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Structure and dynamics of rockpool fish assemblages in Southeastern Australia

Shane P. Griffiths
University of Wollongong

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For my parents,
 Alan and Denise.
 For never losing faith.
STRUCTURE AND DYNAMICS OF ROCKPOOL FISH ASSEMBLAGES IN SOUTHEASTERN AUSTRALIA.

A thesis submitted in fulfilment of the requirements for the award of the degree

DOCTOR OF PHILOSOPHY

from

UNIVERSITY OF WOLLONGONG

by

SHANE P. GRIFFITHS

ENVIRONMENTAL SCIENCE

2002
"The intertidal zone is the place of origin of most fish groups. From there they spread seaward onto the shelf platform and into the open sea and landward to deltaic (and into the rivers) and supratidal areas" (Shultze, 1999).

Frontispiece. A typical intertidal landscape during low tide at Maloney's Bay, Bass Point, New South Wales, Australia.
DECLARATION

I, Shane P. Griffiths, declare that this thesis, submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in Environmental Science, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Shane Paul Griffiths

24 October 2002
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To say that a PhD thesis can be one of the greatest pieces of work anyone could imagine compiling, in my opinion, would be a drastic understatement. Many times I considered the task all too difficult but only now after finally coming to the end and compiling all my research findings in a single volume do I realise how fortunate I have been to have the opportunity to pursue my personal research in ichthyology. I have always been a keen recreational fisher, and in the early 1980's when I saw Dr Julian Pepperell talk on the television program "Go Fish Australia" about the fascinating migrations of tagged game fish, I knew fisheries was the only field I wanted to work in. From my first day of high school work experience at NSW Fisheries at Cronulla back in August 1991, I was determined to become an ichthyologist, perhaps 11 years later but nonetheless I reached my goal.

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I thank David Barker, Bruce Pease and Veronica Silberschneider from NSW Fisheries, Robin Gibson, Mike Chotkowski and Donald Buth who critically reviewed drafts of Chapter 1 in the form of a scientific paper published in the *Journal of Fish Biology*. Kirsten Benkendorff generously allowed use of her aquaria for laboratory experiments. Jade Butler, Adrian Ferguson, Alisa Eustace, Alan Griffiths, and Kane Organ assisted with fieldwork and laboratory experiments. I am grateful to Ken Russell, Mick Gregory, Catherine Pfister and Marti Anderson for statistical advice. Rob Whelan, Kris French and Bill Buttemer are thanked for helpful discussions. Glenn Johnstone generously donated nets and preliminary tagging equipment. Jeremy Nicol and Eric Hockey for supplying equipment needed for the manipulation experiments. Staff at the Environmental Science unit are thanked, namely Professor John Morrison for accepting me into his department and Sandra Quinn for help with all aspects of administration. Peter Bergman and Daniel Thompson from Northwest Marine Technology are thanked for the extremely generous donation of very expensive visible implant tags. I thank Peter Macdonald from Ichthus Data Systems who generously donated a copy of his MIX computer program and Malcolm Haddon for providing me with a copy of the GROTAG program (his Microsoft Excel version). Nikki James from the Oceanic Research Institute, South Africa is thanked for help analysing growth data.

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Papers and Manuscripts Associated with Thesis Chapters

Chapter 2- Methods for sampling rockpool fishes

Chapter 3- Overview of rockpool fish assemblages

Chapter 4- Spatial and temporal variation in rockpool fish assemblages

Chapter 5- Effects of rockpool elevation on fish assemblages

Chapter 6- Recolonisation of rockpools by intertidal fishes
Chapter 7- Movements and homing in rockpool fishes


Chapter 8- Effects of habitat complexity on rockpool fish assemblages


Manuscripts Associated with this Thesis

ABSTRACT

The structure and dynamics of intertidal rockpool, or tidepool, fish assemblages were studied along the south coast of New South Wales (NSW), Australia. This work aimed to fulfil a number of objectives that contribute to three key components in fish ecology. These are: 1) the structure and patterns of variation in rockpool fish assemblages, 2) the role of fish movements (recruitment, relocation and homing) in influencing fish population dynamics and 3) the role of structural heterogeneity in structuring fish assemblages.

Since sampling rockpool fishes is difficult owing to the variable-sized rockpools, and their small secretive fishes, the effectiveness of three sampling methods was assessed. Emptying water from rockpools with a battery-powered bilge pump proved the best method, which accounted for significantly more species and individuals than a fish anaesthetic (clove oil) and visual census. Despite being more time consuming and cumbersome, bilge-pumping provides access to crevices and under rocks, thus results in a more accurate census than the other methods trialled.

The rockpool fish assemblages of the NSW south coast comprised 50 species, mainly permanent residents endemic to Australian waters. The main families represented were: Blenniidae, Clinidae, Tripterygiidae, Gobiidae and Gobiesocidae. At the level of family, NSW rockpools fish assemblages were different from those in the United States, Spain, France and Portugal, but similar to Chile and New Zealand. They were surprisingly similar to those in South Africa, to the extent of sharing species. At a regional scale, south coast NSW fish assemblages differed from those to the north in having different relative abundance of the species common in each region. Some species of economic
and conservation importance were caught, such as *Girella elevata* and the protected black rockcod, *Epinephelus daemelii*. Their presence exclusively as juveniles indicates that rockpools may be possible nursery areas for such species that live their adult lives subtidally.

The rockpool fish assemblages were dynamic across various spatial and temporal scales. Horizontal spatial variability across scales of kilometres to hundreds of kilometres may be due to barriers to larval dispersal (e.g. local currents or upwelling events) or barriers to fish migration (e.g. sandy beaches between headlands). Across scales of metres to kilometres, the presence of different microhabitats within and among locations favours species having specific requirements for a particular habitat. In contrast, vertical spatial variability may be controlled by differences in fish physiology, which appears to broadly separate species by their intertidal residential status. Highly adapted resident species generally occupy rockpools of highest elevations where the environment can be harsh and variable, whereas opportunists and transients possessing few or no adaptations for intertidal life occupy lower rockpools where water chemistry is similar to the adjacent ocean.

Temporal variability in rockpool fish assemblages across scales of months to years was due to seasonal recruitment that occurs from summer to autumn (February to April) for most species studied. During recruitment pulses the abundance of each species varies but the relative change is minimal, resulting in highly stable and persistent assemblages. In the short-term (weeks to months), fish assemblages are resilient to perturbations and recolonise rockpools within weeks. This process was primarily due to sub-adult and adult fishes moving in from nearby rockpools, although many fishes displaced up to 20
m have the ability to home. This homing ability may be facilitated by identification of specific topographic cues learned by swimming over a limited geographic range at high tide. Juveniles appear only to be a major contributor to the recolonisation process if perturbations coincide with recruitment periods. The high stability of rockpool fish assemblages both in the long and short term may be a result of only fishes with specialised adaptations being able to utilise vacant habitats in the highly variable rockpool environment. Despite occupying a highly variable environment, the high resilience and stability detected indicates that NSW rockpool fish assemblages are probably regulated by deterministic, rather than stochastic, processes. However, a longer study period is needed to determine the effects of natural stochastic elements on these fish assemblages.

Manipulation experiments explored the effects of varying structural complexity of two major habitat types (suspended algae and substratum cover) on rockpool fish assemblages. Fish did not discriminate between different habitat types so long as some shelter was available. The amount of substrate rock cover afforded the most attractive shelter to fish, since most rockpool fishes are benthic. However, increased habitat complexity only increased the numbers of species and fish in a rockpool to a threshold where other factors (possibly food) probably become limiting. Alternatively, the lack of habitat specificity of fishes indicates fish may only utilise rockpools as temporary refuges before moving throughout the intertidal zone during high tide. Since rockpool fishes may be still vulnerable to predation at low tide (i.e. terrestrial predators), they appear to select rockpools with shelter where predators may have difficulty of access.
By undertaking experiments that manipulated both fish assemblages and habitats in rockpools, the dynamics of rockpool fish populations can be better understood. Establishing a link between regulation processes allowed the development of the "Nearest Neighbour Model", which describes the dynamics of rockpool fish assemblages being primarily dependent upon fish populations and habitats in neighbouring rockpools. This model opposes population regulation of reef and estuarine fish assemblages, which are primarily controlled by recruitment processes, and stochastic availability of resources.

The paucity of data on rockpool fishes in Australia and the increasing potential of anthropogenic impacts on coastal ecosystems highlight an urgent need to document, protect and manage its biological integrity. The most appropriate means of managing intertidal fishes may be the use of intertidal protected areas (IPA) where human activity is restricted. The limited movements and larval dispersal of intertidal fishes and the small scale patchiness of assemblage structure indicate that several small reserves may be better than a single large reserve. However, there are many socio-economic issues that need to be carefully addressed before implementation of IPAs.
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Chapter 1
General Introduction

The rocky intertidal zone is a highly productive, dynamic and ecologically important habitat that has long attracted the attention of marine scientists. Ease of access has made rocky foreshores a popular environment for study of aquatic flora and fauna (Connell, 1972). As a result, much is known of the biology of intertidal rocky shore organisms and the ecological interactions among them (Dayton, 1971; Connell, 1972; Dethier, 1984; Astles, 1993; Metaxas and Scheibling, 1993). Algal and invertebrate communities have generally received greatest attention of scientists, owing to their abundance, ease of study and obvious presence on rocky shores. However, in regards to motile organisms, and fishes in particular, their occupation of a range of physically complex habitats within the rocky intertidal zone, such as rockpools (Gosline, 1965; Yoshiyama, 1981), boulder fields (Gibson, 1972; Cross, 1981) and crevices (Faria and Almada, 2001), have contributed to this area as being one marine environment where ecological research is still very much in its infancy.

Intertidal fishes are particularly interesting animals because many spend a large majority of their lives out of water in the narrow transition zone between the land and the ocean (Gordon et al. 1970; Cross, 1981; Martin, 1995; Yoshiyama et al. 1995). They are also fascinating because they are subjected to, and have adapted to cope with, a wide variation in biological and physico-chemical environments that present fish with significant challenges. These range from predictable rhythmic tidal, lunar, diurnal and seasonal cycles that greatly influence factors such as temperature, salinity and dissolved oxygen (Morris and Taylor, 1983; Martin, 1995), food availability (Thomson and
Lehner, 1976; Moring, 1990) and risk of predation (Black and Miller, 1991; Gibson et al. 1996), to more stochastic events such as storms, cyclones (Moring, 1996) and anthropogenic impacts (e.g. harvesting and pollution) (Kingsford et al. 1991; Barber et al. 1995). As a result of these challenging conditions, the rocky intertidal zone is often occupied by only a small number of fish species and individuals, compared to adjacent subtidal waters (Smale and Buxton, 1989; Black and Miller, 1991; Table 1). Most of these species are 'permanent residents' of the rocky intertidal zone and mainly represent a small number of families including Blenniidae, Gobiidae, Cottidae, Stichaeidae, Gobiesocidae and Tripterygiidae (Table 1). They are generally small (<10 cm), cryptically coloured species, which cope with the variable conditions of the intertidal environment by possessing various morphological, behavioural and physiological adaptations. These include adaptations such as, 'suckers' built from pelvic fins (Gordon et al. 1970; Zander et al. 1999) and the ability to leave the water during unfavourable conditions (Davenport and Woolmington, 1981; Martin, 1991, 1995) and periodically breathe air (Bridges, 1988; Martin and Bridges, 1999). However, not all species of fish found within the intertidal zone utilise this habitat for their entire life history. Many 'opportunistic' species, or 'secondary residents' (Thomson and Lehner, 1976), possessing few or no adaptations to intertidal life utilise the intertidal zone as a breeding ground (Haegele and Schweigert, 1985), feeding area (Black and Miller, 1991; Rangley and Kramer, 1995a, 1995b) or as a nursery before moving to subtidal sites (Valle, 1989; Stepien, 1990). Other 'transient' species, or 'accidental visitors' (Gibson and Yoshiyama, 1999), can be occasionally found in low numbers, for example when they become stranded in the intertidal after high tide feeding excursions. These transient species are often only seasonally present when currents may disseminate them from where they would normally occur (Stepien et al. 1991).
Intertidal fishes are often found concentrated in rockpools (or tidepools) at low tide. Rockpools are one of the most common and obvious intertidal habitats on rocky shores. They can provide a productive shallow water habitat for a range of juvenile and small-sized fish species where they can exist, at least during low tides, with minimal threat from larger subtidal predators (Yoshiyama, 1981). Rockpools are of great interest to ecologists because they exist as discrete communities in a natural environment. The wide distribution throughout the world, general small size, accessibility and low cost of sampling make them excellent areas for testing the validity of existing principles in ecology (see Thomson and Lehner, 1976; Grossman, 1982; Pfister, 1995, 1997, 1998) or for developing new ecological hypotheses.

Despite their apparent ease of study, rockpool fish assemblages have undergone few quantitative investigations compared to fishes of adjacent subtidal and nearshore environments. Furthermore, few of these studies have been undertaken for periods greater than one year (Table 1). The relatively small size and high variability of rockpool environments (e.g. volume, water surface area, and habitat complexity) may contribute to difficulties in capturing fish using a single conventional shallow water fish sampling method, such as netting, making quantitative comparisons of data among rockpools difficult or impossible. However, the development of a range of effective sampling methods, particularly ichthyocides and anaesthetics, has resulted in increasing attempts to quantify ecological patterns and processes for intertidal fishes (Table 1), promoting awareness of their importance in intertidal and nearshore food webs (Coull and Wells, 1983; Connell and Anderson, 1999).
The general lack of economic importance of resident rockpool fishes, except to some aquarists and recreational fishers (see Eschmeyer et al. 1983), may also contribute to these fish assemblages being overlooked by ichthyologists. However, in some countries rockpools are believed to be nursery habitats for many species that spend their adult lives subtidally (Stepien, 1990; Varas and Ojeda, 1990), some of which are important to commercial and/or recreational fisheries (Beckley, 1985b; Lardner et al. 1993; Bennett, 1987). In South Africa, rockpools can function as alternative nursery areas for many economically important species, such as some Sparids and Mugilids, which primarily utilise estuaries and surf zones during their juvenile phases (Beckley, 1985a, 1985b; Bennett, 1987). In southeastern Australia, the rocky intertidal zone has not been widely identified as an important fish habitat (see NSW Fisheries 2001). There has apparently been only three studies undertaken on Australian rockpool fish assemblages (Wilson, 1989; Lardner et al. 1993; Silberschneider and Booth, 2001), and only one has been undertaken for a period longer than one year. However, aspects of the biology of single taxa, namely Clinids, have received some attention (Thresher et al. 1989; Gunn and Thresher, 1991). The possible nursery function of rockpools at some Australian locations (see Wilson, 1989; Lardner et al. 1993) may have wide-reaching implications for fisheries conservation and management, since anthropogenic degradation of major estuarine nursery habitats may result in increased reliance upon 'supplementary' nursery habitats, such as rockpools, to support local fisheries. In addition, the recognition that abundances of economically important species may rely upon the presence of other species of little or no perceived economic value (Auster et al. 1996; Blaber et al. 2000) has resulted in an increasing acceptance of an ecosystem approach to management (Hall, 1999).
A popular tool for managing and protecting marine biodiversity in many countries, including Australia, is the use of Marine Protected Areas (MPAs). Ironically, despite the possible nursery function of rockpools and resident intertidal fish being a significant component of intertidal community structure elsewhere (Norton and Cook, 1999), rocky intertidal fishes have yet to be included in frameworks set out to protect coastal biodiversity (Horn et al. 1999; NSW Fisheries, 2001). Instead, the design and establishment of marine reserves is often highly dependent on the stock structure of subtidal fishes, invertebrates and conspicuous and easily censused organisms, such as algae and molluscs (Roberts and Polunin, 1991; Edgar and Barrett, 1999). The successful management of Australia's coastal environment requires sound scientific knowledge of coastal ecology in order for rational management policies or frameworks to be adopted. Without baseline information on biodiversity there is no justification for conservation or management of species, nor are there any means of quantifying or assessing the potential impacts of future natural or anthropogenic perturbations. This highlights the need for research in order to fill the gaps in our scientific knowledge regarding these important fish habitats.

The main goal of the research described in this thesis was to gain an understanding of the ecological processes driving the dynamics of rockpool fish assemblages in southeastern NSW. However, the paucity of information on intertidal fishes in Australia requires an understanding of patterns of variation in rockpool fish assemblages before any processes can be examined. Taking into account the restrictions of time and resources, the objectives of the present research were to:
1) Determine the most appropriate means by which to quantitatively sample intertidal rockpool fishes at low tide using a safe and environmentally-friendly technique.

2) Document the fish fauna of intertidal rockpools across a wide spatial scale in southeastern New South Wales, Australia, and determine their residential and biogeographic affinities.

3) Quantitatively investigate variation in the fish assemblage structure across various spatial (vertical and horizontal) and temporal (within- and among-season) scales.

4) Quantitatively investigate the time scales at which fishes recolonise intertidal rockpools after disturbance.

5) Investigate the movements of some common rockpool fish species, particularly with reference to alleged homing behaviour.

6) Quantitatively investigate the influence of habitat complexity on structuring intertidal rockpool fish assemblages.

7) Develop a simple conceptual model that describes the processes that are fundamental to controlling the patterns of variation observed in rockpool fish assemblages.

In order to logically describe the structure and dynamics of intertidal rockpool fish assemblages in the Illawarra Region this thesis has been divided into seven inter-related Chapters based on the above objectives. In this thesis, only the ichthyofaunas of southeastern Australian rockpools have been investigated. Flora and invertebrate fauna of rockpools has been the focus of other research (Underwood and Jenakoff, 1984; Astles, 1993; Underwood and Skilleter, 1996).
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The importance of intertidal habitats for fish and the need for research for the purposes of assessment, conservation and management of biodiversity has been introduced in the present Chapter. This Chapter concludes below with definitions of terms and justification for their use throughout this thesis. The methods for sampling rockpool fishes are described in Chapter 2. Assessments are made with regards to the effectiveness of clove oil as a fish anaesthetic and method for sampling rockpool fishes. An overview of the composition, biogeographic and residential affinities of fish species recorded in rockpools along 300 km of the southeast Australian coast are described in Chapter 3. Investigation of long-term monitoring of spatial and temporal variations in rockpool fish assemblage structure are presented in Chapter 4, as well as exploration of the environmental and biotic variables that appear to influence fish assemblage structure. Chapter 5 continues to investigate the spatial variation of rockpool fish assemblages, but with respect to height of rockpools above sea level. The rates of rockpool recolonisation by fishes after experimental eliminations are explored in Chapter 6 to help provide a logical basis for the interval between sampling trips for future monitoring studies of rockpool fish assemblages. Chapter 7 begins by assessing the effectiveness of visible implant tags for monitoring the movements of rockpool fishes. A tagging experiment then investigates the movements and homing ability of common rockpool fish species. The influence of structural heterogeneity on rockpool fish assemblages was investigated by experimental manipulations in Chapter 8. Chapter 9 draws together the results of Chapters 2 to 8, and links various processes to explain observed patterns of spatial and temporal variation in rockpool fish assemblages. The implications for management are also discussed and the thesis concludes with directions for future research and a short overview of this research. Two papers have been included in the Appendix, which has been published in a peer-reviewed scientific journal; the use
Definitions of commonly used terms

Before exploring the patterns of variation in fish assemblages and processes controlling these patterns, it is necessary to provide definitions of commonly used terms, species nomenclature and justify their use. Identification and nomenclature of fishes follow a large number of sources including Hutchins and Swainston (1986), Kuiter (1993, 1996), Grant (1997), Randall et al. (1997) and Neira et al. (1998). However, due to the large number of taxa examined in this thesis and the presence of cosmopolitan species having various common names for the same species, only Latin scientific names have been cited. Reference to these names in the text is given in full when first mentioned in each paragraph but abbreviated in successive references within that paragraph.

Researchers studying coastal rocky shores and shallow water habitats have tended to use a number of terms to describe a particular habitat, although many seem to be used interchangeably, creating confusion. Generally, the "intertidal zone" is the term given to the region between the low and high water mark, although "littoral" has also been widely used (Raffaelli and Hawkins, 1996). The region below the low water mark can be considered "subtidal" or "sublittoral" (Ruitton et al. 2000) and the region above the high tide mark is "supratidal" (Zander et al. 1999) or "supralittoral" (McGregor, 1963). Therefore, those fish species that inhabit or can be captured in the zone between high and low water can be generally considered "intertidal fishes". In addition, many authors refer to rocky shores, sandy and gravel beaches (Schoeman et al. 2000) and estuaries
(Connell and Anderson, 1999) as intertidal or littoral habitats and the fishes that inhabit them as "intertidal fishes", "shore fishes" or "littoral fishes". However, some authors have used littoral to describe purely subtidal habitats, such as submerged rocky reefs (Mazzoldi and De Girolamo, 1997) and shallow estuarine habitats (Whitfield, 1986), whereas others describe the littoral zone to be what is normally referred to as the supratidal zone above the high tide mark. Similarly, many authors have used the term "shore fishes" to describe intertidal fishes, but this can comprise fishes found close to the shore but with variable depth limits (Leis and Trnski, 1989). In this thesis, only the terms intertidal, subtidal, supratidal and intertidal fishes are used.

The vast majority of studies examining the same or similar habitats as in this thesis have been termed "tidepools" (Beckley, 1985a; Collette, 1986; Davis, 2000a, 2000b) and "splash pools" (Gosline, 1965), which describe pools being inundated by the tide on a regular basis, or pools being intermittently splashed by waves. However, some pools, depending on tide and wave heights at a particular locality may not conform to such a definition. All pools being studied in this thesis can be simply defined as "shallow water habitats formed by rocky holes or depressions located in the intertidal zone", and subsequently termed "rockpools".

Many fish species found in rockpools often move between the intertidal and subtidal zones at high tide (see Black and Miller, 1991; Rangley and Kramer, 1995a, 1995b), although this thesis examines only those fishes that can be captured in rockpools during low tide and are thus termed "rockpool fishes". By slightly altering the definition of Gibson (1982) to describe intertidal fishes, rockpool fishes can be defined as "a fish species that can be found in rockpools during any part of its life history".
Chapter 1 General Introduction

There are also many terms analogous with describing the dynamics of rockpool fish assemblages that are used throughout this thesis. The recovery process of fish populations to vacant rockpools is often termed "recolonisation" (Beckley, 1985a; Lardner et al. 1993; Willis and Roberts, 1996; Polivka and Chotkowski, 1998) and can be defined as "the re-establishment of a fish population in a previously occupied habitat following a perturbation". This differs from "recruitment" which occurs "when larvae settle from the oceanic phase to the demersal juvenile phase" (Hixon, 1998). The term "resilience" is also commonly used to describe "how fast the variables (i.e. fish assemblage structure) return towards their equilibrium following a perturbation" (Pimm, 1984). The term "persistence" has been used to describe "the time a variable (i.e. fish assemblage structure) lasts before it is changed to a new value" (Pimm, 1984), whereas "stability" is used to describe "the ability of an assemblage to maintain its structure despite environmental uncertainty" (Gibson and Yoshiyama, 1999).

Description of the study region

The studies described in this thesis were undertaken in the intertidal zone at 14 rocky headlands situated along the high-energy coastline of southeastern Australia (southern New South Wales) from Coalcliff Point in the north to Narooma in the south (Fig. 1). However, the main focus of this research was the Illawarra region. This is generally regarded as the coastal plain that begins around 40 km south of Sydney from Stanwell Park (34°15'S, 150°58'E) to Gerroa (Black Head) (35°07'S, 150°37'E) around 50 km further south. The Illawarra region was chosen as the main focus of this research as it supports a range of rocky headlands that penetrate several kilometres into the Tasman Sea as well as smaller rocky platforms and outcrops at the ends of beaches (Plate 1).
Figure 1. Map of the study region located in southern New South Wales (NSW), Australia. The 14 locations sampled in various studies reported in this thesis are shown.
Plate 1. Photograph of the north Illawarra region in New South Wales (NSW), Australia, including Coalcliff (foreground) to Port Kembla (Background) (reprinted with permission from Smith, 2000).

The Illawarra and South Coast Region is a major population growth centre for New South Wales (NSW) indicating that the coastal zone in this region is under increasing anthropogenic pressure, such as housing and foreshore developments. However, at this point in time, the Illawarra coastal zone can still be considered to be in relatively pristine condition. It is appropriate that this research be conducted prior to major impacts, such as foreshore developments (see Griffiths, 1998). Making data available from this thesis
from this thesis may provide a basis for future management and increase the awareness of conservation issues of the rocky intertidal zone before any such impacts are experienced.

The geological environment of the Illawarra has been well studied. The coastal plain is situated at the base of an escarpment of between 400-600m in elevation formed as a result of tectonic uplift over between 80-60 million years ago. Although the Illawarra’s geology is dominated by the predominantly marine sequence of sedimentary rocks known as the Shoalhaven group, continued volcanism up until about 30 million years ago was responsible for several volcanic members evident in the region such as the Dapto and Bumbo latites (Derbyshire and Allen, 1984). Such volcanic members are responsible for the abundance of rock platforms in the Illawarra, such as Bass Point and Black Head. These rock platforms are gently-sloping and are generally 40-90 m in width, with an intertidal zone of approximately 10-30 m.

The climate affecting the Illawarra is characterised by its lack of extremes due to its close proximity to the sea and the escarpment that forms a boundary to the coastal plain some 20 km inland (Derbyshire and Allen, 1984). Mean monthly temperatures on the coastal plain range from 9.8°C in winter (June-August) to 24.4°C in summer (December-February) (Derbyshire and Allen, 1984). Although rainfall does not follow distinct seasonal patterns in the Illawarra, however the prevailing winds can be considered seasonal. Light to moderate southeast and northeast winds occur during spring and summer, while stronger winds from the west and southwest generally predominate throughout late autumn and winter (Derbyshire and Allen, 1984).
The southeastern NSW coastline lies along a high-energy coastline which experiences average ocean swells of 1-1.5m for most of the year, although strong south and southeasterly winds generate larger swells (2-4 m) during winter (Manly Hydraulics Laboratory, 2002). Tides in the Illawarra are similar to most NSW waters, being semi-diurnal and having a range of less than 2 metres (Manly Hydraulics Laboratory, 2002). The Illawarra region is subjected to similar oceanographic conditions as the rest of the mid-NSW coastline in that the continental shelf is situated relatively close to the coast, approximately 20 km off Narooma (Knight, 1989). The East Australian Current (EAC) is a primary factor influencing sea surface temperatures in the Illawarra region. Eddies from the EAC during summer can heat surface waters to 20-28°C, whereas during winter the EAC contracts northward resulting in cooler water temperatures of 14-21°C (CSIRO, 2000; Zann, 2000).

The Interim Marine and Coastal Regionalisation for Australia (IMCRA) have divided the NSW coast into five "bioregions" distinguished by biological and physical characteristics (IMCRA, 1998). The Illawarra region is located in the southern extremity of the Hawkesbury Shelf bioregion (which extends from Port Stephens to Shellharbour) and the northern portion of the Batemans Shelf bioregion (which extends from Shellharbour to Tathra). The location of the Illawarra region is considered to have mainly warm temperate marine species with some strong seasonal influences in assemblages due to the south-flowing EAC. This can contribute to nearshore fish assemblages containing high numbers of tropical fishes after the warm current transport them further south than would normally be expected (Kuiter, 1993; Smith and Suthers, 1999; Zann, 2000).
Chapter 2
Methods for sampling rockpool fishes

INTRODUCTION

As outlined in Chapter 1, despite a large number of studies on rocky intertidal areas, there have been surprisingly few quantitative investigations their fish assemblages (but see Gibson and Yoshiyama, 1999). Quantitative sampling of intertidal rockpool fishes is problematic in that the unique physical characteristics (e.g. volume, water surface area, physico-chemical regimes, habitat complexity) of individual rockpools often inhibits the use of a single sampling method. Ichthyologists have employed a variety of methods to capture intertidal fishes including ichthyocides, anaesthetics, bailing or siphoning, hand nets, seine nets, visual census, baited hooks and traps. Unfortunately, even the use of several methods in tandem may not permit quantitative comparisons of data as each method has different levels of sampling efficiency. For example, the use of dip nets often underrepresents cryptic or secretive species that are more effectively sampled using an anaesthetic (Yoshiyama et al. 1986), whereas baited traps fail to sample fishes that are best captured by angling (Beja, 1995). Considering such limitations for sampling rockpool fishes with conventional fish sampling methods, the possible quantitative methods that can be used for sampling rockpool fishes can be broadly categorised as chemical and manual methods.

Chemical sampling methods

Collection of rockpool fishes using chemical methods is relatively simple and involves addition of a particular chemical to a rockpool which anaesthetise, immobilise or comatose the fishes present, allowing collection by hand or with small dip nets. There
are two types of chemical sampling methods, anaesthetics and ichthyocides (poisons), but each has its own application depending on the research objective. Nonetheless, ichthyocides, for example rotenone, are most widely used in assemblage-level rockpool fish studies (for recent examples see Beckley, 2000; Silberschneider and Booth, 2001). However, the potential of ichthyocides for residual effects on subsequent catches and relative effectiveness to other methods has attracted recent consideration (Christensen and Winterbottom, 1981; Mok and Wen, 1985; Yoshiyama et al. 1986). Although ichthyocides are an efficient sampling method, fish mortality is obviously high and ethical issues must be justified, hence there are strict regulations for their use in most countries. Furthermore, its toxicity to humans and other rockpool animals may make it a less desirable sampling method.

Anaesthetics, such as quinaldine and tricaine methanesulfonate or MS-222 (3-aminobenzoic acid ethyl ester methanesulfate), are a far less destructive sampling method as fish mortality is greatly minimised. By adding an anaesthetic to a rockpool, fishes can be quickly immobilised and collected with dip nets without excessive stress or physical harm and can then be released alive after observations are recorded. There are a variety of fish anaesthetics available, although the most commonly used anaesthetic used in fisheries science, MS-222, has limited use in the field. The U.S. Food and Drug Administration (FDA) requires fish exposed to MS-222 to undergo a 21 day withdrawal period before being released into the wild or consumed by humans. Significant disadvantages also exist for other anaesthetics such as carbon dioxide (CO₂), which induces only shallow anaesthesia, excessively long induction and recovery times (Gilderhus and Marking, 1987) and high mortality in rainbow trout (Bernier and Randall, 1998).
Recently there has been growing interest in fisheries in the use of clove oil as an alternative fish anaesthetic. Clove oil, containing its active principal Eugenol (4-allyl-2-methoxyphenol), is derived from the stem, flowers and leaves of clove trees (Eugenia caryophyllata and Eugenia aromatica). It is a highly versatile chemical used in a range of applications such as an antifungal and antibacterial agent (Karapmar and Aktug, 1987; Karapmar, 1990; Moleyar and Narasimham, 1992), as an antioxidant (Cort, 1974; Pulla Reddy and Lokesh, 1992) and as a local anaesthetic in dentistry (Curtis, 1990). It has many advantages over other fish anaesthetics by being a natural compound that is user-safe, inexpensive, can generally be used in lower concentrations than other anaesthetics for similar anaesthetising effects (Keene et al. 1998). As well, it promotes rapid induction and recovery from anaesthesia for a number of fish species in both freshwater (Anderson et al. 1997; Keene et al. 1998; Waterstrat, 1999) and marine (Soto and Burhanuddin, 1995; Munday and Wilson, 1997) environments. Furthermore, unlike MS-222, fish exposed to clove oil do not require a 21 day withdrawal period before being released back into the wild (Anderson et al. 1997). Considering the numerous advantages and successful use of clove oil as an anaesthetic for a number of fish species its application to intertidal rockpool fishes has yet to be investigated, although appears to be an impressive alternative to the widely used, but potentially hazardous, quinaldine.

**Manual sampling methods**

With concerns of potential adverse effects of chemical sampling methods on rockpool fishes and the researcher, numerous authors have developed manual means of sampling rockpool fishes. These include fish traps (Beja, 1995), visual census (Christensen and Winterbottom, 1981), a range of nets such as dip, seine and pop nets (Rangley and
Kramer, 1995a, 1995b), or draining water from rockpools using battery or petrol-powered pumps, by siphoning (Davis, 2000a, 2000b) or bailing with buckets (Hussain and Knight-Jones, 1995). The main advantage of manual methods is that they generally permit rapid census and have little obvious impact on the rockpool biota. However, the main disadvantage of using physical sampling methods is that most are species selective and underrepresent secretive or cryptic species (see Christensen and Winterbottom, 1981; Yoshiyama et al. 1986). Emptying rockpools is probably the most accurate manual sampling method. In addition, it causes minimal stress in fish because most rockpool fishes have the ability to withstand at least short periods of aerial exposure (Martin and Bridges, 1999). Hussain and Knight-Jones (1995) suggest emptying rockpools is a more effective sampling method than using quinaldine as secretive fish are more easily found by being able to search crevices and under rocks when rockpools are empty. However, there are also some disadvantages in using water extraction methods to sample rockpool fishes: i) large pools require long periods to empty, especially employing bailing and/or siphoning; and, ii) a heavy 12 volt battery which is needed to power a bilge pump is difficult to transport to remote locations.

This Chapter aims to justify the use of a particular sampling method in the various studies comprising this dissertation. Since clove oil has only recently come into use as a fish anaesthetic, it was necessary to conduct two separate experiments. First, to determine a single desirable concentration of clove oil for anaesthetising some intertidal fishes, and second, to use this concentration to assess the effectiveness of clove oil as a stand-alone sampling method compared to two commonly used methods, namely bilge pumping and visual census.
MATERIALS AND METHODS

Experiment 1: Determination of a desirable clove oil concentration

To determine a suitable concentration of anaesthetic to sample rockpool fish populations, the tolerance of eight intertidal fish species to clove oil was assessed. Fish were caught by completely draining water from a number of 1000-2000 litre (l) rockpools at Maloney's Bay, Bass Point (34°35'S, 150°52'E) (see Fig. 1) with a battery-powered submersible VMC bilge pump of 9092 l hr\(^{-1}\) capacity. Some species were also caught with a small seine net from \textit{Zostera capricorni} seagrass beds at Lake Illawarra where they could be caught in larger numbers. When captured, fish were immediately transferred to a 60 l container of continuously aerated seawater (mean water temperature 18.1 ± S.E. 0.5 °C) in preparation for exposure to clove oil.

Four identical aquaria were filled with 20 l of continuously aerated seawater (18.3 ± 0.6 °C) containing clove oil concentrations of 30, 40, 50 and 60 mg l\(^{-1}\). These concentrations were selected after reference to other studies (Soto and Burhanuddin, 1995; Anderson \textit{et al.} 1997; Keene \textit{et al.} 1998) and short preliminary trials. Clove oil is insoluble in seawater and therefore it was necessary to dissolve it in ethanol in the ratio of 1:5 (clove oil : ethanol). An additional aquarium containing the highest concentration of ethanol used (i.e. the same as in the 60 mg l\(^{-1}\) treatments) was maintained as a control. A few fish representing each of the eight species were subjected to the ethanol treatment and no variation in opercular rate or swimming behaviour was observed over a period of 15 min.
No less than five fish of each species for each clove concentration (i.e. at least 20 fish per species) were placed in each aquarium. Fish were monitored continuously and induction time to anaesthesia was measured to the nearest second. Successful induction to anaesthesia was determined as the stage where total loss of equilibrium first became evident (i.e. when the fish could no longer swim and maintain a vertical position in the water). Concentrations of clove oil were considered suitable if induction to anaesthesia was less than 3 min (see Marking and Myer, 1985). As soon as the fish were fully anaesthetised they were transferred immediately to a 30 l container of continuously aerated seawater (18.2 ± 0.4 °C) and time to recovery was measured. Recovery was defined as the stage when the fish regained equilibrium (i.e. maintained a vertical position in the water). A recovery time of less than 5 min was considered desirable (Marking and Myer, 1985), which would probably be adequate time to record weight, length and identify fish in a larger study before they emerged from anaesthesia.

**Experiment 2: Effectiveness of clove oil as a quantitative sampling method**

After a suitable concentration of clove oil was established in experiment 1, its effectiveness for sampling wild fish populations in intertidal rockpools was investigated. The rockpools sampled were situated along an exposed south-facing rocky platform at Maloney's Bay, Bass Point (Fig. 1) and were selected for similarity of habitat, size and vertical elevation (tidal height) in the intertidal zone. All rockpools were largely devoid of aquatic macrophytes, but the bedrock substratum of all rockpools was covered in cobbles and small boulders, which is characteristic of rockpools in the area. Since rockpool size was a possible determinant of the number of fish collected with a single sampling method (i.e. more difficult to catch small secretive species in large pools), rockpools were categorised *a priori* by volume as small (8-21 l) or large
To add the correct clove oil concentration to rockpools, the volume of each pool was calculated by emptying with the bilge pump two months prior to the study, which allowed adequate recolonisation of rockpools by fishes (see Chapter 4). For a balanced experimental design eight large and eight small pools were sampled with each method.

**Census of fishes**

Prior to addition of clove oil to rockpools (30-60 min), an above-water visual census of fishes was made over a period of 10 min. In some large pools, a diving mask was used to search deep crevices. Fish were identified to species and total length of fish estimated to the nearest 5 mm. After the visual census was complete, 40 mg l\(^{-1}\) of clove oil was added to the same pool and mixed thoroughly with a wooden stirring rod. Usually anaesthetised fish surfaced within five minutes and were collected with a small dip net. However, some fish sank to the bottom or swam under rocks and could not be captured. All anaesthetised fish caught were identified immediately, measured and transferred to a 30 l container of continuously aerated seawater (18 ± 0.5 °C) to recover. Fifteen minutes after the last fish was captured, the rockpool was emptied completely with the bilge pump and a thorough search of the rockpool was carried out. All fish caught were identified, measured for their total length and transferred to the recovery tank.

Fishes were collected from the rockpools by hand after completely emptying rockpools using a 12V battery-powered submersible VMC bilge pump of 9092 l hr\(^{-1}\) capacity (Plate 2). A small hand net was also set over the end of the hose when rockpools were being emptied to capture any fish that were accidentally drawn into the pump (Plate 2). A thorough search of each pool was conducted systematically from one side of the pool...
to the other, overturning all rocks and boulders and shaking foliose algae until all fish were removed. A second search was then conducted to collect fish that may have been overlooked upon the first search, although, in the vast majority of pools the second search yielded no additional fish. These fishes collected were transferred to a 60 l drum containing fresh aerated seawater for identification and measurement of their total length (TL). However, fork length (FL) was also measured for species considered being of economic importance, namely *Girella elevata*. This allowed the results in the present study to be discussed in relation to the vast majority of studies that use this length measurement (see Gray *et al.* 1996). Fish were then released alive into nearby rockpools or the shallow subtidal at least 10 metres away from the pool being sampled, unless voucher specimens were retained for identification. This collection method was utilised in all studies reported in this thesis.

Fish collected and used in both experiments were handled in accordance with the regulations of an approved animal ethics permit (No. AE99/13).

**Statistical analyses**

Two-factor analysis of variance (ANOVA) was used to compare the number of species and individual fish sampled by clove oil, bilge pumping and visual census in large and small rockpools. Both factors were considered fixed. Data were examined for normality and homoscedasticity using Shapiro-Wilk and Cochran's Test, respectively. Abundance data were transformed by $\log_{10} (x+1)$ to remove heteroscedasticity. Tukey's Honestly Significant Difference (HSD) test was used to determine significantly different means.
illustrate whether particular sampling methods were selective for specific size classes of fish.

Plate 2. Use of a bilge pump (VMC 9092 l hr\(^{-1}\) capacity) to drain water from a typical rockpool. A 12-volt battery powers the pump. Water is strained through a fine-mesh net to captured fishes accidentally drawn into the pump.
RESULTS

Experiment 1: Determination of a desirable clove oil concentration

A total of 181 fish representing the eight most common intertidal fish species were exposed to clove oil. No mortalities were documented during the experiment. Size and number of fish representing each species used in the study and temperature of aquaria water in each treatment is given in Table 2.

Time to induction and recovery from anaesthesia varied markedly interspecifically and to a lesser extent intraspecifically (Fig. 2). *Enneapterygius rufopileus* appeared to have the lowest tolerance to clove oil. This species had induction times of less than 30 sec for all concentrations tested and excessively long recovery times of 6.5 min at 30 mg l\(^{-1}\) and 9.5 min at 60 mg l\(^{-1}\) (Fig. 2). *Myxus elongatus* was most tolerant of clove oil exhibiting long induction times (e.g. 187±42 sec at 30 mg l\(^{-1}\)) and short recovery times at high concentrations (63±28 sec at 60 mg l\(^{-1}\)). However, recovery times varied among individuals (Fig. 2) even though they were of similar size (Table 2). Induction to anaesthesia was short for all species at all concentrations, with the only exception being *M. elongatus*, which took a little over 3 min at 30 mg l\(^{-1}\) (Fig. 2). Recovery from anaesthesia was short for *M. elongatus*, *Afurcagobius tamarensis*, *Meuschenia trachylepis* and *Girella elevata* at all concentrations (Fig. 2). Recovery times for *Favonigobius lateralis*, *Bathygobius cocosensis* and *Scorpis lineolatus* were also short at concentrations of 30 and 40 mg l\(^{-1}\), although recovery times were in excess of 5 min for these species at concentrations of 50 and 60 mg l\(^{-1}\) (Fig. 2).

Apart from *Enneapterygius rufopileus*, all species displayed respective induction and recovery times of less than 3 and 5 mins respectively at a clove oil concentration of 40...
Although *E. rufopileus* had a recovery time of 438.8 (±5.4) sec at 40 mg l⁻¹, which is higher than the recommended 5 min (300 sec) maximum recovery time for anaesthetised fish (Marking and Meyer 1985), no mortalities were observed. Therefore, a clove oil concentration of 40 mg l⁻¹ appeared to be most desirable for sampling wild populations of rockpool fishes.

**Table 2.** Number and length range (total length in mm) of fish representing eight species anaesthetised by clove oil combined for each of the four concentrations (30, 40, 50 and 60 mg l⁻¹). Mean (±SE) water temperature in aquaria is also listed.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of fish anaesthetised</th>
<th>Length range (mm)</th>
<th>Mean (± SE) aquaria water temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>20</td>
<td>43-57</td>
<td>18.3 (± 0.1)</td>
</tr>
<tr>
<td><em>Enneapterygius rufopileus</em></td>
<td>26</td>
<td>31-49</td>
<td>18.1 (± 0.2)</td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>24</td>
<td>69-81</td>
<td>17.9 (± 0.3)</td>
</tr>
<tr>
<td><em>Afurcagobius tamarensis</em></td>
<td>22</td>
<td>41-57</td>
<td>18.6 (± 0.1)</td>
</tr>
<tr>
<td><em>Favonigobius lateralis</em></td>
<td>23</td>
<td>34-48</td>
<td>18.3 (± 0.1)</td>
</tr>
<tr>
<td><em>Scorpis lineolatus</em></td>
<td>21</td>
<td>29-35</td>
<td>18.3 (± 0.2)</td>
</tr>
<tr>
<td><em>Meuschenia trachylepis</em></td>
<td>25</td>
<td>119-131</td>
<td>18.2 (± 0.1)</td>
</tr>
<tr>
<td><em>Myxus elongatus</em></td>
<td>20</td>
<td>61-70</td>
<td>18.3 (± 0.2)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>181</strong></td>
<td><strong>29-131</strong></td>
<td><strong>18.3 (± 0.3)</strong></td>
</tr>
</tbody>
</table>
Figure 2. Mean (±SE) induction and recovery times (in seconds) for eight intertidal fishes anaesthetised with clove oil at concentrations of 30, 40, 50 and 60 mg l\(^{-1}\).
Experiment 2: Effectiveness of clove oil as a quantitative sampling method

A total of 100 fish representing 10 species were captured from the censused rockpools (Table 3). Rockpools sampled using clove oil accounted for 49 fish from eight species, the bilge pump method accounted for 51 fish from seven species, whereas visual census accounted for only 18 fish of four species (Table 3). The most abundant species in pools were *Lepidoblennius haplodactylus* and *Bathygobius cocosensis*, representing 21% and 58% of the catch, respectively.

ANOVA revealed both number of species and individuals differed significantly between sampling methods but not in regard to pool size (Table 4). The number of species caught by clove oil sampling did not differ significantly from the bilge pump samples in small and large pools, although both methods accounted for significantly more species and individuals than visual census (Fig. 3). The number of individuals caught by clove oil sampling did not differ from the bilge pump samples in small pools, although both methods accounted for significantly more species and individuals than visual census (Fig. 4). However, in large pools clove oil and visual census samples did not differ and both methods accounted for significantly fewer individuals than bilge pumping (Fig. 4).

