January 2010

Patterns of demography for rocky-shore, intertidal invertebrates approaching their geographical range limits: tests of the abundant-centre hypothesis in south-eastern Australia

Eszter Z. Hidas
ezh998@uow.edu.au

David J. Ayre
University of Wollongong, david_ayre@uow.edu.au

Todd E. Minchinton
University of Wollongong, tminch@uow.edu.au

Patterns of demography for rocky-shore, intertidal invertebrates approaching their geographical range limits: tests of the abundant-centre hypothesis in south-eastern Australia

Abstract

The abundant-centre hypothesis predicts that species' abundances peak at the centre of their geographical ranges and decline gradually towards their range limits. We tested predictions of this hypothesis for three rocky-shore, intertidal invertebrates with planktonic larvae (the whelk, Morula marginalba, the snail, Afrolittorina pyramidalis, and the barnacle, Tesseropora rosea) by quantifying their patterns of abundance and size, and inferring pulses of recruitment from size-frequency distributions, at multiple spatial scales spanning a 600-km region in south-eastern Australia and encompassing roughly the southern third of their geographical ranges. At the regional scale, abundances for all species were, as predicted, dramatically lower at their range limits. This decline was not gradual, however, because there were large variations in abundance at smaller spatial scales, and abrupt declines at the south-eastern corner of Australia. Size did not change towards the range limit for any species, but size-frequency distributions suggested a decline in the frequency of recruitment events at the range limit for T. rosea. We conclude that the abundant-centre hypothesis is not an appropriate model for abundance distributions of benthic marine invertebrates with planktonic larvae, because of the vagaries of dispersal and recruitment interacting with complex current patterns along non-uniform coastlines.

Keywords

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

Publication Details

Patterns of demography for rocky-shore, intertidal invertebrates approaching their geographical range limits: tests of the abundant-centre hypothesis in south-eastern Australia

Eszter Z. Hidas[A], *David J. Ayre*[A] *and Todd E. Minchinton*[A,B]

[A]Institute for Conservation Biology & School of Biological Sciences,
 University of Wollongong, NSW 2522, Australia.
[B]Corresponding author. Email: tminch@uow.edu.au

Abstract.   The abundant-centre hypothesis predicts that species' abundances peak at the centre of their geographical ranges and decline gradually towards their range limits. We tested predictions of this hypothesis for three rocky-shore, intertidal invertebrates with planktonic larvae (the whelk, *Morula marginalba*, the snail, *Afrolittorina pyramidalis*, and the barnacle, *Tesseropora rosea*) by quantifying their patterns of abundance and size, and inferring pulses of recruitment from size-frequency distributions, at multiple spatial scales spanning a 600-km region in south-eastern Australia and encompassing roughly the southern third of their geographical ranges. At the regional scale, abundances for all species were, as predicted, dramatically lower at their range limits. This decline was not gradual, however, because there were large variations in abundance at smaller spatial scales, and abrupt declines at the south-eastern corner of Australia. Size did not change towards the range limit for any species, but size-frequency distributions suggested a decline in the frequency of recruitment events at the range limit for *T. rosea*. We conclude that the abundant-centre hypothesis is not an appropriate model for abundance distributions of benthic marine invertebrates with planktonic larvae, because of the vagaries of dispersal and recruitment interacting with complex current patterns along non-uniform coastlines.

Additional keywords: abundant-centre hypothesis, biogeography, dispersal, distribution, planktonic larvae, recruitment, size-frequency.

