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Eszter Zsafia Hidas
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**The Patterns of Abundance and Demography of Rocky
Intertidal Marine Invertebrates Indicate That
Recruitment Can Set Geographical Range Limits**



**A thesis submitted in fulfillment of the requirements for the
award of the degree of Master of Science (Research) from the
University of Wollongong by**

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BSc (Hons) (UNSW)

**School of Biological Sciences and Institute for Conservation
Biology, 2007**

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Abstract

The geographical distributions of species are limited by either physical or biogeographic boundaries that inhibit their dispersal, or by changes in abiotic or biotic factors that affect their survival towards their range limits. Benthic marine invertebrates display an array of reproductive modes and dispersal mechanisms, from 'poor' dispersers that produce direct developing crawl-away juveniles to 'good' dispersers that produce planktotrophic larvae, which is likely to influence their population structure and connectivity across the range and at their range limits. Few empirical studies have assessed, however, how the distribution, adult abundance, recruitment and fecundity vary and relate at large spatial scales towards the geographical range limits of benthic marine species, despite the importance of such information for effective conservation practices.

Firstly, I surveyed the large-scale patterns of community composition and species richness of sessile and sedentary rocky intertidal macro-invertebrates at five locations on either side of a biogeographic barrier, and at an isolated habitat patch within the barrier on the southeast coast of Australia, to test the hypothesis that patterns of distribution of these species relate to their reproductive modes across these coastal features. I found that species richness and composition were significantly different north and south of the barrier. Of the total of 40 species sampled, an average of 30 were found in the north, and 27 in the south. Surprisingly, all 8 species that were limited to either side of the barrier were planktonically developing, while the 3 direct developing species were present on both sides. The isolated habitat patch supported 19 of the 32 species that were distributed across the barrier, and all these were planktonically developing. Contrary to my simplistic expectations, therefore, patterns

of species distributions across the barrier were not obviously related to species' reproductive and dispersive modes.

Second, I used surveys of the adult abundances and size-frequency distributions of three planktonically developing rocky intertidal invertebrates that were limited to the north side of the biogeographic barrier to test the predictions of the abundant-centre hypothesis, which states that species are most abundant at the middle of their ranges and least abundant on the edges. I sampled three times, from May 2005 to January 2006, at small (hundreds of m) to large (hundreds of km) spatial scales over a 600 km stretch of coast, from the middle of the range to the range limit of these species. I found that over all three sampling times, the adult abundances of the three species were consistently high within the middle of their ranges, but declined dramatically and significantly at the range limit. Patterns of size-frequency distributions, however, varied towards the range limit among the three species, with one showing no apparent changes, one lacking small individuals, and one lacking large individuals at locations near the range limit. These results indicated that all three species had abundant-centre distributions, but this distribution was not necessarily related to changes in patterns of recruitment.

Lastly, I assessed how demographic processes such as recruitment and fecundity change towards the range limit for the only sessile species that is limited at the barrier, the barnacle *T. rosea*, and explored how these changes related to adult abundance at small to large spatial scales, to reveal the changes in the population dynamics and connectivity of this species from the middle of its range to its range limit. This yielded a complex pattern. Adult and recruit densities, and the proportions of adults producing mature larvae were all consistently large within the middle of the range, but declined

dramatically and significantly at the range limit, indicating a close link between life-history changes and therefore, a relatively closed population structure. However, a significant relationship was only found between adult and recruit densities at large scales at the range limit, whereas fecundity and recruitment did not relate, suggesting that recruitment plays a key role in determining adult abundance at the range limit.

In this thesis, I demonstrated empirically that the adult abundances of three planktonically developing species, and the fecundity and recruitment of one of these species, decline dramatically towards their range limits. Therefore, suboptimal conditions towards the range limits of planktonically developing, rocky intertidal marine invertebrates impact on their demographic processes and thus, adult abundances, despite their potential for long distance dispersal and recolonisation. In this sense, therefore, benthic marine invertebrates with a planktonic larval stage may indeed have ephemeral and vulnerable populations at the edge of their ranges, and may at least partially rely on populations in the middle of the range for survival. Essentially, range edge populations may therefore act as 'sink' populations, however, this proposition should now be tested using genetic assessments of populations across the range and at the range limit.

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CHAPTER 1

General Introduction

Predicting how species are distributed across their geographical ranges has been a long standing challenge to ecologists (Grinnell, 1917; Orton, 1920). It is known that species generally have a patchy distribution, as a consequence of spatial variability in abiotic and biotic conditions across their ranges (Gaston, 2003). However, the resulting patterns of distribution in abundance across species' geographical ranges, and the underlying processes responsible for these distributions, are less well understood.

Theoretical models imply that the key determinant of species' ranges is the spatial variation in factors driving local extinction, and the ability of species to recover from local extinction through dispersal (Carter and Prince, 1981; Kirkpatrick and Barton, 1997; Case and Taper, 2000; Hixon *et al.*, 2002; Case *et al.*, 2005; Guo *et al.*, 2005; Holt *et al.*, 2005). Dispersal enables recurrent immigration from 'source' populations (*sensu* Pulliam, 1988) to sites where a species would not normally survive and reproduce, and hence allows range expansion. Furthermore, dispersal can elevate local abundances and reduce extinction risk for populations in temporally variable 'sink' habitats (*sensu* Pulliam, 1988), and permit sites to be recolonised after extinction or disturbance (Guo *et al.*, 2005). At the range limit of a species, therefore, extinction arises when the births and immigrants simply become too small or the deaths and emigrants too large to sustain a population for sufficient periods (Gaston, 2003).

Measuring the large scale connectivity, via dispersal, among local populations is critical for understanding spatial patterns of species' abundance. Conservation management practices rely heavily on such information for the appropriate spatial arrangement of national park and marine reserve networks (Roberts, 1998; Crowder *et al.*, 2000; Botsford *et al.*, 2003; Gaines *et al.*, 2003; Lubchenco *et al.*, 2003; Palumbi, 2003; Holt *et al.*, 2005; Parmesan *et al.*, 2005; Sale *et al.*, 2005). Moreover, global climatic change threatens to shift species' ranges (Fields *et al.*, 1993; Sagarin *et al.*, 1999; Perry *et al.*, 2005), highlighting the need to understand the factors setting the patterns of distribution of species at their range limits (Holt and Keitt, 2005; Parmesan *et al.*, 2005).

Several empirical studies in terrestrial systems have found that species are most abundant at the centre of their geographical ranges and least abundant at the edges (e.g. Brown, 1984; Caughley *et al.*, 1988; see review in Gaston, 2003), resulting in an 'abundant-centre' distribution (Sagarin and Gaines, 2002a). This pattern of distribution is generally attributed to the more favourable abiotic conditions at the centre of species' ranges than at the edges (Brown, 1984). Similar assessments of such patterns in marine systems are, however, rare (Sagarin and Gaines, 2002a; Sagarin and Gaines, 2002b; Parmesan *et al.*, 2005). Moreover, decreased levels of fecundity and recruitment, and smaller individuals towards the range limit have been noted for some species in both terrestrial (Jump and Woodward, 2003; Zaidan *et al.*, 2003) and marine habitats (Westerbom *et al.*, 2002; Zacherl *et al.*, 2003; Lima *et al.*, 2006). However, little is known about how these factors influence the population dynamics and consequently, the abundances of species towards their range limits.

Benthic marine invertebrate species display an array of different reproductive modes, from direct developing crawl-away juveniles to planktotrophic larvae that can spend months in the water column (Strathmann, 1985; Pechenik, 1999). The larvae of direct developing species are released directly onto the benthic habitat, thus forming a closed population structure, whereby local populations are predominantly determined by the recruitment of local larvae (Hixon *et al.*, 2002). Planktonically developing species, however, release their larvae into the water column, which then drift, mostly passively, with the oceanic currents (Palmer and Strathmann, 1981; Strathmann, 1985; Pechenik, 1999; Kinlan and Gaines, 2003). Depending on the length of time spent in the plankton, they can be carried from a few metres to hundreds of kilometres away from their origins (Caley *et al.*, 1996; Eckman, 1996; Pechenik, 1999). The enormous potential for dispersal of these species has major implications for their population dynamics and connectivity at large scales (Caley *et al.*, 1996; Eckman, 1996; Pechenik, 1999; Cowen *et al.*, 2000; Hixon *et al.*, 2002; Dethier *et al.*, 2003; Eckert, 2003).

Local adult population densities and sizes can be determined by a mix of local and distantly sourced recruits, thus forming an open population structure (Caley *et al.*, 1996; Eckman, 1996; Pechenik, 1999; Cowen *et al.*, 2000; Carr *et al.*, 2003; Grantham *et al.*, 2003). Due to the often unidirectional flow of major oceanic currents (Gaylord and Gaines, 2000), some downstream 'sink' populations may exist predominantly due to the supply of larvae from upstream 'source' populations (*sensu* Pulliam, 1988; Crowder *et al.*, 2000). These unique life history characteristics and dispersal abilities are, therefore, likely to have a large influence on the patterns of recruitment and ultimately, adult abundance towards the range limits of these species. Simple predictions, however, are confounded by the fact that even species with little

or no time spent in the plankton may be widely distributed, and that even species with larvae that are apparently capable of widespread dispersal may form closed populations maintained by locally derived larvae (Johannesson, 1988; Wares *et al.*, 2001; Dethier *et al.*, 2003; Miner *et al.*, 2006).

In this thesis, I investigate the large scale patterns of distribution and demography of rocky intertidal marine macro-invertebrates on the southeast coast of Australia, by examining changes in their patterns of abundance, recruitment and fecundity. In chapter 2, I begin with an initial investigation on the patterns of rocky intertidal community composition and species richness across a marine biogeographic barrier on the southeast coast of Australia. The purpose of this chapter is to contrast the ability of species with direct and planktonic development to overcome large gaps in suitable habitat and, consequently, to identify species whose distributions are limited by the biogeographic barrier. In chapter 3, I then investigate the patterns of abundance and size frequency distributions of 3 planktonic developing species that are limited to the northern side of the biogeographic barrier, and one species that has a distribution that crosses the barrier. The purpose of this chapter is to test the predictions of the abundant-centre hypothesis. Finally, in chapter 4 I focus on one of the planktonic developing species from Chapter 3, the intertidal barnacle *Tessieropora rosea*, which has been relatively well studied, and for which the recruit and adult stages are easily distinguishable. I investigate the patterns of fecundity, recruitment and adult abundance of this species towards its southern range limit, and the relationships between these three stages of the life-cycle at several spatial scales. The purpose of this chapter is to reveal how patterns of fecundity and recruitment vary in space towards the range limit of this species, and how this ultimately affects patterns of

abundance. Chapters 2, 3 and 4 have been written as separate manuscripts. In chapter 5, I sum up my findings in a general discussion.

CHAPTER 2 ¹

Is The Species Composition of Rocky Intertidal Invertebrates Across A Biogeographic Barrier In Southeast Australia Related To Their Potential for Dispersal?

Introduction

Physical features of the coastal landscape have the potential to influence the dispersal and recruitment of organisms and, consequently, the large-scale patterns of diversity of species assemblages (Connolly and Roughgarden, 1998; Broitman *et al.*, 2001; Wares *et al.*, 2001). Large areas of unsuitable habitat, such as sandy beaches for rocky intertidal organisms, can form barriers that potentially restrict the geographical distribution of species (Crisp and Southward, 1958; Myers, 1997). In contrast, isolated patches of habitat, such as small rock platforms on sandy beaches, may act as stepping-stones and facilitate dispersal between geographically isolated populations (Valentine, 1966; Brown, 1995b).

The influence of these coastal features on the richness and composition of species assemblages will depend on the dispersal abilities of their member species (e.g. Johannesson, 1988; Scheltema, 1989; Parker and Tunnicliffe, 1994). Intertidal, rocky shore invertebrates have various modes of reproduction, development and dispersal, ranging from species that brood and lay benthic egg masses with direct developing and crawl-away juveniles, which are often considered ‘poor’ dispersers, to those with pelagic larvae that can disperse for up to a year in the plankton, which are typically considered ‘good’ dispersers (Strathmann, 1985). Consequently, the influence of

¹ This chapter is a manuscript written in collaboration with a B. Marine Science Honours student, Trudy L. Costa. The manuscript has been submitted to, and reviewed by Marine and Freshwater Research, and is likely to be accepted for publication after minor changes.

barriers and isolated patches of habitat on the distribution of these organisms is likely to be species-specific, but studies investigating how these features affect large-scale patterns of richness and composition of rocky intertidal species are rare (but see Wares *et al.*, 2001; Dethier *et al.*, 2003).

Species with a planktonic larval stage ('good' dispersers) are generally more successful than direct developers ('poor' dispersers) at reaching isolated locations, such as islands (Scheltema, 1986). It may therefore be predicted that large areas of unsuitable habitat would limit the distribution of 'poor' dispersers and that isolated habitats would be comprised predominantly of 'good' dispersers. Nevertheless, 'poor' dispersers may reach remote habitats by rafting and, once there, may persist more easily through greater local retention of their offspring (Highsmith, 1985; Johannesson, 1988). Indeed, two recent studies provide evidence that 'poor' dispersers may disperse more widely than predicted by their life histories. First, Wares *et al.* (2001) assessed the distribution of rocky intertidal invertebrates across a barrier formed by complex oceanic current patterns at Point Conception, along the coast of Californian, USA, and found that many species with planktonic larvae were limited by the barrier, whereas direct developing species had a continuous distribution across the barrier. Second, Dethier *et al.* (2002) found that a small, isolated jetty surrounded by soft-sediment habitat on the west coast of the USA supported a range of species with direct and planktonic development, and had species compositions similar to those at distant rocky platforms to the north and south. Therefore, although it seems logical that reproductive mode and larval type will influence the spatial scale of dispersal, there is no clear consensus as to whether these traits are related to the geographic distributions of species.

Along the southeast coast of Australia, a 300 km stretch of sandy shore (Ninety Mile Beach) and mangrove forest (between Cape Conran and Wilson's Promontory; see Fig. 2.1) separates the nearest rocky intertidal habitats. This habitat barrier coincides with the convergence zone of two major currents, the East Australian Current carrying warm temperate water from the north and the Zeehan Current carrying cool temperate water from the west (Bennett and Pope, 1953; Knox, 1963; O'Hara and Poore, 2000). The combination of differences in sea surface temperature, complex flow patterns and lack of suitable habitat has been postulated to form a significant biogeographic barrier (Ninety Mile Beach biogeographic barrier) and to delineate two biogeographic provinces for species on rocky intertidal shores (Bennett and Pope, 1953; Knox, 1963). The Ninety Mile Beach biogeographic barrier is also broken by a small, isolated rocky intertidal platform at Red Bluff (Fig. 2.1), which may provide a potential stepping-stone linking through dispersal populations of intertidal invertebrates north and south of the barrier.

Recent genetic studies provide evidence for the presence of a barrier, with significant population differentiation detected between regions on either side of the barrier for several intertidal species. These include two planktonically dispersing anemones, *Actinia tenebrosa* and *Anthothoe albocincta*, that are largely dependent on asexual recruitment to maintain local populations (Ayre *et al.*, 1991; Billingham and Ayre, 1996), the direct developing sea star *Patiriella exigua* (Hunt, 1993) and one archetypal 'good' disperser with planktonic larvae, the gastropod *Nerita atramentosa* (Waters *et al.*, 2005). Moreover, the geographical range limits for some species correspond with the presence of the barrier, including intertidal limpets (Bennett and Pope, 1953; Knox, 1963; Knox, 1980), macro-algae (King, R.J., unpublished data) and some bivalves and crustaceans (Bennett and Pope, 1953; Edgar, 1986; Wilson and

Allen, 1987; O'Hara and Poore, 2000). Nevertheless, there has been no rigorous assessment of the large-scale patterns of richness and composition of invertebrate assemblages on rocky intertidal shores across the region and how these relate to the life history and dispersal potential of the member species.

This natural configuration of habitat provides an excellent opportunity to test hypotheses about the effects of barriers and isolated patches of habitat on the large-scale patterns of richness and composition of marine communities comprised of species with different modes of reproduction, larval development and dispersal abilities. We therefore conducted a large-scale survey of intertidal macro-invertebrates at rocky shores on both sides of the biogeographic barrier at Ninety Mile Beach and at the small, isolated rock platform at Red Bluff. We tested the hypotheses that (1) there is a difference in species richness and composition north and south of the barrier and at Red Bluff; and (2) the patterns of distribution of species across the barrier are related to their potential dispersal abilities.

Methods

Study Area

The study area comprised 11 intertidal, rock platforms (hereafter locations) separated by at least 50 km along a 700 km stretch of the southeast coast of Australia from Bermagui, New South Wales (NSW) to Flinders, Victoria (Fig. 2.1). Five locations were sampled on the northern side of the barrier (Bermagui, Merimbula, Mallacoota, Point Hicks, Cape Conran) and five on the southern side (Sealers Cove, Picnic Bay, Cape Liptrap, Cape Patterson, Flinders), along with the isolated rock platform within the barrier at Red Bluff (Fig. 2.1). All platforms were subject to similar levels of wave exposure (medium to high) and had slopes of less than 45°. Rock type could not be controlled for due to the natural changes in geomorphology along the NSW and Victorian coasts. Platforms at Bermagui, Merimbula, Mallacoota, Cape Liptrap, Cape Conran and Cape Patterson are composed predominantly of sandstone and siltstone, those at Point Hicks, Sealers Cove, and Picnic Bay are granite and Flinders is basalt. It should be noted that some of the invertebrate species recorded on natural rock platforms in this study are also present on hard, artificial substrata (e.g. seawalls, breakwaters) at Lakes Entrance (unpublished data of authors), which is only about 3 km from Red Bluff and located in a generally more sheltered habitat.

Sampling Design and Methods

Sampling was conducted in winter (26 May to 15 June 2004) and summer (17 January to 8 February 2005) to ensure that seasonally occurring species were captured in the surveys. The number of species was counted at two sites at each of the five locations on either side of the barrier (Fig. 2.1). This hierarchical sampling design was used to capture spatial variability in species richness and composition over tens of metres

(between sites), tens of kilometres (among locations), and hundreds of kilometres (across the barrier) (Schoch and Dethier, 1996; Underwood and Chapman, 1996). Sites (except Red Bluff) extended 30 m alongshore and had intertidal limits from the seaward edge at mean low tide to the landward distributional limit of all intertidal animals. Sites at each location were separated by 10 m to 100 m, and varied naturally in intertidal extent from 6 m to 60 m depending on the slope of the shore. At Red Bluff, the entire area of the intertidal platform was sampled, which extended 18 m alongshore and 20 m from low to high on shore.

At each site and sampling time, sessile and sedentary invertebrate macrofauna inhabiting strictly intertidal habitats were identified through a single, 40 min search at low tide. This search excluded mobile species, such as amphipods and crabs, sponges (because of poor taxonomic resolution), and species < 1 cm. Intertidal species that have a distribution extending into the subtidal region, such as the anemone *A. albocincta* and the ascidian *Pyura stolonifera* among others, were also excluded, as it was impossible to distinguish whether these species were absent from a site or simply undetected due to the strictly intertidal search. A study quantifying the relationship between the search time and number of species at a range of sites of various sizes indicated that a time-per-area search of 40 min was sufficient to encounter most of the species present (unpublished data of authors).

Statistical Analysis

A two-factor, nested analysis of variance (ANOVA) was used to test for differences in species richness (i.e. the number of species from both seasons; untransformed data) among locations nested within regions (random factor) and between regions (fixed factor) north and south of the barrier using the JMP 5.1 statistical package. ANOVA's

assumptions of independence and normality were tested using the Chi-Squared test of independence and the Shapiro-Wilk test for normality respectively. Ordination by non-metric multidimensional scaling (MDS) using Bray-Curtis measures of dissimilarity was used to illustrate differences in species composition between sites and locations north and south of the barrier and at Red Bluff, using the PRIMER 5 software package (Clarke and Warwick, 1994). Analysis of similarity (ANOSIM) was used to test for differences in species composition between sites on either side of the barrier (Clarke and Warwick, 1994). Similarity percentage (SIMPER) was used to determine which species contributed to the differences in composition between sites on either side of the barrier, and between Red Bluff and all other sites.

Results

Species Richness and Composition

A total of 40 species were found across all locations north and south of the barrier, representing a wide range of taxonomic and trophic groups (Table 2.1). Species richness ranged from 24 to 32 species at individual sites and was significantly greater in the north (30.1 ± 0.8 ; mean \pm SE; $n = 10$ sites) than in the south (27.2 ± 0.8 ; mean \pm SE; $n = 10$ sites) ($F_{1,8} = 5.33$, $P < 0.05$), but did not vary significantly among locations ($F_{8,10} = 1.73$, $P = 0.21$). In contrast, only 19 species were found at Red Bluff (Table 2.1).

There were distinct species assemblages across the biogeographic barrier, with locations to the north clearly separate from those to the south (Figs. 2.1 and 2.2). Indeed, there was a greater similarity in species composition among sites and locations both north and south of the barrier than there was between these regions (ANOSIM, $R = 0.942$, $P = 0.008$). With the exception of one site at Cape Conran (N5A, Fig. 2.2), which lacked a number of species common to all other northern sites, variation in species composition among sites and locations within the northern region was less than in the southern (Fig. 2.2). Species composition at both northern and southern sites was distinct from that at Red Bluff (Fig. 2.2).

Of the 40 species, 32 were common to both sides of the barrier and 8 species were restricted to one side of the barrier: four to the northern side and four to the southern side (Table 2.1). Species that were unique to either side of the barrier (see Table 2.1) accounted for 58% of the differences in species composition between northern and southern locations (SIMPER analysis). All 19 species recorded at Red Bluff were from the pool of 32 species that were common to northern and southern sites (Table

2.1). The absence of the 13 other common species not present at Red Bluff explained more than 80% of the difference in species composition between Red Bluff and the other sites (SIMPER analysis).

Dispersal Potential

There were no clear trends in the dispersal potential of species and their presence on either side of the barrier. Seven of the eight species limited to either side of the barrier have pelagic development of larvae that disperse in the plankton, and the mode of reproduction and dispersal of the other species is unknown (Table 2.1). Further, the three species with direct development of juveniles in the benthic habitat were present on both sides of the barrier, as were another 27 species with a planktonic larval stage, and one species with unknown modes of reproduction and dispersal (Table 2.1). Nevertheless, all 19 species present at Red Bluff have planktonic larvae, and there were no species with direct development (Table 2.1).

Table 2.1 Presence of forty intertidal macro-invertebrate species at Red Bluff (RB) and regions north (N) and south (S) of the barrier, and their mode of gamete, egg or larval release (BS = Broadcast spawn; EM = Egg mass deposit; BR = Brooded) and mode of development and juvenile dispersal (PL = pelagic development of larvae in the plankton; DD = direct development of juveniles in benthic habitat, * = unknown).