Although clove oil and visual methods accounted for only 54% and 20% of the total number of fish in rockpools, the length-frequency distributions of fish did not differ among sampling methods (Kolmogorov-Smirnov two sample test; $Z=0.942; P=0.337$). However, fish in the 36-46 mm range were represented most poorly by clove oil sampling, which represented mainly *Bathygobius cocosensis* and *Enneapterygius*
and surprisingly, many larger fish (>60 mm), mainly *Istiblennius meleagris* (Table 3), were not detected by visual census (Fig. 5).

**Table 3.** Number of fish and length range (mm) for each species captured after: bilge pumping; addition of clove oil; and observed by visual census. Number of small (S) and large (L) pools contributing to the total number of fish representing each species is shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Clove oil</th>
<th>Bilge pump</th>
<th>Visual census</th>
<th>Number and size of pools</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Abudeufduf vaigiensis</em></td>
<td>1 (56)</td>
<td>-</td>
<td>-</td>
<td>1L</td>
</tr>
<tr>
<td><em>Acanthistius ocellatus</em></td>
<td>-</td>
<td>2 (50-52)</td>
<td>-</td>
<td>1S, 1L</td>
</tr>
<tr>
<td><em>Aspasmogaster costatus</em></td>
<td>1 (18)</td>
<td>-</td>
<td>-</td>
<td>1L</td>
</tr>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>18 (26-52)</td>
<td>34 (34-66)</td>
<td>9 (30-55)</td>
<td>5S, 8L</td>
</tr>
<tr>
<td><em>Chironemus marmoratus</em></td>
<td>2 (28-43)</td>
<td>-</td>
<td>-</td>
<td>1S</td>
</tr>
<tr>
<td><em>Enneapterygius rufopileus</em></td>
<td>4 (33-39)</td>
<td>3 (36-40)</td>
<td>1 (35)</td>
<td>2S, 3L</td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>3 (52-91)</td>
<td>1 (49)</td>
<td>2 (50-70)</td>
<td>3L</td>
</tr>
<tr>
<td><em>Heteroclinus whiteleggi</em></td>
<td>-</td>
<td>1 (32)</td>
<td>-</td>
<td>1L</td>
</tr>
<tr>
<td><em>Istiblennius meleagris</em></td>
<td>3 (55-69)</td>
<td>8 (54-109)</td>
<td>-</td>
<td>2S, 4L</td>
</tr>
<tr>
<td><em>Lepidoblenius haplodactylus</em></td>
<td>17 (25-80)</td>
<td>2 (45-60)</td>
<td>6 (39-79)</td>
<td>4S, 4L</td>
</tr>
</tbody>
</table>
Table 4. Results of ANOVAs testing for significant differences in number of species and number of individuals between sampling methods (M) and pool size (S). Number of fish data was transformed by $\log_{10} (x+1)$ prior to analysis, which eliminated heteroscedasticity in the data. Mean squares (MS) and significance levels are shown and significant results are in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Number of Species</th>
<th>Number of Individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>MS</td>
</tr>
<tr>
<td>Pool Size (S)</td>
<td>1</td>
<td>4.08</td>
<td>0.00</td>
</tr>
<tr>
<td>Method (M)</td>
<td>2</td>
<td><strong>11.52</strong></td>
<td><strong>1.06</strong>*</td>
</tr>
<tr>
<td>S x M</td>
<td>2</td>
<td>1.40</td>
<td><strong>0.20</strong>*</td>
</tr>
<tr>
<td>Residual</td>
<td>42</td>
<td>1.52</td>
<td>0.06</td>
</tr>
<tr>
<td>Cochran’s C</td>
<td></td>
<td>0.39</td>
<td>0.36</td>
</tr>
</tbody>
</table>

$P<0.05 (*)$; $P<0.01 (**)$; $P<0.001 (***)$. df = degrees of freedom.
Figure 3. Mean (±SE) number of species caught by bilge pumping, clove oil sampling (40 mg l⁻¹) and observed by visual census in small and large rockpools. Horizontal lines join means that did not significantly differ in Tukey's HSD tests.

Figure 4. Mean (±SE) number of individual fish caught by bilge pumping, clove oil sampling (40 mg l⁻¹) and observed by visual census in small and large rockpools. Horizontal lines join means that did not significantly differ in Tukey's HSD tests.
Figure 5. Length-frequency distributions for all species combined, caught by clove oil, observed by visual census and after emptying rockpools with a bilge pump.
DISCUSSION

Desirable concentration of clove oil

This study aimed to determine a single clove oil concentration to sample wild rockpool fish assemblages, but tolerances to clove oil varied among species. Moring (1970) also encountered this problem when assessing the efficacy of quinaldine on Californian rockpool fishes. In the present study, *Myxus elongatus* showed large variability in induction times among individuals at high concentrations, even considering they were all of similar size. In contrast, *Enneapterygius rufopileus* took more than six minutes to recover from anaesthesia at all concentrations of clove oil tested, whereas other benthic species of similar size such as *Bathygobius cocosensis* and *Favonigobius lateralis* only displayed long recovery times at high concentrations. Considering that recovery times for all species were not excessively long (i.e. >15 min) and no mortalities were evident, clove oil can be considered an ideal anaesthetic for rockpool fishes by the criteria of Marking and Meyer (1985). Furthermore, 40 mg l\(^{-1}\) was the optimal concentration for sampling temperate Australian rockpools with clove oil. Induction and recovery times at this concentration were long enough to record biological data. However, due to the temperate climate at the location of the present study, results may differ significantly in tropical or boreal climates where fishes may differ physiologically to fish exposed to clove oil in the present study. Similar experiments to the present study need to be conducted in these locations before selecting a particular clove oil concentration for sampling.

At a clove oil concentration of 40 mg l\(^{-1}\) rockpool fishes in the present study generally exhibited induction and recovery from anaesthesia in less than one and five minutes respectively. This was similar or shorter than those recorded for other species exposed
to similar concentrations of clove oil. For example, juvenile rainbow trout, *Oncorhynchus mykiss*, exhibited induction and recovery times of 1-4 minutes and 4-14 minutes respectively, at 40 mg l\(^{-1}\) (Anderson *et al.* 1997; Keene *et al.* 1998). Furthermore, induction to anaesthesia in juvenile rabbitfish, *Siganus lineatus*, took around two minutes at 50 mg l\(^{-1}\) (Soto and Burhanuddin, 1995). However, Waterstrat (1999) recorded recovery times within four minutes for juvenile channel catfish, *Ictalurus punctatus*, which were subjected to higher concentrations of clove oil (100 mg l\(^{-1}\)) than the rockpool fishes in the present study.

The efficiency of other anaesthetics, such as the widely used quinaldine (2-methylquinolone), as quantitative methods for sampling rockpool fishes have yet to be properly assessed. Some authors have commented on the effectiveness of quinaldine as an anaesthetic and sampling method (see Yoshiyama, 1981; Gibson, 1982, 1999a; Yoshiyama *et al.* 1986) but there have been few instances where concentrations and induction and recovery times have been cited (but see Gibson, 1967b; Yoshiyama *et al.* 1986). Moring (1970) published early information on the anaesthetising effects of quinaldine on fish. He used concentrations of between 7 and 13 ppm and found 13 ppm induced adequate anaesthesia for the majority of the 16 species examined, although fish mortality was high. In contrast, no mortalities were documented in the present study using clove oil. While Moring (1970) recorded short induction times (0.5-4 minutes), recovery times were excessively long (5-14 minutes). If subjected to the criteria of Marking and Myer (1985) quinaldine may not be considered a suitable anaesthetic for intertidal fishes due to excessive recovery times.
Anderson et al. (1997) and Keene et al. (1998) both found that higher concentrations of MS-222 (60 mg l$^{-1}$ and 120 mg l$^{-1}$) were needed to anaesthetise juvenile rainbow trout, *Oncorhynchus mykiss*, compared to clove oil. Bernier and Randall (1998) assessed the anaesthetising efficiency of carbon dioxide (CO$_2$) for *O. mykiss* and found induction and recovery times to be in excess of 10 minutes and recorded 33% mortality, which is indicative of a poor fish anaesthetic (Marking and Myer, 1985).

**Comparisons of sampling methods**

Sampling of rockpool fishes has long been considered a difficult task, mainly due to the variable physical parameters among rockpools. To combat this problem, researchers have used a variety of sampling methods to suit local intertidal environments including ichthyocides (Mahon and Mahon, 1994; Polivka and Chotkowski, 1998), anaesthetics (Moring and Moring, 1991; Pfister, 1998), hand nets (Yoshiyama 1980; Faria and Almada, 1999), traps (Green 1971a, 1971b), seine nets (Moring, 1981; Rangley and Kramer, 1995a, 1995b), visual census (Christensen and Winterbottom, 1981) and baited hooks (Butler, 1982). However, very few studies have quantitatively demonstrated the effectiveness of a particular sampling method to justify its use, particularly in assemblage-level studies (but see Christensen and Winterbottom, 1981).

In the present study, samples obtained using clove oil were similar to those obtained by bilge pumping. However, the effectiveness of clove oil as a sampling method appeared to be influenced by rockpool size. In small rockpools, clove oil and bilge pump samples were similar, but in large rockpools, the number of individuals caught was significantly lower than that for bilge pumping. Clove oil may have also been less effective in large
rockpools due to fish being more difficult to catch in the dip net in the deeper water during induction to anaesthesia.

It is evident in the present study that bilge pumping was a very effective sampling method. Rockpools were more thoroughly sampled using bilge pumping than by either clove oil or visual census, as crevices can be searched and boulders overturned to search for hiding fishes. However, the major disadvantage of bilge pumping is that it is an extremely time-consuming. Large rockpools take 20-30 minutes to empty and re-fill and at least 30 minutes to perform adequate searches of the substratum and all crevices. Therefore, a maximum of three or four rockpools (i.e. one rockpool per hour) can be sampled at low tide before rockpools are inundated by the incoming tide. A second disadvantage of the bilge pump method is a heavy 12-volt battery has to be carried into the field to power the pump, which can be difficult to transport to remote locations.

Visual census was the least effective sampling method, especially for large rockpools, and resulted in underestimates of both the numbers of species and individuals present. Christensen and Winterbottom (1981) encountered similar problems when applying visual census to large rockpools, but suggested results can be as accurate as rotenone sampling with application of correction factors to compensate for cryptic species that were overlooked. However, small pools lacking cracks and other areas of cover may be as effectively sampled by visual census as by use of clove oil. Visual census can be at least as effective as in the present study if there is adequate knowledge and skill to discriminate local rockpool fishes. Some cryptic species, such as *Bathygobius cocosensis*, *Lepidoblennius haplodactylus* and *Enneapterygius rufopileus*, appear very similar at small sizes (<40 mm). Because many species quickly hide under rocks upon
disturbance from an observer, identification and census accuracy may be further reduced. Visual census may be an appropriate sampling technique where resources, particularly time, are limited as large rockpools can be censused well within a period of ten minutes. However, in most instances visual census may prove to be of little value.

Although the compositions of fish recorded by the three sampling methods varied markedly, the length-frequency distributions for fish obtained by each sampling method did not differ. This indicates that these methods may not be as size selective as many other intertidal fish sampling methods, such as seine nets and traps (see Gibson, 1982, 1999a). However, clove oil samples and visual census failed to represent larger size classes (>60 mm FL) of fish. Although it would be assumed larger fish would be readily observed in a visual census, the large individuals of *Bathygobius cocosensis* and *Istiblennius meleagris* are highly secretive. These species also failed to emerge from under rocks after being exposed to clove oil.

This study has quantitatively compared the effectiveness of two methods (clove oil and visual census) for sampling intertidal rockpool fishes in south eastern Australia, and the fishes not accounted for using these methods were determined using bilge pumping. Clove oil is an effective, inexpensive, user-safe anaesthetic for rockpool fishes. It is also an effective stand-alone sampling method and samples can be collected in a fraction of the time taken using the bilge pumping method. The major disadvantage of the clove oil sampling method is the underrepresentation of cryptic species and its pungent odour. Although bilge pumping is a more time-consuming and cumbersome method to use, it was considered the most accurate and quantitative of the methods tested, since it accounted for fishes not sampled by the two other methods. Therefore, it was decided
the bilge pump method would be adopted in this research program as the principal sampling method of rockpool fishes.
Chapter 3

Overview of rockpool fish assemblage structure

INTRODUCTION

The distribution of marine fishes is influenced by numerous environmental factors. These include water temperature (e.g. Maree et al. 2000), wind stress and wave action (e.g. Milicich, 1994), currents (e.g. Ayvazian and Hyndes, 1995), water chemistry (e.g. Riginos and Nachman, 2001) and biological factors including planktonic production (e.g. Thresher et al. 1989). The spatial variation in these factors can affect the local structure of fish assemblages and determine their similarity to nearby or distant assemblages (Maree et al. 2000). However, the most important elements for determining the 'connectiveness' of geographically separated fish assemblages are probably regional current patterns, which control temperature and plankton production, physical geographic barriers and the life history of the fishes themselves. For example, Beckley (2000) found that regions along the South African coast shared similar fish species due to widespread dispersal of their larvae by the Agulhus Current. Similarly, Ayvazian and Hyndes (1995) found that the Leeuwin Current that flows south along the Western Australian coast was responsible for sharing species among northern and southern regions. In contrast, Horn and Allen (1978) found that the cold upwelling water off the coast of Baja created a distinct boundary that defined northern and southern fish assemblages.

As stated previously (see Chapters 1 and 2), there have been surprisingly few quantitative investigations of rockpool fishes (Gibson, 1982), especially in Australia. There are however, numerous accounts worldwide of the biology of single taxa or
qualitative checklists of rocky intertidal species of local areas (see Chapter 1), but most of these studies have concentrated on a single locality and rarely been undertaken for periods of more than a few months. Nonetheless, these studies have shown rockpool fish assemblages to generally support low species richness (<30 species), when compared to the hundreds of species that can be found on coral reefs (Doherty and Williams, 1988), and low densities of fish that often do not exceed more than a few fish per pool (Moring, 1976; Mgaya, 1992). However, some tropical regions are an exception, such as Taiwan, where species richness has been documented to range from 139 to 194 species in studies that only span a period of 10-12 months (Chang et al. 1977; Mok and Wen, 1985). Furthermore, rockpool fish assemblages generally comprise species from only a few families including Blenniidae, Gobiidae, Cottidae, Clinidae, Gobiesocidae, Tripterygiidae and Stichaeidae (see Table 1, Chapter 1). These mainly constitute permanent residents in the intertidal zone. The majority of these families have a wide distribution, although in many parts of the world some families are more dominant than others. For example, Cottidae, Stichaeidae and Scorpaenidae are dominant in the United States (Yoshiyama, 1981; Grossman, 1982); Clinidae, Sparidae and Blenniidae in South Africa (Beckley, 1985b, 2000; Prochazka, 1996); Tripterygiidae and Gobiesocidae in New Zealand (Willis and Roberts, 1996); Blenniidae and Girellidae in Chile (Stepien, 1990; Varas and Ojeda, 1990); Blenniidae, Gobiidae and Gobiesocidae in Spain (Macpherson, 1994), France (Gibson, 1968, 1972) and Portugal (Faria and Almada, 1999, 2001).

The distribution of rockpool fishes is interesting because rockpools can be separated by a range of physical barriers at various scales. At the smallest scale of a single rock platform, individual rockpools are spatially separated by various distances ranging from
a few metres to a few kilometres. However, they are also temporarily separated at low tide where they exist as 'island' habitats, and the extent of this isolation may vary with the tidal height of individual rockpools. At larger spatial scales of ten to hundreds of kilometres, fish assemblages may be isolated by beaches which separate rocky headlands, and furthermore, by wide expanses of ocean which separate continents (Riginos and Nachman, 2001). The degree of connectiveness between local, regional and continental rockpool fish communities is little understood but attracting some attention. Stepien et al. (1991) found that rockpools adjacent to the region of cold upwelling at Point Conception in Mexico supported a unique species-rich fish assemblage derived from a mixture of warm and cool temperate. They suggest that this could be maintained through the larval existence of many species and their transport by the California Current. Similarly, Stepien (1990) found a species rich mixture of warm temperate and cool temperate rockpool fishes in central Chile, along the boundary of two biogeographic provinces.

In Australia, the coastal waters of southeastern Australia define a biogeographically distinct region between tropical and warm temperate provinces. This biogeographic region is often defined by the southern boundary of the south-flowing East Australian Current (EAC) before it separates from the coast and meanders east towards New Zealand (Zann, 2000). The convergence zone of the tropical waters of the EAC with temperate waters is known to have a highly diverse ichthyofauna as it defines the southern limits of the distributions of many tropical fishes and the northern limits of cool temperate species (Kuiter, 1993; Smith and Suthers, 1999). The number of species recorded from the three studies of rockpool fish communities in Australia ranges from 23 (Silberschneider and Booth, 2001), 28 (Wilson, 1989) to 99 species (Lardner et al.)
However, the number of species found in these studies largely reflects the duration of the study and the size of rockpools sampled. Dominant taxa recorded in these studies represent a large number of families including Tripterygiidae, Gobiidae, Girellidae, Clinidae, Blenniidae, Tetradontidae, Pomacentridae, Mugilidae, and Chironemidae. However, it is probably the first five of these families that are representative of the rockpool fish assemblages in NSW.

Apparently all published studies of rockpool fishes in Australia have been undertaken north of Sydney in NSW and in Tasmania. As a result, there is an enormous gap in the scientific knowledge of rockpool fish communities along the coast of southeastern NSW. This study aimed to provide a large-scale account of the rockpool fish assemblages along the south coast of New South Wales (NSW), Australia with a primary emphasis on describing species composition, biogeographic and residential affinities of rockpool fishes. Due to the natural variability in rockpool fishes, it may not be possible for a single study to achieve this aim, as the relative abundances of fish species can vary significantly among locations (Yoshiyama, 1981; Yoshiyama et al. 1986) and years (Collette, 1986). There are also many instances where some species are only represented by a few individuals in some localities and not others. This Chapter has combined the samples collected throughout the various sections of this thesis, to provide an overview of the rockpool fish assemblages found along the south coast of NSW.
MATERIALS AND METHODS

Study Sites

Between the period of 17 August 1999 and 13 September 2001, fishes were collected in 1336 samples from 296 intertidal rockpools at 14 locations along the NSW south coast. These locations were situated between Coalcliff Point in the northern Illawarra region, to Wagonga Head located near Narooma 300 km to the south (Fig. 1). Further descriptions and photographs of these locations are given in Appendix 3. Although the number of rockpools sampled varied greatly depending on the studies being undertaken, at least eight rockpools were sampled at each location and most were sampled on at least three occasions. The most northerly and most southerly headlands sampled were located approximately 40 km and 400 km south of Sydney, respectively. Rockpools of various sizes and vertical elevation in the intertidal zone were sampled in these studies, although the vast majority of pools had a substratum consisting of cobbles and small boulders.

Census of rockpool fishes was undertaken using a range of methods including dip nets, visual census, addition of clove oil as an anaesthetic or emptying rockpools with buckets, by siphoning or use of a bilge pump (see Chapter 2). However, the majority of studies used the bilge pumping method described in Chapter 2.

Categorisation of fishes

To better understand the structure of the NSW rockpool fish assemblages, species were broadly categorised by their geographic distribution relative to the major marine provinces described by Briggs (1974) (Fig. 6). Similar categorisation of subtidal rocky
reef fish assemblages have been undertaken for the Sydney region (Burchmore et al. 1985). These categories consisted of:

i. Tropical (Tr), species which are primarily distributed in the warm tropical region of the Solenderian/Banksian province although they can seasonally occur throughout the Peronian province when warm currents transport them further south than is normally expected;

ii. Warm temperate (W), species which primarily occur in the warm temperate waters of the Peronian province but their distribution can also partly include the Solenderian/Banksian and Maugean Provinces;

iii. Cool temperate (C), species that primarily occur in the cool to cold temperate waters of the Maugean province but their distribution can include the southern extremities of the Peronian province.

Species were also categorised by their utilisation of rockpool habitats as:

i. Permanent residents (R) are fishes which spend their entire life within the rocky intertidal zone. They are generally small, cryptic species that possess specialised morphological, physiological or behavioural adaptations for intertidal life, such as 'suckers' or compress body forms that reduce the risks of fish being swept from rockpools by waves. Permanent residents tend to move only small distances (<10 metres; Green 1971a) and have exceptional knowledge of their surroundings, which may aid in escaping from predation and searching for food and mates.

ii. Partial or secondary residents, or opportunists (O) as they are termed here, generally spend only a part of their life history in the intertidal, usually as juveniles, and generally possess few morphological adaptations for intertidal life. However, some
species enter the intertidal on a tidal basis to feed (Black and Miller, 1991; Rangley and Kramer, 1995a, 1995b), while others use the intertidal as a spawning ground (Blaxter and Hunter, 1982).

iii. Intertidal visitors, or transients (T) are often warm temperate or tropical species that only occasionally enter rockpools, usually when warm currents transport them further south than normal. They generally possess no specialised adaptations for inhabiting the intertidal zone and normally only utilise rockpools for short durations as juveniles (Beckley, 1985b), or to spawn (Haegele and Schweigert, 1985) but spend the majority of their lives subtidally. Transients are often pelagic planktivores that sometimes enter the intertidal zone during high tide feeding excursions or to seek shelter from subtidal predators. They become trapped in rockpools as the tide recedes. Their abundance is largely dependent upon seasonal currents that may transport fishes further from where they would normally occur (Stepien et al. 1991), but their relatively low numbers probably contribute little to rockpool population dynamics.

The behavioural affinities of each species was categorised as:

i. Solitary (S), species which are normally observed alone or in pairs but not in schools.

ii. Aggregating (A), species that form schools or small congregations.

iii. Cryptic (C), species which possess camouflage pattern and colouration and/or tend to be secretive by hiding in crevices, algae and under rocks.

iv. Territorial (T), species which display aggressive behaviour to defend a particular area.
Life-history stages of all species caught were also determined by comparing the length ranges of fish from each species with published records for juveniles (Lardner et al. 1993; Neira et al. 1998) and adults (Edgar et al. 1982; Hutchins and Swainston, 1986; Kuiter, 1993, 1996; Randall et al. 1997).

Figure 6. Major biogeographic marine provinces of eastern Australia (tropical, warm temperate and cool temperate) after Briggs (1974). Locations of the 14 rocky headlands studied in southeastern NSW are shown.
RESULTS

Taxonomic composition

A total of 14,225 fish comprising 50 species and representing 26 families was captured in 1,336 samples from at least 296 rockpools at the 14 locations for the period between 17 August 1999 and 13 September 2001. The dominant families in terms of numbers of species were Clinidae (6 species), Gobiidae and Blenniidae (4 species), Tripterygiidae, Gobiesocidae and Labridae (3 species), while a number of families were represented by two species, including Scorpididae, Serranidae, Muraenidae, Pomacentridae, Scorpaenidae, Tetradontidae, Syngnathidae, Chaetodontidae (Table 5). In terms of numbers of fish, the dominant families were Gobiidae (4,836 fish or 34% of the total catch), Tripterygiidae (3,589 fish or 25%), Clinidae (1,672 fish or 12%), Girellidae, which was represented by a single species, *Girella elevata* (1,190 fish or 8%), and Blenniidae (1,084 fish or 8%) (Fig. 7).

![Pie chart showing relative contributions of major families to rockpool fish assemblages of the NSW south coast.](image)

**Figure 7.** Relative contributions of major families (in terms of numbers of individuals) to the rockpool fish assemblages of the NSW south coast (n=14225).
The most common fish species were (in deceasing order of abundance): *Bathygobius cocosensis* (Gobiidae; 34% of the total catch), *Enneapterygus rufopileus* (Tripterygiidae; 15%), *Lepidoblennius haplodactylus* (Tripterygiidae; 11%), *Girella elevata* (Girellidae; 8%), *Heteroclinus fasciatus* (Clinidae; 5%), *Heteroclinus whiteleggi* (Clinidae; 5%), *Aspasmogaster costatus* (Gobiesocidae; 5%), *Parablennius intermedius* (Blenniidae; 4%); *Istiblennius meleagris* (Blenniidae; 2%); and *Scorpis lineolatus* (Scorpididae; 2%) (Table 5).

A species that is worthy of special mention is the black rock cod, *Epinephelus daemelii*, which is currently listed as vulnerable under the *Fisheries Management Act 1994*. Although only nine individuals were captured, intertidal rockpools may provide a valuable nursery habitat for this species as all fish caught were less than 87 mm TL.

The vast majority of fish represented small-growing fishes or juveniles of larger growing fishes that live their adult lives subtidally. As a result, 76% and 89% of fish were less than 50 mm TL and 100 mm TL, respectively (Fig. 8). However, a few primarily subtidal adult fish were captured, mainly *Notolabrus gymnogenis*, which probably resulted from stranding during intertidal feeding excursions.

Many fish species important to the commercial and/or recreational fishing sectors that are abundant as adults around shallow subtidal reefs areas adjacent to each sampling location were conspicuously absent from intertidal rockpools. These species include luderick, *Girella tricuspidata*; yellowfin bream, *Acanthopagrus australis*; snapper, *Pagrus auratus*; silver drummer, *Kyphosus sydneyanus*; tailor, *Pomatomus saltatrix*;
Table 5. Fish species (including common name) caught from at least 296 rockpools from 14 locations from Coalcliff Point to Wagonga Head, NSW, during the period 17 August 1999 to 13 September 2001. Each species is categorised by family, biogeographic affinity (BiA), behavioural affinity (BeA) and residential status. Total numbers of each species is shown as well as their life history stage when captured.

<table>
<thead>
<tr>
<th>Species (Authority)</th>
<th>Common Name</th>
<th>Family</th>
<th>BiA</th>
<th>BeA</th>
<th>Number caught</th>
<th>Resident status</th>
<th>Life-history stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bathyogobius cocosensis (Bleeker, 1854)</td>
<td>Cocos Goby</td>
<td>Gobiidae</td>
<td>W</td>
<td>S, C, T</td>
<td>4775</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Enneapterygus rufopileus (Waite, 1904)</td>
<td>Black-cheek Threefin</td>
<td>Tripterygiidae</td>
<td>W</td>
<td>S, C, T</td>
<td>2069</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Lepidoblennius haplodactylus Steindachner, 1867</td>
<td>Eastern Jumping Blenny</td>
<td>Tripterygiidae</td>
<td>W, C</td>
<td>S, C, T</td>
<td>1498</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Girella elevata Macleay, 1881</td>
<td>Eastern Rock Blackfish</td>
<td>Girellidae</td>
<td>W</td>
<td>S, C, T</td>
<td>1190</td>
<td>O</td>
<td>J</td>
</tr>
<tr>
<td>Heteroclinus fasciatus (Macleay, 1881)</td>
<td>Banded Weedfish</td>
<td>Clinidae</td>
<td>W</td>
<td>S, C</td>
<td>759</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Heteroclinus whiteleggi (Ogilby, 1894)</td>
<td>Whitelegg's Weedfish</td>
<td>Clinidae</td>
<td>W</td>
<td>S, C</td>
<td>748</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Aspasmogaster costatus (Ogilby, 1885)</td>
<td>Pink Clingfish</td>
<td>Gobiosocidae</td>
<td>W</td>
<td>S, C</td>
<td>672</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Parablennius intermedius (Ogilby,1915)</td>
<td>False Tasmanian Blenny</td>
<td>Blenniidae</td>
<td>W</td>
<td>S, C, T</td>
<td>623</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Istiblennius meleagris (Valenciennes, 1836)</td>
<td>Spotted Blenny</td>
<td>Blenniidae</td>
<td>Tr, W</td>
<td>S, C, T</td>
<td>271</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Scorpis lineolatus Kner, 1865</td>
<td>Silver Sweep</td>
<td>Scorpidae</td>
<td>W</td>
<td>Ag</td>
<td>253</td>
<td>O</td>
<td>J</td>
</tr>
<tr>
<td>Acanthistius ocellatus (Gunther, 1859)</td>
<td>Eastern Wirrah</td>
<td>Serranidae</td>
<td>W</td>
<td>S</td>
<td>222</td>
<td>O</td>
<td>J-SA</td>
</tr>
<tr>
<td>Aspasmogaster liorhyncha Briggs, 1955</td>
<td>Smooth-snout Clingfish</td>
<td>Gobiosocidae</td>
<td>W</td>
<td>S, C</td>
<td>213</td>
<td>R</td>
<td>J-A</td>
</tr>
<tr>
<td>Istiblennius edentulus (Schneider and Forster, 1801)</td>
<td>Peacock Blenny</td>
<td>Blenniidae</td>
<td>Tr</td>
<td>S, C, T</td>
<td>190</td>
<td>R</td>
<td>J-A</td>
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<tr>
<td>Myxus elongatus Gunther, 1861</td>
<td>Sand Mullet</td>
<td>Mugilidae</td>
<td>W</td>
<td>Ag</td>
<td>125</td>
<td>O</td>
<td>J</td>
</tr>
<tr>
<td>Gymnotherax prasinus (Richardson, 1848)</td>
<td>Green Moray Eel</td>
<td>Muraenidae</td>
<td>W</td>
<td>S, C, T</td>
<td>132</td>
<td>R</td>
<td>J-A</td>
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<tr>
<td>Ophichinus gracilis Waite, 1906</td>
<td>Black-back Snake Blenny</td>
<td>Clinidae</td>
<td>W, C</td>
<td>S, C</td>
<td>111</td>
<td>R</td>
<td>J-A</td>
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<tr>
<td>Chironemus marmoratus Gunther, 1860</td>
<td>Eastern Kelpfish</td>
<td>Chironemidae</td>
<td>W</td>
<td>Ag, C</td>
<td>86</td>
<td>O</td>
<td>J</td>
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<tr>
<td>Callogobius depressus (Ramsay and Ogilby, 1886)</td>
<td>Flathead Goby</td>
<td>Gobiidae</td>
<td>Tr</td>
<td>S, C</td>
<td>56</td>
<td>R</td>
<td>J-A</td>
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<tr>
<td>Abudelfadwa vaigensis (Quoy and Gaimard, 1825)</td>
<td>Sergeant Major</td>
<td>Pomacentridae</td>
<td>Tr</td>
<td>Ag</td>
<td>54</td>
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<tr>
<td>Heteroclinus heptaeolus (Ogilby, 1885)</td>
<td>Seven-bar Weedfish</td>
<td>Clinidae</td>
<td>W, C</td>
<td>S, C</td>
<td>49</td>
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<td>Tripterygiidae</td>
<td>W</td>
<td>S, C</td>
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<td>J-A</td>
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<td>Pomacentridae</td>
<td>W, C</td>
<td>Ag, T</td>
<td>12</td>
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<td>Eastern Fortesque</td>
<td>Scorpaenidae</td>
<td>W</td>
<td>S, C, T</td>
<td>10</td>
<td>O</td>
<td>J</td>
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<td>Black Rockcod</td>
<td>Serranidae</td>
<td>W</td>
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<td>9</td>
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<td>Kuhlina mugil (Forster, 1801)</td>
<td>Fivebar Flagtail</td>
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Table 5 continued

<table>
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<tr>
<th>Family name</th>
<th>Habitat</th>
<th>Biogeographic affinity</th>
<th>Behavioural affinity</th>
<th>Residential status</th>
<th>Life-history stages</th>
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<tr>
<td>Torquigener pleurogramma (Regan, 1903)</td>
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<td>Filicampus tigris (Castelnau, 1879)</td>
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<td>Alabes dorsalis (Richardson, 1845)</td>
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<td>Chaetodon auriga Forsskal, 1775</td>
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<td>Cnidoglanis macrocephalus (Valenciennes, 1840)</td>
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<td>Achoerodus viridis (Steindachner, 1866)</td>
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<td>Tetractenos glaber (Fremieville, 1813)</td>
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<td>Urocanus carinostris Castelnau, 1872</td>
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<td>Apogon cuscineus Ruppell, 1838</td>
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<td>Iso rhotophilus (Ogilby, 1895)</td>
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<tr>
<td>Scopanea cardinalis Solander and Richardson, 1842</td>
<td></td>
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<td>Trachinops taeniatus Gunther, 1961</td>
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</tbody>
</table>

| Total number of fish | 14225 |
| Total number of species | 50 |
| Total number of families | 26 |
Figure 8. Length-frequency distributions of the 14 most abundant fish species combined for all catches from rockpools at 14 locations along the NSW south coast between 17 August 1999 to 13 September 2001. Total length (mm) of fish is shown for all species except Girella elevata, where fork length (mm) is shown.
Residential categories

The relative contribution of the number of species and individuals to each residential category is illustrated in Figure 9. Twenty-one of the species and 12203 fish (86% of the catch) of intertidal rockpool fishes had morphological and/or physiological adaptations for intertidal life indicating they were permanent residents in the intertidal zone. Nineteen species represented by 1939 fish (14% of the catch) were considered to be secondary rockpool residents, that either use rockpools during their juvenile phases (possibly as nurseries) or are occasionally caught as sub-adults and adults when they become stranded in rockpools during high tide feeding excursions as the tide recedes. The remaining ten species represented by 83 fish (<0.5% of the catch) were considered to be transients, which are species that are very occasionally found in intertidal rockpools and have no specialised adaptations for intertidal life. These species were often tropical species that were found during the warmer months of the years when warm currents transported them south of their normal distributions.

Figure 9. Fishes classified as residents, opportunists and transients as a percentage of overall numbers of species and individuals caught in rockpools at 14 locations along the NSW south coast between 17 August 1999 and 13 September 2001.
Biogeographic affinities

A large number of species recorded in the present study were endemic to Australia (32 species or 64% of the total catch), 15 species (or 30% of the catch) have an Indo-Pacific distribution, whereas the remaining three species, namely *Chironemus marmoratus*, *Epinephelus daemelii*, *Scorpaena cardinalis*, are distributed throughout the Tasman Sea from eastern Australia, including Lord Howe Island and Norfolk Island, to western New Zealand. These three species comprised 6% of the total catch.

The relative contribution of species and individuals representing the three major biogeographic categories is illustrated in Figure 10. Twenty-nine species, including the three most abundant species (*Bathygobius cocosensis*, *Enneapterygius rufopileus* and *Lepidoblennius haplodactylus*) occur predominantly in the warm temperate Peronian biogeographic province that extends from southern Queensland to the Victorian border. These species represented 95% (13442 fish) of the total number of individuals caught. Thirteen species, including the two most abundant blennies (*Istiblennius meleagris* and *I. edentulus*) are primarily found in warm tropical waters of the Solenderian/Banksian biogeographic province, which extends from the Cape York Peninsula to the southern tip of Fraser Island in Queensland. However, these species comprised only 4% (598 fish) of the total number of individuals caught. Eight species, which were all found in relatively low numbers, occur in the cool temperate waters of the Maugean biogeographic province, which extends from the Victorian border to Spencer's Gulf in South Australia. These species comprised only 1% (185 fish) of the total number of individuals caught.
Seventeen (or 63%) of the twenty-one resident species are endemic to Australia. Of these, only two are normally restricted to waters outside the study region in tropical (*Callogobius depressus*) and cool temperate (*Heteroclinus johnstoni*) waters. The remaining 15 species are therefore endemic to temperate waters of NSW. Thirteen of the 19 opportunist species were endemic to Australia and confined to warm temperate waters, while three species were wide-ranging throughout the Indo-Pacific, and the remaining three species are distributed across the Tasman Sea to New Zealand. Of the ten transient species only two species *Ammotretis rostratus* and *Apogon coccineus* are endemic to Australia, whereas the remaining eight species are of tropical distribution and are wide-ranging throughout the Indo-Pacific.

![Bar chart showing biogeographic affinity of fish species](image)

**Figure 10.** Fishes classified as tropical, warm temperate and cool temperate as a percentage of overall numbers of species and individuals caught in rockpools at 14 locations along the NSW south coast between 17 August 1999 and 13 September 2001.
DISCUSSION

The intertidal rockpool ichthyofauna of Australia's NSW south coast is a diverse mixture of species that are primarily endemic to Australia or at least largely confined to the west and southwest Indo-Pacific. The vast majority of fishes are representative of the warm temperate Peronian biogeographic province, but also there are large contributions made to assemblages by species characteristic of tropical (Solenderian/Banksian) and cool temperate (Maugean) biogeographic provinces. The fish assemblages were mainly comprised of small-growing (<150 mm TL) species that are permanent residents in the rocky intertidal zone. However, there was some evidence to suggest that these rockpools may act as nurseries for larger-growing species that spent their adult lives subtidally, namely *Chironemus marmoratus*, *Acanthistius ocellatus* and *Abudefduf vaigiensis*, and some of significance to recreational and commercial fishing sectors, namely *Girella elevata*, *Myxus elongatus* and *Scorpis lineolatus*.

**Comparisons with other rockpool fish communities**

The species richness of these NSW rockpool fish assemblages (50 species) is significantly lower than the number of species recorded from studies on coral reefs, but comparable to temperate subtidal rocky reefs and estuaries (Table 6). However, the number of species recorded in the present study is higher than has been found in the vast majority of rockpool studies undertaken for similar time frames as the present study (11-31 species; see Beckley, 1985a; Moring, 1986; Varas and Ojeda, 1990; Hussain and Knight-Jones, 1995; Willis and Roberts, 1996), although Taiwan rockpool fish assemblages appear to contain unusually high numbers of species (124-194 species; see Chang *et al.* 1977; Lee 1980; Mok *et al.* 1985).
Table 6. Number of fish species recorded in selected studies from coral reefs, temperate rocky reefs and temperate estuaries. Data has been taken from studies documenting representative fish assemblages of each habitat in various countries and being conducted for 6 months to 3 years.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Number of Species</th>
<th>Country</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coral Reefs</td>
<td>56-143</td>
<td>Australia</td>
<td>Sale and Dybdahl, 1975; Sale and Douglas, 1984</td>
</tr>
<tr>
<td></td>
<td>150</td>
<td>Hawaii</td>
<td>Friedlander and Parrish, 1998b</td>
</tr>
<tr>
<td></td>
<td>138</td>
<td>Taiwan</td>
<td>Tzeng et al. 1997</td>
</tr>
<tr>
<td>Temperate Rocky Reefs</td>
<td>30-37</td>
<td>Australia</td>
<td>Lincoln Smith et al. 1989; Kingsford et al. 1991</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>Spain</td>
<td>Macpherson, 1994</td>
</tr>
<tr>
<td></td>
<td>59</td>
<td>South Africa</td>
<td>Smale and Buxton, 1989</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>Italy</td>
<td>Guidetti, 2000</td>
</tr>
<tr>
<td></td>
<td>46</td>
<td>France</td>
<td>Ruitton et al. 2000</td>
</tr>
<tr>
<td></td>
<td>7-20</td>
<td>New Zealand</td>
<td>Jellyman et al. 1997; Sutherland and Closs, 2001</td>
</tr>
<tr>
<td></td>
<td>41</td>
<td>Portugal</td>
<td>Gordo and Cabral, 2001</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>Italy</td>
<td>Mariani, 2001</td>
</tr>
<tr>
<td></td>
<td>31</td>
<td>France</td>
<td>Laffaille et al. 2000</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>USA</td>
<td>Horn, 1980</td>
</tr>
</tbody>
</table>

With regards to assemblage structure, rockpool fish communities in the present study bear a remarkable resemblance to those along the eastern and southern Cape of South Africa, where Clinidae, Gobiidae and Gobiesocidae are also the dominant families (Bennett and Griffiths, 1984; Beckley, 1985a, 2000). There are also many generic similarities in the rockpool fish assemblages between South Africa and Australia, namely the presence of *Gymnothorax* (Muraenidae), *Acanthistius* and *Epinephelus* (Serranidae), *Bathygobius* (Gobiidae), *Istiblennius* and *Parablennius* (Blenniidae) and
Abudefduf (Pomacentridae). Furthermore, some transient species with Indo-Pacific distributions such as, Chaetodon auriga, Abudefduf vaigiensis, Istiblennius edentulus and Kuhlia mugil are also shared between South Africa and Australia (Beckley, 1985a; Bennett, 1987). The largest differences between Australian and South African rockpool fishes are in the high number of Sparids in South African rockpools. For example, Diplodus sargus capensis, Diplodus cervinus hottentotus, Rhabdosargus holubi and Sarpa salpa are important angling species in South Africa and are also common in estuarine and nearshore habitats, and, apparently use rockpools opportunistically for initial settlement (Prochazka, 1996; Beckley, 1985b) before moving subtidally as they grow. It is interesting to note that in Australia, similar Sparid species also use estuaries as their nursery habitats, such as Acanthopagrus australis, Rhabdosargus sarba and Pagrus auratus (see Gray et al. 1996; Griffiths, 2001b, 2001c), but do not appear to utilise NSW rockpools during their juvenile stages. However, adults of these species can be caught by angling in large rockpools at night and in subtidal waters during the day (unpublished data; Kingsford et al. 1991). In contrast, the rockpool fish assemblages of South Africa's west coast are species depauperate and only two families, Clinidae and Gobiesocidae have been reported (Prochazka and Griffiths, 1992). Although many of these species are also common to the south and east coasts of South Africa they bear little taxonomic resemblance, even at the generic level, to Clinid species found in southeastern Australia.

A few species in the present study have a trans-Tasman distribution into New Zealand waters, namely Chironemus marmoratus, Scorpaena cardinalis and Epinephelus daemelii; however, in general, the NSW fish assemblages appeared to differ to those in Wellington, New Zealand. This is mainly due to rockpools being nearly exclusively
dominated by high numbers of species representing the families Tripterygiidae and Gobiesocidae (Willis and Roberts, 1996). However, none of the species recorded by Willis and Roberts (1996) were common to Australian Tripterygiids or Gobiesocids at generic or specific levels.

The rockpool fish assemblages in the present study are also similar to those along the central Chilean coast, where Girellidae, Tripterygiidae, Clinidae and Blenniidae are dominant families (Stepien, 1990; Varas and Ojeda, 1990). However, (except for the presence of the Girellid, *Girella laevifrons*), the rockpool fish assemblages found in southeastern Australia do not share species or genus with the Chilean rockpool fishes.

In contrast to the similarities of rockpool fish assemblages in temperate regions, at least at familiar and generic levels, the fish assemblages of the present study bare little or no resemblance to those in countries on non-Gondwanan origin, namely the United States, Canada, France, Spain and Portugal. Not only are many of the dominant families, and thus species, different to those found in temperate regions, but their rockpool fish assemblages are also largely species depauperate, often only comprising less than twenty species (Grossman, 1986; Collette, 1986; Moring 1986; Yoshiyama et al. 1986). Nonetheless, generalisations can be made about the fish assemblages in each of these countries.

Rockpools in the United States of America (USA) are largely dominated by the families Cottidae and Stichaeidae, although Scorpaenidae and Pholidae make substantial contributions to mainly boreal regions such as Maine (Moring, 1996) and New England
(Collette, 1996). These families, as well as some species common in the USA, are also dominant in regions of Canada and Nova Scotia (Black and Miller, 1991).

The rockpools along the coastlines of England, France and Portugal generally have low species richness with the dominant families being Blennidae, Gobiidae, Gobiesocidae and Gadidae (Gibson, 1972; Macpherson, 1994; Hussain and Knight-Jones, 1995). As expected, the dominant species vary between countries, since they are separated by large distances and are thus probably influenced by different environmental conditions. For example, the Blenniid, *Lophorus gunnellus*, is an abundant species both in England and France, whereas in Portugal, *Lipophrys pholis* and *Istiblennius* spp. are abundant (Beja, 1995; Faria and Almada, 1999, 2001).

**Comparisons with other Australian rockpool fish communities**

Information on the rockpool ichthyofaunas is available for only three other locations in Australia, all north of Sydney in NSW. These include the Wooli region in northern NSW (Wilson, 1989), Seal Rocks in central NSW (Lardner *et al.* 1993), and north Sydney (Silberschneider and Booth, 2001). These study regions are located around 500 km, 300 km and 100 km north of the northern-most point of the present study region, respectively. The position of the Illawarra and south coast study region fills the gap in the scientific knowledge of intertidal rockpool fishes in temperate NSW. The 50 fish species recorded in the present study exceeds the 28 species found by Wilson (1989) in northern NSW and the 23 species recorded by Silberschneider and Booth (2001) from the rockpools around Sydney. However, the number of species found in the present study was significantly lower than the 99 species recorded by Lardner *et al.* (1993) at Seal Rocks in central NSW, although their study concentrated on a very large low
intertidal rockpool over a 19 year period. To a large extent, the numbers of species found in these studies reflects sampling intensities.

