	10.58	3.18	0.32
	Mean depth (m)	0.056	0.217	0.114	0.009	0.052	0.263	0.111	0.005
	Maximum depth (m)	0.115	0.465	0.260	0.018	0.095	0.455	0.247	0.010
	Volume (l)	59	3166	608	176	47	2115	390	50
Substrate composition (proportion)	Bare rock	0.055	0.743	0.345	0.036	0.014	0.650	0.274	0.018
	Sand	0.000	0.684	0.102	0.034	0.000	0.325	0.064	0.008
	Seagrass	0.000	0.420	0.079	0.026	0.000	0.620	0.067	0.016
	Rubble	0.000	0.211	0.082	0.013	0.000	0.319	0.082	0.008
	Coralline turf	0.016	0.775	0.343	0.046	0.016	0.833	0.397	0.030
	Hormosira banksii	0.000	0.580	0.154	0.033	0.000	0.644	0.190	0.023
	Foliose algae	0.000	0.567	0.078	0.024	0.000	0.920	0.160	0.032
Shelter and complexity	Number of crevices	2.0	258.0	49.8	12.5	0.0	316.0	53.8	7.0
	Crevice density	0.011	0.358	0.128	0.017	0.000	0.485	0.175	0.013
	Estimate algal cover	0	5	2.038	0.263	0	5	2.386	0.175
	Estimate rock cover	0	5	3.308	0.287	1	5	3.171	0.142
	Estimate rugosity	0	5	2.962	0.291	1	5	2.743	0.138

2.4.2) Fish fauna

A total of 6133 fish from 24 species and 13 families was collected. Tripterygiids dominated numbers (70%) and biomass (64%) (Table 3). A single species, the robust triplefin *Grahamina capito* composed 57% of the total catch and 52% of total biomass. The nine most abundant species (*G. capito*, *Ericentrus rubrus*, *Acanthoclinus fuscus*,



*Bellapiscus medius*, *Forsterygion lapillum*, *Trachelochismus melobesia*, *Notolabrus celidotus*, *Dellichthys morelandi*, and *Lissocampus filum*) composed 97.5% of the total numbers and 97.4% of the total biomass. Eighteen species (approximately 96% of the individuals collected) that occur in rockpools as adults (true and partial residents) and juveniles of 6 surge zone species (approximately 4% of the individuals collected) were collected. The labrid *N. celidotus* was the most common surge-zone species, comprising 76% of the non-resident catch and 8% of the total biomass.

**Table 3 Numbers and weights of all species caught. \* denotes endemic species; intertidal resident status and NZ distribution from Paulin & Roberts 1992, 1993. RC = resident classification (TR = true resident, PR = partial resident, SZ = surge zone species); W = widespread; N = northern; S = southern; n = number; b = biomass (g); f = % of samples (n=226) containing each sp.).**

Species	Family	RC	NZ distribution	n	%n	b	%b	f
<i>Grahamina capito</i> *	Tripterygiidae	PR	W	3492	56.94	3277.37	51.96	86.28
<i>Ericentrus rubrus</i> *	Clinidae	PR	N	556	9.07	303.22	4.81	33.63
<i>Acanthoclinus fuscus</i> *	Plesiopidae	TR	W	489	7.97	1217.25	19.30	61.50
<i>Bellapiscus medius</i> *	Tripterygiidae	TR	W	403	6.57	354.71	5.62	53.54
<i>Forsterygion lapillum</i> *	Tripterygiidae	PR	W	341	5.56	343.06	5.44	37.17
<i>Trachelochismus melobesia</i> *	Gobiesocidae	PR	W	196	3.20	14.33	0.23	20.80
<i>Notolabrus celidotus</i> *	Labridae	SZ	W	180	2.93	507.88	8.05	15.04
<i>Dellichthys morelandi</i> *	Gobiesocidae	PR	W	174	2.84	67.67	1.07	18.14
<i>Lissocampus filum</i> *	Syngnathidae	PR	W	146	2.38	57.23	0.91	24.34
<i>Scorpaena papillosus</i>	Scorpaenidae	SZ	W	42	0.68	30.5	0.48	8.41
<i>Gastroscyphus hectoris</i> *	Gobiesocidae	PR	W	36	0.59	7.83	0.12	6.64
<i>Ruanoho decemdigitatus</i> *	Tripterygiidae	PR	W	22	0.36	45.14	0.72	3.54
<i>Gobiopsis atrata</i> *	Gobiidae	PR	W	16	0.26	30.48	0.48	3.54
<i>Parablennius laticlavus</i> *	Blenniidae	PR	N	13	0.21	9.63	0.15	4.87
<i>Peltorhamphus latus</i> *	Pleuronectidae	SZ	W	8	0.13	27.59	0.44	1.33
<i>Notoclinus fenestratus</i> *	Tripterygiidae	PR	W	7	0.11	3.2	0.05	0.88
<i>Notoclinus compressus</i> *	Tripterygiidae	PR	W	3	0.05	4.34	0.07	1.33
<i>Parma alboscapularis</i>	Pomacentridae	SZ	N	2	0.03	0.58	<0.01	0.88
<i>Cristiceps aurantiacus</i>	Clinidae	PR	N	2	0.03	2.54	0.04	0.44
<i>Diplocrepis puniceus</i> *	Gobiesocidae	PR	W	1	0.02	0.03	<0.01	0.44

Table 3 continued...

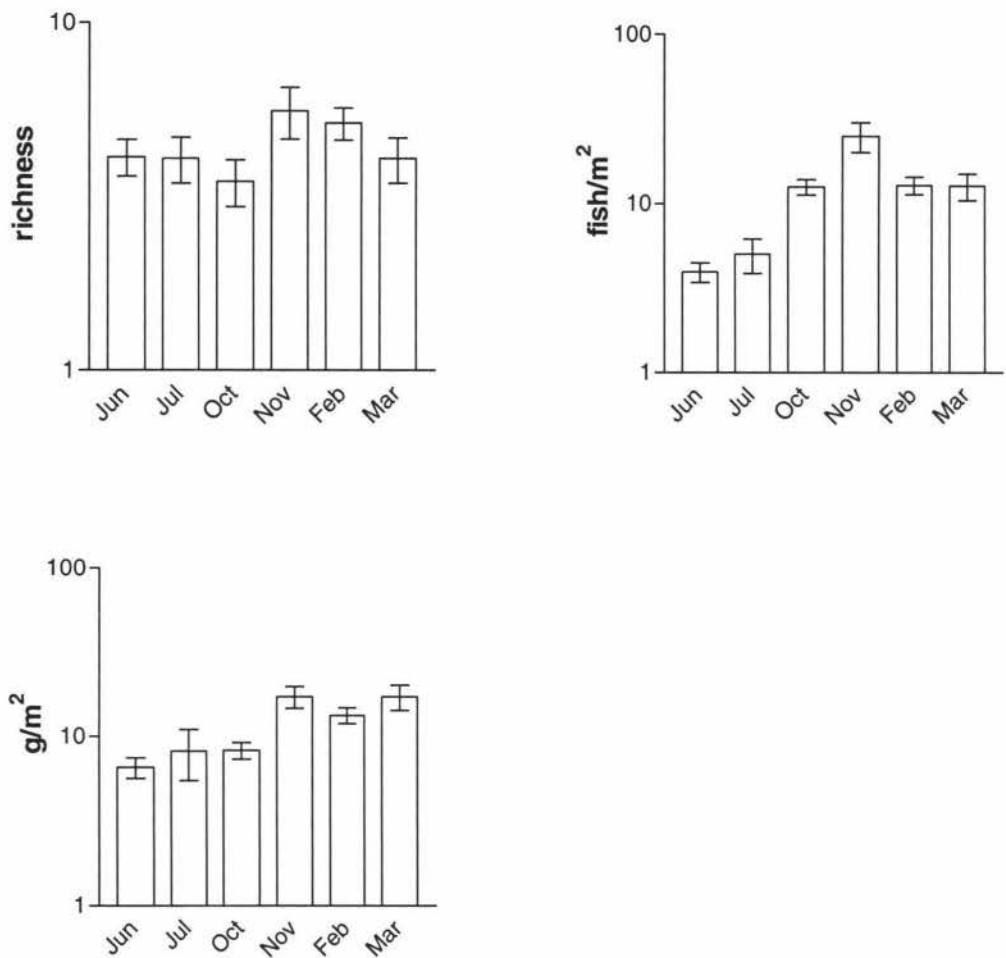
Species	Family	RC	NZ distribution	n	%n	b	%b	f
<i>Bovichtus variegatus</i> *	Bovichthyidae	SZ	S	1	0.02	1.87	0.03	0.44
<i>Ruanoho whero</i> *	Tripterygiidae	PR	W	1	0.02	0.29	<0.01	0.44
<i>Conger verreauxi</i>	Congridae	SZ	W	1	0.02	0.87	0.01	0.44
<i>Gastrocyathus gracilis</i> *	Gobiesocidae	PR	W	1	0.02	0.04	<0.01	0.44
				6133		6307.65		

The majority of species collected are widespread around New Zealand. Four typically northern species were collected while only 1 specimen of a typically southern species, *Bovichtus variegatus*, was collected. Northern and southern species comprised 9.36% of total numbers and 5.04% of total biomass although these figures were dominated by one northern species, *E. rubrus* (Table 3). No species was endemic to the Hawke’s Bay but 20 (83%) were endemic to New Zealand. The remaining four species (*Cristiceps aurantiacus*, *Parma alboscapularis*, *Conger verreauxi*, and *Scorpaena papillosus*) have Australasian distributions.

Examination of surface and benthic captures from 40 pools during March 2001 revealed that 16% of the total number of fish (n = 786) were found dead on the bottom or hidden in algae. In particular, 42% of *F. lapillum* (the 5th most abundant species) and 28% of *A. fuscus* (the 3rd most abundant species) were benthic captures. No additional species were found in benthic searches. Hermit crabs (*Pagurus* spp) were occasionally observed scavenging on a dead fish, and the fish was removed before significant damage occurred to the specimen. It is likely though that a small number of fish were not recovered. Freshly ingested fish were only found in *A. fuscus* and *G. capito* although the number found was negligible (n = 10).

Average species richness was consistent in control pools over time (ANOVA;  $F_{5,90} = 1.46$ ,  $P = 0.212$ ; Fig. 2) but abundance and biomass (standardised by pool surface area) were significantly greater during the latter 3 collection months ( $F_{5,90} = 28.52$ ,  $P < 0.001$ ;  $F_{5,90} = 8.65$ ,  $P < 0.001$  respectively; analyses performed on  $\log_{10}(x+1)$  transformed data). This was due to large numbers of settling larvae during late spring and summer.

Variation over time in the experimental pools includes both seasonal and recovery dynamics and will be covered in Chapter 4.



**Figure 2** Mean  $\pm$  S.E. richness, abundance and biomass of fish in control pools over time. Abundance and biomass are standardised for pool surface area. y axis =  $\log_{10}$

**2.5) Discussion**

**2.5.1) Sampling efficiency**

Rotenone is an ichthyocide historically used by ancient peoples to capture fish and now used as an effective tool to a) manage pest fishes and b) to sample fishes for the purposes of research (Betolli & Maceina 1996; Willis & Ling 2000; Willis 2001). Destructive sampling with rotenone was used in the present study for three reasons;

1. sampling simulated a catastrophic disturbance necessary for the resilience study (Chapter 4);
2. many small cryptic fishes, especially juvenile Tripterygiids, are difficult to identify without microscopic examination;
3. non-destructive sampling greatly underestimates density and diversity of cryptic fishes (Christensen & Winterbottom 1981; Beckley 1985; Ackerman & Bellwood 2000; Griffiths 2000; Willis 2001).

Christensen & Winterbottom (1981) suggest poisoning techniques may be quantitatively inaccurate because of i) immigration/emigration to and from the area being sampled; ii) water currents removing the poison before the full effect takes place; iii) variable susceptibility of the fish to the poison, and; vi) subsequent immigration of predators unaffected by the poison which then feed on the dead fish before they can be collected. The first two reasons are not relevant to this study because the environment being examined (rockpool) is a discrete habitat at low tide, unaffected by water currents and immigration/emigration. Variable susceptibility to the ichthyocide, and predation of moribund fish was observed in the present study. *Acanthoclinus fuscus* and *Dellichthys morelandi* were the last species to be captured alive on return to a pool while sampling a subsequent pool, and the juvenile conger-eel (*Conger verreauxi*) took over forty-five minutes to emerge from the hole in the pool it occupied. This is particularly relevant because the former two species composed approximately 11% of the total number of fish captured. The large number of *A. fuscus* and *Forsterygion lapillum* collected from benthic searching may also reflect variable susceptibility to rotenone. Both species have preferences for crevice and rock shelter (Paulin & Roberts 1992), and may remain there before eventually succumbing to the poison. Fish abundance may have been grossly underestimated had searching ceased when fish activity apparently ceased. The number of fish found in the digestive tract of potentially piscivorous species was negligible but nevertheless these results suggest conventional rotenone sampling in which only surface recoveries are made, may result in underestimates of the abundance of some species. Prochazka & Griffiths (1992) and Chotkowski (1994) also recorded increases in the abundance of some species when bottom searches and bailing were used in addition to rotenone treatment. Neither study found additional species in benthic searches.

### 2.5.2) Fish fauna

Rockpool fish assemblages at both study sites were taxonomically dominated by the Tripterygiidae and Gobiesocidae. One species of triplefin (*Grahamina capito*) dominated numerically and in terms of biomass. Overall there was little seasonal variation in average species richness in the control pools. Summer increases in richness due to an influx of juvenile resident and subtidal species have been reported in a number of studies (Moring 1986; Beja 1995; Beckley 2000), and decreases in diversity and richness have been related to adverse winter weather (Thomson & Lehner 1976; Lee 1980; Willis & Roberts 1996). On the South African west coast, Prochazka (1996) observed no seasonality in richness and attributed it to the absence of transient and partial resident species. In the present study, spring/summer recruitment pulses were comprised of fish found in rockpools as adults. The common surge zone species (*Notolabrus celidotus* and *Scorpaena papillosus*) occurred year round while the other four surge zone species (*Parma alboscapularis*, *Peltorhamphus latus*, *C. verreauxi* and *Bovichthys variegatus*) occurred in small numbers (combined  $n = 12$ ) and had no appreciable impact on mean richness.

Eighty-three percent of the species collected were endemic to New Zealand compared to 50% of the coastal, intertidal and estuarine species ( $n = 74$ ) described for the Hawke's Bay by Roberts & Stewart (1992). This likely reflects differences in vagility between rockpool and subtidal species. In the present study, most of the species collected were widespread but the relative proportions of northern and southern species probably reflect the geographic position of the Central Hawke's Bay. Roberts & Stewart (1992) collected a greater proportion of northern to southern species in their Hawke's Bay study and attributed it to the close proximity of their study sites to the East Cape – North Cape region with its characteristically large number of northern species. In rockpools further south on the Wellington coast, Willis & Roberts (1996) collected 2 southern species (*Gaidropsarus novaezealandiae* and *B. variegatus* combined  $n = 10$ ) but only 1 northern species (*Ericentrus rubrus*  $n = 143$ ). Many species of fish are rare at their distributional extremities (Francis 1996) and this is apparent for most northern and southern species in this study and on the Wellington south coast (Willis & Roberts 1996). However, *E. rubrus* is common in the present study and on the Wellington south coast (Willis & Roberts 1996). It has also been found in the Marlborough Sounds and is

common on the Kaikoura Coast (both south of Cook Strait) in habitat similar to that sampled in the present study (Duffy 1988; Francis 2001). This species is clearly not at the southern limit of its distribution at Cook Strait. Lack of sampling, or possibly suitable habitat in southern locations may account for the apparent scarcity of *E. rubrus* on parts of the South Island coast. Further collections south of Cook Strait are required to determine the distributional extremity of this species.

Of the 42 Gisborne–Hawke’s Bay rockpool species listed by Paulin & Roberts (1993) 21 were collected in the present study and 3 species were added. Two of the additional species (*P. latus* and *B. variegatus*) are subtidal as adults and the third (*Gastroscypus hectoris*) is common subtidally (Paulin & Roberts 1992). Most of the species in Paulin & Roberts’ (1993) list that were not recorded in this study are surge zone fishes (e.g. *Ellerkeldia huntii*, *Aplodactylus artidens*, *Aldrichetta forsteri*, *Notolabrus fuciola*) although 10 widespread resident species listed in Paulin & Roberts (1993) were not collected (e.g. *Trachelochismus pinnulatus*, *Acanthoclinus littoreus*, *Gilloblennius tripennis*, *Notoclinops segmentatus*). The absence of surge zone species reflects the distribution of collection effort. However, the absence of resident fishes from 226 rockpool collections suggests that these species may be restricted to surge guts, channels, and pools open to the ocean.

Of particular interest is the absence of the variable triplefin (*Forsterygion varium*). Creswell & Warren (1990) reported that *F. varium* was one of the most common intertidal fish in Central Hawke’s Bay. They reported it from intertidal platforms at Mangakuri, Paoanui Point, Pourerere/Aramoana (Ouepoto Platform), Aramoana/Blackhead beach, Kairakau, and Blackhead reef (Pohatupapa Point). This species was also listed as an intertidal species in the Te Angiangi Marine Reserve application (Department of Conservation 1994), and is included among the rockpool fishes by Paulin & Roberts (1992). *Forsterygion varium* is a common subtidal species and also occurs in surge channels in the subtidal fringe (Thompson 1981; Duffy 1992; Paulin & Roberts 1992; Francis 1996; pers. obs). Duffy (1992) recorded *F. varium* from large channels and pools open to the ocean at low tide on the Ouepoto platform but did not record it from large pools on the same reef that were completely isolated from the ocean at low tide. These observations and the absence of *F. varium* from my collections indicate this species is not part of the true intertidal fauna in the Central Hawke’s Bay. It



therefore seems likely that Creswell & Warren's (1990) references to intertidal *F. varium* are either based on observations made in the subtidal fringe, or misidentifications of *G. capito* (syn. *Forsterygion robustum*). As the taxonomy of *Grahamina* has only recently been resolved (Fricke 1994; Clements *et al.* 2000) misidentification is a possibility but as no specimens of triplefins collected by Creswell & Warren (1990) survive in collections this can not be confirmed.

The absence of *Bellapiscis lesleyae* from the present collections is also interesting given this species has been recorded from the area (Roberts & Stewart 1992; Fricke 1994) and is described as an obligate intertidal species (Paulin & Roberts 1992; 1993). However, *B. lesleyae* is not listed as an intertidal species in the Te Angiangi Marine Reserve Application (Department of Conservation 1994), although it is included in the subtidal list. In addition, Duffy (1992) did not collect *B. lesleyae* from intertidal pools (on the same reef complex as those sampled in this study) that were closed to the open ocean at low tide, but did collect it from a large lagoon that is open to the ocean during all stages of the tidal cycle. The results of the present study suggest that the intertidal resident status of *B. lesleyae* has yet to be fully qualified.

Whether species absent from rockpools in this study but present in surge channels and large low tide pools connected to the subtidal can be accurately described as rockpool species is debatable. The subtidal fringe is more thermally and chemically stable, and the composition of the present collections compared to previous collections made in the subtidal fringe suggest there is some difference in the fish fauna. The nature of this difference is reflected in the absence of subtidally fringing species (residents and surge zone species) from rockpools, but not vice versa. However, it is possible that some species collected from rockpools are not as common in surge guts and channels. The olive rockfish *A. fuscus* was one of the most common species collected in the present study, but Roberts & Stewart (1992) considered this species is scarce in the Central Hawke's Bay. Intertidal collections in the latter study were confined to the low intertidal (A. Stewart, pers comm). Also worthy of note is the fact that a species previously classified as predominantly subtidal (*G. capito*; Willis & Roberts 1996) was much more abundant in rockpools in the present study than the two true resident species collected (*B. medius* & *A. fuscus*). Further investigation may reveal that the main distribution of *G. capito* is intertidal, at least in the Central Hawke's Bay.

## Chapter 3: Spatial and temporal variability in rockpool fish assemblage structure

### Abstract

Rockpool fish assemblage composition in 96 rockpools on two broad mudstone intertidal reef platforms was determined by destructive sampling with the ichthyocide rotenone. Rockpools were defaunated in winter 2000, spring 2000 and summer 2001. Assemblage structure in each pool was described in terms of diversity, abundance, density, biomass and fish size. Multiple regression analyses and Detrended Correspondence Analysis showed that taxonomic and numeric similarity was a function of intertidal height, pool size, shelter (algal and rock), rugosity and substrate type, and that richness, abundance, biomass, and fish size were generally greater in larger pools with more shelter situated closer towards the low tide mark. Partial resident species contributed significantly to the rockpool fish community, especially to assemblages in larger pools with more shelter situated closer towards the low tide mark. In addition, a suite of true resident species was identified including *Acanthoclinus fuscus*, *Grahamina capito*, and *Bellapiscus medius*. The latter two species were common shore-wide, and *A. fuscus* was the dominant high-shore species. Discriminant Function Analyses (DFA) were used to determine which combination of habitat variables best predicted the presence of certain common species. The results further supported the finding that shelter and shore level are important determinants of rockpool fish assemblage structure. It is most likely that physiological tolerance of environmental fluctuations associated with the tidal cycle, combined with microhabitat partitioning is responsible for the distribution of fish in rockpools on the Central Hawke's Bay coast. Seasonal patterns in community structure were distinguishable, but these were almost entirely due to the influx of juveniles of resident species.

### 3.1) Introduction

Habitat selection by rockpool fish has been related to rockpool tidal height, depth and rugosity (Horn & Riegle 1981; Bennett & Griffiths 1984; Prochazka & Griffiths 1992; Davis 2000), substrate type (Marliave 1977; Faria *et al.* 1998) and exposure (Ibanez *et*



*al.* 1989; Mgaya 1992). Species richness, abundance, and biomass have been positively related to pool size and the amount of rock and weed cover available (Marsh *et al.* 1978; Bennett & Griffiths 1984; Prochazka & Griffiths 1992; Mahon & Mahon 1994; Silberschneider & Booth 2001) as well as topographic complexity and pool stability (Faria & Almada 1999).

### **3.1.1) Pool size**

Rockpool size can have a number of effects on fish assemblage composition. Smaller pools are more likely to undergo pronounced physio-chemical changes during the ebb tide (e.g. salinity variation due to evaporation and rainfall) while larger pools may closely resemble the subtidal condition (Knox 2001). Studies have shown that different fish species vary in their tolerance to temperature, salinity and dissolved oxygen extremes (reviews in Gibson 1969, 1982) such that behavioural, morphological and physiological adaptations allow certain species to exploit rockpools, or parts of pools, less favourable to other species (Nakamura 1976a,b; Congleton 1980; Horn & Riegler 1981; Zander *et al.* 1999; Fanguie *et al.* 2001). Other studies have shown that fish diversity, abundance and biomass are positively correlated with measures of pool size such as surface area, volume, and depth (Marsh *et al.* 1978; Bennett & Griffiths 1984; Mgaya 1992). Mahon & Mahon (1994) also showed that larger rockpools have a larger number of partial residents, and that fish are on average bigger in larger pools.

Most rockpool fish are inactive at low tide, using the pool as a refuge. For those fish that move out of pools at high tide to feed (Norris 1963; Green 1971a; Ralston & Horn 1986), larger pools provide a greater “collection area” as the tide ebbs (Gibson & Yoshiyama 1999). This may explain some of the described relationships between pool size and assemblage structure. However, most rockpool fish are morphologically adapted to use crevices and holes so a simple ‘area effect’ is confounded with microhabitat availability which is usually correlated with pool size (Bennett & Griffiths 1984; Mahon & Mahon 1994; Underwood & Skilleter 1996).