Taxa	Release Mode	Dispersal Mode	Species Present			Reference
			N	RB	S	
Cnidaria						
<i>Actinia tenebrosa</i>	BS / BR	PL / DD	×		×	Ayre (1983)
<i>Aulactinia veratra</i>	*	*	×	×	×	*
<i>Oulactis mucosa</i>	BS	PL	×	×	×	Hunt and Ayre (1989)
Unidentified brown anemone	*	*	×			*
Platyhelminthes						
<i>Notoplana australis</i>	BS	PL			×	Anderson (1977)
Annelida						
<i>Galeolaria caespitosa</i>	BS	PL	×	×	×	Andrews and Anderson (1962)
Arthropoda						
<i>Catomerus polymerus</i>	BR	PL	×	×	×	Poore (2004)

<i>Chthamalus antennatus</i>	BR	PL	×	×	×	×	Poore (2004)
<i>Chaemosipho tasmanica</i>	BR	PL	×	×	×	×	Poore (2004)
<i>Tetracitella purpurescens</i>	BR	PL	×	×	×	×	Poore (2004)
<i>Tesseropora rosea</i>	BR	PL	×				Poore (2004)
Mollusca							
<i>Sypharochiton pelliserpentis</i>	BS	PL	×				Sakker (1986)
<i>Plaxiphora albida</i>	BS	PL	×			×	Otway (1994)
<i>Chypidina rugosa</i>	BS	PL	×	×	×	×	Creese (1980a)
<i>Patella peronii</i>	BS	PL	×	×	×	×	Underwood (1974)
<i>Cellana tramoserica</i>	BS	PL	×	×	×	×	Anderson (1962)
<i>Cellana solida</i>	BS	PL	×	×	×	×	Fretter <i>et al.</i> (1998)
<i>Patelloida alticostata</i>	BS	PL	×	×	×	×	Anderson (1965)
<i>Patelloida latistrigata</i>	BS	PL	×	×	×	×	Creese (1982)
<i>Notoacmea mayi</i>	BS	PL	×	×	×	×	Lindberg (1998)
<i>Notoacmea petterdi</i>	BS	PL	×	×	×	×	Creese (1980b)
<i>Austrocochlea constricta</i>	BS	PL	×			×	Hickman (1998)
<i>Austrocochlea porcata</i>	BS	PL	×			×	Hickman (1998)
<i>Austrocochlea concamerata</i>	BS	PL	×			×	Hickman (1998)
<i>Nerita atramentosa</i>	EM	PL	×			×	Underwood (1974)
<i>Bembicium nanum</i>	EM	PL	×			×	Anderson (1961)
<i>Bembicium melanostomum</i>	BS	PL				×	Reid (1998a)

<i>Austrolittorina unifasciata</i>	BS	PL	×	×	×	×	Underwood (1974)
<i>Afrolittorina praetermissa</i>	BS	PL	×			×	Reid (1998a)
<i>Afrolittorina pyramidalis</i>	BS	PL	×				Underwood (1974)
<i>Lepsiella vinosa</i>	EM	DD	×			×	Ward and Quinn (1988)
<i>Morula marginalba</i>	EM	PL	×				Underwood (1974)
<i>Siphonaria diemenensis</i>	EM	PL	×		×	×	Mapstone (1978)
<i>Siphonaria funiculata</i>	EM	PL	×		×	×	Ward and Quinn (1988)
<i>Siphonaria zelandica</i>	EM	PL	×		×	×	Creese (1980c)
<i>Onchidella patelloides</i>	EM	PL				×	Stanisic (1998)
<i>Brachiodontes rostratus</i>	BS	PL	×		×	×	Reid (1998b)
<i>Xenostrobus pulex</i>	BS	PL	×		×	×	Reid (1998b)
<i>Saccostrea glomerata</i>	BS	PL	×		×	×	Nell <i>et al.</i> (2000)
Echinodermata							
<i>Patiriella exigua</i>	EM	DD	×			×	Hunt (1993)

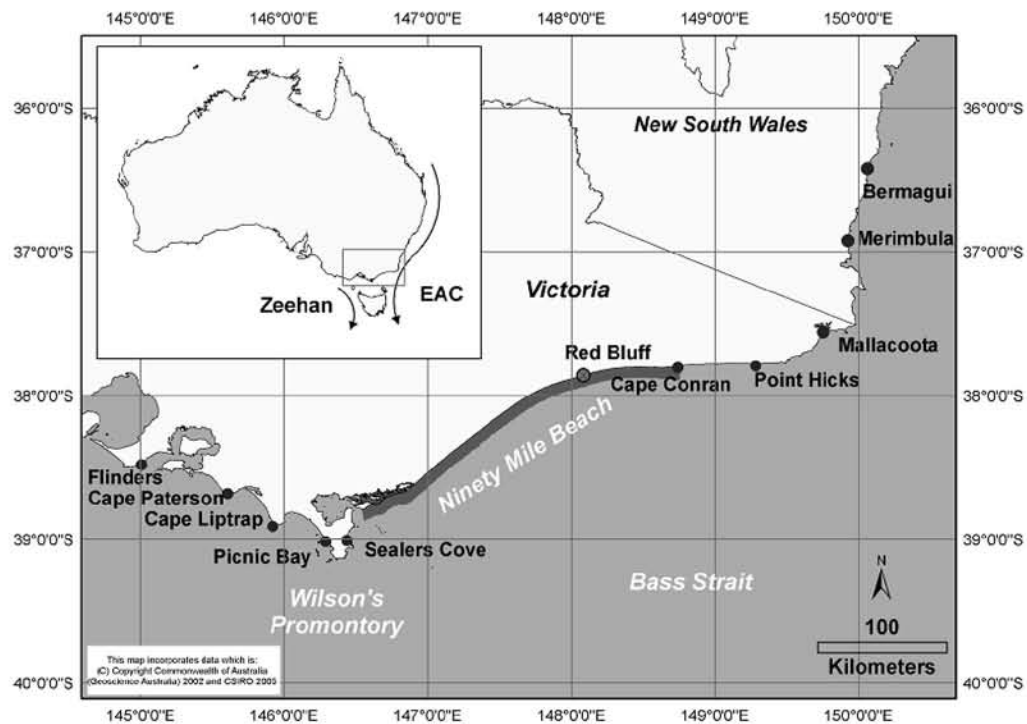


Fig. 2.1 Map of locations of 11 rocky intertidal platforms sampled to determine macro-invertebrate species richness and composition on either side of the Ninety Mile Beach biogeographic barrier, which extends from Cape Conran to Wilson's Promontory, and at Red Bluff within the barrier, on the southeast coast of Australia. Inset map shows Australia, and the dominant warm temperate East Australian Current (EAC) and cold temperate Zeehan Current that converge in Bass Strait along the Ninety Mile Beach biogeographic barrier.



Fig. 2.2 MDS plot of invertebrate species assemblages at 11 rocky intertidal platforms: two sites (A or B) at each of five locations (1 to 5) north (N) or south (S) of the Ninety Mile Beach biogeographic barrier, and at Red Bluff (RB) within the barrier, on the southeast coast of Australia. Northern locations are Bermagui (N1A, N1B), Merimbula (N2A, N2B), Mallacoota (N3A, N3B), Point Hicks (N4A, N4B), and Cape Conran (N5A, N5B). Southern locations are Sealers Cove (S5A, S5B), Picnic Bay (S4A, S4B), Cape Liptrap (S3A, S3B), Cape Paterson (S2A, S2B) and Flinders (S1A, S1B). Note that N3A and N3B are on top of each other.

Discussion

Our study provides further evidence for the importance of the Ninety Mile Beach region as a potential biogeographic barrier that separates two distinct biogeographical provinces for intertidal species (Bennett and Pope, 1953; Knox, 1963; Edgar, 1986; Wilson and Allen, 1987), but little support for an association between the dispersal potential of a species, as indicated by its mode of larval development, and its geographic distribution across a potential barrier (see also Dethier *et al.*, 2002). Indeed we found that seven 'good' dispersers were restricted either to the north or south of the barrier while other 'good' and 'poor' dispersers were found to span the barrier. Our data also support the potential of even tiny areas of suitable shore to act as stepping-stones, as about half of the species surveyed were detected at Red Bluff within the barrier. This finding may have important implications for the connectivity of intertidal communities at large spatial scales and, consequently, for the size and spacing of marine reserve networks (Shanks *et al.*, 2003).

Patterns of oceanic currents and associated changes in sea surface temperature might explain the significant difference in species richness and composition north and south of the barrier. The complex flow patterns arising from the convergence of the East Australian and Zeehan Currents result in the formation of often long-lived eddies and erratic patterns of long-shore water movements (Knox, 1963) that might restrict larval transport of the seven 'good' dispersers across the barrier (see Gaylord and Gaines, 2000). This scenario is consistent with the findings of Wares *et al.* (2001) at Point Conception on the Californian coast of the USA, who found that several rocky intertidal species with planktonic larvae were limited across a barrier formed by complex oceanic patterns. In addition, differences in the extremes of sea surface

temperature, which can differ by several degrees across the barrier (Knox, 1963; O'Hara and Poore, 2000), may limit the reproductive success of these organisms or the settlement and early survival of their larvae. Unfortunately, detailed information on reproduction, larval duration in the plankton and recruitment is not available for the vast majority of species in this study.

The three 'poor' dispersers that were distributed across the barrier may not be limited because they are able to traverse the distance by rafting on large drift algae or other floating debris (e.g. Highsmith, 1985; Johnson *et al.*, 2001; Aliani and Molcard, 2003). Once they are established, apparently poor dispersing direct developers may be better at retaining their offspring compared to planktonic species (Johannesson, 1988; Dethier *et al.*, 2002), and thus be better equipped to maintain viable local populations at distant and isolated locations (Johnson *et al.*, 2001). Once again this would be consistent with Wares *et al.* (2001), who found that poor dispersing direct developers successfully crossed a barrier and established viable populations on the other side.

Alternatively, shoreline changes associated with sea level rise may explain the distribution patterns of macro-invertebrates across the Ninety Mile Beach biogeographic barrier (Marko, 2004). This barrier has emerged fairly recently in geological time, as sea level only reached its present state approximately 6000 years ago (Lambeck and Nakada, 1990). Before this time, the 'poor' dispersers, and even some 'good' dispersers, may have been established across the barrier and had a continuous distribution. As sea level rose (Eisenhauer *et al.*, 1996), the populations may have become isolated, preventing larval exchange. If this separation of populations from sea level rise did occur, some genetic differentiation may be inherent in populations of a number of organisms on either side of the barrier

(Johnson and Black, 1998). There is already evidence of such genetic differentiation between northern and southern populations for the asexually viviparous anemone *A. tenebrosa* (Ayre *et al.*, 1991), the direct developing sea star *P. exigua* (Hunt, 1993), and the planktonic dispersing gastropod *N. atramentosa* (Waters *et al.*, 2005). Further genetic data for a range of taxa from populations on either side of the barrier is needed to explore this supposition.

Red Bluff had a distinct species assemblage, primarily due to the absence of ten species with planktonic larvae and three direct developers, which were common at all or most sites north and south of the barrier. In contrast, Dethier *et al.* (2002) found that, on an isolated jetty surrounded by soft-sediment habitat on the west coast of the USA, only a very small proportion of species were absent compared to those found on distant, larger rocky platforms to the north and south. The smaller number and different set of species at Red Bluff could be attributed to a number of factors. First, several studies have found that the number of benthic invertebrate species generally increases with patch area (Connor and McCoy, 1979; Keough, 1984; Butler, 1991) and, therefore, it is possible that the rock platform at Red Bluff supports fewer species because it is relatively small. This explanation is unlikely, however, as platform size varied among the other sites north and south of the barrier, and larger platforms did not always result in greater species richness or such a distinct species composition. Second, some of the 13 species may have been absent from Red Bluff because of a naturally patchy distribution at the site level. For example, nine of the 13 species absent from Red Bluff were only present at 50 to 75 % of northern and southern sites. Nevertheless, two gastropods, *N. atramentosa* and *Bembicium nanum*, and the anemone *A. tenebrosa*, which were not present at Red Bluff, occupied 90 to 100 % of northern and southern sites, suggesting that if this explanation were correct, then they

should also have been present at Red Bluff. Third, disturbances, such as sand scour (Littler *et al.*, 1983) and varying levels of wave impact (Brown and Quinn, 1988), which may be amplified by the isolation of Red Bluff, may prevent some species from colonising or surviving at Red Bluff. Moreover, if these populations become locally extinct, then they may not be able to recolonise this platform as their larvae might not reach the site, recruitment might be too sporadic, or recently settled juveniles might not be sufficiently robust to survive disturbance conditions. Lastly, it is possible that populations of the species absent from Red Bluff are more closed than has been previously assumed (e.g. Swearer *et al.*, 1999), and discrete populations exist on either side of the barrier, with no exchange of propagules between northern and southern locations. Indeed there is evidence of genetic differentiation between populations north and south of the barrier for two species that are not found at Red Bluff (Ayre *et al.*, 1991; Waters *et al.*, 2005).

We recognise that the patterns of species distributions detected in our study are a snapshot of those in geological time. Patterns of species richness and composition of intertidal assemblages can vary from year to year and over decades and centuries (e.g. Lawson, 1957; Barry *et al.*, 1995; Sagarin *et al.*, 1999). As sea level and climate change over time, more habitat patches may emerge within the Ninety Mile Beach biogeographic barrier (Bird, 1993), or Red Bluff may be completely submerged, altering habitat availability and, consequently, species composition and richness within the region.

CHAPTER 3

Demographic Structure of Populations of Marine Invertebrates Approaching Their Geographical Range Limits

Introduction

A long-standing hypothesis in ecology is that the abundance of a species is typically greatest at the centre of its geographical range and declines towards the edges, thus forming an abundant-centre distribution (Grinnell, 1917; Wulff, 1950; Andrewartha and Birch, 1954). This type of distribution has been proposed to be a result of either the dispersal of individuals outwards from a 'metropolis' of high abundance (Grinnell, 1917) or the decreasing physiological tolerance of individuals to changes in abiotic conditions (e.g. temperature) along an environmental gradient towards their range limits (Shelford, 1911; Andrewartha and Birch, 1954). Although a few terrestrial species have been shown to conform to the abundant-centre distribution (e.g. Brown, 1984; Caughley *et al.*, 1988; see review in Gaston, 2003), recent empirical investigations in marine habitats have found little support for this hypothesis (Sagarin and Gaines, 2002a; Sagarin *et al.*, 2006).

Many sessile and sedentary marine benthic species, particularly those with a planktonic larval stage, depend largely on the movements of oceanic currents for dispersal (Scheltema, 1986; Gaylord *et al.*, 2002; Kinlan and Gaines, 2003). Adult abundance at locations across the ranges of these species is determined by a combination of recruits from local populations, recruits that have been transported from other populations and, local mortality rates (Caley *et al.*, 1996; Eckert, 2003). Because of the often unidirectional flow of coastal currents (Gaylord and Gaines,

2000), areas of greatest local abundance across the range may simply be locations downstream from productive upstream 'source' populations (*sensu* Pulliam, 1988; Shanks *et al.*, 2003). In this sense, dispersal may play the largest role in determining the patterns of abundance of these species, and may not lead to abundant-centre distributions. Tests of this prediction at appropriately large spatial scales are, however, scarce.

In the first study examining large-scale patterns of distribution of marine species, Sagarin and Gaines (2002b) found that four of twelve rocky intertidal invertebrate species on the west coast of the USA increased in abundance from their most upstream northern range edge to their downstream southern range edge. The abundances of 2 species decreased along this same gradient, in a similar fashion to the intertidal limpet *Collisella scabra* (Gilman, 2005), whereas four species showed no apparent patterns, and only two had abundant-centre distributions. The geographic patterns of abundance of rocky, intertidal marine invertebrates on the west coast of the USA are therefore highly variable and, as yet, no general explanations are available for their distribution patterns.

Recruitment is a key determinant of adult distribution and abundance of benthic marine species (Gaines and Roughgarden, 1985; Minchinton and Scheibling, 1991; Caley *et al.*, 1996) and, therefore, quantifying the large-scale patterns of recruitment towards the range limits of benthic marine invertebrates may give insight into their patterns of adult abundance. Such information at large-scales is mostly limited to sessile species, such as corals and barnacles, whose larvae settle appropriately on larval collectors (Hughes *et al.*, 1999; Connolly *et al.*, 2001). For other more mobile species, such as gastropods, measuring recruitment is more difficult as the small and

often cryptic recruits sometimes occupy different habitats to the adults, and arrive to the shore at variable places and times (Zacherl *et al.*, 2003; Gilman, 2005). For these species, a suitable alternative is measuring size-frequency distributions of already established populations (e.g. Zacherl *et al.*, 2003; Gilman, 2005). The absence of small individuals at range edges can indicate sporadic or limited recruitment, whereas the absence of large individuals can reveal post-recruitment mortality, or lack of growth due to unfavourable conditions in the benthic habitat. For example, Zacherl *et al.* (2003) investigated the recent northward range extension of the marine coastal shelf neogastropod *Kellettia kelletti* across Point Conception on the Californian coast of the USA, and found that the recently established population on the northern side of the point was characterised by irregular size classes made up predominantly of large individuals, suggesting that recruitment was sporadic in the area. No such studies of recruitment patterns towards the range limits of benthic species have yet been carried out in the Southern Hemisphere.

Along the east coast of Australia, the warm temperate East Australian Current (EAC) flows dominantly southwards (Fig. 3.1) (Ridgway and Dunn, 2003) and, therefore, has the potential to influence the large-scale patterns of distribution of marine species. In summer, the current partially deflects away from the coast just north of Sydney, and partially continues southward as a weaker current, occasionally forming coastal eddies as it approaches the border of New South Wales and Victoria (Fig. 3.1). In winter, however, it can reach as far south as the border before deflecting away from the coast (Ridgway and Dunn, 2003). It has therefore been suggested that the transport of larvae of benthic marine species may be increasingly less reliable from Sydney towards the south (Murray-Jones and Ayre, 1997).

In this chapter I use surveys of the patterns of abundance and size structure of three planktonically developing rocky intertidal invertebrate species that have a southern range limit on the southeast coast of Australia (from here on, target species), and one species that does not have a limited distribution across this region (from here on, reference species) to test the predictions of the abundant-centre hypothesis. I predict that if the three target species are limited on the southeast coast of Australia due to the decreased reliability of the EAC for dispersal, they may exhibit a decline in adult abundance, and also a decline in the proportion of small individuals and cohorts (or similar individuals indicating a single recruitment event), towards their range limits. If however, dispersal is not limited towards the range limits of these species, which is a possibility as the effect of the EAC may potentially vary at different times of the year (Ridgway and Dunn, 2003), the abundances of these species may stay constant or increase, and there may be a high proportion of small individuals towards and at the range limit. The abundance and size structure of the reference species, however, is unlikely to be affected across this section of coast, which is located within the middle of its range.

Methods

Study Species

I measured the abundances and size-frequency distributions of four planktonic developing rocky intertidal marine invertebrates: the whelk *Morula marginalba* (Plate I), the littorinids *Afrolittorina pyramidalis* (Plate II) and *Nodilittorina unifasciata* (Plate III), and the barnacle, *Tesseropora rosea* (Plate IV), along 600 km of shoreline, from Sydney in New South Wales (NSW) (S 34° 10', E 151° 04') to Cape Conran in Victoria (S 37° 08', E 148° 07') (Fig. 3.1) in southeast Australia, in May 2005, September 2005, and January 2006.

The three target species, *M. marginalba*, *A. pyramidalis* and *T. rosea*, were found to have a southern range limit at Cape Conran on the northern side of a biogeographic barrier (see Chapter 2 and Edgar, 1997), and therefore made suitable study species to assess large-scale changes in patterns of abundance and demography of marine invertebrates approaching their geographical range limits. The distribution of *Nodilittorina unifasciata*, however, was not limited across this same biogeographic barrier (see Chapter 2), and therefore it made a suitable reference species to make appropriate comparisons in patterns of abundance and size-frequency among these species.

Morula marginalba has a distribution from north Queensland to Ram Head in eastern Victoria (Fig. 3.1, Table 3.1), although 6 individuals have recently been found as far south as Cape Conran (C. Perrin, personal communication). *Afrolittorina pyramidalis* and *T. rosea* are also distributed from Queensland to Cape Conran (Fig. 3.1, Table 3.1), although there has been one confirmed sighting of *T. rosea* at one location in

each of the states of Victoria and Tasmania (Edgar, 1997), and it is present in Western Australia due to its introduction from ballast water (Jones, 1990).



Plate I The predatory whelk *Morula marginalba*.



Plate II The littorinid, *Arolittorina pyramidalis*.



Plate III The littorinid, *Nodilittorina unifasciata*.



Plate IV The barnacle, *Tesseropora rosea*.

Nodilittorina unifasciata, in contrast, is distributed abundantly from Queensland to Western Australia (Table 3.1).

These four species inhabit various microhabitats, live at different heights on the shore, and feed on an array of different organisms (Table 3.1). However, their main breeding periods are all from mid-summer to late autumn (Table 3.1), and although they have variable modes of larval release, they all have a planktonic larval stage at some phase in their development. The larval durations of the two littorinids, *A. pyramidalis* and *N. unifasciata*, are unknown, but the larvae of *M. marginalba* and *T. rosea* are thought to spend up to several weeks in the water column (Table 3.1). Therefore, three sampling events separated by four months, from May 2005 to January 2006, were considered appropriately spaced to capture temporal variability in recruitment for these species.

Table 3.1 Distributions, habitat preferences, diets, breeding and reproductive characteristics of the rocky intertidal marine invertebrates *Morula marginalba*, *Afrolittorina pyramidalis*, *Tesseropora rosea*, and *Nodilittorina unifasciata* on the southeast coast of Australia.

	<i>Morula marginalba</i>	<i>Afrolittorina pyramidalis</i>	<i>Tesseropora rosea</i>	<i>Nodilittorina unifasciata</i>
Type of invertebrate	whelk	littorinid	barnacle	littorinid
Northern distribution limit	Cape York, north QLD	Townsville, North QLD	Townsville, North QLD	southern QLD
Southern distribution limit	Cape Conran, East VIC	Cape Conran, East VIC	Cape Conran, East VIC	southern WA
Preferred height on shore	mid to low	high	mid to low	high
Preferred microhabitat	crevice, rockpool	"honeycomb" shaped rock, crevice	emergent rock	all
Diet	barnacles, molluscs, polychaetes	microalgae	plankton	microalgae
Breeding season	December to March	December to April	January to May, but also at variable times throughout the year	December to May
Mode of gamete release	lays egg masses	release into water column	release into water column	release into water column
Larval type	planktotrophic	planktotrophic	planktotrophic	planktotrophic
Time spent in plankton	up to several weeks	unknown	3 to 5 weeks	unknown
Size at maturity	aperture length of about 15-20 mm	unknown	aperture length of 3 to 4 mm	unknown
References	1, 2, 3, 4, 5, 6, 7, 8	3, 5, 9	5, 10, 11, 12	3, 5, 13, 14, 15

References 1. Moran *et al.*, 1984 2. Moran, 1985 3. Underwood, 1974 4. Anderson, 1965 5. Edgar, 1997 6. Kohn and Leviten, 1976 7. Fairweather, 1988b 8. Peter Fairweather, pers. comm. 9. Chapman and Underwood, 1994 10. Caffey, 1985 11. Wisely and Black, 1964 12. Denley, 1981 13. Chapman, 1995 14. Chapman and Underwood, 1996 15. Chapman, 1997

Sampling Design and Study Locations

I used a hierarchical sampling design to assess the changes in patterns of abundance and size-frequency of the four study species, at small to large spatial scales. I divided the 600 km study region into four sectors (each spanning between 70-110 kilometres of coastline), four representative locations within each sector (each covering 100 to 140 metres of coastline), and three sites at each location (each covering 30 metres of coastline) (Fig. 3.1). This allowed an assessment of the changes in patterns of abundance and size-frequency across the entire study region, among sectors, and among locations. Sectors were separated by 30-100 km, locations by 10-50 km, and sites by 0-50 m. Sectors 1 to 4 represented regions furthest to closest to the range limit of the target species respectively, although sectors 1, 2 and 3 were all considered to be within the middle of the species' ranges, while sector 4 was considered to be at the range limit of the target species (Fig. 3.1).

Locations were predominantly chosen for their accessibility, safety, and regular spacing within sectors, but were also selected to be as uniform as possible in their physical characteristics (see Table 3.2). For example, locations where rock platforms lacked rockpools and crevices were avoided because of the known strong positive association between these microhabitats and the densities of some of the study species (see Table 3.1). Wherever possible, locations were located on either side of moderately exposed headlands, with an orientation facing the open ocean and, except at two locations, a platform slope of no more than 10 degrees. Rock type, however, could not be controlled as this varied naturally between siltstone, sandstone, mudstone, granite and basalt, with the majority being sandstone/siltstone. Sites were

approximately 30 m alongshore, and of variable intertidal extent (from 6 to 50 m) depending on the slope of the platform.

Table 3.2 Physical characteristics of the intertidal rock platforms at each of 16 locations from Garie Beach in Sydney in the north, to Cape Conran in the south on the southeast coast of Australia, used to assess the abundances and size-frequency distributions of rocky intertidal marine invertebrates. 'Free standing platform' refers to platforms surrounded by beach on either side. Platform slope is an approximation only, and is given in degrees.