The composition of rockpool ichthyofaunas in the present study were mainly characterised by permanent resident species from the families Clinidae, Gobiidae, Blenniidae and Tripterygiidae, but also the secondary resident, *Girella elevata*, which was the sole representative of Girellidae. The fish assemblages of southeastern NSW were comparable to the temperate rockpool fish assemblages of northern NSW and around the Sydney region, both in terms of species richness and species composition, although some differences were evident. Wilson (1989), Lardner *et al.* (1993) and Silberschneider and Booth (2001) all found a similar number of species from similar families as the present study. However, the warmer climate of the study regions of Wilson (1989) and Lardner *et al.* (1993) and the extended study period of Lardner *et al.* (1993) probably resulted in the capture of species from numerous families not found in the present study, such as Acanthuridae, Bothidae, Bythitidae, Cheilodactylidae, Solidae, and Lutjanidae.

When considering the number of individuals from the dominant families, the fish assemblage structure of the present study differed markedly from those undertaken in northern NSW. For example, Gobiidae, Clinidae, Tripterygiidae, Blenniidae and Girellidae were the most numerically dominant families overall in the present study, whereas Tetradontidae, Pomacentridae and Mugilidae dominated the Seal Rocks assemblage (Lardner *et al.* 1993). These differences are probably attributable to the differences in rockpool characteristics. The description of the rockpool studied by Lardner *et al.* (1993) suggests it is a large (~100 m$^2$), shallow extension of a subtidal
area. This could explain the capture of high numbers of *Torquigener pleurogramma*, *Tetractenos glaber* and *Myxus elongatus* by Lardner *et al.* (1993). These are species common at most sampling locations in the present studies, but appear to prefer the shallow subtidal or large rockpools where there is little chance of being stranded for extended periods (personal observation).

The rockpools studied by Wilson (1989) were comparable to those in the present study, although he found an overwhelming numerical dominance of *Chironemus marmoratus* (Chironemidae), *Myxus elongatus* (Mugilidae) and *Vauclusella annulata* (Tripterygiidae). This suggests that rockpool fish assemblages differ between northern and southern NSW. This is further supported by a comparison the present study and that of Silberschneider and Booth (2001). *Enneapterygius rufopileus*, which is found in southern waters, appears to be replaced by the closely related *Vauclusella annulata*, which reportedly has a more northerly distribution (Kuiter, 1993).

The fish assemblage structure of Sydney rockpools (see Silberschneider and Booth, 2001) is, however, very similar to that of the present study with *Enneapterygius rufopileus*, *Heteroclinus whiteleggi* and *Lepidoblennius haplodactylus* being numerically dominant (Silberschneider and Booth, 2001). However, it is interesting to note that *Bathygobius padangensis* (a synonym for *B. coalitus*) was the second most dominant species overall recorded by Silberschneider and Booth (2001). This species was not recorded in the present study or by Wilson (1989) or Lardner *et al.* (1993), although the closely related *Bathygobius cocosensis* was abundant in each of these studies. It is possible that Silberschneider and Booth (2001) may have misidentified *B.*
cocosensis because B. padangensis is not thought to occur in the Sydney region (personal communication; Doug Hoese, Sydney Museum).

**Residency and biogeographic affinities of NSW rockpool fishes**

The residential status of intertidal fishes (i.e. residents, opportunists or transients) found in south coast NSW rockpools appeared to be a direct reflection of their geographic distributions. For example, the majority of residents were endemic to southeastern Australia and thus had restricted geographical ranges. Species identified as opportunists usually had slightly larger geographic ranges, whereas the majority of transient species had circum-Indo-Pacific distributions and thus, few were endemic to Australia. A requisite for resident intertidal fishes to make permanent use of the intertidal zone is to be suitably adapted to cope with the extremes in the environmental conditions of rockpools (i.e. swell and water temperature). Many species have evolved specialised morphological, physiological and/or behavioural adaptations to cope in this dynamic environment (Zander et al. 1999). Increasing specialisation of these adaptations to cope with localised conditions may have also evolved in some species to allow them to exist as permanent intertidal residents and thus, may limit their geographic range.

Although opportunists can periodically cope with the variable conditions of the intertidal zone, usually as juveniles (Valle, 1989) or during high tide feeding excursions (Black and Miller, 1991), they do not normally breed within rockpools (Gibson and Yoshiyama, 1999). Opportunists most often spawn subtidally and produce planktonic larvae that are distributed by near-shore currents (Stevens et al. 1989), although their larvae generally resist being transported great distances from the coast (Marliave, 1986). Consequently, opportunists generally have larger geographic ranges than permanent
Chapter 3 Overview of rockpool fish assemblage structure

intertidal residents. Many species found in the present studies, such as *Girella elevata*, *Myxus elongatus* and *Scorpis lineolatus*, appear to mainly use rockpools as juveniles before moving to the subtidal as they grow (see Bell et al. 1980; Burchmore et al. 1985).

At the other end of the scale, transient species identified in this study normally have extended pelagic larval phases, probably to increase dispersal by ocean currents (Shulman, 1998). Examples are the tropical reef species *Abudefduf vaigiensis* and *Chaetodon auriga*, which have an extended distribution throughout the Indo-Pacific (Leis and Rennis, 1983). Given that most of these species are distributed throughout tropical waters, they were normally only found in this study during summer and late autumn, when the warm East Australian Current (EAC) extends into southern waters (CSIRO, 2000; Zann, 2000). Although transient species were only ever caught as small juveniles, such as *Abudefduf vaigiensis*, *Kuhlia mugil*, *Chaetodon auriga* and *Scatophagus argus*, most would probably not be sufficiently mobile to migrate northward against the EAC to return to their natal tropical climate before the temperate waters cool during late autumn. Most of these species probably perish and therefore, make little contribution to the dynamics of rockpool fish assemblages in southeastern NSW.

This Chapter has provided the first large-scale description of the species composition, residential and biogeographic affinities of rockpool fishes along the south coast of NSW, Australia. It is clear that these rockpool habitats support species-rich ichthyofaunas, which have a high degree of endemism to Australian waters. The assemblages are comprised of permanent residents, opportunists that are most often
present as juveniles and, transients that utilise rockpools seasonally during the warmer months. The next Chapter explores the natural patterns of spatial and temporal variation in these fish assemblages.
Chapter 4
Spatial and temporal variation in rockpool fish assemblages

INTRODUCTION
The success of many ecological investigations hinge on the ability to understand spatial and temporal variability in abundances. Understanding these parameters using descriptive or "mensurative" studies (Hurlbert, 1984) is essential before testing specific hypotheses. They provide a logical starting point for experimentation using manipulative experiments which may provide definitive explanations of the patterns observed (Underwood et al. 2000). However, ecological patterns can extend across varying spatial scales, meaning that the patterns observed, and those that are missed, in an investigation will depend upon the spatial scale used (Sale, 1998). Despite rockpools being a common and obvious feature of most rocky shores, little is known of the patterns of variations of their fish assemblages.

The spatial distribution of rocky habitats can generally be regarded as being patchy and multiscalar (Underwood et al. 1991). Individual rockpools act as isolated habitat patches, or 'islands', at low tide and occur irregularly along the rocky shore. Physical barriers, such as sandy beaches, often isolate the rocky shores themselves, and separation of rockpools also occurs at wider spatial scales, such as across oceans. Consequently, the patterns of spatial and temporal variation in rockpool fish assemblages across these various scales may also be patchy. That is, assemblages on separate rocky headlands may vary independently due to differing influences from the environment. Since many studies of rockpool fish assemblages are only undertaken at a
single location (Grossman, 1982; Lardner et al. 1993; Beckley, 2000), it is often inappropriate to extrapolate findings across patch boundaries and assume the same patterns might exist elsewhere (Sale, 1998). However, with an increasing number of workers using larger spatial scales in their studies of rockpool fishes (Faria and Almada, 1999, 2001; Silberschneider and Booth, 2001), the extent of spatial variation should become clearer (see Chapter 3).

Good information on the spatial variation of rockpool fish assemblages is available from South Africa where a great deal of research has been undertaken. Prochazka and Griffiths (1992) found that two locations on the west coast of South Africa shared 7 of 14 species recorded, while on the Cape Peninsula two sites separated by some 30 km shared 8 of the 21 species recorded (Bennett and Griffiths, 1984). In contrast, Bennett (1987) found that 5 locations interspersed along some 1000 km of the southern Cape of South Africa shared only 3 of 65 species recorded. The differences in fish assemblages separated by these large spatial scales can be due to the presence of different microhabitats at each location which are utilised by different species (Marsh et al. 1978, Yoshiyama, 1981; Bennett and Griffiths, 1984; Prochazka and Griffiths, 1992). These studies suggest that, at locations where rockpools are dominated by rock cover, gobies and blennies dominate the assemblages, whereas other locations, algal habitats are present and are often dominated by Clinids, which rely upon this type of cover for camouflage.

However, differences in rockpool fish assemblages can also be evident at smaller spatial scales, for example at less than a few kilometres. On the Atlantic coast of France, Gibson (1972) found different fish assemblages on exposed and sheltered shorelines at
the same location, because some species possess more specialised adaptations to cope with the greater variability of environmental conditions on exposed shores. Furthermore, the extent of wave action on exposed shorelines increased the intertidal area available to fish, and was considered to allow more species to coexist. Increasing our knowledge of small-scale patterns of variation across regional scales of metres to kilometres should help in understanding the observed patterns across larger geographic scales.

With respect to temporal variability, marine and coastal fish assemblages are generally dynamic, which is often attributable to the high diversity of species, variety of different breeding sites and subsequent variability in recruitment times among species (Doherty and Williams, 1988). Despite this generality, rockpool fish assemblages appear to display high taxocene persistence and resilience (Grossman, 1982, 1986; Thomson and Lehner, 1976; Prochazka, 1996), even considering they inhabit a continually varying and particularly harsh environment. Their resilience can operate in the space of weeks (Faria and Almada, 1999), while assemblages structure can persist for decades (Moring, 1970; Lardner et al. 1993). Despite this taxocene persistence, variation in the abundance of individual species is seasonally evident when recruitment is driven by the availability of larvae (Willis and Roberts, 1996) or when resident fish emigrate from rockpools when environmental conditions become unsuitable (Thomson and Lehner, 1976; Moring, 1990). However, this normally results in a greater change in demographic composition rather than species composition.

Chapter 3 has documented the structure of the fish assemblages along the NSW south coast with emphasis on biogeographic and residential affinities of constituent species.
This Chapter presents two studies related to spatial and temporal variation in rockpool fish assemblages. The first study intensively studied rockpool fishes at three locations in the Illawarra region, with the aim to quantitatively document the patterns of variation in fish assemblage structure across various spatial scales (hundreds of metres to hundreds of kilometres) and temporal (months to years) scales. The second study aimed to provide a quantitative 'supplementary' account of the fish assemblage structure across 14 locations along the NSW south coast by sampling intermittently. It was postulated that, if fish assemblages were similar along the entire coast, the patterns of variation at the more intensively studied locations (Study 1) could be extrapolated to include these additional locations. Chapter 3 also described the overall assemblage structure for rockpool fishes in the southeastern Australia, by combining data from all studies in this thesis using various collection methods. This second study considered fishes caught only by the bilge pump sampling method, which allowed a more quantitative approach.

**MATERIALS AND METHODS**

**Study 1: Long-term spatial and temporal variation in fish assemblages**

Forty-eight rockpools were sampled every three months between 7 September 1999 to 13 September 2001 at Bass Point, Bellambi Point, and Caravan Point in southeastern Australia, which are located approximately 40-60 km south of Sydney (Fig. 1). For ease of interpretation of the results, each sampling event is named after the season in which it was undertaken. The months included within each season are: spring (September-November), summer (December-February), autumn (March-May) and winter (June-August). Four sites were selected to represent the typical topography at each location, which mainly consists of gently sloping rock platforms and small boulder fields. Although each site could not be strictly defined as either sheltered or exposed to
predominant swell conditions, sites 1 and 2 were considered to be more exposed than sites 3 and 4. Each site was separated by between 200-500 m and four rockpools were studied at each site, with each rockpool being separated by 50-200 m.

**Study 2: Large-scale spatial variation in fish assemblages**

Rockpools were sampled at 14 rocky headlands spanning about 300 km of the southeastern Australian coastline (Fig. 1). The furthest north and south headland are located approximately 40 km and 400 km south of Sydney, respectively. Fishes were collected from two sites at each headland (each separated by at least 100m) on three occasions between 15 May 2000 and 4 July 2001, except for Tuross Heads, Mollymook Point and Wagonga Head which were only sampled once (17-23 December 2000). Four rockpools were sampled at each site, a total of 8 rockpools at each location.

**Data collection: Study 1 and 2**

In order to compare data among locations, rockpools were selected for similarity in volume, surface area, substrate type (cobbles and small boulders) and, especially, their vertical position along the intertidal zone (mid-intertidal; 1-1.5 m above mean low of low water (MLLW)). Such factors have been shown to influence rockpool fish assemblage structure (Gibson, 1972; Mahon and Mahon, 1994). The height of each rockpool above MLLW was measured using a surveyor's level and strata rod. The time and date of each measurement was recorded, and by then adding the actual tidal height for each measurement, the height of each rockpool was calculated. These heights were validated on a second occasion at Bass Point, which confirmed measurements to be accurate to within 10 cm.
Prior to fish collections, temperature, salinity, pH and dissolved oxygen (DO) were measured in each rockpool using a Yeo-Kal meter. All measurements were taken within 1 hour of low tide at a similar time of day (approximately between 11:00 and 14:00), since the physico-chemical environment in rockpools can vary significantly during the day (Huggett and Griffiths, 1986). Rockpool volume was measured to the nearest litre by draining water into a graduated 60 l drum using the bilge pump. After fish collection, percentage of algal cover within rockpools was calculated by placing a layer of fishing net (with 2 cm x 2 cm diamond mesh) around the walls of the empty rockpool and recording the presence or absence of algae in 100 haphazardly chosen net squares. Homogeneity of the rockpool substrate was calculated by dividing the linear distance between two points in the rockpool by the distance between the points following contours of rocks and crevices with a flexible tape measure (see Raffaelli and Hawkins, 1996). This was performed five times in different directions to give an average substratum heterogeneity value that was between zero and one and was converted to a percentage by multiplying by 100. Substrata having values of 0 and 100 were most heterogeneous and homogeneous, respectively. Both algal cover and homogeneity data were arcsine transformed before use in any analyses, since variances are larger for means of around 50% than they are for means that are small (i.e. 10%) or large (i.e. 90%), which can lead to heterogeneous data (Underwood, 1997).

Fishes were collected from rockpools using the bilge pump sampling method described in Chapter 2. Fish were identified, total length (TL) measured and released. Each species was later assigned to a residential category using the criteria described in Chapter 3 to improve the understanding of the dynamics of the fish assemblages.
Chapter 4 Spatial and Temporal Variation in Rockpool Fish Assemblages

Statistical analyses

Univariate analyses

For study 1 an aim was to determine whether the mean numbers of species and individuals differed among locations. For study 2 an aim was to determine whether the mean numbers of species and individuals differed among locations, sites within locations, seasons and degree of exposure. Rockpools were repeatedly sampled in this study, so the assumption for a general factorial ANOVA of temporal independence among times of sampling was generally violated. A repeated-measures ANOVA is often required in such situations (Underwood, 1997). In this case, however, a repeated-measures ANOVA was not been used in either study. Recent work has revealed that due to the high resilience of rockpool fish assemblages, samples taken only a few days apart can be as similar as samples taken months, or even years, apart (see Chapter 6; Yoshiyama, 1981; Willis and Roberts, 1996; Davis, 2000a). Therefore, samples separated by at least three months, as in the present study, can be considered independent. For this reason a nested analysis of variance (ANOVA) was adopted for both studies. Since the first study only aimed to compare species richness and abundance of fish among locations, data were pooled for each sampling event, and a one-factor nested ANOVA was used to test for differences in numbers of species and individuals between locations (fixed factor) and sites nested within locations (random factor). For the second study, a four-factor nested ANOVA was used to test for differences in numbers of species and individuals between months (fixed factor), locations (fixed factor), degree of exposure (fixed factor) and sites nested within locations (random factor).
Since rockpools differed in their physical parameters it was necessary to standardise the data. This is because sites that naturally had larger pools were more likely to accommodate higher numbers of species and individuals (see Bennett and Griffiths, 1984). Pool volume was used as a standardisation factor, as it could be measured most accurately and it was considered to incorporate other rockpool parameters such as depth, surface area, perimeter and submerged substrate area (SSA) (see Willis and Roberts, 1996). Data were standardised by dividing the number of fish and individuals in each sample by the pool volume and expressed as numbers of species and individuals m$^{-3}$. Cochran's tests were used to test for homogeneity of variances and data was transformed by $log_{10}(x+1)$ where necessary. Formal tests for normality were not undertaken since ANOVA is robust to violations of normality so long as experimental designs are balanced (Underwood, 1997). Nevertheless, data were examined visually for violation of the normality assumption. All ANOVAs were tested at the significance level of $P=0.05$, but where heteroscedasticity was not removed after transformation, analyses were still performed on the transformed data, but the significance level was set to $P=0.01$ to minimise the chance of incurring Type I errors (Underwood, 1981). Student-Newman-Keuls (SNK) tests were used for \textit{a posteriori} comparison among means (numbers of species and individuals) compared in ANOVAs. All analyses were performed using the GMAV5 computer program.

\textit{Multivariate analyses}

Non-metric multidimensional scaling (nMDS) was used to examine similarities in fish assemblages (both in terms of presence/absence of species and relative abundances) between seasons, sites and degree of exposure (Clarke, 1993). Data were then fourth-root transformed, to reduce the influence of highly abundant taxa. This is desirable since
the abundances of common or schooling species can be highly spatially variable, which can reduce the importance of species that may naturally have lower abundances. A similarity matrix was then constructed from the transformed data using the Bray-Curtis similarity coefficient (Clarke, 1993). Analysis of similarities (ANOSIM) was used to test whether fish assemblages in _a priori_ groups differed statistically (Clarke, 1993). Similarity percentages (SIMPER) were used to determine which species were responsible for differences between selected groups. All multivariate analyses were carried out using the PRIMER (Plymouth Routines In Multivariate Ecological Research) package (version 5.2.2).

For both studies, the influence of physico-chemical variables in rockpools (intertidal height, substrate homogeneity, algal cover, rockpool volume, temperature, salinity and dissolved oxygen) on the overall numbers of fish and species, as well as the number of fish representing the six most abundant species, was investigated using multiple regression. However, the assumption of independent and uncorrelated independent variables in multiple regression analysis was violated in every case due to many of the rockpool physico-chemical variables being inter-correlated. To circumvent this problem principal component analysis (PCA) was employed which examine correlations and variability of non-independent variables (Manly, 1986). Linear combinations of the 7 variables (principal components or PCs were constructed to examined the variability among factors combined for each site and season. This resulted in seven PCs representing orthogonal and independent variables. The PC scores for the seven PCs were then used as independent variables and regressed against the number of species and fish as well as numbers of fish representing the six most abundant species using standard least square multiple regression. Dependent variables were often non-normal
which required $\log_{10}(x+1)$ transformations prior to analysis. Independent variables were examined for multicollinearity using Durbin-Watson's test, although data were found to be uncorrelated in each case.

RESULTS

Study 1: Long-term spatial and temporal variation in fish assemblages

Variation in the physico-chemical environment

Physico-chemical factors varied considerably in rockpools during the two-year study period, with the exception of pH, which only ranged between 8.3 and 8.5 pH units (Fig. 11). Mean monthly temperatures varied between 17.3 ($\pm 0.1)$ °C (spring 2000) and 27.0 ($\pm 0.4)$ °C (autumn 2001). Temperature varied significantly but in a similar pattern at each location where the highest and lowest temperatures were recorded during spring-summer and autumn-winter (Fig. 11). Mean salinities ranged between 34.3 ($\pm 1.1)$ % and 37.4 ($\pm 1.8)$ % and were generally highest during autumn to winter. Dissolved oxygen (DO) varied between 6.6 ($\pm 0.9)$ mg l$^{-1}$ and 9.7 ($\pm 0.2)$ mg l$^{-1}$. Variation in DO closely followed that of temperature where the highest and lowest values were generally recorded during spring-summer and autumn-winter, respectively (Fig. 11).

Numbers of species and individuals

Between 7 September 1999 to 13 September 2001, a total of 5244 fish were caught comprising 46 species and 25 families in a total of 384 samples from 48 rockpools (Table 7).

ANOVA revealed that the mean number of species and individuals differed significantly among seasons, locations and sites [exposure] (Table 8). There was also a
significant interaction between location and site [exposure] for mean number of species. A means comparison test (SNK) revealed that the mean numbers of species differed among sites within exposed and sheltered regions at each site with the exception of Bellambi Point where no differences were found among the two sheltered sites. Exactly the same outcome was obtained with respect to the mean number of individuals, except that for Caravan Point where no differences were found among sheltered sites (SNK test).

The mean numbers of species and individuals varied significantly between some sampling events (SNK tests), although the main difference appeared to be the high numbers of species and individuals which were caught during autumn 99/00 and winter 00/01 (Figure 12).

The mean number of species differed with respect to location which was due to Bass Point having significantly fewer species than Bellambi Point and Caravan Point, although there was no difference between the latter two locations (SNK test).
Figure 11. Mean (±SE) values for dissolved oxygen, pH, salinity and temperature, recorded during each season between 7 September 1999 and 13 September 2001 from Bass Point (□), Bellambi Point (□) and Caravan Point (●). Data was collected from 16 rockpool at each location in the mid intertidal zone (0.5-1.5 m above MLLW). The months included within each season are: (Sp) spring (September-November), (Su) summer (December-February), (Au) autumn (March-May) and (Wi) winter (June-August).
Table 7. Numbers of individuals of each fish species caught from rockpools at Bass Point, Bellambi Point and Caravan Point between 7 September 1999 to 13 September 2001. Samples were collected from the same sixteen rockpools at each location every three months.

<table>
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<th>Bellambi Point</th>
<th>Caravan Point</th>
<th>Total</th>
</tr>
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</tr>
<tr>
<td></td>
<td>Heteroclinus whiteleggi</td>
<td>274</td>
<td>14</td>
<td>27</td>
<td>315</td>
<td></td>
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<tr>
<td></td>
<td>Ophiclinus gracilis</td>
<td>46</td>
<td>2</td>
<td>2</td>
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<tr>
<td>Gobidae</td>
<td>Bathygobius cocosensis</td>
<td>1068</td>
<td>345</td>
<td>271</td>
<td>1684</td>
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<td></td>
<td>Callogobius depressus</td>
<td>3</td>
<td>20</td>
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<tr>
<td></td>
<td>Callogobius mucosus</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Priolepis cincta</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Microdesmidae</td>
<td>Gunnellichthys monostigma</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pleuronectidae</td>
<td>Ammotretils rostratus*</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetraodontidae</td>
<td>Tetractenos glaber</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Torquigener pleurogramma</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* denotes species of commercial and/or recreational importance.

- Total number of fish: 3012, 1261, 971, 5244
- Total number of species: 44, 24, 18, 46
- Total number of families: 23, 14, 11, 25
Table 8. Results of ANOVAs testing for significant differences in number of species and number of individuals (per m³) among seasons, locations, exposure and sites nested within exposure. Both numbers of species and individuals data were $\log_{10}(x+1)$ transformed before analysis, which removed heteroscedasticity in the data. Mean squares and significance levels are shown and significant results are in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Number of species</th>
<th>Number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season (Se)</td>
<td>7</td>
<td>0.582*</td>
<td>3.749**</td>
</tr>
<tr>
<td>Location (L)</td>
<td>2</td>
<td>38.111*</td>
<td>18.722</td>
</tr>
<tr>
<td>Exposure (E)</td>
<td>1</td>
<td>0.215</td>
<td>0.860</td>
</tr>
<tr>
<td>Site [Exposure] (S[L])</td>
<td>2</td>
<td>1.742**</td>
<td>2.041*</td>
</tr>
<tr>
<td>Se x L</td>
<td>14</td>
<td>0.048</td>
<td>0.445</td>
</tr>
<tr>
<td>Se x E</td>
<td>7</td>
<td>0.220</td>
<td>0.866</td>
</tr>
<tr>
<td>Se x S[L]</td>
<td>14</td>
<td>0.185</td>
<td>0.791</td>
</tr>
<tr>
<td>L x E</td>
<td>2</td>
<td>10.057</td>
<td>16.367</td>
</tr>
<tr>
<td>L x S[L]</td>
<td>4</td>
<td>4.489***</td>
<td>8.386***</td>
</tr>
<tr>
<td>Se x L x E</td>
<td>14</td>
<td>0.136</td>
<td>0.571</td>
</tr>
<tr>
<td>M x L x S [E]</td>
<td>28</td>
<td>0.147</td>
<td>0.544</td>
</tr>
<tr>
<td>Residual</td>
<td>288</td>
<td>0.326</td>
<td>0.561</td>
</tr>
<tr>
<td>Cochran's C</td>
<td></td>
<td>0.073</td>
<td>0.061</td>
</tr>
</tbody>
</table>

* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. 
Figure 12. Mean (±SE) number of species and individuals caught at Bass Point (□), Bellambi Point (□) and Caravan Point (●) (pooled for four sites within each location) during each season between 7 September 1999 and 13 September 2001. The months included within each season are: (Sp) spring (September-November), (Su) summer (December-February), (Au) autumn (March-May) and (Wi) winter (June-August).
Relationships with environmental variables

Multiple regression revealed that rockpool volume and salinity explained a significant amount of the variation for numbers of species and individuals as well as numbers of individuals representing the six most abundant species (Table 9). Additionally, substrate homogeneity and algal cover explained a significant amount of the variation in the numbers of *Bathygobius cocosensis* and *Lepidoblennius haplodactylus* (Table 9). These results reveal little about the microhabitat preference of common species, which is probably a result of a large portion of the unexplained variance in each regression (6-43%). However, the experience gained during sampling indicated that fish assemblage structure in rockpools was related to rockpool characteristics. For this reason it is considered that qualitative accounts may provide a valuable insight into the microhabitat preferences and behaviour of common species, particularly those which were caught in numbers too low to lend them to statistical analyses (Table 10).
Table 9. Multiple regressions of number of fish and species overall and number of fish representing the six most abundant species combined for three locations (Bass Point, Bellambi Point and Caravan Point) against rockpool principal components based on physico-chemical variables (substrate homogeneity, algal cover, rockpool volume, salinity, temperature and dissolved oxygen). Overall regression statistics are shown as well as probabilities and slopes for each factor. All dependent variables were log10(x+1) transformed before analysis, which resulted in normal distributions. Significant results are in bold.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Dependent variable</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number of species</td>
</tr>
<tr>
<td>Tidal Height</td>
<td>-95.199</td>
</tr>
<tr>
<td>Substrate homogeneity</td>
<td>0.145</td>
</tr>
<tr>
<td>Algae cover</td>
<td>-0.251</td>
</tr>
<tr>
<td>Volume</td>
<td><strong>2.412</strong>*</td>
</tr>
<tr>
<td>Salinity</td>
<td><strong>-0.909</strong>*</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.228</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
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</tr>
<tr>
<td>p value</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>R²</td>
<td>0.432</td>
</tr>
</tbody>
</table>

* = P<0.05; ** = P<0.01; *** = P<0.001.

<table>
<thead>
<tr>
<th>Species</th>
<th>Description of habitat preference and behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cocos Goby, <em>Bathygobius cocosensis</em></td>
<td>Extensively found throughout the full vertical range of the intertidal and one of the very few fish that can be found in supratidal rockpools. Can withstand high temperatures and salinities, low dissolved oxygen levels and some time out of water. An extremely robust species. Found in a range of microhabitats but prefers cobbles and bare substratum. If encountered in a particular pool this species usually dominates as they appear aggressive and territorial.</td>
</tr>
<tr>
<td>Black-cheek threefin, <em>Enneapterygius rufopileus</em></td>
<td>Although this species appears highly adapted for intertidal life by being able to withstand extended periods out of water, it is normally restricted to mid-low rockpools where rockpool conditions are similar to that of seawater. Normally in pools with cover of cobbles and algae, particularly pink upright coralline algae. Usually found in male/female pairs or as groups of 5-6. Can be very territorial and aggressive, especially during spawning times around November-December.</td>
</tr>
<tr>
<td>Eastern rock blackfish, <em>Girella elevata</em></td>
<td>Prefers to inhabit pools in the high intertidal but is found throughout the full vertical range of the intertidal providing there is adequate cover, usually large boulders, cobbles, crevices and overhanging ledges. Can withstand high temperatures and salinities, low dissolved oxygen levels and some time out of water where it lays still with gills opened until covered in water where it will quickly seek cover. An extremely robust species. Usually solitary or in groups of 2-3, although in larger lower pools forms schools of 10-20 comprising juveniles to adults.</td>
</tr>
<tr>
<td>Eastern jumping blenny, <em>Lepidoblennius haplodactylus</em></td>
<td>Can be found throughout the full vertical range of the intertidal but is normally restricted to mid-low rockpools. Adults often solitary but juveniles found in small social groups of 3-6. Can withstand high temperatures and salinities, low dissolved oxygen levels and extended periods out of water. Has excellent knowledge of surroundings and even when out of water makes educated leaps to cover under rocks. Prefers substratum of sand or small cobbles and small boulders particularly with extensive green algal growth (esp. <em>Enteromorpha</em> sp.).</td>
</tr>
<tr>
<td>Spotted blenny, <em>Istiblennius meleagris</em> and Peacock blenny, <em>Istiblennius edentulus</em></td>
<td>Rarely solitary and often in pairs or groups of 4-5. Both species often found sympatrically, although <em>I. meleagris</em> appear more common. Both extremely robust species that can withstand high temperatures and salinities and low dissolved oxygen levels and extended periods out of water. Both can be found throughout the full vertical range of the intertidal including supratidal rockpools. Both prefer mid-high pools with crevices and substratum of cobbles and boulders, particularly with green algae growth (esp. <em>Enteromorpha</em> sp.). Both truly adapted intertidal fishes having exceptional knowledge of surroundings and when out of water makes educated leaps towards cover.</td>
</tr>
</tbody>
</table>
Table 10 continued

<table>
<thead>
<tr>
<th>Fish Species</th>
<th>Habitat and Behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pink clingfish, <em>Aspasmogaster costatus</em></td>
<td>Generally restricted to mid-low rockpools with high cover of cobbles and boulders. One of the more social rockpool species and often found in small groups of 4-10 fish. Often found associated with sea urchins or adhered to smooth rocks of various size by clinging with its ventral 'sucker' fin. When in this state and are further disturbed they often secrete mucous which makes them very difficult to handle.</td>
</tr>
<tr>
<td>Banded weedfish, <em>Heteroclinus fasciatus</em> and Whitelegg's weedfish, <em>Heteroclinus whiteleggi</em></td>
<td>Mostly restricted to mid-low rockpools, and from their obvious similarity to algae and seaweeds, are nearly exclusively associated with algal fronds. <em>Heteroclinus fasciatus</em> can be found among any algae species, whereas <em>H. whiteleggi</em> prefers brown and pink coralline algae. Both species often found in pairs. Can withstand some time out of water but considering the habitats they utilise it is likely that they rarely find themselves stranded out of water.</td>
</tr>
<tr>
<td>False Tasmanian blenny, <em>Parablennius intermedius</em></td>
<td>Abundant in rockpools throughout the intertidal zone but often more abundant in mid-high pools with high substrate complexity, particularly with cobbles or deep crevices. Often found associated with brown algae. Appears to occur sympatrically with other common blennies, <em>I. meleagris</em> and <em>I. edentulus</em>. Another species having excellent knowledge of surroundings and when out of water makes directional leaps to rocks or crevices.</td>
</tr>
<tr>
<td>Black-back snake-blenny, <em>Ophiclinus gracilis</em></td>
<td>Can be found throughout the full vertical range of the intertidal, occasionally in supratidal rockpools. Apparently one of the most tolerant Clinid species to harsh rockpool environments. Normally associated with boulders and found in pools where there are large amounts of detached macroalgae debris. Normally solitary or in pairs.</td>
</tr>
<tr>
<td>Green Moray, <em>Gymnothorax prasinus</em></td>
<td>By far the largest permanent rockpool resident fish being captured to 449 mm in length in the present rockpool studies. Prefer mid-low rockpools with high substrate complexity, particularly large boulders or deep crevices. Usually solitary in rockpools where there are high numbers of shrimps (probably prey). Can withstand significant periods out of water and has been observed moving short distances over land between rockpools.</td>
</tr>
<tr>
<td>Eastern Wirrah, <em>Acanthous ocellatus</em></td>
<td>Normally restricted to mid-low rockpools with high substrate complexity, particularly large boulders, cobbles or deep crevices. However, it is one of the few non-residents that can be found in rockpools high in the intertidal. Often solitary and is often found sympatrically with <em>Gymnothorax prasinus</em> in rockpools containing high numbers of shrimps (probably prey).</td>
</tr>
</tbody>
</table>
Variation in abundance of common species

ANOVA revealed that the mean numbers of the six most abundant species caught at Bass Point, Bellambi Point and Caravan Point differed with respect to sites nested within locations but not among locations. The exception was for *Lepidoblennius haplodactylus*, which was caught in significantly lower numbers at Bass Point. However, it appeared that differences in abundances among sites was probably not related to exposure of individual sites, except for *Bathygobius cocosensis* at Bass Point which was more abundant at more sheltered sites (Fig. 13).

Patterns of temporal variation in abundance of each species were consistent among locations for all species except for *Heteroclinus whiteleggi*. This species had a significant season x location interaction (Table 11). Although there were a large number of combinations where the mean numbers of individuals differed among seasons for each species, generally *Bathygobius cocosensis*, *Enneapterygius rufopileus* and *Girella elevata* were more abundant between summer and autumn, whereas *Lepidoblennius haplodactylus* was more abundant between winter and spring (Fig. 14). Both *H. whiteleggi* and *Aspasmogaster costatus* appeared to be more abundant between spring and summer, although both species did not show a consistent trend among years (Fig. 14).
Table 11. Results of ANOVAs testing for significant differences in number of individuals (per m$^3$) representing the six most abundant species among seasons, locations, exposure and sites nested within exposure. All data was $\log_{10}(x+1)$ transformed prior to analysis, which removed heteroscedasticity in the data. Mean squares (MS) and significance levels are shown and significant results are in bold. Degrees of freedom are shown in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season (Se)</th>
<th>Location (L)</th>
<th>Site (S) [Location]</th>
<th>Se x L</th>
<th>Se x S[L]</th>
<th>Residual (288)</th>
<th>Cochran's C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bathygobius cocosensis</td>
<td>21.342***</td>
<td>0.830</td>
<td>17.161***</td>
<td>1.497</td>
<td>1.341</td>
<td>1.010</td>
<td>0.043</td>
</tr>
<tr>
<td>Enneapterygus rufopileus</td>
<td>4.459***</td>
<td>6.328</td>
<td>13.292***</td>
<td>0.938</td>
<td>1.000*</td>
<td>0.7075</td>
<td>0.066</td>
</tr>
<tr>
<td>Girella elevata</td>
<td>0.875</td>
<td>8.212</td>
<td>6.452***</td>
<td>0.877</td>
<td>0.699</td>
<td>0.555</td>
<td>0.059</td>
</tr>
<tr>
<td>Heteroclinus whiteleggi</td>
<td>0.853</td>
<td>3.476</td>
<td>2.583***</td>
<td>1.266**</td>
<td>0.453</td>
<td>0.347</td>
<td>0.083</td>
</tr>
<tr>
<td>Parablellinus intermedius</td>
<td>1.864**</td>
<td>0.304</td>
<td>3.960***</td>
<td>0.606</td>
<td>0.529</td>
<td>0.480</td>
<td>0.060</td>
</tr>
<tr>
<td>Lepidoblenius haplodactylus</td>
<td>8.798***</td>
<td>99.133*</td>
<td>15.230***</td>
<td>2.691</td>
<td>1.777***</td>
<td>0.890</td>
<td>0.052</td>
</tr>
</tbody>
</table>

* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$.  

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**Figure 13.** Mean (±SE) number of individuals (per m$^3$) representing the six most abundant species caught at four sites (four rockpools at each site) at Bass Point, Bellambi Point and Caravan Point between 7 September 1999 and 13 September 2001. Data has been pooled for eight sampling occasions at each site.
**Figure 14.** Mean (±SE) number of individuals (per m$^3$) representing the six most abundant individuals caught during each season at Bass Point, Bellambi Point and Caravan Point between 9 September 1999 and 13 September 2001. Data has been pooled for four sites (each containing four rockpools) at each location. The months included within each season are: (Sp) spring (September-November), (Su) summer (December-February), (Au) autumn (March-May) and (Wi) winter (June-August).
Fish assemblage structure

Among-location comparisons

Ordination of the nMDS data revealed differences in fish assemblage structure among the three locations during the two-year study (Fig. 15). ANOSIM indicated that fish assemblage structure differed significantly among locations but not among seasons (Table 12). Pairwise comparisons of locations showed that the fish assemblages of Bass Point were significantly different to those of both Bellambi Point and Caravan Point, whereas no differences were detected between the latter two locations (Table 12). SIMPER revealed that Bass Point differed from Bellambi Point and Caravan Point fish assemblages primarily due to higher abundances of *Bathygobius cocosensis*, *Enneapterygius rufopileus*, *Girella elevata*, *Heteroclinus fasciatus* and *Heteroclinus whiteleggi* and lower abundances of *Lepidoblennius haplodactylus*. Bellambi Point differed from Caravan Point due to higher abundances of *B. cocosensis*, *L. haplodactylus*, *G. elevata* and *E. rufopileus* and lower abundances of *Aspasmogaster costatus*. 
Figure 15. Non-metric MDS plot comparing centroids of fish assemblages from rockpools at four sites within three rocky headlands (Bass Point, Caravan Point, and Bellambi Point) sampled every three months between 7 September 1999 and 13 September 2001 (n=8). Centroid values (mean of 8 samples) were calculated from principal coordinates of Bray-Curtis similarities.
Table 12. Results of two way crossed ANOSIM testing for differences in fish assemblage structure among locations (Bass Point, Bellambi Point and Caravan Point) and seasons between 9 September 1999 and 17 September 2001 showing $R$ statistics and significance values. Pairwise comparisons of all possible combinations of samples within each main effect are shown. SIMPER results show species (in decreasing order) contributing to at least 10% of the dissimilarity among groups in pairwise comparisons and the site (in parentheses) at which they were most abundant. Significant results are shown in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>$R$ statistic</th>
<th>$P$ value</th>
<th>SIMPER results</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Main Effects</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Location</td>
<td>0.201</td>
<td><strong>0.001</strong></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>0.047</td>
<td>0.149</td>
<td></td>
</tr>
<tr>
<td><strong>Pairwise comparisons</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bass Point vs Bellambi Point</td>
<td>0.302</td>
<td><strong>0.001</strong></td>
<td>Be (1), Er (1), Lh (2), Ge (1), Hw (1), Hf (1)</td>
</tr>
<tr>
<td>Bass Point vs Caravan Point</td>
<td>0.426</td>
<td><strong>0.001</strong></td>
<td>Be (1), Er (1), Lh (3), Ge (1), Hw (1), Hf (1)</td>
</tr>
<tr>
<td>Bellambi Point vs Caravan Point</td>
<td>-0.105</td>
<td>0.934</td>
<td>Bc (2), Lh (2), Ge (2), Er (2), Ac (3)</td>
</tr>
</tbody>
</table>

Key to species abbreviations in SIMPER:
- Ac = Aspasmogaster costatus;
- Bc = Bathygobius cocosensis;
- Er = Enneapterygus rufopileus;
- Ge = Girella elevata;
- Hf = Heteroclinus fasciatus;
- Hw = H. whiteleggi;
- Lh = Lepidoblennius haplodactylus;

Key to site abbreviations: 1 = Bass Point; 2 = Bellambi Point; 3 = Caravan Point.
Within-location comparisons

Since there were significant differences in fish assemblage structure among the three locations (Table 12), it was considered necessary to analyse spatial and temporal patterns in assemblage structure separately for each location. Such subdivision of data is not recommended in testing for differences between factors using ANOSIM (i.e. the equivalent of investigating an interaction term in a univariate ANOVA) as it increases the chances of incurring a Type II error (Clarke, 1993). However, the number of samples within each location group was considered sufficiently large to allow unbiased P values to be estimated.

Ordination of the nMDS data revealed apparent differences in fish assemblage structure among sites for two of the three locations (Bass Point and Bellambi Point) during the two-year study (Fig. 16). ANOSIM confirmed that fish assemblage structure differed significantly among sites within each of the three locations, but not among seasons (Table 13). The lack of obvious differences in fish assemblages among sites for the ordination plot of Caravan Point may therefore have been due to a poor discrimination using nMDS, as indicated by the high stress value (0.16).

Pairwise comparisons of sites at Bass Point showed that each of the four sites supported significantly different fish assemblages (Table 13). SIMPER revealed that this was mainly due to higher abundances of *Bathygobius cocosensis*, *Enneapterygius rufopileus*, *Parablennius intermedius* and *Girella elevata* at the more sheltered sites (Sites 3 and 4), and higher abundances of *Heteroclinus whiteleggi*, *Heteroclinus fasciatus* and *Aspasmogaster costatus* at more exposed sites (Sites 1 and 2) (Table 13).
Pairwise comparisons of sites at Bellambi Point revealed that each of the four sites supported significantly different fish assemblages with the exception of sites 1 and 4 and sites 2 and 3. SIMPER revealed that site 1 was different to sites 2 and 3 due to higher abundances of *Bathygobius cocosensis*, *Lepidoblennius haplodactylus*, *Girella elevata* and *Enneapterygius rufopileus* and lower abundances of *Istiblennius meleagris*, *H. fasciatus* and *Aspasmogaster liorhyncha* (Table 13). Site 4 differed to sites 2 and 3 due to higher abundances of *B. cocosensis* and *G. elevata* and lower abundances of *L. haplodactylus*, *E. rufopileus*, *I. meleagris*, *Heteroclinus fasciatus* and *A. liorhyncha* (Table 13).

Pairwise comparisons of sites at Caravan Point revealed that site 1 differed from sites 3 and 4, while site 2 differed from site 3. SIMPER revealed that site 1 was different to sites 2 and 4 due to higher abundances of *Lepidoblennius haplodactylus*, *Enneapterygius rufopileus*, *H. fasciatus* and *Heteroclinus whiteleggi*, and lower abundances of *Bathygobius cocosensis* and *Istiblennius meleagris* (Table 13). Site 2 differed to site 3 due to higher abundances of *L. haplodactylus*, *Aspasmogaster costatus*, *H. fasciatus* and *Parablennius intermedius* and lower abundances of *B. cocosensis* (Table 13).
Figure 16. Non-metric MDS plot comparing centroids of fish assemblages from rockpools at four sites within a) Bass Point, b) Caravan Point, and c) Bellambi Point, which were sampled every three months between 7 September 1999 and 13 September 2001 ($n=8$). Centroid values (mean of 8 samples) were calculated from principal coordinates of Bray-Curtis similarities.
Table 13. Results of two-way crossed ANOSIM testing for differences in fish assemblage structure among sites and seasons at Bass Point, Bellambi Point and Caravan Point. Samples were collected every three months between 9 September 1999 and 17 September 2001. Pairwise comparisons of all possible combinations of samples within each main effect are shown including $R$ statistics and significance values. SIMPER results show species (in decreasing order) contributing to at least 10% of the dissimilarity among groups in pairwise comparisons and the site (in parentheses) at which they were most abundant. Significant results are shown in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>$R$ statistic</th>
<th>$P$ value</th>
<th>SIMPER</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Main Effects - Bass Point</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>0.424</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>0.109</td>
<td>0.069</td>
<td></td>
</tr>
<tr>
<td><strong>Pairwise comparisons</strong></td>
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<td>&lt;0.0001</td>
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Key to species in SIMPER: Ac=Aspasmogaster costatus; Al=Aspasmogaster liorhyncha; Bc=Bathygobius cocosensis; Er=Enneapterygus rufopileus; Ge=Girella elevata; Hf=Heteroclinus fasciatus; Hw=Heteroclinus whiteleggi; Im=Istiblennius meleagris; Lh=Lepidoblennius haplodactylus; Pi=Parablennius intermedius; Sl=Scorpis lineolatus.

Key to site numbers: 1=Site 1; 2=Site 2; 3=Site 3; 4=Site 4.
Length-frequency distributions of common species

Length-frequency distributions of dominant species suggested that juvenile *Bathygobius cocosensis* (8-24 mm TL), *Enneapterygius rufopileus* (9-31 mm TL), and *Girella elevata* (8-42 mm FL) recruited to rockpools at Bass Point, Bellambi Point and Caravan Point primarily during late spring and early summer (March-May). This trend was consistent for both years of study (Figs 17, 18 and 19). In contrast, juvenile *Lepidoblennius haplodactylus* (12-27 mm TL) recruited to rockpools at Bellambi Point and Caravan Point slightly later (May-September) for both years; although some recruitment occurred during spring in the first year of study (Fig. 20).