### 3.1.2) Habitat complexity, shelter, and substrate

Microhabitat availability and habitat complexity may influence population and community processes through its effect on survival and behaviour (Aburto-Oropeza & Balart 2001). Several studies have shown that an increase in the number of available refuges or topographic complexity can lead to an increase in fish survivorship, abundance or diversity in subtidal (Werner *et al.* 1983; Behrents 1987; Choat & Ayling 1987; Holbrook & Schmitt 1988; Diehl 1993; Persson & Ecklov 1995; Aburto-Oropeza & Balart 2001) and intertidal rockpool habitats (Gibson 1972; Bennett & Griffiths 1984; Prochazka & Griffiths 1992; Davis 2000). Rocky refuges provide nesting sites, shelter from predators, and may contain higher densities of potential prey.

In most studies algae is also seen as a source of shelter, rather than food (Silberschneider & Booth 2001), probably because herbivory is rare in intertidal fish (Gibson & Yoshiyama 1999; Horn & Ojeda 1999). Fish diversity, abundance and biomass in rockpools have been positively correlated with algal cover (Marsh *et al.* 1978; Prochazka & Griffiths 1992), although Bennett & Griffiths (1984) found no correlation between richness, abundance and biomass, and weed cover in rockpools on the South African west coast. Additionally, Black & Miller (1991) noted there was no effect on fish abundance after weed removal from a shore in Nova Scotia.

Substrate selection by rockpool fish has been described by relatively few authors. Specific algal taxa in conjunction with rock overhangs are important for the triplefin *Enneapterygius rufopileus* in intertidal rockpools in Sydney (Silberschneider & Booth 2001), and algal type (foliose, coralline and seagrass) explained some of the variation in recruitment in rockpools in Washington (Pfister 1995). In captive studies, Marliave (1977) showed that settling larvae of intertidal species exhibited differences in substratum preference, and Faria *et al.* (1998) showed that juveniles of 3 co-occurring species also differed in their substratum preferences.

### 3.1.3) Rockpool height

Fish diversity, abundance and biomass tend to decline with increasing rockpool tidal height (Bennett and Griffiths 1984; Prochazka & Griffiths 1992; Davis 2000). This may

occur because of because of the progressively more variable and extreme physical conditions in high shore pools (Newell 1979) but also due to increased exposure to avian predators during high-tide (Gibson & Yoshiyama 1999). In some rockpool fish communities there are marked vertical zonation patterns (reviews: Gibson 1982; Zander *et al.* 1999). Penrith (1970), Marsh *et al.* (1978), and Prochazka & Griffiths (1992) suggest this type of habitat separation results from territoriality and aggressive species occupying pools at more favourable heights. However, overlap in vertical distribution has been described in a number of studies (Nakamura 1976a; Horn & Riegle 1981; Barton 1982; Prochazka & Griffiths 1992; Santos *et al.* 1994). Prochazka & Griffiths (1992) linked the apparent lack of broadscale habitat separation in their study to low species richness although others suggest that species may differ in terms of microhabitat specialisation when there is overlap in vertical distribution (Nakamura 1976a; Gibson 1982; Zander *et al.* 1999).

#### **3.1.4) Seasonality in community structure**

Seasonality in fish diversity and abundance in rockpools has been described in a number of studies, and has been attributed to extreme low temperatures and adverse weather conditions during winter which prevent some species from occupying rockpools during this time (Thompson & Lehner 1976; Jones & Clare 1977; Moring 1990; Willis & Roberts 1996) or to an influx of juveniles of transient and resident species following their breeding season (Gibson 1982; Beckley 1985a,b; Bennett 1987; Ali & Hussein 1990). However, Prochazka (1996) found no seasonal trends in density, densities of individual species, diversity or evenness of intertidal fish on the South African west coast. This was attributed to the absence of transient species year-round. Several studies suggest that the seasonal presence of juvenile transients in rockpools means the intertidal zone may be an important nursery ground for subtidal species (Beckley 1985a; Varas & Ojeda 1990; Lardner *et al.* 1993; Mahon & Mahon 1994; Pequeno & Lamilla 1995). Comparative studies suggest otherwise. Bennett (1987) and Smale & Buxton (1989) found juvenile transients in rockpools but they were more abundant subtidally. Additionally, Prochazka (1996) and Willis & Roberts (1996) found comparatively few juveniles of subtidal species in their rockpools but found large numbers of juveniles of common intertidal residents.

Although factors regulating the taxonomic and numerical composition of intertidal fish have received increasing attention, there is a lack of research addressing the relationships between habitat structure and New Zealand rockpool fish communities. This chapter's aims are: (i) to assess the importance of rockpool size and tidal height, shelter availability and substrate type on fish assemblages inhabiting rockpools on the Central Hawkes' Bay coast, North Island, New Zealand and, (ii) to examine seasonal changes in the composition of the rockpool fish fauna.

## **3.2) Methods**

### **3.2.1) Fish sampling**

Fish were censused from 96 rockpools on Pohatupapa Point and the Ouepoto platform (Chapter 2 Fig. 1) between June 2000 and March 2001. Forty pools were censused in June/July 2000 (winter), 28 in October/November 2000 (spring), and 28 in February/March 2001 (summer). These pools represent the initial and control collections described in Chapter 2. Fish were captured with the aid of the ichthyocide rotenone and care was taken to collect all fish from each pool. Fish were placed in labelled plastic bags and stored at -20°C. In the laboratory fish were thawed and identified to species. Nomenclature follows Paulin & Roberts (1992), except for the Tripterygiidae, which follow Fricke (1994) and Clements *et al.* (2000). All fish were weighed to the nearest 0.01g using a Mettler-Toledo PB 3002 electronic balance. Total length (TL) was measured to the nearest mm using a small fish board constructed from a piece of half-pipe with metric rulers set on the inner walls. Eleven variables were used to describe assemblage structure in each rockpool (Table 1). Assemblage structure variables were checked for normality and log transformed ( $\log_{10}(x+1)$ ) if necessary.

### **3.2.2) Habitat assessment**

Pools were selected to represent the full range of habitat variables measured including: surface area, pool depth, pool volume, substrate composition, shelter from predators, physical complexity and height above low water. Refer to Chapter 2 for habitat methods. Habitat variables were checked for normality and log transformed ( $\log_{10}(x+1)$ ) if necessary (Table 2).

**Table 1** Assemblage structure variables measured and calculated for 96 rockpool fish assemblages on Pohatupapa Point and the Ouepoto platform:  $s$  = total number of species;  $P_i$  = proportion of individuals in the  $i$ th species;  $N$  = total number of individuals;  $N_{\max}$  = number of individuals in the most abundant species.

Assemblage structure variables	Description	Log transformed ( $\log_{10}(x+1)$ )
Mean length (mm)	Mean total length (TL) of all fish in a pool	No
Mean weight (g)	Mean weight (g) of all fish in a pool	Yes
Maximum length (mm)	Maximum total length (TL) of the longest fish in a pool	No
Maximum weight (g)	Maximum weight (g) of the heaviest fish in a pool	Yes
Species richness	Number of species in a pool	Yes
Abundance	Number of fish in a pool	Yes
Biomass (g)	Total weight (g) of all fish in a pool	Yes
Density	Number of fish/m <sup>2</sup> surface area	Yes
Biomass density (g)	g/m <sup>2</sup> surface area	Yes
Shannon-Weiner diversity	$H' = -\sum_{i=1}^s p_i \log_{10} p_i$	No
Berger-Parker dominance	$D = N_{\max} / N$	No

**Table 2** Seventeen habitat variables measured in 96 rockpools on Pohatupapa Point and the Ouepoto platform.

Habitat variable		Measurement	log transformed ( $\log_{10}(x+1)$ )
Position	Height (cm asl)	Measured during spring-tide using a Laser Plane PX665 laser level	No
Size	Surface area m <sup>2</sup>	Sum of 10cm x 10cm grids covering surface area	Yes
	Mean depth (m)	Average of min. 50 random depth measurements	
	Maximum depth (m)	Max. value of random depth measurements	
	Volume (l)	Surface area x Mean depth	
Substrate composition (proportion)	Bare rock	Estimated by recording the substrate category beneath a wooden pointer passed through a predetermined corner of at least 75 randomly selected grids placed over the pool surface area	Yes
	Sand		
	Seagrass		
	Rubble		
	Coralline turf		
	<i>Hormosira banksii</i>		
	Foliose algae		

Table 2 continued ...

Habitat variable		Measurement	log transformed (log <sub>10</sub> (x+1))
Shelter and complexity	Number of crevices	Number of 10cm x 10cm grids covering a rock crevice	Yes
	Crevice density	Number of crevices standardised by surface area	Yes
	Estimate algal cover		
	Estimate rock cover	Estimated visually on a subjective scale of 0 (low) to 5 (high)	No
	Estimate rugosity		

3.2.3) Statistical analysis

Relationships between the habitat and assemblage structure variables were examined by stepwise multiple regression in SYSTAT Version 8.

Rockpool samples were grouped into three seasons; winter (June and July 2000), spring (October and November 2000) and summer (February and March 2001). Variability in assemblage structure between seasons was examined using one-way ANOVA in SYSTAT Version 8.

Detrended correspondence analysis (DCA, PCORD Ver. 4) was used to explore gradients in assemblage structure. Ordination axes were constructed using the density of each species in a rockpool to control for pool size. Densities were log transformed (log<sub>10</sub>(x+1)) to downweight the disproportionate contribution of one very abundant species (*Grahamina capito*).

Stepwise Discriminant Analysis (SDA) was used to determine which habitat variables best predicted the presence or absence of each species in a rockpool. Collinearity among predictor variables was determined by checking the tolerance value for variables selected by the model. If two highly correlated variables had tolerance values <0.1, the variable with the lowest r<sup>2</sup> in a simple linear regression on the density of the species in question was removed. Criteria for Discriminant Function Analyses (DFA) require that the sample size of each group (present vs absent) exceed the number of predictor



variables (Quinn & Keough 2002) therefore only species occurring in >17 but <79 rockpools were considered. The performance of each model was examined using Cohens' Kappa:

$$\frac{((a + d) - (((a + c)(a + b) + b + d)(c + d)) / n))}{(n - (((a + c)(a + b) + (b + d)(c + d)) / n))}$$

where  $n$  = the number of overall cases,  $a$  = true positive values,  $b$  = false positive values,  $c$  = false negative values, and  $d$  = true negative values substituted from the jackknifed classification matrix calculated in the DFA. Cohens' Kappa allows an assessment of the extent to which models correctly predict occurrence at rates that are better than chance expectation (Forbes 1995; Fielding & Bell 1997; Manel *et al.* 2001). Values of 0.0 – 0.4 are considered slight to fair model performance in medical applications, values of 0.4 – 0.6 moderate, 0.6 – 0.8 substantial and 0.8 – 1.0 almost perfect (after Landis & Koch 1977). Discriminant analyses were performed in SYSTAT Version 8.0.

### 3.3) Results

#### 3.3.1) General description

A total of 2748 fish from 19 species was collected from 96 rockpools (Table 3). The collections were taxonomically and numerically dominated by the Tripterygiidae (*Grahamina capito*, *Bellapiscus medius*, *Forsterygion lapillum*, *Ruanoho decemdigitatus*, *Notoclinus fenestratus* and *N. compressus*). Other families represented by large numbers of resident fish included: the Clinidae (*Ericentrus rubrus*), Plesiopidae (*Acanthoclinus fuscus*), Gobiesocidae (*Dellichthys morelandi* and *Trachelochismus melobesia*) and the Syngnathidae (*Lissocampus filum*). Most of the resident species captured were partial residents, in that they are also abundant subtidally. Species considered true residents (*B. medius* and *A. fuscus*) made up 16% of the total numbers. Surge zone species, dominated numerically by the labrid *Notolabrus celidotus* were captured in low numbers (Table 3). There was great variability in richness, abundance, biomass and density in rockpools. Richness ranged from 1 to 15



species, abundance from 1 to 125, biomass from 0.65g to 373g, and density from 0.4 to 85 fish per m<sup>2</sup>. A description of the rockpools is provided in Chapter 2 and Appendix 2.

**Table 3 Species of fish captured from 96 intertidal rockpools on Pohatupapa Point and the Ouepoto platform between June 2000 and March 2001. n = number captured; %n = percent of total; frequency = number of pools species was captured from. \* denotes surge zone species (Paulin & Roberts 1992).**

Species	N	%n	Frequency
<i>Grahamina capito</i>	1292	47.02%	86
<i>Ericentrus rubrus</i>	317	11.54%	31
<i>Acanthoclinus fuscus</i>	257	9.35%	64
<i>Forsterygion lapillum</i>	219	7.97%	42
<i>Bellapiscus medius</i>	186	6.77%	55
<i>Dellichthys morelandi</i>	119	4.33%	25
<i>Lissocampus filum</i>	117	4.26%	34
<i>Trachelochismus melobesia</i>	69	2.51%	17
<i>Notolabrus celidotus</i> *	68	2.47%	16
<i>Gastroscyphus hectoris</i>	32	1.16%	11
<i>Ruanoho decemdigitatus</i>	19	0.69%	7
<i>Gobiopsis atrata</i>	16	0.58%	8
<i>Scorpaena papillosus</i> *	13	0.47%	8
<i>Parablennius laticlavus</i>	10	0.36%	8
<i>Notoclinus fenestratus</i>	7	0.25%	2
<i>Notoclinus compressus</i>	3	0.11%	3
<i>Peltorhamphus latus</i> *	2	0.07%	1
<i>Diplocrepis puniceus</i>	1	0.04%	1
<i>Bovichthys variegatus</i> *	1	0.04%	1
	2748		

3.3.2) Multiple regression

In general the multiple regression analyses of assemblage structure on habitat variables were robust with the models explaining from 22% (biomass density) to 66% (species richness) of the variation in each measure of assemblage structure (Table 4). Tolerance levels of potentially correlated habitat variables selected by the models never fell below 0.1, consequently no habitat variable was omitted from the analyses. All habitat variables except maximum depth were selected by at least one of the 11 models.

The predictive contributions (*F* ratio) of measures of rockpool size were particularly important. Richness, abundance, biomass, Shannon-Weiner diversity, and fish size were all greater in pools with a large volume, surface area or mean depth (Table 4). Fish density decreased in pools with a large surface area but increases were associated with mean depth. Rock and algal shelter were also important. Increases in richness, abundance, biomass, Shannon-Weiner diversity, and density were associated with one or more of the measurements and estimates of shelter. Small pool size with little shelter was associated with high Berger-Parker dominance values (low diversity). Rockpool height was also particularly important. Richness, abundance, density, Shannon-Weiner diversity and maximum fish length decreased in pools further from the low tide mark. Sand cover was negatively associated with all measurements of assemblage structure except mean fish size and Berger-Parker dominance. There was a strong association between mean fish size (length and weight) and the proportion of algal cover, in that the former increased in pools with low algal cover. Dominance was positively associated with % sand and *Hormosira banksii* cover. The other substrate variables most important in the regression models were rubble and bare rock. Increases in abundance, biomass and maximum fish size were associated with high % rubble cover. Abundance and density decreased with high % bare rock cover but an increase in mean fish size was positively associated with the same habitat variable.

**Table 4** Stepwise multiple regressions of rockpool fish assemblage structure variables against habitat variables. Stepwise selection is forward with *P* = 0.15 to enter and remove. Only habitat variables selected by the models are shown. Assemblage structure variables ordered by descending *R*<sup>2</sup>.

Variable	Model <i>R</i> <sup>2</sup>	Factor	Slope	<i>F</i>
Richness	0.66	Volume	0.229	54.1
		% sand	-0.836	6.5
		Height	-0.003	36.2
		Algal cover	0.021	4.4
Shannon-Weiner	0.59	Mean depth	3.842	7.3
		% sand	-0.828	3.1
		Height	-0.003	14.5
		Rock cover	0.036	4.7
		Surface Area	0.239	10.8

Table 4 continued ...

Variable	Model R <sup>2</sup>	Factor	Slope	F
Abundance	0.57	Volume	0.367	10.8
		Crevice	0.274	5.8
		% sand	-1.776	4.1
		% <i>Hormosira banksii</i>	1.957	7.9
		% bare rock	-2.188	12.7
		% rubble	3.095	6.2
		% foliose algae	1.765	10.2
		Height	-0.005	7.3
		Rugosity	-0.073	5.4
Biomass	0.56	Crevice Density	2.624	8.4
		% sand	-1.663	3.5
		% rubble	3.019	6.3
		Surface Area	1.28	105.3
Maximum Length	0.51	% sand	-71.398	3.0
		% rubble	198.462	11.0
		Height	-0.126	3.0
		Surface Area	54.267	84.0
Density	0.49	Mean depth	4.061	2.5
		Crevice Density	2.67	8.5
		% sand	-3.275	13.0
		% bare rock	-4.473	24.4
		% coralline turf	-3.176	20.2
		% seagrass	-2.857	12.1
		Height	-0.006	16.3
		Rugosity	-0.059	4.0
		Surface Area	-0.387	7.7
Berger-Parker	0.43	Volume	-0.094	3.8
		% sand	1.278	6.3
		% <i>Hormosira banksii</i>	0.713	5.8
		Algal cover	-0.023	2.6
		Rock cover	-0.038	3.9
Maximum Weight	0.36	% sand	-1.177	2.9
		% rubble	2.001	4.0
		Surface Area	0.728	49.1
Mean Length	0.31	% bare rock	44.333	10.4
		% foliose algae	-46.3	23.1
		Surface Area	13.634	22.0
Mean Weight	0.25	% bare rock	0.727	9.6
		% foliose algae	-0.624	14.5
		Surface Area	0.206	17.3
Biomass Density	0.22	Crevice Density	2.748	7.1
		% sand	-2.392	5.5
		% rubble	3.198	5.5

### 3.3.3) Seasonal variability

Richness did not vary significantly between the three sampling seasons ( $F_{2,93} = 0.685$ ,  $P = 0.506$ ; Fig. 1). Abundance ( $F_{2,93} = 26.25$ ,  $P < 0.001$ ), biomass ( $F_{2,93} = 8.67$ ,  $P < 0.001$ ), biomass density ( $F_{2,93} = 16.04$ ,  $P < 0.001$ ), and density ( $F_{2,93} = 60.89$ ,  $P < 0.001$ ) were significantly greater in spring and summer due to recruitment events (Fig. 1). For the same reason, mean total length and mean weight were lower in spring and summer ( $F_{2,93} = 49.9$ ,  $P < 0.001$ ;  $F_{2,93} = 16.44$ ,  $P < 0.001$  respectively; Fig. 1), but maximum fish length and weight did not vary significantly (ANOVA;  $F_{2,93} = 0.471$ ,  $P = 0.626$ ;  $F_{2,93} = 1.594$ ,  $P = 0.209$  respectively; Fig. 1). Shannon-Weiner diversity was consistent between seasons (ANOVA;  $F_{2,93} = 1.72$ ,  $P = 0.185$ ) although Berger-Parker dominance was significantly greater (ANOVA;  $F_{2,93} = 6.28$ ,  $P < 0.05$ ) in the spring/summer recruitment months (Fig. 1). High Berger-Parker scores are attributable to large numbers of settling larvae of a single species, *Grahamina capito*.

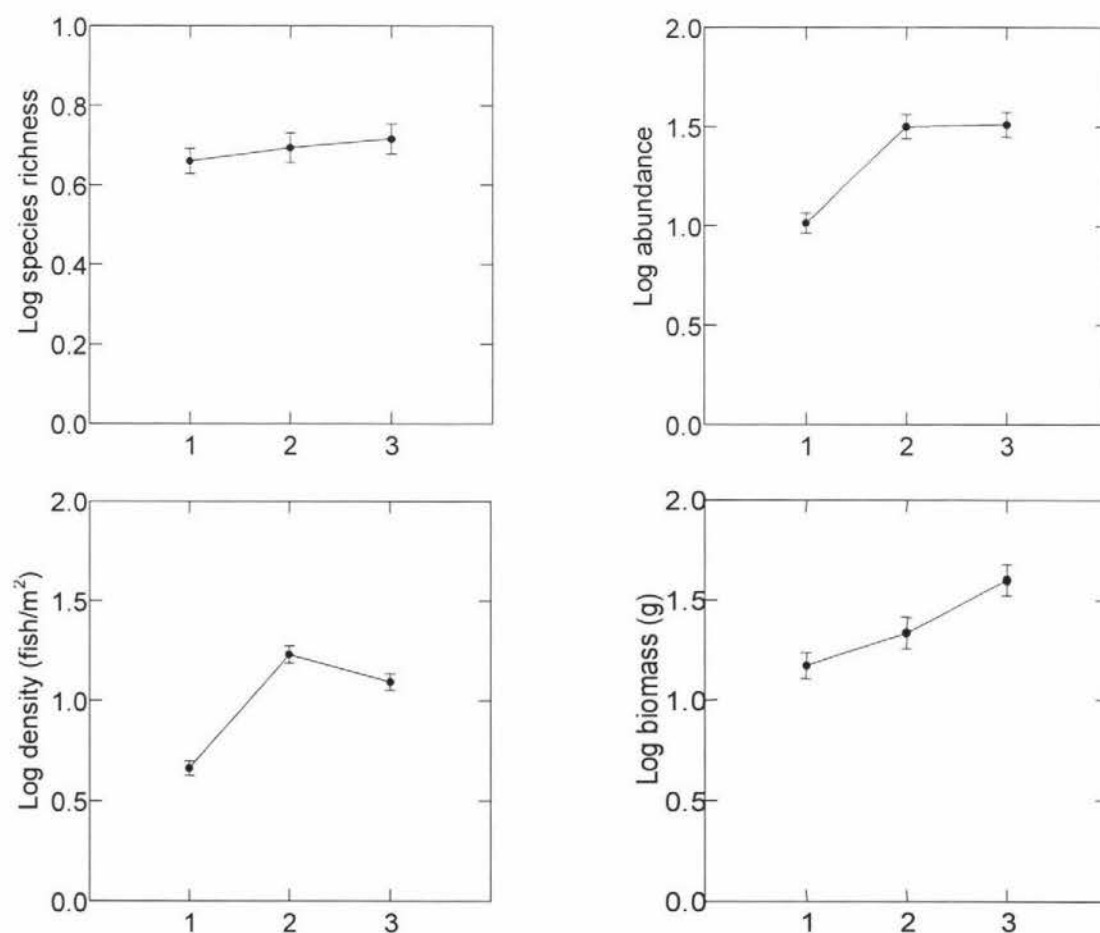


Figure 1 Seasonal change in 11 rockpool fish assemblage structure variables. Fish censused from 96 rockpools on Pohatupapa Point and the Ouepoto platform during winter 2000, spring 2000, and summer 2001. Log transformation is  $\log_{10}$ . 1 = winter; 2 = spring; 3 = summer.