Location	Landform	Rock Type	Orientation	Platform Slope
Garie Beach	Free standing platform	Sandstone/Siltstone	East	5
Wollongong	Headland	Sandstone/Siltstone	South	5
Kiama	Headland	Sandstone/Siltstone	North	5
Gerroa	Headland	Sandstone/Siltstone	South	5
Kioloa	Headland	Sandstone/Siltstone	South	10
Malua Bay	Headland	Sandstone/Shale	South	5
Tuross Heads	Free standing platform	Sandstone/Siltstone	East	10
Dalmeny	Headland	Sandstone/Siltstone	North	5
Bermagui	Headland	Sandstone/Siltstone	North/North-East	10
Mimosa Rocks	Free standing platform	Sandstone/Mudstone/ Basalt	East	5
Merimbula	Headland	Sandstone/Siltstone	North/North-East	5
Haycock Point	Headland	Sandstone/Siltstone	East	5
Mallacoota	Headland	Sandstone/Siltstone	East	5
Ram Head	Headland	Granite	South/South-East	30
Point Hicks	Free standing platform	Granite	South	30
Cape Conran	Headland	Sandstone/Siltstone	East/South-East	10

Sampling Methods

Patterns of abundance of the four rocky intertidal invertebrate species were assessed by measuring density at each site using haphazardly placed quadrats within all microhabitats (i.e. rockpools, crevices and emergent rock) on the height on the shore that each species was found. Preliminary sampling showed that ten, 2 m x 2 m quadrats for *M. marginalba*, twenty, 0.5 m x 0.5 m quadrats for *A. pyramidalis*, twenty, 0.25 m x 0.25 m quadrats for *N. unifasciata*, and twenty, 0.15 x 0.15 m quadrats for *T. rosea* gave appropriate estimates of density. The densities of *M. marginalba*, *A. pyramidalis* and *N. unifasciata* were estimated *in situ*. The density of *T. rosea* was estimated from photoquadrats.

Size-frequency distributions for each species at each location were obtained by measuring to the nearest 0.5 mm with Vernier calipers a random sample of 300-500 individuals across two sites (i.e. 150-200 per site) at each location. At locations near the range limit of the target species in sector 4 (i.e. Mallacoota, Ram Head, Point Hicks, Cape Conran - see Fig. 3.1), less than 100 individuals were measured for some species, due to their low abundances. Bias towards any size class relating to position on shore or microhabitat was avoided by measuring only approximately 20 individuals at any one area within a site, and by moving around to cover the entire vertical and horizontal extent of species within a site. For *A. pyramidalis* and *N. unifasciata*, measurements were made from the apex to the outermost tip of the aperture (Chapman, 1997), and for *M. marginalba* and *T. rosea*, the length of the aperture (Denley, 1981; Moran *et al.*, 1984).

Data and Statistical Analyses

Density

I used linear regression analyses, using the SYSTAT 10 statistical package, to assess the relationships between density and distance from the range limit across the entire study region, for each of the four study species. Density values were the means of the three sampling seasons at each location.

To test whether there were significant differences in densities (log-transformed data) among sectors (fixed factor) and among locations nested within sectors (random factor) for each of the study species, I used mixed model analyses of variance (ANOVA) with the statistical package SPSS 12. Analyses were carried out separately for each of the three sampling times (May 2005, September 2005, and January 2006), and for the mean of the three sampling times (from here on, overall mean) for each species, using the mean values at each site. Data during some sampling seasons were not obtained at some locations due to adverse weather conditions. Therefore, for the analyses on total means, data were omitted for any sites that had fewer than two sampling times.

For a mixed model ANOVA, a standard F ratio is used to assess statistical significance for the fixed factor, and a Wald-Z value for the nested random factor. The Wald test is commonly used to test the statistical significance of covariance parameters in a mixed model, and allows calculation of a Z-statistic by dividing the parameter estimate by its standard error (Littell *et al.*, 1996).

Size-frequency

To look for evidence of recruitment, indicated by the appearance of small individuals, and growth, indicated by the modal shift of size classes over time, temporal variations in size-frequency distributions were compared visually for each species by comparing May 2005, Sept 2005 and January 2006 distributions at each location for each species. For analysis of spatial variations in size-frequency distributions towards the range limit, however, size distributions from all three sampling times were combined, to increase sample sizes and to maximise the chances of identifying possible recruitment events. For all three gastropod species, a unimodal distribution was observed at all locations, for each of the three sampling times and the total of the sampling times (see Results) and, therefore, no further analysis was done. For *T. rosea*, however, cohort analysis was carried out on the data combined from the three sampling events, using the probability paper technique (Harding, 1949; Cassie, 1954). This method involves plotting on probability paper the cumulative percentage distribution of sizes of a species at each location, and identifying points of inflexion that represent the separation of distinct size cohorts.

Linear regression analyses were used to test for significant relationships between mean sizes at each location and distance from the range limit for each species, and for the mean sizes of small (<3 mm - juvenile) and large (≥ 3 mm - adult) individuals, and the number of cohorts at each location, and distance from the range limit for *T. rosea*, using the SYSTAT 10 statistical package.

Results

Patterns of Density Across the Study Region

Across the 600 km study region, there was a significant negative linear relationship between overall mean density and distance from the range limit for two of the target species: *M. marginalba* and *T. rosea*, (Fig. 3.2). This relationship was not significant for the third target species, *A. pyramidalis*, as this species appeared to have a bell shaped distribution towards the range limit. Nevertheless, *A. pyramidalis* also had smallest densities at the range limit. As expected, density did not decline significantly across the study area for the reference species, *N. unifasciata*.

Patterns of Density Across Sectors

At the sector level, the three target species, *M. marginalba*, *A. pyramidalis* and *T. rosea*, had overall mean densities 5- to 100-fold greater in sectors 1 to 3 within the middle of the range, ranging from 24.3 to 41.9, from 6.3 to 18.1 and, from 74.6 to 134.4 individuals per quadrat respectively, than in the range limit sector 4, which only had mean densities of 0.4, 0.6 and 16.4 respectively for the three species (Fig. 3.3). *Tesseropora rosea* appeared to exhibit a gradual decline in density towards the range limit, while the densities of the two gastropods, *M. marginalba* and *A. pyramidalis*, appeared to peak in sector 2 before declining again at the range limit. Nevertheless, for all three species mean density was significantly lower in sector 4 than in all other sectors (Table 3.3). In contrast, the reference species, *N. unifasciata*, which does not have a limited distribution within the study region, had consistently high mean densities, ranging from 38.1 to 60.2 individuals per quadrat across the four sectors (Fig. 3.3) and, therefore, had no significant differences in density among sectors (Table 3.3)

The three sampling times of May 2005, September 2005 and January 2006 separately revealed similar patterns of density than described above for the overall mean, for all four species (Fig. 3.3, Table 3.3). The only two exceptions were in January 2006, when densities of *T. rosea* only varied between 20.4 and 82.7 individuals per quadrat among the four sectors and therefore, no significant differences were found in the densities of *T. rosea* among the four sectors, and densities of *N. unifasciata* were significantly higher in sector 3 than in other sectors.

Patterns of Density Across Locations

The overall mean densities of each of the four species varied among locations within sectors (Fig. 3.4). However, for the three gastropods, *M. marginalba*, *A. pyramidalis* and *N. unifasciata*, there were only 2- to 3-fold differences among locations within any sector, while for *T. rosea*, there were some differences of much greater magnitude, particularly in sector 2. Indeed, overall mean densities at locations within sectors only varied significantly for *T. rosea*, and there were no significant differences for the other three species (Table 3.3). These patterns held constant across all three sampling times (and, consequently, data are not presented), with the exception of May 2005 for *N. unifasciata*, when there was a significant difference in density among locations within sectors for this species.

Patterns of Size-frequency

The size-frequency distributions of the three gastropods, *M. marginalba*, *A. pyramidalis* and *N. unifasciata* did not show any patterns either spatially across locations or temporally across seasons (Figs. 3.5, 3.6 and 3.8 respectively). For *M. marginalba* (Fig. 3.5) and *N. unifasciata* (Fig. 3.8) each location appeared to have a unimodal distribution, and there were no obvious recruitment events. For *A.*

pyramidalis, the only obvious change was a lack of small individuals at the most southern location at Point Hicks, nearest to the range limit (Fig. 3.6). Mean size decreased slightly towards the range limit for *M. marginalba*, and increased slightly for *A. pyramidalis*, but did not change significantly towards range limit locations for any of the three gastropod species (Fig. 3.9).

The size-frequency distribution of *T. rosea*, however, showed both spatial and temporal patterns (Fig. 3.7). At the range limit locations of Mallacoota, Ram Head and Point Hicks, there appeared to be a smaller proportion of large (> 6 mm) individuals, although this was also seen at Garie Beach and Kioloa within the middle of the range (Fig. 3.7). There was, therefore, no significant relationship between total mean size at locations and distance from the range limit (Fig. 3.9). However, when mean size of juveniles (< 3 mm) and adults (≥ 3 mm) were plotted separately against distance from the range limit (Fig. 3.10), there was a significant increase in the mean size of small, and a non-significant decrease in the mean size of large individuals towards the range limit. Furthermore, cohort analysis implied that the number of age classes on rocky platforms at each location decreased towards the range limit, with 3 or 4 cohorts present in the most northern locations of Garie Beach, Wollongong, Kiama, Gerroa, Kioloa and Tuross Heads, but only predominantly 2, but a maximum of 3 cohorts present at more southern locations (Fig. 3.7). This decline in number of cohorts towards the range limit was indeed significant (Fig. 3.11).

Peaks in recruitment of *T. rosea*, indicated by peaks in the number of small individuals, were generally detected in May 2005 across all locations. Interestingly, however, these peaks appeared to shift to larger size classes by January 2006 in the northern locations, whereas in the southern range limit locations, they appeared to

persist through this same time period (Fig. 3.7).

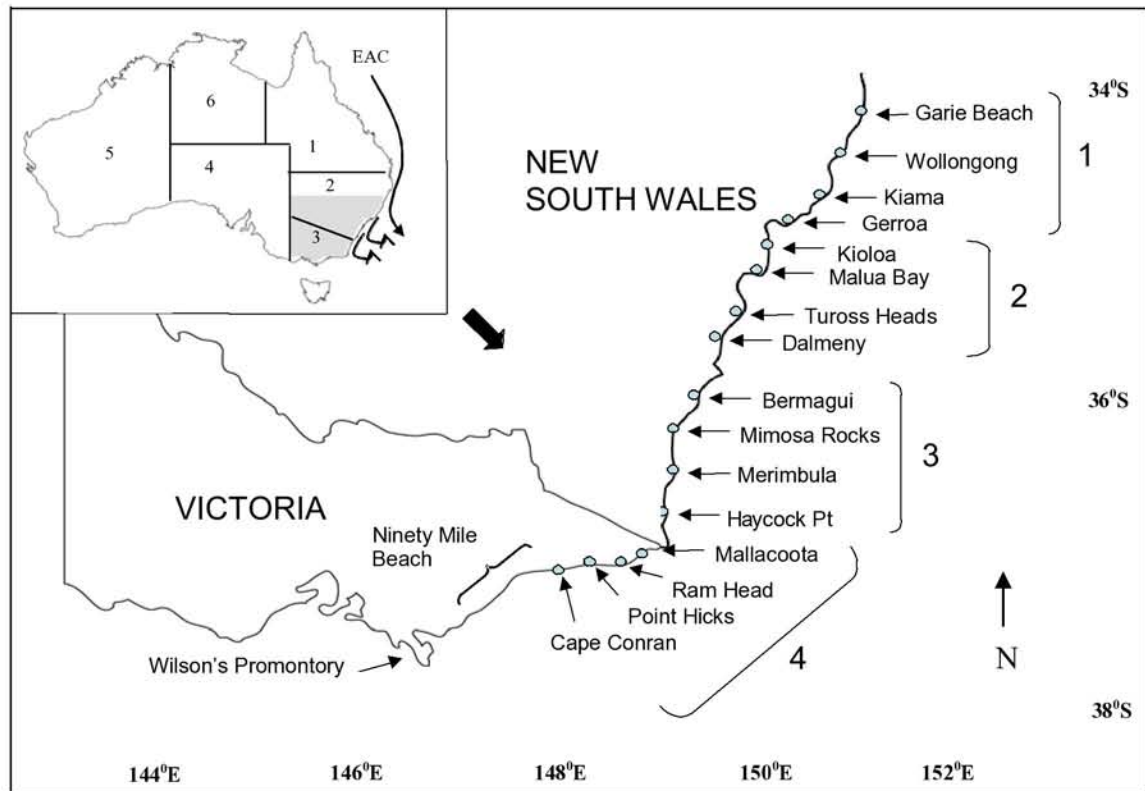


Fig. 3.1 Map of the southeast coast of Australia showing the four sectors (1 to 4) and corresponding 16 locations used to assess the density and size frequency distributions of four rocky intertidal invertebrate species. Ninety Mile Beach is a 150 km stretch of continuous sandy beach, followed southward by mangrove forests to Wilson's Promontory, together forming a 300 km gap in suitable habitat for any rocky intertidal species. Inset map shows Australia with its major states and territories numbered 1 to 6 (1=Queensland, 2=New South Wales, 3=Victoria, 4=South Australia, 5=Western Australia and 6=Northern Territory), and the shaded area showing the location of the key map of this figure. Flow patterns of the dominant southward flowing East Australian Current (EAC) are also shown, which partially deflects away from the coast just north of Sydney, and partially continues as a weaker current, occasionally forming coastal eddies as it approaches the border of New South Wales and Victoria.

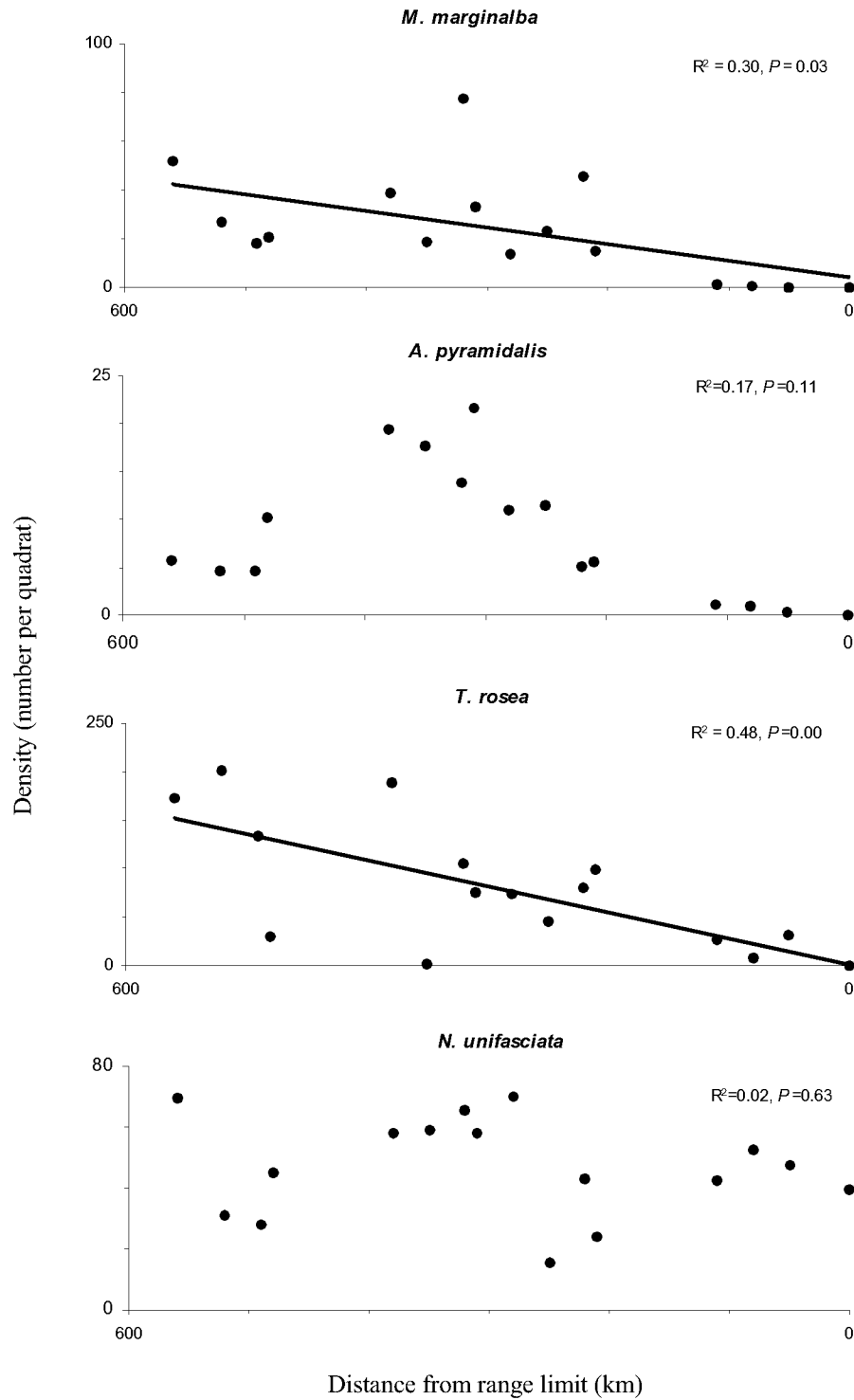


Fig. 3.2 The relationship between mean densities of four rocky intertidal invertebrates, and distance from the range limit of *M. marginalba*, *A. pyramidalis* and *T. rosea* at Cape Conran, Victoria (Fig. 1) from May 2005 to January 2006 at 13 to 16 locations (depending on the location of the range limit of each species) on the southeast coast of Australia.

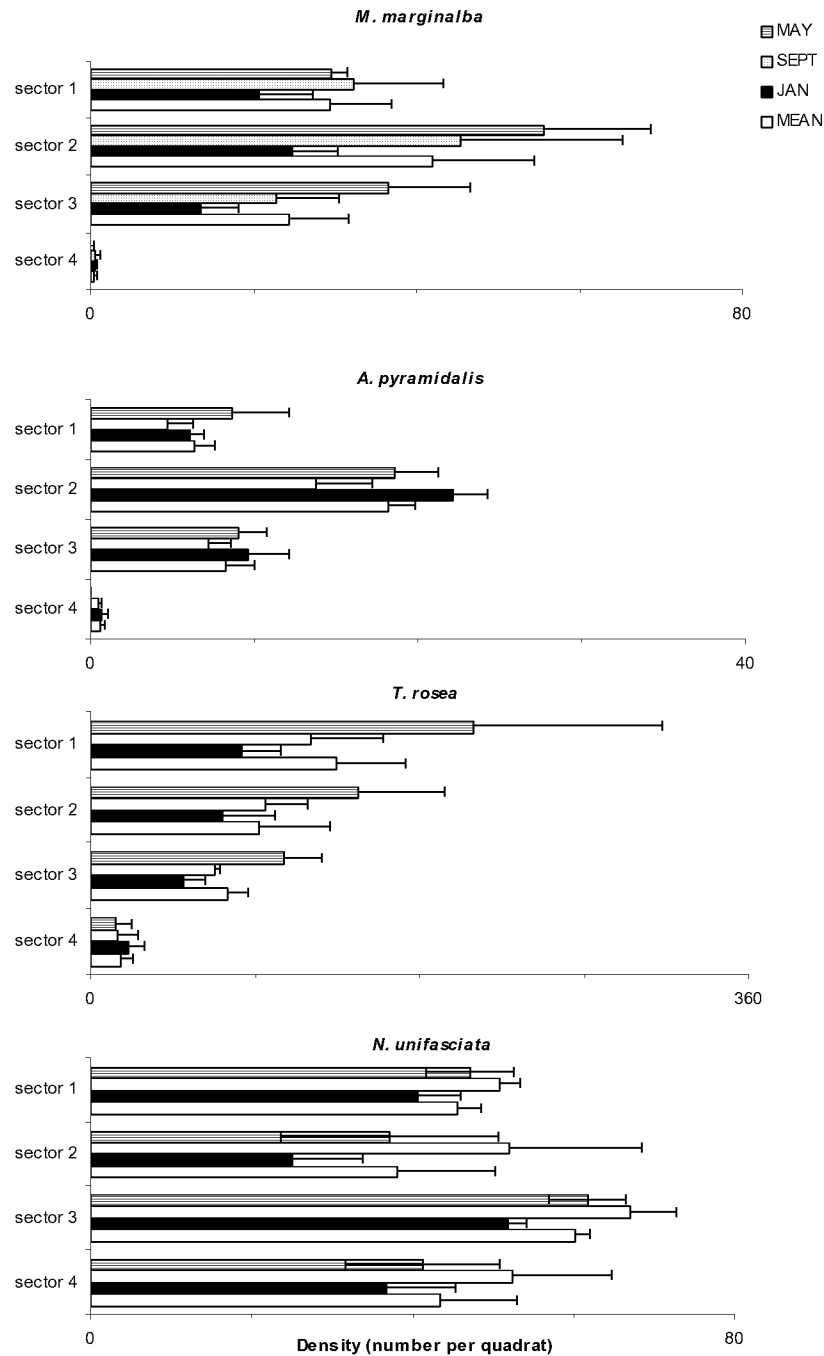


Fig. 3.3 Mean (+SE) densities of four rocky intertidal invertebrate species in four sectors (numbered from north to south, see Fig. 3.1) on the southeast coast of Australia in May 2005, September 2005, January 2006, and the mean of these three sampling periods. *M. marginalba*, *A. pyramidalis* and *T. rosea* have a southern range limit in sector 4, whereas *N. unifasciata* does not have a range limit across these four sectors.

Table 3.3 Mixed model analyses of variance of the densities of four rocky intertidal invertebrates, *M. marginalba*, *A. pyramidalis*, *T. rosea* and *N. unifasciata* on the southeast coast of Australia, with fixed sectors and random locations nested within sectors, on log-transformed data from May 2005, September 2005, January 2006, and the mean of these three sampling events. The Wald Z tests the significance of the nested random factor. Results of Tukey's post-hoc tests are shown with sectors listed in order of 1 (most northern, within the middle of the range) to 4 (most southern, range limit). Sectors with different letters are significantly different from each other, with 'A' representing sectors with the greatest densities, and consecutive letters of the alphabet representing a decrease in abundance.