By tracing the growth of prominent cohorts in length-frequency distributions of *Enneapterygius rufopileus* and *Bathygobius cocosensis* through time, it was apparent that growth through during their juvenile stages is rapid and fish are capable of reaching around 40 mm TL and 50 mm TL respectively in their first year. It is also apparent that very few individuals of these species, found in rockpools, exceed 50 mm TL and 60 mm TL respectively (Figs 17 and 18). Similarly, *Girella elevata* and *Lepidoblennius haplodactylus* appear to grow rapidly reaching around 100 mm FL and 80 mm TL, respectively, in their first year (Figs 19 and 20). However, growth of these four species appears to slow between autumn and winter when water temperatures decreases.
Figure 17. Length-frequency distributions (in 1 mm intervals) for *Bathygobius cocosensis* caught during each season between 7 September 1999 and 13 September 2001 at Bass Point, Bellambi Point and Caravan Point. Samples sizes are shown.
Figure 18. Length-frequency distributions (in 1 mm intervals) for *Enneapterygius rufopileus* caught during each season between 7 September 1999 and 13 September 2001 at Bass Point, Bellambi Point and Caravan Point. Samples sizes are shown.
Figure 19. Length-frequency distributions (in 5 mm intervals) for *Girella elevata* caught during each season between 7 September 1999 and 13 September 2001 at Bass Point, Bellambi Point and Caravan Point. Samples sizes are shown.
Figure 20. Length-frequency distributions (in 2 mm intervals) for *Lepidoblennius haplodactylus* caught during each season between 7 September 1999 and 13 September 2001 at Bass Point, Bellambi Point and Caravan Point. Samples sizes are shown.
Study 2: Large-scale spatial variation in fish assemblages

A total of 2215 fish from 30 species comprising 20 families were caught from rockpools at 14 between 15 May 2000 and 4 July 2001 (Table 14). Only one species, Girella elevata, was common to all sites, whereas thirteen species were only captured at one or other of the sites (Table 14). Abundances of these species was always low (<7 fish).

ANOVA showed number of species and individuals significantly differed among locations (Table 15, SNK tests). Highest mean numbers of species were recorded at Cowrie Island, Caravan Point and Mollymook Point and the lowest mean numbers of species at Flagstaff Point, Bass Point and Wagonga Head (Fig. 21). Highest mean numbers of individuals were recorded at Caravan Point, Marsden Head and Bellambi Point and the lowest mean numbers of individuals were recorded at Coalcliff Point and Wagonga Head (Fig. 21).

The nMDS ordination plot revealed differences in fish assemblages among locations (Fig. 22). ANOSIM revealed significant differences in fish assemblages among locations (Global $R=0.563; P<0.001$) and pairwise comparisons identified locations having similar fish assemblages. Generally, those locations only sampled once or having low species richness were isolated. However, this may be due to fewer samples being taken at some of these locations. Locations comprising three groups were identified by ANOSIM as having similar fish assemblages (Fig. 22). SIMPER revealed that these groups mainly differed due to differences in the relative contribution of the same species. For example, the first group (Coalcliff Point, Puckey's Bombora and Sandon Point) were similar due to high catches of Lepidoblennius haplodactylus and Heteroclinus fasciatus. The second group (Caravan Point, Marsden Head and Black
Head) were similar due to high abundances of species such as *L. haplodactylus*, *Bathygobius cocosensis* and *Girella elevata*. The third group (Bass Point, Bellambi Point and Flagstaff Point) were similar due to high abundances of *B. cocosensis* and *G. elevata*. 
Table 14. Numbers of individuals representing each fish species caught from rockpools at 14 locations along the NSW south coast between 15 May 2000 and 4 July 2001. Length range (total in mm) of each species is also shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Coalcliff Point</th>
<th>Sandon Point</th>
<th>Bellambi Point</th>
<th>Bucky's Point</th>
<th>Flagstaff Point</th>
<th>Barrack Point</th>
<th>Cowrie Island</th>
<th>Caravan Point</th>
<th>Bass Point</th>
<th>Marsden Head</th>
<th>Black Head</th>
<th>Mollymook Point</th>
<th>Tuross Heads</th>
<th>Wagonga Head</th>
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<td>Scatophagidae</td>
<td><em>Scatophagus argus</em></td>
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Table 14 continued

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<tr>
<td><em>Flicampus tigris</em></td>
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| **Total number of fish** | 125 | 77  | 343 | 115 | 246 | 44  | 78  | 207 | 562 | 187 | 95  | 49  | 36  | 51  | 1964 | 8  |
| **Total number of species** | 8   | 7   | 19  | 9   | 10  | 7   | 5   | 13  | 22  | 13  | 6   | 5   | 7   | 10  | 31  |
| **Number of rockpools**    | 8   | 8   | 8   | 8   | 8   | 8   | 8   | 8   | 8   | 8   | 8   | 8   | 8   | 112 |
| **Number of samples**      | 24  | 24  | 24  | 24  | 24  | 24  | 24  | 24  | 24  | 24  | 8   | 8   | 8   | 288 |
Table 15. Results of ANOVAs testing for significant differences in number of species and number of individuals (per m\(^3\)) among locations (fourteen locations) and sites nested within locations (two sites). Both numbers of species and individuals data were \(\log_{10}(x+1)\) transformed before analysis, which removed heteroscedasticity in the data. Mean squares and significance levels are shown and significant results are in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Number of species</th>
<th>Number of Individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>13</td>
<td><strong>0.582</strong>*</td>
<td><strong>0.765</strong>*</td>
</tr>
<tr>
<td>Site [Location]</td>
<td>14</td>
<td><strong>0.185</strong></td>
<td><strong>0.032</strong></td>
</tr>
<tr>
<td>Residual</td>
<td>260</td>
<td>0.376</td>
<td>0.128</td>
</tr>
<tr>
<td>Cochran's C</td>
<td></td>
<td>0.091</td>
<td>0.081</td>
</tr>
</tbody>
</table>

* = \(P<0.05\); ** = \(P<0.01\); *** = \(P<0.001\).
Figure 21. Mean (±SE) number of species (per m$^3$) caught in rockpools at 14 rocky headlands along the NSW south coast during three sampling occasions between 15 May 2000 and 4 July 2001. Data at each locality for each sampling occasion have been pooled from two sites, each containing four rockpools. Note: Mollymook Point, Tuross Heads and Wagonga Head were only sampled once. Sampling locations are listed from north to south.
Figure 22. Non-metric MDS plot comparing centroids of fish assemblages in rockpools at 14 locations along the NSW south coast, which were sampled on three occasions between 15 May 2000 and 4 July 2001. Centroids (mean of eight rockpools combined for three samples) were calculated from principal coordinates of Bray-Curtis similarities.
DISCUSSION

Rockpool fish assemblages in southeastern Australia were found to vary significantly across spatial scales from hundreds of metres to hundreds of kilometres, and across temporal scales from months to years. Generally, spatial variation could be attributed to differences in the physico-chemical environment of rockpool, whereas temporal variability appeared to be a result of fish recruitment, immigration and emigration.

Both numbers of species and individuals and the numbers of the six most abundant species were captured in higher numbers in rockpools with higher volume, but captured in lower numbers in rockpools with higher water salinity. Natural differences in rockpool volume among locations probably explain the differences in numbers of species and individuals among individual rockpools. For example, rockpools at Bass Point and Bellambi Point are, on average, an order of magnitude larger than rockpools at other locations and these rockpools supported higher number of fish species. Mahon and Mahon (1994) found a similar relationship between the numbers of species and fish with rockpool volume and suggested that this may be due to larger rockpools providing more habitat for additional fish species to exploit. However, the catches of fish at Bass Point revealed that higher rockpool volume does not necessarily increase fish density, especially where substratum area is not increased in the same proportion as volume (i.e. increases in rockpool depth and not surface area) (also see Willis and Roberts, 1996). In the present study, habitats associated with substratum area (i.e. substratum heterogeneity and algal cover) were shown to be important in influencing the numbers of *Bathygobius cocosensis* and *Lepidoblennius haplodactylus*. Similar findings have been reported elsewhere. For example, increased algal cover in South African rockpools (Bennett and Griffiths, 1984) and substrate heterogeneity or "rugosity" in southern
Californian (Davis, 2000a), have both been suggested as factors responsible for increased numbers of fish in rockpools. These studies attributed this relationship to the increased number of microhabitats available for fish to exploit.

The significant influence of salinity on the rockpool fish assemblages is far more ambiguous than the effects of rockpool volume. Although salinity has not been shown to directly influence rockpool fish assemblages, water temperature has been shown previously to be an influence on the distribution of individual taxa (see Graham, 1970; Nakamura, 1976a, 1976b). Temperature can dramatically change with vertical elevation of rockpools (Huggett and Griffiths, 1986). In contrast, tidal height was not a significant factor influencing the variation in the numbers of species and individuals in the present study, and thus the effects of salinity may act independently. An alternative explanation may be the exposure time of rockpools to flood tides, which is generally influenced by the tidal height of rockpools. However, some rockpools at the same tidal height may have significantly different exposure times due to physical barriers to water flow such as crevices, gullies and other rockpools. Salinity may increase in rockpools with longer exposure times at low tide and cause fish greater physiological stress. As a result, these rockpools may be avoided by species having less tolerance to such conditions.

A large percentage of the variation in rockpool fishes was not explained by the environmental variables measured. This large residual variation may be explained by a combination of variables or by those not measured. At the largest spatial scales investigated in this study (tens to hundreds of kilometres), the structure of rockpool fish assemblages differed significantly among locations, although this was due mostly to differences in the relative abundances of individual species common to most locations,
such as *Bathygobius cocosensis*, *Lepidoblennius haplodactylus* and *Girella elevata*. The similarity in species composition among locations may be facilitated by the dispersal of larvae by the East Australian Current, which influences the ocean adjacent to the 14 locations studied (see Zann, 2000). However, differences between headlands was also found, which appears to be due to species that are common at particular locations, such as *Heteroclinus whiteleggi*, *Aspasmogaster costatus* and *Parablennius intermedius*. These local populations may exist and be isolated as a result of barriers for larval dispersal or post-settlement migrations, such as local currents and upwelling events (Stepien *et al.* 1991) or beaches between headlands (Gibson and Yoshiyama, 1999).

Across smaller spatial scales of kilometres, differences in fish assemblages may be due to preferences of species for particular habitats. Of the three locations studied intensively in the Illawarra region, Bass Point has distinctly different fish assemblages. At Bass Point, rockpools have holes and crevices formed by layers of cobbles and boulders that create habitat for secretive species, such as *Girella elevata*. Further, large 'mats' of pink coralline algae on the rockpool floors and brown algae (*Zonaria* spp. and *Phyllospora* spp.) suspended through the water column are habitats for *Enneapterygius rufopileus* and the weedfishes, *Heteroclinus fasciatus* and *Heteroclinus whiteleggi*.

In contrast, the rockpool fish assemblages at Bellambi Point and Caravan Point are similar to each other but different to Bass Point, perhaps due to differences caused by a lower structural heterogeneity within rockpool habitats. The substratum of rockpools at Bellambi Point and Caravan Point generally consist of gravel, small cobbles or broken shells. There is little algal cover in these rockpools except for green turf algae (*Enteromorpha* spp.) and larger macroalgae, such as *Caulerpa filiformis* at Bellambi.
Point and *Hormosira banksii* at Caravan Point. These structural components attract a different suite of species to Bass Point including *Lepidoblennius haplodactylus* and the blennies, *Istiblennius meleagris* and *Istiblennius edentulus*. However, large numbers of the sea urchins, *Centrostephanus rogersii* and *Heliocidaris tuberculata*, provided additional cover within the Caravan Point rockpools and may have resulted in catches of high numbers of *Aspasmogaster costatus*, which were often found living among urchin spines.

At smaller spatial scales, differences in rockpool fish assemblages at sites within headlands separated by hundreds of metres may have been due to their relative exposure to wave action. Although interactions occurred between the factors site and exposure, some general patterns appeared evident, particularly at Bass Point and Bellambi Point. For example, *Bathygobius cocosensis*, *Enneapterygius rufopileus* and *Lepidoblennius haplodactylus* were generally more abundant at sheltered sites, whereas *Girella elevata*, *Istiblennius meleagris* and *Parablennius intermedius* were generally more abundant at exposed sites. Similar results have been obtained on the Atlantic coast of Spain, where exposed rocky shores are mainly dominated by blennies, whereas gobies are more abundant on sheltered shores (Ibanez et al. 1989). In Shirahama (Japan), the composition of a guild of blenniid fishes changes from being dominated by *Scartella cristata* on exposed shores, to *Entomacrodus stellifer* on more sheltered ones (Fukao, 1985). The relative adaptiveness of species to the harsh and more variable conditions on exposed shores may be responsible for these patterns of variation (see Zander et al. 1999).
With regards to temporal variability, the present study has shown that rockpool fish assemblages in the Illawarra region can vary in terms of abundance of constituent species, but ANOSIM revealed that the composition of species was quite stable, both among and within locations through time. At Bass Point *Bathygobius cocosensis*, *Enneapterygius rufopileus* and *Girella elevata* were consistently the most abundant species, while *Lepidoblennius haplodactylus*, *B. cocosensis* and *E. rufopileus* were consistently the most abundant species at Bellambi Point and Caravan Point. Similar persistence in rockpool fish assemblages has been documented for numerous study sites. For example, Collette (1986) documented two species, *Pholis gunnellus* and *Tautogolabrus adspersus*, to be consistently abundant over a period of 19 years. Even more striking, Faria and Almada (1999) found fish assemblages in Portugal to have remained consistent over three years even after physically manipulating substratum heterogeneity within rockpools. They suggest persistence existed because rockpools are only permanently occupied by a small number of species possessing specialised adaptations to cope with the highly variable intertidal environment.

Patterns of temporal variability in rockpool fish assemblages in the present study appear to be a result of recruitment peaks in at least the four of the most abundant species. For example, seasons where abundances of fish were highest (summer to autumn of both years) coincide with the recruitment of juveniles (<30 mm TL) of the species *Bathygobius cocosensis*, *Enneapterygius rufopileus* and *Girella elevata*. However, a smaller peak in fish abundance during winter (May) of each year coincides with recruitment of the third most abundant species, *Lepidoblennius haplodactylus*. This contrasts to recruitment patterns recorded by Beckley (2000) who found that *Helcogramma obtusirostre* (Tripterygiidae) and *Bathygobius* sp. (Gobiidae) recruited
year-round to rockpools in KwaZulu-Natal, South Africa. The three most abundant species in the present study, *Bathygobius cocosensis* (Gobiidae), *Enneapterygius rufopileus* and *Lepidoblennius haplodactylus* (both Tripterygiidae), are closely related to these species but do not have juveniles present year-round. The warmer climate of Beckley’s study location (27°57’S, 30°59’E) compared to the south coast of NSW, may provide more conducive conditions for recruitment throughout the year. This is supported by the results of Willis and Roberts (1996) who found a number of Tripterygiids recruit only once each year, albeit at different times, in the cool temperate waters near Wellington, New Zealand.

Despite the widespread stability and persistence of the ‘resident’ rockpool fish assemblages, the number of species showed a distinct peak between summer and autumn during both years of the present study. This was mainly attributed to the appearance of warm water transient species, such as *Chaetodon aguira* and *Kuhlia mugil*, which are transported south from the tropical waters of northern Queensland by the warm East Australia Current. The Illawarra region is well outside the normal distribution of these transient species so when the water temperature in the Illawarra declines these fish probably leave the rockpools and may try to migrate northward to warmer waters, although most probably perish in the process. Thus, a decline in the number of species has been documented between autumn and summer.

This Chapter has quantitatively documented the patterns of variation in the rockpool fish assemblages of the NSW south coast across various temporal and horizontal spatial scales. To compliment these results, Chapter 5 will investigate the patterns of variation in rockpool fish assemblages along the vertical plane in the intertidal zone.
Chapter 5

Effects of rockpool elevation on fish assemblage structure

INTRODUCTION

The rocky intertidal zone is a dynamic yet extremely harsh environment for most organisms, where physico-chemical variables can vary significantly across an array of spatial (e.g. wave exposure) and temporal (days, months, years) scales (Morris and Taylor, 1983; Huggett and Griffiths, 1986). Perhaps the most dramatic changes in environmental conditions occur along the vertical plane of the intertidal zone, where the tide and wave conditions constantly vary the height of the interface between land and sea. The tolerance of particular sessile organisms to environmental variables results in the establishment of well defined vertical zonation patterns in the intertidal zone, which has attracted significant attention among ecologists in the past few decades (see reviews by Connell, 1972; Raffaelli and Hawkins, 1996). Numerous studies have quantitatively compared fish assemblage structure within rockpools across various horizontal spatial scales (see Chadwick, 1976; Yoshiyama et al. 1986; Davis, 2000a) and studies in Chapter 4 have already identified some of these patterns in south eastern Australia. However, less is known about the vertical zonation patterns of fish assemblages in the intertidal zone (see Gosline, 1965; Gibson, 1972; Yoshiyama, 1981; Prochazka and Griffiths, 1992), although some attention has been paid to single taxa (Nakamura, 1976a, 1976b; Barton, 1982; Horn et al. 1986; Ralston and Horn, 1986; Mgaya, 1992).

Gibson (1972) found that vertical elevation of rockpools played a significant role in the distribution of species along the Atlantic coast of France, although this 'snap-shot' study
was undertaken over a period of only one month. Nonetheless, he revealed a well-defined turnover in species with increasing vertical elevation, from a domination of blennies and gobies in the high intertidal, to others, such as the Gobiesocids, in the lower intertidal. Gosline (1965) also made similar qualitative observations in the rockpools of the Hawaiian Islands, where blennies and gobies occupied higher level "splash pools" that are not always inundated by the tide on each day. In the lower rockpools of the "surge zone", far more diverse fish assemblages were found, including many species from the families Labridae, Acanthuridae, Muraenidae and Holocentridae. Most of these were not permanent intertidal residents. There are various opinions about the cause of vertical zonation patterns among intertidal fishes, such as tolerance to temperature extremes (Hiat and Strasberg, 1960; Nakamura, 1976a, 1976b; Kotrschal and Reynolds, 1982) and hypoxic conditions (Martin, 1995). However, Gibson (1972) suggests physical conditions do not entirely account for the zonation patterns in intertidal fishes and that competition for space and food may also be important factors.

In Chapter 4, the variation in fish assemblages across various spatial and temporal scales was investigated. In the present Chapter, the patterns of spatial variation in the rockpool fish assemblages are further explored by quantitatively investigating the effect of vertical elevation on the fish assemblage structure and demographic composition of dominant species. An *a priori* expectation was that the number of species and individuals would decline with increasing elevation (see Bennett and Griffiths, 1984). Furthermore, it was predicted that a greater change species composition would occur at lower elevations, where species not being well adapted for intertidal life (transients and opportunists) would be found. These species should be replaced by permanent resident
Chapter 5 Effects of Rockpool Elevation on Fish Assemblage Structure

species, which possess adaptations to cope with the physiological demanding conditions of higher intertidal rockpools.

MATERIALS AND METHODS

Study sites and collection of fishes

This study was carried out concurrently with the research described in Chapter 4, but involved sampling separate groups of rockpools. Forty-eight intertidal rockpools were sampled on three occasions (between 15 March and 19 September 2001) at Bass Point, Bellambi Point, Caravan Point and Puckey's Bombora in southeastern NSW, Australia (Fig. 23). At each site, four pools considered to be representative of low (0.6-0.99 m above MLLW), medium (1.0-1.39 m) and high (1.4-1.8 m) elevations in the intertidal were sampled. Tidal heights of pools were measured using the methods described in Chapter 4. The sampling site at each location were selected only along exposed stretches of the shoreline as the level of wave exposure influences the upper limits of sessile intertidal biota (Gibson, 1972), which may subsequently influence fish distribution. Rockpools were selected for similarity of size (surface area and volume) and substrate type (cobbles and small boulders) as such factors have been shown to influence rockpool fish assemblage structure (Mahon and Mahon, 1994).

Collection of fish and environmental data (temperature, salinity, pH and dissolved oxygen, volume, algal cover and substratum homogeneity) from each rockpool was undertaken using the methods described in Chapters 2 and 4 respectively. Each fish species captured was categorised as resident (R), opportunist (O) or transient (T) using the criteria described in Chapter 3.
Figure 23. Map of the Illawarra study region showing the sampling locations at Bellambi Point, Puckey’s Bombora, Caravan Point and Bass Point in New South Wales (NSW), Australia.
Statistical analyses

A three factor orthogonal ANOVA was performed in the G-MAV 5 computer program to test for significant differences in numbers of species and individuals between locations (four levels), intertidal rockpool height (three levels) and sampling times (three levels). All factors were considered fixed. Although the same rockpools were sampled on each occasion a repeated-measures ANOVA was not used for the reasons given in Chapter 4. Since rockpools differed in volume, data was standardised and expressed as number of fish or species per m$^3$ before analyses (see Chapter 4).

The influence of environmental variables of rockpools (intertidal height, substrate homogeneity, algal cover, rockpool volume, temperature, salinity and dissolved oxygen) on the numbers of individuals and species was investigated using multiple regression analyses described in Chapter 4.

Non-metric multidimensional scaling (nMDS) was used to examine similarities in fish assemblages among locations, sampling occasions and rockpool height. A two-way crossed ANOSIM was used to determine whether \textit{a priori} groups of tidal height and location differed statistically and SIMPER was then used to determine which species were responsible for significant differences among these groups. Detailed descriptions of these methods are given in Chapter 4.

Kolmogorov-Smirnov tests were used to determine whether the length-frequency distributions for abundant species differed among low, medium and high rockpools.
RESULTS

Physico-chemical environment

Most environmental variables changed very little over the study period, with the exception being mean monthly temperatures, which varied between 21.0 (±SE 0.4) °C (June 2001) and 25.6 (±0.2) °C (March 2001). Mean monthly salinities ranged between 35.7 (±0.1) %o (June 2001) and 35.9 (±0.7) %o (March 2001). Mean monthly DO values ranged between 6.1 (±0.2) mg l⁻¹ (March 2001) and 6.6 (±0.2) mg l⁻¹ (September 2001). With respect to intertidal height, a significant positive correlation (r=0.824; P<0.0001) existed with salinity, although no significant relationships were evident with DO (r=-0.084; P=0.318), temperature (r=0.017; P=0.841), algal cover (r=0.012; P=0.886) or substrate homogeneity (r=-0.052; P=0.534).

Numbers of species and individuals

A total of 1515 fish from 23 species and 13 families were caught at the four sites (Table 16). ANOVA showed that only the mean number of species differed significantly among locations (Table 17). This was due to significantly more species being caught at Puckey's Bombora compared to the other locations. No differences in the mean number of species were evident between Bass Point, Caravan Point and Bellambi Point (SNK test; Fig. 24). ANOVA also revealed that mean number of individuals did not differ for location, rockpool height, month, or any combination of these (Table 17).

Multiple regression of PC scores revealed that rockpool variables explained 32% and 26% of the variation for the number of species and individuals, respectively (Table 18). Rockpool height, substrate homogeneity and salinity each explained a significant portion of the variation in numbers of species (Table 18). Numbers of species
significantly decreased with increasing height, whereas positive relationships occurred with both substrate homogeneity and salinity. Substrate homogeneity, algal cover and salinity each explained a significant portion of the variation for numbers of individuals. Each of these variables showed positive relationships with the number of individuals (Table 18).
Table 16. Number of fish for each species caught from rockpools at low (L), medium (M) and high (H) intertidal levels at four rocky headlands pooled for three sampling occasions undertaken between 15 March and 19 September 2001. Asterisks denote species of economic significance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Bass Point</th>
<th>Bellambi Point</th>
<th>Caravan Point</th>
<th>Puckey's Bombora</th>
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<tr>
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<td>L  M  H</td>
<td>L  M  H</td>
<td>L  M  H</td>
<td>L  M  H</td>
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<td><strong>Gobiesocidae</strong></td>
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<td>2 - - -</td>
<td>9 - -</td>
<td>5 1</td>
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<td>- - -</td>
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<tr>
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<td>1 - 4</td>
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<tr>
<td><em>Girella elevata</em></td>
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<td>11 18 16</td>
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<td>5 1 1</td>
</tr>
<tr>
<td><em>Istiblennius meleagris</em></td>
<td>3 - -</td>
<td>- 1 8</td>
<td>4 5 22</td>
<td>- - -</td>
</tr>
<tr>
<td><em>Parablennius intermedius</em></td>
<td>2 6 8</td>
<td>1 2 10</td>
<td>1 5 1</td>
<td>3 1 5</td>
</tr>
<tr>
<td><strong>Tripterygiidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lepidoblennius haplodactylus</em></td>
<td>2 1</td>
<td>28 49</td>
<td>6 51 16</td>
<td>9 20 3</td>
</tr>
<tr>
<td><em>Enneapterygus rufipilus</em></td>
<td>5 45</td>
<td>14</td>
<td>28 5</td>
<td>34 - 4</td>
</tr>
<tr>
<td><strong>Clinidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Heteroclinus fasciatus</em></td>
<td>11 10</td>
<td>4 - 10</td>
<td>- 17 1</td>
<td>1 12 15</td>
</tr>
<tr>
<td><em>Heteroclinus whiteleggi</em></td>
<td>9 - -</td>
<td>4 1</td>
<td>- 9 -</td>
<td>3 1</td>
</tr>
<tr>
<td><em>Ophiclinus gracilis</em></td>
<td>3 2 -</td>
<td>- 1</td>
<td>- - -</td>
<td>- - -</td>
</tr>
<tr>
<td><strong>Gobiidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>73 95</td>
<td>104 64</td>
<td>64 71 83</td>
<td>16 24 85 5</td>
</tr>
<tr>
<td><em>Callogobius depressus</em></td>
<td>- -</td>
<td>- 8</td>
<td>- 3</td>
<td>- - -</td>
</tr>
<tr>
<td><strong>Total numbers of fish</strong></td>
<td>201 101</td>
<td>182 95</td>
<td>187 186</td>
<td>158 39 135 86</td>
</tr>
</tbody>
</table>
Table 17. Results of ANOVAs testing for significant differences in number of species and number of individuals (per m\(^3\)) among locations, rockpool height, and months. Number of individuals data was \(\log_{10}(x+1)\) transformed prior to analysis but did not remove heteroscedasticity the significance values was set to \(P=0.01\). Mean squares and significance levels are shown and significant results are in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Number of species</th>
<th>Number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location (L)</td>
<td>3</td>
<td>1090.735***</td>
<td>0.967</td>
</tr>
<tr>
<td>Pool Height (H)</td>
<td>2</td>
<td>409.995</td>
<td>1.326</td>
</tr>
<tr>
<td>Month (M)</td>
<td>2</td>
<td>26.258</td>
<td>0.033</td>
</tr>
<tr>
<td>L x H</td>
<td>6</td>
<td>116.101</td>
<td>0.391</td>
</tr>
<tr>
<td>L x M</td>
<td>6</td>
<td>58.130</td>
<td>0.816</td>
</tr>
<tr>
<td>H x M</td>
<td>4</td>
<td>29.986</td>
<td>0.354</td>
</tr>
<tr>
<td>L x H x M</td>
<td>12</td>
<td>76.056</td>
<td>0.347</td>
</tr>
<tr>
<td>Residual</td>
<td>108</td>
<td>158.337</td>
<td>0.678</td>
</tr>
<tr>
<td>Cochran's C</td>
<td></td>
<td>0.117</td>
<td>0.203**</td>
</tr>
</tbody>
</table>

* = \(P<0.05\); ** = \(P<0.01\); *** = \(P<0.001\).

Table 18. Multiple regressions of number of species and individuals (data pooled for four locations) against rockpool principal component scores based on environmental variables. Overall regression statistics are shown as well as probabilities and slopes for each factor. All dependent variables were \(\log_{10}(x+1)\) transformed prior to analysis to normalise data. Significant results are shown in bold.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Dependent variable</th>
<th>Number of species</th>
<th>Number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td>-5.643*</td>
<td></td>
<td>-1.987</td>
</tr>
<tr>
<td>Substrate homogeneity</td>
<td>0.666***</td>
<td></td>
<td>0.586*</td>
</tr>
<tr>
<td>Algae cover</td>
<td>0.192</td>
<td></td>
<td>0.623*</td>
</tr>
<tr>
<td>Volume</td>
<td>0.207</td>
<td></td>
<td>0.455</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>0.150</td>
<td></td>
<td>0.096</td>
</tr>
<tr>
<td>Salinity</td>
<td>0.843***</td>
<td></td>
<td>1.693***</td>
</tr>
<tr>
<td>Temperature</td>
<td>-0.034</td>
<td></td>
<td>-0.169</td>
</tr>
<tr>
<td>(F)</td>
<td>9.235</td>
<td></td>
<td>6.604</td>
</tr>
<tr>
<td>(P) value</td>
<td>&lt;0.0001</td>
<td></td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(R^2)</td>
<td>0.322</td>
<td></td>
<td>0.255</td>
</tr>
</tbody>
</table>

* = \(P<0.05\); ** = \(P<0.01\); *** = \(P<0.001\).
Figure 24. Mean (±SE) number of species and individuals (per m$^3$) caught at Bass Point, Bellambi Point, Caravan Point and Puckey’s Bombora from rockpools located at low (0.6-0.99 m), mid (1.0-1.39 m) and high (1.4-1.8 m) elevations above mean low of low water (MLLW). Each bar comprises samples of four rockpools repeatedly sampled on three occasions between 15 March and 19 September 2001.
Fish assemblage structure

After performing nMDS on the data combined for all four locations (ordination not shown), ANOSIM revealed that fish assemblages significantly differed among rockpool heights but also with respect to location (Table 19). Therefore, it was considered necessary to examine the differences in fish assemblage structure with respect to rockpool elevations for each site separately. As was discussed in Chapter 4, the subdivision of data to examine within-factor variation is possible where the number of permutations of data is sufficient, as was the case here.

Ordination plots from nMDS revealed no obvious grouping with respect to intertidal height of rockpools at any site, with the exception of Caravan Point, where low, medium and high pools appeared to be separated (Fig. 25). Nonetheless, ANOSIM revealed that fish assemblages significantly differed with respect to tidal height at all four locations (Table 19). Pairwise comparisons showed that fish assemblages differed among medium and high pools at Bass Point, Caravan Point and Puckey's Bombora; low and medium pools at Bellambi Point and Caravan Point; and low and high pools at Caravan Point (Table 19).

Generally, SIMPER revealed that differences among medium and high rockpools across all sites was mainly driven by the species *Bathygobius cocosensis*, *Girella elevata* and *Istiblennius meleagris* which were most abundant in high pools, and the species *Lepidoblennius haplodactylus*, *Enneapterygius rufopileus* and *Heteroclinus fasciatus*, which mainly occupied medium-level rockpools (Table 19). Differences in fish assemblage structure among low and medium rockpools across all sites was mainly driven by the fishes, *L. haplodactylus*, *E. rufopileus* and *H. fasciatus* which were more
abundant in lower pools, whereas *B. cocosensis* and *G. elevata* were mainly captured in medium-level rockpools (Table 19). Surprisingly, low and high-level rockpools only had significantly different fish assemblages at Caravan Point, which was mainly due to the species *B. cocosensis* and *I. meleagris* occupying high rockpools, and species *L. haplodactylus*, *E. rufopileus* and *H. fasciatus* found in low rockpools (Table 19). A general diagrammatic summary of the vertical distribution of fishes within the intertidal zone is shown in Fig. 26.
Figure 25. Non-metric MDS plot comparing centroids of fish assemblages from rockpools at low, medium and high intertidal elevations at Bass Point, Bellambi Point, Caravan Point and Puckey's Bombora, which were sampled on three occasions between 15 March and 19 September 2001. Centroid values (mean of 3 samples for each rockpool) were calculated from principal coordinates of Bray-Curtis similarities. Stress values are shown.
Table 19. Results of ANOSIM testing for differences in fish assemblage structure among four locations and intertidal rockpool height (low, medium, high) pooled across three sampling occasions between 15 March and 19 September 2001. Pairwise comparisons of samples within the height factor are shown and species contributing to at least 10% of the dissimilarity among significantly different samples in SIMPER analysis, and the level (low, medium or high) where their relative abundance was highest.

<table>
<thead>
<tr>
<th>Source</th>
<th>R statistic</th>
<th>P value</th>
<th>SIMPER</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Two factor ANOSIM</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rockpool height</td>
<td>0.125</td>
<td>&lt;0.0001</td>
<td>N/A</td>
</tr>
<tr>
<td>Location</td>
<td>0.260</td>
<td>&lt;0.0001</td>
<td>N/A</td>
</tr>
</tbody>
</table>

Pairwise comparisons of samples within the 'rockpool height' factor.

**Bass Point**
- Low vs. Medium: 0.040, 0.328
- Low vs. High: 0.030, 0.592
- Medium vs. High: 0.123, 0.049, Be (H), Er (M), Ge (H), Hf (M).

**Bellambi Point**
- Low vs. Medium: 0.135, 0.037, Be (M), Lh (L), Er (L), Ge (M).
- Low vs. High: 0.011, 0.321
- Medium vs. High: 0.006, 0.444

**Caravan Point**
- Low vs. Medium: 0.311, 0.002, Lh (L), Er (L), Be (M), Hf (L).
- Low vs. High: 0.292, 0.003, Be (H), Lh (L), Er (L), lm (H).
- Medium vs. High: 0.215, 0.009, Be (H), lm (H), Lh (L).

**Puckey's Bombora**
- Low vs. Medium: 0.036, 0.718
- Low vs. High: 0.087, 0.081
- Medium vs. High: 0.294, 0.001, Be (H), Er (M), Lh (M), Hf (M).

Key to species in SIMPER: Bc=Bathygobius cocosensis; Er=Enneapterygius rufopileus; Ge=Girella elevata; Lh=Lepidoblennius haplodactylus; lm=Istiblennius meleagris; Hf=Heteroclinus fasciatus.
Rockpool heights where species were most abundant: L=low, M=medium and H=high.
Bathygobius cocosensis
Girella elevata
Istiblennius meleagris
Parablennius intermedius
Abudefduf vaigiensis

Enneapterygius rufopileus
Lepidoblennius haplodactylus
Heteroclinus fasciatus
Acanthistius ocellatus

Aspasmogaster costatus
Myxus elongatus
Heteroclinus whiteleggi

High
(1.8-1.4 m)

Medium
(1.39-1.0 m)

Low
(0.99-0.6 m)

Intertidal Zone

**Figure 26.** Diagrammatic representation of the intertidal zone showing the distributions of twelve common fish species in relation to vertical elevation of rockpools. Many of fishes shown can be found throughout the entire intertidal zone, particularly those common in high level rockpools; however this diagram groups fish into zones where they are most abundant.

**Length-frequency distributions**

Length-frequency distributions for at least four of the five most abundant species revealed that there were no obvious demographic segregation among low, medium and high intertidal rockpools as similar wide ranges in sizes were evident at each intertidal height (Fig. 27). The only species that appeared to have different size compositions among tidal heights was *Enneapterygius rufopileus*, where modal lengths were significantly larger in low pools (30-32 mm TL) than in medium (14-16 mm TL; Kolmogorov-Smirnov test $Z=2.362$, $P<0.0001$) and high pools (16-18 mm TL; Kolmogorov-Smirnov test $Z=1.726$, $P=0.005$) (Fig. 27).
Figure 27. Length-frequency distributions (in 2 mm intervals) of the five most abundant species caught on three occasions between 15 March and 19 September 2001 from low (L), medium (M) and high (H) intertidal rockpools pooled for catches from Bass Point, Bellambi Point, Caravan Point and Puckey's Bombora. Total length is given for all species except for *Girella elevata*, where fork length is shown.
DISCUSSION

The present study revealed that the vertical elevation of intertidal rockpools has a significant effect on fish assemblage structure. For example, the species composition changed with increasing rockpool elevation. Higher rockpools contained specialist resident species that were probably better suited to the more variable environmental conditions of higher rockpools (see Fig. 26). Rockpool characteristics other than height and water chemistry of rockpool, such as algal cover and substrate homogeneity, had greater influence on the number of individuals, but these factors were not influenced by rockpool elevation. It was interesting to note that tidal height was not a significant factor in the ANOVA for number of species, but was significant in multiple regression analysis. This may be a result of data included in the multiple regression analysis being based on principal component scores. This was necessary to satisfy an assumption of multiple regression analysis that there is no collinearity among variables (Manly, 1986).

The vertical zonation in fish distribution may be considered a reflection of the life cycles of individual species. The residential status of fishes may be good predictors of their distribution within the intertidal zone (Martin, 1995; Zander et al. 1999) and this trend appears to be confirmed in the present study. For example, the lowest rockpools often contained opportunists and transients that are pelagic planktivores and not specifically adapted to intertidal life, such as *Myxus elongatus* and *Chaetodon auriga*. Consequently, these species can probably only survive within low level rockpools that are more frequently inundated by the flooding tide and have water properties approximately that of the surrounding seawater (Huggett and Griffiths, 1986). These species probably do not actively seek rockpools as low tide refuges but probably accidentally become stranded in rockpools as the tide ebbs during high tide feeding.
excursions or escaping subtidal predators (Black and Miller, 1991; Rangley and Kramer, 1995a, 1995b). Since the time of isolation is minimal and low pools are usually inundated even by the smallest high tides, fish may be able to move out with the next tide and most individuals probably survive. However, some resident species are adapted to the high turbulence and surge conditions of lower rockpools, such as the Gobiesocids, *Aspasmogaster costatus* and *Aspasmogaster liorhyncha*, which posses a 'sucker' ventral fin that allows them to adhere to rocky surfaces.

Opportunistic species possessing some physiological or behavioural adaptations to intertidal environments, such as flexible thermoregulatory and osmoregulatory abilities, generally occupy lower to medium level rockpools where conditions are more variable than the lowest level rockpools (Fig. 26). A range of species inhabits the mid-intertidal as it comprises the upper and lower limits of the distributions of species adapted to low and high intertidal rockpool conditions, respectively. The main species found in this zone are the resident Tripterygiids, *Lepidoblennius haplodactylus* and *Enneapterygius rufopileus*, the Clinid, *Heteroclinus fasciatus* and the opportunistic Serranid, *Acanthistius ocellatus*.

The high intertidal zone can have extremely variable environmental conditions (Huggett and Griffiths, 1986). Diurnal variability in environmental conditions was not shown explicitly in the present study because sampling was generally undertaken at the same time of day on each occasion. However, water temperatures and salinity increase during the day (Metaxas and Scheibling, 1993), while dissolved oxygen levels can dramatically decline during the night (Morris and Taylor, 1983). These fluctuations can be amplified with increasing tidal height where rockpools are subjected to greater periods of isolation.
from the sea (Martin, 1995). Consequently, fishes possessing specialised adaptations cope better with such variable conditions. Specialised adaptations, such as flexible osmoregulatory ability and periodic air breathing, allow some species to make permanent use of higher intertidal rockpools (Martin, 1995). These species are most often resident intertidal fishes that spend their entire life history within the rocky intertidal zone. The main species found in this zone are *Bathygobius cocosensis* and *Istiblennius meleagris*, which both possess various adaptations for intertidal life. Kuiter (1996) wrote that *I. meleagris* is "often seen hanging on rocks out of water...and when disturbed jump to other pools". Although little is known of the physiology *Istiblennius* spp. in Australia, similar rocky intertidal blennies have the ability to breathe air (Lamming *et al.* 1982; Luck and Martin, 1998), which may further facilitate utilisation of high-level rockpools.

Although the vertical distribution of rockpool fishes can be a reflection of their residential status, many of the assemblages in present study do not strictly conform to such a model. Instead, a better prediction of fish distributions throughout the intertidal zone is achieved by incorporating information of their morphological and physiological adaptations to the intertidal environment. Martin (1995) categorised intertidal fishes, not exclusively rockpool fishes, as being "skippers", "remainers" or "tidepool emergers". Skippers readily move between water and land for purposes of feeding, courtship and to avoid competitive intraspecific confrontations (Todd, 1976; Zander *et al.* 1999). 'Remainers' define those species that remain hidden under various types of cover as the tide recedes. However this category can include rockpool fishes that posses no capacity for even temporary amphibious behaviour. Finally, 'tidepool emergers'
remain within rockpools during low tide period but during hypoxic conditions they move to land and temporarily reside near cover until the next high tide.

In the present study, no species appeared to be strictly amphibious and being 'skippers', but many could be classified as 'remainers' and 'tidepool emergers'. This categorisation appears far more relevant than the division relative to residential status, which can be best seen using the secondary residents as an example, such as *Abudeffuf vaigiensis* and *Girella elevata*. The physiology of these species may be better determinants of their vertical intertidal distribution than their residential status. For example, *Girella elevata* does not posses morphological adaptations for an intertidal existence as it spends its adult life subtidally (Bell *et al.* 1980). However, this opportunist appears to have behavioural and possibly physiological adaptations for an intertidal existence. When stranded out of water in an empty rockpool, this species was observed moving to the bottom of the rockpool in a series of leaps and wriggles, probably in an attempt to access water at the lowest point in the rockpool. On other occasions, stranded fish were seen to remain motionless for long periods with their opercula widely opened. Once these fish were returned to water they quickly swam to cover, indicating that such short-term aerial stranding does not pose a problem for their survival. These observations indicate that *G. elevata* may have the ability to breathe air, at least for short periods. A similar Californian species, *Girella nigricans*, behave in a similar way (Valle, 1989) and are capable of breathing air (Martin, 1993).

In contrast, permanent rockpool residents possessing specialised adaptations for such an existence cannot always be assumed to dominate the highest rockpools. Good examples are the Gobiesocids, *Aspasmogaster costatus* and *Aspasmogaster liorhyncha*, which
have a mucous body covering, which may reduce the risk of desiccation if stranded out of water. Furthermore, they possess a 'sucker' ventral fin, which may reduce the risk of fish being swept from lower rockpools where there is high wave action. Such morphological adaptations could enable these fishes to occupy rockpools at a wide range of elevations, although the inability of many Gobiesocids to breathe air (Eger, 1971; Cross, 1981; Martin, 1993) probably excluded these fishes from rockpools where there is a high chance of hypoxic conditions or the pool drying up completely.

Further complicating the issue of vertical distribution of fishes may be interspecific competition (Faria and Almada, 1999) and predation (Yoshiyama, 1981). Competition, or 'right of priority' for some microhabitats (Faria and Almada, 1999), can be best illustrated in the Tripterygiids, *Enneapterygius rufopileus* and *Lepidoblennius haplodactylus*, which appear highly adapted both morphologically and physiologically for intertidal life, like their air-breathing New Zealand relatives, *Acanthoclinus fuscus* and *Forsterygion nigripenne robustum* (Berger and Mayr, 1992; Hill *et al.* 1996). These species have characteristics that indicate that they could easily reside in high-level rockpools, such as strengthened pectoral fins for terrestrial locomotion and possibly air breathing (see Berger and Mayr, 1992; Hill *et al.* 1996), although their abundances may be influenced by the competitive goby, *Bathygobius cocosensis*, which is abundant in these habitats (see Chapter 6). With regards to predation, Yoshiyama (1981) found a consistent pattern among a number of taxa, where smaller fishes occupied rockpools of higher elevation because larger fish may be more conspicuous to avian and subtidal piscivores. However, this pattern was not evident in the present study, in that the size of fish from each abundant species did not differ dramatically among rockpool elevations,
perhaps with the exception of *Enneapterygius rufopileus* (see Fig. 27 and Kolmogorov-Smirnov test results).

Chapter 4 examined the variation in rockpool fish assemblages across various horizontal spatial scales. The present Chapter completed the documentation of spatial patterns of variation by exploring the distribution of rockpool fishes along the vertical plane in the intertidal zone. The following Chapter will begin to investigate the processes that underpin these observed patterns by manipulating the rockpool fish assemblages in an attempt to explore the recolonisation process of rockpools by fish after disturbance.
Chapter 6
Recolonisation of rockpools by fishes

INTRODUCTION

Rocky intertidal fishes are faced with many biotic (competition and food availability) and abiotic factors (temperature and salinity) which can influence their distribution and abundance (Gibson, 1982). Despite occupying a dynamic environment, the structure of fish assemblages in intertidal rockpools has been widely shown to remain persistent through time (Grossman, 1982; Collette, 1986, also see Chapter 4). The communities have also been shown to rapidly return to their original state after major or even catastrophic perturbations (Moring, 1996). Such resilience is less common among assemblages of invertebrates (Connell, 1976; Astles, 1993) since recolonisation of substrata is normally dependent upon successful larval settlement (Paine and Levin, 1981) (for definition of the terms resilience and recolonisation see Chapter 1). In contrast, fish can rapidly inhabit new and existing habitat by larval recruitment from the plankton (Willis and Roberts, 1996) but also by relocation of sub-adults and adults from adjacent rockpools (Beckley, 1985). Under natural conditions rockpools can be defaunated by events such as hurricanes (Moring, 1996) and, in some regions, seasonal freezing of rockpool water (Thomson and Lehner, 1976). These events can create new microhabitats or open existing ones for fish to colonise, and therefore have the potential to change fish assemblage structure.