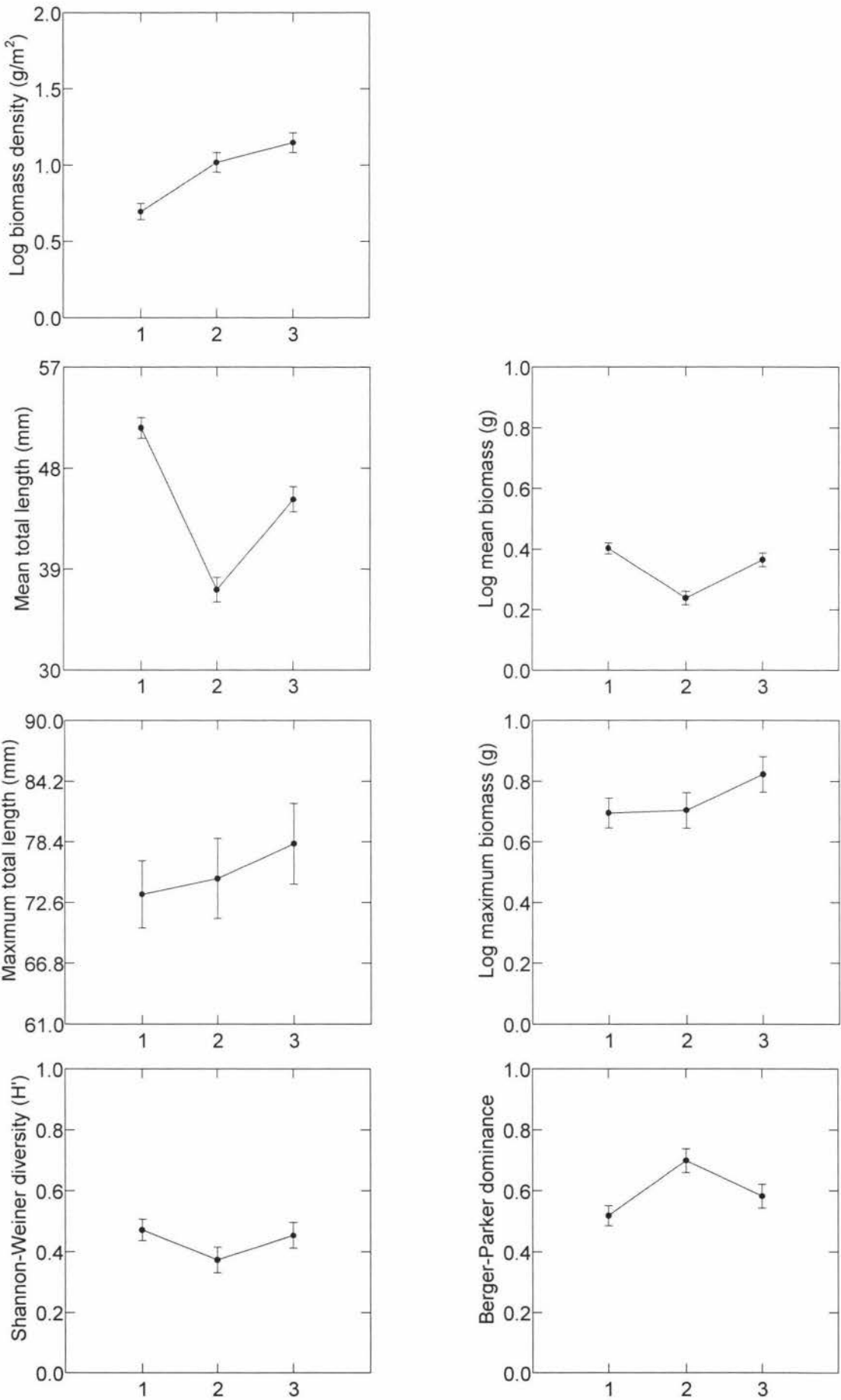


Figure 1 continued ...

3.3.4) Ordination analysis

The percent variance explained by axes 1 and 2 in the DCA ordination (Figure 2) of rockpools was 38% and 19% respectively (Sorenson distance). The densities of eleven species used to construct the DCA axes were significantly correlated (Bonferroni adjusted) with one or more of the first three axes (Table 5; Fig. 3). Rockpools with higher axis 1 scores (right of Fig. 3) typically had greater densities of *E. rubrus*, *T. melobesia*, *F. lapillum*, *D. morelandi* and *Gastroscyphus hectoris*. Pools with lower scores had greater densities of *A. fuscus* (Table 5; left of Fig. 3). The most common species, *G. capito*, showed no relationship with axis 1. Axis 2 was positively correlated (top of Fig. 3) with *G. capito* and *T. melobesia* density, and negatively correlated with *D. morelandi*, *N. celidotus* and *Gobiopsis atrata* density (Table 5; bottom of Fig. 3). Axis 3 (not shown) was positively correlated with *F. lapillum* and *B. medius* density and negatively correlated with *L. filum* density (Table 5).

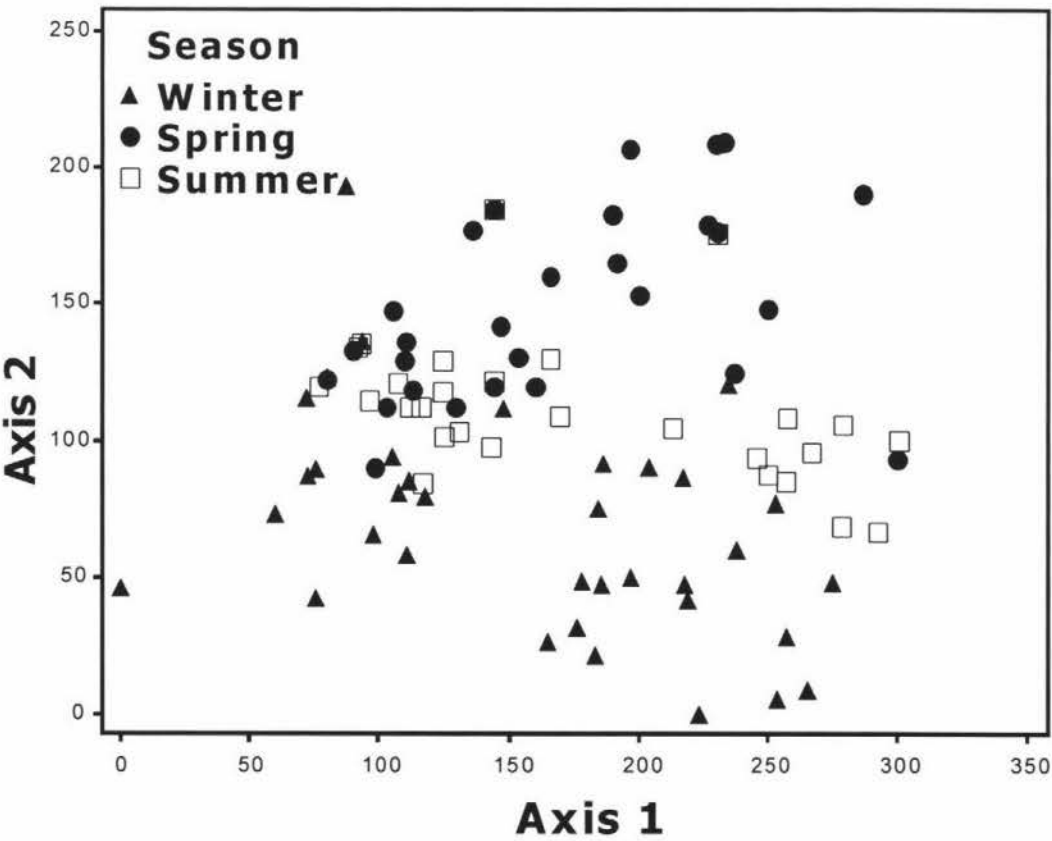
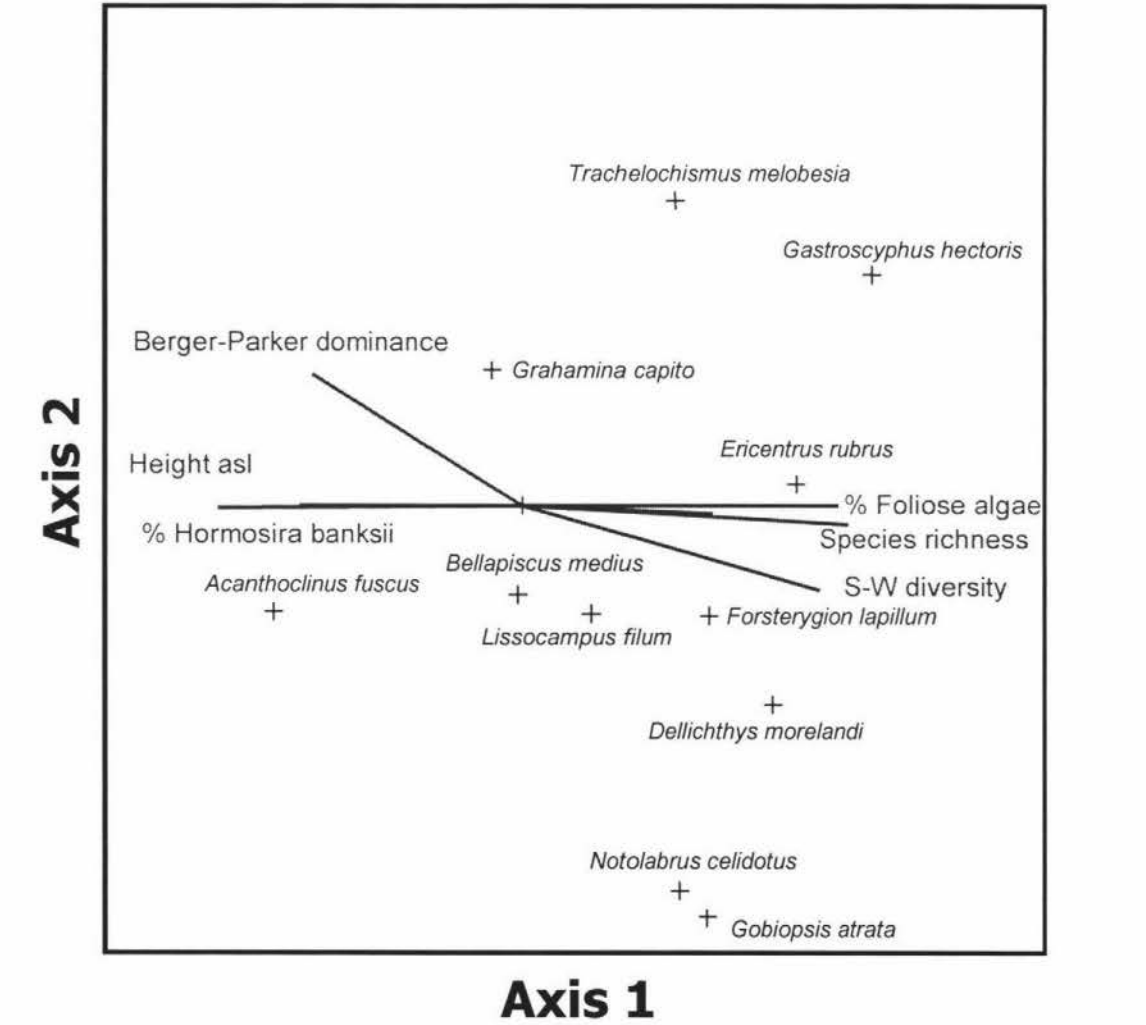


Figure 2 DECORANA ordination of 96 rockpools from Pohatupapa Point and the Ouepoto platform. Axes constructed using species density (fish/m<sup>2</sup> surface area) in pools. Density is log transformed (log<sub>10</sub>(x+1)). The season a rockpool was sampled is indicated by the symbol.

**Table 5** Bonferroni adjusted probabilities for Pearson correlations between species density and the first 3 axes of the DCA ordination. + = positive correlation; — = negative correlation; ns = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.001$ .

Species	Axis 1	Axis 2	Axis 3
<i>Notolabrus celidotus</i>	ns	—*	ns
<i>Acanthoclinus fuscus</i>	—**	ns	ns
<i>Ericentrus rubrus</i>	+**	ns	ns
<i>Grahamina capito</i>	ns	+**	ns
<i>Bellapiscus medius</i>	ns	ns	+**
<i>Forsterygion lapillum</i>	+**	ns	+**
<i>Dellichthys morelandi</i>	+**	—*	ns
<i>Lissocampus filum</i>	ns	ns	—*
<i>Gastroscyphus hectoris</i>	+*	ns	ns
<i>Trachelochismus melobesia</i>	+ $P=0.057$	+**	ns
<i>Gobiopsis atrata</i>	ns	—*	ns



**Figure 3** Position of species correlated with axes 1, 2 or 3 of the DECORANA ordination of rockpools sampled at Pohatupapa Point and the Ouepoto platform. Vectors are correlations between habitat variables, assemblage structure variables, and ordination axes. Cut off  $R^2$  value for vectors = 0.3.



All but five of the habitat variables were significantly correlated with one or both of the first two axes (Table 6). Axis 1 contrasts pools higher on the shore with high percent cover of *H. banksii* and rubble (left of Fig. 2) with deep, rugose pools lower on the shore with more foliose algae and crevices (right of Fig. 2; Table 6). The vectors on Figure 3 show the relationship between the habitat variables with the strongest  $r^2$  in a linear regression on axes scores, and the species correlated with the 1st three axes. High shore pools were dominated by *A. fuscus* while the assemblages in high complexity low shore pools were more diverse. The 2nd axis was negatively correlated with rock cover and rugosity.

**Table 6 Bonferroni adjusted probabilities for Pearson correlations between habitat variables and the first 2 axes of the DCA ordination. + = positive correlation; — = negative correlation; ns = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.001$ .**

Habitat variable		Axis 1	Axis 2
Position	Height asl	—**	ns
Size	Surface area	ns	ns
	Volume	+ *	ns
	Maximum depth	+ *	ns
	Mean depth	+ **	ns
Substrate composition (proportion)	% Sand	ns	ns
	% Bare rock	ns	ns
	% Rubble	—*	ns
	% <i>Hormosira banksii</i>	—**	ns
	% Foliose algae	+ **	ns
	% Eelgrass	ns	ns
	% Coralline turf	ns	ns
Shelter and complexity	Number of crevices	+ *	ns
	Crevice density	+ p=0.098	ns
	Rock cover (estimate)	+ **	—**
	Rugosity (estimate)	+ *	—**
	Algal cover (estimate)	+ **	ns

The position of rockpools on axis 2 varied significantly with season (ANOVA;  $F_{2,93} = 39.1$ ,  $p < 0.001$ ; Fig. 2). Rockpools sampled in winter scored lowest on axis 2 followed by summer then spring with the highest scores. This represents an increase in abundance due to larval recruitment of *G. capito* and *T. melobesia* during October and November (Table 7). *Gobiopsis atrata* was negatively correlated with the second axis. This is also a seasonal effect. *Gobiopsis atrata* was found in 7 pools in winter and 1 in spring. The density of two species (*N. celidotus* and *D. morelandi*) negatively correlated with the 2nd axis did not change over the three sampling seasons (ANOVA: *N. celidotus*,  $F_{2,93} = 1.846$ ,  $p = 0.164$ ; *D. morelandi*,  $F_{2,93} = 1.14$ ,  $p = 0.249$ ). However, both species were typical of rugose pools with shelter, two habitat variables negatively correlated with the 2nd axis (Table 6). Axis 3 (not shown) only explained 8% of the variance. No habitat variable varied significantly with axis 3 but a one-way ANOVA separated rockpools sampled in summer from the other two groups ( $F_{2,93} = 4.64$ ,  $p < 0.05$ ). The densities of *F. lapillum* and *B. medius* (positively correlated with axis 3; Table 5) were greater in summer due to large numbers of larval recruits (Table 7).

**Table 7 Seasonal change in total density of species with large numbers of larval recruits. Total density calculated as number of fish/pool surface area of all occupied rockpools combined. Inferred recruitment peaks are shaded.**

		<i>Grahamina capito</i>	<i>Trachelochismus melobesia</i>	<i>Forsterygion lapillum</i>	<i>Bellapiscus medius</i>
Winter	Proportion of pools occupied	0.78	0.05	0.4	0.58
	Total density in occupied pools	0.86/m <sup>2</sup>	0.42/m <sup>2</sup>	0.52/m <sup>2</sup>	0.39/m <sup>2</sup>
Spring	Proportion of pools occupied	1.0	0.43	0.36	0.46
	Total density in occupied pools	8.9/m <sup>2</sup>	1.22/m <sup>2</sup>	1.3/m <sup>2</sup>	0.73/m <sup>2</sup>
Summer	Proportion of pools occupied	0.96	0.11	0.57	0.68
	Total density in occupied pools	4.98/m <sup>2</sup>	0.52/m <sup>2</sup>	2.0/m <sup>2</sup>	1.72/m <sup>2</sup>

Six assemblage structure variables (Table 2) were significantly correlated with the 1st two DECORANA axes (Table 8). Density, abundance, richness, and Shannon-Weiner diversity were greater to the right of axis 1, and Berger-Parker dominance to the left. Density and Berger-Parker dominance were positively correlated with axis 2 while

Shannon-Weiner diversity and mean total length were negatively correlated with axis 2. The relationships with the 2nd axis reflect high larval density during summer and lower diversity due to numerical dominance by the recruits.

**Table 8 Bonferroni adjusted probabilities for Pearson correlations between assemblage structure variables and the first two axes of the DCA ordination. + = positive correlation; — = negative correlation; ns = not significant; \* = P < 0.05; \*\* = P < 0.001.**

Assemblage structure variables	axis 1	axis 2
Density (fish/m <sup>2</sup> surface area)	+ *	+ **
Abundance	+ **	Ns
Richness	+ **	Ns
Mean total length (mm)	ns	—**
Shannon-Weiner diversity	+ **	—*
Berger-Parker dominance	—**	+ **

**3.3.5) Discriminant analysis**

Six species fit the criteria for discriminant analyses (see methods). Overall prediction success was generally high for all models although Cohens’ Kappa performance measure was low (<0.4) for 2 models (Table 9).

*Ericentrus rubrus* was correctly predicted absent in 61/65 pools and present in 28/31 pools. The variables included in the discriminant function (algal cover, *H. banksii* and tidal height) indicate *E. rubrus* is common in pools closer to low water that have high % cover of foliose algae. Overall prediction success for *A. fuscus* was 86%. The most highly weighted variables in the discriminant function were the number of crevices, tidal height, rugosity (all positive), and % foliose algae (negative).

*Dellichthys morelandi* and *L. filum* occurred most frequently in pools lower on the shore with high % cover of coralline turf. Respective discriminant functions differed in other variables however. High algal cover, many crevices and little rubble was important for *D. morelandi* (85% overall predictive success), while the discriminant function for *L.*

*filum* indicated that it was more likely to be found in large pools (volume), with little sand and low rock cover (79% overall predictive success).

Group membership (presence/absence) for *B. medius* and *F. lapillum* was relatively equal but both models performed rather poorly (Table 9). Deep rugose pools were important for *B. medius* and low rugose pools with many crevices and little rubble were the most important variables in the discriminant function predicting *F. lapillum* presence/absence. Despite the low performance power of these last two models, the absence of height in the discriminant function for *B. medius* is significant given it was included in the models for the other 5 species. *Bellapiscus medius* was found in pools at all shore levels whereas other species showed some degree of zonation.

**Table 9 Stepwise Discriminant Function Analyses (DFA) of species presence/absence in rockpools against habitat variables. Canonical discriminant functions are standardised by within group variances. 0 groups are absence; 1 groups are presence.**

Species	0 group centroid	1 group centroid	Total % correct prediction (jackknifed)	Cohens' Kappa	Discriminant function	F	Canonical discriminant functions
<i>Ericentrus rubrus</i>	-0.977	2.049	93%	0.83	% <i>Hormosira banksii</i>	16.7	-0.584
					Height	5.56	-0.364
					Algal cover	65.35	0.818
<i>Acanthoclinus fuscus</i>	-1.54	0.77	86%	0.69	Crevice	18	0.853
					Crevice density	6.54	-0.432
					% foliose algae	34	-0.976
					% seagrass	2.49	-0.245
					Height	12.88	0.554
					Rugosity	7.53	0.503
<i>Dellichthys morelandi</i>	-0.53	1.506	85%	0.65	Crevice	10.56	0.503
					% coralline turf	2.48	0.287
					% rubble	2.67	-0.269
					Height	6.88	-0.438
					Algal cover	5.69	0.405
<i>Lissocampus filum</i>	-0.634	1.157	79%	0.54	Volume	46.61	1.126
					% sand	10.34	-0.567
					Coralline turf	4.01	0.365
					Height	4.19	-0.367
					Rock cover	8.99	-0.626
<i>Bellapiscus medius</i>	-0.555	0.414	68%	0.35	Maximum depth	2.87	0.463
					Rugosity	6.39	0.679

Table 9 continued ...

Species	0 group centroid	1 group centroid	Total % correct prediction (jackknifed)	Cohens' Kappa	Discriminant function	F	Canonical discriminant functions
<i>Forsterygion lapillum</i>	-0.705	0.907	68%	0.35	Crevice	7.04	0.482
					% bare rock	3.53	0.317
					% rubble	5.85	-0.411
					Rugosity	2.51	0.302
					Height	9.82	-0.517

3.4) Discussion

Sufficient evidence was gathered in the present study to suggest that fish assemblage structure in rockpools on the central Hawkes' Bay coast is not random but structured by habitat and tidal height. All habitat variables contributed to some aspect of assemblage structure but due to the large number of variables, it is necessary to discuss the relative importance of each sequentially.

3.4.1) Rockpool size

Rockpool size had an important influence on assemblage structure. The results of the multiple regression analyses and inference from the DCA ordination show that diversity, abundance and biomass increase in larger rockpools. This is not entirely unexpected and others (e.g. Marsh et al. 1978; Bennett & Griffiths 1984; Mgaya 1992; Mahon & Mahon 1994) have reported similar patterns.

The relationship between pool volume and species richness could be explained by an area effect, although large pools higher on the shore were not necessarily diverse in terms of their fish assemblage. Greater densities of partial residents including *Dellichthys morelandi*, *Forsterygion lapillum* and *Ericentrus rubrus* were associated with larger pools. Although the physiological tolerances of these species are unknown, the relative physiochemical stability in larger pools may be more suitable habitat for these species that are not strictly intertidal (Paulin & Roberts 1992; Willis & Roberts 1996). Conversely, the true resident *Acanthoclinus fuscus* was not necessarily



associated with larger rockpools. This is likely to be testimony to the tolerance of environmental extremes described for this species (Davison 1984; Berger & Mayr 1992; Mayr & Berger 1992). The other true resident captured, *Bellapiscus medius*, was not necessarily associated with larger rockpools and was also found in pools at all shore levels. Innes & Wells (1985) described a moderate level of tolerance to exposure to low aquatic PO<sub>2</sub> and air for *B. medius*. These properties are more likely to be associated with smaller pools. Another aspect of rockpool size, depth, was important for fish density and diversity. Although oxygen concentration, temperature and salinity in a rockpool may change during the low tide, it is likely that the bottom of a deeper pool is more stable due to vertical stratification in these properties (Green 1971c; Wright & Raymond 1978; Congleton 1980). This stability means a deeper rockpool is likely to be more suitable for partial residents.

Pool size was also important for fish size. Multiple regression analyses revealed that mean and maximum length and weight were positively associated with surface area. This relationship is significant given that fish density decreased with surface area. Larger, but relatively fewer individuals in large pools possibly reflects intra- and interspecific competition (Neider 1993). The largest fish in 73% of the rockpools censused in the present study were *A. fuscus* and *Grahamina capito*. These species typically defend shelter, and their success in doing so is related to fish size (Mayr & Berger 1992), which is usually an indicator of dominance in rockpool fish (Gibson 1968; Faria *et al.* 1998). Predation on smaller fish in larger pools could also explain why fish size increased in large pools. Small fish were recovered from the digestive tracts of *A. fuscus* and *G. capito*, and *A. fuscus* particularly is known to take small fish (Paulin & Roberts 1992). Larger fish may also be absent from small pools due to habitat-dependent mortality. In smaller pools they risk greater exposure to avian predators and to the physical action of currents and waves (Mahon & Mahon 1994).