Introduction

A long-standing hypothesis in ecology predicts that the abundance of a species is typically greatest at the centre of its geographical range and declines towards the edges, forming an abundant-centre distribution (Grinnell 1917; Andrewartha and Birch 1954; Brown *et al.* 1995). This type of distribution has been attributed to 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). Although a few terrestrial species have been shown to conform to the abundant-centre distribution (e.g. Brown 1984; Caughley *et al.* 1988; review in Gaston 2003), recent empirical investigations in marine habitats have found little support for this hypothesis (Sagarin and Gaines 2002*a*, 2002*b*; Gilman 2005; 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 a species range is determined by a combination of the supply of larvae originating from local and distant populations and local mortality rates (Caley *et al.* 1996; Eckert 2003). Because of the typically unidirectional flow of major 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), especially for species that have larvae with long planktonic duration (Shanks *et al.* 2003). Dispersal may therefore play the largest role in determining the patterns of abundance of benthic marine species, and may not lead to abundant-centre distributions. Tests of this prediction at appropriately large spatial scales are, however, limited to a few studies in the northern hemisphere. On the western coast of the USA, only 2 of 13 intertidal marine invertebrates had abundant-centre distributions, whereas others either showed no obvious patterns or had a skewed distribution in abundance from north to south (Sagarin and Gaines 2002*b*; Gilman 2005). These studies concluded that the underlying assumptions of the abundant-centre hypothesis may conflict with specific characteristics of the life histories and patterns of environmental variation across the
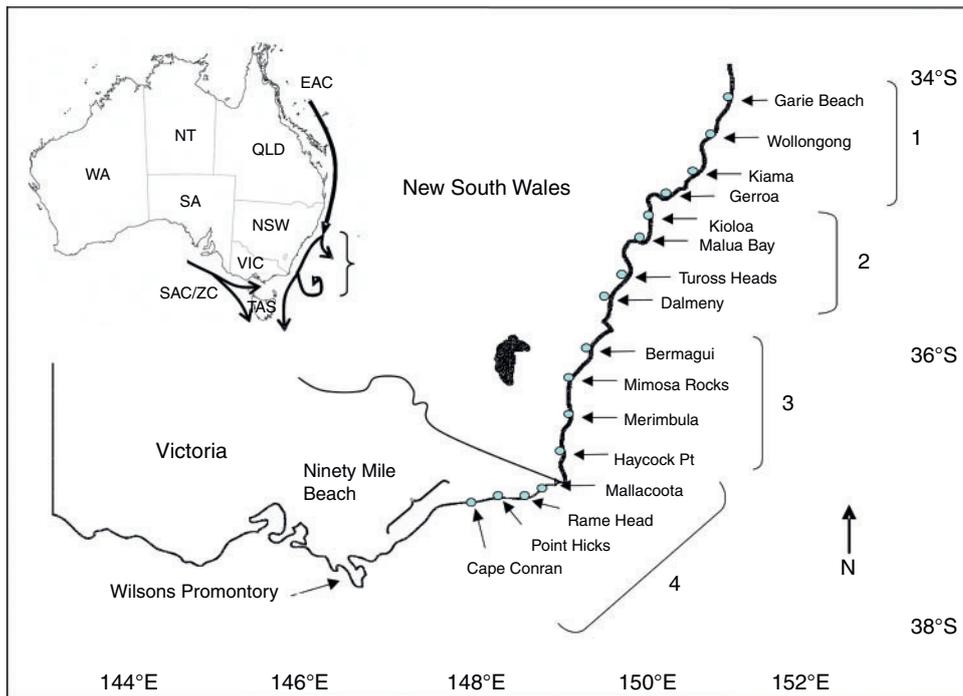
Fig. 1. Map of the south-eastern coast of Australia, showing the four sectors and corresponding 16 locations used to assess the densities and sizes of three rocky-shore, intertidal marine invertebrate species from Garie Beach, New South Wales (Sector 1), to their southern range limits at Cape Conran, Victoria (Sector 4). Ninety Mile Beach is a 150-km stretch of continuous sandy beach, followed southward to Wilsons Promontory by mangrove forests, together forming a 300-km gap in suitable habitat for rocky-shore, intertidal species. Flow patterns of the East Australian Current (EAC) and South Australian and Zeehan Currents (SAC/ZC) are also shown.

ranges of marine species (Gilman 2005), and that future studies should combine sampling geographical distributions of abundance with demographic and physical data (Sagarin and Gaines 2002*b*).

Recruitment can be a key determinant of adult distribution and abundance for benthic marine species (Gaines and Roughgarden 1985; Minchinton and Scheibling 1991). Therefore, quantifying the large-scale patterns of recruitment towards the range limits for benthic marine invertebrates may give insight into patterns of adult abundance. Measuring the size-frequency distributions of already established populations has proven a useful method of assessing changes in patterns of recruitment (e.g. Zacherl *et al.* 2003; Gilman 2005; Lima *et al.* 2006). 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 as a result of unfavourable environmental conditions in the benthic habitat. Additionally, a decrease in size at range edges may reflect a decline in individual performance (Gaston 2003; Gilman 2005).

Marine species along the eastern coast of Australia are subjected to the southward-flowing, warm temperate East Australian Current (EAC) (Fig. 1), which may have the potential to influence their patterns of dispersal and abundance. The EAC flows dominantly southwards from the Coral Sea to the north of Sydney. Here, a large proportion of it deflects eastwards or recirculates (Ridgway and Godfrey 1997), whereas about a third

continues southwards to the Tasman Sea, as a weaker, less reliable current (Tilburg *et al.* 2001). This most southerly flow is twice as strong in the austral summer than in winter, reflecting seasonal changes in the intensity of anti-cyclonic eddies formed along its path (Ridgway and Godfrey 1997). The transport of larvae of benthic marine species may, therefore, be increasingly less reliable from Sydney towards the south (Murray-Jones and Ayre 1997; Sherman *et al.* 2008).

Here, we test predictions of the abundant-centre hypothesis for three rocky-shore, intertidal invertebrate species with planktonic larvae (*M. marginalba*, *A. pyramidalis* and *T. rosea*) and southern range limits on the south-eastern coast of Australia (Edgar 1997; Hidas *et al.* 2007). Specifically, we use surveys of abundance and size structure across 600 km of the coast, encompassing roughly the southern third of the geographical ranges of these highly dispersive species, to test predictions that recruitment occurs less frequently and abundance and mean size decline gradually as these species approach their southern range limits. A decline in abundance and episodic recruitment events towards species' range limits may reflect the decreased influence of the EAC as a source of immigrants into southern populations, whereas a decline in mean size may reflect the five-degree change in sea surface temperature that occurs across this geographical range (Knox 1963; Ridgway and Dunn 2003). Nevertheless, natural variations in habitat availability (Hidas *et al.* 2007), together with the seasonal and inter-annual variability of the EAC (Ridgway and Godfrey 1997),

may contribute to very different patterns of recruitment, size and adult distributions.