Numerous studies have attempted to test natural spatial and temporal variation and recolonisation processes in rockpool fish assemblages (Beckley, 1985a, 2000; Polivka and Chotkowski, 1998). However, the widespread use of ichthyocides to sample
Recolonisation of rockpools by fishes has identified that sampling in itself can eliminate a large proportion of fishes present and create a disturbance far beyond the magnitude of disturbances experienced under natural conditions. This issue has led to many investigations of the recovery process in rockpool fish assemblages after disturbance. Such investigations have identified patterns in the rates of recovery, variation in species and demographic composition of recolonising fish assemblages (Polivka and Chotkowski, 1999), and homing abilities of many intertidal fishes (Williams, 1957; Green 1971, Yoshiyama et al. 1986).

Rockpools can be regarded as 'island' habitats (Underwood and Skilleter, 1996) among an inhospitable rocky landscape. Therefore, the balance between the immigration (recruitment and relocation) and emigration (mortality) of fishes after a disturbance may be predicted under the equilibrium theory of island biogeography (MacArthur and Wilson, 1967). That is after a period of time, the number of species and individuals in a defaunated rockpool can be expected to reach an asymptote where some type of carrying capacity is reached. Recolonisation of rockpools by fishes has been found to be a rapid process, beginning within days, or even hours, after defaunation (Collette, 1986). However, the time period needed for rockpools to be repopulated to pre-perturbation levels greatly varies from study to study. Unfortunately most studies have used only small sample sizes (<10 pools) and sampled at a range of time intervals (Table 20). The time when sampling is undertaken may also contribute to the species and demographic compositions of fishes in recolonised assemblages as recolonisation is both driven by juveniles settling from the plankton, which is dependent on the breeding times of individual species (Willis and Roberts, 1996; Pfister, 1997), and adult fish relocating from nearby rockpools (Beckley, 1985).
Although generalisations regarding fish recolonisation patterns can be proposed from the literature, it is important to note that the majority of published studies have two major drawbacks (Table 20). First, researchers sample fish using an anaesthetic or ichthyocide which may affect subsequent catches (Yoshiyama et al. 1986) and may result in fish assemblages never reaching pre-perturbation conditions (see Mok and Wen, 1985). Second, small samples sizes, poor experimental design, a lack of spatial and temporal replication, as well as limited use of powerful statistical analyses, have meant that reliable conclusions can rarely be drawn from data. A well designed experiment requires large numbers of rockpools and quantitative comparisons using statistical analyses.

Table 20. Summary of studies examining recolonisation of rockpools by fishes. Location of study, number of rockpools studied, sampling method used, time between sampling events, and the suggested time needed between sampling for rockpools to recolonise to pre-perturbation levels are listed.

<table>
<thead>
<tr>
<th>Country</th>
<th>Number of pools</th>
<th>Sampling Method</th>
<th>Time between sampling</th>
<th>Recolonisation time</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>U.S.A.</td>
<td>24</td>
<td>Ichthyocide</td>
<td>4, 8, 12 weeks</td>
<td>&lt;1 month</td>
<td>Cross (1981)</td>
</tr>
<tr>
<td>U.S.A.</td>
<td>21</td>
<td>Ichthyocide</td>
<td>1-90 day</td>
<td>2-3 months</td>
<td>Polivka &amp; Chotkowski (1998)</td>
</tr>
<tr>
<td>U.S.A.</td>
<td>1</td>
<td>Ichthyocide</td>
<td>43 day</td>
<td>&gt;43 days</td>
<td>Matson et al. (1986)</td>
</tr>
<tr>
<td>U.S.A.</td>
<td>6</td>
<td>Ichthyocide</td>
<td>1 day-2 weeks</td>
<td>&gt;2 weeks</td>
<td>Mistry et al. (1989)</td>
</tr>
<tr>
<td>U.S.A.</td>
<td>2</td>
<td>Ichthyocide</td>
<td>2 weeks</td>
<td>&lt;1 month</td>
<td>Collette (1986)</td>
</tr>
<tr>
<td>Mexico</td>
<td>2</td>
<td>Ichthyocide</td>
<td>3-14 months</td>
<td>&lt;3 months</td>
<td>Thomson &amp; Lehner (1976)</td>
</tr>
<tr>
<td>New Zealand</td>
<td>4</td>
<td>Ichthyocide</td>
<td>2 &amp; 5 months</td>
<td>1-3 months</td>
<td>Willis &amp; Roberts (1996)</td>
</tr>
<tr>
<td>Australia</td>
<td>12</td>
<td>Ichthyocide</td>
<td>1 month</td>
<td>&lt;1 month</td>
<td>Wilson (1989)</td>
</tr>
<tr>
<td>Australia</td>
<td>1</td>
<td>Ichthyocide</td>
<td>1 year</td>
<td>&lt;1 year</td>
<td>Lardner et al. (1993)</td>
</tr>
<tr>
<td>Australia</td>
<td>12</td>
<td>Ichthyocide</td>
<td>&lt;2, 7, 10 weeks</td>
<td>&lt;2 - &gt;10 weeks</td>
<td>Silberschneider &amp; Booth (2001)</td>
</tr>
<tr>
<td>South Africa</td>
<td>3</td>
<td>Ichthyocide</td>
<td>1, 3, 6 months</td>
<td>&lt;3 months</td>
<td>Beckley (1985a)</td>
</tr>
<tr>
<td>South Africa</td>
<td>12-16</td>
<td>Ichthyocide</td>
<td>1 month</td>
<td>&lt;1 month</td>
<td>Prochazka (1996)</td>
</tr>
<tr>
<td>Taiwan</td>
<td>1</td>
<td>Ichthyocide</td>
<td>3-4 months</td>
<td>&lt;3 months</td>
<td>Lee (1980)</td>
</tr>
<tr>
<td>Taiwan</td>
<td>&gt;10</td>
<td>Ichthyocide</td>
<td>3 months</td>
<td>3-6 months</td>
<td>Mok &amp; Wen (1985)</td>
</tr>
<tr>
<td>Barbados</td>
<td>19</td>
<td>Anaesthetic</td>
<td>1 year</td>
<td>&lt;1 year</td>
<td>Mahon &amp; Mahon (1994)</td>
</tr>
<tr>
<td>Portugal</td>
<td>43</td>
<td>Dip nets</td>
<td>15 &amp; 30 days</td>
<td>2 weeks</td>
<td>Faria &amp; Almada (1999)</td>
</tr>
</tbody>
</table>
Chapter 6 Recolonisation of Rockpools by Fishes

The present Chapter investigates some of the processes that underpin patterns observed in Chapter 4. The major factors that may control the structure of rockpool fish assemblages are i) habitat characteristics ii) larval recruitment and iii) disturbance. The latter can create new niches or open existing habitats to be recolonised with new individuals or species from a nearby source or again, through recruitment. In Chapter 4, the process of recruitment was documented to operate independently of disturbance. However, the present Chapter explores the role of disturbance in structuring rockpool fish assemblages. The aims of this Chapter were to determine: i) the period required for intertidal rockpools to recover to pre-perturbation levels, ii) which fish species were responsible for recolonising rockpools, iii) if recolonisation patterns differed across temporal and spatial scales, and iv) whether there were demographic consequences of disturbance in rockpools and whether interspecific or intraspecific competition is a contributing factor to contributing fish assemblage structure.

MATERIALS AND METHODS

Experimental design

Spatial and temporal variation in fish recolonisation patterns were investigated in three separate studies. Two short-term recolonisation studies were undertaken in spring-summer and autumn-winter (herein referred to as spring and autumn studies, respectively), and a long-term recolonisation study spanned the entire 12 month period. The long-term study was conducted to serve as a 'control' experiment for the short-term experiments. That is, variability in fish assemblages in rockpools given a significant time to recolonise (i.e. 6 months) could be compared to those defaunated more frequently. Rockpools for each of the three studies were selected at the same four sites at Bass Point, NSW, which are named Maloney's Bay, The Chair, Gravel Loader and
Beaky Bay (Fig. 28; Plate 3). Each of the four sites are separated by around 1 km. Rockpools were selected at each site (50-200 m apart) based on similar physical parameters (i.e. volume, surface area and substrate type) and particularly, their vertical elevation on the rock platform. It was considered that higher pools might have less chance of fish recolonisation because they are less frequently inundated by seawater. Every effort was made to select pools located in the mid-intertidal zone (1-1.5 m above MLLW) and, although pools were visually similar, they varied in volume, ranging from 762 to 2160 l (or 0.76-2.16 m³). The bottom of the rockpools consisted of pebbles, cobbles and small boulders.

For the short-term studies, four rockpools were sampled at each of the four sites. In the spring study (beginning 7 September 1999), they were then resampled 1 week, 1 month and 3 months after the preceding sampling date. This study ended on 8 February 2000, after a period of 5 months. After this date a period of at least three months was given for pools to re-establish fish assemblages before beginning the autumn study on 15 May 2000. Rockpools were sampled in exactly the same manner as for the spring study, with sampling ending on 17 September 2000. For each study 64 samples were taken, a total of 128 samples for the short-term studies. It is important to note that although every effort was made to resample pools after exactly the same time intervals this was not possible due to, daily time and height of tides and wave heights. For example, for the '1 week' samples, the number of days between samples was actually between 7 and 10 days.

For the long-term study, four different rockpools were sampled at the same four sites. Rockpools were initially sampled on 22 September 1999 and then resampled twice at
intervals of six months (20 April 2000 and 11 September 2000). A total of 48 samples were taken for this study.

Figure 28. Map illustrating the four sampling sites at Bass Point and the location of the study location in the Illawarra region, New South Wales, Australia.
Plate 3. Photograph showing the four sampling sites at Bass Point, New South Wales, Australia. As can be seen by the white water caused by wave action, Maloney's Bay and The Chair sites are on exposed shores, while the Gravel Loader and Beaky Bay are on more sheltered shores (Photograph from Smith, 2001).

Statistical analyses

In the present studies the same pools were repeatedly sampled at intervals that may not allow complete replenishment of fish assemblages. This violates the assumption of independence among sampling times which is necessary for using a general factorial ANOVA (Underwood, 1997). As a result, a repeated-measures ANOVA (RM-ANOVA) was used, which takes into account an expected correlation in values in successive samples of the same experimental subject (Underwood, 1997). Since the recolonisation study was comprised of short-term and long-term experiments, it was
necessary to perform two RM-ANOVAs (SPSS Version 6.1). Both analyses tested for differences in the numbers of species and individuals between sampling intervals (within subjects factor) and sites (among subjects factor). For the short-term study a third factor of season (i.e. spring or autumn; among subjects factor) was added. All factors were considered fixed. Assumptions of sphericity of the variance-covariance matrix were tested using Mauchly's criterion and if violated, $F$ tests were performed using Greenhouse-Geisser adjusted degrees of freedom. In cases where Mauchly's criterion was violated, the multivariate approach of performing RM-ANOVA were not undertaken as they are generally less powerful than the univariate approach (Nielsen, 2001). Simple within subjects contrasts and Student-Newman-Keuls (SNK) tests were used for \textit{a posteriori} comparisons among means for within subjects and among subjects factors respectively.

Non-metric multidimensional scaling (nMDS) was used to examine similarities in fish assemblages between sampling intervals, sites and degree of exposure. Total abundances of each species were fourth-root transformed to reduce the influence of highly abundant taxa, and a similarity matrix among samples constructed using the Bray-Curtis similarity coefficient (Clarke, 1993). A series of one factor ANOSIMs were used to determine whether fish assemblages differed statistically among sampling intervals for each site within each of the three studies. SIMPER was then used to determine which species were responsible for significant differences among \textit{a priori} groups. Detailed descriptions of these methods are given in Chapter 4.


**Competition**

It was considered important to determine whether inter- and intra-specific competition was a major factor determining species composition during recolonisation. This was investigated by performing multiple regression analyses of the numbers of fish for each species as a function of environmental variables and then saving the residuals, which provided the variance unexplained by environmental variables and which can be a reflection of heterospecific competition (Pfister, 1995). It is important to note that unexplained variance could also be explained by other sources such as unmeasured variables, natural heterogeneity in fish numbers and associated with food organisms. The residuals for each species were then regressed against each other in a separate multiple regression analysis. Determining whether competition existed within and among recolonising species was investigated by calculating competition coefficients between the three most numerically dominant species using the dynamic regression model of Pfister (1995). Significant negative competition coefficients imply intraspecific or interspecific competition, whereas significant positive competition coefficients can imply gregarious or mutualistic behaviour within or among species. A dynamic regression model was used instead of a static model because it best examines whether variation in the abundance of one species is associated with variation in another species using time series data (Pfister, 1995). The dynamic regression model is based on Lotka-Volterra differential equations and can be expressed as:

\[ N_i(t + 1) = N_i(t) \exp\{r[K_1 - N_i(t) - \alpha_{2i}N_2(t)]K_1\} \]

This can also be expressed as:

\[ \ln[N_i(t + 1)/N_i(t)] = r[K_1 - N_i(t) - \alpha_{2i}N_2(t)]/K_1, \]
where \( N_1 \) and \( N_2 \) are population sizes of species 1 and 2, respectively, \( K_1 \) is the carrying capacity of species 1 and \( \alpha_{21} \) is the competition coefficient between species 1 and 2.

RESULTS

**Numbers of species and individuals**

A total of 3658 fish from 38 species and 19 families were caught in 176 samples taken from 32 rockpools at Bass Point between 7 September 1999 and 22 September 2000 (Table 21).

For the short-term studies, RM-ANOVA revealed that the mean number of species differed between sampling intervals and sites (Table 22). With respect to the site factor, there were significantly more species caught at Beaky Bay compared to the other three sites, which in turn did not differ (SNK test). When investigating the time interval factor more closely, only the 1 week samples accounted for significantly fewer species than the initial samples (Simple Within Subjects Contrasts; Fig. 29). However, the mean number of species caught in the 1 and 3 month samples did not differ from the initial samples, which was consistent at all sites (Simple Within Subjects Contrasts; Fig. 29).

RM-ANOVA revealed that the mean number of individuals differed between sampling intervals and sites, although there was also a significant time x site interaction (Table 22). A close investigation of the significant interval x site interaction, with primary interest in the interval factor, revealed that the number of individuals in the initial samples did not significantly differ from samples taken after three months at the exposed sites (Maloney's Bay and The Chair), but they did at sheltered locations (The
Loader and Beaky Bay) (Fig. 29). It appeared that the Loader and Beaky Bay sites initially supported unusually high numbers of individuals. This may give the impression that significantly fewer individuals were being caught in subsequent samples (Fig. 29).

For the long-term study, RP-ANOVA revealed a significant difference among sampling times for number of individuals but not number of species (Table 23). The significant difference in the mean number of individuals was due to fewer individuals being caught in the 12 month samples when fish numbers were pooled for all sites (Fig. 30).

Table 21. Number of fish for each species caught from rockpools at four sites at Bass Point, NSW during short-term (spring and autumn) and long-term recolonisation studies conducted between 7 September 1999 and 22 September 2000.

<table>
<thead>
<tr>
<th>Family</th>
<th>Scientific name</th>
<th>Spring study</th>
<th>Autumn study</th>
<th>Long-term study</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Muraenidae</td>
<td>Gymnothorax prasinus</td>
<td>41</td>
<td>13</td>
<td>16</td>
<td>70</td>
</tr>
<tr>
<td></td>
<td>Gymnothorax sp.</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Plotosidae</td>
<td>Cnidoglanis macrocephalus</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Gobiesocidae</td>
<td>Alabes dorsalis</td>
<td>-</td>
<td>2</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Aspasmogaster costatus</td>
<td>134</td>
<td>41</td>
<td>65</td>
<td>240</td>
</tr>
<tr>
<td></td>
<td>Aspasmogaster liorhyncha</td>
<td>5</td>
<td>20</td>
<td>4</td>
<td>29</td>
</tr>
<tr>
<td>Sygnathidae</td>
<td>Sygnathidae sp.</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Scorpaenidae</td>
<td>Scorpaena cardinalis</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Serranidae</td>
<td>Acanthistius ocellatus</td>
<td>33</td>
<td>35</td>
<td>16</td>
<td>84</td>
</tr>
<tr>
<td></td>
<td>Epinephelus daemelii</td>
<td>-</td>
<td>2</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>Plesiopidae</td>
<td>Trachinops taeniatus</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Girellidae</td>
<td>Girella elevata *</td>
<td>210</td>
<td>93</td>
<td>74</td>
<td>377</td>
</tr>
</tbody>
</table>
Table 21 continued.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Count 1</th>
<th>Count 2</th>
<th>Count 3</th>
<th>Count 4</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Scorpididae</strong></td>
<td><em>Microcanthus strigatus</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Scorps lineolatus</em></td>
<td>94</td>
<td>10</td>
<td>16</td>
<td>120</td>
</tr>
<tr>
<td><strong>Pomacentridae</strong></td>
<td><em>Abudefu vaigiensis</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Parma microlepis</em></td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><strong>Chironemidae</strong></td>
<td><em>Chironemus marmoratus</em></td>
<td>30</td>
<td>11</td>
<td>10</td>
<td>51</td>
</tr>
<tr>
<td><strong>Mugilidae</strong></td>
<td><em>Myxxus elongatus</em></td>
<td>3</td>
<td>4</td>
<td>-</td>
<td>7</td>
</tr>
<tr>
<td><strong>Labridae</strong></td>
<td><em>Halichoeres nebulosus</em></td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Notolabrus gymnogenis</em></td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><strong>Blennidae</strong></td>
<td><em>Parablennius intermedius</em></td>
<td>102</td>
<td>78</td>
<td>47</td>
<td>227</td>
</tr>
<tr>
<td></td>
<td><em>Isitiblennius meleagris</em></td>
<td>8</td>
<td>10</td>
<td>4</td>
<td>22</td>
</tr>
<tr>
<td><strong>Tripterygiidae</strong></td>
<td><em>Lepidoblennius haplodactylus</em></td>
<td>22</td>
<td>26</td>
<td>22</td>
<td>70</td>
</tr>
<tr>
<td></td>
<td><em>Norfolktia clarkei</em></td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td><em>Enneapterygus rufopileus</em></td>
<td>354</td>
<td>188</td>
<td>157</td>
<td>699</td>
</tr>
<tr>
<td><strong>Clinidae</strong></td>
<td><em>Heteroclinus fasciatus</em></td>
<td>59</td>
<td>48</td>
<td>38</td>
<td>145</td>
</tr>
<tr>
<td></td>
<td><em>Heteroclinus nasutus</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Heteroclinus heptaeolus</em></td>
<td>24</td>
<td>-</td>
<td>1</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td><em>Heteroclinus johnstoni</em></td>
<td>-</td>
<td>2</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td><em>Heteroclinus whiteleggi</em></td>
<td>138</td>
<td>66</td>
<td>39</td>
<td>243</td>
</tr>
<tr>
<td></td>
<td><em>Ophiclinus gracilis</em></td>
<td>15</td>
<td>16</td>
<td>6</td>
<td>37</td>
</tr>
<tr>
<td><strong>Gobiidae</strong></td>
<td><em>Bathygobius cocosensis</em></td>
<td>583</td>
<td>293</td>
<td>285</td>
<td>1161</td>
</tr>
<tr>
<td></td>
<td><em>Callogobius depressus</em></td>
<td>6</td>
<td>2</td>
<td>7</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td><em>Callogobius mucosus</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Prioepis cincta</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td><em>Gobiidae sp.</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><strong>Microdesmidae</strong></td>
<td><em>Gunnellichthys monostigma</em></td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><strong>Tetraodontidae</strong></td>
<td><em>Tetraodontidae sp.</em></td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td></td>
<td>1880</td>
<td>968</td>
<td>810</td>
<td>3658</td>
</tr>
</tbody>
</table>

(*) = Species of commercial and/or recreational significance.
Table 22. Results of repeated-measures ANOVAs testing for significant differences in number of species and number of individuals (per m\(^3\)) caught at Bass Point during two short-term recolonisation studies among sampling intervals (time) (within subjects factor), seasons (spring and autumn) and sites (among subjects factors). Both numbers of species and individuals data were \(\log_{10}(x+1)\) transformed before analysis, which removed heteroscedasticity in the data. Mauchly's criterion for sphericity of variances was violated for number of species \((P=0.025)\) so analysis was performed using Greenhouse-Geisser adjusted degrees of freedom. Mean squares (MS) and significance levels are shown and significant results are in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>Number of species</th>
<th>Number of fish</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>MS</td>
</tr>
<tr>
<td><strong>Among subjects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season (SE)</td>
<td>1</td>
<td>14.94</td>
</tr>
<tr>
<td>Site (S)</td>
<td>3</td>
<td>46.80**</td>
</tr>
<tr>
<td>S x SE</td>
<td>3</td>
<td>3.66</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>9.38</td>
</tr>
<tr>
<td><strong>Within subjects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time (T)</td>
<td>2.16</td>
<td>18.03***</td>
</tr>
<tr>
<td>T x S</td>
<td>6.47</td>
<td>2.93</td>
</tr>
<tr>
<td>T x SE</td>
<td>2.16</td>
<td>2.54</td>
</tr>
<tr>
<td>T x S x SE</td>
<td>6.47</td>
<td>1.89</td>
</tr>
<tr>
<td>Residual</td>
<td>51.75</td>
<td>1.41</td>
</tr>
<tr>
<td>Mauchly's criterion (W)</td>
<td>0.569*</td>
<td></td>
</tr>
</tbody>
</table>

\* = \(P<0.05\); ** = \(P<0.01\); *** = \(P<0.001\).

Table 23. Results of repeated-measures ANOVAs testing for significant differences in number of species and number of individuals (per m\(^3\)) caught at Bass Point during the long-term recolonisation study among sampling intervals (within subjects factor) and sites (among subjects factors). Both numbers of species and individuals data were \(\log_{10}(x+1)\) transformed before analysis, which removed heteroscedasticity in the data. Mean squares (MS) and significance levels are shown and significant results are in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>Number of species</th>
<th>Number of fish</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>MS</td>
</tr>
<tr>
<td><strong>Among subjects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site (S)</td>
<td>3</td>
<td>86.93</td>
</tr>
<tr>
<td>Residual</td>
<td>12</td>
<td>27.49</td>
</tr>
<tr>
<td><strong>Within subjects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time (T)</td>
<td>2</td>
<td>3.26</td>
</tr>
<tr>
<td>T x S</td>
<td>6</td>
<td>4.44</td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>2.84</td>
</tr>
<tr>
<td>Mauchly criterion (W)</td>
<td>0.622</td>
<td></td>
</tr>
</tbody>
</table>

\* = \(P<0.05\); ** = \(P<0.01\); *** = \(P<0.001\).
Figure 29. Mean (±SE) number of species and individuals (per m$^3$) caught in rockpools from four sites at Bass Point, NSW between 7 September 1999 to 17 September 2000 during the short-term recolonisation studies (combined for spring and autumn) between sampling intervals separated by 1 week, 1 month and 3 months. Key to sites: Maloney’s Bay (MB), The Chair (TC), Gravel Loader (GL) and Beaky Bay (BB).
### Figure 30

Mean (±SE) number of species and fish (per m$^3$) caught in rockpools at Bass Point, NSW between 22 September 1999 to 11 September 2000 (pooled for all four sites) during the long-term recolonisation study between sampling intervals separated by six months.
Variation in abundance of major recolonising species

The rank abundances of the numerically dominant species were consistent for *Bathygobius cocosensis* and *Enneapterygius rufopileus*, among sampling all intervals for all studies, even though their relative abundances varied considerably (Table 24). In contrast, the ranks of the least common of the six species, namely *Heteroclinus whiteleggi*, *Parablennius intermedius*, *Aspasmogaster costatus*, varied considerably among sampling intervals for each study. This probably reflects their generally low abundances as differences in ranks can be a result of a few incidences of low individual counts.

The mean number of the six most abundant recolonising species showed considerable variability in space and time. For the short-term study, each of these species significantly differed for the main effects of site and time or at least for higher order interactions containing these effects (Table 25). No definitive conclusions can be made as to the effects of defaunation on these species as short-term recolonisation patterns for each species was clearly variable within and among seasons (Fig. 31). However, the mean number of fish was generally highest in initial samples and lowest in the '1 week' samples at each site for the majority of numerically dominant species. For the long-term study only the mean number of *B. cocosensis* and *E. rufopileus* differed among sampling times (Table 25), and this was due to lower numbers being caught in the 12 month samples (Figure 31).
Table 24. Ranked abundances of the six most abundant species overall for each sampling interval in the spring, autumn and long-term experiments. Total numbers of fish caught during each sampling occasion from 16 rockpools from four sites are shown in parentheses. 1=Initial samples; 2=samples taken after 1 week; 3=samples taken after 1 month; 4=samples taken after 3 months. Species having the same rank are denoted by =.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spring Study</th>
<th></th>
<th>Autumn Study</th>
<th></th>
<th>Long-term Study</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Bathygobius cocosensis</td>
<td>1 (153)</td>
<td>1 (69)</td>
<td>1 (73)</td>
<td>1 (59)</td>
<td>2 (81)</td>
<td>1 (20)</td>
</tr>
<tr>
<td>Enneapterygius rufopileus</td>
<td>2 (109)</td>
<td>2 (50)</td>
<td>4 (33)</td>
<td>2 (46)</td>
<td>1 (84)</td>
<td>2 (12)</td>
</tr>
<tr>
<td>Girella elevata</td>
<td>3 (46)</td>
<td>3 (36)</td>
<td>3 (40)</td>
<td>3 (38)</td>
<td>3 (34)</td>
<td>3 (10)</td>
</tr>
<tr>
<td>Heteroclinus whiteleggi</td>
<td>6 (11)</td>
<td>=4 (7)</td>
<td>2 (51)</td>
<td>5 (35)</td>
<td>6 (9)</td>
<td>=4 (5)</td>
</tr>
<tr>
<td>Parablennius intermedius</td>
<td>4 (27)</td>
<td>=4 (7)</td>
<td>6 (10)</td>
<td>6 (23)</td>
<td>=4 (14)</td>
<td>=4 (5)</td>
</tr>
<tr>
<td>Aspasmogaster costatus</td>
<td>5 (21)</td>
<td>=4 (7)</td>
<td>5 (13)</td>
<td>4 (36)</td>
<td>=4 (14)</td>
<td>6 (3)</td>
</tr>
</tbody>
</table>
Table 25. Results of repeated-measures ANOVAs testing for significant differences in number of individuals (per m$^3$) representing the six most abundant species caught at Bass Point during the short-term recolonisation studies among sampling intervals (within subjects factor) and sites and seasons (among subjects factors). Data were $\log_{10}(x+1)$ transformed before analysis, which removed heteroscedasticity in the data. Mauchly's criterion for sphericity of variances was violated ($P<0.001$) for species denoted by (G) so analysis was performed using Greenhouse-Geisser adjusted degrees of freedom. Mean squares and significance levels are shown and significant results are in bold. Degrees of freedom are shown in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Among subjects factors</th>
<th>Within subjects factors</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Season (Se) (1) Site (S) (3) Se x S (3) Residual (24)</td>
<td>Time (T) (3) Se x T (3) S x T (9) Se x S x T (9) Residual (72)</td>
</tr>
<tr>
<td>Bathygobius cocosensis$^G$</td>
<td>5.20 24.50*** 3.62 2.18</td>
<td>43.99*** 2.21 10.68** 3.22 1.70</td>
</tr>
<tr>
<td>Enneapterygius rufopileus$^G$</td>
<td>0.66 4.38*** 0.01 0.17</td>
<td>0.70*** 0.05 0.08* 0.07* 0.04</td>
</tr>
<tr>
<td>Girella elevata</td>
<td>0.22 0.49 0.03 0.28</td>
<td>0.12** 0.07 0.05* 0.07** 0.03</td>
</tr>
<tr>
<td>Heteroclinus whiteleggi$^G$</td>
<td>12.09 20.77* 1.65 4.90</td>
<td>18.99*** 6.61* 4.31* 4.22 1.72</td>
</tr>
<tr>
<td>Parablennius intermedius</td>
<td>0.00 4.85* 0.20 1.20</td>
<td>7.88** 0.20 1.92 0.29 1.07</td>
</tr>
<tr>
<td>Aspasmogaster costatus</td>
<td>0.37 0.54* 0.15 0.10</td>
<td>0.11* 0.09 0.03 0.07* 0.03</td>
</tr>
</tbody>
</table>

* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$.

Greenhouse-Geisser degrees of freedom used for within subjects factors where Mauchly's criterion for sphericity of variances was violated ($P<0.001$):

Time (T) = 1.55; Se x T = 1.55; S x T = 4.64; Se x S x T = 4.64; Residual = 34.14
Figure 31. Mean (±SE) number of fish from the eight most abundant species caught from rockpools at four sites during short-term (spring and autumn) (4 sampling intervals) and long-term (3 sampling intervals) recolonisation studies undertaken between 7 September 1999 and 22 September 2000. Key to sites: Maloney’s Bay (MB), The Chair (TC), Gravel Loader (GL) and Beaky Bay (BB).
Figure 31 continued.
**Fish assemblage structure**

No clear patterns emerged in the nMDS ordination plots with the exception of separation of the '1 week' samples from all other samples at Beaky Bay during the autumn study (Fig. 32 a-c). ANOSIM supported this visual interpretation of ordination plots and revealed that fish assemblages did not significantly differ among sampling times at any of the four sites for the spring and long-term studies (Table 26). This was due to *Enneapterygius rufopileus*, *Bathygobius cocosensis*, *Heteroclinus fasciatus* and *Parablennius intermedius* being common to all samples (SIMPER analysis). For the autumn study, the results of ANOSIM complemented those of RM-ANOVA in that significant differences among sampling intervals were only detected at Beaky Bay (Table 26). At this site the initial samples and one week samples differed in their fish assemblages, which was due to higher numbers of *Girella elevata* and *B. cocosensis* in the initial samples (SIMPER analysis).

**Table 26.** Results of ANOSIM testing for differences in fish assemblage structure among sampling intervals at four sites at Bass Point during the spring, autumn and long-term recolonisation studies. Significant results are shown in bold.

<table>
<thead>
<tr>
<th>Site</th>
<th>Spring</th>
<th>Autumn</th>
<th>Long-term</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>p value</td>
<td>R</td>
</tr>
<tr>
<td>Maloney's Bay</td>
<td>0.002</td>
<td>0.474</td>
<td>0.029</td>
</tr>
<tr>
<td>The Chair</td>
<td>0.185</td>
<td>0.057</td>
<td>0.014</td>
</tr>
<tr>
<td>Gravel Loader</td>
<td>0.083</td>
<td>0.165</td>
<td>0.027</td>
</tr>
<tr>
<td>Beaky Bay</td>
<td>0.025</td>
<td>0.383</td>
<td>0.726</td>
</tr>
</tbody>
</table>

* = *P*<0.05; ** = *P*<0.01; *** = *P*<0.001.
Figure 32. Non-metric MDS plots of fish assemblages from four sites at Bass Point comparing initial samples with those taken after 1 week, 1 month and 3 months during a) spring and b) autumn short-term studies, and after 6 months and 12 months during c) the long-term study. Each symbol represents a single rockpool sample. Stress values are shown.
Chapter 6 Recolonisation of rockpools by fishes

Length-frequency distributions and competition

Removal of fishes from rockpools did not have any apparent effects on the length frequency distributions for at least the three species for which there was sufficient data (B. cocosensis, E. rufopileus and G. elevata). Rockpools were mainly recolonised by sub-adults and adults for each species in all three studies (Figs 33, 34 and 35). However, cohorts of small juveniles (15-30 mm) were evident in the 3 month samples during spring and the initial autumn studies (February to June), which could then be clearly identified in subsequent samples (Figs 33, 34 and 35). Unfortunately, the less dominant recolonising species, namely Parablennius intermedius, Aspasmogaster costatus and Heteroclinus whiteleggi, were caught in too few numbers to ascertain the impacts of defaunation on their demography.

The dynamic regression model (equation 1) revealed highly significant negative competition coefficients for Bathygobius cocosensis upon Enneapterygius rufopileus and Girella elevata. These values are consistent with interspecific competition, although the significant negative competition coefficient on itself is indicative of significant intraspecific competition for this species (Table 27). In contrast, significant positive competition coefficients were evident for both Enneapterygius rufopileus and Girella elevata upon B. cocosensis, which may indicate mutualistic or gregarious behaviour of these species. However, there was no evidence for significant interspecific competition between Enneapterygius rufopileus and Girella elevata, but there were positive competition coefficients for each of these species (Table 27).
Figure 33. Length-frequency distributions (in 2 mm intervals) for Bathygobius cocosensis caught in the initial samples and after 1 week, 1 month and 3 months pooled for all sites during a) spring and b) autumn short term recolonisation studies, and after 6 months and 12 months for c) the long-term recolonisation study conducted between 7 September 1999 and 22 September 2000. Samples sizes are shown.
Figure 34. Length-frequency distributions (in 2 mm intervals) for *Enneapterygius rufopileus* caught in the initial samples and after 1 week, 1 month and 3 months pooled for all sites during a) spring and b) autumn short term recolonisation studies, and after 6 months and 12 months for c) the long-term recolonisation study conducted between 7 September 1999 and 22 September 2000. Samples sizes are shown.
Figure 35. Length-frequency distributions (in 2 mm intervals) for *Girella elevata* caught in the initial samples and after 1 week, 1 month and 3 months pooled for all sites during a) spring and b) autumn short term recolonisation studies, and after 6 months and 12 months for c) the long-term recolonisation study conducted between 7 September 1999 and 22 September 2000. Samples sizes are shown.
Table 27. Results of dynamic regression models involving numbers of the three most numerically abundant recolonising species, *Bathygobius cocosensis* (*Nc*), *Enneapterygus rufopileus* (*Nr*) and *Girella elevata* (*Ne*) censused from 16 rockpools. The variable *N* refers to the number or density of each fish species per rockpool. *F* ratios, *r*² and *P* values are shown. Significant results are shown in bold.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th><em>Nc</em>&lt;sub&gt;t+1&lt;/sub&gt;/<em>Nc</em>&lt;sub&gt;t&lt;/sub&gt;</th>
<th><em>Nr</em>&lt;sub&gt;t+1&lt;/sub&gt;/<em>Nr</em>&lt;sub&gt;t&lt;/sub&gt;</th>
<th><em>Ne</em>&lt;sub&gt;t+1&lt;/sub&gt;/<em>Ne</em>&lt;sub&gt;t&lt;/sub&gt;</th>
<th><em>F</em></th>
<th><em>r</em>²</th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>ln (<em>Nc</em>&lt;sub&gt;t+1&lt;/sub&gt;/<em>Nc</em>&lt;sub&gt;t&lt;/sub&gt;)</td>
<td>-0.798***</td>
<td>0.215***</td>
<td>0.606***</td>
<td>39.037</td>
<td>0.520</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>ln (<em>Nr</em>&lt;sub&gt;t+1&lt;/sub&gt;/<em>Nr</em>&lt;sub&gt;t&lt;/sub&gt;)</td>
<td>-0.246**</td>
<td>0.194*</td>
<td>0.087</td>
<td>3.721</td>
<td>0.094</td>
<td>0.014</td>
</tr>
<tr>
<td>ln (<em>Ne</em>&lt;sub&gt;t+1&lt;/sub&gt;/<em>Ne</em>&lt;sub&gt;t&lt;/sub&gt;)</td>
<td>-0.124**</td>
<td>0.002</td>
<td>0.215**</td>
<td>5.029</td>
<td>0.123</td>
<td>0.003</td>
</tr>
</tbody>
</table>

* = *P*<0.05; ** = *P*<0.01; *** = *P*<0.001.
DISCUSSION

The present study has revealed that rockpool fish assemblages at Bass Point were resilient and many can quickly return to their original state within weeks of defaunation. Not only does this provide an insight into the ecology of rockpool fish assemblages, but this information may also provide a basis for future sampling protocols where the confounding effects of sampling may be minimised. A period of one week between sampling the same rockpool appears to be unsuitable, as this does not permit adequate recolonisation of all species. Intervals of between one and three months appear suitable for recolonisation of rockpools at exposed localities where there may be greater water exchange between the rockpool and the sea, thus allowing fish greater opportunity to recolonise. At sheltered locations, rockpools may require more than three months for fish assemblages to reach pre-perturbation levels. Therefore, it can be proposed that in southeastern Australia between at least three months is an adequate period before resampling the same rockpool regardless the wave exposure at a particular location. This should not provide a foundation for future studies using other methods, such as anaesthetics or ichthyocides. The possible residual effect of these sampling methods is an additional factor that may complicate fish recolonisation patterns and certainly requires additional investigation.

Spatial variability in fish recolonisation patterns were not definitive with regards to species composition since samples were generally widely dispersed in nMDS ordination plots (generally stress values were low (<0.2) indicating that high variability in fish assemblages at the level of individual rockpools is probably responsible for patterns observed). However, spatial variability in fish recolonisation patterns appeared to be dependent to some extent on exposure of sites to predominant swell (see Chapter 4).
There is considerable evidence to suggest that wave exposure can affect the distribution of intertidal fishes (Gibson, 1972; Ibáñez et al. 1989), although there is apparently no study which has investigated this effect in relation to fish recolonisation in rockpools. In the present study, recolonisation appears more rapid at sites located on wave-exposed shorelines of Bass Point (The Chair and Maloney’s Bay). These sites may receive a more frequent and greater magnitude of water exchange with the sea than more sheltered sites (The Loader and Beaky Bay sites). This may allow fish greater opportunity to locate denuded pools than at sheltered sites where lower wave action may not provide access to all rockpools.

In contrast, fish recolonisation patterns were not influenced by the time of year that rockpools were defaunated in either short-term or long-term studies. The number of species and individuals consistently returned to pre-perturbation levels within one month, which may partially be a consequence of the relatively small numbers of species that are normally found in rockpools at any given time (see Chapter 4). In such situations a significant differences could only occur if large-scale changes in abundances were recorded. The lack of temporal variation in recolonisation rates was surprising, as recolonisation was expected to be more rapid during summer, when the larvae of residents and warm water transients were expected to be available for settlement (Beckley, 1985; Willis and Roberts, 1996). It seems that recruitment was not the major mechanism driving fish recolonisation in the present study, as the majority of recolonisers were sub-adults and adults, which would have ‘relocated’ from nearby rockpools.
The movement of benthic fishes from adjacent rockpools also appears to control the resilience of rockpool fish assemblages. Therefore, the composition of species in newly recolonised rockpools is probably dependent upon the relative abundances of species in nearby rockpools (for a similar coral reef example see Sale and Dybdahl, 1975). Species having the highest local abundances, such as *Bathygobius cocosensis* and *Enneapterygius rufopileus*, are therefore more likely to be the primary recolonisers as vacant habitats have a higher probability of being located by these species during high tide excursions throughout the intertidal. These species are also versatile and can exploit a range of microhabitats, and as a result, can occupy almost any rockpool within the intertidal zone. This is particularly true for *B. cocosensis* (see Chapter 3). In contrast, less abundant species such as *Heteroclinus whiteleggi* and *Parablennius intermedius* often occupy more specific, and perhaps less abundant, microhabitats that may require longer periods to locate than more abundant habitats, such as cobble-covered substratum.

The structure of multispecies assemblages can generally be regarded as being regulated by either deterministic or stochastic processes (see Grossman, 1982). Assemblages regulated by deterministic or equilibrium processes generally occur in environments where conditions are constant or fluctuate predictably over time. The structure of these assemblages is often predictable, that is, the composition of species and their relative abundance are persistent through time. Such stability of assemblages structure can be maintained through a number of factors including partitioning of resources in finite supply (Schoener, 1974; Behrents, 1987); and, interspecific competition that prevents any single species being competitively dominant (Buss and Jackson, 1979). In contrast, assemblages regulated by stochastic, or non-equilibrial, processes generally exist in...
environments that are unpredictable. Here, the resources are available on a random or periodic basis, which prevents superior competitors from dominating the assemblage (Sale, 1977, 1978). Consequently, stochastically regulated assemblages are generally species rich (Sale, 1977). However, resource partitioning among species does not necessarily control the coexistence of species, as many species show similar acquisition of resources but do not incur competitive exclusion (Doherty and Williams, 1988). The composition of the assemblage is therefore controlled by the availability of recruits and vacation of space by post-settlement mortality.

In many marine and estuarine systems there is often a dynamic turnover in abundant species which is seen to be a result of certain species winning a 'lottery' to settle from the plankton to available resources (i.e. habitat). This 'lottery hypothesis' (Sale, 1977, 1978, 1982) is a stochastically driven non-equilibrial model that has been deemed relevant for some reef fish populations and which proposes that the composition of species will vary randomly over time. In contrast, rockpool fish assemblages are often persistent for lengthy periods, even after catastrophic natural disturbances, such as hurricanes (Moring, 1996), and continual experimental eliminations (Grossman, 1982; Collette, 1986). For example, Collette (1986) found two species, *Pholis gunnellus* and *Tautogolabrus adspersus*, to be dominant over 19 years of study in two New England rockpools, while the rank of dominant species in the rockpools of Barbados showed no evidence of change over six years (Mahon and Mahon, 1994). Similar stability and persistence was evident in the present study, where *Bathygobius cocosensis*, *Enneapterygius rufopileus* and *Girella elevata* were most often the highest ranked species in each collection for all three studies, regardless of the period between sampling. Although the dynamic regression models revealed possible competition
among these species, they may coexist by fulfilling different microhabitats. For example, *G. elevata*, occupies the upper water column and resides among large overhangs and boulders, *B. cocosensis* prefers bare rocky substratum (Butler, 1980), whereas *E. rufopileus* normally resides over coralline algae (personal observation).

The persistence of the Bass Point fish assemblages suggests they are regulated by deterministic processes. At first, this may seem ironic as the intertidal zone is subjected to a high frequency of stochastic events. It would be easy to assume that these events could eliminate fishes from rockpools, vacating microhabitats for other species to exploit. This has been documented for sessile intertidal invertebrate assemblages that rely upon the availability of vacant substratum for successful recruitment of larvae (see examples by Raffaelli and Hawkins, 1996). However, the locomotory capabilities and morphological and physiological adaptations of resident intertidal fishes allow them to cope with such disturbances by being able to temporarily cope with adverse conditions (Martin, 1995). As a result, the abundance of resident species is probably little affected under normal disturbance regimes. In contrast, those species having few or no adaptations for an intertidal existence (i.e. opportunists and transients) are at greater risk of mortality and therefore make substantially less contribution to rockpool fish populations. However, the disturbances created by sampling in the present studies (i.e. removal of all fish in rockpools) were probably far greater in magnitude than any natural perturbation experienced at these sites, yet resilience and persistence of taxocene structure was clearly evident. The deterministic regulation of rockpool fish assemblages will be further investigated greater detail in Chapter 9.
Despite the Bass Point fish assemblage appearing to be persistent through time, it must be noted that this may be a result of the size of the populations removed from rockpools relative to the size of the entire populations at each site. In the present study, it is possible that recolonisation rates are more rapid than what may occur after natural perturbations. For example, the experimental removal of fishes in the present study may be the equivalent of natural catastrophic disturbances, but these disturbances were restricted to only a subset of rockpools along a rock platform. Nearby rockpools remaining undisturbed may have sufficient populations of fish to replenish disturbed rockpools, since many species of intertidal fishes move between a number of rockpools in a "home range" (Williams, 1957; Valle, 1989; Yoshiyama et al. 1992). In contrast, catastrophic natural disturbances may affect all rockpools within an area, and as a result, there may be few nearby populations to supply fish to disturbed rockpools. In this case, one may expect populations to be replenished by recruitment of those species having planktonic larvae. It is probable that this process of recolonisation would be slower than what has been recorded in the present study, which was mainly facilitated by post-settlement movements.