Many studies (Marsh *et al.* 1978; Bennett & Griffiths 1984; Mgaya 1992; Prochazka & Griffiths 1992; Mahon & Mahon 1994; Davis 2000; Silberschneider & Booth 2001) report positive relationships between pool size (volume, surface area, perimeter, depth) and fish assemblage structure (namely richness, abundance, and biomass). However, most discussion tends to focus on the influence of increasing shelter in larger pools and not pool size *per se*. Silberschneider & Booth (2001) determined that richness was best

predicted by a regression on pool perimeter, yet their discussion focused on rock cover and perimeter wasn't mentioned. Mahon & Mahon (1994) determined that volume was the best predictor of richness in their rockpools and inferred co-existence from microhabitat partitioning, despite finding no relationship between richness and habitat diversity (Simpsons index). Bennett & Griffiths (1984) determined that pool size was important for fish diversity and abundance, only because larger pools contained more cover. In the present study, larger pools also contained more crevices. This, and the fact that the number of crevices alone was the best predictor of diversity and abundance confounds the relationship between pool size and assemblage structure.

### **3.4.2) Habitat complexity, shelter, and substrate**

The predictive analyses used in the present study cannot determine cause and effect, but there are some significant and logical benefits to fish choosing to remain under rock/algal shelter during low tide. The impact of predation from within the resident fish community is generally considered to be low whereas the influence of external predators may be considerable (Gibson & Yoshiyama 1999) and there is evidence to suggest that access to shelter is important in reducing predation of small fish (Markel 1993). Predation on intertidal fish by other residents (Grossman 1986a,b; Wells 1986; Varas & Ojeda 1990), subtidal species foraging at high tide (Marsh *et al.* 1978; Paulin & Roberts 1992) and birds (Yoshiyama 1981; Mahon & Mahon 1994) has been described in a number of studies. In New Zealand, gulls, terns, shags, kingfishers and herons are all predators of rockpool fish (Paulin & Roberts 1992), and the study area is well populated by a number of sea-birds that forage in intertidal rockpools (Department of Conservation 1994; pers. obs.). Fish were removed from the digestive tracts of two common intertidal residents (*G. capito* and *A. fuscus*), and it is also likely that piscivorous subtidal species (e.g. banded wrasse – Duffy (1988) Appendix 3 Table 1) forage over the platforms at high tide. Additionally, the study reefs are adjacent to small coastal settlements and caravan parks, and both study platforms are frequented by children often seen capturing animals in rockpools.

The role of competition in structuring the assemblages in the present study is difficult to assess given agonistic behaviour was not examined. However, others have observed aggressive interactions between intertidal fish that appear to influence the structure of

assemblages. Marsh *et al.* (1978) suggested that aggressive interactions between adult and juvenile *Clinus superciliosus* could result in smaller fish being forced into open areas, and Prochazka & Griffiths (1992) hypothesized that size-specific partitioning of pools based on shore height by individual species may be the result of territoriality and aggressive behaviour. The amount of shelter in a pool may limit inter- and intra-specific competition for space. Although most rockpool fish are generally inactive during the low tide, more crevices would tend to limit intra-specific interactions. This would be especially important for conspecific nest-guarders, represented by at least two families in the present study, the Tripterygiidae and Gobiesocidae (Thompson 1981; Paulin & Roberts 1992). Additionally, increased rock cover may increase the number of microhabitats available for different species and therefore limit interspecific interactions. Stephens *et al.* (1970), Koppell (1988), and Mayr & Berger (1992) showed that different shelter preferences by co-occurring intertidal fish species influences microhabitat segregation. In the present study, pools with the most shelter were the most diverse and abundant in terms of the fish assemblage, being able to accommodate a wider range of species. Axis 2 of the DCA ordination was particularly interesting in that although it was essentially seasonal in structure, it was also negatively correlated with rugosity and rock cover. This relationship indicated that low complexity pools had extremely high densities of *G. capito* recruits. It is possible that these small fish may have been excluded from complex rockpools by larger territorial fish through competition or predation. In the present study, rugosity was positively correlated with axis 1 of the DCA ordination suggesting that rugose pools promote diversity and abundance of fish. Given rockpool fish are generally benthic, this relationship is probably a response to the provision of more substrate than would be found in pools with a regular shaped bottom. Rugosity featured in the discriminant function models of *B. medius*, *A. fuscus*, and *F. lapillum*, but not for other species. Difference in response to this variable indicates that rugosity may be a factor involved in microhabitat partitioning.

While some studies have shown that the presence of algae is not related to fish diversity and abundance (Black & Miller 1991; Bennetts & Griffiths 1994), others have shown that algal cover is important (Marsh *et al.* 1978; Prochazka & Griffiths 1992; Silberschneider & Booth 2001). The role of algae as recruit habitat is also debatable. Pfister (1995) showed that the recruitment density of particular species is negatively

related to algal cover, and Thompson (1979), in examining a subtidal habitat, found that juveniles of common triplefin species settle into all habitat types. In another study, Marliave (1977) showed that while some rockpool fish species settled preferentially onto gravel, sand and pebbles, others settled primarily into algae. In addition, Duffy (1988) observed that juvenile *Notolabrus celidotus* settle directly into finely branching brown algae.

The results of the present study suggest that algal cover is important for rockpool fish assemblages. The regression models predicting mean length and weight showed that the smallest fish were common in pools with abundant algal cover. The multiple regression analyses, and the relationship between axis 1 of the DCA ordination, the habitat variables, and the assemblage structure variables, showed that species richness and abundance were positively related to foliose algal cover.

Foliose algae provides shelter from potential predators, and this may be especially important for abundant settling larvae that are potential prey for larger conspecifics. The increase in mean fish size with decreasing algal cover is possibly a result of a change in substratum preference with growth, as has been described for intertidal fish by Shiogaki & Dotsu (1971) and Marliave (1977). Diversity and abundance in algal rich pools may have been promoted by food availability. New Zealand fucoid algae typically harbours high densities of small crustaceans that are prey for many rockpool fish species (Russell 1983; Choat & Ayling 1987). However, it is difficult to determine whether foliose algae promoted diversity and abundance primarily through the provision of shelter or as a food resource. In the present study, no typically herbivorous fish were found but many species collected from diverse assemblages (eg. *Notoclinus fenestratus*, *N. compressus*, *E. rubrus*) feed on small weed dwelling crustaceans (Russell 1983; Paulin & Roberts 1992). However, the cryptic colouration and laterally compressed body form of these, and other species found in algal-filled pools (eg. *Scorpaena papillosus*) makes them difficult to observe. These species are morphologically and behaviourally adapted to living in foliose algae, suggesting also that they use algae for shelter. This argument is probably artificially polarized, and it is likely that algae is used as food and shelter by rockpool fish. Manipulative experiments are required to determine the relative contribution of each. In addition, some of the species collected from diverse assemblages (e.g. *Gastroscyphus hectoris* and *D. morelandi*) are known to lay eggs on

algal fronds (Paulin & Roberts 1992), and this may also explain part of the relationship between richness and algal cover, as access to suitable nest sites is likely to be important.

In the present study diversity and abundance were negatively associated with % sand cover. Sand tends to simplify habitat by infilling crevices hence reducing shelter and potentially the number of microhabitats. Similar relationships between sand cover and assemblage structure have been described by others (Macpherson 1994; Aburto-Oropeza & Balart 2001), and Syms & Jones (1999) found that sand was infrequently used as habitat by a guild of blennoid fish (including 4 species captured in the present study) in north-eastern New Zealand. Abundance and density were generally lower in pools with high % bare rock cover. Bare rock, like sand, offers fish little in the way of food resources and shelter. Density was also negatively associated with coralline turf and seagrass. Both these substrates trap sand that may lower microhabitat availability, however, they also provide habitat for potential prey. It may be that food was not necessarily limiting in rockpools but that space was more important. This is supported by the fact that the density of crevices in a pool was positively related to fish density. It is also significant that maximum fish size was positively related to % bare rock and rubble. These habitat variables were characteristic of higher pools (DCA) that were dominated by *A. fuscus*, in many cases the largest fish in a pool. Again this is testimony to the ability of *A. fuscus* to persist in what would be sub-optimal habitat for most other species.

Discriminant function analyses were not particularly useful in separating rockpool selection between common species. This indicated that there was significant overlap in habitat selection, at least on the scale of the rockpool. All species for which discriminant functions could be calculated, except *B. medius* and *A. fuscus*, were predicted to be more common in pools lower on the shore and all but *B. medius* were better predicted in pools with some form of algal or rock cover. Interestingly, the number of crevices was a significant positive predictor of *A. fuscus* presence, but crevice density was a negative predictor of its presence. Given the territorial and aggressive nature of this species (Berger & Mayr 1992; Mayr & Berger 1992), the negative correlation with crevice density maybe due to defense of multiple crevices, or entire pools by *A. fuscus*.



### 3.4.3) Rockpool height

In the present study, fish assemblage structure changed with rockpool height. Multiple regression showed that richness, Shannon-Weiner diversity, abundance, density, and maximum length decreased in pools upshore. The correlation between axis 1 of the DCA ordination and pool height showed that sparsely populated, low diversity assemblages in pools high on the shore gave way to more abundant and diverse assemblages in pools towards the low tide mark.

Discriminant function analyses (DFA) and axis 1 of the DCA ordination separated higher pools dominated by *A. fuscus* from lower pools with a suite of partial residents including *E. rubrus*, *D. morelandi*, *Lissocampus filum*, *Trachelochismus melobesia*, and *F. lapillum*. The density of *G. capito* was not significantly correlated with axis 1 of the DCA ordination (essentially the pool height axis), and a discriminant function could not be calculated for this species because of its prevalence. *Grahamina capito* was found throughout the height range of the platform. Similarly, there was no suggestion that *B. medius* selected pools based on shore level. Three distribution patterns were obvious. Pools higher on the shore dominated by *A. fuscus* but also present, *G. capito* and *B. medius*; shore-wide distributions of *G. capito* and *B. medius*; and lower pools with *F. lapillum*, *E. rubrus*, *T. melobesia*, *D. morelandi* and rarer species. These analyses confirm that *A. fuscus* is a high-shore specialist, and suggest that *G. capito* and *B. medius* are intertidal generalists.

The mechanisms by which species separated pools based on shore level are most likely related to differences in physiological tolerance. *Acanthoclinus fuscus*, as noted earlier is generally considered an intertidal specialist and is able to exploit high-shore pools that undergo greater physiochemical change. Conversely, partial residents are unlikely to be able to tolerate to such a degree physiochemical change, and were largely restricted to low-shore pools. *Bellapiscus medius* is mostly intertidal in distribution (Paulin & Roberts 1993) and may also be tolerant of a range of environmental conditions, hence its shorewide distribution. *Grahamina capito* is considered to be a subtidal species (Willis & Roberts 1996 Table 3). However, in the present study the abundance and distribution of *G. capito* relative to *B. medius* and *A. fuscus* suggests that

in the Central Hawke's Bay, this species may be considered a true resident. Subtidal collections are required to determine the full extent of its distribution.

It is possible that other mechanisms contributed to greater diversity, abundance and density downshore. Low shore pools are emerged for shorter periods and hence the length of exposure to avian predators is much shorter. However, the length of exposure to foraging fish would be longer in low shore pools that are emerged for greater periods of time. Predation of intertidal fish has been observed in other studies, but it is unknown if the intensity of predation in this study was sufficient to cause the large-scale distribution patterns observed. It is also possible that the length of access to, and availability of food accounted for some of the observed distribution in the fish assemblages. Although little is known of the high tide movement of New Zealand rockpool fish, stomach contents of fishes in overseas studies clearly reveal that some species forage outside of rockpools during high tide (Horn *et al.* 1986; Ralston & Horn 1986; John & Lawson 1991). Zander *et al.* (1999) suggest vertical distribution of fish in the intertidal zone is correlated with temporal restriction of access to food, and Wyttenbach & Senn (1993) also suggest that the nutritional condition of a fish can be influenced by the shore level on which it resides. The length of time species have to forage over the tidal platform is much shorter if they reside in high-shore pools that are emerged for shorter periods. Additionally, turfing algae harbours high densities of invertebrate prey and was not as dense on the upper part of the tidal platform. It is unlikely however, that predation pressure and food availability were solely responsible for the distribution of fish in rockpools in the present study. High and midshore pools were dominated almost exclusively by *A. fuscus*, *G. capito* and *B. medius*. Unless these species outcompete all others for food and space (assuming these are limiting), one would expect to collect other species in high-shore pools in densities reflective of their relative abundance. However, this was not the case.

Habitat separation as a function of height was obscured to a large degree by overlap within and between the three vertical distributions identified. Similar patterns of species overlap and coexistence have been attributed to low species richness (Prochazka & Griffiths 1992) and also to microhabitat separation (Nakamura 1976a,b; Horn & Riegler 1981; Gibson 1982; Pfister 1992). The positive relationship between shelter and diversity/density in the present study suggests the latter may be the case here.

Unfortunately, because of the cryptic nature of rockpool fish, microhabitat separation is difficult to observe *in situ*.

Pool height also featured in the regression model predicting maximum fish length indicating that fish size increases downshore. This may have been due to intraspecific changes in mean fish size (Gibson 1972; Mahon & Mahon 1994) or to shifts in species composition with larger subtidal fish being added downshore. The former explanation is likely to be the case, and it is important to note that the contribution of pool height to this model was low. *Grahamina capito* and *A. fuscus* were the largest fish in 73% of the pools that were sampled while in only 3 cases was a surge zone fish (*N. celidotus*) the largest fish in a pool. The partial residents that were added downshore were not necessarily larger than the true resident species but their presence in low shore pools does suggest that the rockpool fish assemblage grades into the subtidal assemblage downshore. Mahon & Mahon (1994) described a similar pattern whereby more partial residents were present in larger pools, and other studies have shown that partial residents contribute significantly to intertidal fish communities (Thompson & Lehner 1976; Beckley 1985b; Lardner *et al.* 1993). However, Yoshiyama *et al.* (1986) determined that parts of the Californian coast had distinct intertidal and subtidal fish assemblages, and Prochazka (1996) noted that there were no transient species on the South African west coast.

#### 3.4.4) Seasonality

In previous studies it has been demonstrated that seasonality in diversity, abundance and density of intertidal fish is related to an influx of settling juveniles usually (Beckley 1985a, 2000; Bennett 1987), but not always (Ali & Hussein 1990) during summer. Juveniles of transient species account for most of the variability while resident species often show no seasonal trends in relative abundance (Yoshiyama *et al.* 1986) or richness (Bennett 1987). In the present study, seasonality in community structure was related primarily to recruitment events in the true and partial resident community. Surge zone (transient) species contributed little to the observed variation. Richness and Shannon-Weiner diversity were consistent between seasons, while abundance, density, and Berger-Parker dominance were greater during periods of peak recruitment (Spring and Summer).

Three surge zone species (*Scorpaena papillosus*, *Peltorhamphus latus* and *Bovichthys variegatus*) were rare ( $n = 16$ ), and there was no seasonal variation in the density of the most common surge zone fish, *Notolabrus celidotus* ( $n = 68$ ) in occupied pools. Conversely, the density of the resident fauna increased markedly during recruitment events. For example, higher densities of *T. melobesia*, *F. lapillum*, *G. capito*, *B. medius*, and *E. rubrus* were associated with periods of peak recruitment for each species. Adult densities were much lower but it is not known if this was due to migration to the subtidal or post settlement density-dependent mortality. If the former were true, then rockpools may be significant nursery habitat for these species. The results of this study are consistent with the views of Bennett (1987), Smale & Buxton (1989), and Willis & Roberts (1996) that the intertidal zone is not a significant nursery area for surge zone (transient) species. Large numbers of juveniles were present in pools, but they belonged primarily to species comprising the bulk of the adult community.

Seasonal variation in Tripterygiid density showed a similar pattern to that described by Willis & Roberts (1996) for 4 rockpools on the Wellington south-coast. However, in their rockpools Willis & Roberts (1996) found an alternating pattern of triplefin dominance in summer and Gobiesocid (clingfish) dominance in winter. This was attributed to natural mortality of triplefins during inclement winter weather. In the present study, triplefins were numerically dominant every month. This difference may be an artifact of the type of pools studied. Clingfish were relatively restricted to low shore pools while the common triplefins *G. capito* and *B. medius* were found shore wide. The Wellington south-coast pools were all large and close to low water. Alternatively, differences in exposure between the sites in the present, and Wellington south-coast studies may have explained the differences in seasonal dominance patterns. Willis & Roberts (1996) hypothesised that triplefins suffered large-scale episodic mortality during rough weather due to mechanical injury, whereas clingfish appeared immune due to their ability to adhere to the substratum using their ventral sucker. The study sites in the present study were much more sheltered in comparison, and the triplefin population may not have been subject to such rough weather as described for the Wellington south-coast.

Recruitment peaks differed for the three most common triplefins. *Grahamina capito* recruitment peaked in October/November while *B. medius* and *F. lapillum* recruitment peaked in February/March. Staggered recruitment may reduce interspecific competition for space and food (Willis & Roberts 1996). It is interesting that *B. medius* recruitment in the Central Hawkes Bay peaked in February/March, compared to November on the Wellington south-coast (Willis & Roberts 1996). This may be due to interannual variation in recruitment timing but it is also possible that *B. medius* recruitment in Central Hawkes Bay is offset to avoid competition with *G. capito*. *Bellapiscus medius* was much more abundant than *G. capito* on the Wellington south-coast.

### 3.4.5) Conclusion

The present study demonstrated patterns in the composition of fish assemblages present in rockpools that are associated with specific attributes of the pools, including upper shore vs lower shore, and simple vs complex habitats. Specifically, diverse and abundant assemblages were associated with large, complex, low shore pools. These assemblages included a number of partial resident species that are commonly recorded from subtidal habitats. A suite of apparently obligate intertidal species was also identified. *Grahamina capitio* and *B. medius* were ubiquitous species, collected shore wide, and also from small, less complex rockpools. *Acanthoclinus fuscus*, although collected shore wide, was more common on the upper part of the intertidal platform.

Mechanisms that acted to separate species over the shore are probably related to the physiological tolerance levels of each species, with some, particularly *G. capito*, *B. medius*, and *A. fuscus* apparently able to tolerate greater change in the rockpool environment. Partial residents may not have extended far upshore due to the fact their main distribution is quite likely subtidal, and their high-tide movements may be limited. Lower pools are also likely to provide a much more stable low-tide habitat. However, there was significant overlap in species distribution, specifically on the lower shore, sometimes with up to 10 – 15 species collected in any one pool. The positive relationship between pool size, shelter, diversity and abundance would tend to suggest that the availability of microhabitats mediated coexistence in rockpools. *In situ* observations of microhabitat preference in pools with high species richness would allow one to observe whether species differ in the type of microhabitat they occupy.



Alternatively, species occupying shelter in crevice rich pools may have simply arrived on a 'first come, first served' basis. In either case, shelter provides the obvious benefits of a refuge from predation and competition during low tide, suggesting that these interactions, past or present, may play a role in the organisation of this intertidal fish community. Although far from obvious, this hypothesis is supported by others who suggest that rocky intertidal fish communities are regulated by deterministic controls (Grossman 1982; Faria & Almada 1999). It must be stated though, that habitat structure appears to be the template over which these interactions are modified. For example, the life history of a partial resident or transient species means it is unlikely to compete for space with *A. fuscus*, or be exposed to wading avian predators for as long as the main intertidal distribution of *B. medius* and *G. capito*.

Seasonal effects on assemblage composition, and on the intertidal community as a whole, were directly related to recruitment events in the true and partial resident populations. Surge zone (transient) species, with the exception of *N. celidotus*, contributed little to the intertidal fish community. Comparison of the relative contribution of true and partial residents, and transient species, between this, and other studies would be interesting. However, inconsistency among authors in the designation of species as true and partial residents, and transient species, make direct comparison of published results difficult (Mahon & Mahon 1994). It is clear that in New Zealand it is difficult to classify a species by intertidal resident status given all intertidal fish have been collected subtidally around the New Zealand coast. It would appear however, that temporal variation in rockpool fish community structure on the Central Hawkes Bay coast is related to seasonal variability in the abundance of species that occur in rockpools as adults, and not to the seasonal presence of transient species as described in other studies.

## Chapter 4: Resilience of rockpool fish community structure on the Central Hawke's Bay coast

### Abstract

The fish assemblages in 26 intertidal rockpools on Pohatupapa Point, Central Hawke's Bay, New Zealand were repeatedly censused between June 2000 and March 2001 to determine the extent and rate of recovery, with an aim to assess the resilience of assemblage structure. Assemblages were censused at 1- and 3-month intervals during different times of the year to assess seasonal effects on resilience, and to determine if there was any difference in the level of recovery between these two time periods, as has been suggested by others. The assemblages in these resampled pools were compared to assemblages in a suite of control pools to control for natural seasonal variability in assemblage structure. They were also compared to the original collection to determine if recovery was directional.

The partial resident species collected were particularly poor recolonisers, relying mainly on larval recruitment to repopulate pools. Species that can be considered true residents including *Acanthoclinus fuscus*, *Grahamina capito*, and *Bellapiscus medius*, recolonised pools as larval fish and as larger fish. The level and rate of resilience was seasonally dependent, being greater in summer than in winter and spring. This was manifested by lower diversity, abundance, and biomass of recolonisers compared to control assemblages during winter and spring. During summer, there was generally no appreciable difference in the experimental and control communities. Some variability was observed in the ranks of recolonisers, but rank concordance analysis indicated that the taxonomic structure of the recolonising fish community was stable. The ranks of species in the recolonising community were not significantly different to the ranks of species in the control community, indicating that deterministic processes contribute to the regulation of this fish community. Stochastic events (sampling) and seasonal variability in community dynamics, particularly larval recruitment, contributed to the variability in the recovery of this fish community.

## 4.1) Introduction

The ability of rocky intertidal fish assemblages to recover from periodic disruptions to community structure (resilience) has direct bearing on the stability and persistence of the community (Gibson & Yoshiyama 1999). By nature, rocky intertidal fish live in a highly variable environment that fluctuates on scales of hours (tidal cycles), months (season) and years (e.g. Southern Oscillation). Despite this, studies have shown that in the long-term, rocky intertidal fish communities are remarkably persistent in terms of species composition (Thomson & Lehner 1976; Grossman 1982; Collette 1986; Yoshiyama *et al.* 1986; Mahon & Mahon 1994). In the short-term rockpool fish also recolonise rapidly after experimental defaunation (Collette 1986; Lardner *et al.* 1993; Polivka & Chotkowski 1998). Long-term and short-term stability has led to the conclusion that rocky intertidal fish assemblages are regulated by deterministic processes (Grossman 1982; Faria & Almada 1999). However, Beckley (1985b) and Willis & Roberts (1996) observed a pattern of variable recovery of defaunated rockpools whereby fish assemblages were slower to recover during winter but faster during summer. Willis & Roberts (1996) suggested that short-term stochastic events such as environmental disruption, recruitment variability and episodic mortalities may obscure broad-scale, deterministic patterns. The high level of resilience and persistence in intertidal fish communities is interesting given intertidal algal and invertebrate assemblages appear to be regulated by stochastic processes (Dayton 1971, 1974; Sousa 1979, 1984 Paine & Levin 1981). This is not entirely surprising given sessile organisms cannot escape disturbance, and recovery depends initially on the seasonal and local availability of propagules (Paine & Levin 1981). Intertidal fish are able to avoid disturbance by escaping to rockpool refuges, and their mobility relative to sessile organisms enables recovery of defaunated rockpools by movement of post-settlement fish from unaffected areas.

Rockpool fish studies that have examined patterns of persistence or resilience tend to focus on fish in a limited number of very large rockpools (e.g. Lardner *et al.* 1993 – 1 pool, 100m<sup>2</sup>; Collette 1986 – 2 pools, 1m deep; Beckley 2000 – 1 pool, 23m<sup>2</sup>; Willis & Roberts 1996 – 4 pools, 15m<sup>2</sup> – 17m<sup>2</sup>; Beckley 1985b – 3 pools, 21m<sup>2</sup> – 41m<sup>2</sup>; Thomson & Lehner 1976 – 2 pools, 600m<sup>2</sup> and 60m<sup>2</sup>). However, Mahon & Mahon

(1994) examined resilience in range of pool sizes and found only the very largest had similar fish communities in consecutive collections. As species richness increases with rockpool size (Chapter 3 this thesis; Bennett & Griffiths 1984; Prochazka & Griffiths 1992; Mahon & Mahon 1994; Silberschneider & Booth 2001) diverse rockpool assemblages may be more resilient and hence more stable. Connell & Sousa (1983) suggest that populations or communities on small areas are unlikely to be stable since even small perturbations may cause local extinction. It is not clearly established whether this is the case for rockpool fish because, apart from one study, resilience has been assessed only in large pools with diverse fish assemblages.