M. marginalba

		d.f.	SS	F ratio	Wald Z	P	Post-hoc
May 2005	Sector	3	41.323	29.056		0.000	A A A B
	Location(Sector)	9	1.369		0.474	0.635	
	Residual	25					
Sept 2005	Sector	3	9.471	7.223		0.007	A A A B
	Location(Sector)	10	12.332		1.631	0.103	
	Residual	28					
Jan 2006	Sector	3	13.158	8.93		0.004	A A A B
	Location(Sector)	10	5.040			0.277	
	Residual	28					
Mean	Sector	3	15.225	12.378		0.001	A A A B
	Location(Sector)	10	6.462		1.333	0.183	
	Residual	28					

A. pyramidalis

		d.f.	SS	F ratio	Wald Z	P	Post-hoc
May 2005	Sector	3	7.414	9.637		0.008	A A A B
	Location(Sector)	7	2.694		1.076	0.282	
	Residual	20					
Sept 2005	Sector	3	12.527	20.028		0.000	A A A B
	Location(Sector)	11	3.401		1.361	0.174	
	Residual	30					
Jan 2006	Sector	3	17.198	27.171		0.000	B A B C
	Location(Sector)	12	3.731		1.417	0.157	
	Residual	32					
Mean	Sector	3	13.329	40.341		0.000	B A B C
	Location(Sector)	12	2.526		1.574	0.116	
	Residual	32					

T. rosea

		d.f.	SS	F ratio	Wald Z	P	Post-hoc
May 2005	Sector	3	12.502	6.252		0.012	A A A B
	Location(Sector)	10	25.267		1.748	0.08	
	Residual	27					
Sept 2005	Sector	3	4.038	9.05		0.013	A AB A B
	Location(Sector)	10	29.397		2.076	0.038	
	Residual	26					
Jan 2006	Sector	3	0.782	1.289		0.323	
	Location(Sector)	12	64.575		2.359	0.018	
	Residual	31					
Mean	Sector	3	2.716	5.277		0.017	A A AB B
	Location(Sector)	11	30.046		2.201	0.028	
	Residual	30					

N. unifasciata

		d.f.	SS	F ratio	Wald Z	P	Post-hoc
May 2005	Sector	3	0.468	1.153		0.371	
	Location(Sector)	11	9.585		2.019	0.043	
	Residual	28					
Sept 2005	Sector	3	1.349	0.829		0.503	
	Location(Sector)	12	1.128		0.321	0.748	
	Residual	32					
Jan 2006	Sector	3	1.199	3.520		0.049	AB B A AB
	Location(Sector)	12	3.953		1.799	0.072	
	Residual	32					
Mean	Sector	3	0.973	2.021		0.165	
	Location(Sector)	12	3.344		1.517	0.129	
	Residual	32					

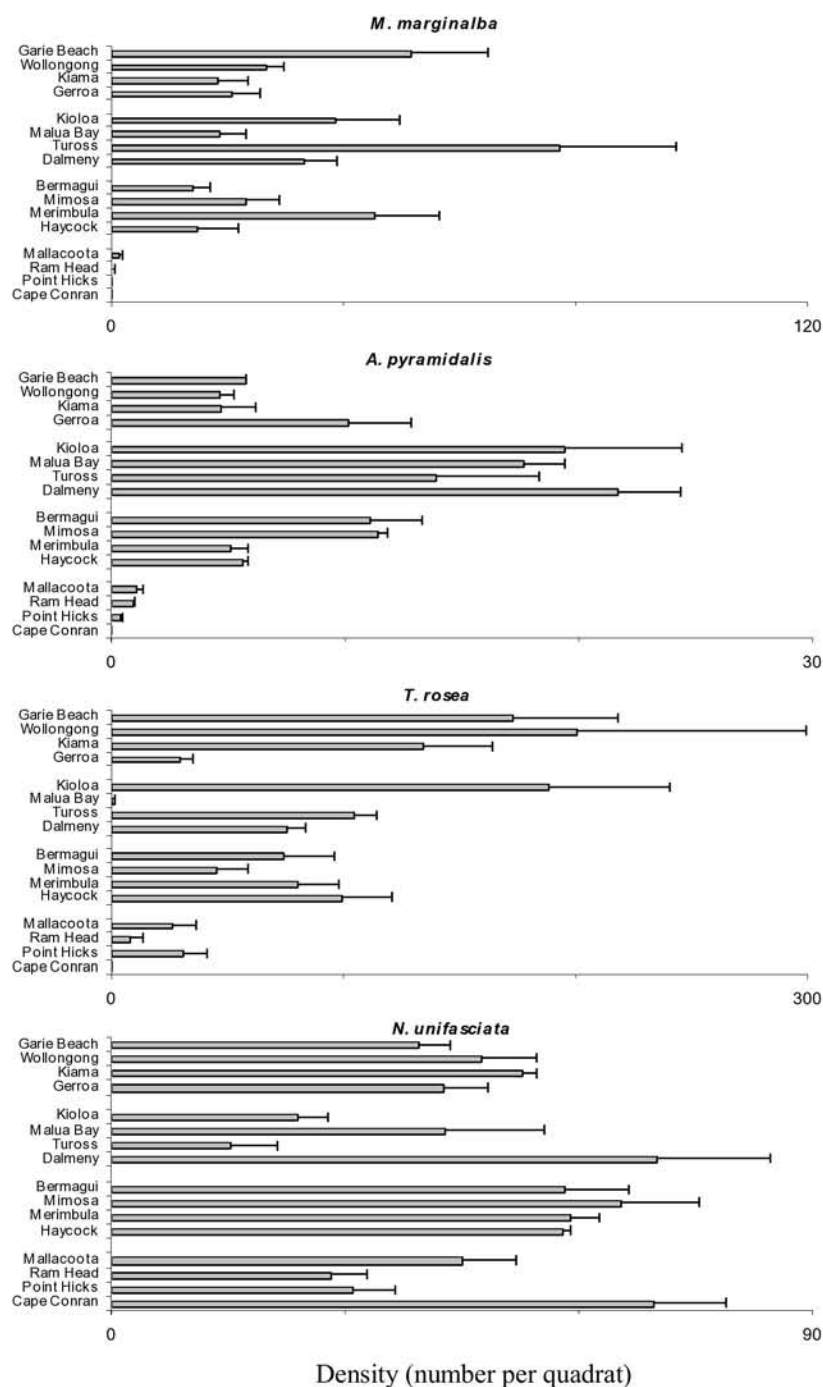


Fig. 3.4 Mean (+SE) densities of four rocky intertidal invertebrate species at 16 locations within four sectors (see Fig. 3.1) on the southeast coast of Australia between May 2005 and January 2006. *M. marginalba*, *A. pyramidalis* and *T. rosea* have a southern range limit at Cape Conran, while *N. unifasciata* does not have a range limit across these locations.

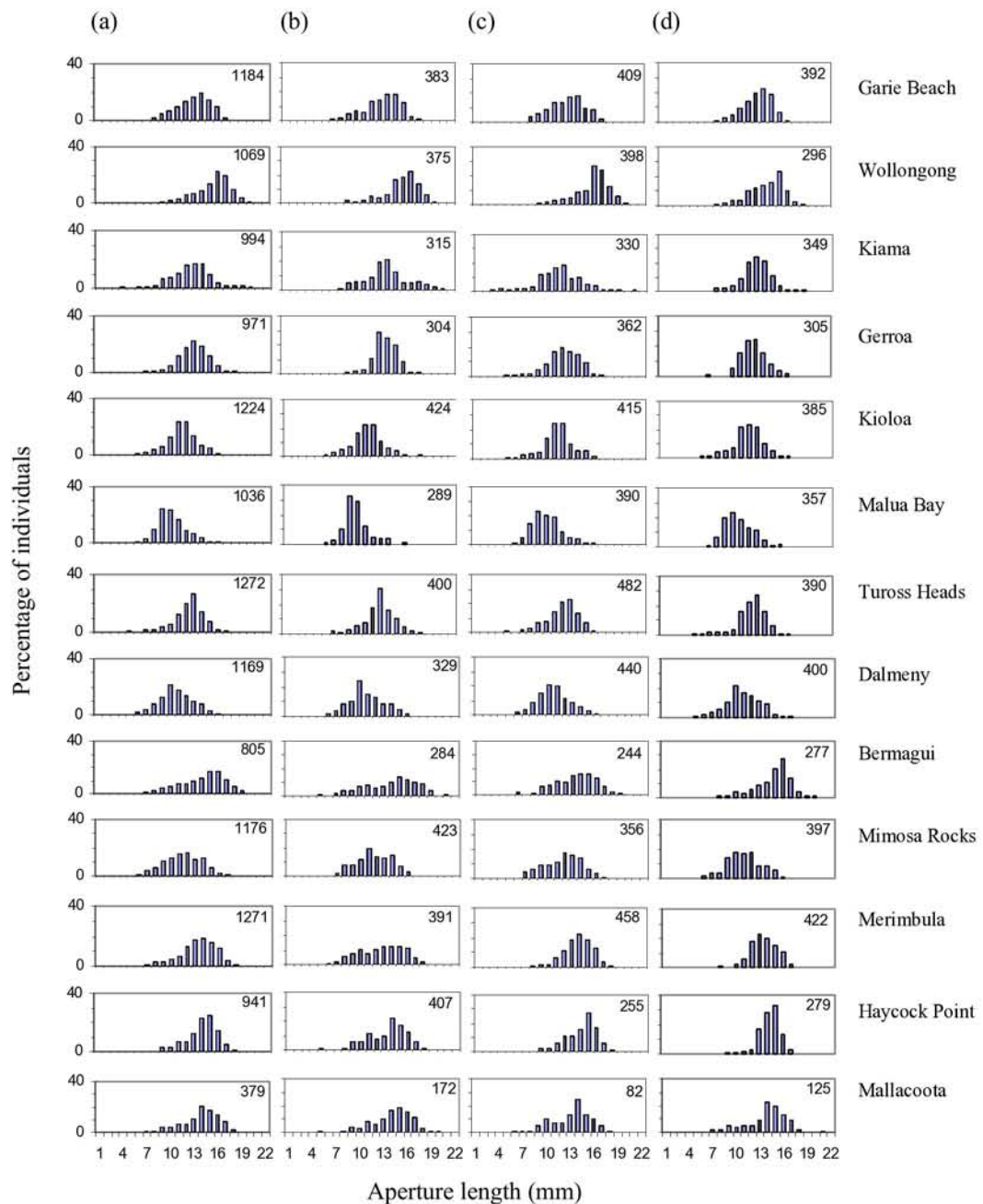


Fig. 3.5 Size-frequency distributions (a) over the total sampling period, and separately in (b) May 2005, (c) September 2005, and (d) January 2006 for *M. marginalba* at 13 locations, from within the middle of its range at Garie Beach in Sydney, NSW, to near its southern range limit at Mallacoota, Victoria. Numbers in top right hand corner show the number of individuals measured. Three range limit locations, Ram Head, Point Hicks and Cape Conran (see Fig. 3.1) are not included here, as insufficient number of individuals were available at these locations.

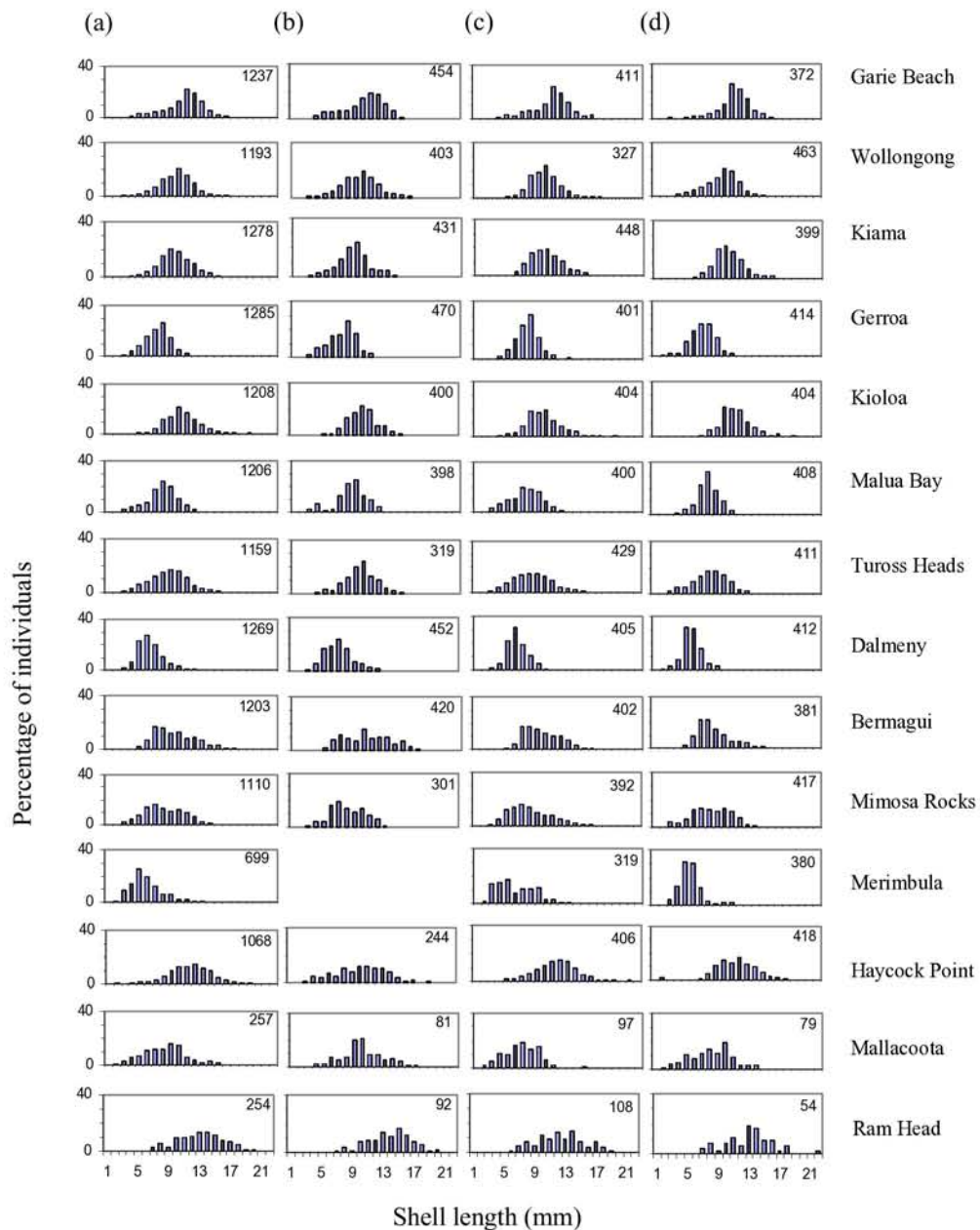


Fig. 3.6 Size-frequency distributions (a) over the total sampling period, and separately in (b) May 2005, (c) September 2005, and (d) January 2006 for *A. pyramidalis* at 14 locations, from within the middle of its range at Garie Beach in Sydney, NSW, to near its southern range limit at Ram Head, Victoria. Numbers in top right hand corner show number of individuals measured. Two range limit locations, Point Hicks and Cape Conran (Fig. 3.1) are not included here, as insufficient number of individuals were available at these locations. Furthermore, data for Merimbula in September 2005 could not be obtained due to adverse weather conditions.

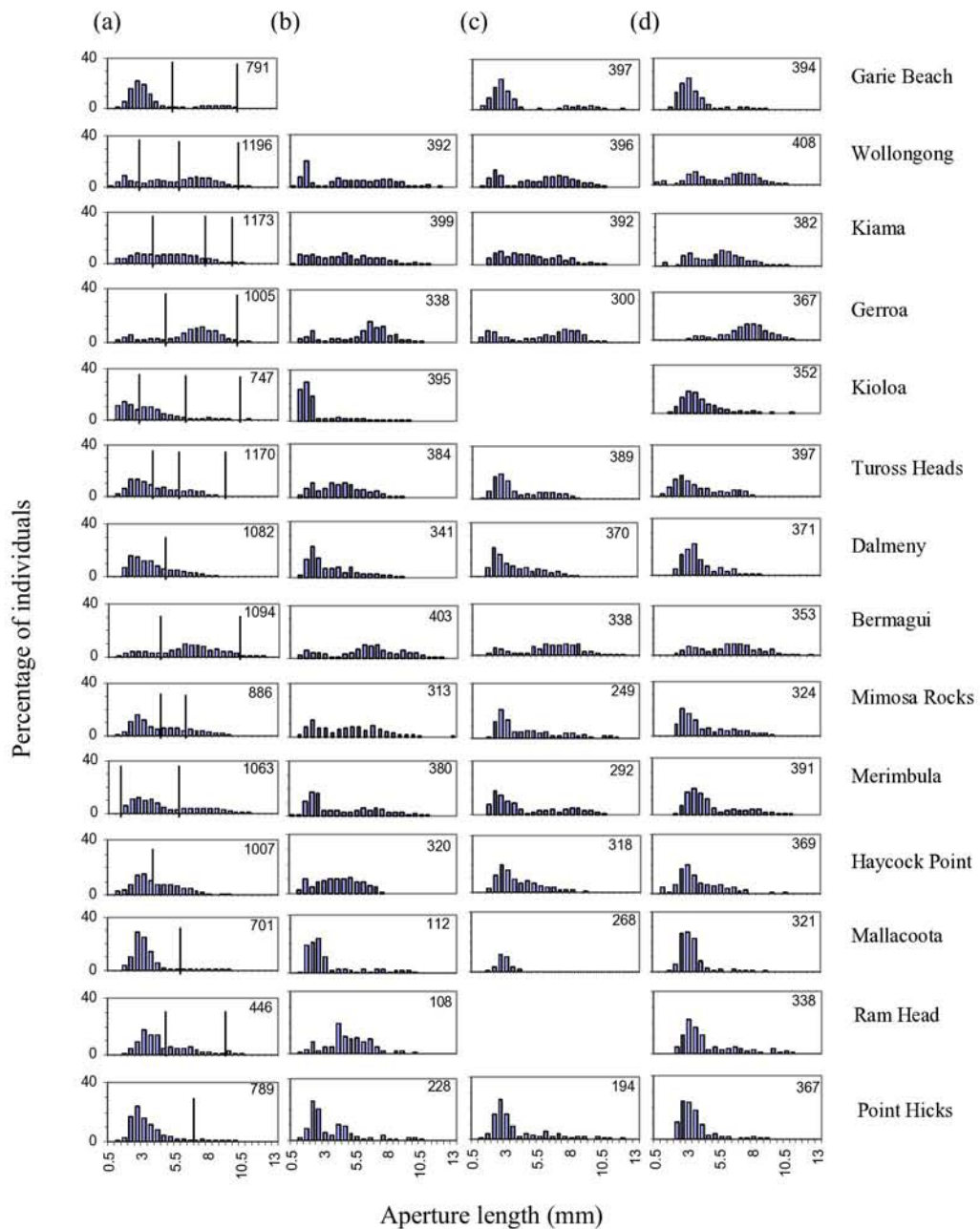


Fig. 3.7 Size-frequency distributions (a) over the total sampling period, and separately in (b) May 2005, (c) September 2005, and (d) January 2006 for *T. rosea* at 14 locations, from within the middle of its range in Sydney, NSW, to near its southern range limit at Point Hicks, Victoria. Numbers in top right hand corner show sample sizes. Black vertical lines separate cohorts. Missing graphs represent locations and sampling times for which data could not be obtained. Two range limit locations, Point Hicks and Cape Conran (Fig. 3.1) are also not included here, as insufficient numbers of individuals were available at these locations.

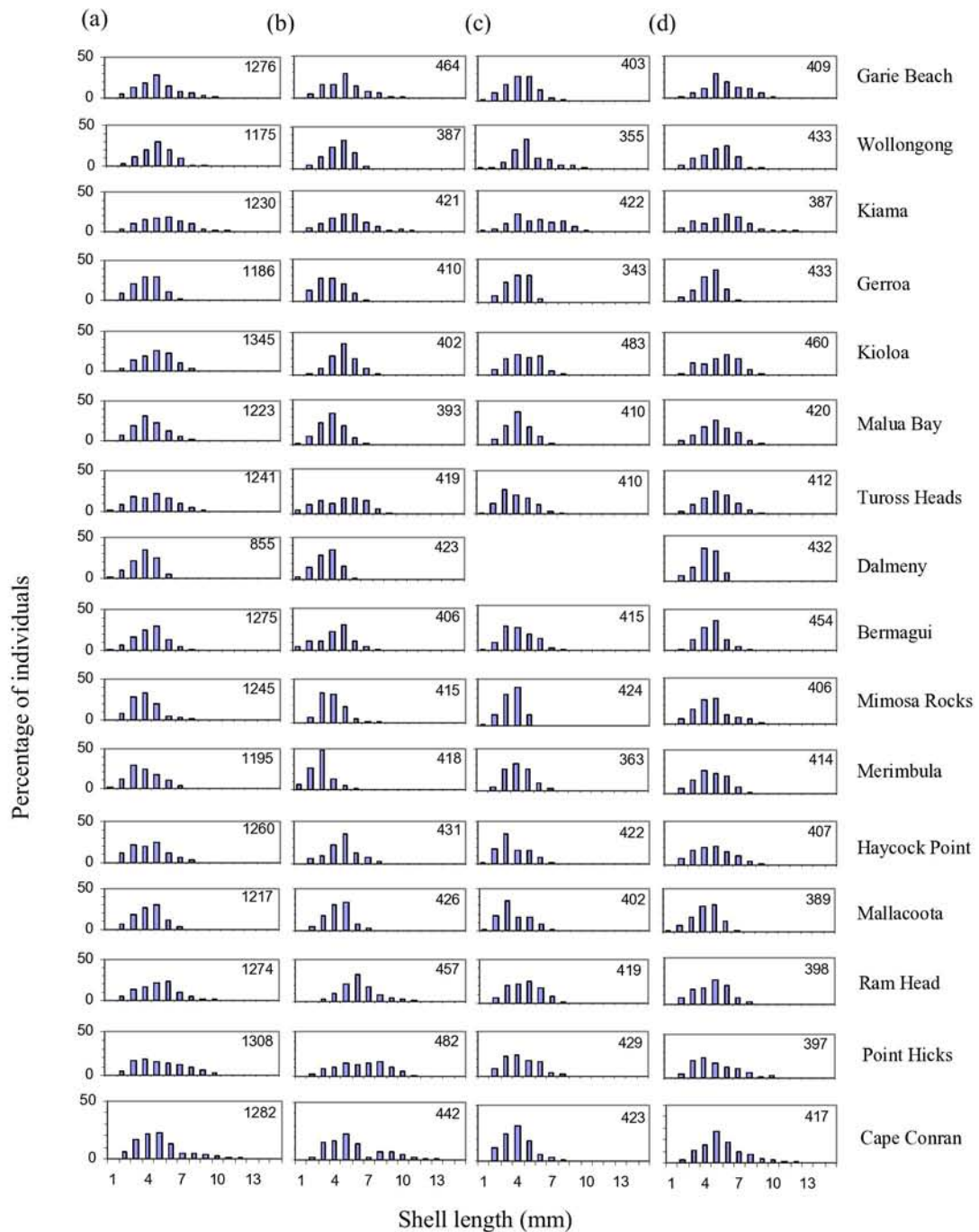


Fig. 3.8 Size-frequency distributions (a) over the total sampling period, and separately in (b) May 2005, (c) September 2005, and (d) January 2006 for *N. unifasciata* at 16 locations across its range from Garie Beach in Sydney, NSW, to Cape Conran, Victoria. Numbers in top right hand corner show number of individuals measured. Data could not be obtained for Dalmeny in September 2005.

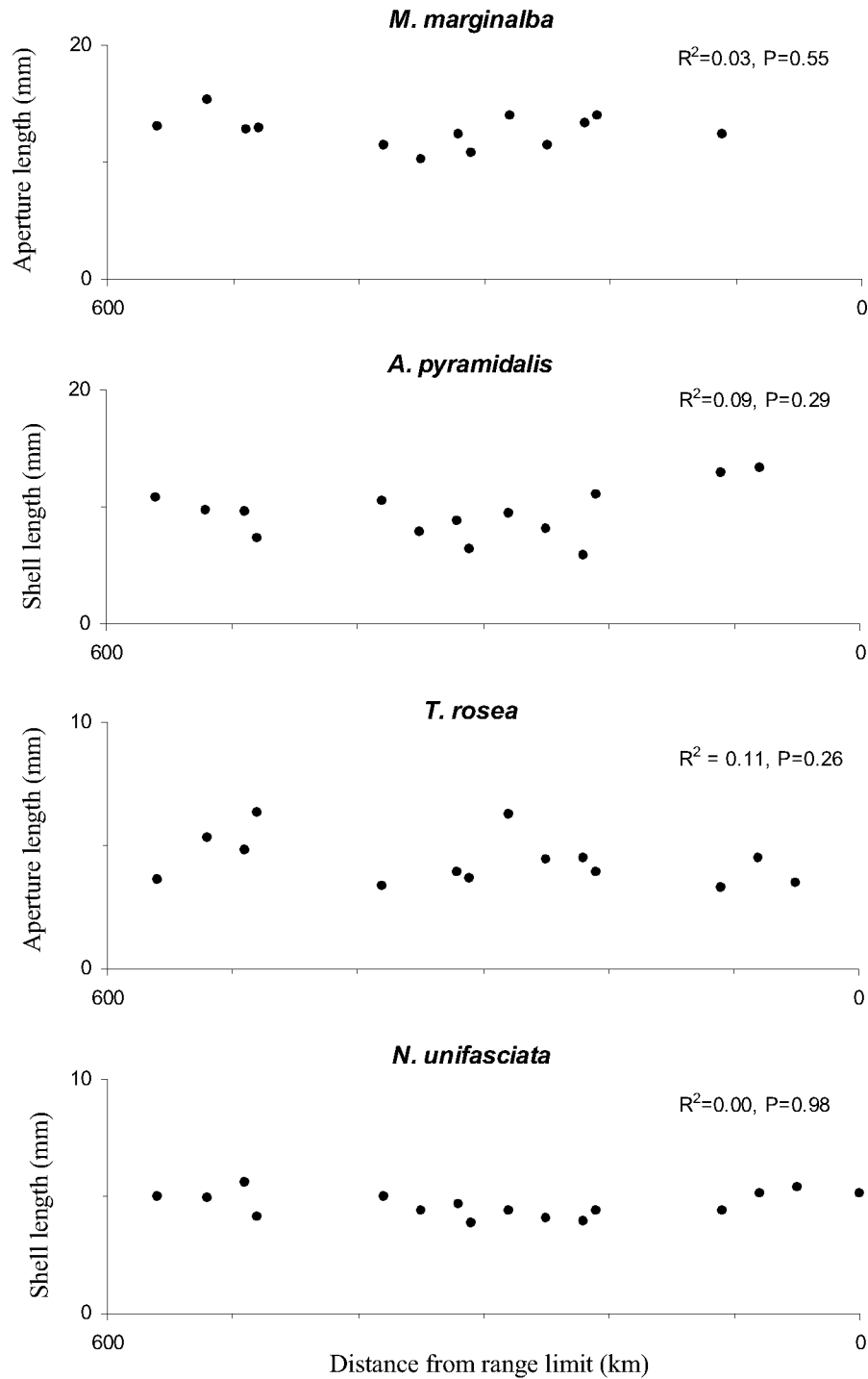


Fig. 3.9 The relationships between the mean sizes of four rocky intertidal marine invertebrates, and distance from the range limit of *M. marginalba*, *A. pyramidalis* and *T. rosea* at Cape Conran, Victoria (Fig. 3.1), at 13 to 16 locations on the southeast coast of Australia.