The results of the present study may implicitly infer different trends about the re-establishment and maintenance of fish assemblage structure in rockpools than what may occur under natural conditions. To assess the effects of large scale natural disturbances, fish from all rockpools in an isolated area would need to be removed simultaneously and the recovery process examined over time. However, this would be nearly impossible to perform since sampling rockpools is extremely time consuming (at least one hour to sample a single rockpool) and fish often move from other rockpools into vacant rockpools within a single tidal cycle (personal observation), thus hindering such
an experiment. Entire populations are often unable to be censused, and this certainly appears to be the case with rockpool fish assemblages. The closest scientists may get to understand the processes controlling the dynamics of fish populations is to perform experiments such as the one in the present study, where an adequate sample of rockpools is taken and the results extrapolated to be relevant to the entire population.

This Chapter has shown that fish assemblages can quickly return to pre-perturbation levels after significant disturbance. This resilience appears to be mainly driven by post settlement migration, although recruitment may also periodically play a significant role in population replenishment. Chapter 7 further explores the movements of fishes within the rockpool environments to determine whether displaced individuals display some degree of site fidelity or homing behaviour.
Chapter 7

Movements and homing of rockpool fishes

INTRODUCTION

The dynamics of most marine fish populations is primarily driven by larval recruitment filling habitats left vacant by adult mortality (Doherty and Williams, 1988). However, many fishes display the ability to home to specific location after being displaced. Homing ability and site fidelity has been documented for many fish species in marine (Gibson, 1967a; Sale, 1971; Green, 1973; Green and Wroblewski, 2000), estuarine (Lotrich, 1975) and freshwater (Donaldson and Allen, 1957; Blair and Quinn, 1991; Armstrong and Herbert, 1997) systems. Homing can be defined as "the return to a place formerly occupied instead of going to other equally probable places" (Gerking, 1959). Perhaps the most well known fishes that display such behaviour are the salmonids that travel thousands of kilometres to spawn in rivers or streams where they were hatched (Neave, 1964; Dittman and Quinn, 1996).

Williams (1957) was among the first ichthyologists to document the homing ability of intertidal rockpool (or tidepool) fishes, however numerous researchers worldwide have since documented homing behaviour for various rocky intertidal fish species. These experiments involve the removal of individuals from their home pool and relocating them to other pools. Species shown to have homing ability are generally permanent residents, that is, they complete their entire life cycle in the rocky intertidal zone (Gibson, 1969). These species are from a number of families including Blennidae (Gibson, 1967a; Stephens et al. 1970), Cyclopteridae (Moring and Moring, 1991), Girellidae (Williams, 1957; Valle, 1989), Acanthoclinidae and Tripterygiidae (Berger
and Mayr, 1992), and Cottidae, which have probably been studied most extensively (Green 1971a, 1971b, 1973; Khoo, 1974; Richkus, 1978; Craik, 1981; Yoshiyama et al. 1992). Homing success is often a function of displacement distance. For example, the opaleye, *Girella nigricans*, can home to their rockpool of capture when displaced by up to 54 m, although the percentage of fish returning to pools greatly decreases with increasing distance of displacement (Valle, 1989).

The ability of intertidal fishes to home may function as a safeguard so that, after high tide feeding excursions, fish can return to a specific pool where it has knowledge of its normal environmental conditions and microhabitat availability. This is often an advantage as these fishes avoid adverse conditions and predators that might be present in other rockpools. There are numerous suggestions as to how intertidal fish may return to a specific pool after displacement and these include: orientation relative to tidal variations (Norris, 1963); phototaxic navigation (Berti *et al.* 1994); olfactory cues (Khoo, 1974); topographic characteristics (Green, 1971; Craik, 1981; Markel, 1993); and, environmental factors, such as wave exposure (Yoshiyama *et al.* 1992). All these suggestions remain speculative. Permanent resident fishes of intertidal rockpools tend only to move small distances over a limited geographic range, and thus appear to have intricate knowledge of their immediate surroundings, which appears to enhance their homing ability (Green, 1971a).

Chapter 6 concluded that rockpools were primarily recolonised by fishes moving in from adjacent rockpools. Although fish removed from rockpools in those experiments were relocated to other rockpools or the shallow subtidal, it was possible that the homing of some fish species was responsible for the recolonisation of rockpools.
Extensive searches of the literature revealed there has been no study of the movements or homing ability of intertidal rockpool fishes in Australia. Therefore, tagging experiments were designed to determine i) which fish species, if any, commonly found in southeastern Australian rockpools display homing behaviour, and ii) the strength of this homing ability, as a function of displacement distance, fish size and time at liberty.

Although tagging is a widely used method in fisheries for estimating growth and monitoring the movements of fish, the large size of conventional external tags, such as t-bar, dart, spaghetti and streamer tags, make their application to the study of small intertidal fishes very limited. Furthermore, external tags are highly susceptible to loss and increased potential for infections or disease around the insertion point, which can affect growth, behaviour and survivorship (see discussions by Willis and Babcock, 1998; Malone et al. 1999).

The recent development of small internal tags overcomes many of these problems. Visible implant tags are increasingly popular and relatively inexpensive internal tags that are suited for study of small fishes. Visual implant alphanumeric (VIA) tags and visual implant fluorescent elastomer (VIFE) tags are two types of visual implant tags successfully used for marking small fishes in both freshwater (Blankenship and Tipping, 1993; Niva, 1995; Dewey and Zigler, 1996) and marine environments (Forrester, 1995; Willis and Babcock, 1998; Malone et al. 1999). VIA tags are small (1.0 x 2.5 mm) fluorescent polyester pieces imprinted with a three digit alphanumeric code. The tags are injected into the transparent tissue of a fish using a specialised injector. VIFE tagging involves injection of a viscous fluorescent liquid elastomer that sets to form a permanent, biocompatible mark. When exposed to ultraviolet light the tag
fluoresces, allowing identification of fishes by colour or tag location. VIFE tags are useful for monitoring groups of very small fish as the tag size can be varied to suit fish size, and, with the use of two elastomer colours, 243 fish may be given unique markings (Dewey and Zigler, 1996). There have been attempts to use other methods for marking intertidal fishes using various dyes (Hart and Pritcher, 1969; Ross et al. 1987), acrylic paints (Lotrich and Meredith, 1974; Pfister, 1995, 1996) and latex (Riley, 1973), which can last for several years (Yoshiyama et al. 1992). However, compounds such as paint harden over time, which may affect the behaviour, growth or survivorship of the marked fishes. Therefore, before undertaking the homing experiment, laboratory studies were undertaken to assess their retention and mortality associated with their use with two rockpool fishes, *Bathygobius cocosensis* and *Girella elevata*.

**MATERIALS AND METHODS**

**Experiment 1: Assessment of tag utility**

Fish were collected from rockpools in the Illawarra region (34°58'S, 150°93'E), New South Wales, Australia and transported to six flow-through seawater aquaria where they were allowed to acclimate for 3-8 weeks. In preparation for tagging, fish were anaesthetised in a 30 mg l⁻¹ solution of clove oil using the methods described in Chapter 2.

VIA and elastomer tags were implanted into the transparent cheek tissue of *Bathygobius cocosensis*. Since *Girella elevata* have few suitable tag locations due to dark skin pigmentation, VIA and elastomer tags were inserted into the semi-transparent tissue in the nape and cheek, respectively (Plates 4 and 5). Fluorescent yellow VIA tags were implanted with a syringe-like applicator (Northwest Marine Technologies, Appendix 4).
Fluorescent orange and red elastomer tags implanted using a 0.3 cc syringe (Northwest Marine Technologies, Appendix 5). All fish were measured (total length (TL) in mm) and weighed (to the nearest 0.1 gram) during the tagging procedure and again after 15, 30, 60 and 90 days, where the presence and readability of a tag was also recorded. Number and sizes of individuals of each species with each tag type is shown in Table 28, although it is important to note that fish tagged with VIA tags were generally larger than elastomer-tagged fish. As a result, it is possible that differences observed between tag treatments are due in part to differences in retention by differently-sized fish.

Six aquaria maintained at the same seawater temperature (17-21°C) and flow rate were used for the laboratory experiment. Each aquarium was considered a single replicate and contained all individuals of one of the six experimental groups (2 species: Girella elevata and B. cocosensis, and 3 tag types: VIA, elastomer, and control). Fish were fed a selection of fresh Ulva, freeze dried brine shrimp and krill or frozen blood worms every 2-3 days.

ANOVA was used to test for differences in the mean retention among tag types and associated mortality rates of fish. Fish species was ignored as a factor in comparing retention and mortality among tag types. That is, retention percentages for both aquaria (one of each species) of VIA and elastomer treatments were used as replicates. Sample size within the two treatments was 2. Similarly, mortality percentages for both aquaria (one of each species) of VIA, elastomer and control treatments were used as replicates. Sample size within the three treatments was 2. Data were examined for homogeneity of variances using Cochran’s test. No transformation of data was necessary. Tukey’s
Honestly Significant Difference (HSD) test was used to determine significantly different means.

**Table 28.** Number, mean (±SE) weight (grams) and total length (mm), and length range (mm) of *Girella elevata* and *Bathygobius cocosensis* implanted with VIA and elastomer tags and used as untagged controls.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number</th>
<th>Length range (mm)</th>
<th>Mean length (mm)</th>
<th>Mean weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>VIA tags</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>20</td>
<td>60-148</td>
<td>84.9 (5.8)</td>
<td>11.5 (2.9)</td>
</tr>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>25</td>
<td>43-64</td>
<td>53.6 (0.9)</td>
<td>1.4 (0.1)</td>
</tr>
<tr>
<td><strong>Elastomer tags</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>12</td>
<td>47-69</td>
<td>57.9 (1.9)</td>
<td>2.3 (0.2)</td>
</tr>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>21</td>
<td>32-46</td>
<td>39.8 (0.9)</td>
<td>0.6 (0.1)</td>
</tr>
<tr>
<td><strong>Control</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>15</td>
<td>52-101</td>
<td>76.2 (4.4)</td>
<td>9.3 (1.8)</td>
</tr>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>23</td>
<td>34-59</td>
<td>47.5 (0.8)</td>
<td>1.1 (0.1)</td>
</tr>
</tbody>
</table>
Plate 4. Photographs showing visible implant alphanumeric (VIA) tags after being injected into transparent cheek tissue of a fish. Images show the visibility of tags under natural (left) and UV light (right). Note the clarity of alphanumeric digits for identification of individuals. Tag length is 2 mm.

Plate 5. Photographs showing visible implant fluorescent elastomer (VIFE) tags after being injected into transparent cheek tissue of a fish. Images show the visibility of tags under natural (left) and UV light (right). Tag length is approximately 2 mm.

Experiment 2: Pilot study of fish homing

In order to determine the homing ability of rockpool fishes, a small displacement experiment was conducted to obtain an indication of the distances fish are capable of homing. Previous studies of rockpool fishes have revealed that there is great variability in the distances that fish are capable of homing. For example, Williams (1957) found that some species are not capable of homing when displaced at distances of less than
two metres, whereas others can home when displaced over one hundred metres from their rockpool of capture (Green, 1971a; Khoo, 1974). Therefore, the homing ability of the two most abundant permanent residents, *Bathygobius cocosensis* and *Enneapterygius rufopileus*, was tested over three displacement distances in the pilot study: 5 m, 20 m and 50 m. Adequate numbers of the opportunistic species *Girella elevata* and *Acanthistius ocellatus* could not be obtained, so their homing ability was only tested over two displacement distances, 5 m and 20 m.

The pilot study was undertaken at Maloney's Bay, Bass Point (Fig. 28) between 20 September 1999 and 17 November 1999. An isolated group of four small (80-210 l) rockpools being no more than 2 m apart were selected for the study. Since the closest rockpool outside this group of pools was approximately 10 m away, the study pools were considered to possibly represent a home range for some fish. Fish were collected from rockpools (using methods described in Chapter 2) and tagged with a unique colour VIFE tag (for procedure see Experiment 1 in this Chapter) depending on the distance it was intended to be displaced. Fish were then relocated in a bucket to other pools at the specified displacement distances. The original group of four rockpools were then repeatedly sampled every two weeks and the recapture of a tagged fish in any of the four rockpools was considered successful homing.
Experiment 3: Main homing study

Study sites and fish collection

Homing studies were undertaken at four rocky headlands (Bass Point, Caravan Point, Bellambi Point and Puckey's Bombora) in the Illawarra region, New South Wales, Australia (Fig. 25) between 9 September 1999 and 7 August 2001. Rockpools at each location generally occurred as distinct groups of around 4-8 rockpools across areas, or plots, of approximately 100 m², presumably a result of small-scale geological variations (Plate 6). These plots were assumed to comprise home ranges of resident fishes, if in fact, their movements were restricted to only a few metres of shoreline, which is generally the case for most intertidal fishes (Green, 1971a; Gibson, 1999b). All rockpools in two plots (4-8 rockpools per plot), or home ranges, separated by 300-800 m were repeatedly sampled at 1 to 3 monthly intervals at each location in order to give fish adequate time to locate the rockpool of original capture. These rockpools were within 10 m of each other. Only plots containing rockpools that were each situated along the mid-intertidal zone (0.5-1.2 m above MLLW) sharing similar volume (about 100-500 l) and substrate type (mainly cobbles) were selected for study. Fish were collected from rockpools using the bilge pump sampling method described in Chapter 4. Fish were transferred to a 60 l drum containing fresh aerated seawater for identification and measurement of their total length (TL) and the rockpool then refilled. Fish larger than 20 mm TL were tagged using VIFE tags and fish >60 mm TL were tagged with VIFE or VIA tags. Identification of individuals was possible using both tag types as each VIA tag has a unique 3 digit code, while numerous colour and tag location combinations were used for VIFE tags. Tagging procedures followed those described in Experiment 1 (this Chapter).
Plate 6. Photograph showing a typical group of rockpools comprising a plot, or home range, used for testing homing abilities of rockpool fishes. In this plot at Maloney's Bay, Bass Point there was four rockpools.

Displacement distances of <5 m and 10-20 m were used to test the strength of homing ability, established in Experiment 2. Only two displacement distances were used since gaining adequate sample sizes of fish was extremely difficult, as the number of fish per rockpool does not normally exceed a few fish of any one species. Fishes caught in a single plot at each location were relocated to rockpools at each distance in both directions from the rockpool where fish were initially captured. This ensured that homing ability was independent of orientation and influences of small-scale environmental variations (i.e. currents), which may bias homing success. To further ensure that homing behaviour was being assessed, one rockpool within each plot was assigned as a control. Fishes captured from these rockpools were tagged and returned to
the same rockpool within a period of three hours of being removed, after the rockpool was refilled by the tide or the bilge pump. Fish from control groups were treated in the same way as experimentally displaced fish. If the mean proportion of fish recaptured in control rockpools was significantly higher than for displaced fishes, then homing behaviour may be questionable. That is, recaptured fish may incidentally find their way into the rockpool of original capture and does not constitute homing *per se*.

The influence of fish size on homing success was investigated by arbitrarily categorising fish of each species as being juveniles, subadults and adults based on their total lengths and relocating these fish to rockpools approximately 10 m from the original rockpool of capture. This experiment was undertaken at a separate plot at each location and simultaneously determined whether the time at liberty of displaced fish influenced homing success, since the displacement distance was equal for all fish. Time at liberty is defined here as the period (in days) from the date of capture to the date of recapture of a tagged fish.

On each sampling occasion fish possessing a tag were measured and the colour and body location combinations (for VIFE tags) or tag number (for VIA tags) recorded. Any tagged fish recaptured during other studies being conducted concurrently near the study sites (i.e. outside home range plots) (studies in Chapters 4 to 8) were also recorded. This also provided greater insight as to the extent of movements of fish that failed to home to the rockpool of original capture.
Statistical analyses

Two separate one-factor ANOVAs were used to test for differences in the mean percentage of individuals from the most abundant species displaying homing behaviour among i) displacement distances (0 m for control, <5 m, 10-20 m) and ii) fish sizes (juvenile, sub-adult, adult). Numerous species appeared to display homing behaviour; however analyses were restricted to four species for which there was sufficient data. Although spatial variation in homing for each species may be possible, the number of recaptures was generally too low to perform statistical comparisons of data among the four locations, so data from each location was pooled. Test of assumptions and a posteriori comparisons among means are described in Experiment 1 (this Chapter). The relationship between homing success (number of fish homing) and the time at liberty was assessed using a simple linear correlation.

RESULTS

Experiment 1: Assessment of tag utility

Both VIA and elastomer tags were easily implanted for both species, even considering some fish were less than 35 mm TL. Identification of tags with the naked eye was excellent for all species after 90 days, although the use of either an infrared or black light in low light conditions significantly enhanced the readability of VIA tags (Plate 4 and 5).

There were considerable differences in retention rates among tag types, although the greatest proportion of fish generally lost VIA and elastomer tags 15 days and 60-90 days after tagging respectively (Fig. 36). After 90 days the mean retention of VIA tags was 32 (± 20)%, while higher retention rates 77 (± 19)% were recorded for elastomer tags.
ANOVA revealed that the mean retention rate was significantly higher for elastomer-tagged fish ($F_{1,2}=5.771, P=0.043$).

After 90 days, the mean mortality of VIA-tagged fish was 20 ($\pm$ 5%), which was higher than the mean mortality rates of elastomer-tagged fish (7 $\pm$ 2)% and the control group (11 $\pm$ 2%) (Fig. 37). ANOVA revealed that the overall mean mortality rates differed among tag types ($F_{2, 3}=11.421, P=0.002$). Tukey's HSD test revealed that the mean mortality rate was significantly higher among VIA-tagged fish than elastomer-tagged or control fish, although mean mortality rate did not differ among the latter two treatments.

**Figure 36.** Percentage (mean $\pm$ SE) of visible implant alphanumeric (VIA) tags and visible implant fluorescent elastomer (VIFE) tags retained by fish 15, 30, 60 and 90 days after tagging. Data has been pooled for *Girella elevata* and *Bathygobius cocosensis.*
Experiment 2: Pilot study of fish homing

The results of the study are summarised in Table 29. Overall, of the 42 fish tagged 11 (or 26%) were recaptured. The two resident species, *Bathygobius cocosensis* and *Enneapterygius rufopileus*, were capable of homing after being displaced by 5 m and 20 m but not 50 m. The two opportunist species, *Girella elevata* and *Acanthistius ocellatus*, successfully homed after being displaced by 5 m, although only *G. elevata* was capable of homing from 20 m.

Although the sample sizes used in the pilot study were small, the results indicate that some fish species are capable of homing after being displaced at distances of up to 20 m. Fish may be capable of homing from 50 m or more, but the time taken for fish to navigate back to their home pool may be long and therefore the use of such distances is not feasible in a larger study. Considering the densities of fish in rockpools are often
low (see Chapter 4) two displacement distances would provide adequate data that would lend itself to statistical analyses. Therefore, the strength of homing in a larger experiment could be determined by using displacement distances that are small (<5 m) and large (10-20 m).

**Table 29.** Results of preliminary homing experiments carried out between 20 September 1999 and 17 November 1999. Species tagged, distance and number of fish displaced, and the number of fish recaptured is shown for a set of four rockpools.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distance displaced</th>
<th>No. of fish displaced</th>
<th>No. of fish recaptured</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>5 m</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>20 m</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>50 m</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td><em>Enneapterygius rufopileus</em></td>
<td>5 m</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>20 m</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>50 m</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>5 m</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>20 m</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td><em>Acanthistius ocellatus</em></td>
<td>5 m</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>20 m</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total number of fish</strong></td>
<td></td>
<td>42</td>
<td>11</td>
</tr>
</tbody>
</table>

**Experiment 3: Main homing study**

A total of 1380 fish representing 20 species were tagged and displaced for examination of homing behaviour, while 207 fish from 10 species were tagged but not displaced to investigate their intertidal movements (Table 30). Of the fishes displaced, 154 individuals (or 20% of tagged fish) comprising 11 species were recaptured. The nine species not recaptured were represented by less than twelve individuals (Table 30). The percentage of fish recaptured for individual species ranged from 3% to 41%. This constitutes a mean (±SE) recapture rate of 19 (±3)% for all species combined. Of the recaptured fish representing each species, at least 50% returned to their original pool of capture (Table 30). All recaptured fish from six species were found in their original pool, most notably *Enneapterygius rufopileus*, which was the second most abundant
species overall (Table 30). Comparatively smaller percentages (0-50%) of fish were recaptured in other rockpools within sampling plots. Only seven fish were recaptured in rockpools outside sampling plots and none were more than 19 m from the rockpool of original capture.

Of the fishes tagged and not displaced, 50 individuals (or 24% of tagged fish) were recaptured. The percentage of fish recaptured for individual species ranged from 13% to 100%. This constitutes a mean recapture rate of 29 (±8)% for all species combined. At least 50% of recaptured fish from eight species returned to their original pool of capture, while fish from the remaining two species were caught in adjacent rockpools. However, these species were represented by no more than two recaptures (Table 30). No fish from control rockpools were recaptured outside sampling plots at any location.

For the four most abundant species, the mean percentage of recaptured fish did not differ among control groups or those displaced by <5 m and 10-20 m (Fig. 38a; Table 31). This indicates that recapture rates of displaced fish were no different to control groups, and homing success was not affected by displacement distance. Homing success was not significantly influenced by the size of fish for any species after being displaced by approximately 10 m, with the exception *Lepidoblennius haplodactylus*, which showed significantly less tendency to home with increasing size (Fig. 38b; Table 32). Furthermore, the total number of fish recaptured from all species showed no significant correlation with the time that fish were at liberty ($r=0.123; P=0.454$) after being displaced by around 10 m. However, it is clear that after periods of around 120 days the number of fish homing drastically declined. However, it is interesting to note that some fish were found in their original pool after periods of up to 214 days (Fig. 39).
Table 30. Fish species used in homing experiments (displaced groups and control groups) showing number of fish tagged and recaptured overall, in the original rockpool of capture, and adjacent rockpools (<10 m from original rockpool) between 7 September 1999 and 20 August 2001 pooled for four rocky headlands in southeastern NSW. All species were considered residents, except those denoted by an asterisk, which were considered opportunists (for definitions see Chapter 3). Values in parentheses in "number recaptured" columns show percentage of all tagged fish recaptured, whereas for other columns it shows percentage of recaptured fish caught in home pool or adjacent pools. Details of fish recaptured outside sampling plots are shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number tagged</th>
<th>Number recaptured</th>
<th>Number recaptured in home pool</th>
<th>Number recaptured in adjacent pools</th>
<th>Number tagged</th>
<th>Number recaptured</th>
<th>Number recaptured in home pool</th>
<th>Number recaptured in adjacent pools</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bathygobius cocosensis</td>
<td>592</td>
<td>141 (24)</td>
<td>122 (87)</td>
<td>19 (13)</td>
<td>46</td>
<td>13 (28)</td>
<td>11 (85)</td>
<td>2 (15)</td>
</tr>
<tr>
<td>Enneapterygius rufopileus</td>
<td>187</td>
<td>39 (21)</td>
<td>39 (100)</td>
<td>0 (0)</td>
<td>37</td>
<td>9 (24)</td>
<td>9 (100)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Girella elevata</td>
<td>154</td>
<td>19 (12)</td>
<td>16 (84)</td>
<td>3 (16)</td>
<td>21</td>
<td>4 (19)</td>
<td>3 (75)</td>
<td>1 (25)</td>
</tr>
<tr>
<td>Lepidoblennius haplodactylus</td>
<td>94</td>
<td>19 (20)</td>
<td>19 (100)</td>
<td>0 (0)</td>
<td>41</td>
<td>9 (22)</td>
<td>9 (100)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Heteroclinus fasciatus</td>
<td>73</td>
<td>10 (14)</td>
<td>5 (50)</td>
<td>5 (50)</td>
<td>16</td>
<td>2 (13)</td>
<td>0 (0)</td>
<td>2 (100)</td>
</tr>
<tr>
<td>Parablennius intermedius</td>
<td>61</td>
<td>15 (25)</td>
<td>10 (67)</td>
<td>5 (33)</td>
<td>12</td>
<td>3 (25)</td>
<td>3 (100)</td>
<td>0 (0)</td>
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<tr>
<td>Istiblennius meleagris</td>
<td>58</td>
<td>8 (14)</td>
<td>8 (100)</td>
<td>0 (0)</td>
<td>12</td>
<td>2 (17)</td>
<td>2 (100)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Heteroclinus whiteleggi</td>
<td>57</td>
<td>11 (19)</td>
<td>10 (91)</td>
<td>1 (9)</td>
<td>12</td>
<td>2 (17)</td>
<td>1 (50)</td>
<td>1 (50)</td>
</tr>
<tr>
<td>Aspasmogaster costatus</td>
<td>36</td>
<td>1 (3)</td>
<td>1 (100)</td>
<td>0 (0)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Istiblennius edentulus</td>
<td>27</td>
<td>11 (41)</td>
<td>11 (100)</td>
<td>0 (0)</td>
<td>5</td>
<td>5 (100)</td>
<td>4 (80)</td>
<td>1 (20)</td>
</tr>
<tr>
<td>Acanthistius ocellatus</td>
<td>19</td>
<td>2 (11)</td>
<td>2 (100)</td>
<td>0 (0)</td>
<td>5</td>
<td>1 (20)</td>
<td>0 (0)</td>
<td>1 (100)</td>
</tr>
<tr>
<td>Ophiclinus gracilis</td>
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<td>0</td>
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<td>-</td>
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<td>-</td>
<td>-</td>
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<tr>
<td>Parma microlepis</td>
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<td>-</td>
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<td>Abudefuf vaigiensis</td>
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<td>Callogobius depressus</td>
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<td>Chironemus marmoratus</td>
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<tr>
<td>Kuhlia mugil</td>
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<td>0</td>
<td>-</td>
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<td>Norfolkia clarkei</td>
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<tr>
<td>Notolabrus gymnogenis</td>
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<td>0</td>
<td>-</td>
<td>-</td>
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<td>Epinephelus daemonii</td>
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<td>-</td>
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<td>-</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>1380</td>
<td>276 (20)</td>
<td>124 (81)</td>
<td>30 (19)</td>
<td>207</td>
<td>50 (24)</td>
<td>42 (84)</td>
<td>8 (16)</td>
</tr>
</tbody>
</table>

Tagged fish recaptured outside sampling plots during other studies (number caught, distance from home rockpool, size at release (in mm), days at liberty):
Bathygobius cocosensis (5, 14-19 m, 21-55 mm, 23-104 days); Enneapterygius rufopileus (1, 14 m, 38 mm, 44 days); Girella elevata (1, 17 m, 86 mm, 112 days).
Figure 38. Mean (±SE) percentage of fish representing the four most abundant species homing to rockpools a) after being displaced at distances of <5 m and 10-20 m (regardless of fish size), and b) as a function of fish size (after being displaced by approximately 10 m). Data has been pooled for four sampling locations (Bellambi Point, Puckey’s Bombora, Caravan Point and Bass Point). Fish size categories not represented for particular species are denoted by (NC).
Table 31. Results of ANOVA testing for differences in number of tagged fish recaptured for the four most abundant species among controls (not displaced) and after being displaced at distances of <5 m and 10-20 m. Data has been pooled for experiments conducted at four locations (Bellambi Point, Puckey's Bombora, Caravan Point and Bass Point) between 9 September 1999 and 7 August 2001. Degrees of freedom, F ratios and significance values are shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>df</th>
<th>F Ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bathygobius cocosensis</td>
<td>2</td>
<td>0.602</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Enneapterygius rufopileus</td>
<td>2</td>
<td>2.001</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Girella elevata</td>
<td>2</td>
<td>0.012</td>
<td>P&gt;0.05</td>
</tr>
<tr>
<td>Lepidoblennius haplodactylus</td>
<td>2</td>
<td>0.018</td>
<td>P&gt;0.05</td>
</tr>
</tbody>
</table>

Table 32. Results of ANOVA testing for differences in number of fish homing for the four most abundant species representing juveniles (≤50 mm TL), subadults (31-60 mm TL) and adults (>60 mm TL) after being displaced by approximately 10 m. Note that for Enneapterygius rufopileus only subadults and adults were displaced. Data has been pooled for experiments conducted at four locations (Bellambi Point, Puckey's Bombora, Caravan Point and Bass Point) between 9 September 1999 and 7 August 2001. Degrees of freedom, F ratios and significance values are shown. Significant results shown in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>df</th>
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DISCUSSION
Utility of visible implant tags for marking small rockpool fishes

High retention, low mortality and ease of identification of elastomer tags clearly indicate their higher suitability for marking intertidal rockpool fishes compared to VIA tags, particularly for fish of small sizes (<50 mm TL). Elastomer tags are useful for marking batches or cohorts of fish, although with the use of two elastomer colours 243 fish may be given unique markings (Dewey and Zigler, 1996). Since rockpool fishes normally have low densities within the intertidal zone, the use of elastomer tags for the purpose of identifying individuals may be adequate. Although VIA tags resulted in lower survivorship and retention rates, particularly for Girella elevata, their use for individual identification of gobies or similar species with adequate transparent tissue may be successful, although this should be restricted to fish greater than 50 mm TL. However, it is also important to note that differences in retention and mortality rates

Figure 39. Frequency of fish (combined for all species) homing to rockpools as a function of the time taken to home to rockpools being displaced at distances of around 10 m.
among tag types may be partly due to differences in fish sizes among tag treatments. Larger fish were tagged with VIA tags in the present study because of the potentially high trauma of injecting small fish with the relatively large VIA tags and the tag injector.

The main factor influencing tag retention was probably the effect of handling fish during tag inspections. This effect was identified where tags were found on the bottom of containers used to transfer fish between aquaria and the observation laboratory. Kincaid and Calkins (1992) suggest tag loss can be highly influenced by excessive handling after implantation where insertion wounds have not properly healed. Although extreme care was taken when handling fish during all observations, observations of unhealed wounds indicate that this may be a major source of tag loss even after 90 days. The rate of tag loss of both tag types would probably be far lower in field experiments where tagged fish would not be continually handled. However, some tag losses are to be expected as VIFE tags can be lost without handling of fish if tags are not inserted correctly (Willis and Babcock, 1998).

Some interspecific differences in retention rates for VIA tags were noted, which probably related to differences in fish anatomy and behaviour. For example, tag loss in *Girella elevata* may have been in part due to the small amount of semi-transparent tissue at the nape, which probably requires a smaller tag to resist movement by muscular contractions. Second, the secretive behaviour of *G. elevata* may also contribute to tag loss as fish were observed rubbing the tag site upon rocks. Conversely, elastomer tags could be injected into a more suitable tag location (i.e. the cheek) thus resulting in high retention rates. Conversely, *Bathygobius cocosensis* has ample
transparent cheek tissue enabling both VIA and elastomer tags to be implanted further from the insertion point, which probably accounted for high retention rates, particularly for VIA tags.

**Homing experiments**

The present homing study, the first of its kind in Australia, has confirmed the findings of overseas studies that intertidal rockpool fishes are capable of homing after being displaced, often by distances exceeding 10 m (Williams, 1957; Gibson, 1967a; Green, 1971a, 1973; Khoo, 1974; Valle, 1989; Yoshiyama et al. 1992). Furthermore, this study revealed that fish that were not displaced moved only small distances between a few rockpools.

Although the absolute number of individuals representing each species used in the experiments differed, the percentage of fish homing varied significantly indicating that some species display far stronger tendency to home than others. However, determining the existence of homing, as opposed to random movement of fish to the same pool, is confounded by the fact that some species (and individuals) often display a preference for a set of rockpools often termed a "home range" (Gibson, 1967a) which are utilised over time. Therefore there may be a high probability of finding the same fish in a single pool in its home range. However, the return of a fish to any pool which it has occupied within its home range can be considered homing behaviour (see definition by Gerking, 1959). Although without extensive previous knowledge of the movements of an individual, determining which rockpools are included within its home range will be difficult and time consuming, especially if an adequate sample of fish is to be monitored. A further confounding issue is that an individual’s home range may vary
spatially and temporally (Green, 1971a). For instance, fish may show a preference for rockpools located in the lower intertidal on sheltered shores or during warmer months when water temperature and salinity can dramatically increase and dissolved oxygen decrease in higher elevated rockpools (Huggett and Griffiths, 1986). Higher pools may be utilised on exposed shores or during winter when wave action and turbulence increases due to storms, making lower level rockpools less desirable habitats. Furthermore, ontogenetic shifts in rockpool selection have been documented for some intertidal species, such as *Girella nigricans*, which tend to migrate to lower intertidal rockpools as they grow and their food and microhabitat preferences change (Valle, 1989).

Nonetheless, a strong homing tendency was particularly marked for at least four species, *Enneapterygius rufopileus*, *Lepidoblennius haplodactylus*, *Istiblennius meleagris* and *Istiblennius edentulus*, which were always recaptured in the rockpool of their original capture. This strong homing tendency is further supported by the recapture of some individuals of *E. rufopileus* up to four times in the same rockpool during preliminary studies. Such strong homing tendencies for these species may be related to their preference for specific microhabitats as reflected by their cryptic colouration. For instance *E. rufopileus* is a pink/red colour and is normally associated with pink coralline algae found along the walls of some rockpools, particularly those at lower intertidal elevations. Likewise, *L. haplodactylus* is blotched with pink to light brown patterns and is most commonly found in rockpools where there are small cobbles covered with pink encrusting algae, but also in close proximity to substrata covered in green algae (*Enteromorpha* sp.) that comprises a high portion of its diet (unpublished data on 15 individuals). Because of this apparent microhabitat selectivity, it may be more difficult
to find an equally suitable rockpool near a release point than searching for their home pool.

With regards to the most abundant species, *Bathygobius cocosensis*, fish still displayed relatively strong homing behaviour but some of the recaptured fish (13% of the total number recaptured) were caught in adjacent pools within 7 m of the pool in which it was originally captured. It is difficult to determine whether fish returning to adjacent pools are displaying homing behaviour or random relocation to rockpools near their original pool of capture. However, it is likely that this species displays homing behaviour but has a relatively large home range. A similar rockpool species found in the United States, *Bathygobius soporator*, displays site fidelity and makes leaps towards specific rockpools if disturbed during low tide, which comes from knowledge gained by swimming over its home range at high tide (Aronson 1951, 1971 as cited in Gibson, 1999b). The likely mechanism by which fish home is visual cues of specific topographical features within their home range which assists them in determining their location within that range.

**Displacement distance and homing success**

The distances that fish are capable of covering to return to a home pool after being displaced has attracted much attention. Previous research has revealed conflicting results, even when examining the same species at the same location. For example, Williams (1957) found only 8% of Cottids returned to the original pool of capture after they were displaced at distances of up to two metres, while 32% of fish were captured in other pools and the remaining 60% were never recaptured. In contrast, Cottids have been documented to home when displaced at distances of up to 122 m from their
original rockpool even when blinded (Khoo, 1974), although high homing success (>36% of fish) is certainly evident at distances of up to 44 m (Yoshiyama et al. 1992). In the present study it was evident that the distances at which fishes were released were well within their home ranges as there was no difference in the proportion of fish being recaptured at the two distances. Therefore, adoption of a new home pool (and possibly an extension of the original home range) may explain the failure of some fish to be recaptured in their original rockpool of capture, as there were numerous suitable rockpools located in the immediate vicinity of the release points at each site. This may also have been the case at sites sampled by Williams (1957). Settlement to unfamiliar environments is not uncommon among normally site-attached fish, so long as equally suitable resources are available (Armstrong et al. 1997; Belanger and Rodriguez, 2001).

**Effects of fish size on homing success**

Another interesting finding of the present study was that fish size had little influence upon homing success. With regards to resident species, the only species that showed any relationship between fish size and homing success, for which there was sufficient data, was *Lepidoblennius haplodactylus*. This species showed fewer tendencies to home with increasing size. This is an interesting finding considering resident reef and intertidal fishes tend to become increasingly sedentary with age (Hartney, 1996; Gibson, 1999b). Furthermore, larger fish can be expected to have greater homing success, as they have more experience with the general environs, are able to cover greater distances than smaller fish and thus, have greater chance of finding their home range (Bunnell et al. 1998). The main suggestion for homing abilities among resident fishes is that fish identify with topographical features that aid them in locating their original pool after high tide feeding excursions and this knowledge accumulates with age (see references
in Gibson, 1999b). Therefore, the higher proportion of juvenile *L. haplodactylus* displaying homing behaviour was quite unexpected.

However, at Bellambi Point where large numbers of *Lepidoblennius haplodactylus* were tagged, there are very few rockpools. So even if juveniles show no homing ability *per se* there is a good chance that fish will locate the original pool of capture. At other sites, such as Bass Point, there are far more opportunities for fish to relocate to other suitable pools. Juveniles at Bellambi Point may locate these rockpools by remaining close to the shore and travelling horizontally until a suitable rockpool is located. The fact that all fish are removed from the rockpools during sampling (these studies were conducted concurrently with the studies in Chapter 4) probably increases their attractiveness, since fish have little or no competition once that pool is located. In the case of adults, their reduced tendency to home may indicate that rockpools may not play as an important role in their lives as they have been documented to utilise habitats other than rockpools, such as the shallow subtidal zone (Kuiter, 1993).

Gibson (1999b) suggested that strength of homing is greatest among resident fishes, as secondary residents display less tendency to return to a particular rockpool once displaced. However, it was clear that the secondary resident, *Girella elevata*, showed a strong tendency to home even at relatively large sizes (>100 mm FL). This trend was strong in at least one individual, which was first caught at 145 mm FL and subsequently recaptured three times in the same rockpool until it was 170 mm FL after being displaced by 14 m. This same fish was captured one year later at 220 mm FL in an adjacent large lower-level rockpool, which indicates that this species probably remains within a restricted home range for much of its life.
The Californian opaleye, *Girella nigricans*, appears to have an extremely similar life history to *G. elevata* in that fish continue to use the same rockpools for up to two years until they are between 80-90 mm SL (≈90-100 mm FL) before moving to deeper subtidal waters where intertidal homing eventually ceases (Valle, 1989). This period of intertidal occupation for both *G. elevata* and *G. nigricans* is probably sufficient to gain intricate knowledge of the topography of their home range. Therefore, the tendency for homing in this intertidal 'opportunist' may be greater than would normally be the case for a species that utilises the intertidal only during high tide feeding excursions or stray into rockpools as juveniles (Black and Miller, 1991).

*Time at liberty and homing success*

Although there was no significant correlation between the number of fish displaying homing ability and the time at liberty after being displaced by around 10 m, it was evident that after periods of around 120 days the number of fish homing significantly decreased. A possible explanation may be that if a fish cannot locate its home pool after a significant period of searching it might adopt a new home pool in the immediate vicinity of its release point if the pool offers equally sufficient resources as its original home pool. Such cases have been documented for several species of salmonids, which normally display a very strong homing tendency as they can relocate their home site after being displaced by thousands of metres (Miller, 1954; Armstrong and Herbert, 1997). Alternatively, fish may not be physically capable of navigating back to their home pool if the displacement distance is large, or at least large enough to be outside their normal home range where they may have little knowledge of their orientation in relation to their home pool.
Other factors influencing homing success

The number of fish returning to their home pool may also be influenced by tagging artefacts. For example, in Experiment 1 (above) mean mortality rates were as high as 20%, while mean tag loss was also as high as 68%. This may greatly reduce the potential for tagged fish being recaptured in subsequent samples. A further confounding effect on recapture rates may be an increased risk of predation on tagged fish. The fluorescent tag materials are highly visible against the generally dark background of rockpool substrates, particularly in darkened regions amongst large boulders that piscivorous fishes, such as *Acanthistius ocellatus* and *Gymnothorax prasinus*, selectively use to ambush prey (personal observation). However, the important question remains as to the fate or whereabouts of fish that escaped predation, retained a tag and survived the tagging process but were not recaptured. This finding may just be a result of variation in homing ability between individuals, as has been shown for some salmonid species (Saunders and Gee, 1964; Harcup *et al.* 1984). However, the failure to recapture these fish certainly does not indicate that recaptured fish were found in the study sites by chance since the recapture rate of the control groups were no different. Because recapture rates were similar for control and displaced groups, this indicates that both groups were sampled with the same efficiency. If the recapture rate of displaced fish was significantly lower than the control group it is possible that displaced fish may not being sampled as efficiently as those that were not displaced (since they may continue to move after being displaced), and this may also indicate that homing ability is not strong. Since recapture rates of the two groups did not differ, it may be assumed that displaced fishes displayed some initiative to home.
This Chapter has quantitatively identified another mechanism that appears to explain some of the patterns of variation in the rockpool fish assemblages, particularly the recolonisation process documented in Chapter 6. To this point, hypotheses have been mainly been concerned with how fish movement or displacement may contribute to variation in assemblages. The following Chapter will explore the influence of the habitat complexity on structuring rockpool fish assemblages.
Chapter 8

Effects of habitat complexity on rockpool fish assemblages

INTRODUCTION

The interaction between organisms and their environment forms the fundamental basis of ecology. The physical structure of habitats within an environment is an important factor influencing the distribution and abundance of individual species and thus, controls the structure of a community (Grinnell, 1917; Gause, 1934; Huffaker, 1958). The mechanism by which habitat structure influences the overall community is largely dependent upon the requirements of its constituent species. Habitat structure functions as a medium for which physical stresses and major biological interactions, such as competition and predation, can be reduced by providing temporary or permanent refuges (Hixon and Beets, 1993; Caley and St John, 1996; Friedlander and Parrish, 1998a). The physical nature of the habitat structure, or habitat complexity, also varies the availability of resources and their rate of acquisition (Safriel and Ben-Eliahu, 1991). Because the habitat requirements of different species, and even individuals, may vary, an increase in habitat complexity can therefore provide more individuals in an environment with suitable living space than if such structure was not present. Therefore, at the community level, this often results in higher species richness in environments where habitats have greater structural complexity (Kohn, 1967).

Over the past two decades significant research has investigated the influence of habitat complexity on the fish assemblages in estuaries (Bell and Westoby, 1986a, 1986b, 1986c; Bell et al. 1987; Laegdsgaard and Johnson, 2001) and other coastal habitats,
such as coral reefs (Luckhurst and Luckhurst, 1978; Jones and Symms, 1998; Steele, 1999) and temperate reefs (Garcia-Charton and Perez-Ruzafa, 2001; Angel and Ojeda, 2001). The interactions between fish and estuarine habitats, such as seagrasses, have received a large amount of attention owing to the ease of experimental simulation using artificial seagrass units (Bell, 1985; Bell et al. 1985; Virmstein and Curran, 1986; Sogard, 1989; Sogard and Able, 1994; Jenkins and Sutherland, 1997; Jenkins et al. 1998; Edgar, 1999). The higher fish densities and species richness of fish supported by natural and artificial seagrass beds compared to adjacent bare substrata (Bell et al. 1986b; Bell et al. 1987; Bell et al. 1988; Jenkins and Sutherland, 1997) is considered to be attributed to the shelter afforded by increased habitat complexity, making small fish less vulnerable to predation. This hypothesis was further supported by findings that fish do not discriminate between seagrass beds of different leaf heights or densities and appeared to recruit to any available shelter, such as man-made structures (Bell and Westoby, 1986a, 1986b; Bell et al. 1987).

The intertidal zone may also be a highly structurally complex environment; habitat complexity in this environment may also be important in influencing fish assemblages (Horn et al. 1999), although this relationship has attracted little attention by the scientific community. Physical stresses such as turbulence by wave action as well as variation in abiotic variables, such as temperature and insolation, may make living on exposed surfaces physically demanding. Lack of suitable adaptations to this demanding environment may result in mortality from the direct effects of abiotic variables (e.g. desiccation and heat stress) or indirectly through vulnerability to predation. To combat these pressures many intertidal fishes possess specific adaptations. However, these tidally isolated "island" refuges have a finite number of microhabitats available for
utilisation, and so competition for those habitats which offer the best resources (e.g. shelter from the environment and predators or access to food) is often high (Marsh et al. 1978; Faria and Almada, 1999; Gibson and Yoshiyama, 1999). Refinement of adaptations to utilise specific microhabitats may further decrease competitive interactions with conspecifics and heterospecifics (Yoshiyama 1980; Barton, 1982). Therefore, rockpools exhibiting a variety of habitats, and thus greater habitat complexity, can be expected to support greater numbers of fish species at higher abundances.

Rockpools habitats can generally be divided into two main categories, substratum cover and suspended cover. Substratum cover can be comprised of a number of elements including bare sand, gravel or broken shells, where fish can partially or completely bury themselves; rocks of varying in size where fish can reside among the spaces between rocks; and holes, crevices and overhanging ledges that also exist in various shapes and sizes. Substratum cover is therefore important to fishes that spend the vast majority of their time on or near the substratum (Davis, 2000b). Alternatively, the leaves of aquatic macrophytes such as seaweeds create suspended cover. These leaves can vary in size and structure but create shelter in an otherwise featureless water column. Such cover may be important to those species that utilise areas at or near the surface of the water of rockpools.