Measures used to assess resilience and stability of rockpool fish assemblages have included: similarity in rank abundance between paired collections, recovery of richness, abundance, biomass and diversity, taxonomic and numeric similarity indices, recovery of recolonist size structure, and temporal consistency of habitat/community structure relationships (Grossman 1982; Collette 1986; Lardner *et al.* 1993; Mahon & Mahon 1994; Willis & Roberts 1996; Polivka & Chotkowski 1998). In the present study, all but the last measure were used to assess the resilience of rockpool fish assemblages on an intertidal reef in the Central Hawke's Bay, New Zealand. Few studies have examined seasonality in recovery so it was decided to defaunate rockpools over a period covering the Southern Hemisphere winter, spring and summer to look at differences in the extent of recovery by season. I chose one and three month inter-collection intervals to see if recovery times reported elsewhere by Willis & Roberts (1996) and Polivka & Chotkowski (1998) held true for rockpool fish assemblages at Pohatupapa Point. Pools with a range of sizes, heights and physical characteristics were selected to see if recovery and resilience can be predicted by certain habitat characteristics.

## **4.2) Methods**

### **4.2.1) Sampling**

Fish from 26 intertidal rockpools on Pohatupapa Point (experimental site) were collected in June 2000 using rotenone. Collections were repeated around the same day

during July, October and November 2000, and February and March 2001 to examine the extent of recovery over 1- and 3-month periods at different times of the year. Fourteen control (i.e. previously unsampled) rockpools were sampled each time the experimental pools were resampled (Chapter 2 Table 1). Control pools were located on the Ouepoto platform and were as similar as possible to the experimental pools. A separate control site was chosen so harvesting pressure was not concentrated in one area. The positions of experimental and control pools were recorded using digital photographs and a hand-held GPS to aid relocation and ensure control pools were not resampled accidentally (Appendix 1).

All fish were placed in labelled plastic bags and stored at -20°C. In the laboratory fish were thawed and identified to species. Nomenclature follows Paulin & Roberts (1992), except for the Tripterygiidae, which follow Fricke (1994) and Clements *et al.* (2000). All fish were weighed to the nearest 0.01g using a Mettler-Toledo PB 3002 electronic balance. Total length (TL) was measured to the nearest mm using a small fish board constructed from a piece of half-pipe with metric rulers set on the inner walls.

Surface area, pool depth, pool volume, substrate composition, shelter from predators, physical complexity and height above low water were measured or estimated for each pool as described in Chapter 2.

Willis & Roberts (1996) considered that the arrival of freshly metamorphosed larvae in defaunated rockpools is independent of rotenone sampling and may bias estimates of recovery. To examine the influence of recruitment on recovery, I plotted length frequency histograms for each species and identified recruitment modes to determine the minimum size at which fish could be considered 'non-larval'. Comparative analyses were then performed including and excluding larval fish. For the purposes of this chapter, the fish "community" is defined as fish from all pools during a particular sampling period and "assemblage" is defined as fish from one pool.



## **4.2.2) Assessing recovery**

### **4.2.2.1) Rank abundance stability**

Rank abundance stability was examined for communities in experimental and control pools using Kendall's  $W_c$  (coefficient of concordance) (Siegel 1956) for multiple comparisons. Significance was determined using the Friedman chi-square ( $\chi^2_r$ ) (Zar 1984). Significant values suggest the null hypothesis (species ranks vary randomly between months) be rejected and that rank order is seasonally consistent (control site) and resilient (experimental site). To remove rank-order bias caused by zeros in the dataset, only species occurring in 4 or more of the collection months were included in the analyses.

Rank abundance similarity between the experimental and control sites was examined by calculating the Spearman rank correlation ( $r_s$ ) between experimental and control communities for all months combined (mean rank). Analyses were performed on data excluding larvae in SYSTAT Version 8.

### **4.2.2.2) Assemblage properties**

I used a two-way ANOVA to compare species richness, density and biomass between the experimental and control pools each month. If the interaction between pool type (experimental vs control) and month was significant, this was followed by pre-planned contrasts between experimental pools and control pools for each month. To protect against type II error, significance for the interaction was set at  $P < 0.15$ . An overall comparison of the two recovery periods (1-month vs 3-months) was also performed using a pre-planned contrast.

For each month, richness, density and biomass in experimental pools were compared to the first collection (June 2000) by two-way ANOVA (randomised block design; block = pool number, factor = month) and pairwise comparisons using Bonferroni adjustment.

Biomass was standardised for pool surface area and analyses were performed on  $\log_{10}(x+1)$  transformed data to control for differences in variance between experimental and control pools. The null hypothesis is that density, richness, and biomass are the same in the experimental and control pools and do not vary between months. Analyses were performed in SYSTAT Version 8 including and excluding larval fish to assess the influence of recruitment on these aspects of recovery.

#### 4.2.2.3) Multivariate distance

Recovery was also assessed using a multivariate distance measure that calculated the taxonomic and numeric similarity between paired assemblages in the experimental pools. Similarity ( $S$ ) between the original and recolonist assemblage was calculated for each month using a modified Sorenson distance measure:

$$100 \times 1 - \left( \frac{\sum \text{abs}(a_i - b_i)}{\sum a_i + \sum b_i} \right) \text{ where } a_i = \text{the number of individuals of the } i^{\text{th}} \text{ species in}$$

the original assemblage and  $b_i$  = the number of individuals of the  $i^{\text{th}}$  species in the subsequent assemblage, such that total recovery ( $S = 100\%$ ) was achieved when the abundance of each species was restored. Since I was interested only in recovery towards the original assemblage (June 2000), values of  $b_i > a_i$  were truncated to  $a_i$ . To assess the effect of recruitment on this measurement of resilience, distance measures were calculated including and excluding larval fish for comparison.

A two-way ANOVA was used to test for differences in  $S$  between collection months (block = rockpool number, factor = month). One and three month recovery periods were compared with a pre-planned contrast. In addition,  $S$  was averaged over all months for each pool and multiple linear regression was used to see which set of habitat variables (see Chapter 2) best predicted recovery. Analyses were performed in SYSTAT Version 8.

To determine how different species contributed to the distance measure (i.e. best vs worst recolonisers) I calculated the proportion of pools recolonised by each species each

month. For this diagnostic I use the term “recolonised” to describe the arrival of an individual in a pool that had a resident conspecific in June 2000. The abundance of recolonists relative to original resident conspecifics was also used to assess recolonising propensity.

#### **4.2.2.4) Size structure of recolonists**

The size structure of experimental and control populations was compared for common resident species. Length frequency histograms were constructed using fish from experimental and control pools and 3 – 4 size classes were constructed to maximise evenness in each category. Size class frequencies of experimental and control populations were compared in a two-way table and significance of the distribution was determined using Pearson  $\chi^2$ . Analyses were performed in SYSTAT Version 8 both including and excluding larval fish.

### **4.3) Results**

#### **4.3.1) General description**

A total of 6133 fish were taken from 96 rockpools (total number of collections = 226) between June 2000 and March 2001. The collections consisted of 18 resident and 6 surge zone species and were dominated taxonomically by the Tripterygiidae and Gobiesocidae (Table 1). Twenty species were collected from Pohatupapa Point (experimental pools) and 18 from the Ouepoto Platform (control pools) (Table 1). Both sites shared 14 species, and species that were exclusive to each site were rare (Pohatupapa Point: 6 species, 0.4% of total abundance; Ouepoto Platform: 4 species, 0.5% of total abundance). Fourteen species were collected in the first collection from Pohatupapa Point and only one species, the black goby *Gobiopsis atrata* never recolonised. However, 6 additional species were found. Richness in the initial collection ranged from 1 to 11 species per pool with an average of 4.1. Density ranged from 0.38 fish/m<sup>2</sup> to 10 fish/m<sup>2</sup> with a mean of 4. A complete description of the fish fauna from all collections combined, and of the rockpools is presented in Chapter 2 and Appendix 2.

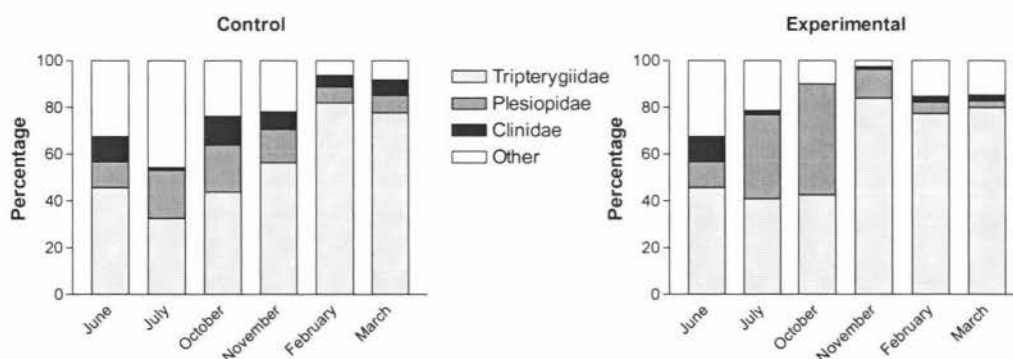
**Table 1 Numbers of all species caught from Pohatupapa Point and the Ouepoto platform. \* denotes captured in first collection from Pohatupapa Point.  $T_n$  = total number of fish. The % of larval and recently metamorphosed juveniles omitted is presented for each species, along with the minimum size for inclusion in the modified (excluding larvae) data set. n/a = included in both data set (surge zone species).**

Species	Family	Pohatupapa Point	Ouepoto Platform	$T_n$ all fish	$T_n$ excluding	% omitted	Minimum size (mm)
<i>Grahamina capito</i> *	Tripterygiidae	2270	1222	3492	1653	53	40
<i>Ericentrus rubrus</i> *	Clinidae	272	284	556	139	75	40
<i>Acanthoclinus fuscus</i> *	Plesiopidae	296	193	489	329	33	39
<i>Bellapiscus medius</i> *	Tripterygiidae	252	151	403	223	45	39
<i>Forsterygion lapillum</i> *	Tripterygiidae	159	182	341	190	44	40
<i>Trachelochismus melobesia</i> *	Gobiesocidae	132	64	196	24	88	25
<i>Notolabrus celidotus</i> *	Labridae	126	54	180	180	0	n/a
<i>Dellichthys morelandi</i> *	Gobiesocidae	98	76	174	80	54	30
<i>Lissocampus filum</i> *	Syngnathidae	65	81	146	130	11	40
<i>Scorpaena papillosus</i> *	Scorpaenidae	33	9	42	42	0	n/a
<i>Gastroscyphus hectoris</i> *	Gobiesocidae	5	31	36	14	61	30
<i>Ruanoho decemdigitatus</i>	Tripterygiidae	3	19	22	7	68	47
<i>Gobiopsis atrata</i> *	Gobiidae	11	5	16	16	0	40
<i>Parablennius laticlavus</i> *	Blenniidae	5	8	13	9	31	35
<i>Peltorhampus latus</i> *	Pleuronectidae	8	absent	8	8	0	n/a
<i>Notoclinus fenestratus</i>	Tripterygiidae	absent	7	7	2	71	40
<i>Notoclinus compressus</i>	Tripterygiidae	absent	3	3	3	0	40
<i>Parma alboscapularis</i>	Pomacentridae	2	absent	2	2	0	n/a
<i>Cristiceps aurantiacus</i>	Clinidae	2	absent	2	2	0	40
<i>Diplocrepis puniceus</i>	Gobiesocidae	absent	1	1	1	0	25
<i>Bovichthys variegatus</i>	Bovichthyidae	absent	1	1	1	0	n/a
<i>Ruanoho whero</i>	Tripterygiidae	1	absent	1	0	100	40
<i>Conger verreauxi</i>	Congridae	1	absent	1	1	0	n/a
<i>Gastrocyathus gracilis</i>	Gobiesocidae	1	absent	1	0	100	30

Larval settlement modes were identified for 18 resident species. Larvae and recently metamorphosed juveniles were generally considered to be fish smaller than the minimum size in the first collection (Table 1). Recruitment peaks of most species occurred in November 2000 and February 2001 so fish collected in June would have been resident intertidally for some months. Most fish in the settlement modes were recently metamorphosed juveniles but some of the slightly larger and very abundant size classes were also considered larvae. Larval fish accounted for approximately half the total abundance of the triplefins *Grahamina capito*, *Bellapiscus medius* and *Forsterygion lapillum*. Other species represented by large numbers of larvae were the banded weedfish *Ericentrus rubrus* (75%), striped clingfish *Trachelochismus melobesia*

(88%) and urchin clingfish *Dellichthys morelandi* (54%). All size classes of surge zone species were included in the full data set (i.e. "including larvae"). Resident species present in too fewer numbers to produce length-frequency histograms were compared to species in the same family that were present in greater numbers to determine if they were larval. If this could not be done, an estimate was made after considering the general size and appearance of the fish.

The major difference in family composition between experimental and control sites was the relative contribution of the Clinidae and families belonging to the "other" group, namely the Gobiesocidae, Sygnathidae and Labridae (Fig. 1). These families comprised a particularly small percentage of the experimental community during late winter and spring. Triplefins were numerically dominant at both sites every month with the exception of October 2000 at the experimental site. During October and July the large relative contribution of the Plesiopidae was due to low numbers of other recolonists rather than large numbers of *Acanthoclinus fuscus*. Family composition was most similar at both sites during summer.



**Figure 1** Family composition of the control community (Ouepoto platform) and the experimental community (Pohatupapa Point), June 2000 to March 2001.

#### 4.3.2) Rank concordance

Rank order stability in the experimental community was significant ( $W_c = 0.628$ ,  $P < 0.0001$ ) but lower than rank order stability in the control community ( $W_c = 0.724$ ,  $P < 0.0001$ ). However, significant concordance in the experimental community may have



been due to the constancy of ranks of *G. capito* and *D. morelandi* (Table 2). I recalculated  $W_c$  excluding these species and still obtained a significant correlation of ranks over time ( $W_c = 0.431$ ,  $P = 0.017$ ). Likewise, rank concordance in the control community was also significant when consistently high and low ranking species were removed (*G. capito*, *Parablennius laticlavius*, *Gastroscyphus hectoris*, *Trachelochismus melobesia*, and *Scorpaena papillosus*) ( $W_c = 0.329$ ,  $P = 0.065$ ). For both communities the probability of occurrence of the calculated  $W_c$  decreases when more species are added to the analysis (Fig. 2). However, at the control site  $W_c$  was significant ( $P < 0.05$ ) with 2 species compared to the 4 needed for significance at the experimental site. This indicates less concordance of rank order among the most common species at the experimental site (Table 2).

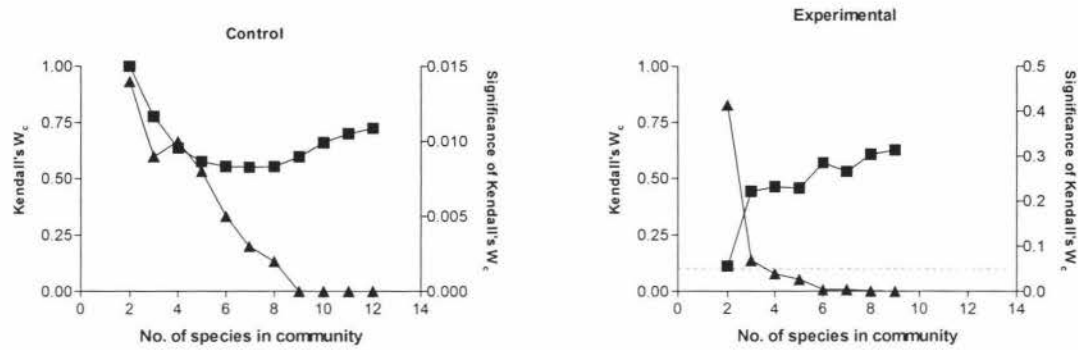
A comparison of average ranks of the 9 most common species between experimental and control collections revealed a significant positive correlation ( $r_s = 0.806$ ,  $P < 0.05$ ). This indicated that collecting did not have a strong effect on rank assemblage structure.

#### 4.3.3) Assemblage properties

Species richness, density and biomass were significantly lower in treatment pools than in control pools for all months combined whether including or excluding larvae (Table 3). However, the significance of the interaction between pool type (experimental vs control) and month was not sufficiently small to ignore ( $P$  always  $< 0.13$ ; two-way ANOVA). Monthly contrasts between experimental and control pools revealed low recovery of each variable during July, October and November, especially when adult recolonists were examined separately (Table 4 and below). Recoveries towards original levels of each variable (June 2000) were also generally lower during July, October and November (Table 4 and below).

**Table 2 Ranks of species at recolonist (experimental) and control sites each collection month (larval fish excluded). Only species used in the rank concordance test are given rank values. Percent of total abundance is shown in parentheses.  $W_c$  is Kendalls coefficient of concordance. Species ordered in average rank order.**

	Recolonist (treatment)								CONTROL						
	Species	Jun-00	Jul-00	Oct-00	Nov-00	Feb-01	Mar-01		Species	Jun-00	Jul-00	Oct-00	Nov-00	Feb-01	Mar-01
	<i>G. capito</i>	1 (23)	2 (26)	2 (33)	1 (82)	1 (71)	1 (60)	<i>G. capito</i>	1 (23)	1 (23)	1 (35)	1 (40)	1 (62)	1 (54)	
	<i>A. fuscus</i>	4 (11)	1 (36)	1 (48)	2 (12)	4 ( 5)	5 ( 3)	<i>A. fuscus</i>	4 (11)	2 (21)	2 (20)	2 (14)	4 ( 7)	3 ( 8)	
	<i>B. medius</i>	4 (11)	3 ( 8)	3 ( 5)	3 ( 1)	3 ( 5)	2 (12)	<i>F. lapillum</i>	2 (12)	6 ( 6)	6 ( 4)	3 (11)	2 (12)	5 ( 6)	
	<i>F. lapillum</i>	2 (12)	4 ( 7)	3 ( 5)	6 (<1)	7 ( 1)	4 ( 8)	<i>B. medius</i>	4 (11)	7 ( 4)	6 ( 4)	8 ( 2)	3 ( 7)	2 (17)	
	<i>L. filum</i>	3 (12)	5 ( 3)	3 ( 5)	4 ( 1)	9 ( 1)	7 ( 1)	<i>L. filum</i>	3 (12)	3 (19)	4 (10)	4 ( 8)	8 ( 1)	8 ( 2)	
	<i>N. celidotus</i>	8 ( 5)	5 ( 3)	7 ( 1)	8 ( 0)	2 (10)	2 (12)	<i>E. rubrus</i>	6 (11)	9 ( 1)	3 (12)	4 ( 8)	5 ( 5)	4 ( 7)	
	<i>E. rubrus</i>	6 (11)	7 ( 2)	8 ( 0)	4 ( 1)	6 ( 2)	6 ( 3)	<i>D. morelandi</i>	7 ( 9)	5 (10)	5 ( 7)	8 ( 2)	8 ( 1)	7 ( 2)	
	<i>S. papillosus</i>	9 ( 1)	7 ( 2)	8 ( 0)	6 (<1)	5 ( 3)	8 ( 1)	<i>N. celidotus</i>	8 ( 5)	4 (14)	11 ( 0)	6 ( 5)	6 ( 1)	6 ( 3)	
	<i>D. morelandi</i>	7 (10)	9 ( 0)	6 ( 3)	8 ( 0)	8 ( 1)	9 (<1)	<i>T. melobesia</i>	10 ( 1)	10 ( 0)	6 ( 4)	7 ( 4)	7 ( 1)	11 ( 0)	
	<i>G. atrata</i>	( 4)						<i>S. papillosus</i>	9 ( 1)	8 ( 2)	10 ( 1)	12 ( 0)	11 ( 1)	10 ( 1)	
	<i>P. latus</i>	( 1)	( 5)		( 1)			<i>G. hectoris</i>	12 (<1)	10 ( 0)	11 ( 0)	11 ( 1)	8 ( 1)	8 ( 1)	
	<i>G. hectoris</i>	(<1)	( 5)					<i>P. laticlavius</i>	10 ( 1)	10 ( 0)	9 ( 1)	8 ( 2)	12 (<1)	11 ( 0)	
	<i>T. melobesia</i>	( 1)	( 3)					<i>G. atrata</i>	( 4)	( 2)		( 1)			
	<i>P. laticlavius</i>	( 1)						<i>R. decemdigitatus</i>				( 3)		(<1)	
	<i>P. alboscaphularis</i>					(<1)	(<1)	<i>N. compressus</i>				( 1)	(<1)		
	<i>C. aurantiacus</i>					(<1)		<i>P. latus</i>	( 1)						
	<i>C. verauxi</i>			( 1)				<i>N. fenestratus</i>				(<1)	(<1)		
								<i>D. puniceus</i>				(<1)	(<1)		
								<i>B. variegatus</i>							
Abundance		308	61	80	274	728	274	Abundance	308	199	139	239	434	320	
	W <sub>c</sub> = 0.628; P < 0.0001; df = 8								W <sub>c</sub> = 0.724; P < 0.0001; df = 11						



**Figure 2** The effect of adding rarer species on community resilience as measured by Kendalls Rank Concordance ( $W_c = \blacksquare$ ). Probability of  $W_c = \blacktriangle$ ; horizontal line =  $P = 0.05$ .

**Table 3** Partial results of two-way ANOVA testing for variation in richness, density and biomass by pool type (experimental vs control) and month, including and excluding larvae. Data shown for all months combined.

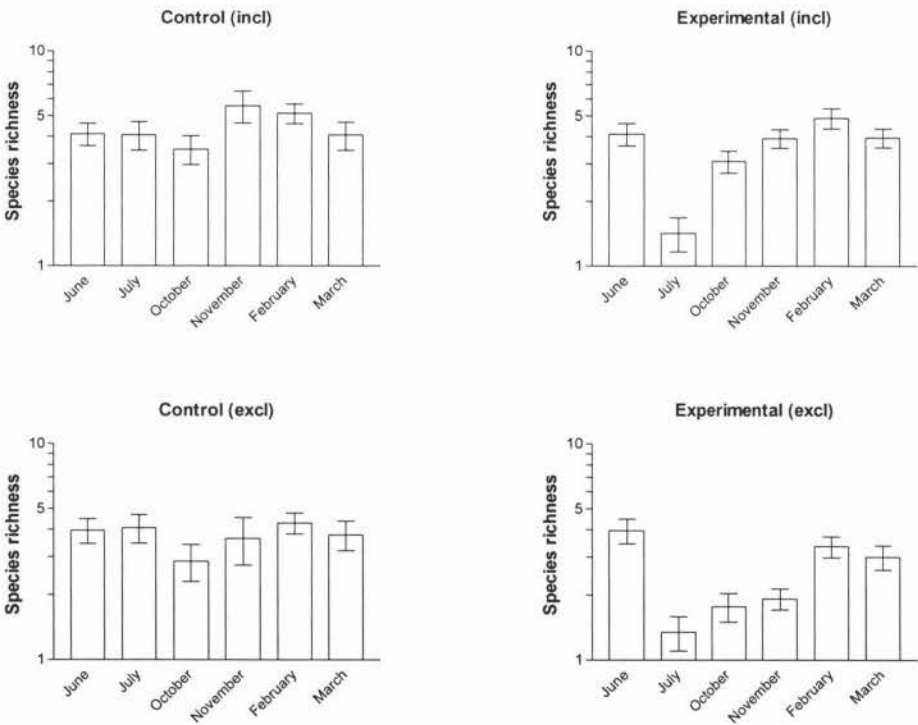
	Including larvae		Excluding larvae	
	$F_{1,4}$	P	$F_{1,4}$	P
Species richness	13.77	< 0.001	28.91	< 0.001
Density (fish/m <sup>2</sup> )	63.52	< 0.001	85.84	< 0.001
Biomass (g/m <sup>2</sup> )	79.55	< 0.001	74.39	< 0.001

*Richness*

Richness was generally consistent in the control pools over the sampling period (including larvae: mean 3.5 – 5.6 species per pool; excluding larvae: mean 2.8 – 4.3 species per pool) but fluctuated considerably in the experimental pools (Fig. 3). When larvae were excluded, richness in experimental pools was lower than original and control levels in all but the summer collections (Table 4). When larvae were included the only significant difference between experimental and control/original richness was after the first inter-collection interval (Table 4). There was no significant difference in recovery between 1- and 3-month periods (including larvae –  $F_{1,190} = 2.97$ ,  $P = 0.086$ ; excluding larvae –  $F_{1,190} = 1.21$ ,  $P = 0.272$ ). For adult fish it appears recovery of richness is seasonally dependent being rapid during summer and non-existent during winter and spring.