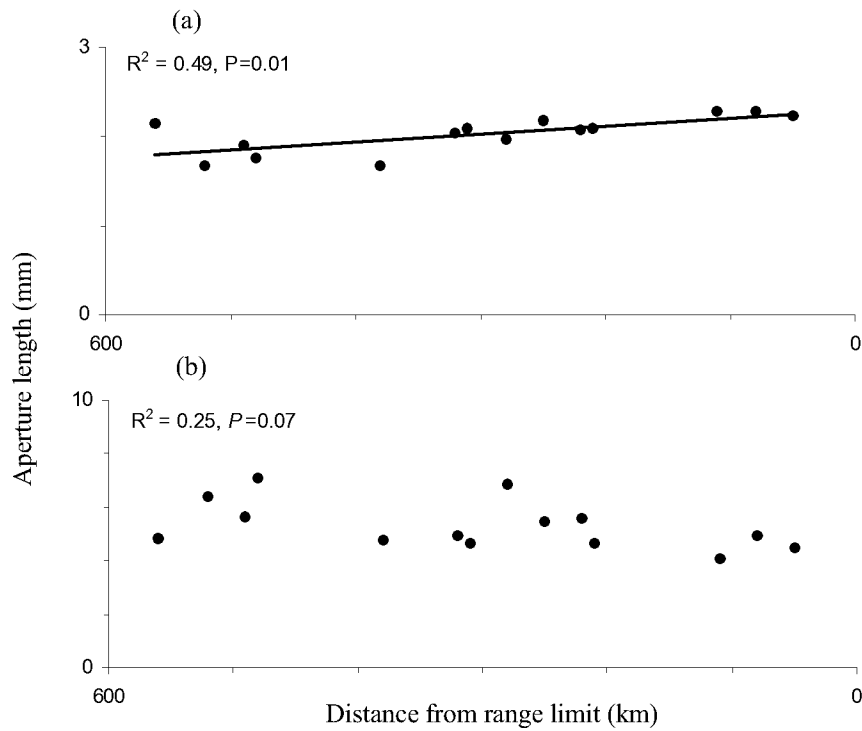


Fig. 3.10 The relationship between mean aperture length of (a) juvenile (<3 mm) and (b) adult (≥ 3 mm) *T. rosea*, and distance from the species' range limit at Cape Conran, Victoria (Fig. 3.1) at 14 locations on the southeast coast of Australia.

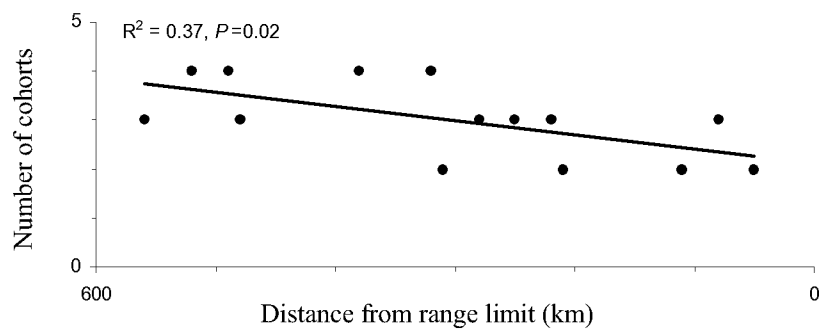


Fig. 3.11 The relationship between the number of cohorts of *T. rosea* at 14 locations on the southeast coast of Australia, and distance from the range limit at Cape Conran, Victoria (Fig. 3.1).

Discussion

This study assessed the patterns of abundance and size-frequency distributions of four planktonically developing, rocky intertidal invertebrate species on the southeast Australian coast, to test the predictions of the abundant-centre hypothesis. My results showed that the three target species, *M. marginalba*, *A. pyramidalis* and *T. rosea* are more abundant at the middle of their ranges than at their southern range edges, though the relationship between abundance and distance from the range limit was not always linear. Although these patterns need to be also assessed at their northern range limits, where different range limit factors and processes may bring about different patterns of abundance towards the range limit (Sagarin and Gaines, 2002a; Gaston, 2003), my results suggested that these species may indeed have abundant-centre distributions. Three other benthic marine invertebrates have also been documented to decline towards their downstream range edges on the west coast of the USA (Sagarin and Gaines, 2002b; Gilman, 2005). However, six others were found to increase in abundance along this same gradient (Sagarin and Gaines, 2002b).

The dramatic decline in abundance towards the range limits of the three target species, compared to the consistently high abundance of the reference species, *N. unifasciata*, across the study area, clearly indicates that the factors determining the adult abundances of the three target species vary sharply at their range limits. However, size-frequency distributions did not reveal any general, consistent patterns towards the range limit of these species. There was no evidence of a distinct disappearance of small individuals at the range limit, indicating sporadic or limited recruitment, as was found by other studies investigating changes in patterns of size-frequency of benthic marine invertebrates (Zacherl *et al.*, 2003; Lima *et al.*, 2006). However, these studies

dealt with species that had recently expanded their geographic ranges, which is not the case here.

The mean size of *M. marginalba* did not change significantly at locations towards the range limit, and there were no apparent changes in terms of proportions of small individuals in the intertidal habitat. Firstly, this suggests that recruitment was not affected, and therefore did not determine the decline in abundance towards the range limit of this species. However, it is also possible that recruitment was just particularly poor during my year of sampling, and there were actually no recruits on the shore during this time. Although it is known that this species breeds and spawns from December to March (Underwood, 1974), perhaps successful recruitment events occur more occasionally. Indeed, Moran *et al.* (1984) found that recruitment success of this species varies highly among years. Alternatively, despite my sampling covering the entire horizontal and vertical extent of this species on the shore, and special effort made to look closely for small recruits within microhabitats, I may have failed to notice small individuals on the substratum, although this is unlikely. Zacherl *et al.* (2003) also failed to find small individuals of the neogastropod *Kelletia kelletii* on the west coast of the USA, even after rigorous searching, and also concluded that recruits remain cryptic or exploit a different habitat from adults.

If patterns of size-frequency distributions obtained for *M. marginalba*, however, were a true representation of the size structure across my study region, then results suggest that some factor or process, other than recruitment, may be limiting the distribution of this species at its range limit. Post-recruitment abiotic factors, such as a five degree sea surface temperature difference around the border of New South Wales and Victoria (Knox, 1963; Ridgway and Dunn, 2003), may limit the survival of adults on

the shore, although there is no evidence of this from the size-frequency distributions at the range limit. Alternatively inter-specific interactions may limit the survival or persistence of populations at the range limit (Gaston, 2003). Small scale distributions of *M. marginalba* on a rocky platform have been shown, for example, to be strongly associated with the availability of their preferred prey such as barnacles (Fairweather, 1988a; Fairweather, 1988b). Changes in prey availability at large spatial scales may therefore have the potential to limit the distribution of this species, however, this requires further experimental investigation. Alternatively, a potential competitor, *Lepsiella vinosa*, overlaps in distribution with *M. marginalba* towards its range limit, occupies similar habitat and feeds on similar prey to *M. marginalba* (personal observation, and see also Chapter 2). This species may therefore outcompete *M. marginalba* in food consumption or habitat occupation, however, this again needs to be examined experimentally, through exclusion or transplant experiments.

Afrolittorina pyramidalis showed relatively consistent patterns of size-frequency distributions towards its range limit, similar to the reference species *N. unifasciata*, but it was lacking small individuals at the location closest to the range limit at Point Hicks, suggesting that there may be sporadic recruitment of this species at this location. However, the dramatic decline in abundance of *A. pyramidalis* occurred at locations further north, at Mallacoota and Ram Head, suggesting that it is not exclusively recruitment that may limit the distribution and abundance of this species. It has been experimentally shown that this species prefers complex microhabitats such as cracks, crevices and pits in the rock, and avoids topographically simple areas (Chapman and Underwood, 1994). The recruitment of this species has also been found to be limited to shores with topographically complex substratum (Chapman, 1994). Granite platforms at Ram Head and Point Hicks are smooth, and cracks only

occur high on the shore. Indeed, these platforms were found to lack the presence of some otherwise commonly occurring species in Chapter 2. Therefore, these platforms may be unsuitable for *A. pyramidalis* to recruit to, or persist on, and this may explain the absence of small individuals at Point Hicks (Fig. 5). The other littorinid, *N. unifasciata*, which does not have a range limit within the study region lives at the same height on the shore, and feeds on the same sources of food as *A. pyramidalis* (Chapman and Underwood, 1994), yet its abundance was not affected by these platforms. This supports the idea that *A. pyramidalis* may be limited by microhabitat availability at its range limit.

For the barnacle *T. rosea*, there were fewer large individuals towards the range limit, and there was a significant decrease in the number of cohorts at locations close to the range limit. At first impression, these results suggest that some post-recruitment factor may limit either the survival of adults, or limit the maximum size reached by individuals at the range limit. As mean size did not change significantly towards the range limit and, peaks in recruitment detected in May 2005 were still obviously detectable in January 2006 at the range limit, perhaps growth rate may be reduced at the range limit. However, if this reduction in growth rate does occur at the range limit, it is also possible that small individuals at the range limit may not necessarily represent recent recruitment events, but instead, slow growing individuals from past recruitment events and therefore, there may be sporadic recruitment at the range limit. The timing, frequency, or success of reproduction of this species may therefore be affected at its range limit, which would explain the lower number of cohorts present onshore compared to the middle of the range. Caffey (1985) assessed the spatial and temporal variation in settlement and recruitment of *T. rosea* along 550 km of coastline

in NSW in the central part of the species' distribution, and found evidence of more frequent recruitment at his most northern location.

The shortcoming of this study is that the size-frequency distribution patterns offered little explanation for the decline in abundances of the three target species. However, it is nevertheless an intriguing finding that the abundances of these species declined so dramatically despite their large potential for dispersal towards their range limits. It has been previously proposed that the effect of the EAC for larval dispersal gradually decreases south of Sydney (Murray-Jones and Ayre, 1997), and this may partially explain the decline in abundance of the target species. However, the continuously high abundance of the reference species across my study region, which also has a planktonic larval stage, and the lack of evidence for limited recruitment of the target species towards the range limit contradicts and questions this hypothesis. This raises the question of whether range edge populations of these target species may be relying on local recruitment for the maintenance of their populations.

CHAPTER 4

Population Dynamics of a Marine Invertebrate Approaching its Geographical Range Limit

Introduction

The geographical distributions of species are limited by either physical boundaries that inhibit their dispersal, or by changes in abiotic or biotic factors that affect survival towards the range limit (Gaston, 2003). Little is known, however, about how these factors impact on crucial population processes towards species' range limits (Gaston, 2003; Parmesan *et al.*, 2005; Sagarin *et al.*, 2006). In marine habitats, for example, no empirical studies have yet assessed the extent and scale at which local populations are connected by dispersal from the middle to the limits of their ranges, and how this varies for species with different life-histories (Sagarin and Gaines, 2002b; Parmesan *et al.*, 2005; Sagarin *et al.*, 2006). Determining these relationships is, however, crucial for predicting the shift in species' ranges from climatic change (Barry *et al.*, 1995; Perry *et al.*, 2005), for identifying potential source-sink dynamics and ultimately, the correct positioning of marine reserve networks (Roberts, 1998; Crowder *et al.*, 2000; Palumbi, 2003; Shanks *et al.*, 2003).

For benthic marine invertebrates with a planktonic larval stage, adult population sizes and densities throughout the range are thought to be largely determined by the recruitment of larvae (Gaines and Roughgarden, 1985; Underwood and Fairweather, 1989; Minchinton and Scheibling, 1991; Grosberg and Levitan, 1992), though other processes are also important. Thus, recruitment may be a crucial process that limits the distributions of species at their range limits. Recruitment at a particular locality,

however, depends on larval supply, which in turn depends on the intensity and success of larval production (i.e. fecundity) (Hughes, 1990), mortality in the plankton, and the strength and direction of oceanic currents for dispersal (Gaylord and Gaines, 2000). Understanding changes in connectivity towards the range limits of benthic marine species' populations therefore requires the assessment of changes in fecundity, recruitment, adult abundance, and the links between these stages of the life cycle.

Large-scale changes in patterns of fecundity towards the geographical range limits of benthic marine invertebrate species are virtually unknown. However, one study along the European Atlantic coast found that rocky intertidal invertebrates were characterised by shortened breeding periods towards their northern range limits, which correlated with a decline in sea surface temperature (Lewis, 1986). Indeed, temperature is known to have an impact on the fecundity of marine invertebrates (Ramirez Llorda, 2002). Given that many benthic species, particularly those inhabiting the intertidal zone, are distributed along a latitudinal temperature gradient along the north-south orientation of continental coasts, it may thus be expected that fecundity may decline for these species towards their range limits at higher latitudes. However, marine species are also subjected to the often unidirectional flow of dominant surface currents along a latitudinal gradient which, depending on the length of the larval stage, may have large and variable effects on their patterns of recruitment towards the range limit (Gaylord and Gaines, 2000). Range limit populations with low fecundity that are located downstream of productive source populations may still be potentially supplied with sufficient larvae to maintain large, functional populations, assuming that there are no abiotic or biotic post-settlement factors affecting recruit or adult survival. A weak or non-existent link between fecundity and recruitment towards the range limit may therefore be expected for a species with high dispersal

ability, high degree of connectivity among local populations and an open population structure. Conversely, a strong link is likely to indicate localised effects of fecundity on recruitment and, therefore, a low degree of connectivity among local populations and a more closed population structure.

The only previous large-scale study that has explored adult-fecundity-recruitment relationships of benthic marine species focused on broadcast spawning corals on the Great Barrier Reef in Australia (Hughes *et al.*, 2000). Although recruits were only identified to family or genus level for these corals, thus potentially affecting the accuracy of the relationships found, adult abundance and recruitment did not relate at either small or large spatial scales, but most of the variance in recruitment at small and large spatial scales was explained by the fecundity of the adults. This result is likely to reflect the highly limited dispersal, low degree of population connectivity and, therefore, relatively closed population structure of at least some coral species (Ayre and Dufty, 1994; Ayre and Hughes, 2000).

Here I attempt to examine life-history relationships at several spatial scales for an organism believed to have more widespread dispersal than many coral species, and for which the recruit stage of the life-cycle is easily recognisable. I assessed the adult abundance, fecundity and recruitment of the intertidal, rocky shore barnacle, *Tessieropora rosea*, along 600 km of shore, from within the middle of its range in Sydney, to its southern distributional limit in eastern Victoria (Fig. 1), on the southeast coast of Australia. Along much of the eastern coast of Australia, the warm temperate East Australian Current (EAC) flows dominantly southwards (Ridgway and Dunn, 2003). At approximately the latitude of Sydney, the EAC partially deflects away from the coast, and partially continues southwards as a weaker current, forming

occasional coastal eddies as it reaches the southeast corner of Australia (Fig. 1). Here, sea surface temperatures dramatically change by up to five degrees compared to the north (Knox, 1963; Ridgway and Dunn, 2003). Given that the larvae of *T. rosea* have been estimated to spend from 3 to 5 weeks in the water column as planktotrophic larvae (Wisely and Blick, 1964; Denley, 1981), the EAC may have a substantial influence on the patterns of abundance of *T. rosea* along this coast (Gaylord and Gaines, 2000). There may be several possible distributions towards the range limit that result from these conditions, however, I predict that if the larvae of this species are carried southward by the EAC, then although fecundity may be reduced towards the range limit due to the decreasing sea surface temperature, recruitment may in fact increase due to the accumulation of larvae, and adult abundance may also increase as an effect of increasing recruitment, thus forming an open population structure. If, however, larvae are retained close to their populations of origin by some process, then the decrease in fecundity towards the range limit may be mirrored by a corresponding decrease in recruitment and adult abundance, thus forming a more closed population structure. These two scenarios will ultimately affect the relationships between the three stages of the life cycle, with a weak link expected towards the range limit for an open population structure, and a strong link expected for a more closed population structure.

Methods

Study Area and Study Species

My study area extended along 600 km of coastline, from Garie Beach in Sydney, New South Wales (NSW) (S 34° 10', E 151° 04') to Cape Conran in Victoria (S 37° 08', E 148° 07') in southeast Australia (Fig. 4.1), covering the southern third of the total distributional range of *Tesseropora rosea*. This species is one of the most common and abundant rocky shore barnacles on the east coast of Australia, usually found on moderately exposed to exposed emergent rock platforms in the mid shore regions of the intertidal zone (Denley, 1981; Caffey, 1985; Edgar, 1997). *Tesseropora rosea* is a hermaphroditic species, whereby adults cross-fertilise their nearest neighbours by the use of a long retractable penis (Greenaway, 1998). Fertilised eggs are then brooded, and mature larvae are released into the water column predominantly from January to April (Wisely and Blick, 1964), but also sporadically throughout the year (Denley, 1981; Caffey, 1985; Egan and Anderson, 1988).

Sampling Design and Study Locations

I sampled the adult and recruit abundances, and the fecundity of *T. rosea* in May and September 2005, and January and May 2006, to capture variability in these patterns and processes throughout the year. Furthermore, I surveyed at three different spatial scales using a hierarchical sampling design to assess these patterns at small to large spatial scales, with four sectors each encompassing between 70-110 kilometres of coastline, four representative locations within each sector (each covering 100 to 140 metres of coastline), and three sites at each location (each covering 30 metres of coastline) (Fig. 4.1). Sectors were separated by 30-100 km, locations by 10-50 km, and sites by 0-50m. Sites were approximately 30 m alongshore and of variable

intertidal extent (from 6 to 50 m). Sectors 1 to 4 represented regions furthest to closest to the range limit respectively, although sectors 1, 2 and 3 were all considered to be within the middle of the range of the species, while sector 4 was considered to be the range limit (Fig. 4.1).

Locations were predominantly chosen for their accessibility, safety, and regular spacing within sectors, but were also selected to be as uniform as possible in their physical characteristics. For example, sheltered locations were avoided, as they do not provide suitable habitat for *T. rosea* (Caffey, 1985; Edgar, 1997). The majority of locations were positioned on either side of moderately exposed headlands, with an orientation facing the open ocean, and a platform slope of no more than 30 degrees. Rock type, however, could not be controlled for and varied between siltstone, sandstone, mudstone, granite and basalt. However, this was not considered a problem, as *T. rosea* has been shown to settle indiscriminately on all these rock types (Caffey, 1982).

Abundance

The densities of adults and recruits of *T. rosea* were measured using 20 haphazardly placed 0.15 x 0.15 m quadrats at each site, and sampling was done only within the height on the shore that *T. rosea* is found. Quadrats at each site were placed next to a metric scale and photographed with a digital camera. Adult and recruit densities within each quadrat were estimated from photographs, by categorizing individuals as either reproductively mature adults (≥ 3 mm aperture) or immature recruits (< 3 mm aperture) (Wisely and Blick, 1964).

Fecundity

The fecundity of *T. rosea* at each location was assessed by determining the proportion of adults with gonads, and the proportion of adults with gonads containing ready-to-release mature larvae. I collected a total of between 20 to 40 haphazardly chosen mature adults (>3 mm aperture) across the three sites at each location. Individuals were preserved in 10% formalin, then later observed under a binocular microscope, and the gonads graded into the categories: empty (no gonad present), developing (milky, or yellow eggs), or mature (orange or brown eggs with obvious eyed nauplii (larvae)) (Wisely and Blick, 1964).

Statistical Analyses

To test for differences in mean adult and recruit densities (both log-transformed data), and the mean proportions of adults with gonads and larvae (untransformed data) among sectors, and among locations within sectors, along the southern distributional range of *T. rosea* in May and September 2005, January and May 2006, and the overall mean over this 12 month period (total mean), I used mixed model analyses of variance (ANOVA) with the SPSS 12 statistical package. Locations were treated as random factors and were nested within fixed sectors. For a mixed model ANOVA, this statistical package generates two values: a standard *F* ratio for the fixed factor, and a Wald-Z value for the nested random factor. The Wald test calculates a Z-statistic by dividing the parameter estimate by its standard error (Littell *et al.*, 1996).

Sites were used as replicates for analyses of adult and recruit densities, and locations were used as replicates for the analyses of proportions of adults with gonads or larvae. Data during some sampling seasons were not obtained at some locations due to adverse weather conditions. Therefore, for the analyses on total means, data were

omitted for any sites that had fewer than two sampling times for adult and recruit densities, and any locations with fewer than three sampling times for proportions of adults with gonads and larvae.

Linear regression analyses were used to test for relationships between recruit and adult densities, between proportion of adults with gonads or larvae and recruit densities, and between proportion of adults with gonads or larvae and adult densities of *T. rosea* across the entire 600 km study area, within sectors, and within locations, using the SYSTAT 10 statistical package. To account for the time lags between larval release and settlement, relationships between adults and recruits, and proportions of adults with gonads or larvae and recruits were examined between the means of the May and September 2005, and January 2006 adults and their proportions of gonads or larvae, with the means of the September 2005, and January and May 2006 recruits. Recruit density data were initially transformed, but did not result in a better fit for any of the relationships tested, and hence are presented as untransformed data. Relationships between mean adult density and mean proportions of adults with gonads or larvae were based on total means of the four sampling times.

Because there were differences in replication intensity among the various hierarchical levels of the sampling design (i.e. 4 sectors, 4 locations within each sector, 3 sites at each location, and 20 quadrats at each site), relationships between variables (i.e. adult density, recruit density, and proportions of adults with gonads and larvae), at each of the spatial scales (i.e. across the entire study region, across sectors, and across locations) had to be explored based on values at each of the lower hierarchical levels. So for relationships across the entire 600 km study area, I explored relationships from plots based on values for all sectors, locations and sites; for relationships across

sectors, I plotted values for all locations and sites; and for relationships across locations I plotted values for all sites and individual quadrats.

Results

Patterns of Adult Abundance, Recruitment and Fecundity

Mean adult densities of *T. rosea* over the one year sampling period from May 2005 to May 2006 were 7- to 15-fold higher within sectors 1, 2 and 3 in the middle of the range, ranging from 14.3 to 30.1 adults per quadrat, than within sector 4 at the species' range limit with only 2.8 adults per quadrat (Fig. 4.2 a). There appeared to be a step-wise decrease in adult density towards the range limit (Fig. 4.2 a), with sectors 2 and 3 having considerably lower densities than sector 1. However, due to the significant variations in densities among locations within sectors ($Z_{12,32}=2.206$, $P=0.027$), particularly in sectors 1 and 2 (Fig. 4.2 e), the decline in adult density across sectors was only significant at the range limit sector 4 ($F_{3,10}=5.4$, $P=0.014$).

Recruit density of *T. rosea* showed similar patterns to adult density across the four sectors (Fig. 4.2 b). There was a non-significant decline towards the range limit across sectors 1, 2 and 3, ranging from 73.4 to 118.6 recruits per quadrat, but a significant drop at the range limit within sector 4 with only 11.1 recruits per quadrat ($F_{3,10}=5.053$, $P=0.017$). Recruit densities also varied highly and significantly among locations within sectors ($Z_{12,32}=2.262$, $P=0.024$) (Fig. 2 f), particularly in sector 2, where the rock platform at Kioloa had a 15-fold greater recruit density than the nearby rock platform at Malua Bay.

Interestingly, the proportions of adults with gonads were consistently 95-100 % across all four sectors (Fig. 4.2 d), and there was little variation of this among locations within sectors (Fig. 4.2 h). In contrast, the proportions of adults with mature larvae were consistently low across sectors 1, 2 and 3, ranging from 16.5 to 27.2 %, but were

significantly lowest at the range limit with 6.3 % adults with mature gonads ($F_{3,10}=3.45$, $P=0.05$) (Fig. 4.2 c & g).