There have been numerous attempts to identify the most important factors influencing the structure of rockpool fish assemblages (Marsh et al. 1978; Bennett and Griffiths, 1984). Unfortunately, the vast majority are mensurative studies that can provide an understanding of general patterns of association but cannot verify cause effects
Nevertheless, rockpools containing algal cover has been shown to support higher numbers of species and individuals (Bennett and Griffiths, 1984), particularly for Clinids (Marsh et al. 1978). In contrast, bare substratum generally supports lower numbers of species and individuals but attract a different suite of species including blennies and gobies (Bennett and Griffiths, 1984).

There have been comparatively few studies aiming at experimentally determining the importance of rockpool habitats on fish assemblages, and all of which have exclusively concentrated on manipulating substratum cover, which is also termed substratum heterogeneity or 'rugosity' (Davis, 2000b). Unfortunately, the results of most studies are relatively unconvincing due to poor experimental designs and inappropriate statistical analyses and a failure to consider temporal scale. Nonetheless, Davis (2000b) found the numbers of species and individuals to increase and decrease in rockpools where substratum cover was increased and decreased. However, only two days separated samples in the manipulated rockpools, which may severely impede the recruitment and recolonisation opportunities of intertidal fishes. At this time there is apparently no study that has specifically investigated the influence of suspended cover on the structure of intertidal rockpool fish assemblages (but see Cross, 1981; Silberschneider and Booth, 2001).

Studies in Chapters 6 and 7 uncovered some of the effects of physically manipulating fish numbers on fish assemblages. The present Chapter aimed to investigate the role of manipulating the physical shape of the environment to assess its role in structuring rockpool fish assemblages by removing or adding two major rockpool habitat types, substratum and suspended (algal) cover.
MATERIALS AND METHODS

Study design

Using the bilge pump sampling method described in Chapter 2, fish were collected from 20 rockpools at both Puckey’s Bombora and Bass Point (Fig. 25) between 7 February and 7 August 2001. Rockpools at each site were situated 50-200 m apart, and were selected for similarity of physical parameters, mainly volume (105-570 l), substratum type (pebbles, cobbles and small boulders) and position in the mid-intertidal zone (0.5-1.2 m above MLLW). Before any manipulation of rockpool characteristics was undertaken each rockpool was sampled twice, separated by about 4 weeks to allow recolonisation of rockpools by fishes among samples (see Chapter 6). After fish were removed following the second sampling occasion, rockpool characteristics were manipulated. Fishes removed from these rockpools were released to rockpools or the shallow subtidal at least 10 m away from the rockpools being sampled.

At each site pools were randomly allocated to represent one of five treatments, each treatment was replicated using four pools at each site:

1) Control pools: rocks and attached algae removed and replaced.
2) -Rock-Algae: all rocks and algae removed
3) +Rock-Algae: additional rocks added only after algae removed
4) +Algae-Rock: algae added and all rocks removed.
5) +Algae+Rock: algae and additional rocks added

The effects of disturbance were accounted for in the control rockpools where all algae and rocks were removed and then replaced during each sampling event. All rockpools were resampled on two occasions after manipulation at intervals of about 4 weeks,
which has been shown to be sufficient time for fish to recolonise rockpools (see Chapter 6; Beckley, 1985) and to recruit to artificial cover (Bell et al. 1987). Since algae commonly found in rockpools could not be transplanted successfully between rockpools, algal cover was simulated in quantitative units by using artificial seagrass units (ASUs), which have been used extensively in estuaries (Bell, 1985; Bell et al. 1985; Virmstein and Curran, 1986; Sogard, 1989; McNeill and Fairweather, 1993; Sogard and Able, 1994; Jenkins and Sutherland, 1997; Edgar 1999). The main objective of this procedure was not to physically mimic actual algae found in rockpools, but to introduce physical structure in a similar form. Eighteen lengths of blue nylon strapping (800 mm in length) were doubled around a 40 x 40 cm square of reinforced steel mesh and secured with nylon cable ties (Plate 7) to create shoot lengths of 400 mm and a density of 225 shoots per m$^2$. This density was considered to be sufficient as fish settling from the plankton have been shown not to discriminate between artificial seagrass beds of different leaf densities but recruit to any available shelter (Bell et al. 1987). This was considered to be a single ASU and only one was designated to each pool. The metal frame was secured in rockpools by fitting the frame with two metal saddles on opposite sides and securing them to 8 mm Dynabolts, which were anchored by drilling holes in the rocky substratum.
Plate 7. Photograph showing the installation of an artificial seagrass unit (ASU) into an empty rockpool at Maloney's Bay, Bass Point after all rocks and foliose algae has been removed. The 40 x 40 cm metal frame is secured to the substratum with metal saddles attached to Dynabolts drilled into the substratum.

After revision of results after the last manipulation samples it was clear that substratum heterogeneity was an important factor but few obvious trends were found involving the two artificial algae treatments. Therefore, additional experimentation was undertaken only using substratum heterogeneity. Treatments were reversed in rockpools that had rock cover added or removed in the first manipulation with the expectation that the numbers of fish and species and species composition would show the opposite trend observed after the first manipulation (samples 3 and 4). Rockpools receiving artificial algal treatments were included in this study by removing the artificial algae and reversing the rock cover treatments introduced in the first manipulation. The overall experimental design is shown diagrammatically in Figure 40.
Figure 40. Experimental design used to test the influence of habitat heterogeneity on the structure of rockpool fish assemblages after physically manipulating algal cover and substratum rock cover. Duration between samples (arrows) is 4-5 weeks.
Statistical analyses

Since the same pools were being repeatedly sampled at relatively short intervals (4 weeks) it is possible that samples may not be independent. Studies in Chapter 6 revealed rockpool fish assemblages generally return to pre-perturbation structure within 1-3 months. To safeguard against the possibility of non-independence, a three factor repeated-measures ANOVA (RM-ANOVA) was used to test for differences in the numbers of species and individuals between months (within subjects factor), sites and treatments (among subjects factors). All factors were considered fixed. For detailed descriptions of this method and tests of assumptions see Chapter 6.

Non-metric multidimensional scaling (nMDS) was used to examine similarities in fish assemblages among locations, treatments and sampling times. Before the analysis, abundances of each species in each sample were fourth-root transformed, to reduce the influence of highly abundant or schooling species. A similarity matrix was then constructed from the transformed data using the Bray-Curtis similarity coefficient (Clarke, 1993). ANOSIM was used to determine whether fish assemblages statistically differed after manipulation of rockpool habitats (times) for each treatment at the two locations. SIMPER was then used to determine which species were responsible for significant differences among a priori groups. Detailed descriptions of these methods are given in Chapter 4.
RESULTS

**Numbers of species and individuals**

A total of 1746 fish from 27 species were caught in rockpools during the study. The significant treatment x time interaction and the highly significant differences for the time factor for both numbers of species and individuals is the most important feature in the results of RP-ANOVAs (Table 33). This indicates that differences in the numbers of species and individuals are evident over time but is dependent upon the treatment examined. Although the patterns of variation in the numbers of species and individuals do not differ among locations, as indicated by a non-significant location x treatment x time interaction term, data could not be pooled across locations due to the significant location main effect (Table 33). This was due to higher numbers of species and individuals being captured at Puckey’s Bombora (SNK test). However, Figure 41 reveals nearly identical patterns in the variation of number of species and individuals for each treatment at both locations. Therefore, the patterns being described will incorporate both locations. For ease of interpretation, variation in numbers of species and individuals were examined separately for each of the manipulations. For the first manipulation, samples from time 1 and 2 (“before” samples) were compared with samples from time 3 and 4 (“after” samples) (see Fig. 40). For the second manipulation, samples from time 3 and 4 (“after” samples) were compared with samples from time 5 and 6 (“reverse” samples) (see Fig. 40).

In the first set of manipulations the number of species and individuals were not significantly different in rockpools used for controls, +algae-rock, +algae+rock, and +rock-algae treatments (Fig. 41; Within subjects simple contrast tests). However, both
the number of species and individuals were significantly lower in rockpools receiving the -rock -algae treatment (Fig. 41; Within subjects simple contrast tests).

In the second manipulation experiment involving manipulation of only substratum complexity, both the number of species and individuals were significantly lower in rockpools after rocks were removed (Fig. 41; Within subjects simple contrast tests). In contrast, both the number of species and individuals were significantly higher in rockpools after rocks were added, with the exception of the +algae-rock treatment (where rocks were added) at Bass Point, where no differences were detected after the manipulation (Fig. 41; Within subjects simple contrast tests). These effects of these manipulations are further reinforced in that the number of species and individuals did not differ in the control rockpools after treatments were reversed in other rockpools (Fig. 41).
Table 33. Results of repeated-measures ANOVAs testing for significant differences in number of species and number of individuals (per m$^3$) among locations (Bass Point and Puckey's Bombora), treatments (+rock-algae, +algae-rock, +rock+algae, -rock-algae, control) and time (six sampling events). Both numbers of species and individuals data were $\log_{10}(x+1)$ transformed before analysis, which removed heteroscedasticity in the data. Mauchly's criterion for sphericity of variances was violated for number of species ($P<0.001$), so analysis was performed using Greenhouse-Geisser adjusted degrees of freedom. Mean squares (MS) and significance levels are shown and significant results are in bold.

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* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. 
**Bass Point**

**Number of Species**

![Graph showing number of species before and after manipulation](image)

**Number of Individuals**

![Graph showing number of individuals before and after manipulation](image)

**Treatment**

**Figure 41.** Mean (±SE) number of species and individuals caught before and after manipulating water-column and substratum complexity of rockpools at Bass Point and Puckey's Bombora and after reversal of substratum complexity treatments ("reverse"). For treatments involving addition of algae in the first manipulation, the algae were removed and substratum complexity treatment reversed. Each before, after and reverse treatment consists of replicate samples which have been pooled for two sampling events.
Puckey's Bombora

Number of Species

Number of Individuals

Figure 41 continued.
Variation in abundance of individual species

Repeated-measures ANOVAs revealed there were significant effects of manipulations upon the number of individuals representing the four most abundant species as the treatment x time interaction and the time main effect were both significant for each species (Table 34). Because patterns of variation in the numbers of species and individuals were no different between Bass Point and Puckey's Bombora, as indicated by a non-significant location x treatment x time interaction term (Table 34), data for each site were pooled and the variation in numbers of species and individuals for treatment over time examined in detail.

During the first set of manipulations significant differences in the numbers of individuals were only evident in rockpools receiving the -rock-algae treatment (Table 34, SNK test; Fig. 42). The numbers of fish for three of the most abundant species were significantly lower after manipulation, with the exception of *Lepidoblennius haplodactylus*, which did not differ for any factor (Table 34, SNK test; Fig. 42).

For the second manipulation the number of *Bathygobius cocosensis* was significantly lower where rocks were removed but increased or did not differ where rocks were added (Table 34, SNK test; Fig. 42). Similarly, the number of *Enneapterygius rufopileus* was significantly lower where rocks were removed, but also decreased or did not differ where rocks were added (Table 34, SNK test; Fig. 42). *Lepidoblennius haplodactylus* clearly showed significant increases in numbers where rocks were added, but also increased or did not differ where rocks were removed (Table 34, SNK test; Fig. 42). The number of *Heteroclinus fasciatus* dramatically decreased after both removal and addition of rock cover, although this probably reflects a decrease in the local abundance.
as numbers in the control pools also declined after other pools were manipulated (Fig. 42).
Table 34. Results of repeated-measures ANOVAs testing for significant differences in number of individuals (per m$^3$) for the four most abundant species among locations (Bass Point and Puckey's Bombora), treatments (+rock-algae, +algae-rock, +rock+algae, -rock-algae, control) and time (six sampling events). Both numbers of species and individuals data were $\log_{10}(x+1)$ transformed before analysis, which removed heteroscedasticity in the data. Mauchly's criterion for sphericity of variances was satisfied ($P>0.05$) in each case so analysis was performed using unadjusted degrees of freedom. Mean squares and significance levels are shown and significant results are in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Bathygobius cocosensis</th>
<th>df</th>
<th>Enneapterygus rufopileus</th>
<th>df</th>
<th>Lepidoblenius haplodactylus</th>
<th>df</th>
<th>Heteroclinus fasciatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among subjects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Location</td>
<td>1</td>
<td>3.37**</td>
<td>1</td>
<td>18.90***</td>
<td>1</td>
<td>14.63***</td>
<td>1</td>
<td>1.71</td>
</tr>
<tr>
<td>Treatment</td>
<td>4</td>
<td>1.56*</td>
<td>4</td>
<td>0.73</td>
<td>4</td>
<td>1.31*</td>
<td>4</td>
<td>1.31*</td>
</tr>
<tr>
<td>Location x Treatment</td>
<td>4</td>
<td>0.28</td>
<td>4</td>
<td>0.06</td>
<td>4</td>
<td>1.76**</td>
<td>4</td>
<td>0.24</td>
</tr>
<tr>
<td>Residual</td>
<td>30</td>
<td>0.43</td>
<td>30</td>
<td>0.36</td>
<td>30</td>
<td>0.35</td>
<td>30</td>
<td>0.47</td>
</tr>
<tr>
<td>Within subjects</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>3.20</td>
<td>1.92***</td>
<td>3.55</td>
<td>6.05***</td>
<td>3.14</td>
<td>7.63***</td>
<td>3.29</td>
<td>6.96***</td>
</tr>
<tr>
<td>Location x Time</td>
<td>3.20</td>
<td>2.34***</td>
<td>3.55</td>
<td>0.62*</td>
<td>3.14</td>
<td>0.53**</td>
<td>3.29</td>
<td>0.38</td>
</tr>
<tr>
<td>Treatment x Time</td>
<td>12.79</td>
<td>0.74***</td>
<td>14.18</td>
<td>0.41*</td>
<td>12.55</td>
<td>0.41***</td>
<td>13.16</td>
<td>0.46**</td>
</tr>
<tr>
<td>Location x Treatment x Time</td>
<td>12.79</td>
<td>0.19</td>
<td>14.18</td>
<td>0.23</td>
<td>12.55</td>
<td>0.13</td>
<td>13.16</td>
<td>0.29</td>
</tr>
<tr>
<td>Residual</td>
<td>95.89</td>
<td>0.16</td>
<td>106.35</td>
<td>0.22</td>
<td>94.16</td>
<td>0.12</td>
<td>98.68</td>
<td>0.15</td>
</tr>
<tr>
<td>Mauchly sphericity test, $W$</td>
<td>0.041***</td>
<td>0.052***</td>
<td>0.055***</td>
<td>0.066***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greenhouse-Geisser Epsilon</td>
<td>0.639</td>
<td>0.709</td>
<td>0.628</td>
<td>0.658</td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$. 

Figure 42. Mean (±SE) number of individuals representing the four most abundant species caught before and after manipulation of rockpool habitat complexity and following reversal of substratum complexity treatments ("reverse"). Each bar comprises eight samples pooled for two sampling events separated by 4-5 weeks.
**Fish assemblage structure**

**Manipulation 1**

Since ANOSIM revealed that the fish assemblages of Bass Point and Puckey's Bombora were significantly different ($R=0.220; P<0.0001$), it was necessary to investigate the effects of experimental treatments separately for each site. Ordination of abundance data revealed some differences in community structure after manipulations for some treatments, mainly -rock-algae, although due to high stress values for two-dimensional ordination plots these differences were not obvious or convincing (Fig. 43). However, ANOSIM revealed fish assemblage structure differed after manipulations involving the -rock-algae and +algae-rock treatments (Table 35a). Differences in fish assemblages after manipulations involving these two treatments was primarily due to lower abundances of *Bathygobius cocosensis*, although for the +algae-rock treatment *Istiblennius edentulus* was higher before manipulation (Table 35a).
Figure 43. Non-metric MDS ordination plots comparing centroids of fish assemblages in rockpools at Bass Point and Puckey's Bombora before and after the first manipulations of physical rockpool features were undertaken. Four rockpools comprised each treatment type at each location and each rockpool was sampled twice before and after manipulations were undertaken. Centroid values (mean of 8 samples) were calculated from principal coordinates of Bray-Curtis similarities. Stress values are shown.
Table 35. Results of one-way ANOSIM testing for differences in fish community structure after application of treatments into rockpools a) control, +algae-rock, +algae+rock, +rock-algae and -rock-algae and b) reversal of substratum treatments applied in manipulation 1 at Bass Point and Puckey's Bombora. SIMPER analysis indicates species contributing to at least 10% of the dissimilarity among significantly different groups. Percentage contribution and whether abundances of individual species were higher before (B) or after (A) habitat manipulations are shown in parentheses. Key to species in SIMPER: Ac=Aspasmogaster costatus; Al=Aspasmogaster liorhyncha; Bc=Bathygobius cocosensis; Er=Enneapterygius rufopileus; Ge=Girella elevata; Hf=Heteroclinus fasciatus, Hw=Heteroclinus whiteleggi; Ie=Istiblennius edentulus; Lh=Lepidoblennius haplodactylus; Pi=Parablennius intermedius; Sl=Scorpis lineolatus. *=P<0.05; **=P<0.01; ***=P<0.001. Significant results are shown in bold.

a)  

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bass Point</th>
<th>Puckey's Bombora</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>SIMPER</td>
</tr>
<tr>
<td>Control</td>
<td>0.004</td>
<td>-</td>
</tr>
<tr>
<td>+ Rocks</td>
<td>0.053</td>
<td>-</td>
</tr>
<tr>
<td>- Rocks &amp; Algae</td>
<td><strong>0.451</strong></td>
<td>Bc (B), Hf (B), Ac (B).</td>
</tr>
<tr>
<td>+ ASU</td>
<td><strong>0.355</strong></td>
<td>Bc (B), Ac (B), Ie (B).</td>
</tr>
<tr>
<td>+ Rocks &amp; ASU</td>
<td>0.081</td>
<td>-</td>
</tr>
</tbody>
</table>

Global R = 0.216***

Global R = 0.189***

b)  

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Bass Point</th>
<th>Puckey's Bombora</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R</td>
<td>SIMPER</td>
</tr>
<tr>
<td>From -Rock to +Rock</td>
<td><strong>0.098</strong></td>
<td>Bc (A), Er (A), Im (A).</td>
</tr>
<tr>
<td>From +Rock to -Rock</td>
<td><strong>0.493</strong></td>
<td>Bc (B), Ie (B), Ge (B).</td>
</tr>
<tr>
<td>Control</td>
<td><strong>0.499</strong></td>
<td>Bc (B), Ac (B), Hf (B).</td>
</tr>
</tbody>
</table>

Global R = 0.286***

Global R = 0.169***
Manipulation 2

Ordination of abundance data revealed obvious differences in fish species composition with respect to treatments, although separation of control rockpools that were not manipulated was also apparent (Fig. 44). ANOSIM revealed that +rock and -rock treatments and control rockpools produced significantly different fish assemblages after manipulations at both locations (Table 35b). Differences among +rock treatments were due to higher abundances of resident benthic species after addition of rocks at Bass Point and Puckey's Bombora although *Enneapterygius rufopileus* was caught in higher numbers before manipulations at Puckey's Bombora (Table 35b). The -rock and +rock treatments reflected similar results at both locations in that benthic resident species had highest abundances when rock cover was present (Table 35b). It was interesting to note that removal of rocks also resulted in lower numbers of the mid-water dweller, *Girella elevata*.

The cause effects of addition and removal treatments are well supported by investigating the results of the control rockpools. Although significant differences in control rockpools were detected after manipulations were undertaken at the other rockpools, the species which were responsible for differences were not those contributing to at least 10\% of the dissimilarity among samples, namely *Aspasmogaster costatus* and *Heteroclinus fasciatus* at Bass Point. Furthermore, high abundance of some species in control rockpools was not consistent with the periods where the same species were in highest abundance in treatment rockpools (Table 35b). This reinforces treatment effects. There are two clear examples of the latter case. First, at Bass Point *Bathygobius cocosensis* was in highest abundance in control pools before manipulations took place, whereas numbers were higher after manipulation among +rock treatments.
Second, at Puckey's Bombora *Lepidoblennius haplodactylus* was more abundant in control pools after manipulations in other rockpools, but was more abundant before rocks were removed in the -rock treatment (Table 35b).
Figure 44. Non-metric MDS ordination plots comparing centroids of fish assemblages in rockpools at Bass Point and Puckey's Bombora before and after the second manipulations (substratum heterogeneity only). Four rockpools comprised each treatment type at each location and each rockpool was sampled twice before and after manipulations were undertaken. Centroid values (mean of 8 samples) were calculated from principal coordinates of Bray-Curtis similarities. Stress values are shown.
Length-frequency distributions

There appeared to be no obvious variation in length-frequency distributions for the four most abundant species after the first set of manipulations of rockpool habitats at Bass Point or Puckey's Bombora. Although in numerous instances the absolute number of fish was lower before or after manipulations, depending upon the treatment administered, length-frequency distributions of fish in less abundant samples generally appeared to be a subset of those in samples where catches were higher (Fig. 45).

There were two exceptions to this case with *Bathygobius cocosensis* and *Lepidoblennius haplodactylus*, although it could be seen that variation was unlikely due to manipulation of rockpool habitats. For example, *B. cocosensis* were mainly represented by fishes less than 30 mm TL before manipulations in +rock-algae pools, but after rocks were added the most abundant fishes were 40-51 mm TL (Fig. 45e). However, samples taken from control pools revealed a similar pattern in that smaller fish (<25 mm TL) were more abundant before manipulations were undertaken in pools receiving treatments, but larger (40-52 mm TL) after manipulations (Fig. 45a).

Similarly, *Lepidoblennius haplodactylus* were mainly represented by fishes larger than 40 mm TL before manipulations in pools receiving any treatment, but after manipulations the most abundant fish represented a single cohort of less than 30 mm TL (Fig. 45b-e). Again, control pools revealed a nearly identical pattern (Fig. 45a) and thus, changes in demographic composition probably reflect variations across the entire intertidal population and are unlikely to be attributable to changes in habitat.
Figure 45. Length-frequency distributions of the four most abundant species caught in rockpools (combined for Bass Point and Puckey's Bombora) before and after manipulations of rockpool variables. Treatments shown are a) control (unmanipulated), b) -rock-algae, c) +rock-algae, d) +algae-rock and e) +algae+rock. Before and after samples each comprise two sampling occasions where eight rockpools (four pools from each location) represented each treatment.
Figure 45 continued.
DISCUSSION

These manipulation experiments revealed a number of significant findings that improves the understanding of processes controlling fish assemblage structure in rockpools. Most importantly, fish assemblages are highly dependent upon the presence of physical structure of habitats within rockpools and fish assemblage structure can be altered by manipulating the complexity of these habitats. The amount of substratum cover appeared most important when offered, although fish readily utilised suspended cover in the absence of substratum cover. However, the amount of cover available only appears to be important to a point where other resources, possible food, in rockpools may become limiting. Finally, the use of artificial seagrass units was successful in attracting similar fish assemblages, both species and demographic composition, as natural algae habitat and is therefore useful for future experiments.

Suspended cover (ASUs)

The present study has shown that increasing suspended structural heterogeneity does not appear to increase fish abundance or species richness at Bass Point and Puckey's Bombora. This finding opposes strongly with evidence that has shown increased algal cover increases the number of species and fish in intertidal habitats (see Bennett and Griffiths, 1984; Davis 2000b). These studies have all reached this conclusion on the basis of multiple regression analysis from mensurative studies, which are unable to define cause effects (Underwood et al. 2000). Nevertheless, Bennett and Griffiths (1984) suggested that the presence of algal cover may increase species richness and abundance of fish due to an increase in the number of microhabitats, but they could not conclude whether this was due to shelter or dietary preference by fishes. In a study of algal-dwelling Clinids in South African rockpools, Marsh et al. (1978) found the diets
of most fish to contained items that are not associated with algae, and thus feeding
probably occurs elsewhere within the rockpool or adjacent intertidal zone.

The use of artificial seagrass units (ASUs) in the present study allowed the effects of
suspended cover (apart from associated food sources) on rockpool fish assemblages to
be isolated. The finding that fish assemblage structure was no different after
introduction of ASUs reveals two important results. First, ASUs attract similar fish
communities as natural seaweeds and algae and are therefore suitable for manipulation
studies of this type. Second, cover alone in the water column has a significant influence
on fish assemblage structure of rockpools. This can be illustrated clearly when
considering that the blue colour of the "shoots" does not resemble any natural algae or
sponges, which many fish appear to use as shelter in the rockpools at the two study
sites. Many fishes are camouflaged against the generally dark brown and green algae in
rockpools, so their stark contrast against the blue shoots may provide evidence that the
artificial cover provides adequate refuge from predators and/or harsh environmental
conditions (wave surge and direct sunlight). The hypothesis that fishes resided in the
experimental rockpools purely for the purpose of gaining shelter is further reinforced
since all sponges and foliose algal cover were removed in experimental pools, and
shoots did not support any significant epiphytic cover to attract fishes by providing any
type of significant food source. Black and Miller (1991) found that removal of intertidal
weed cover had no effect on the abundance of fishes in Nova Scotia, although their
catches mainly comprised subtidal species that only entered the intertidal to feed during
high tide and not permanent residents.
Because this is apparently the first study that has introduced artificial 'algal' cover into rockpools, there are unfortunately no comparisons to be made with other studies. However, these results are in close agreement with those of Bell et al. (1985, 1987) who found that ASUs attract similar fish assemblages as natural cover located nearby, such as Zostera capricorni and Posidonia australis seagrass beds within estuaries. The lack of epiphytic biota associated with the artificial shoots used in these studies provided sufficient evidence that cover alone is probably the most significant factor for attracting settling estuarine fishes. Bell et al. (1987) suggests that fish probably recruit to any available shelter after finding that species commonly among seagrasses also recruited to other artificial structures such as man-made jetties and metal cages. This model also seems applicable for rockpools as fish consistently recruited to rockpools where ASUs were added even where there was no substratum cover.

Although Bell et al. (1987) were able to determine the role of seagrasses in the recruitment of postflexion and juvenile fishes, a large number of the fishes he examined only use seagrasses during their juvenile life phases (but see Bell and Westoby, 1986c). They gradually move to habitats that offer different food sources and less structural complexity. For example, the yellowfin bream, Acanthopagrus australis, recruits to estuarine seagrass beds and remain there until they are a few months old and then move to bare sand and mud substrata (West, 1993; Griffiths, 2001c). In contrast, rockpools ichthyofaunas are primarily comprised of permanent residents that may utilise the same microhabitat type for their entire lives. In the present study the vast majority of fish (80%) were greater than 30 mm TL and were thus not juveniles recruiting to the manipulated rockpools for the first time, but were fish relocating from adjacent rockpools or were possibly the same fish originally captured that were returning to their
home pool (see Chapter 7). These results suggest that cover is still a significant factor for rockpool selection by adults and suggests they are vulnerable to predation even at larger sizes during low tide when the rockpools become isolated and easily accessible to large terrestrial predators, such as piscivorous birds (Gibson and Yoshiyama, 1999).

**Substratum heterogeneity**

It was clear that substratum heterogeneity was the most significant factor for influencing fish assemblage structure, as significant increases and decreases in the numbers of species and individuals could be predicted by adding and removing rock cover, respectively. These findings are in agreement with the results of Cross (1981) and Davis (2000b) who manipulated substratum heterogeneity (which they term 'rugosity') in US rockpools and found more fish to recolonise pools of high heterogeneity than pools with low heterogeneity. However, the results of the present study revealed that an increase in rock cover (substratum heterogeneity) in rockpools where rock cover was already present did not necessarily increase the number of fish or species or even significantly influence species composition. However, the complete removal of rocks resulted in dramatic declines in species numbers and fish to the stage where most rockpools did not contain a single fish. These changes may be attributed to the fact that the vast majority of dominant taxa found in these rockpools, which mainly represent the families Gobiidae, Tripterygiidae, Gobiesocidae and Blennidae are benthic, or at least demersal. Thus, an increase in substratum heterogeneity would potentially increase the number of microhabitats available and result in higher numbers of fish being able to make use of a rockpool. However, in the first manipulation increasing rock cover in a rockpool may not have a dramatic effect on fish assemblage structure if its carrying capacity has already been reached. Addition of rock cover may increase the number of microhabitats
available for additional fish to exploit but not increase the carrying capacity if other resources are limited, such as food, so there may be little incentive for fish to remain in those pools. On the other hand, where rocks are completely removed there is no protection from predation and thus, shelter becomes the limiting resource. This was clearly observed between sampling events where pools having no rock cover often did not contain fish. However, a few small cobbles were often washed into these pools during large seas, which appeared to be sufficient cover for small fish to exploit as fish, mainly *Bathygobius cocosensis* and *Istiblennius* spp., were often found huddling around these isolated rocks.

These findings are similar to those of Davis (2000a) who found no increase in the number of species and individuals where rock cover was added to rockpools, but a significant ($P<0.001$) decrease in the number of species and individuals where rock cover was completely removed. However, the results appear to largely reflect the dependence on rock cover by the most abundant species found in her study pools (*Clinocottus analis*, *Girella nigricans* and *Gobiesox rhessodon*) and not necessarily the entire community. In contrast, Cross (1981) arrived at the rigid conclusion that cover is not a limiting resource for fish in rockpools after finding that fish numbers did not change when all cover was experimentally removed from rockpools at three localities in North America. However, he also suggests that a 25-69% decrease in water depth in rockpools receiving additional rock cover may have confounded the results for numerous species (mainly representing the families Cottidae, Stichaeidae and Pholidae) that prefer deeper pools.
Another possible explanation for these results is that fish display no preference for rockpool habitats for food at all. There is good evidence to suggest that most fishes only utilise rockpools as temporary refuges before moving throughout the intertidal zone during high tide to feed (Bennett et al. 1983). For example, Marsh et al. (1978) found that Clinids in South Africa travel throughout the intertidal zone to feed at high tide but become less active and seek cover among algal fronds in rockpools at low tide. This would certainly explain the lack of variation in fish assemblages where rock cover was added to existing rock cover, as there is probably already sufficient cover for the short time fish intend using the pool. However, it is possible there may be a time lag for fish to eventually find a rockpool with additional cover, which may only become obvious after a major recruitment event. In pools where there is no cover, fish would obviously be at significantly greater risk of predation from terrestrial predators such as piscivorous birds (see Robertson, 1974; Yoshiyama, 1981; Gibson and Yoshiyama, 1999) and snakes (Batts, 1961) and so they probably seek alternative refuge. However, it cannot be ignored on some occasions fish were still found in pools have absolutely no algae or rock cover, albeit in very low numbers. This may indicate that some fish may accidentally become stranded by the receding tide during high tide movements and may resort to finding any available refuge. Even such featureless pools would no doubt offer fishes greater low tide protection from predators and desiccation than being stranded out of water.

Although substratum heterogeneity appeared to be the most important factor influencing rockpool fish assemblages, they are probably affected by the combined effects of both substratum and suspended cover, but individual species probably have the capacity to utilise, at least in the short-term, either habitat type. For example, dominant species that
are nearly exclusively benthic, such as *Bathygobius cocosensis*, *Enneapterygius rufopileus* and *Lepidoblennius haplodactylus*, were still seen to be in higher abundances, albeit not statistically, in pools where only suspended algal cover was offered. Furthermore, the abundance of Clinids is often closely related to the presence of algae (Marsh *et al.* 1978), although in the present study it appeared that the presence of both habitats is important for the most abundant Clinid, *Heteroclinus fasciatus*. These combined effects of habitats were well illustrated at the assemblages level, particularly in the first manipulation study. Here significantly lower numbers of species and individuals were found in pools where both rocks and natural algae cover was removed, whereas fish assemblage structure was maintained at pre-perturbation levels in other rockpools so long as at least one habitat type was offered.

The previous two Chapters have described experiments that investigated the effects of manipulating rockpool fish assemblages and the present Chapter quantified the effects of manipulating the physical structure of the rockpool environment. These Chapters provide a general understanding of some important processes operating in rockpool fish assemblages and have attempted to provide an explanation of patterns of variation observed in Chapters 3 and 4. The following Chapter will attempt to bring together the results of these studies and discuss the dynamics of NSW rockpool fish assemblages.
Chapter 9
General Discussion

The ease of access and low cost of sampling intertidal rockpool fish assemblages make them convenient study subjects for testing existing principles or developing new hypotheses in fish ecology. A small number of researchers have realised this potential and tested some general ecological principles using rockpool fish communities such as competition (Pfister, 1995), recolonisation and extinction processes (Beckley, 1985a; Pfister, 1998), habitat dependence (Faria and Almada, 1999, 2001; Davis 2000b), consequences of recruitment variability (Pfister, 1996) and population regulation mechanisms (Grossman, 1982). However, the vast majority of studies of rockpool fishes have only attempted to describe the fish assemblages and their patterns of variation (see Chapter 3). The recognised paucity of data on rockpool fishes in Australia highlights an urgent need to document the current state of the fish assemblages for both the purposes of natural history and to provide additional scientific information to enhance management of intertidal biodiversity (i.e. Marine Protected Areas). However, after documenting the structure and patterns of variability within these fish assemblages, an excellent opportunity is provided to test some important ecological principles in a little studied system.

Chapter 1 identified seven objectives to be met in this thesis and these can be seen to contribute to the scientific understanding of three key components in fish ecology. These are: 1) the structure and patterns of spatial variation in rockpool fish assemblages, 2) the role of fish movements (recruitment, relocation and homing) in influencing population dynamics and 3) the role of structural heterogeneity in structuring fish
assemblages. Discussion of each of these components will now be taken in turn and then to link these processes, a simple conceptual model has been developed to provide an understanding of the population dynamics of NSW rockpool fish assemblages. The limitations of this model and the possible directions for future research will then be discussed. Finally, management of the intertidal zone will be discussed in relation to the findings of the present study.

Structure and spatial variation in rockpool fish assemblages

The 50 species comprising the rockpool fish assemblages of the NSW south coast is significantly lower than the number of species on coral reefs, is comparable to most temperate subtidal rocky reefs and estuaries, and species rich compared to rockpools at other locations at similar latitudes. The reason for the relatively high species diversity in this region is likely to be the convergence of temperate waters with both tropical and cool temperate waters (Kuiter, 1993; Smith and Suthers, 1999). The latitude of this convergence zone is dependent on the seasonal effect of the warm waters of the East Australian Current along the NSW coast (Zann, 2000). The important role of the current is demonstrated by, for example, the seasonal occurrence of tropical fishes transported further south than they are normally distributed. As a result, 30% of species found in rockpools during the present research have an Indo-Pacific distribution. However, the vast majority of species found were endemic to Australian waters, and representing the families Blenniidae, Clinidae, Tripterygiidae, Gobiidae and Gobiesocidae. The vast majority of species found in rockpools from these families are permanent intertidal residents possessing various specialised adaptations for intertidal life. Adaptations such as 'walking' fins and air breathing, allow them to cope with the harsh and variable environmental conditions of intertidal rockpools which are normally too severe for most
fishes to contend with (Martin, 1995). However, some secondary residents with seemingly few morphological adaptations for intertidal life, such as *Girella elevata*, appear to possess behavioural and possibly physiological adaptations that aid them in being able to opportunistically utilise rockpools, mainly as juveniles, before moving to the subtidal waters to complete the rest of their lives.

In light of the increasing anthropogenic impacts upon aquatic environments such as overfishing and habitat degradation, identification and protection of nursery habitats of economically important fish species has been recognised as a management priority in recent decades (Blaber et al. 2000). Therefore, it is particularly important to note that this research has found that rockpools in southeastern Australia may provide important nursery habitat for some species of economic or conservation importance. Although many economically important species including *Girella elevata, Myxus elongatus, Scorps lineolatus, Achoerodus viridis, Ammotretis rostratus* and *Scorpaena cardinalis* were caught in low numbers, this may merely reflect the relatively small rockpools sampled during the present research. From casual observations of larger rockpools (greater than about 5 m$^2$) the diversity and number of fish representing economically significant species greatly increases. Particularly conspicuous species in these larger rockpools are the leatherjackets (Monacanthidae), sea breams (Sparidae), mullets (Mugilidae), wrasses (Labridae), trevallies (Carangidae), drummers (Kyphosidae and Girellidae) and morwongs (Cheilodactylidae).

The capture of juvenile black rockcod, *Epinephelus daemelii*, from south coast NSW rockpools is particularly noteworthy as this once prolific species is now listed as vulnerable to extinction under the *Fisheries Management Act 1994*. This species has
also been captured in low numbers as juveniles in rockpools at two other locations in northern (Wilson, 1989) and central NSW (Lardner et al. 1993), which indicates that rockpools may be one of the key nursery areas for *E. daemelii*.

A growing literature has shown that the structure of rockpool fish assemblages varies significantly over various spatial scales (for recent examples see Faria and Almada, 1999; Beckley, 2000; Davis 2000a, 2000b). The rockpool fish assemblages investigated in this research certainly appear no different, as Chapters 4 and 5 revealed that variation in the structure of fish assemblages occurred with respect to both vertical and horizontal separation of rockpools across spatial scales from metres to hundreds of kilometres. Not only were these patterns probably attributable to the preferences of rockpool fishes to particular habitat types for shelter or food (Chapter 8; Marsh *et al.* 1978; Berger and Mayr, 1992; Faria and Almada, 2001), but it is possible that fish physiology may also influence the spatial organisation of species. This was particularly evident with respect to the vertical distribution of fishes (Chapter 5). Highly adapted resident species generally occupy rockpools of the highest elevations where environmental conditions can be particularly harsh and extremely variable (Huggett and Griffiths, 1986). In contrast, transients and opportunists possessing few or no adaptations for intertidal life occupy lower rockpools where water chemistry is similar to that of the adjacent ocean. Similar explanations for a turnover in species composition with respect to tidal height have been given by researchers undertaking studies in the United States (Nakamura, 1976b; Yoshiyama, 1981), France (Gibson, 1972) and the Hawaiian Islands (Gosline, 1965). Yoshiyama (1981) also documented a decline in fish size for numerous species with increasing tidal height of rockpools. He suggests that this may be due to larger fish being more conspicuous to terrestrial predators. The lack of ontogenetic shifts among
species with tidal height of rockpools in the present research may reflect the low numbers of piscivorous terrestrial predators observed during the study period.

The role of fish movements in rockpool fish assemblages

In the present research, the combined effects of recruitment and inter-rockpool movements by fish were found to be responsible for temporal variability in rockpool fish assemblages, although a consistent finding was the stability and persistence of taxocene structure. On the scale of months to years, the same species dominated at each location studied (Chapter 4), although their abundances varied over time. This appeared to be mainly driven by the recruitment of juveniles which, for most species, occurs during summer through to autumn (February to April). At these times the abundance of individuals representing each species changes but the relative change is minimal, resulting in persistent and stable community structure. The most dynamic component of the rockpool fish assemblages were the less common species, such as Parablennius intermedius, Heteroclinus fasciatus, Istiblennius meleagris, and Aspasmogaster costatus, that varied greatly in abundance over time. However, their generally low abundances and seemingly sporadic presence at some locations (and rockpools) made it difficult to identify patterns in the variation of their abundances.

In Chapter 5, short-term (weeks to months) temporal variability was shown to be far less obvious due to the high resilience of fish assemblages. After sampling, which may resemble natural catastrophic disturbances, fish rapidly recolonised rockpools to pre-perturbation levels, often within the space of weeks. Such rapid colonisation of vacant habitat is not uncommon among marine fish assemblages. For instance, Shulman (1985) found fish colonisation of denuded patch reefs began within hours, although the speed
of colonisation is dependent upon the timing of the disturbance relative to the availability of recruits (Doherty and Williams, 1988). Population replenishment is primarily driven by larval recruitment in other coastal fish assemblages such as coral reef patches (Doherty, 1983; Jones, 1990) and intermittently open estuaries (Griffiths, 1999). In contrast, sub-adult and adult fishes moving in from adjacent rockpools primarily drive recolonisation of rockpools examined in the present research. Similar mechanisms for rapid initial fish recolonisation in rockpools exist in other countries including South Africa (Beckley, 1985a, 2000), the United States (Grossman, 1982; Matson et al. 1986) and Australia (Lardner et al. 1993), although these studies also highlight that this may be secondary to recruitment in the longer term. The rapid movement of fish from nearby habitats to vacant habitat may signify competition for a finite number of quality rockpools, and microhabitats within rockpools, in the intertidal zone and is indicative of post-recruitment density-dependant regulation (Faria and Almada, 1999). The fact that some species may range widely throughout the intertidal zone at high tide (Williams, 1957; Green, 1971a) may also contribute to rapid colonisation of vacant rockpools. Further, the persistent taxocene structure of recolonised assemblages may be a result of only a small number of fishes with specialised adaptations to permanently reside within rockpools. The relative abundances of these species are therefore probably determined by their relative abundances in nearby rockpools (Polivka and Chotkowski, 1998). Juveniles only appear to be a major contributor to the recolonisation process if perturbations coincide with major recruitment periods (also see Beckley, 1985a; Willis and Roberts, 1996).

Despite rockpool fish assemblages occupying a highly variable environment, their high resilience and persistence suggest that rockpool fish assemblages are regulated by
deterministic, rather than stochastic, processes (Grossman, 1982, 1986; Mahon and Mahon, 1994; Faria and Almada, 1999). Detailed descriptions of some of these processes are provided in Chapter 4. However, Willis and Roberts (1996) suggest New Zealand rockpool fish assemblages are regulated by a combination of both processes. This contrasts markedly with a stochastic non-equilibrium model assumed to regulate some coral reef fish assemblages, best known in the literature as the 'Lottery Hypothesis' (Sale, 1977, 1978, 1982). This model assumes a continuous saturation of larvae but a limiting resource is partitioned randomly among species each having a similar competitive ability. The species that can exploit an available resource is therefore determined randomly from species present in the larval pool. This model does not appear to apply in the present study nor apparently to most other rockpool fish populations, as it predicts that species composition varies randomly over time. Patterns of variation in the rockpool fish assemblages appear more consistent with a deterministic model of single-species equilibrium (sensu Grossman, 1982). This model suggests that assemblages are consistent (=persistent) and stable through time due to replenishment from individuals seeking to 'upgrade' from less suitable habitats or recruit as larvae. This reflects the movement of fishes from a benthic source in nearby rockpools to establish a denuded rockpool and the timing of the disturbance governs the extent of recruitment by juveniles. This model is also relevant as it suggests that assemblages will be fragmented into several local populations which may only show a high degree of similarity when the larval pool for all species saturates all local populations (i.e. recruitment periods) (Doherty and Williams, 1988).

An additional factor contributing to the high resilience of rockpool fish assemblages is the homing ability of many rockpool fishes. In Chapter 7, recolonisation experiments
revealed fish assemblages can be replenished within a period of one week and it appears that many of the primarily recolonists are homing fish. Homing has not been addressed in the various models of reef fish assemblages (see review by Doherty and Williams, 1988) as most models assume that a fish vacating a habitat during a disturbance constitutes mortality.

Rockpools can be considered 'island' habitats among an otherwise desolate inhospitable rocky landscape at low tide (Underwood and Skilleter, 1996). Therefore, the recolonisation process of denuded rockpools by fishes is an example of 'Island Biogeography'. The equilibrium theory of island biogeography (MacArthur and Wilson, 1967) proposes that the number of species on an island is a dynamic balance between the number of species colonising from the 'mainland source pool', and the number of species becoming extinct after colonisation. At some number of species, these two processes will be in equilibrium and this number will often depend on the number of habitats available for individuals to exploit and the extent of interspecific interactions. Although this theory has been derived using oceanic islands (MacArthur and Wilson, 1967), it has been widely applied to habitat 'islands' such as fragmented grassland (Robinson and Quinn, 1988), mountaintops (Brown, 1971), forests (Lomolino et al. 1989), drifting kelp rafts (Hobday, 2000), coral reefs (Scheltema, 1987) and seagrass beds (Virnstein and Curran, 1986; Sogard, 1989).

In the context of the present research, the 'source' pool of new fishes for the rockpool 'islands' is the ocean, which can be assumed to contain a certain density of intertidal fish larvae at any time. This density will depend upon the breeding times of constituent species and the local environmental conditions (Thresher et al. 1989). As a result, the
Chapter 9 General Discussion

colonisation rate of rockpools can be expected to vary with respect to the time of year that a habitat becomes vacant (Beckley, 1985a; Willis and Roberts, 1996). However, in the intertidal zone nearby rockpools provide additional 'source' pools to supply colonists to available niches in the rockpool 'islands'. In Chapter 6 it was revealed that these smaller sources probably supply the bulk of colonists to defaunated rockpools, as adults and subadults were by far the dominant fish found after recolonisation. This may be a result of the reproductive strategies of resident rockpool fishes, as many species produce demersal eggs (Marliave and DeMartini, 1977; DeMartini, 1978; Ruck, 1980) and show parental care (DeMartini and Patten, 1979). As a result, larvae may not travel great distances and many resist being transported offshore by currents, and hence remain close to their natal habitats (Marliave, 1986). Tagging experiments in Chapter 7 revealed that small juveniles display homing behaviour and may not move great distances for much of their life history. There are some suggestions that fish assemblages on a single rocky shore or adjacent locations may support genetically distinct populations (Cross, 1981). Although this area has attracted little attention (but see Yoshiyama and Sassaman, 1987; Steprien and Rosenblatt, 1991), there is increasing evidence to support this notion (but see Waples, 1987; Terry et al. 2000; Riggins and Nachman, 2001).