**Table 4** Changes in species richness, density and biomass in experimental pools compared to the original collection (June 2000) and control collections made each month from the Ouepoto platform. ↔ = no significant difference; ↑ = significantly greater than original/control; ↓ = significantly lower than original/control. P is set at < 0.05 and was determined by i) pairwise comparison with Bonferroni adjustment for experimental vs June comparisons and, ii) by monthly contrasts for experimental vs control comparisons. Comparisons are including and excluding larvae. Analyses performed on log<sub>10</sub>(x+1) transformed data.

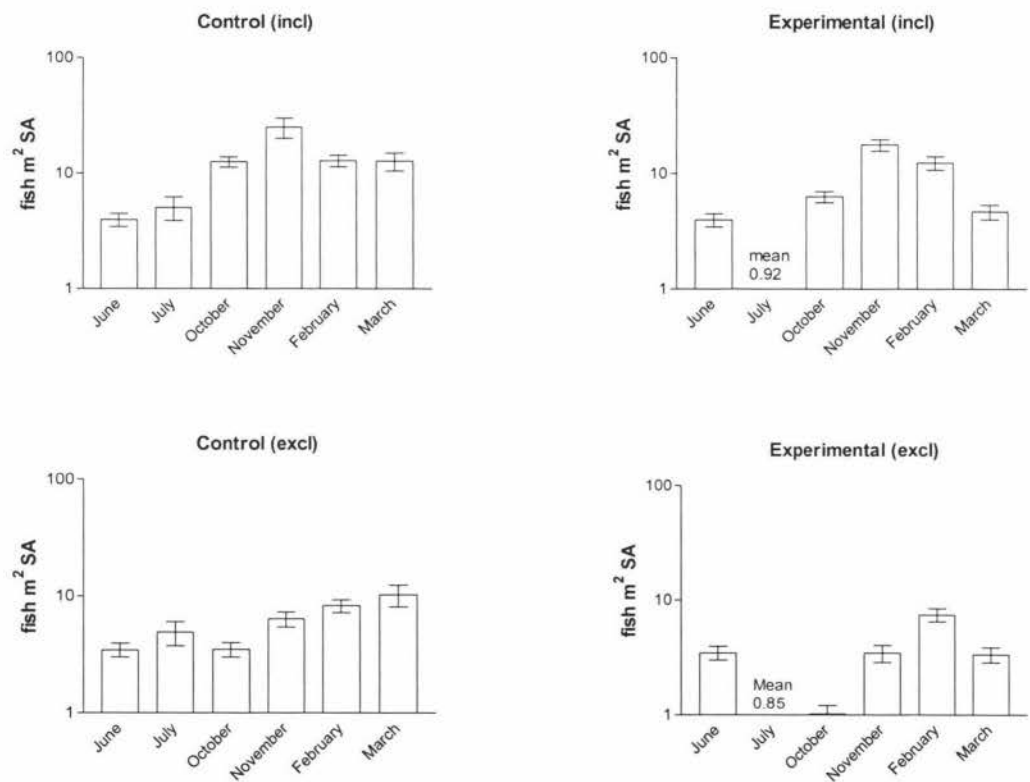
	Richness				Density (fish/m <sup>2</sup> SA)				Biomass (g/m <sup>2</sup> SA)			
	incl larvae		excl larvae		incl larvae		excl larvae		incl larvae		excl larvae	
	June	Ctrl	June	Ctrl	June	Ctrl	June	Ctrl	June	Ctrl	June	Ctrl
Experimental pools												
July	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓
October	↔	↔	↓	↓	↑	↓	↓	↓	↓	↓	↓	↓
November	↔	↔	↓	↓	↑	↔	↔	↓	↔	↓	↔	↓
February	↔	↔	↔	↔	↑	↔	↑	↔	↑	↔	↔	↔
March	↔	↔	↔	↔	↔	↓	↔	↓	↔	↓	↔	↓



**Figure 3** Mean species richness ± S.E. in control and experimental rockpools including (upper graphs) and excluding (lower graphs) larval fish. Scale is log<sub>10</sub> mean number of species per pool.

Density

When larval fish were excluded, density in control pools increased steadily from October (mean 3.5 fish/m<sup>2</sup>) to March (mean 10.26 fish/m<sup>2</sup>). The increase was the same in experimental pools, although there was a significant decrease after the 1-month inter-collection interval in summer (Fig. 4). Including larvae, density peaked in November in control and experimental pools (Fig. 4) but decreased in February and March presumably due to post-settlement mortality. Recovery of density was significantly greater over a 3-month period compared to a 1-month period irrespective of season (including larvae –  $F_{1,190} = 4.63$ ,  $P < 0.05$ ; excluding larvae –  $F_{1,190} = 5.48$ ,  $p < 0.05$ ) although (with the exception of February) when larvae were excluded, density in experimental pools was always lower than the control levels (Table 4).

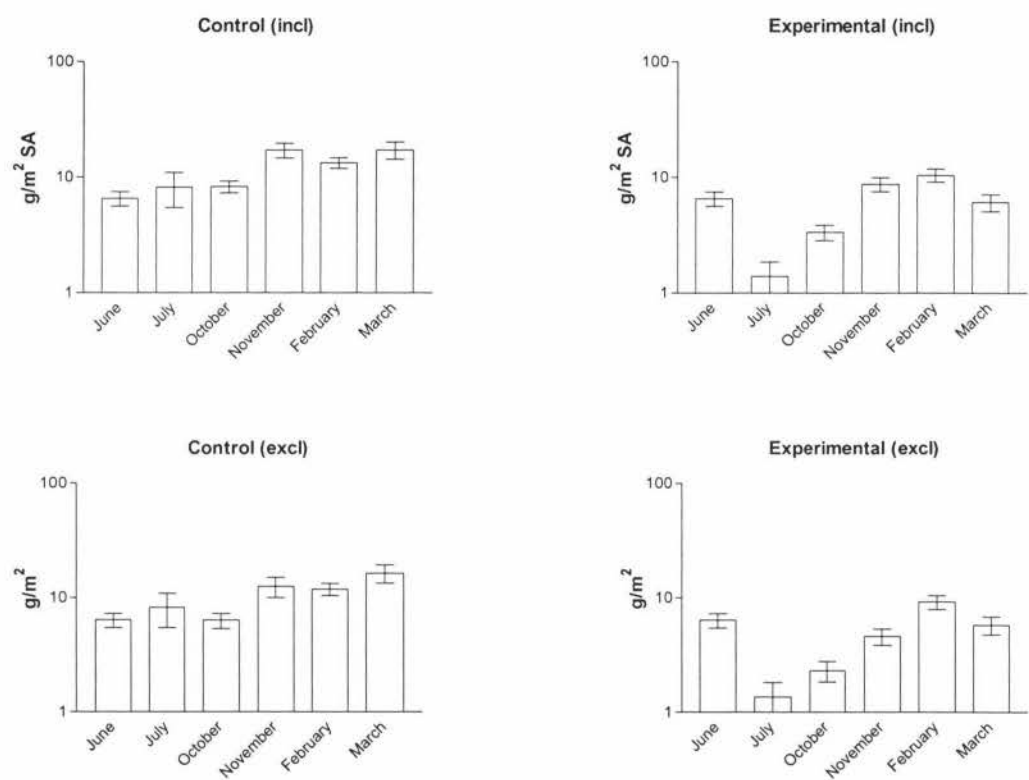


**Figure 4** Mean fish density (fish/m<sup>2</sup> pool surface area) in control and experimental rockpools including (upper graphs) and excluding (lower graphs) larval fish. Scale is log<sub>10</sub> mean density of fish per pool.



Biomass

Biomass increased in the November, February and March collections (control and experimental – Fig. 5) and the biomass in experimental pools was similar to, or significantly greater than original biomass in all but July and October (Table 4). In the experimental pools, recovery of biomass was significantly greater over a 3-month period compared to a 1-month period irrespective of season (including larvae –  $F_{1,190} = 4.3$ ,  $P < 0.05$ ; excluding larvae –  $F_{1,190} = 4.96$ ,  $p < 0.05$ ) but, with the exception of February never recovered to control levels whether larvae were included or excluded from analyses (Table 4).



**Figure 5 Mean fish biomass ( $g/m^2$  pool surface area) in control and experimental pools including (upper graphs) and excluding (lower graphs) larval fish. Scale is  $log_{10}$  mean biomass of fish per pool.**

#### 4.3.4) Multivariate distance

##### *Including larvae*

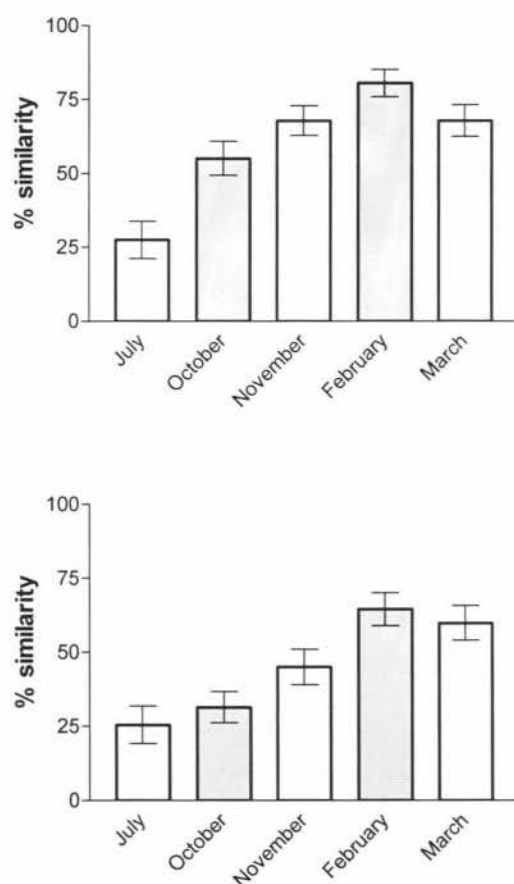
Recovery as assessed by multivariate distance ranged from  $S = 0\%$  (no recovery) to  $S = 100\%$  (complete recovery) and varied significantly depending on month ( $F_{4,100} = 10.214$ ,  $P < 0.001$ ) but not specific pool ( $F_{25,100} = 1.483$ ,  $P = 0.09$ ). Mean  $S$  increased in consecutive collections (Fig. 6) and was significantly greater over the two 3-month recovery periods ( $F_{1,100} = 7.96$ ,  $P < 0.05$ ). The major contributor to this difference was extremely low recovery during July 2000 (1-month recovery period) when there were no larval recruits. When July 2000 was removed from analyses, there was no significant difference between 1- and 3-month recovery periods ( $F_{1,75} = 0.00$ ,  $P = 0.991$ ). Multiple regression analysis revealed that a combination of positive % cover of seagrass and negative % cover of coralline turf was the best predictor of mean  $S$  ( $r^2 = 0.354$ ). However, the  $F$  values of both predictor variables were low (2.35 and 3.39 respectively) and neither had a  $P$  value  $< 0.05$ .

##### *Excluding larval fish*

Recovery was generally lower when larval fish and recently metamorphosed juveniles were excluded from analyses. Paired comparisons of recovery each month including and excluding larval fish showed that, except for July 2000, recovery was greater using the complete data set (Table 5). However when larval fish were excluded,  $S$  still ranged from 0% (no recovery) to 100% (complete recovery) and varied significantly depending on month, but also specific pool ( $F_{4,100} = 10.214$ ,  $P < 0.001$ ;  $F_{25,100} = 1.886$ ,  $P < 0.05$  respectively). Mean  $S$  increased in consecutive collections (Fig. 6) but recovery over a 1-month recovery period was not significantly different from recovery over a 3-month period ( $F_{1,100} = 0.864$ ,  $P = 0.355$ ). A combination of positive mean depth, intertidal height and negative % cover of coralline algae was the best predictor of mean  $S$  ( $r^2 = 0.635$ ;  $F = 6.7, 8.1, 6.9$  respectively;  $P < 0.05$ ).

**Table 5 Comparison of mean recovery ( $S$  = modified Sorenson-distance) of experimental pools including and excluding larvae. Significance determined by Wilcoxon matched pairs test.**

Month	Including larvae ( $S$ )	Excluding larvae ( $S$ )	Significance
July 2000	18.67%	6.67%	$P = 0.011$
October 2000	58.04%	29.23%	$P < 0.001$
November 2000	69.05%	38.84%	$P < 0.001$
February 2001	85.71%	67.79%	$P = 0.008$
March 2001	73.35%	59.82%	$P = 0.003$



**Figure 6 Mean  $\pm 1$  S.E. % similarity (modified Sorenson-distance) between fish assemblages in 26 rockpools sampled during 5 different months and the original assemblages sampled during June 2000. Top graph includes larval fish that are excluded from the lower graph. 3-month recovery periods are shaded.**

The graphical diagnostics used to assess recolonising propensity (Fig. 7) revealed that, for the resident species, recolonisation by larger fish was generally low in winter and higher during summer. Adults of four partial residents never recolonised original pools and three of those species (*P. laticlavus*, *G. hectoris* and *G. atrata*) never recolonised as larvae either. The species that recolonised best as adults were *G. capito* and *A. fuscus*, both abundant, predominantly intertidal species. *Ericentrus rubrus*, *F. lapillum*, *D. morelandi* and *L. filum* recolonised most of their original pools as larvae, and adult abundance of these species in recolonised pools was always lower than original levels. These species are also common in shallow subtidal habitats.

#### 4.3.5) Size structure of recolonists

Seven species were present in large enough numbers to examine differences in the size structure of experimental and control populations. Defaunated rockpools were recolonised by all size classes (Table 6). For most species, the frequency of large recolonists (experimental pools) was significantly lower than the frequency of large conspecifics in control populations (Pearson  $\chi^2$ ,  $P < 0.05$ ). The greatest differences in the frequency of the largest size class between control and experimental populations were seen in *E. rubrus* (>56mm: 49%, 19% respectively), *F. lapillum* (>58mm: 20%, 2.6% respectively), *D. morelandi* (>36mm: 26%, 11% respectively) and *L. filum* (>74mm: 35%, 19% respectively,  $P = 0.103$ ). Experimental and control populations of *G. capito* and *A. fuscus* had more comparable distributions among size classes (Table 6) although smaller fish still comprised the greater proportion of recolonists ( $P < 0.0001$  and  $P < 0.05$  respectively). For *B. medius*, there was no significant difference in the frequency of size classes between experimental and control populations when larval fish were excluded from the analysis.

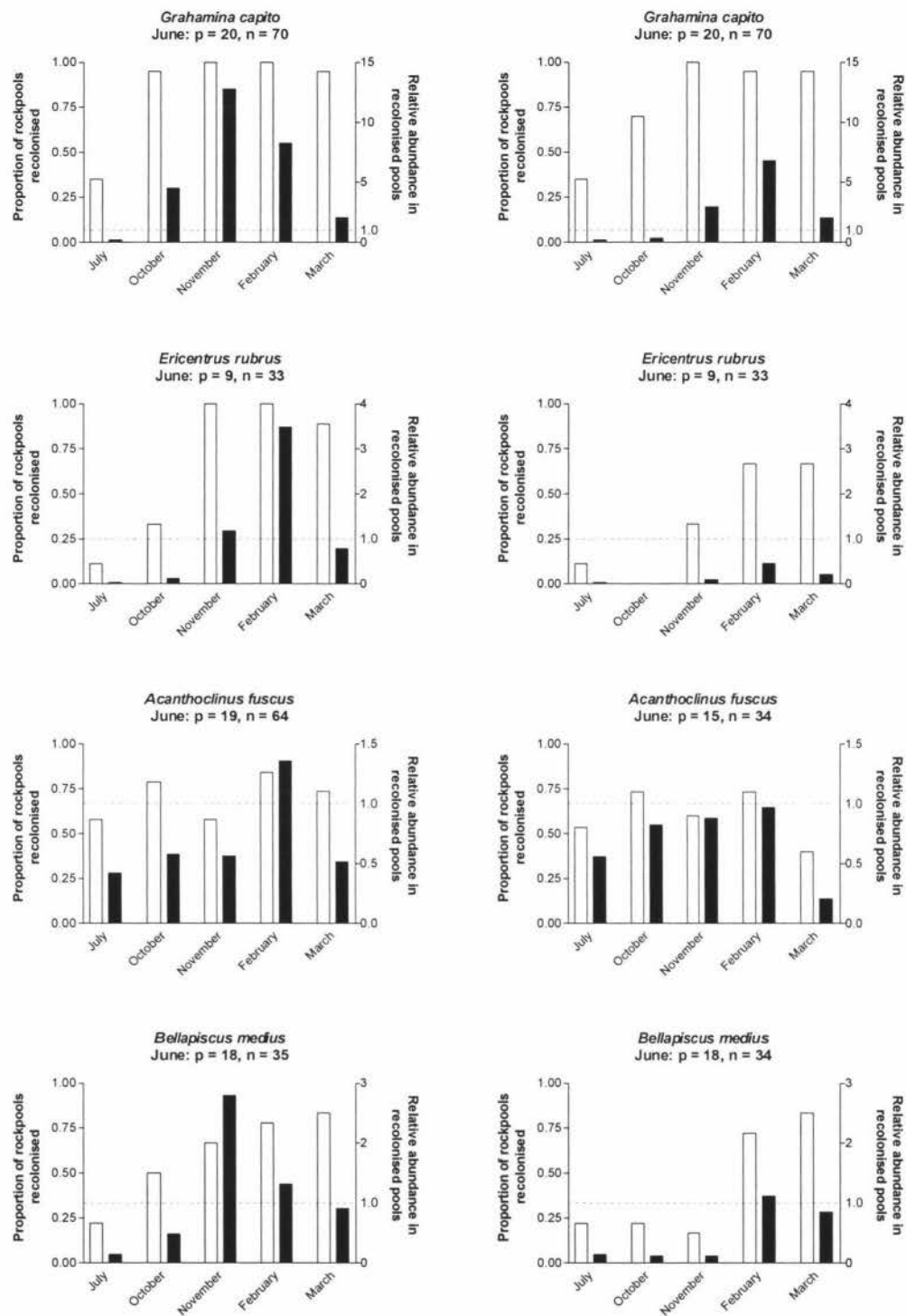


Figure 7 Recolonising propensity of species collected from rockpools on Pohatupapa Point during June 2000, expressed as the proportion of rockpools recolonised ( $\square$ ), and abundance in recolonised pools as a proportion of original abundance ( $\blacksquare$ ). Graphs on the left include larval fish; graphs on the right exclude larval fish. The number of pools occupied (p) and abundance (n) in June 2000 are shown in each graph title. Horizontal line is  $\blacksquare = 1.0$ . Graphs for 3 species that were present in June 2000 (*G. hectoris*, *G. atrata* and *P. laticlavus*) but never recolonised are not shown.



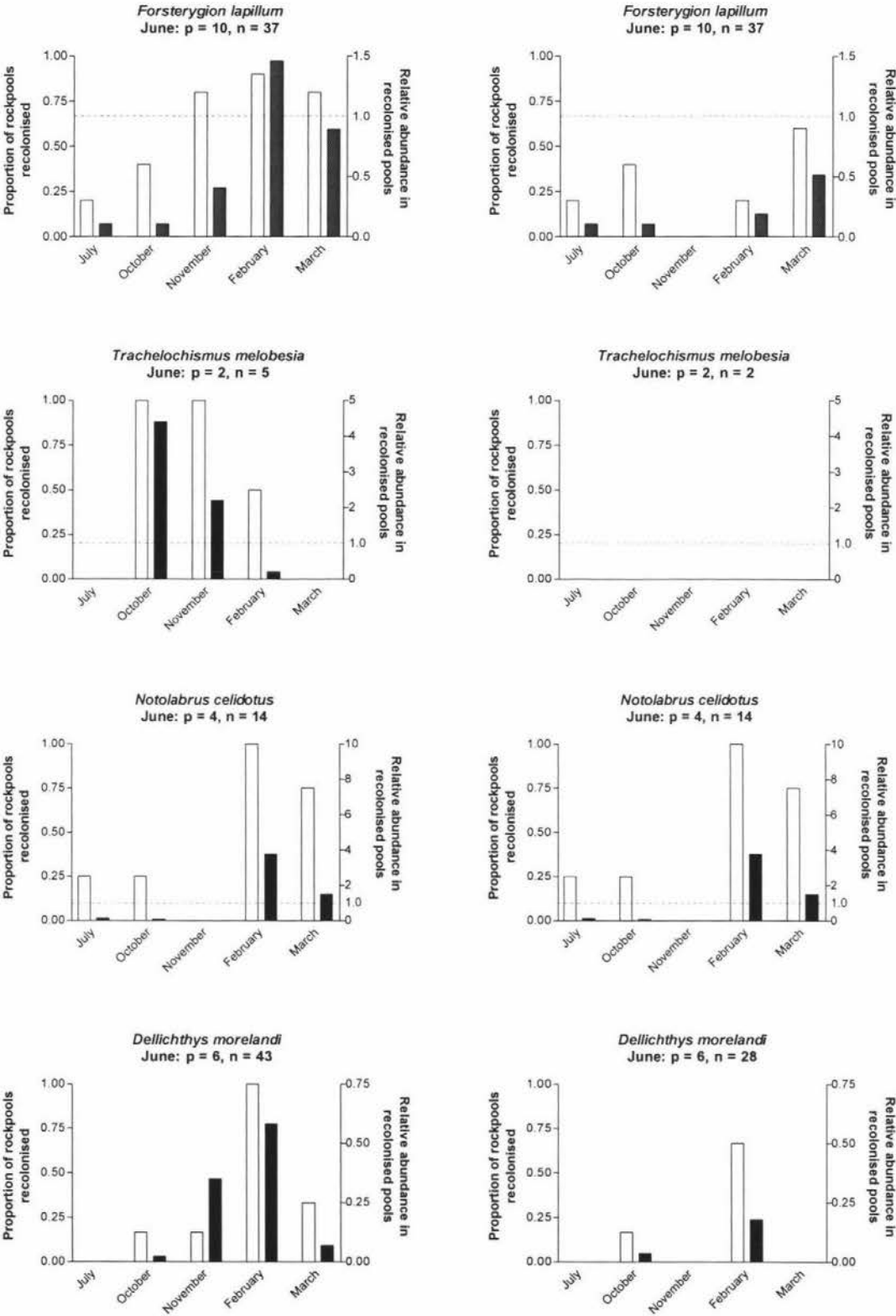


Figure 7 continued ...