Variations in Patterns Among Sampling Times

Within sectors, recruit densities and the proportions of adults with mature larvae varied greatly among sampling seasons, whereas adult densities and the proportions of adults with gonads were relatively consistent across seasons (Table 4.1). Recruit density, for example, was clearly greatest in May 2005 and May 2006 in all three sectors within the middle of the range, ranging from 91.7 to 176.8, and from 110.4 to 156.3 recruits per quadrat respectively, compared to 55.0 to 92.7 during September 2005, and from 32.6 to 60.7 in January 2006. However, these pulses of recruitment were not present at sector 4, closest to the range limit, where recruit density only varied between 1.9 and 16.6 individuals per quadrat across the four sampling times (Table 4.1). Proportions of adults with larvae were also highest in May 2006 for all three northern sectors, ranging from 24.4 to 50.2 %, but again, this increase was not observed at the range limit, where only an average of 1.3 % of adults had gonads containing mature larvae.

Despite these variations among sampling times, adult and recruit densities were generally lowest at the range limit (Table 4.2). The only exception was in January 2006, when there was relatively low recruit density across all sectors (Table 4.1), and therefore no significant differences in recruit density were found among sectors (Table 4.2). The proportions of adults with gonads were significantly lower at the range limit sector 4 in September 2006, but did not differ among sectors during any other of the other 3 sampling times. Lastly, the proportions of adults with mature

larvae were consistently significantly lowest in sector 4 during the main spawning seasons in May 2005 and 2006 (Table 4.2).

Adult-Fecundity-Recruit Relationships

Across the entire 600 km study area, recruit and adult densities were not significantly correlated at a sector level (Fig. 4.3 a), although the relationship was clearly similar to the significant positive correlations revealed by plotting adult density against recruit density for all locations and sites (Fig. 4.3 b & c respectively). At a smaller spatial scale, within individual sectors, plots of adult-recruit relationships based on both locations and sites revealed similar patterns in sectors 1 (Fig. 4.4 a & e), 3 (Fig. 4.4 c & g), and 4 (Fig. 4.4 d & h), showing no significant relationships. In sector 2, however, the plot based on locations showed no significant relationship (Fig. 4.4 b), whereas the plot based on sites showed a significant positive relationship between adult and recruit densities (Fig. 4.4 f). At the smallest spatial scale, within individual locations, there were no significant relationships between adult and recruit densities based on mean values at each of the three sites, and therefore these results are not presented. However, there was a significant negative relationship at Garie Beach, Wollongong, Mimosa Rocks, and Point Hicks, and a significant positive relationship at Bermagui, between adults and recruits based on mean values for 46 to 60 quadrats across the 3 sites (Table 4.3). The locations for which there were significant relationships, were widely distributed throughout the study area, from the middle of the range to the range limit.

Recruit density did not correlate with either the proportions of adults with gonads (Fig. 4.5 a & c), or the proportion of adults with mature larvae (Fig. 4.5 b & d), at either the sector or location level. Similarly, there were no significant relationships

between adult density and the proportions of adults with gonads (Fig. 4.6 a & c) or larvae (Fig. 4.6 b & d) at either the sector or location level.

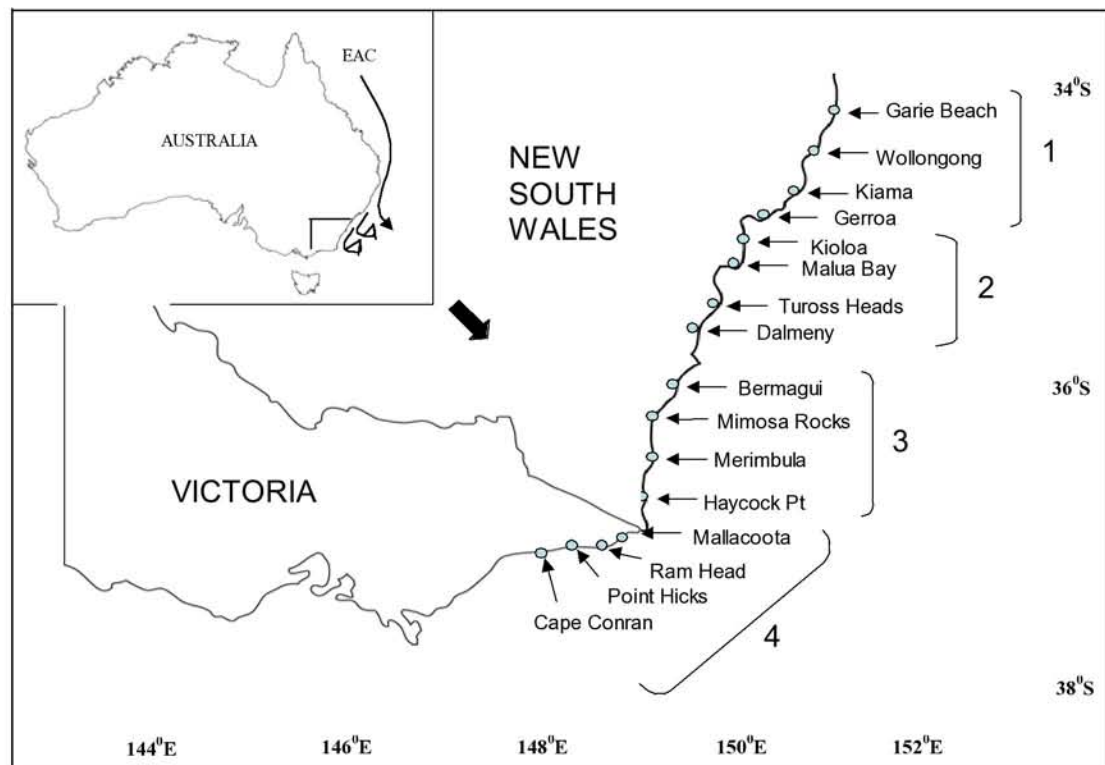


Fig. 4.1 Map of the southeast coast of Australia, showing the hierarchical sampling design used to assess the adult abundance, recruitment and proportion of fecund individuals of *T. rosea*. There were 16 locations nested within four sectors, from within the middle of the range (1) to the range limit (4) of the species. Inset map shows the position of the study site within Australia, and the flow pattern of the dominant southward flowing East Australian Current (EAC), which partially deflects away from the coast just north of Sydney, and partially continues as a weaker current, occasionally forming coastal eddies as it approaches the border of New South Wales and Victoria.

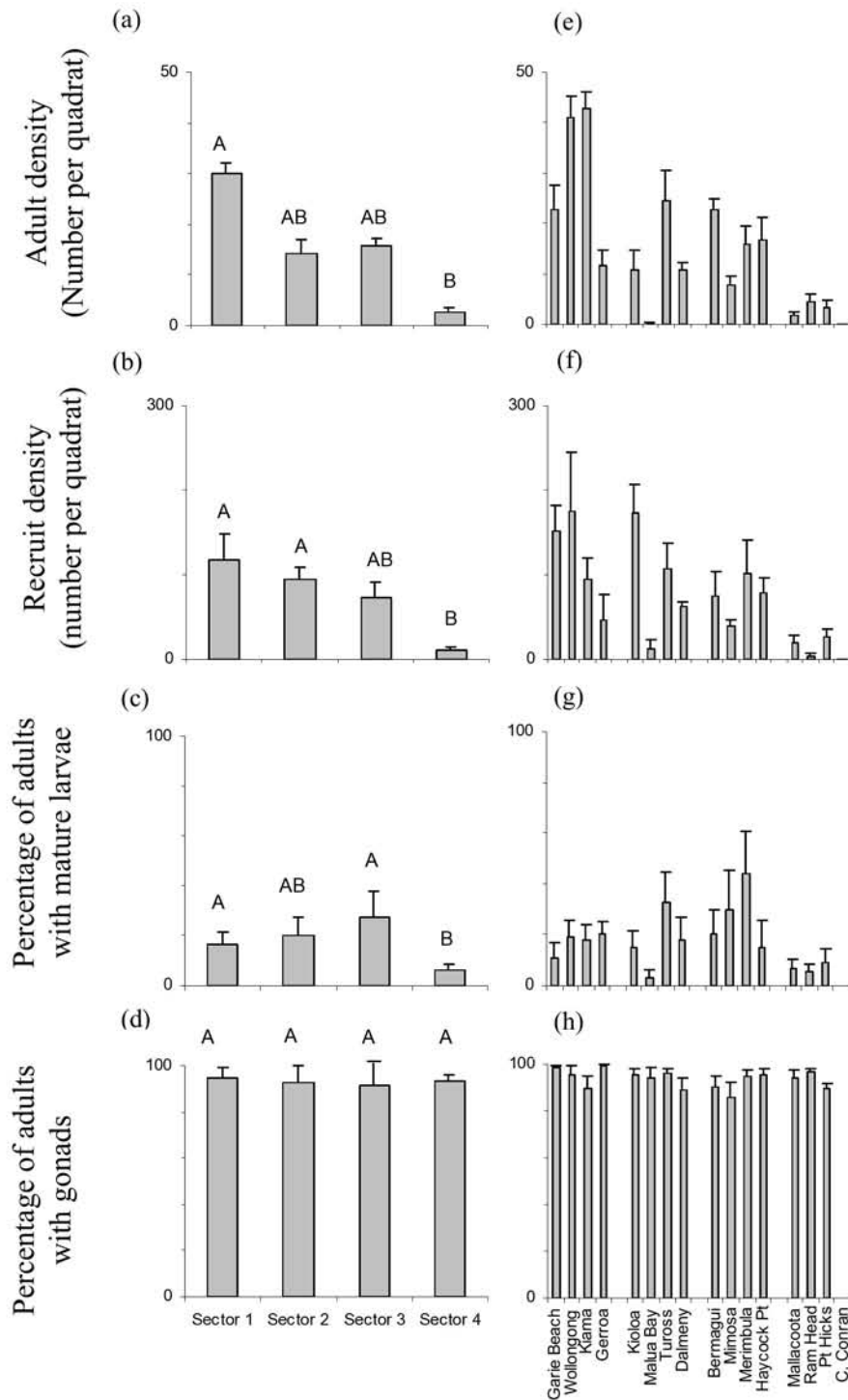


Fig 4.2. Mean (+SE) adult (a & e) and recruit densities (b & f), and percentages of adults with gonads (c & g) and mature larvae (d & h) of *T. rosea* across four sectors and corresponding 16 locations, from the middle of the range (Sector 1, Garie) to the range limit (Sector 4, C. Conran) of the species on the southeast coast of Australia, between May 2005 and May 2006. Within each graph, sectors marked by different letters are significantly different from one another.

Table 4.1 Mean (\pm SE) adult and recruit densities (number per quadrat), and proportions of adults with gonads and mature larvae, in May and September 2005, and January and May 2006, at four sectors from the range centre (Sector 1) to the range limit (Sector 4) of *T. rosea*, on the southeast coast of Australia.

		Sector 1	Sector 2	Sector 3	Sector 4
Adult density	May 2005	32.5 (11.6)	19.7 (10.0)	13.8 (4.2)	1.6 (0.6)
	Sept 2005	27.5 (10.0)	17.7 (11.0)	12.7 (4.6)	1 (0.4)
	Jan 2006	34.3 (7.0)	11.8 (4.1)	18 (5.3)	3.9 (1.8)
	May 2006	26 (6.3)	8.1 (3.0)	18.6 (2.2)	4.7 (1.8)
Recruit density	May 2005	176.8 (92.7)	126.6 (54.0)	91.7 (19.4)	12.4 (8.0)
	Sept 2005	92.7 (40.0)	77.9 (12.5)	55 (6.2)	13.7 (10.5)
	Jan 2006	48.4 (20.6)	60.7 (24.2)	32.6 (6.9)	16.6 (8.0)
	May 2006	156.3 (25.2)	110.4 (42.7)	114.2 (39.9)	1.9 (0.2)
Proportion of adults with gonads	May 2005	94.2 (3.3)	92.4 (0.8)	92.7 (3.5)	98.6 (1.4)
	Sept 2005	100.0	100.0	99.5 (0.5)	94.7 (2.8)
	Jan 2006	97.6 (1.7)	93.1 (3.0)	88 (6.4)	90.4 (3.2)
	May 2006	88.4 (5.7)	86.6 (6.7)	86.6 (2.8)	90.1 (3.7)
Proportion of adults with mature larvae	May 2005	12.7 (5.4)	19.6 (0.7)	7.3 (1.7)	6 (0.6)
	Sept 2005	5.4 (3.4)	3.1 (2.6)	40 (18.7)	5.2(4.0)
	Jan 2006	23.5 (4.0)	20.6 (8.1)	11.4 (7.4)	12.7 (6.2)
	May 2006	24.4 (4.1)	37.6 (13.7)	50.2 (4.2)	1.3 (1.3)

Table 4.2 Mixed model analyses of variance on the (a) adult and (b) recruit densities, and the proportions of adults with (c) gonads and (d) larvae of *T. rosea*, with fixed sectors, and random locations nested within sectors, in May and September 2005, and January and September 2006. Wald Z is a measurement of the nested random factor. Results of Tukey's post-hoc tests are shown with sectors listed in order of 1 (most northern, range centre) to 4 (most southern, range limit). Sectors not connected by same letter are significantly different from each other, with 'A' representing sectors with the highest abundances, and consecutive letters of the alphabet representing a decrease in abundance.

(a) Adult density

		d.f.	SS	F ratio	Wald Z	P	Post-hoc
May 2005	Sector	3	9.22	8.315		0.005	A A A B
	Location(Sector)	10	10.687		1.632	0.103	
	Residual	27					
Sept 2005	Sector	3	8.251	7.043		0.008	A AB A B
	Location(Sector)	10	13.842		1.735	0.083	
	Residual	26					
Jan 2006	Sector	3	2.423	7.325		0.005	A AB AB B
	Location(Sector)	12	31.777		2.246	0.025	
	Residual	31					
May 2006	Sector	3	9.878	3.442		0.052	A AB A B
	Location(Sector)	12	17.653		0.063	0.063	
	Residual	32					

(b) Recruit density

		d.f.	SS	F ratio	Wald Z	P	Post-hoc
May 2005	Sector	3	19.328	5.119		0.022	A A AB B
	Location(Sector)	10	25.336		1.454	0.146	
	Residual	27					
Sept 2005	Sector	3	4.48	4.787		0.025	A AB AB B
	Location(Sector)	10	31.536		2.031	0.042	
	Residual	26					
Jan 2006	Sector	3	0.722	0.596		0.629	
	Location(Sector)	12	70.056		2.288	0.022	
	Residual	31					
May 2006	Sector	3	24.511	12.436		0.001	A A A B
	Location(Sector)	10	11.995		1.414	0.158	
	Residual	28					

(c) Proportion of adults with gonads

		d.f.	SS	F ratio	P	Post-hoc
May 2005	Sector	3	0.000	1.0717	0.414	
	Residual	8				
Sept 2005	Sector	3	64.745	4.6676	0.024	A A AB B
	Residual	11				
Jan 2006	Sector	3	0.000	1.0632	0.404	
	Residual	11				
May 2006	Sector	3	0.000	0.1158	0.949	
	Residual	11				

(d) Proportion of adults with larvae

		d.f.	SS	F ratio	P	Post-hoc
May 2005	Sector	3	0.000	9.5524	0.005	AB A B B
	Residual	8				
Sept 2005	Sector	3	3216.066	3.0133	0.0761	
	Residual	11				
Jan 2006	Sector	3	0	0.696	0.574	
	Residual	11				
May 2006	Sector	3	2930.831	7.607	0.006	AB A A B
	Residual	10				

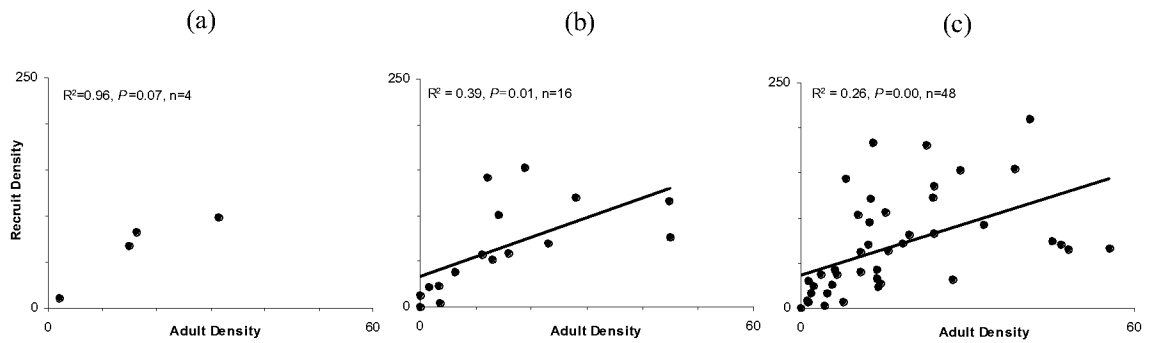


Fig. 4.3 The relationships between mean adult and recruit densities of *T. rosea* along 600 km of coastline, from the middle of its range to its range limit on the southeast coast of Australia at (a) four sectors, (b) corresponding 16 locations and (c) 48 sites, between May 2005 and May 2006. Recruit density values are lagged by three months compared to adult density values (see pg. 68).

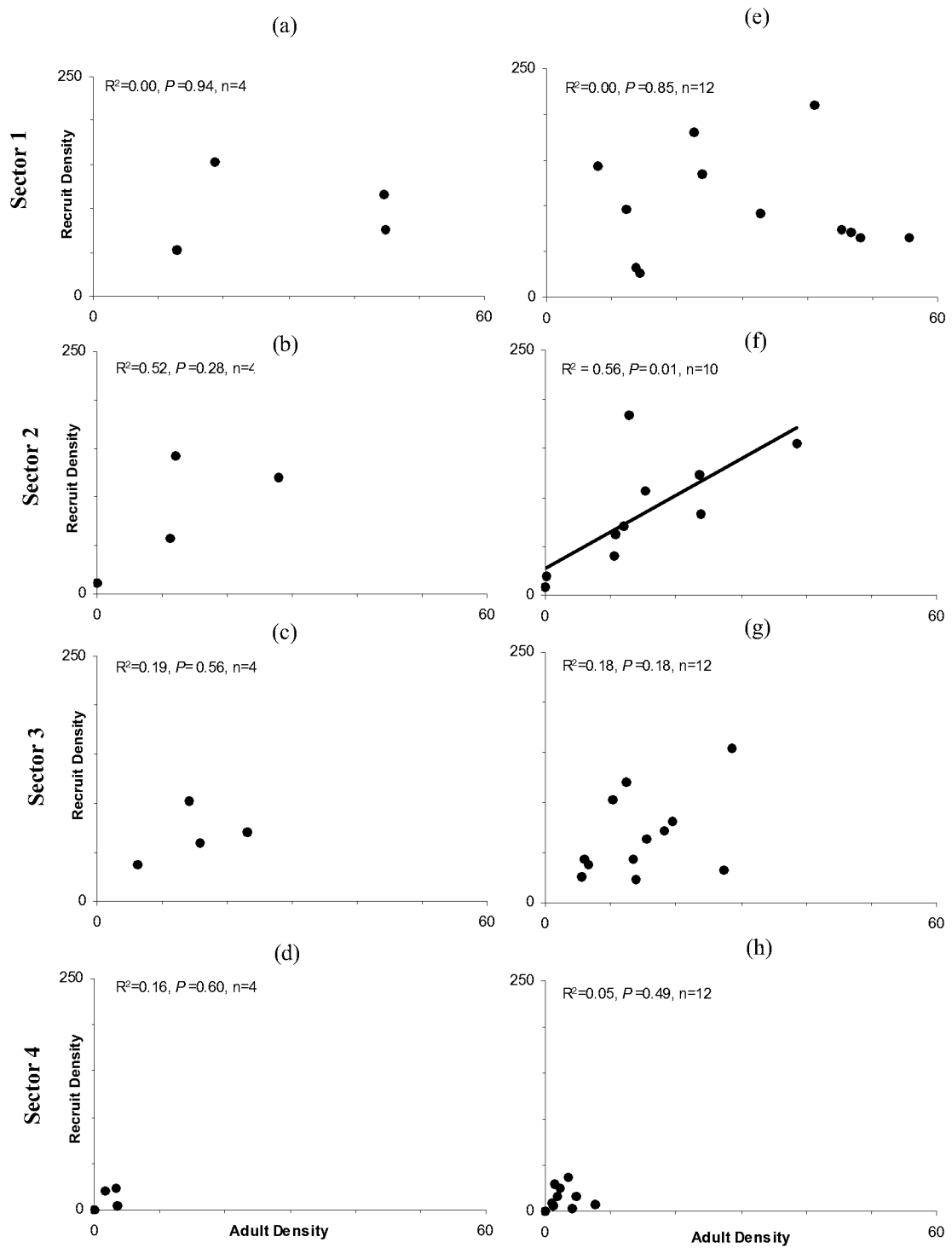


Fig. 4.4 The relationships between mean adult and recruit densities of *T. rosea* within four sectors consisting of 70 to 110 km of shoreline, from within the middle of the range (sector 1) to the species' southern range limit (sector 4) based on values at 4 locations (a to d) and corresponding 12 sites (e to h), on the southeast coast of Australia. Recruit density values are lagged by three months compared to adult density values (see pg 68).

Table 4.3 The relationships between adult and recruit densities of *T. rosea* at each of 16 locations covering approximately 140 m of coastline, from Sydney's Garie Beach in the middle of the range, to Point Hicks at the range limit of this species on the southeast coast of Australia, based on mean values from 46 to 60 quadrats of 0.15 x 0.15 cm, from May 2005 to May 2006. For locations marked by 'n/a' (i.e. non-applicable), insufficient replication was achieved to carry out such an analysis. Significant relationships are highlighted in bold. Recruit density values are lagged by three months compared to adult density values (see pg. 68).

Location	R ²	P	n	Type of relationship
Garie Beach	0.12	0.011	54	negative
Wollongong	0.14	0.004	60	negative
Kiama	0.06	0.053	60	
Gerroa	0.01	0.462	55	
Kioloa	0.01	0.634	46	
Malua Bay	n/a	n/a	n/a	
Tuross Heads	0.02	0.293	60	
Dalmeny	0.02	0.263	60	
Bermagui	0.08	0.033	60	positive
Mimosa Rocks	0.12	0.008	60	negative
Merimbula	0.06	0.051	60	
Haycock Point	0.05	0.100	60	
Mallacoota	0.01	0.477	60	
Ram Head	0.02	0.247	59	
Point Hicks	0.10	0.014	60	negative
Cape Conran	n/a	n/a	n/a	

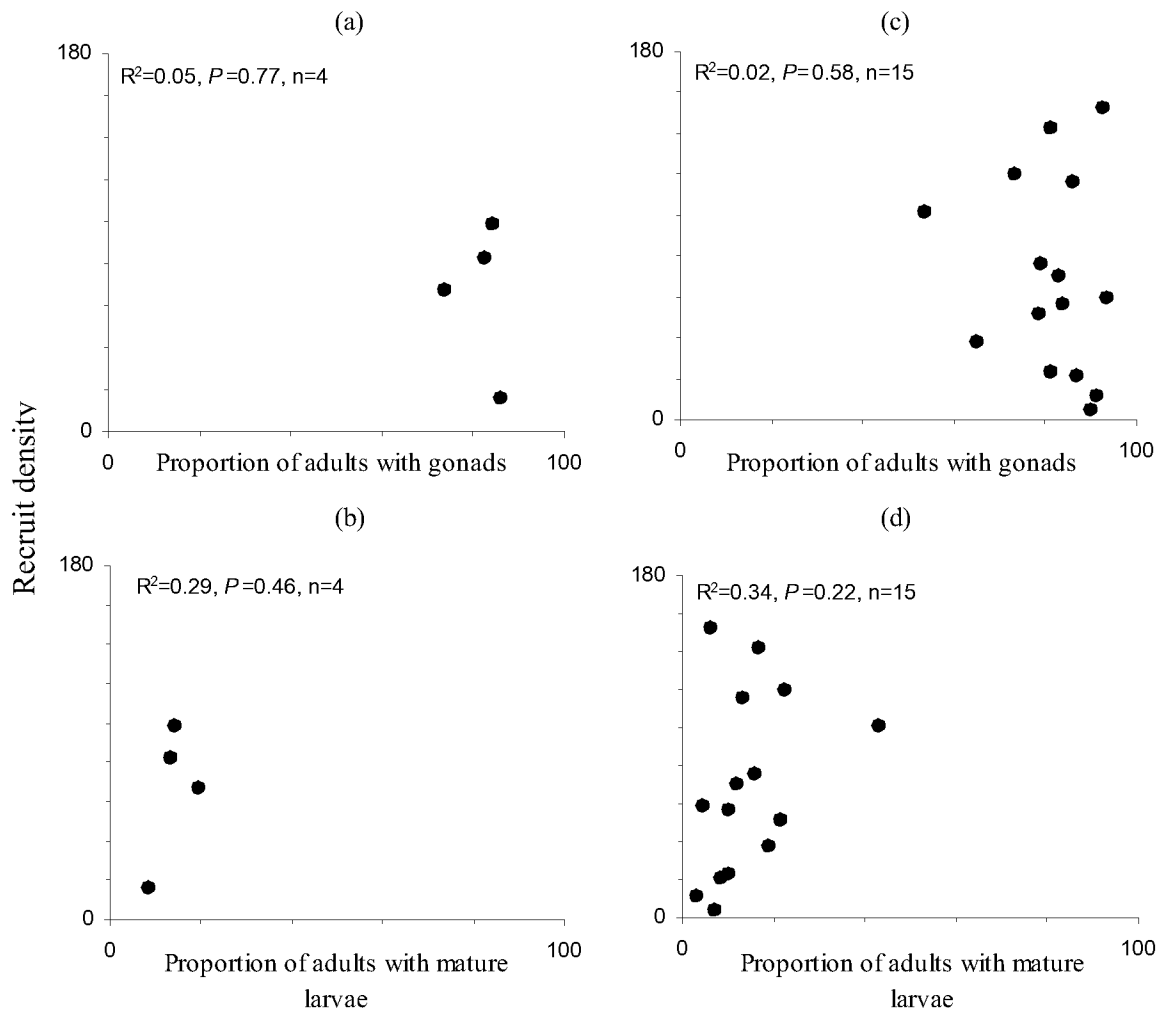


Fig. 4.5 The relationships between the mean proportion of adults with gonads and mature larvae, and mean recruit density of *T. rosea* along 600 km of coastline, from the range centre to the range limit of this species on the southeast coast of Australia, based on mean values at four sectors (a & b), and corresponding 16 locations (c & d), from May 2005 to May 2006. Values for proportions of adults with mature gonads and larvae are lagged by three months compared to recruit density values (see pg. 68).