In contrast to rockpools in the present research, recruitment of planktonic larvae from this ocean 'source' pool is the major source for colonisation in other coastal fish assemblages, such as coral reefs (Sale et al. 1994) and estuaries (Kok and Whitfield, 1986; Griffiths, 1999a, 2001c). Equivalent smaller sources in these habitats, such as adjacent patch reefs, tend to supply only a 'supplementary' source of colonists to vacant habitat (Bohnsack et al. 1994; Hixon, 1998). This may similarly be a result of the
reproductive strategy of fishes in these systems. For instance, coral reef fishes mainly produce pelagic larvae with long planktonic phases to maximise dispersal (Leis and Rennis, 1983; Victor, 1986; Leis, 1989). This often results in low genetic divergence within populations, even when separated by thousands of kilometres (Shulman, 1998; but see Doherty et al. 1995 when this may not apply). Therefore, in the context of coral reefs, the ocean provides the greatest source pool of potential colonists than do benthic fishes of adjacent reefs. The recruitment dependent population dynamics of coral reef fish again reiterates why a non-equilibrium population model such as the lottery hypothesis is not relevant to rockpools and why the single-species equilibrium model is more useful as it assumes some degree of population differentiation.

The role of cover in rockpool fish assemblages

There is widespread belief that many rockpool fishes display preferences for specific microhabitats within rockpools. Most of this evidence is derived from 'mensurative' studies which correlate patterns of variation in fish assemblages with variation in environmental parameters, such as algae and rock cover (Marsh et al. 1978; Bennett and Griffiths, 1984; Prochazka and Griffiths, 1992; Faria and Almada, 2001). Unfortunately, such studies are often only useful to ecologists for providing a logical start point for further study, as only manipulation experiments can define causal effects (Underwood et al. 2000). The small number of well designed manipulation studies in rockpool fish ecology means there is still relatively little conclusive scientific evidence of processes which underpin observed patterns (but see Pfister, 1995). Studies in Chapter 4 provided correlative evidence that suggested the distribution of rockpool fishes were influenced by particular habitats such as substratum and algal cover. However, the manipulation experiments in Chapter 8 were able to better define the role
that structural complexity of abundant habitat types play in controlling fish assemblage structure.

The amount of substratum rock cover appeared to afford the most attractive shelter to rockpool fishes, since the vast majority of species are benthic or at least demersal. However, fish do not discriminate between different habitat types so long as some shelter is available. This may be due to many rockpool fishes only utilising rockpools as temporary low tide refuges before moving throughout the intertidal zone during high tide (Marsh et al. 1978). Although rockpools are shallow tidally isolated habitats for fish, they are easily accessible by terrestrial predators such as wading birds (see Robertson, 1974; Yoshiyama, 1981), and so fish are also temporarily vulnerable to predation. To safeguard against this situation rockpool fishes may select rockpools containing adequate shelter, where predators have difficulty of access.

At first glance, the utilisation of any available cover by rockpool fishes is a trend synonymous with the role that cover plays in the colonisation process of estuarine seagrasses by fish (see Bell, 1985). Bell et al. (1987) revealed that juvenile fishes recruit to any available shelter such as natural and artificial seagrass beds of various densities or even artificial metal cages, as they all offer significantly greater structural complexity than adjacent bare substratum. Although they suggest that recruitment of juveniles to cover may reduce the risk of predation, small-growing fishes from the benthic source, such as Bathygobius krefftii, did not display preference for any cover so long as there was adequate macroinvertebrate prey (Bell and Westoby, 1986c). In contrast to this model, manipulation experiments in Chapter 8 revealed cover was most important for predicting the numbers of species and individuals from the benthic source, since the
majority of recolonists were sub-adults and adults that had probably relocated from surrounding habitats. Furthermore, in the present study fish of all sizes utilised the artificial seagrass units, which followed the complete removal of natural algae, and most likely, their major food source (Butler, 1982; Silberschneider and Booth, 2001). The most parsimonious explanation for such strong dependence on cover may be predation pressure by several large piscivorous fishes which are common in NSW rockpools, namely *Acanthistius ocellatus* and *Gymnothorax prasinus*. Furthermore, terrestrial predators, such as wading birds, have also shown to prey upon intertidal fishes (see Robertson, 1974; Yoshiyama, 1981), although there was less evidence of this in the present study. Refuge from predation has also been the major source of habitat dependence by among reef fishes (Doherty and Sale, 1985; Beets, 1997). The increased complexity of these habitats contributes to a higher number of fish being able to coexist in an area while simultaneously reducing the risk of predation (Hixon and Beets, 1993; Beukers and Jones, 1997; Steele, 1999).

**Modelling the dynamics of rockpool fish assemblages**

The present Chapter identified fish movements (recruitment and relocation) and the presence of cover as two major processes responsible for the patterns of variation observed in both the numbers of species and individuals in NSW rockpool fish assemblages. By establishing a link between these processes a good understanding of rockpool fish population dynamics can be obtained. To establish this link I propose a simple conceptual model I will term the "Nearest Neighbour Model". This model arises from the observation that the dynamics of a fish assemblage in a single rockpool may depend upon the habitats and fish populations present in neighbouring rockpools (Fig. 46). This model is best understood using a simple scenario where all the fish are
eliminated from a single rockpool within a group of rockpools by, for arguments sake, a catastrophic natural disturbance. However, the physical rockpool environment is unchanged. While this scenario suggests that the model primarily describes recolonisation of completely vacant habitat, the same processes are likely to be in effect under normal disturbance regimes but on a smaller scale.

"Nearest Neighbour Model"

Figure 46. Diagrammatic representation of the "Nearest Neighbour Model" which illustrates the role that fish movement and the presence of cover have upon the dynamics of intertidal rockpool fish assemblages. Size of arrows indicates relative importance of each factor.
For convenience, the first component in the model is the presence of some type of cover in a rockpool, as this is important for a rockpool's 'attractiveness' to fish (see Chapter 8). Its relative importance as a fish habitat depends on the number of microhabitats it offers (i.e. structural complexity). The number of fish and species able to occupy a rockpool might be expected to increase with the number of microhabitats, until a threshold is met where other factors may become limiting, possibly food (see Chapter 8). However, additional factors may control the capacity of some species to utilise particular rockpools, such as the rockpool's vertical elevation and subsequent severity in environmental conditions, and the possession of adequate adaptations to cope with these factors (see Chapter 5). Furthermore, the presence of predators and the competitive ability of fish species already present may also determine which species can utilise a rockpool. The number of fish and species available to occupy these microhabitats will depend upon the abundance of fishes in adjacent pools that are willing or capable of relocating to the vacant habitat (see Chapter 6). Once the vacant pool is recolonised these adjacent pools may also share the fishes in the previously vacant pool. These fishes will primarily be sub-adults and adults. Recruitment may also play an important role, although this role is dependent upon the breeding times of each species (DeMartini, 1999) and the time of year when habitats become available. The abundance of juveniles from intertidal species that produce pelagic larvae may further be influenced by several deterministic and stochastic events, such as variations in ocean currents and plankton production (Thresher et al. 1989). However, juveniles may also play a role if they actively move between rockpools in a home range (see Chapter 6; Yoshiyama, 1981) and do not conform to the 'settle and stay' model of Bell and Westoby (1985). Their model assumes recruits do not move from their settlement habitat until they are large enough to avoid predation. The cycle of the Nearest
Neighbour Model is completed by assuming that the abundance of fishes in adjacent rockpools, regardless of demographic composition, will be influenced by the presence of cover in these rockpools.

**Limitations of the model and directions for future research**

The present research has shown rockpools to provide a convenient 'testing ground' for general ecological principles. By testing some of these principles and developing a model describing how these processes integrate, a good understanding of the dynamics of NSW rockpool fish assemblages was gained. However, there is scope for testing the validity or improving the Nearest Neighbour Model by studying other locations. Reginald Aldworth Daly suggests, "The best model is one that works best. The perfect model, working infinitely well, is not for men now living". The major limitation to this model, and any model of rockpool fish populations for that matter, is that non-intrusive sampling is not possible where an accurate census of rockpool fishes is required (see Chapter 2). Even by returning fish to the same rockpools after sampling there is still an element of disturbance. The extent that assemblages may differ in subsequent samples because of such disturbances is not yet known and certainly requires further investigation. Some workers have attempted to account for such problems by sampling different rockpools each time (see Willis and Roberts, 1996), but results are confounded by individual rockpools having their own unique fish assemblages. As a result, the Nearest Neighbour Model and other models may only predict the dynamics of artificially disturbed rockpool fish assemblages.

Studies contributing to the evolution of this model have identified a clear need for further research. Before testing the validity of any model, or suggesting alternatives
ones, there are many fundamental questions about rockpool fish ecology that need attention. Most of the important questions simply revolve around how little we know about the ecology and biology of rockpool fishes. Although the structure of rockpool fish assemblages and patterns of variation are becoming well documented, most information comes from North America. In Australia, there is little data available on rockpool fish assemblages from Victoria, South Australia, Western Australia, Northern Territory and Queensland. Therefore, there is good reason to undertake quantitative studies in locations where data is lacking, which may also be valuable for future conservation and management strategies, such as designing marine protected areas. The possibility that rockpools may provide important nursery areas for some species of economic significance certainly warrants closer investigation, especially if a species' primary nursery habitat (i.e. estuaries) continue to be degraded by anthropogenic impacts (see Short and Burdick, 1996).

Furthermore, there is very little quantitative information on the biology of even common rockpool fish species, except some Clinids (Thresher et al. 1989; Gunn and Thresher, 1991), such as growth, longevity, migrations and reproductive biology. The task of investigating the growth and movements of small fish has become easier in recent years with the development of small implant tags (Chapter 7) and the increasing understanding and analysis of otolith microstructure and microchemistry (Campana and Neilson, 1985; Thresher, 1999; Kennedy et al. 2000; Campana and Thorrold, 2001). This information is of importance to further investigate the dynamics of rockpool fish communities, particularly for understanding the relationship between geographically separated rockpool fish assemblages through larval dispersal or post-settlement movements. Investigation of the genetic isolation of geographically separated
populations would also be illuminating as it may be of importance for marine reserve
design.

Despite the need to increase the knowledge of rockpool fish assemblages, the current
methods of sampling rockpool fishes require closer assessment of their effectiveness for
collecting quantitative data. Although the most appropriate sampling method will vary
between locations and habitats, the widespread use of chemical sampling methods
(anaesthetics and ichthyocides) is not well justified. There is apparently no study that
has assessed the possible residual effects of this method on rockpool fish assemblages.
That is, the extent that chemical residues remaining within the rockpool may affect
recolonisation of sensitive species or particular size classes of fish. This would
obviously have an impact upon the species and demographic compositions of the
recolonised fish assemblage, and may also accumulate where resampling of the same
rockpool is undertaken. This may ultimately lead to unjustified conclusions from
patterns observed.

Further manipulation experiments to investigate the processes controlling the dynamics
of fish assemblages would be helpful. Experiments in Chapter 8 used a single artificial
seagrass leaf density and presence/absence of substratum cover as the number of
similar-sized rockpools at the headlands studied was limited. Since these studies have
shown substratum and suspended cover to influence fish assemblages, future studies
could further investigate the influence of these factors by using different densities of
artificial seagrass (or natural algae if translocation is possible) and rocks of various size
categories. Incorporation of these studies with those addressing recruitment and
recolonisation processes may provide even greater understanding of the processes
structuring rockpool fish assemblages. This may facilitate developing new population models or testing the validity of other models such as the 'lottery hypothesis' (Sale, 1977, 1978, 1982) and the Nearest Neighbour Model (this Chapter) at other locations.

**Implications for conservation and management**

The increasing recognition that anthropogenic impacts have reduced the ecological integrity and potential economic value of the world's marine ecosystems has highlighted the need for more stringent management strategies to reduce these negative effects (Costanza et al. 1998). An increasingly popular tool for managing coastal ecosystems is closed areas, such as Marine Protected Areas (MPAs) (also marine parks, sanctuaries etc). The International Union for Conservation of Nature and Natural Resources (IUCN) defines an MPA as "any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which have been reserved by law or other effective means to protect part or all of the enclosed environment" (Kelleher and Kenchington, 1992). MPAs are generally declared for the purposes of protecting biological diversity and specific habitats (Bennett and Attwood, 1991; Roberts, 1995; Edgar and Barrett, 1999), and enhancing depleted fisheries (Carr and Reed, 1993; Edgar and Barrett, 1999; Jamieson and Levings, 2001; Jouvenel and Pollard, 2001).

In New South Wales, Australia, there are two types of MPAs: 1) Marine parks, which are large multiple use areas designed to conserve biodiversity and, 2) aquatic reserves, which are small areas designed to protect biodiversity and meet specific management objectives. There are currently three marine parks and eight aquatic reserves in NSW with a proposal to increase the number of aquatic reserves to 15, which may also
include extensions to the intertidal zone, known as Intertidal Protected Areas (IPA) (NSW Fisheries, 2001). IPAs are a relatively new management strategy established by NSW Fisheries in 1993, which aim to protect intertidal habitat and maintain the biological diversity of intertidal communities (NSW Fisheries, 2001). However, none of the biodiversity studies undertaken to enable nomination of potential IPAs included intertidal fishes. The difficulty of sampling intertidal fishes may have contributed to them being overlooked by environmental consultants conducting biodiversity assessments, which are often conducted in short time frames and can fail to adequately describe the community structure (see Fairweather, 1989; Benkendorff, 1999; Griffiths, 2001a). The importance of intertidal fishes for structuring intertidal communities (Choat, 1982; Coull and Wells, 1983; Connell and Anderson, 1999) should place them among the key organisms in biodiversity assessments which aim to declare such protection zones.

There may be a myriad of approaches for protecting and managing intertidal fishes, but successful approaches will depend on sufficient empirical data to predict the final outcome. It is in these instances where baseline studies of local areas are of importance. Appropriate protection of intertidal fishes may be best achieved by incorporating additional legislation for IPAs to include the prohibition of harvesting fishes of any type. However, the design of IPAs will require some thought, as ecologists remain divided whether species and genetic diversity can be maintained in a single large reserve or several smaller reserves. This concept is known as the SLOSS (Single Large or Several Small) debate (see McNeill and Fairweather, 1993). There is supportive evidence for each case although the appropriate design largely depends upon the mobility of 'target' species (Edgar and Barrett, 1999) and the spatial distribution of
species (McNeill and Fairweather, 1993). Tagging studies in Chapter 7 revealed that most rockpool fishes only move small distances and the presence of homing ability among many species suggests they probably do not venture outside their home range for much of their lives. The limited dispersal of their larvae (DeMartini and Patten, 1979; Marliave, 1986; Ruck, 1980) indicates there may be numerous genetically distinct populations both among and within rocky headlands. Therefore, several small reserves may be most appropriate to maintain the species and genetic diversity of the rockpool fish assemblages. IPAs may be as small as 100 metres wide, which would probably accommodate the restricted larval dispersal and home ranges of the species studied here, which probably do not exceed about 50 metres (see Chapter 7). A consideration for the spatial distribution of these reserves within a single rock headland should take into account the exposure of sites to wave action, since fish assemblage structure can differ among exposed and sheltered shores (see Chapter 4; Gibson, 1972). However, there will be many other factors to consider before implementation of IPAs, such as economic and social issues. For instance, it is unknown how well such a proposal will be accepted, and regulations adhered to, by the wider community. Furthermore, possible conflict with recreational uses of the intertidal (i.e. anglers and spearfishers), may negatively impact small coastal towns where such activities may contribute highly to the local economy.

Conclusions

It is surprising that rockpool fishes have attracted little attention by the scientific community, despite their occupation of highly conspicuous and easily accessible habitats. Rockpool fish assemblages are ecologically distinct since they share little resemblance to fish assemblages of coral reefs, estuaries and even adjacent subtidal
regions, despite some subtidal species also utilising rockpools during their juvenile stages (possibly as nurseries) or occasional feeding areas. The reproductive strategy of many rockpool fishes in limiting dispersal of larvae is quite dissimilar to fishes common in other systems, such as coral reefs, that generally attempt to maximise larval dispersal. Consequently, population dynamics models devised for these systems, which generally predict a continual turnover in species composition, are not applicable to rockpool fish assemblages. Instead, the physiological demanding rockpool environments means that relatively small numbers of fish species possess adequate adaptations to cope with these conditions and make permanent use of rockpools. As a result, rockpool fish assemblages are usually resilient to perturbations and persistent. Furthermore, the limited larval dispersal, site fidelity and apparently high competition for suitable microhabitats among rockpool fishes appear to contribute to individual rockpool assemblages being maintained by relocation of fishes from nearby habitats and to a lesser extent, recruitment from the plankton. Although rockpool fish assemblages may be in part neglected by their relative lack of value to fisheries (compared to other key habitats such as estuaries) and difficulty of sampling, their unique species composition and important role in structuring other intertidal communities certainly warrants their preservation and further research.
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Retention of visible implant tags in small rockpool fishes

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ABSTRACT: Retention and associated fish mortality of visible implant alphanumeric (VIA) and fluorescent elastomer tags was assessed in 2 Australian intertidal rockpool fishes, Girella elevata (Girellidae) and Bathygobius cocosensis (Gobiidae). Mean retention of VIA and elastomer tags after 90 d was 32 ± 20% and 77 ± 19%, respectively. After 90 d the fish mean mortality from VIA tags (20 ± 5%) was significantly higher than from elastomer tags (7 ± 2%) and untagged control groups (11 ± 2%). Elastomer tags appear most suitable for marking batches of fish of various size, while VIA tags appear suitable for identification of larger individuals of species such as many gobies that have adequate transparent tissue for tag recognition.

KEY WORDS: Bathygobius cocosensis • Elastomer • Girella elevata • Girellidae • Gobiidae • Intertidal • Tidepool

Tagging is a widely used method for estimating growth, survival, and mortality, as well as monitoring the movements of fishes and members of other taxa. The development of small implant tags (e.g. visible implant, passive integrated transponder [PIT] and coded wire tags [CWT]) has allowed ichthyologists to study fish considered too small to tag with conventional external tags, such as T-bar and spaghetti tags. Visible implant tags offer the advantages of being small, inexpensive and externally recognised allowing repeated observations of individuals without being sacrificed to retrieve tags (i.e. CWT).

Visible implant alphanumeric (VIA) and visible implant fluorescent elastomer (VIFE) tags manufactured by Northwest Marine Technology are 2 types of visible implant tag that have been successfully used for marking small fishes in both freshwater (Blankenship & Tipping 1993, Dewey & Zigler 1996, Halls & Azim 1998) and marine environments (Forrester 1995, Willis & Babcock 1998, Malone et al. 1999). However, the present study is apparently the first study that assessed the utility of visible implant tags for tagging intertidal fishes. VIA tags are small (1.0 x 2.5 mm) polyester pieces imprinted with alphanumeric codes that are externally visible when implanted into transparent tissue, permitting identification of individuals. Elastomer tagging involves injecting a fluorescent liquid elastomer into transparent tissue that sets to form a permanent, biocompatible mark, which is useful for identifying batches or cohorts of fish.

Tagging studies of intertidal rockpool fishes are relatively few, mainly owing to their small size and subsequent difficulty in marking (Gibson 1999), but with use of visible implant tags more accurate study of their growth and movements may be possible. The present study assessed the retention of VIA and elastomer tags and associated mortality rates for 2 common Australian intertidal rockpool fishes, Girella elevata and Bathygobius cocosensis, under laboratory conditions before undertaking field studies with these species.

Materials and methods. Fish were collected from rockpools in the Illawarra region (34°58' S, 150° 93' E), New South Wales, Australia, and transported to 6 flow-through seawater aquaria where they were allowed to acclimate for 3 to 8 wk. In preparation for tagging, fish were anaesthetised in a 30 mg l⁻¹ solution of clove oil using the methods of Griffiths (2000). VIA and elastomer tags were implanted into the transparent cheek tissue of Bathygobius cocosensis, but since Girella elevata have few suitable tag locations due to dark skin pigmentation, VIA and elastomer tags were inserted into the semi-transparent tissue in the nape and cheek, respectively. Fluorescent
yellow VIA tags were implanted with a syringe-like applicator. Fluorescent orange and red elastomer tags were implanted using a 0.3 cc syringe following the directions of Northwest Marine Technology. All fish were measured (total length [TL] in mm) and weighed (to the nearest 0.1 g) during the tagging procedure and again after 15, 30, 60 and 90 d, where the presence and readability of a tag were also recorded. Number and sizes of individuals of each species with each tag type is shown in Table 1, although it is important to note that fish tagged with VIA tags were generally larger than elastomer-tagged fish. As a result, it is possible that differences observed between tag treatments are due in part to differences in retention by differently sized fish.

Six aquaria maintained at the same seawater temperature (17 to 21°C) and flow rate were used for the laboratory experiment. Each aquarium was considered as a single replicate and contained all individuals of 1 of the 6 experimental groups (2 species: Girella elevata and Bathygobius cocosensis subjected to 3 tag types: VIA, Elastomer and Control). Fish were fed a selection of fresh Ulva, freeze-dried brine shrimp and krill or frozen blood worms every 2 to 3 d.

ANOVA was used to test for differences in the mean retention among tag types and associated mortality rates of fish. Fish species was ignored as a factor in comparing retention and mortality among tag types. That is, retention percentages for both aquaria (1 of each species) of VIA and elastomer treatments were used as replicates. Sample size within the 2 treatments was 2. Similarly, mortality percentages for both aquaria (1 of each species) of VIA, elastomer and control treatments were used as replicates. Sample size within the 3 treatments was 2. Data were examined for homogeneity of variances using Cochran’s test. No transformation of data was necessary. Tukey’s honestly significant difference (HSD) test was used to determine significantly different means.

**Results.** Both VIA and elastomer tags were easily implanted for both species even when some fish were < 35 mm TL. Identification of tags with the naked eye was excellent for all species after 90 d, although the use of either an infrared or black light in low light conditions significantly enhanced the readability of VIA tags.

There were considerable differences in retention rates among tag types, although the greatest proportion of fish generally lost VIA and elastomer tags 15 d and 60 to 90 d after tagging, respectively (Fig. 1). After 90 d the mean retention of VIA tags was 32 ± 20%, while higher retention rates (77 ± 19%) were recorded for elastomer tags (Fig. 1). ANOVA revealed that the mean retention rate was significantly higher for elastomer-tagged fish ($F_{1,2} = 5.771, p = 0.043$). After 90 d the mean mortality of VIA-tagged fish was 20 ± 5%, which was higher than the mean mortality rates of both elastomer-tagged fish (7 ± 2%) and the control group (11 ± 2%) (Fig. 2). ANOVA revealed that the overall mean mortality rates differed among tag types ($F_{2,3} = 11.421, p = 0.002$). Tukey’s HSD test revealed that the mean mortality rate was significantly higher among VIA-tagged fish than among elastomer-tagged or control fish.

**Discussion.** High retention, low mortality and ease of identification of elastomer tags clearly indicate their higher suitability for marking intertidal rockpool fishes than VIA tags, particularly for fish of small sizes (< 50 mm TL). Elastomer tags are useful for marking batches or cohorts of fish, and with the use of 2 elastomer colours 243 fish may be given unique markings (Dewey & Zigler 1996). Since rockpool fishes normally have low densities within the intertidal zone, the use of elastomer tags for the purpose of identifying individuals may be adequate. Although VIA tags resulted in lower survivorship and retention rates, particularly for Girella elevata, their use for individual identification of gobies or similar species with adequate transparent tissue may be successful, although this should be restricted to fish > 50 mm TL. The potentially high trauma of injecting small fish with both relatively large VIA tags and the tag injector is another reason why only larger fish should be tagged. This was the reason for the larger sizes of fish tagged with VIA tags in the present study. However, it is also important to note that differences in retention and mortality rates among tag types may be partly due to differences in fish sizes among tag treatments.

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**Table 1.** Number, mean (±1 SE,) weight (g) and total length (mm), and length range of fish representing *Girella elevata* and *Bathygobius cocosensis* implanted with visible implant alphanumeric (VIA) and visible implant fluorescent elastomer (VIFE) tags. The procedural control groups were left untagged but handled in a similar manner to the tagged fish.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number tagged</th>
<th>Length range (mm)</th>
<th>Mean length (mm)</th>
<th>Mean weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>VIA tags</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>20</td>
<td>60–148</td>
<td>84.9 (5.8)</td>
<td>11.5 (2.9)</td>
</tr>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>25</td>
<td>43–64</td>
<td>53.6 (0.9)</td>
<td>1.4 (0.1)</td>
</tr>
<tr>
<td><strong>VIFE tags</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>12</td>
<td>47–69</td>
<td>57.9 (1.9)</td>
<td>2.3 (0.2)</td>
</tr>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>21</td>
<td>32–46</td>
<td>39.8 (0.9)</td>
<td>0.6 (0.1)</td>
</tr>
<tr>
<td><strong>Control</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Girella elevata</em></td>
<td>15</td>
<td>52–101</td>
<td>76.2 (4.4)</td>
<td>9.3 (1.8)</td>
</tr>
<tr>
<td><em>Bathygobius cocosensis</em></td>
<td>23</td>
<td>34–59</td>
<td>47.5 (0.8)</td>
<td>1.1 (0.1)</td>
</tr>
</tbody>
</table>
Appendix

Griffiths: Retention of implant tags in small fishes

Some interspecific differences in retention rates for VIA tags were noted, which probably related to differences in fish anatomy and behaviour. For example, tag loss in *Girella elevata* may have been in part due to the small amount of semi-transparent tissue at the nape, which probably requires a smaller tag to resist movement by muscular contractions. Second, the secretive behaviour of *G. elevata* may also contribute to tag loss as fish were observed rubbing the tag site upon rocks. Conversely, elastomer tags could be injected into a more suitable tag location (i.e. the cheek), thus resulting in higher retention rates. Conversely, *Bathygobius cocosensis* has ample transparent cheek tissue enabling both VIA and elastomer tags to be implanted further from the insertion point, which probably accounted for high retention rates, particularly for VIA tags.

Acknowledgements. I thank Kirsten Benkendorff for generous use of her aquaria, Jade Butler for assistance in laboratory procedures, Robin Gibson for comments on drafts of this manuscript and Daniel Thompson from Northwest Marine Technology for generous donation of tags. This research comprises a small component of a PhD dissertation by the author funded by an Australian Postgraduate Award. Fish were handled in accordance with the regulations of an animal ethics permit (No. AE99/13).

LITERATURE CITED


Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany
Appendix 3. Photographs and descriptions of the locations sampled during studies in this thesis. Photographs after Smith (2001), except for Puckey's Bombora, Marsden Head, Mollymook Point, Tuross Heads and Wagonga Head, which were taken by the author.

Coalcliff Point. Located about 5 km south of Stanwell Park near the small town of Coalcliff. The two sites sampled at this location were situated near the swimming pool. Rockpools are well defined and habitats are pebbles and cobbles, Caulerpa filiformis but very few crevices. Easy access to the rock platform, but is a very dangerous location where wave conditions can change very quickly.

Sandon Point. Located 2 km from Bulli at the southern end of Machauly's Beach. The two sites sampled at this large rocky headland were situated on the southern flank of the headland. Rockpools are well defined but generally very small "pot holes". Habitats are mainly pebbles and cobbles, Caulerpa filiformis but very few crevices. Easy access to the rock platform via the beach.

Bellambi Point. Located at Bellambi at the south end of Bellambi Beach. The sites sampled at this location were situated near the swimming pool (2 sheltered) and at the end of the point (2 exposed). Rockpools are well defined and habitats are pebbles and cobbles, Caulerpa filiformis and some crevices. Easy access to the rock platform, but exposed sites can be dangerous due to large waves. Generally an ideal intertidal study location.
Appendix

Puckey's Bombora. Although generally known only as "Puckey's", this small rock platform is located at the northern end of North Wollongong Beach. The two sites sampled at this location were situated at the platform's northern and southern extremities. Rockpools are well defined and habitats are pebbles and cobbles, *Caulerpa filiformis* but very few crevices. Easy access to the rock platform.

Flagstaff Point. Located about 2 km from the Wollongong CBD. The two sites sampled at this location were situated near at the front and on the southern flank. Rockpools generally large and well defined with main habitats being cobbles and boulders, brown algae and some crevices. Easy access to the rock platform, but can be a dangerous location in southerly swells.

Barrack Point. Located about 3 km from the Shellharbour township. The two sites sampled at this location were situated near North Shellharbour Beach. Very few rockpools at this location, which are generally undefined gullies, depressions and crevices. Main habitats are large boulders, brown algae and many small crevices. Easy access to the rock platform.

Cowrie Island. Located adjacent to Shellharbour boat harbour. The two sites sampled at this location were situated near "Rocky Bay" and North Shellharbour Beach. Very few rockpools at this location, but are generally well defined with main habitats being pebbles and cobbles, abundant brown algae. Easy access to the rock platform.
Caravan Point. Located adjacent to Shellharbour caravan park. The four sites sampled at this location were situated near the swimming pool and on the southern flank near South Shellharbour Beach. Rockpools not particularly abundant and are generally irregular depressions and isolated crevices, although most are large in size. Main habitats are large boulders, pink and brown algae and many crevices. Relatively easy access to the rock platform.

Bass Point. Located about 3 km from the Shellharbour township at the southern end of South Shellharbour Beach. Probably the largest rocky headland in the Illawarra. The four sites sampled were the gravel loader or "The Shallows", Beaky Bay, Maloney's Bay and "The Chair". Rockpools abundant and well defined of varying size. Main habitats are cobbles and large boulders, pink and brown algae and many crevices. Difficult access to Beaky Bay and Maloney's Bay. An excellent location for intertidal studies, although car theft is a problem.

Marsden Head. Bass Point. Located about 4 km from the Kiama township. The two sites sampled were adjacent to the "Little Blowhole". Few rockpools which are well defined of varying size. Main habitats are cobbles, large boulders, pink and brown algae and a few crevices. Easy access to the rock platform. Can be a dangerous location.
Appendix

Black Head. Located adjacent to the township of Gerroa at the northern end of Seven Mile Beach. This very large rocky headland has very few rockpools, which are generally undefined gullies, depressions and crevices. Main habitats are isolated boulders and many crevices. The two sites sampled were along the southern flank. Easy access to the rock platform.

Mollymook Point. Located about 5 km from Ulladulla. The two sites sampled at this location were toward the southern flank of the platform near the golf course. Very flat rock platform with very few rockpools at this location, which are generally undefined gullies and crevices. Main habitats are crevices. Easy access to the rock platform.

Tuross Heads. Located 1 km from Tuross Heads township at the entrance to the Tuross River. The two sites sampled at this location were situated at the end of the headland. Very few rockpools and variable in size and shape. Main habitats are large boulders, brown algae and crevices. Relatively easy access to the rock platform via the beach. It exposure to swell make it a dangerous study location.
Wagonga Head. Located 3 km from Narooma at the entrance to Wagonga Inlet. The two sites sampled at this location were situated immediately south of the southern breakwall. Rockpools abundant but variable in size and shape. Main habitats are large boulders, brown algae and many crevices. Relatively easy access to the rock platform. The large intertidal area here makes it a generally safe location.
Appendix 4. Instructions for the use of Visible Implant Alphanumeric tags by Northwest Marine Technologies.

INSTRUCTIONS FOR USING SOFT VIALPHA TAGS

Thank you for choosing visible implant (Vialpha) tags! Our mission at NMT is to provide the best tools to help you get results from your research. We are committed to support you in your scientific research, and to that end we offer free Technical Support for our products. For Technical Support regarding Vialpha tags please call Biological Services (360) 754-2500 or biology@nmt-inc.com (email). For equipment questions and to order more supplies, please call Customer Service (360) 468-3375 or office@nmt-inc.com (email). Customer Service personnel are available 8am-5pm (Pacific Time) to help you.

Before tagging please consider the following:

➢ Prior to using the Vialpha system, available reference material relating to its use on fish or other aquatic animals should be reviewed. The biological staff of NMT is available to advise users in this regard and to refer them to others conducting similar research.
➢ If references are lacking, experimentation to determine suitable tag locations, retention rates, and visibility should precede applied use.
➢ Injectors should be sharp and free of contaminants. A fine stone is included with the injector and; should be used to keep tagging needles sharp. Injectors should be cleaned at least daily. We recommend a warm detergent bath, followed by thorough rinsing in freshwater and then alcohol.
➢ The wearing of an optical magnifying visor may be very useful while loading tags into injectors, especially for standard size.
➢ Loading and injecting tags should be practiced until proficient prior to conducting experiments.

Soft Vialpha tags are organized in rows on transparent sheets with the tag codes printed beside them. The tags are lightly adhered to the clear sheet by biocompatible gel. A sheet of white plastic covers the tags for protection until ready for use. Rows of tags have perforated dividing lines so one or more strips can be torn apart for use.

LOADING THE INJECTOR

The injector needle is dipped in water or alcohol, if not already wet. The tags may be loaded into the injectors with either of two methods. For the first method, the white plastic cover is peeled back or removed and the strip of tags is held in the hand with the tag to be loaded curved over the forefinger. At this point the backside of the tag is facing up; so the code on the tag is not visible. The open side of the needle point is turned down, aligned with the long axis of the tag. Slide the needle over the tag until the tag is entirely inside the injector (see figure 1).

For the second method, hold the tags with the clear plastic side up. The code on the tag will be visible with this method. Peel back the white plastic cover just enough to expose the tag to be loaded. The open side of the needle point is turned up, aligned with the long axis of the tag. Slide the needle under the tag until the tag is entirely inside the injector (see figure 2). Rocking the injector from side to side while loading tag will assist in easier loading.

The tag is now loaded and when injected the code will be visible.
INJECTING THE TAG INTO SPECIMEN

The tags cannot be pushed into solid tissue without the aid of the injector needle because of their soft texture. The sharp tip of the needle is used to cut a path for the tag.

The procedure is:
1) the needle cuts a space so the tip is slightly beyond where the far edge of the tag is desired;
2) the tip of the needle is slightly withdrawn;
3) using the palm of the hand the push rod is slightly advanced so the tag fills the opening at the front of the needle*; and
4) the tag is left in place as the fingers withdraw the needle while the push rod is held stationary relative to the tissue using the palm of the hand.

*Please note: The tag will roll up or otherwise become distorted if pushed too much.

The tag injectors supplied with the soft tags differ from those used for the original hard tags. The injectors used for soft tag are shorter in length so the push rod fits the palm of the hand; and the thumbscrew has been replaced with a setscrew.

Here are some tagging tips:

1) The tagging area should be well illuminated.
2) Tags should be stored in a cool, dry location until ready for use.
3) Fish to be tagged should be well anesthetized or restrained, otherwise, they are likely to move when injected causing tearing and enlarging of the tag location, which increase tag loss.
4) Implants should remain just below the skin. Deep tags may become obscured, and if they penetrate into the skin are likely to be lost.
5) If possible, a representative number of tagged specimens should be retained for evaluation of tag loss and visibility for several weeks minimum.
6) Care should be taken in handling the fish immediately after tagging to minimize tag loss. Avoid dropping, tossing, or exposing them to strong water currents.

Again, thank you for choosing our visible implant (Vlalpha) tags. Please contact our Biological Services for more assistance with this product. For references and more information about Vlalpha tags, please see our website: www.nmt-inc.com

The Biological Services Office of Northwest Marine Technology is located at:

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Olympia, WA 98502
Tel: 360-754-2500
Fax: 360-754-4240
E-mail: biology@nmt-inc.com
NMT Website: www.nmt-inc.com
Appendix

Appendix 5. Instructions for the use of Visible Implant Fluorescent Elastomer tags by Northwest Marine Technologies.

Visible Implant Fluorescent Elastomer Hand Injection Kit
Instructions for Use

The Visible Implant Fluorescent Elastomer (VIE) tagging system was developed to provide externally visible internal marks for fish and other aquatic animals. It also provides the opportunity for developing a surprising array of unique identifications. The elastomer system utilizes a specially developed, bio-compatible, two part fluorescent elastomer material. After mixing, the elastomer is a liquid that can be injected into tissue with a hypodermic syringe. Within 24 hours at room temperature, this material cures into a pliable solid. The elastomer functions to hold the fluorescent pigments in a cohesive well defined bio-compatible mark. VIE tagging systems can be purchased as a Master Kit or a Mini Kit.

The materials in each kit are listed below.

Elastomer is available in nine colors and also clear. Red, orange, yellow and green fluoresce under blue light; while blue, black, brown white and purple do not fluoresce under a blue light. Blue and clear will fluoresce under ultraviolet light.

Materials included in the VIE Master Kit:
2 - hand injectors
4 - colors elastomer with curing agent (choose from colors above)
200 - 3/10 cc injecting syringes
200 - 1 cc syringes
field carrying case

Materials included in the VIE Mini Kit:
1 - hand injector
1 - color with curing agent (choose from above)
50 - 3/10 cc injecting syringes
50 - 1 cc syringes
field carrying case

Mixing instructions:
In order for proper curing to occur, the elastomer and curing agent must be properly mixed at a 10:1 ratio.

1. Using the calibrations on the elastomer container, dispense 1 cc colored elastomer into the bottom of a mixing cup.
2. Use a 1 cc syringe to draw up a small amount of curing agent. Remove any air pockets by pushing all the material out and then drawing more up. Dispense 0.1 cc into the cup with the elastomer. Discard this 1 cc syringe.

(rev. 10/00)
3. **MIX THOROUGHLY!** We recommend stirring and scraping the mixing cup walls and bottom for one full minute to ensure complete mixing.

**Warnings:**
(a) Never allow the colored elastomer material (unmixed or mixed with the curing agent) to enter the “sampling bottle” that contains the curing agent. Even a minute amount of colored elastomer will contaminate the curing agent and preclude its future use.
(b) Contact of either the catalyst or elastomer with the rubber plunger tip of the 1 cc syringe for an extended time may inhibit curing of the elastomer. Discard each of these syringes immediately after use, as instructed!

4. Carefully remove the white and orange caps from a 0.3 cc injecting syringe. Remove the plunger.

5. Use a new 1 cc syringe to slowly draw up a small amount of the mixed elastomer material, then wipe off the tip.

6. The tip of the 1 cc syringe will fit tightly into the opening in the injecting syringe. Fill the injecting syringe about one third full. **Throw out the 1 cc syringe.** (More than one injecting syringe can be filled from a single mixing if the mixed material is kept on ice or refrigerated in the mixing beaker.) For best results, deposit mixed elastomer into the syringe so that no air pockets form between the plunger and elastomer.

7. Replace the plunger, pushing it forward till the air is displaced and elastomer appears at the needle tip. Install the injecting syringe into the hand injector body making sure to line up the bevel of the needle with the reference dot.

**Important Note:** We strongly recommend retaining the mixing cup and injecting needle after use to verify that proper curing has occurred. If the elastomer is not curing in a reasonable amount of time (approximately 24 hours at room temperature), contact NMT immediately.

Larger amounts can be mixed at a single time if necessary as long as the 10:1 ratio of elastomer to curing agent is maintained. We recommend mixing as little at a time as is possible to avoid waste and ensure proper curing.

**Tagging instructions:**
With the back piece in place, the injector should be ready to tag. It is designed for the tapered front piece to be held in the thumb and forefinger with the back piece against the palm. In this way, maximum force with minimum effort can be placed on the injector by simply squeezing the palm of the hand against the back piece. Most users inject elastomer with the bevel of the needle up. A sponge or paper towel will be useful to clear the needle of excess elastomer before injection.

Prior to using the elastomer system, available reference material relating to use of the method on the fish, or similar species, should be reviewed. The biological staff of Northwest Marine Technology stands ready to advise users in this regard. If references are lacking, experimentation to determine suitable tag locations, retention rates and visibility should precede applied uses.

Most clear or translucent tissue is a suitable target, providing there are no associated external openings. The adipose eyelids of salmonids and some other fishes, as well as the spaces between fin rays are examples of potential targets. Other possible targets are along fin margins of flatfish, and the abdominal area of shrimps. Elastomer tags can be placed under pigmented skin where they are difficult to see in ambient light, but quite visible when fluoresced.
The use of four different colors in combination with different body locations offers the potential for developing a range of unique identifications. For example, experiments with bull trout indicated that there were eight suitable tag locations using the elastomer system. Using a single mark per fish would thus produce $8 \times 4 = 32$ unique marks. However, use of two different marks per fish, in combination with these same body locations and colors, results in the potential for hundreds of unique marks.

Fluorescence is used primarily for convenience in detecting the tags; a tiny spot of elastomer when fluoresced can be seen at considerable distance. Tags obscured by pigmentation can often be detected by fluorescing them. NOTE that fluorescing the tags changes the apparent color somewhat, in particular yellow appears to be light greenish. If it is necessary to decode tag colors when they are fluoresced - usually when they are obscured - then the reference fish included in your kit should be fluoresced near the detected tag for comparison. When designing experiments using multiple colors, the most contrasting colors should be preferentially used.

Once the elastomer has cured and the wound has healed, the tag should be retained for the life of the animal. However, if the specimens are vigorously handled too soon after tagging, before the material cures or the wound heals, the material can be forced back out the needle wound. Merely dropping the animal into water or subjecting it to heavy current could increase tag loss. Tagged specimens should be handled with care for at least 10 days after tagging. Long term retention of elastomer tags should exceed 90% when done properly.

Care should also be taken to avoid material trailing from the tagging wound. This could cause a percutaneous condition and problems similar to those resulting from external fish tags. This problem is avoided by ending the flow of material before withdrawing the needle and lightly wiping the wound.

The possibility of spreading fish diseases between culture facilities and watersheds is of concern to both our customers and NMT. Rinse the surfaces of the hand injectors with tap water removing any extraneous material in the process. Place the equipment on a clean, disinfected surface and spray liberally with a chlorine solution. (Household bleach comes in a concentration of about 5% so that to achieve the desired concentration one would dilute an ounce of bleach in each two gallons of water—a ratio of 1:250.) Use water to thoroughly rinse away bleach.

Please dispose of the used syringes properly after bending the end of the needles 180 degrees to prevent the risk of needle stick injury. Further, although the elastomer material is non-toxic, properly disposed needles and syringes will also avoid any inquiry from the public about improperly disposed needles around your field site or your marking facility.

The shelf life of the elastomer material is at least 4 months at room temperature. Once mixed, the elastomer will begin to set in one to two hours depending on temperature. Storing the mixed material at low temperatures (such as under ice) greatly extends the working time.
Tag recovery:
Although VIE Tags can usually be easily seen with the naked eye with normal daylight or interior lighting, their visibility can be greatly enhanced with special illumination and viewing conditions. They can be illuminated with bright blue light and viewed through a filter that allows only the green, yellow, orange or red fluorescence to reach your eyes. This will maximize the intensity of tag fluorescence while minimizing the intensity of light reflected from everything else, making the greatest contrast between tag material and surrounding tissue. The waterproof flashlight and amber filter glasses are provided for this purpose.

**CAUTION:** All NMT supplied blue light flashlights come with blue LED (light emitting diodes). LED arrays draw less energy than halogen bulbs and will last longer on a set of batteries. Furthermore, LED lights are almost indestructible. Although LED offers the longest possible usable light, we recommend that you test all blue light flashlights before examining study animals for marks. All NMT Fluorescent Elastomer Hand Injection Kits come with a mark standard for use in testing flashlight performance. We also recommend that you keep a set of spare alkaline batteries with you and that batteries be replaced every 40 hours.

Light filtering system can be adapted to many different tag recovery regimes. NMT can provide amber filter material for scuba goggles, blue filtering material for hatcheries, and supply information about how to obtain other types of lights for fluorescing tags. Regular ultraviolet light will fluoresce these tags under most circumstances, but is considerably less efficient than the blue light and sunglasses where tags are obscured. Please call NMT for any special circumstances to be met.

**Continuing projects:**
When the supplies in this kit have been exhausted, you may purchase a Refill Kit containing a single 15 ml supply of elastomer (one color) and all required disposable materials.

The equipment in this kit is designed for relatively limited applications. Large scale elastomer operations may be best conducted using an air driven injector system. These injectors have been used to tag Pacific Northwest salmon where groups approach a million in number. Please contact NMT for further information.