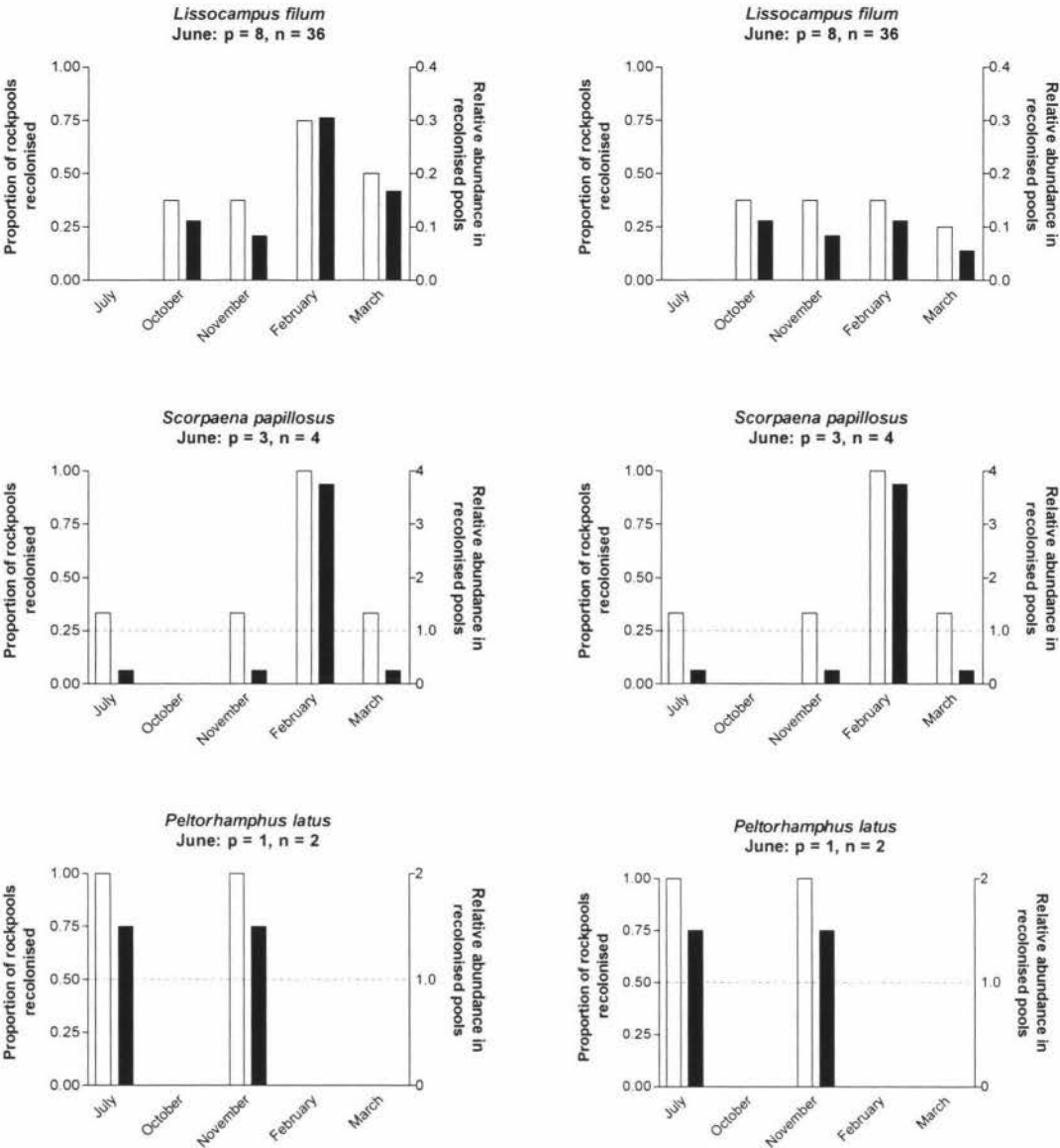


Figure 7 continued ...

**Table 6 Comparison of size class frequency of 7 common resident species from recolonist (experimental) and control populations, including and excluding larval fish. Bold labels are size classes in mm. Figures for each size class are percentage of population (row) total. Significance determined using Pearson  $\chi^2$ .**

Species	Experimental or control	Size classes				n	$\chi^2$	df	P
		1	2	3	4				
<i>Grahamina capito</i>		<b>&lt;30</b>	<b>30-40</b>	<b>41-50</b>	<b>51+</b>		37.9	3	<0.0001
	including larvae Control	18.6	32.8	27.3	21.3	1222			
	Experimental	21.1	40.0	24.5	14.4	2200			
		<b>&lt;51</b>	<b>51-60</b>	<b>61+</b>			15.8	2	<0.0001
	excluding larvae Control	59.1	25.0	15.9		636			
	Experimental	66.5	23.9	9.6		947			
<i>Ericentrus rubrus</i>		<b>&lt;30</b>	<b>30-40</b>	<b>41+</b>			51.4	2	<0.0001
	including larvae Control	26.8	45.8	27.5		284			
	Experimental	55.2	35.1	9.6		239			
		<b>&lt;57</b>	<b>57+</b>				7.9	1	0.005
	excluding larvae Control	50.6	49.4			79			
	Experimental	81.5	18.5			27			
<i>Acanthoclinus fuscus</i>		<b>&lt;30</b>	<b>30-56</b>	<b>57-72</b>	<b>73+</b>		31.4	3	<0.0001
	including larvae Control	14.5	44.0	20.7	20.7	193			
	Experimental	35.7	29.7	23.7	10.8	232			
		<b>&lt;50</b>	<b>50-70</b>	<b>71+</b>			11.7	2	0.003
	excluding larvae Control	33.8	39.5	26.8		157			
	Experimental	21.7	59.4	18.8		138			
<i>Bellapiscus medius</i>		<b>&lt;34</b>	<b>34-46</b>	<b>47+</b>			56.9	2	<0.0001
	including larvae Control	17.2	62.9	19.9		151			
	Experimental	56.2	31.3	12.4		217			
		<b>&lt;46</b>	<b>46-50</b>	<b>51+</b>			0.2	2	<b>0.887</b>
	excluding larvae Control	66.0	18.4	15.5		103			
	Experimental	62.8	20.9	16.3		86			
<i>Forsterygion lapillum</i>		<b>&lt;39</b>	<b>39-54</b>	<b>55+</b>			27.5	2	<0.0001
	including larvae Control	33.5	43.4	23.1		182			
	Experimental	55.7	40.9	3.2		122			
		<b>&lt;49</b>	<b>49-58</b>	<b>59+</b>			7.1	2	0.028
	excluding larvae Control	41.7	38.3	20.0		115			
	Experimental	57.9	39.5	2.6		38			

Table 6 continued ...

Species	Experimental or control	Size classes				n	$\chi^2$	df	P
		1	2	3	4				
<i>Dellichthys morelandi</i>		<25	25-36	37+			29.8	2	<0.0001
	including larvae Control	17.1	56.6	26.3		76			
	Experimental	63.6	25.5	10.9		55			
	excluding larvae Control	To few adult recolonisers for reliable Pearson $\chi^2$							
	Experimental								
<i>Lissocampus filum</i>		<57	57-74	75+			23.4	2	<0.0001
	including larvae Control	13.6	53.1	33.3		81			
	Experimental	58.6	31.0	10.3		29			
	excluding larvae Control	<61	61-74	75+			4.5	2	0.103
	Experimental	15.4	50.0	34.6		78			
	Experimental	37.5	43.8	18.8		16			

4.4) Discussion

To evaluate all potential effects of disturbance, a variety of measures are necessary (Jones & Syms 1998). In the present study, a number of methods were used to examine the resilience of rockpool fish assemblages subjected to periodic disturbance. The results of the study support Jones & Syms’ (1998) recommendation, as the interpretation of each of the different estimates of recovery revealed different information on the recovery dynamics of this rockpool fish community. This information is assessed below, followed by a discussion of the effects of including larval fish as part of the recolonising community.

4.4.1) Community Recovery

4.4.1.1) Rank concordance

Recovery of rank order following repeated defaunation was significant and by definition, this aspect of community structure is resilient. Species that were abundant pre-defaunation (*Grahamina capito* and *Acanthoclinus fuscus*) were generally the most

abundant post-defaunation and rare species (*Dellichthys morelandi* and *Scorpaena papillosus*) consistently recolonised to the lowest ranks. Significant concordance values were obtained despite the impact of defaunation and seasonal variation. However, values less than unity were found even after rare species were excluded from analyses, indicating that the ranks of common species did change. Other studies examining the same system have likewise calculated  $W_c < 1$ , but still inferred persistence of taxocene (a taxonomically-related set of species within a community) structure in the face of disturbance (Grossman 1982; Willis & Roberts 1996). In the present study, there was generally constancy in the top and bottom ranking recolonist species. When they were removed from analyses,  $W_c$  fell and significance rose, indicating that the ranks of moderately abundant species also changed over time. However, the significant rank correlation between the experimental and control communities indicates that in general, the rockpool fish community on Pohatupapa Point is resilient in that the taxonomic composition of the recolonising assemblage appears to be largely deterministic.

The way a community is defined will influence resilience calculated using rank correlation indices (Rahel *et al.* 1984). Grossman *et al.* (1982) considered the lack of rank constancy of fish species in an Indiana stream as evidence to reject the hypothesis that the fish community was regulated by deterministic processes. However, Rahel *et al.* (1984) added the next 4 most abundant species to Grossmans' data and calculated a significant concordance value suggesting the community is not regulated by stochastic processes. In the present study, rank concordance in the control community was significant with 2 species but 4 were needed in the recolonist community before significance for  $W_c$  was  $<0.05$ . This comparison is probably more useful than comparing the  $W_c$  statistic for each community alone and suggests some randomness in recolonisation that may reflect the availability of recolonisers, or possibly the propensity of each species to move between pools in the intertidal zone.

When using rank correlation indices as stability measures, it is possible to infer similarity despite unequal species abundances. No two natural communities have an identical taxonomic and numeric structure (Jumars 1980; Ghent 1983), but gross differences in numbers of the same species from standardised areas suggests something is different. In the present study for example, recolonist density varied over time but more importantly was significantly lower than control density suggesting that fish



numbers had not recovered to 'normal' levels. Despite this, I obtained significant correlations between species ranks in the experimental and control communities (mean ranking). Significant  $W_c$  and Spearman rank ( $S_r$ ) values can only be taken to indicate that there is no significant reordering of ranks among sampling occasions and between different collections (Mahon & Mahon 1994), but as an assessment of resilience must be corroborated with additional analyses.

However, in some occasions, significant  $W_c$  values can be obtained even with significant reordering of ranks. For example, I calculated Kendalls  $W_c$  for a fish community sampled from the same set of pools 4 times over 8 years at Pescadero Point in California (Table 3 Yoshiyama *et al.* 1986) and found a significant and relatively high value of rank concordance among 12 species ( $W_c = 0.654$ ,  $P = 0.002$ ,  $df = 11$ ). However, the most abundant species in this community (*Oligocottus snyderi*) comprised 52% of the total abundance in the first collection (June 1976) but decreased markedly and accounted for 9% of total abundance in June 1984. Yoshiyama *et al.* (1986) did not calculate rank concordance but suggested that the fish community at Pescadero Point may not be persistent. The opposite may have been suggested if rank concordance (Kendalls  $W_c$ ) had been calculated. In studies of intertidal fish, 10 or fewer species tend to dominate the assemblage. It is suggested that with such small numbers of common species, re-ordering of rank can be examined with rank concordance indices, and by corroborating these by directly viewing raw data.

#### **4.4.1.2) Recovery of overall properties**

Previous studies have suggested rockpool fish start recolonising experimentally defaunated pools within two weeks (Collette 1986; Lardner *et al.* 1993) but up to 60 to 90 days are required for restoration of richness and abundance (Willis & Roberts 1996; Polivka & Chotkowski 1998). Seasonality in recovery has also been described where communities recover from disturbance more rapidly during summer (Beckley 1985b; Willis & Roberts 1996). In the present study, recovery of density and biomass to control levels was significantly greater over a 3-month period than a 1-month period. However, more important was the time of year recovery took place. During winter and spring, the density and biomass of non-larval recolonists was significantly lower than control levels

after 1- (July and November) and 3-month (October) post-defaunation intervals. Three months (February) during summer was sufficient time for density and biomass to recover to control levels but 1-month (March) was not. Recovery of non-larval species richness was also seasonally dependent. It was not until the summer months that no appreciable difference was detected between experimental and control richness. In general, the effect of rotenone sampling was still detectable after 3-months during winter and spring, but not after 3-months during summer. This suggests that recovery of this rockpool fish community from a disturbance is seasonally dependent.

Rank concordance gave an overall impression of stability in the rockpool fish community in the present study. The above results indicate that while different taxa consistently recolonised to a similar rank, the numbers of species and of fish recolonising were fewer than what would be considered 'normal' in an undisturbed community. In this case, the community would only be considered resilient during summer.

#### **4.4.1.3) Multivariate distance**

Despite seasonality in abundance and biomass, the taxonomic and numeric composition of recolonising assemblages increased in similarity to original assemblages in consecutive collection months. This suggests that there are deterministic processes operating that regulate community structure, but they may be masked by slow recovery during winter and spring. The contrast between 1- and 3-month recovery periods revealed that there was no significant difference in the extent of recovery. These results support those from the previous section, that resilience is seasonally dependent ie. similarity, as an estimate of resilience, was greatest during the summer months.

The fact that intertidal height was included in the multiple regression model predicting recovery of the post-larval community was interesting given high-shore pools had low species richness (see Chapter 3). It would appear that high-shore and shore-wide species (*A. fuscus*, *G. capito* and *Bellapiscus medius*) were more successful recolonisers than species characteristic of low shore pools (e.g. *Forsterygion lapillum*, *Ericentrus rubrus*, *D. morelandi*). This is probably because intertidal generalists and specialists were able

to colonise experimental pools from nearby, unaffected ones, whereas the source population for partial residents may have been in subtidal habitats.

Differences in the propensity of rockpool fishes to recolonise defaunated pools were confirmed by graphing the recolonising success of species captured in the original collection. *Grahamina capito* and *A. fuscus* typically recolonised most of the pools they were originally collected from although *B. medius* was generally an unsuccessful recoloniser during winter and spring. Post-larval *E. rubrus*, *F. lapillum*, *D. morelandi* and *Lissocampus filum* were particularly poor at recolonising and these species repopulated originally occupied rockpools mainly via larval recruitment. The number of pools recolonised by these post-larval partial residents, and their abundance in these pools did not reach original levels, and recovery by these larger fish generally occurred only during late spring and summer. The clingfish *Trachelochismus melobesia* relied entirely on larval recruitment, and some of the rare partial residents (*Parablennius laticlavius*, *Gastroschypus hectoris* and *Gobiopsis atrata*) never recolonised original pools.

#### **4.4.2) Size distribution of recolonists, and the effect of including larvae as recolonising fish**

When larvae were included in the analyses, resilience was generally calculated to be greater, and more rapid. For example, the onset of the spring/summer recruitment pulses meant that density and species richness in the recolonising community was not significantly different from the control community from spring onwards. There was generally no recruitment during winter, so the addition of larvae to the data made no difference to the level of recovery of density during this period, although recovery of species richness was significantly greater from October on when larvae were included. There was still some indication as to the lack of larger recolonising fish when analyses were conducted including the larval fish – recolonist biomass was, apart from February, always significantly lower than biomass in the control pools.

Recovery, as calculated by multivariate distance, was generally greater when including larvae in the analysis. This indicated that recovery by the adult populations was not sufficient to restore the taxonomic and numeric composition of some pools. Three-

month recovery periods in this case, were only considered better than 1-month periods when July 2000 was considered. There was negligible larval recruitment during this month, meaning the composition of the recolonising community was essentially the same as that examined without larval fish. There was no significant predictive power in the multiple regression model used to find a relationship between habitat structure and the level of recovery when larval fish were included. While recovery is significantly greater when larval fish are considered, the effects of random settlement make it difficult to determine if there is any relationship between the level of recovery and pool structure.

When the recolonising success of species was graphed, it was obvious that the partial resident species in particular rely on larval recruits to recolonise pools. Many of these pools originally occupied by partial residents remain unoccupied by those species until recruits settle during late spring/summer.

The recolonising propensity of partial residents was also reflected in the size distribution of recolonists. There were markedly smaller proportions of larger adults compared to control pools. For these species, the smaller size classes composed the bulk of the recolonists and there was apparently little movement by larger fish. For the ubiquitous triplefins, *G. capito* and *B. medius*, most recolonisation took place by movement of small fish but differences in recolonist and control size structure were not as pronounced as for partial residents. When post-larval fish were examined separately, there was no significant difference in the size structure of *B. medius* between experimental and control populations indicating that there was significant intertidal movement of larger fish. The size structure of *A. fuscus* in the experimental community indicated that larger juvenile fish frequently recolonise empty pools.

#### **4.4.3) Processes involved in recovery**

Previous studies (Craik 1981; Matson *et al.* 1986; Yoshiyama *et al.* 1992) have found a high degree of site fidelity in adult fish of some species, and others have described significant intertidal movement and recolonisation success of juvenile fish (Gibson 1967; Beckley 1985b; Polivka & Chotkowski 1998). The results of the present study are

consistent with these observations. For all species (except *B. medius* when larval fish were excluded), the size class of recolonists were generally smaller than an undisturbed community. This was particularly obvious for the partial resident component of the fauna, that also showed a relatively low propensity to recolonise previously occupied pools.

The high recolonisation propensity of *A. fuscus* and *G. capito* may reflect regular movement within their natural habitat. The upper and midshore pools inhabited by these species were comparatively homogeneous compared to complex low pools, and there may be no adaptive advantage for fish to remain localized in homogeneous environments (Gibson & Yoshiyama 1999). Rapid recolonisation by *A. fuscus* was interesting considering Berger & Mayr (1992) found this species to be relatively sedentary year round on the Kaikoura coast. In addition, Willis & Roberts (1996) noted that this species was a poor recoloniser in their most frequently sampled pool on the Wellington south coast. *Acanthoclinus fuscus* is highly territorial, and contest success for this species depends on fish size (Mayr & Berger 1992). In the present study, most recolonists were between 50–70mm TL (excluding larvae) and fewer of the largest fish (>70mm TL) recolonised pools. This suggests juvenile and small adults that may typically lose contests against larger conspecifics were able to take advantage of cleared rockpools. The size structure of the experimental *B. medius* population also suggested that recolonisation takes place by movement of larger fish, as the size structure of this population was not significantly different from the control population. These results suggest that there is significant intertidal movement of true resident species on the intertidal platforms examined in this study. The true resident community recovered better than the partial resident component, probably because they were able to colonise experimental pools from nearby, unaffected ones. In other studies, many species of intertidal fish are relatively restricted in their lateral movements over the shore (Moring 1976; Gibson & Yoshiyama 1999). The evidence in the present study suggests that this may be more so the case for partial residents.

It is not known why there was greater propensity for juvenile and adult fish to recolonise during summer (Figure 7). One possibility is general inactivity during the typically temperate New Zealand winter. Overseas studies have shown that in turbulent water, rockpool fish tend to limit their activity to the low-tide period (Green 1971b) or



by remaining in crevices (Williams 1957). It is unknown how New Zealand rockpool fish react to extreme water movement (Willis & Roberts 1996), but it is possible that they seek to avoid being displaced during these periods by limiting activity. It is also possible that fish become lethargic and less active in colder water temperatures, as has been described for other species by Thomson & Lehner (1976). This may limit intertidal movement during winter. In addition, some of the common residents including *F. lapillum*, *B. medius*, and *D. morelandi* are nest-guarding species that breed during early spring (Paulin & Roberts 1992). This would tend to limit inter-rockpool movement during high-tide in this period. More larger fish recolonising during late spring and summer may also be a result of recruits searching and competing for space as they grow.

In other studies, the ability of fish to home to a particular pool, or group of pools appears to increase with size (Craik 1981; Gibson 1999). If this is the case for fish in the present study, it may in part explain why larger fish did not make up a large proportion of the recolonising community ie. there was little tendency for large fish to move to a new pool. It was interesting to, that the true resident species were the best recolonisers given they are generally considered to be restricted in their movements (Gibson 1967; Richkus 1978; Gibson 1999), whereas in other studies, visitors to the intertidal zone cover considerable distances (Wright *et al.* 1990; Black & Miller 1991) and might be considered to recolonise better. The partial residents in the present study appear to represent a group in between the true residents and tidal visitors that remain relatively restricted in the intertidal movements. It is unlikely that low recovery during winter and early spring represented an offshore movement of partial residents (eg. Moring 1990). The richness, abundance, and size structure of the control population indicated that partial resident species do occupy the intertidal zone, even in more inclement weather.

#### 4.4.4) Conclusion

Holling (1973) defined resilience as the persistence of a system without extinction. In the present study, a number of different aspects of a recolonist fish community were examined to see if the structure was persistent in the face of repeated defaunation. Persistence of this system was measured against a control community that reflected



seasonal variation, and against an original community. Generally, community structure was more resilient in summer than in winter and spring. Comparative analyses of recovery including and excluding larval fish highlighted the importance of seasonal recruitment to the resilience of rockpool fish community structure.

In their study of recolonisation and recruitment of rockpool fish, Willis & Roberts (1996) determined that, at the broadscale, deterministic processes governed primarily by seasonal factors play a large part in determining rockpool fish community composition and structure. They also suggested that shorter-term stochastic events may obscure these broadscale patterns. The results of the present study agree with this view. The recovery of the rockpool fish community appeared to be directional, but seasonal effects, and short-term stochastic events (sampling) obscured this pattern. However, the level and rate of recovery was generally lower than has been described in other studies (Collette 1986; Willis & Roberts 1996; Polivka & Chotkowski 1998; Faria & Almada 1999).

In assessing the resilience and persistence of the rockpool fish community examined in the present study, consideration must be given to the disturbance fish were subjected to. Most studies, including the present, have examined the resilience of rockpool fish communities to direct disturbance (removing fish) (Thomson & Lehner 1976; Grossman 1982; Lardner *et al.* 1993; Willis & Roberts 1996). Rotenone sampling is a short, pulsed disturbance that kills all the fish present in a rockpool. It is unlikely a natural disturbance would be fatal to a series of entire rockpool fish assemblages. However, most natural and anthropogenic disturbances will be on a much larger scale, and may significantly affect the availability of recolonists. For example, Alaskan intertidal fishes required at least 2 years to recover after the Exxon Valdez oil spill (Barber *et al.* 1995; Gibson & Yoshiyama 1999).

Although the evidence in this, and other studies shows that rockpool fish resilience is seasonally dependent, anecdotal evidence suggests they may not be resilient to certain levels of indirect disturbance (e.g. habitat destruction) (Gibson 1967; Richkus 1978; Moring 1996; Faria & Almada 1999). Experiments involving indirect disturbance are needed, especially given the results described in this thesis (Chapter 3) and elsewhere (Marsh *et al.* 1978; Bennett & Griffiths 1984; Prochazka & Griffiths 1992; Davis 2000)

indicate that there are significant relationships between rockpool fish assemblage structure and rockpool structure.

In addition, there is considerable debate on the importance of variability in larval recruitment to adult fish populations (Shulman 1985; Doherty & Fowler 1994; Pfister 1996, 1999). Pfister (1996) suggested post-recruitment density dependent mortality is more important than variability in larval supply in determining the abundance of adult populations of tidepool sculpins. However, where failure (variability) in recruitment of intertidal fish has been observed, the changes were reflected in adult populations (Yoshiyama *et al.* 1986). This is of significance to the present study because the resilience of partial residents was, to a large extent, dependent on larval recruitment. Additionally, most intertidal fish species are short-lived, meaning recruitment failure is unlikely to be masked by an accumulation of large, old fish in the population. Failure in the recruitment of partial residents that were a significant component of the resident community including *E. rubrus*, *D. morelandi*, and *F. lapillum*, may have significant effects on the structure of the fish community on the central Hawke's Bay coast. However, it is unlikely failure would occur two years in a row.