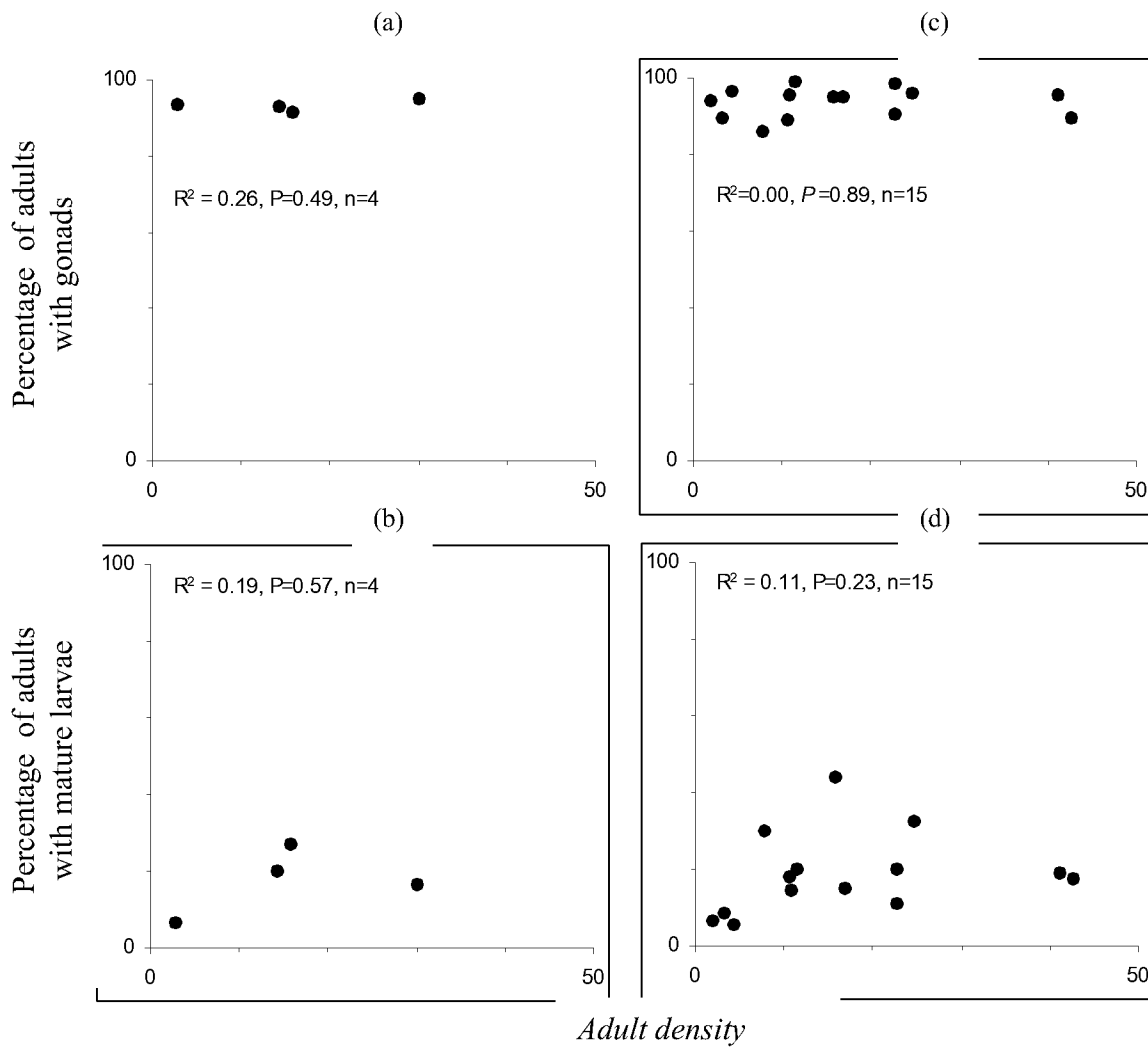


Fig. 4.6 The relationships between the mean adult density and the percentage of adults with gonads and larvae of *T. rosea* along 600 km of coastline, from the range centre to the range limit of this species on the southeast coast of Australia, based on mean values at four sectors (a & b), and corresponding 16 locations (b & d), from May 2005 to May 2006.

Discussion

This study is the first assessment of the large scale patterns of adult abundance, fecundity and recruitment of a temperate, benthic marine invertebrate species with planktonic development. By investigating adult-fecundity-recruitment relationships from small to large spatial scales, I have attempted to determine the changes in population dynamics and connectivity of the intertidal barnacle, *Tessieropora rosea*, towards its range limit on the southeast coast of Australia. Although the outcome is somewhat contradictory, my analyses revealed some striking patterns. Paradoxically, the patterns of adult abundance, fecundity and recruitment of *T. rosea* gave evidence to suggest that this highly dispersive species has a relatively closed population structure towards its southern range limit, whereas correlations among the various stages of the life cycle pointed towards a more open population structure.

I found that patterns of adult abundance, recruitment and the proportions of adult *T. rosea* producing larvae all declined dramatically at the range limit. This suggested that despite the long larval duration (of up to 5 weeks) of *T. rosea* in the water column (Denley, 1981), adult abundance at the range limit is related to the intensity of larval production and recruitment for this species. However, life-history relationships revealed that only recruitment and adult abundance were significantly correlated at large spatial scales. Although these correlations were possibly affected by differences in replication at different hierarchical scales (as discussed in more detail in Chapter 5), this suggested that the effect of fecundity on recruitment operates at some larger spatial scale across the range of this highly dispersive species and, therefore, that *T. rosea* has an open population structure towards its range limit. The fact that there

were no trends in the links between recruits and adults at any smaller spatial scales towards the species' range limit further gave evidence for this.

Positive associations between recruitment and adult abundance of benthic marine species with a planktonic larval stage have been demonstrated by several other studies at both small and relatively large scales (Gaines and Roughgarden, 1985; Minchinton and Scheibling, 1991; Gaines and Bertness, 1992; Menge, 2000). However, these studies explored the effect of recruitment on consequent adult population size, whereas my study explored the reverse, looking at how adult population size affects the intensity of recruitment towards the range limit. Although both are valid approaches, and are likely to give similar results, given that adult *T. rosea* can live for between 8 to 20 years (Peter Fairweather, pers. comm.; Caffey, 1985), I addressed how already established adult populations affect recruitment over a 12 month period in this study. Either way, the strong positive relationship between adults and recruits suggested that temporal variations in recruitment may have large impacts on adult abundance, particularly at range limit populations where adult density is small. For example, Hills and Thomason (2003) found that at low densities, recruit densities of the barnacle *Semibalanus balanoides* were more closely related to adult densities, than at high densities.

The lack of relationship between larval production and recruitment in my study is a sharp contrast to the results found by the only other study that has assessed these patterns at large scales. Hughes *et al.* (2000) found that the fecundity and recruitment of one genus of coral were strongly positively associated at large scales. This difference may be due to the more widespread dispersal of *T. rosea*, compared to coral species, which may increase the scale at which fecundity and recruitment are

related. However, it may also be because in Hughes' (2000) study, coral recruits were only identified to family or genus level, which may have confounded the relationships found between fecundity and recruitment of these species.

The decline in recruitment towards the range limit of *T. rosea* was a surprising result given the long larval duration of this species and, therefore, the great potential for the EAC to distribute its larvae southwards. However, recruitment has been documented to decrease with increasing latitude for several other benthic marine species (Lewis, 1986; Hughes *et al.*, 1999; Connolly *et al.*, 2001; Hughes *et al.*, 2002). Between the northernmost and southernmost locations of my study area (Sydney and Cape Conran), sea surface temperature changes by up to 5 degrees (Knox, 1963; Ridgway and Dunn, 2003), which may limit the survival of larvae or recent settlers.

Alternatively, although the EAC flows dominantly southwards, it also weakens and occasionally forms coastal eddies as it flows towards the southeast corner of Australia (Ridgway and Dunn, 2003). These eddies may fail to transport larvae in large enough numbers from upstream 'source' populations towards the range limit, and may also potentially recirculate larvae back to, or close to their shores of origin (Murray-Jones and Ayre, 1997). The fact that there was a positive relationship between recruitment and adult density within the second sector of my study area, yet no relationships within the sectors furthest and closest to the range limit gives some evidence for this.

Pulses of recruitment found in May 2005 and May 2006 within the range centre are likely to have represented the main spawning season of the species during this time (Wisely and Blick, 1964). Interestingly, however, these pulses were not observed at the range limit, particularly in May 2006. This suggests that recruitment may be limited at the range limit, and contradicts earlier results found in Chapter 3, which

showed, based on the presence of a high proportion of small sized individuals of *T. rosea* at the range limit locations, that recruitment was plentiful. However, because there was also evidence of potentially slower growth of *T. rosea* at range limit locations, and a significant decrease in the number of cohorts towards the range limit in Chapter 3, it may be that small sized individuals at range limit locations do not necessarily represent recent recruitment events but instead, slow growing individuals from previous recruitment events.

If the potential lack of recruitment at the range limit of *T. rosea* is determined at least partially by larval production within the middle of the range, as would be expected for a species with such a long larval duration and high dispersal potential, then recruitment events may not always successfully reach the range limit, maybe due to variable patterns of current flow at time of larval release. If, however, recruitment at the range limit is a result of larval production at the range limit, and range limit populations functioned as separate units with no connections to populations within the range, then larvae may be released less frequently, in less quantities, or may be less abundant or viable compared to the middle of the range.

Changes in fecundity, or reproductive potential of benthic marine species have not been previously assessed specifically towards a geographical range limit, but Hughes *et al.* (2000) found a large drop in fecundity for one genus of broadcast spawning corals towards both the southern and northern end of the 3000 km extent of the Great Barrier Reef in Australia. I also found a distinct and significant drop in the proportion of adults producing ready-to-release larvae at the southern range limit of *T. rosea*, despite an equal proportion of them having mature gonads from the middle of the range to the range limit. This drop at the range limit may be explained in several

different ways. Changes in abiotic factors that favour reproduction, such as a drop in sea surface temperature towards the range limit (Ridgway and Dunn, 2003), may limit the production of larvae (Ramirez Llorda, 2002) at the range limit. A decline in fecundity along a temperature gradient towards the geographical range limit has also been found for a terrestrial plant (Jump and Woodward, 2003). Alternatively, because barnacles cross-fertilise their nearest neighbours (Greenaway, 1998), a drop in adult density may possibly reduce the chances of encountering a neighbour, and therefore affect the success of fertilisation and larval production. However, adult density and proportions of adults with larvae did not relate at large spatial scales, which contradicts this argument. Furthermore, increased density has in fact been shown to negatively impact on egg production for one barnacle species, *Semibalanus balanoides* (Thomason and Hills, 2003). Lastly then, the drop in fecundity at the range limit may be due to a difference in the timing of reproduction. Perhaps the sampling seasons chosen for my study did not encounter the peak periods of reproduction at the range limit. *Tesseropora rosea* is known to reproduce predominantly from January to April (Wisely and Blick, 1964), but the timing and duration of this has been observed to vary among years (Denley, 1981), and larvae have been noticed to settle on rocky shores even in the mid winter months of August at some locations in the middle of the range of this species (Caffey, 1985). Indeed, rocky intertidal marine invertebrates on the European Atlantic coast were also observed to have shorter breeding seasons at their northern range limits (Lewis, 1986).

CHAPTER 5

General Discussion

There are few empirical investigations of the large scale patterns of species composition, abundance and population dynamics of temperate benthic marine invertebrates (but see Connolly *et al.*, 2001; Wares *et al.*, 2001; Sagarin and Gaines, 2002b; Zacherl *et al.*, 2003), and very few that have documented these patterns towards the range limits of species (Zacherl *et al.*, 2003; Gilman, 2005). This thesis provides the first rigorous and quantitative assessment of large scale patterns of distribution, abundance and recruitment of intertidal invertebrate species approaching their range limits on the southeast coast of Australia.

The results found in Chapter 2 suggested that large areas of unsuitable habitat, such as the 300 km stretch of the Ninety Mile Beach and mangrove forests on the southeast coast of Australia, can significantly influence the species composition and richness of rocky intertidal invertebrate communities, by limiting the distributions of some planktonic developing species. The biogeographic barrier at Point Conception on the west coast of the USA, which is composed of a headland where two major oceanic currents collide, was also found to limit only the distributions of planktonically developing species (Wares *et al.*, 2001), supporting the results of my study. This implied that although planktonically developing species are generally considered to be better at dispersing to distant locations than direct developing species (Kinlan and Gaines, 2003; Shanks *et al.*, 2003), they may nevertheless, in some cases, be more susceptible to be limited by physical barriers, consisting of large gaps in suitable habitat that are associated with complex oceanic flow patterns.

Of course, it is also possible that the distributions of rocky intertidal species across the Ninety Mile Beach biogeographic barrier found in my study did not actually reflect the ability of species to cross this barrier through dispersal, but rather their ability to maintain viable populations over the natural historical changes in sea level, and associated changes in habitat availability. Because this barrier only emerged approximately 6000 years ago when the sea reached its current level (Lambeck & Nakada, 1990), it may be that direct developing species may simply maintain more stable populations that are better able to persist in isolated locations over long periods, as they are better able to retain their propagules within local populations (Highsmith, 1985; Johannesson, 1988; Helmuth *et al.*, 1994). Conversely, planktonically developing species may have more ephemeral and temporally variable populations that rely on the exchange of propagules between local populations for the maintenance of viable populations. Importantly, however, the interpretations of my results may have been affected by the fact that my survey on species richness and composition did not include all invertebrate species on the shore. The exclusion of micro-invertebrates, sponges and mobile species may have made a difference in both the species richness and the types of reproductive modes of the species found on either side of the barrier. Moreover, of the forty species found in my survey, only 3 were direct developing, which made general conclusions difficult to draw, regarding the success of different reproductive modes in crossing the barrier. Future surveys aiming to determine differences in distribution among rocky, intertidal marine invertebrates with different life history characteristics may need to consider carrying out more detailed searches, to include all species found on the shore, and to hence increase the likelihood of finding sufficient numbers of species for each unique life history characteristic.

In Chapter 3 I showed that the abundances of 3 planktonically developing species limited to the northern side of the Ninety Mile Beach biogeographic barrier all declined dramatically at several locations leading up to the barrier, while the one species with a continuous distribution across this region remained highly abundant. This suggested that indeed, the truncation in the distributions of the three limited species is not a simple effect of a gap in suitable habitat. Size frequency distributions of the 3 species showed variable patterns, with one showing no changes, one with missing smaller sized individuals, and one with missing large sized individuals towards the range limit. This implied that crucial population processes, such as in some cases a lack of recruitment and, in other cases, post-settlement mortality may contribute to limiting the distributions of these species towards their range limits. A lack of recruitment may be an effect of the weakening of the East Australian Current off the southeast corner of Australia (Murray-Jones and Ayre, 1997; Ridgway and Dunn, 2003), and post-settlement mortality may be due to a change in sea surface temperature by up to five degrees around this same region (Knox, 1963; Ridgway and Dunn, 2003). However, the absence of small individuals for the two gastropod species, *M. marginalba* and *A. pyramidalis*, at most locations of the study region have made these conclusions fairly speculative. Future studies aiming to study the recruitment of mobile species such as gastropods may need to combine a number of different methods, such as larval collectors and size frequency measurements, to assure the detection of recruits on the shore.

Finally, in Chapter 4, I found that the adult abundance, fecundity and recruitment of one of the species from Chapter 3, the intertidal barnacle, *Tessieropora rosea*, all showed similar patterns of decline towards the range limit on the northern side of the barrier. This suggested that despite the long larval stage of this species, local adult

abundance strongly reflects local fecundity and recruitment at the range limit, which is indicative of a closed population structure. However, correlations only revealed a relationship between adult abundance and recruitment, and only at a large spatial scale, which suggested that the influence of larval production on recruitment actually operates at a larger scale than my study region, and gave evidence for a semi-open population structure for this species. Importantly, comparisons of life-history relationships between small and large spatial scales have to be treated with caution in this study, as relationships at these different spatial scales were explored based on regression plots with different replication intensity. Therefore, particularly at small spatial scales, results may have been confounded by insufficient power to detect significant relationships. The sampling design of this study was modeled on the only other study that has addressed life-history relationships of benthic marine invertebrates (Hughes *et al.*, 2000), and was thought to be appropriate for effective comparisons between studies. However, in future, it may be necessary to have greater replication at the larger spatial scales of a hierarchical sampling design addressing such relationships, to improve the assessability of questions at large spatial scales, and also the comparability of correlation results among the various spatial levels.

Results from Chapter 4 nevertheless indicated firstly, that recruitment at the range limit of *T. rosea* may be determined partially by the local production of larvae, and partially by the supply of larvae from upstream locations within the middle of the range of the species and, secondly, that recruitment may be a key determinant of adult abundance at the range limit of this species. *Tesseropora rosea* may therefore be limited near its range limit partially due to post-settlement factors limiting the production of larvae within range limit populations, and partially by the lack of, less frequent, or smaller supply of larvae from upstream populations.

The key contribution of this thesis is, therefore, an empirical demonstration that the adult abundance, fecundity, recruitment, and the link between the three stages of the life cycle of intertidal marine invertebrates vary in space towards their geographical range limits. It appears, based on my data on *T. rosea*, that benthic marine invertebrates with a planktonic larval stage may indeed have ephemeral and vulnerable populations at the edge of their ranges, and may at least partially rely on recruitment from populations in the middle of the range for survival. Essentially, range edge populations may therefore act as ‘sink’ populations (*sensu* Pulliam, 1988). However, to what degree this is true for other species with different life histories along this coast and others, remain to be answered. Future studies should therefore aim to verify and further explore the generality of the patterns found in this study. Assessing the genetic relationships among populations in the middle of the range and range edge for species that are limited by the barrier, as well as among populations on either side of the barrier for species that cross the barrier, may be the most appropriate and beneficial approach to do this (Ayre *et al.*, 1991; Billingham and Ayre, 1996; Murray-Jones and Ayre, 1997; Waters *et al.*, 2005). This can reveal important information about the degree of genetic connectivity across the ranges of these species and the potential historical ancient split between now isolated populations on either side of the barrier, as well as identify potential bottlenecks throughout this region (Johnson and Black, 1998). Furthermore, to address important questions about the effects of post-settlement mortality on the survival of species that are limited to the northern side of the barrier, firstly assessing the relationships between settlers and recruits at the range limit may be beneficial (Connell, 1985; Minchinton and Scheibling, 1991). Secondly, assessing the changes in fecundity of these species at a greater detail towards the range limit, by perhaps measuring the sizes or numbers of

larvae produced compared to the middle of the range, may reveal important information about how reproductive potential is affected towards the range limit.

The results of this study have several implications for the conservation and management of rocky intertidal invertebrate communities. Coastal development that impacts on rocky shore habitats may clearly pose a serious threat to the connectivity and viability of populations of some invertebrate species, particularly some that have a planktonic larval stage, by increasing the distance between, and hence isolating, populations in suitable habitats. Such impacts may be particularly detrimental close to the range limit of some species, as they may decrease the chances of larvae produced within productive ‘source’ populations in the middle of the range from reaching ‘sink’ populations at the range limit (*sensu*. Pulliam, 1988). As human-induced global warming becomes an increasingly serious problem, current range edge populations may soon become critically important populations that may act as the stepping stone for some species to expand and shift into new habitats. The protection and preservation of range edge populations of intertidal marine invertebrates may therefore be essential for ensuring the future survival of these species, and may be necessary to integrate into future marine reserve design.

References

- Aliani, S. and Molcard, A. (2003). Hitch-hiking on floating marine debris: macrobenthic species in the Western Mediterranean Sea. *Hydrobiologica* **503**: 59-67.
- Anderson, D. T. (1961). The reproduction and early life histories of the gastropod *Bambicium nanum* (Lamarck, 1822) (Fam. Littorinidae). *Proceedings of the Linnean Society of New South Wales* **86(1)**: 203-206.
- Anderson, D. T. (1962). The reproduction and early life histories of the gastropods *Bembicium auratum* (Quoy and Gaimard) (Fam. Littorinidae), *Cellana tramoserica* (Sower.) (Fam. Patellidae) and *Melanerita melanotragus* (Smith) (Fam. Neritidae). *Proceedings of the Linnean Society of New South Wales* **37**: 62-68.
- Anderson, D. T. (1965). The reproduction and early life histories of the gastropods *Notoacmea petterdi* (Ten-Woods), *Chiazacmaea flammea* (Quoy and Gaimard) and *Patelloida alticostata* (Angas) (Fam. Acmaeidae). *Proceedings of the Linnean Society of New South Wales* **90**: 106-114.
- Anderson, D. T. (1977). The embryonic and larval development of the turbellarian *Notoplana-australis* Polycladida Leptoplanidae. *Australian Journal of Marine and Freshwater Research* **28**: 303-310.
- Andrewartha, H. G. and Birch, L. C. (1954). The Distribution and Abundance of Animals. Chicago, University of Chicago Press.
- Andrews, J. C. and Anderson, D. T. (1962). The development of the polychaete *Galeolaria caespitosa* Lamarck (Fam. Serpulidae). *Proceedings of the Linnean Society of New South Wales* **37**: 185-188.
- Ayre, D. J. (1983). The effects of asexual reproduction and intergenotypic aggression on the genotypic structure of the populations of the sea anemone *Actinia tenebrosa*. *Oecologia* **58**: 158-165.
- Ayre, D. J. and Dufty, S. (1994). Evidence for restricted gene flow in the viviparous coral *Seriatopora hystrix* on Australia's Great Barrier Reef. *Evolution* **48(4)**: 1183-1201.
- Ayre, D. J. and Hughes, T. P. (2000). Genotypic diversity and gene flow in brooding and spawning corals along the Great Barrier Reef, Australia. *Evolution* **54(5)**: 1590-1605.

