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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

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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., Syms.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; Kotschal 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.