Given the relatively short time frame of the present study, it would be difficult to determine if the rockpool fish community on Pohatupapa Point is persistent over periods extending beyond 1 year. However, within the timeframe of this study it was possible to document the response of the fish community to experimental disturbance at different times within one year and make an assessment of community resilience, a necessary component of long-term stability.

## Chapter 5: Synthesis

The aim of the present study was to address the lack of quantitative information on rockpool fish communities in New Zealand, specifically, on the Central Hawke's Bay coast. Whereas previous studies on New Zealand rockpool fish communities have been conducted mostly in subtidal habitats, this study was interested in the dynamics of fish in intertidal rockpools. Despite the fact that this part of the New Zealand coast is considered interesting by biogeographers due to the mixing of ocean currents, there were remarkably few northern and southern species collected. Rather, the collections consisted mostly of species that are widespread around New Zealand. It would be interesting to see if the same pattern exists subtidally. Subtidal habitats are generally more stable, and may be more suitable for species reaching the limits of their latitudinal distribution.

Like rockpool fish communities from other parts of the world, the community studied for this thesis was composed of true and partial residents. The relative importance of each of these two groups was related primarily to rockpool tidal height, rockpool size, and the amount of shelter in a rockpool. Partial resident species were collected frequently from large, low shore pools with lots of shelter. True residents were captured from low shore pools, but also dominated high shore pools where partial residents were generally absent. Transient, or surge zone species, were not common, and this may explain the lack of seasonal variation in species richness that has been described in other studies where juveniles of common reef fish settle in large numbers in rockpools, usually during summer (Beckley 1985a,b; Lardner *et al.* 1993).

The relationships discovered between these New Zealand rockpool fish assemblages and their habitat are broadly similar to those described elsewhere (Bennett & Griffiths 1984; Prochazka & Griffiths 1992; Mahon & Mahon 1994). The importance of shelter, be it a refuge from predation, a place to escape physiological stress, or a nesting site, was paramount to the structure of assemblages, including the presence of certain species. It may be inferred from this, that habitat, or resource partitioning among species limits the number of species, and of fish, that occupy rockpools. This raises the point that the potential for competition (for shelter) exists, and that this may contribute to the regulation of assemblage structure.

This thesis raises some interesting questions regarding the dynamics of New Zealand rocky intertidal fish communities. Inconsistency in the designation of species resident status between studies means comparison of the relative importance of each group between locations is difficult. Three species collected in the present study displayed traits of true residents, in that they were abundant as juveniles, and adults. Yet, one of these species, *Grahamina capito*, has been previously categorised as a subtidal species (Willis & Roberts 1996). The prevalence, size structure, distribution, and recolonisation success of *G. capito*, relative to *Acanthoclinus fuscus* and *Bellapiscus medius* (two species considered as true residents) leads one to question the validity of categorising this species as primarily subtidal. Although that categorisation may be the case for the Wellington south coast, a case was made for an alternative categorisation in the present study, and this warrants further attention. Subtidal collections are required to determine the relative contribution of *G. capito* to the subtidally fringing community. Of interest also would be tagging and tracking studies that examine the extent of movement within the intertidal zone. The results of the present study suggest that true resident species are relatively mobile within the intertidal compared to the partial residents that are restricted to the lower part of the shore.

Like other studies of rockpool fish, the present showed that rockpool fish assemblages are a stable part of the intertidal biota, in that they start recolonising within at least 1-month after a disturbance. However, the extent, and rate of recovery depended greatly on the season recovery took place. During winter and spring, community recovery was slow, and some species did not recolonise at all during this period. Conversely, during summer, recolonisation was much quicker. When larval fish were considered, recovery was generally greater, highlighting the importance of recruitment events, and their potential failure, to the persistence of this rockpool fish community. Nevertheless, the taxonomic structure of the recolonising community was generally stable, in that common species, particularly the true residents, were usually the first, and most successful recolonisers, and rarer species consistently recolonised to the lowest ranks.

Observational studies such as this one are burdened, as they do not determine cause and effect. However, by describing patterns in community structure, observational studies are a necessary first step in generating testable hypotheses regarding the processes

producing these patterns. This study has determined that similar spatial and temporal patterns observed in overseas studies appear to hold true for fish in New Zealand rockpools, at least those on the Central Hawkes' Bay coast.

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**Appendix 1 GPS waypoints of rockpools sampled for fish. Waypoints recorded on a Garmin etrex 12 channel GPS receiver using New Zealand geodetic map datum 1949. Elevation on this receiver is accurate to 10m and not presented here as no pool was more than 10m asl. Pool designation recorded as Experimental = E; Control = C. \* indicates that the pool was sampled in June 2000, and in each month the control pools were sampled.**

Pool Number	Experimental/ Control	Month Sampled	Easting	Northing
1	E	*	2835987	6107520
2	E	*	2836016	6107563
3	E	*	2835957	6107646
4	E	*	2835955	6107697
5	E	*	2836005	6107784
6	E	*	2836040	6107583
7	E	*	2836085	6107782
8	E	*	2836022	6107823
9	E	*	2836009	6107820
10	E	*	2835991	6107726
11	E	*	2835918	6107646
12	E	*	2836067	6107599
13	E	*	2836005	6107619
14	E	*	2835997	6107568
15	E	*	2836004	6107573
16	E	*	2835921	6107466
17	E	*	2836009	6107602
18	E	*	2835877	6107515
19	E	*	2835941	6107640
20	E	*	2835752	6107341
21	E	*	2835766	6107263
22	E	*	2835763	6107264
23	E	*	2835761	6107324
24	E	*	2836013	6107566
25	E	*	2835861	6107466
26	E	*	2835898	6107481
27	C	July	2835848	6107512
28	C	July	2835892	6107584
29	C	July	2835872	6107341
30	C	July	2835923	6107659
31	C	July	2836019	6107737
32	C	July	2836001	6107791
33	C	July	2836037	6107845
34	C	July	2836066	6107779
35	C	July	2836064	6107780
36	C	July	2836077	6107776
37	C	July	2836075	6107802
38	C	July	2836028	6107639
39	C	July	2836082	6107824
40	C	July	2836035	6107862
41	C	October	2839289	6111740
42	C	October	2839765	6112307
43	C	October	2839275	6111743
44	C	October	2838967	6111522
45	C	October	2838967	6111522
46	C	October	2839097	6111599
47	C	October	2839094	6111558



Appendix 1 *continued* ...

Pool Number	Experimental / Control	Month Sampled	Easting	Northing
48	C	October	2839070	6111493
49	C	October	2839405	6111752
50	C	October	2839060	6111473
51	C	October	2839641	6111923
52	C	October	2839374	6111689
53	C	October	2839380	6111649
54	C	October	2839369	6111687
55	C	November	2839322	6111696
56	C	November	2839948	6113109
57	C	November	2839125	6111557
58	C	November	2839129	6111561
59	C	November	2838532	6111336
60	C	November	2839342	6111712
61	C	November	2839329	6111697
62	C	November	2839288	6111573
63	C	November	2839156	6111468
64	C	November	2838696	6111295
65	C	November	2838702	6111291
66	C	November	2838848	6111333
67	C	November	2838971	6111377
68	C	November	2839055	6111401
69	C	February	2838726	6111381
70	C	February	2839486	6111976
71	C	February	2839796	6112232
72	C	February	2839738	6112220
73	C	February	2839482	6111966
74	C	February	2839351	6111743
75	C	February	2839328	6111782
76	C	February	2838974	6111380
77	C	February	2839050	6111408
78	C	February	2838872	6111346
79	C	February	2839266	6111554
80	C	February	2839400	6111631
81	C	February	2839375	6111656
82	C	February	2839371	6111692
83	C	March	2835959	6107670
84	C	March	2835996	6107711
85	C	March	2839732	6112211
86	C	March	2839761	6112198
87	C	March	2840020	6113164
88	C	March	2839989	6113210
89	C	March	2839299	6111680
90	C	March	2836097	6107719
91	C	March	2835830	6107260
92	C	March	2836046	6107589
93	C	March	2838763	6111337
94	C	March	2840050	6113200
95	C	March	2840068	6113219
96	C	March	2836024	6107555

**Appendix 2** Values of habitat variables measured and estimated for 96 rockpools censused for fish on Pohatupapa point and the Ouepoto platform. Crevice density is the number of crevices standardised for surface area.

Pool number	Position Height (cm asl)	Size				Substrate composition (proportion)							Shelter and complexity				
		Surface area (m <sup>2</sup> )	Mean depth (m)	Maximum depth (m)	Volume (l)	Bare rock	Sand	Seagrass	Rubble	Coralline turf	<i>Hormosira banksii</i>	Foliose algae	Number of crevices	Crevice density	Estimate algal cover	Estimate rock cover	Estimate rugosity
1	36	1.17	0.14	0.30	159	0.29	0.08	0.00	0.16	0.50	0.03	0.15	11	0.09	2	4	4
2	36	1.18	0.10	0.29	115	0.23	0.02	0.00	0.08	0.62	0.02	0.04	15	0.13	1	4	4
3	91	2.37	0.08	0.19	182	0.63	0.02	0.06	0.18	0.02	0.26	0.00	30	0.13	1	4	4
4	97	4.33	0.06	0.12	260	0.06	0.53	0.00	0.02	0.33	0.25	0.00	6	0.01	2	1	1
5	94	2.70	0.07	0.24	197	0.56	0.06	0.14	0.02	0.03	0.44	0.00	9	0.03	2	1	1
6	35	1.24	0.09	0.22	112	0.27	0.05	0.00	0.06	0.57	0.01	0.21	32	0.26	3	5	5
7	45	1.60	0.07	0.15	114	0.56	0.14	0.00	0.06	0.39	0.00	0.13	37	0.23	1	3	4
8	78	2.14	0.10	0.25	207	0.56	0.03	0.16	0.03	0.07	0.35	0.00	17	0.08	1	3	3
9	90	2.58	0.15	0.32	392	0.74	0.07	0.00	0.09	0.07	0.27	0.00	54	0.21	1	4	3
10	98	2.66	0.06	0.15	150	0.17	0.68	0.00	0.04	0.36	0.20	0.00	12	0.05	1	1	1
11	93	5.51	0.12	0.22	639	0.15	0.43	0.30	0.17	0.04	0.00	0.00	34	0.06	1	2	1
12	45	2.71	0.14	0.29	379	0.28	0.00	0.00	0.00	0.44	0.03	0.57	31	0.11	5	5	4
13	64	10.09	0.17	0.47	1721	0.13	0.02	0.42	0.05	0.31	0.14	0.03	90	0.09	2	4	3
14	63	1.74	0.09	0.21	160	0.39	0.00	0.00	0.17	0.42	0.19	0.00	19	0.11	2	3	3
15	68	2.36	0.13	0.25	318	0.24	0.07	0.00	0.07	0.66	0.07	0.00	10	0.04	1	4	3
16	55	2.20	0.10	0.26	230	0.16	0.00	0.00	0.00	0.77	0.08	0.18	37	0.17	3	5	5
17	51	2.05	0.08	0.18	171	0.49	0.00	0.00	0.03	0.39	0.08	0.03	43	0.21	1	4	2
18	87	1.18	0.08	0.17	96	0.52	0.01	0.00	0.13	0.22	0.40	0.00	11	0.09	1	3	1
19	92	1.37	0.09	0.20	121	0.32	0.22	0.06	0.13	0.04	0.58	0.00	12	0.09	4	3	3
20	57	1.84	0.08	0.26	155	0.52	0.04	0.00	0.00	0.44	0.00	0.00	2	0.01	0	0	0
21	46	1.09	0.12	0.24	134	0.50	0.00	0.36	0.09	0.06	0.03	0.10	39	0.36	2	2	2
22	46	7.03	0.22	0.38	1524	0.27	0.08	0.28	0.21	0.10	0.08	0.21	148	0.21	5	5	5
23	46	19.10	0.17	0.40	3166	0.31	0.04	0.26	0.05	0.27	0.01	0.12	152	0.08	4	4	4
24	54	16.26	0.18	0.43	3006	0.19	0.03	0.00	0.00	0.72	0.00	0.18	177	0.11	3	5	4
25	45	9.75	0.21	0.43	2036	0.19	0.01	0.02	0.16	0.59	0.03	0.07	258	0.26	3	5	5
26	57	0.90	0.07	0.18	59	0.25	0.02	0.00	0.13	0.49	0.42	0.02	9	0.1	1	2	2
27	84	6.97	0.12	0.30	809	0.36	0.10	0.25	0.13	0.04	0.44	0.00	47	0.07	3	4	3
28	90	6.37	0.15	0.30	940	0.25	0.06	0.45	0.08	0.08	0.31	0.00	49	0.08	3	3	2

## Appendix 2 continued ...

Pool number	Position Height (cm asl)	Size				Substrate composition (proportion)							Shelter and complexity				
		Surface area (m <sup>2</sup> )	Mean depth (m)	Maximum depth (m)	Volume (l)	Bare rock	Sand	Seagrass	Rubble	Coralline turf	<i>Hormosira banksii</i>	Foliose algae	Number of crevices	Crevice density	Estimate algal cover	Estimate rock cover	Estimate rugosity
29	87	1.82	0.10	0.16	149	0.51	0.01	0.00	0.13	0.23	0.40	0.00	16	0.09	1	3	1
30	95	1.69	0.06	0.13	105	0.42	0.18	0.00	0.05	0.23	0.32	0.00	11	0.07	2	3	2
31	96	2.19	0.06	0.10	124	0.34	0.09	0.00	0.06	0.47	0.32	0.00	21	0.10	2	2	1
32	89	1.85	0.08	0.22	157	0.41	0.03	0.18	0.07	0.23	0.36	0.00	14	0.08	1	2	2
33	63	1.64	0.06	0.14	92	0.11	0.04	0.00	0.17	0.59	0.10	0.00	34	0.21	1	3	2
34	65	7.55	0.13	0.35	996	0.12	0.06	0.00	0.11	0.76	0.09	0.02	192	0.25	1	3	4
35	67	7.15	0.09	0.24	668	0.24	0.05	0.43	0.01	0.17	0.21	0.02	64	0.09	2	2	2
36	62	0.82	0.07	0.21	58	0.22	0.01	0.00	0.03	0.74	0.10	0.00	18	0.22	1	3	3
37	53	1.15	0.10	0.20	115	0.32	0.00	0.00	0.08	0.62	0.06	0.00	31	0.27	1	5	4
38	44	0.94	0.11	0.21	99	0.32	0.02	0.00	0.03	0.63	0.02	0.07	23	0.24	1	4	1
39	41	2.22	0.11	0.28	240	0.14	0.03	0.00	0.02	0.80	0.01	0.15	25	0.11	3	4	5
40	62	3.16	0.12	0.26	381	0.19	0.09	0.00	0.02	0.76	0.09	0.00	50	0.16	1	4	4
41	82	4.94	0.08	0.28	410	0.33	0.04	0.16	0.10	0.19	0.37	0.00	105	0.21	2	4	3
42	75	6.04	0.11	0.32	672	0.16	0.09	0.32	0.11	0.32	0.10	0.01	75	0.12	1	2	2
43	86	1.76	0.12	0.35	216	0.06	0.02	0.00	0.07	0.83	0.03	0.01	38	0.22	1	4	3
44	103	1.43	0.12	0.35	174	0.01	0.03	0.62	0.01	0.26	0.13	0.00	15	0.10	4	2	4
45	103	1.95	0.16	0.32	314	0.33	0.03	0.00	0.29	0.17	0.30	0.00	11	0.06	3	3	4
46	104	0.80	0.08	0.19	65	0.20	0.00	0.20	0.09	0.11	0.55	0.00	17	0.21	3	3	2
47	96	1.30	0.07	0.13	95	0.20	0.14	0.00	0.17	0.15	0.64	0.00	13	0.10	3	2	1
48	62	6.49	0.26	0.46	1709	0.28	0.00	0.00	0.03	0.69	0.02	0.21	234	0.36	3	5	4
49	32	5.82	0.12	0.25	682	0.17	0.09	0.20	0.07	0.51	0.01	0.05	22	0.04	2	3	3
50	50	1.83	0.11	0.20	205	0.48	0.10	0.15	0.18	0.02	0.10	0.08	34	0.19	1	3	2
51	9	1.12	0.05	0.18	58	0.14	0.09	0.00	0.04	0.67	0.04	0.07	13	0.12	1	1	1
52	37	1.14	0.10	0.26	112	0.18	0.09	0.00	0.02	0.65	0.12	0.01	17	0.15	1	3	2
53	23	1.00	0.09	0.22	94	0.17	0.03	0.00	0.14	0.67	0.00	0.33	5	0.05	3	2	1
54	42	0.68	0.07	0.11	47	0.09	0.17	0.00	0.09	0.64	0.12	0.00	3	0.04	0	1	2
55	77	3.42	0.17	0.42	573	0.18	0.03	0.01	0.08	0.67	0.18	0.03	81	0.24	1	4	4
56	50	6.27	0.12	0.35	726	0.10	0.04	0.00	0.13	0.68	0.12	0.13	94	0.15	3	3	3

Appendix 2 continued ...

Pool number	Position Height (cm asl)	Size				Substrate composition (proportion)							Shelter and complexity				
		Surface area (m <sup>2</sup> )	Mean depth (m)	Maximum depth (m)	Volume (l)	Bare rock	Sand	Seagrass	Rubble	Coralline turf	<i>Hormosira banksii</i>	Foliose algae	Number of crevices	Crevice density	Estimate algal cover	Estimate rock cover	Estimate rugosity
57	74	1.57	0.08	0.18	130	0.30	0.12	0.07	0.12	0.08	0.52	0.02	24	0.15	2	2	1
58	80	0.83	0.10	0.19	87	0.53	0.00	0.10	0.32	0.04	0.24	0.00	19	0.23	2	3	3
59	72	1.96	0.11	0.25	210	0.54	0.10	0.03	0.07	0.02	0.43	0.01	20	0.10	2	3	3
60	70	1.31	0.12	0.30	157	0.43	0.03	0.00	0.10	0.38	0.26	0.04	33	0.25	2	4	4
61	77	0.75	0.08	0.18	62	0.13	0.06	0.00	0.15	0.36	0.47	0.00	0	0.00	2	1	3
62	14	10.58	0.20	0.40	2115	0.59	0.01	0.00	0.04	0.30	0.00	0.74	316	0.30	5	5	5
63	37	8.36	0.14	0.27	1136	0.48	0.08	0.00	0.01	0.17	0.07	0.80	127	0.15	5	3	4
64	56	0.86	0.08	0.18	66	0.06	0.04	0.50	0.06	0.35	0.00	0.00	14	0.16	1	2	1
65	50	1.11	0.10	0.17	110	0.15	0.14	0.00	0.02	0.58	0.06	0.20	23	0.21	3	4	2
66	43	0.68	0.09	0.18	62	0.04	0.11	0.00	0.04	0.73	0.00	0.18	4	0.06	2	1	1
67	32	1.47	0.07	0.14	107	0.28	0.07	0.00	0.08	0.42	0.03	0.45	8	0.05	4	3	3
68	41	1.79	0.16	0.30	288	0.31	0.02	0.00	0.00	0.58	0.00	0.71	43	0.24	5	4	3
69	69	9.40	0.13	0.28	1261	0.29	0.28	0.16	0.05	0.04	0.38	0.00	94	0.10	2	3	2
70	55	6.87	0.12	0.23	819	0.38	0.01	0.10	0.25	0.10	0.32	0.01	105	0.15	2	4	4
71	75	2.43	0.06	0.17	154	0.33	0.04	0.00	0.08	0.04	0.63	0.00	6	0.02	2	1	1
72	72	3.14	0.11	0.27	342	0.15	0.08	0.29	0.06	0.17	0.32	0.03	31	0.10	3	3	3
73	58	3.56	0.07	0.16	265	0.54	0.01	0.00	0.22	0.08	0.34	0.00	18	0.05	2	3	3
74	69	1.04	0.06	0.14	60	0.50	0.05	0.08	0.06	0.08	0.51	0.01	10	0.10	1	1	2
75	66	2.09	0.08	0.23	176	0.21	0.03	0.01	0.04	0.46	0.38	0.03	31	0.15	1	3	2
76	46	8.51	0.17	0.37	1461	0.43	0.03	0.00	0.02	0.11	0.00	0.92	125	0.15	5	5	4
77	36	10.04	0.10	0.20	995	0.15	0.04	0.00	0.05	0.48	0.00	0.56	226	0.23	5	5	4
78	42	1.35	0.21	0.36	285	0.65	0.00	0.00	0.05	0.05	0.00	0.75	50	0.37	5	5	4
79	32	2.67	0.15	0.25	412	0.54	0.01	0.00	0.11	0.29	0.01	0.74	49	0.18	5	4	3
80	23	1.72	0.13	0.27	220	0.56	0.05	0.00	0.00	0.35	0.00	0.67	49	0.28	5	5	4
81	27	2.69	0.07	0.18	195	0.05	0.32	0.00	0.01	0.58	0.03	0.01	25	0.09	1	2	1
82	46	1.93	0.12	0.39	225	0.13	0.00	0.00	0.03	0.83	0.00	0.17	45	0.23	4	3	3
83	93	9.67	0.08	0.20	821	0.27	0.26	0.04	0.03	0.17	0.63	0.00	78	0.08	4	2	2
84	97	2.14	0.09	0.20	183	0.15	0.07	0.00	0.17	0.44	0.42	0.00	40	0.19	1	2	2

## Appendix 2 continued ...

Pool number	Position Height (cm asl)	Size				Substrate composition (proportion)							Shelter and complexity				
		Surface area (m <sup>2</sup> )	Mean depth (m)	Maximum depth (m)	Volume (l)	Bare rock	Sand	Seagrass	Rubble	Coralline turf	<i>Hormosira banksii</i>	Foliose algae	Number of crevices	Crevice density	Estimate algal cover	Estimate rock cover	Estimate rugosity
85	75	1.45	0.14	0.27	196	0.27	0.00	0.18	0.21	0.32	0.12	0.04	62	0.43	1	4	3
86	68	1.61	0.09	0.19	140	0.32	0.08	0.15	0.08	0.04	0.50	0.00	18	0.11	1	1	1
87	47	2.97	0.11	0.24	331	0.22	0.01	0.00	0.09	0.68	0.03	0.00	39	0.13	1	3	2
88	78	0.83	0.14	0.31	119	0.39	0.00	0.00	0.15	0.32	0.27	0.01	29	0.35	1	3	2
89	69	1.09	0.09	0.34	101	0.22	0.02	0.00	0.11	0.44	0.29	0.00	49	0.45	1	5	4
90	40	4.24	0.12	0.27	517	0.31	0.02	0.00	0.00	0.52	0.02	0.67	133	0.31	5	5	4
91	47	6.27	0.15	0.44	943	0.26	0.03	0.00	0.02	0.61	0.00	0.60	125	0.20	4	5	4
92	43	1.67	0.15	0.32	258	0.24	0.11	0.00	0.00	0.63	0.00	0.59	81	0.49	5	4	4
93	69	3.86	0.10	0.22	398	0.11	0.20	0.00	0.07	0.56	0.08	0.09	68	0.18	1	4	3
94	43	1.97	0.08	0.19	167	0.20	0.14	0.00	0.12	0.47	0.12	0.12	36	0.18	2	3	3
95	57	1.95	0.10	0.24	200	0.11	0.03	0.00	0.04	0.75	0.17	0.11	62	0.32	2	4	3
96	46	2.53	0.16	0.28	411	0.30	0.03	0.00	0.00	0.58	0.03	0.73	79	0.31	5	5	5