- Ayre, D. J., Read, J. and Wishart, J. (1991). Genetic subdivision within the eastern Australian population of the sea anemone *Actinia tenebrosa*. *Marine Biology* **109**: 379-390.
- Barry, J. P., Baxter, C., Sagarin, R. and Gilman, S. E. (1995). Climate related, long-term faunal changes in a California rocky intertidal community. *Science* **267**: 672-675.
- Bennett, I. and Pope, E. C. (1953). Intertidal zonation of the exposed rocky shores of Victoria, together with a rearrangement of the biogeographical provinces of temperate Australasian shores. *Australian Journal of Marine and Freshwater Research* **4**: 105-159.
- Billingham, M. and Ayre, D. J. (1996). Genetic subdivision in the sub-tidal, clonal sea anemone *Anthothoe albocincta*. *Marine Biology* **125**: 153-163.
- Bird, E. C. F. (1993). The coast of Victoria: The shaping of scenery. Melbourne, University Press Carlton.
- Botsford, L. W., Micheli, F. and Hastings, A. (2003). Principles for the design of marine reserves. *Ecological Applications* **13**(1): S25-S31.
- Broitman, B. R., Navarette, S. A., Smith, F. and Gaines, S. D. (2001). Geographic variation of southeastern Pacific intertidal communities. *Marine Ecology Progress Series* **224**: 21-34.
- Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist* **124**(2): 255-279.
- Brown, J. H. (1995b). Macroecology. Chicago, University of Chicago Press.
- Brown, K. M. and Quinn, J. F. (1988). The effect of wave action on growth of three intertidal gastropods. *Oecologia* **75**: 420-425.
- Butler, A. J. (1991). Effect of patch size on communities of sessile invertebrates in Gulf St Vincent, South Australia. *Journal of Experimental Marine Biology and Ecology* **153**: 255-280.
- Caffey, H. M. (1982). No effect of naturally-occurring rock types on settlement or survival in the intertidal barnacle, *Tessieropora rosea*. *Journal of Experimental Marine Biology and Ecology* **63**: 119-132.

- Caffey, H. M. (1985). Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* **55**(3): 313-332.
- Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P. and Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**: 477-500.
- Carr, M. H., Neigel, J. E., Estes, J. A., Andelman, S., Warner, R. R. and Largier, J. L. (2003). Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications* **13**(1): S90-S107.
- Carter, R. N. and Prince, S. D. (1981). Epidemic models used to explain biogeographical distribution limits. *Nature* **293**: 644-645.
- Case, T. J., Holt, R. D., McPeck, M. A. and Keitt, T. H. (2005). The community context of species' borders: ecological and evolutionary perspectives. *Oikos* **108**: 28-46.
- Case, T. J. and Taper, M. L. (2000). Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *The American Naturalist* **155**(5): 583-605.
- Cassie, R. M. (1954). Some uses of probability paper in the analysis of size frequency distributions. *Australian Journal of Marine and Freshwater Research* **5**: 513-522.
- Caughley, G., Grice, D., Barker, R. and Brown, B. (1988). The edge of the range. *Journal of Animal Ecology* **57**: 771-785.
- Chapman, M. G. (1994). Small- and broad-scale patterns of distribution of the upper-shore littorinid *Nodilittorina pyramidalis* in New South Wales. *Australian Journal of Ecology* **19**(1): 83-95.
- Chapman, M. G. (1995). Aggregation of the littorinid snail *Littorina unifasciata* in New South Wales, Australia. *Marine Ecology Progress Series* **126**(1-3): 191-202.
- Chapman, M. G. (1997). Relationships between shell shape, water reserves, survival and growth of highshore littorinids under experimental conditions in New South Wales, Australia. *Journal of Molluscan Studies* **63**(4): 511-529.
- Chapman, M. G. and Underwood, A. J. (1994). Dispersal of the intertidal snail *Nodilittorina pyramidalis*, in response to the topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology* **179**(2): 145-169.

Chapman, M. G. and Underwood, A. J. (1996). Influences of tidal conditions, temperature and dessication on patterns of aggregation of the high-shore periwinkle, *Littorina unifasciata*, in New South Wales, Australia. *Journal of Experimental Marine Biology and Ecology* **196(1-2)**: 213-237.

Clarke, K. R. and Warwick, R. M. (1994). Change in marine communities: An approach to statistical analysis and interpretation. Plymouth, Natural Environment Research Council and Plymouth Marine Laboratory.

Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **93**: 11-45.

Connolly, S. R., Menge, B. A. and Roughgarden, J. (2001). A latitudinal gradient in recruitment of intertidal invertebrates in the northeast pacific ocean. *Ecology* **82(7)**: 1799-1813.

Connolly, S. R. and Roughgarden, J. (1998). A latitudinal gradient in Northeast Pacific intertidal community structure: Evidence for an oceanographically based synthesis of marine community theory. *The American Naturalist* **151**: 311-326.

Connor, E. F. and McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *American Naturalist* **113**: 791-833.

Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Paris, C. B. and Olson, D. B. (2000). Connectivity of marine populations: open or closed? *Science* **287**: 857-859.

Creese, R. G. (1980a). Reproductive cycles and fecundities of four common eastern Australian Archaeogastropod limpets (Mollusca: Gatropoda). *Australian Journal of Marine and Freshwater Research* **31**: 49-59.

Creese, R. G. (1980b). An analysis of distribution and abundance of populations of the high shore limpet, *Notoacmea petterdi* (Tenison-Woods). *Oecologia* **45**: 252-260.

Creese, R. G. (1980c). Reproductive cycles and fecundities of two species of Siphonaria (Mollusca: Pulmonata) in south - eastern Australia. *Australian Journal of Marine and Freshwater Research* **31**: 37-47.

Creese, R. G. (1982). Distribution and abundance of the acmaeid limpet, *Patelloida latistrigata*, and its interaction with barnacles. *Oecologia* **52**: 85-96.

Crisp, D. J. and Southward, A. J. (1958). The distribution of intertidal organisms along the coast of the English Channel. *Journal of the Marine Biological Association of the United Kingdom* **37**: 157-208.

Crowder, L. B., Lyman, S. J., Figuera, W. F. and Priddy, J. (2000). Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* **66(3)**: 799-820.

Denley, E. J. (1981). The ecology of the intertidal barnacle, *Tesseropora rosea*. University of Sydney.

Dethier, M. N., McDonald, K. and Strathmann, R. R. (2003). Colonization and connectivity of habitat patches for coastal marine species distant from source populations. *Conservation Biology* **17(4)**: 1024-1035.

Eckert, G. L. (2003). Effects of the planktonic period on marine population fluctuations. *Ecology* **84(2)**: 372-383.

Eckman, J. E. (1996). Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *Journal of Experimental Marine Biology and Ecology* **200**: 207-237.

Edgar, G. J. (1986). Biogeographical processes in the Southern Hemisphere marine environment. Actas Del Segundo Congreso Sobre Algas Marinas Chilenas, Universidad Austral De Chile, Chile.

Edgar, G. J. (1997). Australian Marine Life: The Plants and Animals of Temperate Waters. Sydney, Reed New Holland.

Egan, E. A. and Anderson, D. T. (1988). Larval development of the coronuloid barnacles *Austrbalanus imperator* Darwin, *Tetraclitella purpurascens* Wood, and *Tesseropora rosea* Krauss Cirripedia Tetraclitidae. *Journal of Natural History* **22(5)**: 1379-1406.

Eisenhauer, A., Ahu, Z. R., Collins, L. B., Wyrwoll, K. H. and Eichstätter, R. (1996). The last interglacial sea level change: New evidence from the Abrolhos islands, west Australia. *Geologische Rundschau* **85**: 606-614.

Fairweather, P. G. (1988a). Correlations of predatory whelks with intertidal prey at several scales of space and time. *Marine Ecology Progress Series* **45**: 237-243.

Fairweather, P. G. (1988b). Movements of intertidal whelks (*Morula marginalba* and *Thais orbita*) in relation to availability of prey and shelter. *Marine Biology* **100**: 63-68.

Fields, P. A., Graham, J. B., Rosenblatt, R. H. and Somero, G. N. (1993). Effects of expected global climate change on marine faunas. *Trends in Ecology and Evolution* **8(10)**: 361-367.

Fretter, V., Graham, A., Ponder, W. F. and Lindberg, D. L. (1998). Prosobranchia Introduction. *Mollusca: The Southern Synthesis. Fauna of Australia Vol. 5 Part B*. P. L. Beesly, G. J. B. Ross and A. Wells. Melbourne, CSIRO Publishing: 605-638.

Gaines, S. and Roughgarden, J. (1985). Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Science USA* **82**: 3707-3711.

Gaines, S. D. and Bertness, M. D. (1992). Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* **360**: 579-580.

Gaines, S. D., Gaylord, B. and Largier, J. L. (2003). Avoiding current oversights in marine reserve design. *Ecological Applications* **13(1)**: S32-S46.

Gaston, K. J. (2003). *The Structure and Dynamics of Geographic Ranges*. New York, Oxford University Press.

Gaylord, B. and Gaines, S. D. (2000). Temperature or transport? Range limits in marine species mediated solely by flow. *The American Naturalist* **155(6)**: 769-789.

Gaylord, B., Reed, D. C., Raimondi, P. T., Washburn, L. and McLean, S. R. (2002). A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. *Ecology* **83(5)**: 1239-1251.

Gilman, S. E. (2005). A test of Brown's principle in the intertidal limpet *Collisella scabra* (Gould, 1846). *Journal of Biogeography* **32**: 1583-1589.

Grantham, B. A., Eckert, G. L. and Shanks, A. L. (2003). Dispersal potential of marine invertebrates in diverse habitats. *Ecological Applications* **13(1)**: S108-S116.

Greenaway, P. (1998). Crustacea. *Invertebrate Zoology*. D. T. Anderson. Melbourne, Oxford University Press: 286-318.

- Grinnell, J. (1917). Field tests of theories concerning distribution control. *The American Naturalist* **51**: 115-128.
- Grosberg, R. K. and Levitan, D. R. (1992). For adults only? Supply-side ecology and the history of larval biology. *Trends in Ecology and Evolution* **7(4)**: 130-133.
- Guo, Q., Taper, M., Schoenberger, M. and Brandle, J. (2005). Spatial-temporal population dynamics across species range: from centre to margin. *Oikos* **108**: 47-57.
- Harding, J. P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. *Journa of the Marine Biological Association of the United Kingdom* **28**: 141-153.
- Helmuth, B., Velt, R. R. and Holberton, R. (1994). Long distance dispersal of a subantarctic brooding bivalve (*Gaimardia trapesine*) by kelp rafting. *Marine Biology* **120**: 421-426.
- Hickman, C. S. (1998). Subfamily Trochoidea. Mollusca: The Southern Synthesis Fauna of Australia Vol 5 Part A & B. P. L. Beesley, G. J. B. Ross and A. Wells. Melbourne, CSIRO Publishing: 671-692
- Highsmith, R. C. (1985). Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Marine Ecology Progress Series* **25**: 169-179.
- Hills, M. and Thomason, J. C. (2003). Recruitment density can determine adult morphology and fecundity in the barnacle, *Semibalanus balanoides*. *Biofouling* **19(3)**: 205-213.
- Hixon, M. A., Pacala, S. W. and Sandin, S. A. (2002). Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology* **83(6)**: 1490-1508.
- Holt, R. D. and Keitt, T. H. (2005). Species' borders: a unifying theme in ecology. *Oikos* **108**: 3-6.
- Holt, R. D., Keitt, T. H., Lewis, M. A., Maurer, B. A. and Taper, M. L. (2005). Theoretical models of species' borders: single species approaches. *Oikos* **108**: 18-27.
- Hughes, T. P. (1990). Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology* **71(1)**: 12-20.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Harriott, V. J., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E. and Willis, B. L. (2002). Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. *Ecology* **83**(2): 436-451.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E. and Willis, B. L. (1999). Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* **397**: 59-63.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E. and Willis, B. L. (2000). Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* **81**(8): 2241-2249.

Hunt, A. (1993). Effects of contrasting patterns of larval dispersal on the genetic connectedness of local populations of two intertidal starfish, *Patiriella calcar* and *P. exigua*. *Marine Ecology Progress Series* **92**: 179-186.

Hunt, A. and Ayre, D. J. (1989). Population structure in the sexually reproducing sea anemone *Oulactis mucosa*. *Marine Biology* **102**: 537-544.

Johannesson, K. (1988). The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? *Marine Biology* **99**: 507-513.

Johnson, M. P., Allcock, A. L., Pye, S. E., Chambers, S. J. and Fitton, D. M. (2001). The effects of dispersal mode on the spatial distribution patterns of intertidal molluscs. *Journal of Animal Ecology* **70**: 641-649.

Johnson, M. S. and Black, R. (1998). Effects of isolation by distance and geographical discontinuity on genetic subdivision of *Littoraria cingulata*. *Marine Biology* **132**: 295-303.

Jones, D. S. (1990). Occurrence of the barnacle *Tesseropora rosea* (Krauss) (Thoracica, Balanomorpha, Tetraclitidae) in Western Australian waters. *Records of the Western Australian Museum* **14**(4): 665-668.

Jump, A. S. and Woodward, F. I. (2003). Seed production and population density decline approaching the range-edge of *Cirsium* species. *New Phytologist* **160**: 349-358.

Keough, M. J. (1984). Effects of patch size on the abundance of sessile marine invertebrates. *Ecology* **65**: 423-437.

- Kinlan, B. P. and Gaines, S. D. (2003). Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* **84**: 2007-2020.
- Kirkpatrick, M. and Barton, N. H. (1997). Evolution of a species' range. *The American Naturalist* **150**(1): 1-23.
- Knox, G. A. (1963). The biogeography and intertidal ecology of the Australasian coasts. *Oceanography and Marine Biology: An Annual Review* **1**: 341-404.
- Knox, G. A. (1980). Plate tectonics and the evolution of intertidal and shallow water benthic biotic distribution patterns of the Southwest Pacific. *Paleogeography, Paleoclimatology, Paleoecology* **31**: 267-297.
- Kohn, A. J. and Leviten, P. J. (1976). Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia* **25**: 199-210.
- Lambeck, K. and Nakada, M. (1990). Late Pleistocene and Holocene sea-level change along the Australian coast. *Palaeogeography, Palaeoclimatology, Palaeoecology* **89**: 143-176.
- Lawson, G. W. (1957). Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. *Journal of Ecology* **45**: 831-860.
- Lewis, J. R. (1986). Latitudinal trends in reproduction, recruitment and population characteristics of some littoral molluscs and cirripedes. *Hydrobiologia* **142**: 1-13.
- Lima, F. P., Queiroz, N., Ribeiro, P. A., Hawkins, S. J. and Santos, A. M. (2006). Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. *Journal of Biogeography* **33**: 812-822.
- Lindberg, D. R. (1998). Order Patellogastropoda. Mollusca: The Southern Synthesis Fauna of Australia Vol 5 Part A & B. P. L. Beesley, G. J. B. Ross and A. Wells. Melbourne, CSIRO Publishing: 639-652.
- Littell, R. C., Milliken, G. A., Stroup, W. W. and Wolfinger, R. D. (1996). SAS system for mixed models. Cary, NC, USA, SAS Institute Inc.
- Littler, M. M., Martz, D. R. and Littler, D. S. (1983). Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Marine Ecology Progress Series* **11**: 129-139.

- Lubchenco, J., Palumbi, S. R., Gaines, S. D. and Andelman, S. (2003). Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications* **13**(1): S3-S7.
- Mapstone, G. M. (1978). Egg capsules and early development in *Siphonaria diemenensis* (Quoy and Gaimard, 1833) and *Siphonaria baconi* (Reeve, 1856). *Journal of the Malacological Society of Australia* **4**: 85-92.
- Marko, P. B. (2004). "What's larvae got to do with it?" Disparate patterns of post-glacial population structure in two benthic marine gastropods with identical dispersal potential. *Molecular Ecology* **13**: 597-611.
- Menge, B. A. (2000). Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. *Ecological Monographs* **70**(2): 265 - 288.
- Minchinton, T. E. and Scheibling, R. E. (1991). The influence of larval supply and settlement on the population structure of barnacles. *Ecology* **72**(5): 1867-1879.
- Miner, C. M., Altstatt, J. M., Raimondi, P. T. and Minchinton, T. E. (2006). Recruitment failure and shifts in community structure following mass mortality limit recovery prospects of black abalone. *Marine Ecology Progress Series* **327**: 107-117.
- Moran, M. J. (1985). Distribution and dispersion of the predatory intertidal gastropod *Morula marginalba*. *Marine Ecology Progress Series* **22**: 41-52.
- Moran, M. J., Fairweather, P. G. and Underwood, A. J. (1984). Growth and mortality of the predatory intertidal whelk *Morula marginalba* Blainville (Muricidae): the effects of different species of prey. *Journal of Experimental Marine Biology and Ecology* **75**: 1-17.
- Murray-Jones, S. E. and Ayre, D. J. (1997). High levels of gene flow in the surf bivalve *Donax deltoides* (Bivalvia: Donacidae) on the east coast of Australia. *Marine Biology* **128**(1): 83-89.
- Myers, A. A. (1997). Biogeographic barriers and the development of marine biodiversity. *Estuarine, Coastal and Shelf Science* **44**: 241-248.
- Nell, J. A., Smith, I. R. and McPhee, C. C. (2000). The Sydney rock oyster *Saccostrea glomerata* (Gould 1850) breeding programme: progress and goals. *Aquaculture Research* **31**: 45-49.

- O'Hara, T. D. and Poore, G. C. B. (2000). Patterns of distribution of marine echinoderms and decapods. *Journal of Biogeography* **27**: 1321-1355.
- Orton, J. H. (1920). Sea-temperature, breeding, and distribution in marine animals. *Journal of Marine Biological Associations* **12**: 339-366.
- Otway, N. M. (1994). Population ecology of the low-shore chitons *Onithochiton quernicus* and *Plaxiphora albida*. *Marine Biology* **121**: 105-116.
- Palmer, A. R. and Strathmann, R. R. (1981). Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia* **48**: 308-318.
- Palumbi, S. R. (2003). Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* **13(1)**: S146-S158.
- Parker, T. and Tunnicliffe, V. (1994). Dispersal strategies of the biota on an oceanic seamount: implications for ecology and biogeography. *The Biological Bulletin* **187**: 336-347.
- Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D. M., Kingsolver, J., Peterson, A. T. and Sagarin, R. (2005). Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* **108**: 58-75.
- Parmesan, C., Gaines, S. D., Gonzalez, L., Kaufman, D. M., Kingsolver, J., Peterson, A. T. and Sagarin, R. (2005). Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* **108**: 58-75.
- Pechenik, J. A. (1999). On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series* **177**: 269-297.
- Perry, A. L., Low, P. J., Ellis, J. R. and Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science* **308**: 1912-1915.
- Poore, G. C. B. (2004). Marine decapod Crustacea of southern Australia. A guide to identification. Melbourne, CSIRO Publishing.
- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *The American Naturalist* **132(5)**: 652-661.

- Ramirez Llorda, E. (2002). Fecundity and life-history strategies in marine invertebrates. *Advances in marine biology* **43**: 87-170.
- Reid, R. G. B. (1998a). Superfamily Littorinoidea. Mollusca: The Southern Synthesis Fauna of Australia Vol 5 Part A & B. P. L. Beesley, G. J. B. Ross and A. Wells. Melbourne, CSIRO Publishing: 737-739.
- Reid, R. G. B. (1998b). Subclass Protobranchia. Mollusca: The Southern Synthesis Fauna of Australia Vol 5 Part A & B. P. L. Beesley, G. J. B. Ross and A. Wells. Melbourne, CSIRO Publishing: 235-247.
- Ridgway, K. R. and Dunn, J. R. (2003). Mesoscale structure of the East Australian Current system and its relationship with topography. *Progress in Oceanography* **56**: 189-222.
- Roberts, C. (1998). Sources, sinks, and the design of marine reserve networks. *Fisheries* **23**(7): 16-19.
- Sagarin, R. D., Barry, J. P., Gilman, S. E. and Baxter, C. H. (1999). Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* **69**: 465-490.
- Sagarin, R. D. and Gaines, S. D. (2002a). The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters* **5**: 137-147.
- Sagarin, R. D. and Gaines, S. D. (2002b). Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography* **29**: 985-997.
- Sagarin, R. D., Gaines, S. D. and Gaylord, B. (2006). Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology and Evolution* **21**(9): 524-530.
- Sakker, E. R. (1986). Seasonal reproductive cycles of three Australian species of chitons (Mollusca: Polyplacophora). *International Journal of Invertebrate Reproduction and Development* **10**: 1-16.
- Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., Planes, S., Polunin, N. V. C., Russ, G. R., Sadovy, Y. J. and Steneck, R. S. (2005). Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution* **20**(2): 74-80.

- Scheltema, R. S. (1986). Long distance dispersal by planktonic larvae of shoal water benthic invertebrates among central Pacific Islands. *Bulletin of Marine Science* **39**: 290-322.
- Scheltema, R. S. (1989). Planktonic and non-planktonic development among Prosobranch gastropods and its relationship to the geographic range of species. Reproduction, Genetics and Distribution of Marine Organisms. J. S. Ryland and P. A. Tyler. Denmark, Olsen and Olsen: 183-188.
- Schoch, G. C. and Dethier, M. N. (1996). Scaling up: the statistical linkage between organismal abundance and geomorphology on rocky shores. *Journal of Experimental Marine Biology and Ecology* **201**: 37-72.
- Shanks, A. L., Grantham, B. A. and Carr, M. H. (2003). Propagule dispersal and the size and spacing of marine reserves. *Ecological Applications* **13**(1): S159-S169.
- Shelford, V. E. (1911). Physiological animal geography. *Journal of Morphology* **22**: 551-618.
- Stanisic, J. (1998). Order Systellommatophora. Mollusca: The Southern Synthesis. Fauna of Australia Vol. 5 Part B. P. L. Beesly, G. J. B. Ross and A. Wells. Melbourne, CSIRO Publishing: 1060-1067.
- Strathmann, R. R. (1985). Feeding and non-feeding larval development and life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics* **16**: 339-361.
- Swearer, S. E., Caselle, J. E., Lea, D. W. and Warner, R. R. (1999). Larval retention and recruitment in an island population of a coral reef fish. *Nature* **402**: 799-801.
- Thomason, J. C. and Hills, M. (2003). The 'ghost of settlement past' determined mortality and fecundity in the barnacle, *Semibalanus balanoides*. *Oikos* **101**: 529-538.
- Underwood, A. J. (1974). The reproductive cycles and geographical distribution of some common eastern Australian Prosobranchs (Mollusca: Gastropoda). *Australian Journal of Marine and Freshwater Research* **25**: 63-88.
- Underwood, A. J. and Chapman, M. G. (1996). Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* **107**: 212-224.
- Underwood, A. J. and Fairweather, P. G. (1989). Supply-side ecology and benthic marine assemblages. *Trends in Ecology and Evolution* **4**(1): 16-20.

Valentine, J. W. (1966). Numerical analysis of marine molluscan ranges on the extra tropical northeastern Pacific shelf. *Journal of Limnology and Oceanography* **11**: 198-211.

Ward, S. and Quinn, G. P. (1988). Preliminary investigations of the ecology of the intertidal predatory gastropod *Lepsiella vinosa* (Lamarck) (Gastropoda: Muricidae). *Journal of Molluscan Studies* **54**: 109-117.

Wares, J. P., Gaines, S. D. and Cunningham, C. W. (2001). A comparative study of asymmetric migration events across a marine biogeographic boundary. *Evolution* **55**(2): 295-306.

Waters, J. M., Kind, T. M., O'Loughlin, P. M. and Spencer, H. G. (2005). Phylogeographical disjunction in abundant high-dispersal littoral gastropods. *Molecular Ecology* **14**: 2789-2802.

Westerbom, M., Kilpi, M. and Mustonen, O. (2002). Blue mussels, *Mytilus edulis*, at the edge of the range: population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea. *Marine Biology* **140**(5): 991-999.

Wilson, B. R. and Allen, G. R. (1987). Major Components and Distribution of Marine Fauna. Fauna of Australia. General Articles, Vol. 1 Part A. G. R. Dyne and D. W. Walton. Canberra, Government Publishing Service: 43-68.

Wisely, B. and Blick, R. A. P. (1964). Seasonal abundance of first stage nauplii in 10 species of barnacles at Sydney. *Australian Journal of Marine and Freshwater Research* **15**: 162-171.

Wulff, E. V. (1950). An Introduction to Plant Geography. Waltham, MA, Chronica Botanica Company.

Zacherl, D., Gaines, S. D. and Lonhart, S. I. (2003). The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). *Journal of Biogeography* **30**: 913-924.

Zaidan, F. I., Krevder, D. L. and Beaupre, S. J. (2003). Testosterone cycles and reproductive energetics: Implications for the northern range limits of the cottonmouth (*Agkistrodon piscivorus leucostema*). *Copeia* **2003**: 231-240.