Materials and methods

Study region and species

We measured the abundances and sizes of three common and abundant rocky-shore, intertidal invertebrates that have planktonic larval stages, namely *M. marginalba*, *A. pyramidalis* and *T. rosea*. Sampling was carried out at 16 locations along 600 km of coastline from Garie Beach in New South Wales (NSW) (34°10′S, 151°04′E) to Cape Conran in Victoria (37°08′S, 148°07′E) in south-eastern Australia (Fig. 1).

Morula marginalba ranges from northern Queensland to Rame Head in eastern Victoria (Edgar 1997; Fig. 1), although six individuals have recently been observed 80 km further south-west at Cape Conran (C. Perrin, pers. comm.). *A. pyramidalis* and *T. rosea* are also distributed from Queensland to Cape Conran (Edgar 1997; Fig. 1), although there have also been occasional sightings of *T. rosea* west of Wilsons Promontory in Victoria (T. Minchinton, pers. obs.), as well as in Western Australia (Jones 1990). Therefore, sampling encompassed roughly the southern third of the geographical ranges for these species.

Morula marginalba, *T. rosea* and *A. pyramidalis* inhabit microhabitats ranging from crevices and rockpools to emergent rock, live at different heights on the shore, and feed on an array of different organisms, from barnacles and molluscs to microalgae and plankton (Denley 1981; Moran *et al.* 1984; Caffey 1985; Moran 1985; Fairweather 1988; Chapman and Underwood 1994). Although the mode of larval release varies among these species, all have a planktonic larval stage at some phase in their development (Wisely and Blick 1964; Underwood 1974; Caffey 1985). The main breeding periods for all three species are similar (Wisely and Blick 1964; Underwood 1974; Caffey 1985), from austral mid-summer to late autumn; therefore, southward transport of their larvae is likely to be strongly influenced by the EAC (Ridgway and Godfrey 1997). Larval duration of *A. pyramidalis* is unknown, whereas the larvae of *M. marginalba* and *T. rosea* are believed to spend up to several weeks in the water column (Caffey 1985; P. Fairweather, pers. comm.). Therefore, to capture temporal variability in recruitment for these species, we sampled on three occasions separated by 4 months, namely May 2005, September 2005 and January 2006.

Sampling design

We used a hierarchical sampling design to assess differences in patterns of abundance and size of the three study species at multiple spatial scales. We divided the 600-km study region, corresponding to the southern third of the distributional range of the species, into four sectors of roughly equal lengths of coastline, with each spanning 70–110 km (Fig. 1). Four representative locations were selected within each sector (each covering 100–140 m of coast) and three replicate sites were selected at each location (each covering 30 m of coast) (Fig. 1). Sectors were separated by 30–100 km, locations by 10–50 km, and sites by up to 50 m. This allowed an assessment across the study region of the changes in patterns of abundance and size among locations within sectors (tens of kilometres) and among sectors (hundreds of kilometres).

Locations were chosen that displayed similar physical characteristics. Wherever possible, they were on moderately exposed headlands, facing the open ocean and, except at two locations, a platform slope of <10 degrees. Rock type could not be controlled because this varied naturally between siltstone, sandstone, mudstone, granite and basalt, with the majority being sandstone/siltstone. Sites were ∼30 m alongshore and of variable intertidal extent (6–50 m), depending on the slope of the platform.

Sampling methods

Abundances for each species at each site were assessed by estimating density with haphazardly placed quadrats on the shore. All microhabitats (i.e. rockpools, crevices and emergent rock) had the opportunity to be sampled, depending on their availability at that site. At each site, we sampled 10 quadrats of $2 \, m \times 2 \, m$ for *M. marginalba*, 20 quadrats of $0.5 \, m \times 0.5 \, m$ for *A. pyramidalis* and 20 quadrats of $0.15 \, m \times 0.15 \, m$ for *T. rosea*. The means of these replicate quadrats gave one estimate of density for each species at each site, and sites were used as replicates in statistical analyses.

Size-frequency distributions for each species at each location were obtained by measuring to the nearest 0.5 mm with Vernier calipers a haphazard sample of 300–500 individuals across two sites (i.e. 150–200 individuals per site). Bias towards any size class relating to the position on shore or microhabitat was avoided by measuring individuals across the entire vertical and horizontal extent of the species within a site. For *A. pyramidalis*, 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 was measured (Denley 1981; Moran *et al.* 1984).

Data and statistical analyses

To test for significant differences in densities among sectors (fixed factor) and among locations nested within sectors (random factor) for each of the study species, we used mixed model, nested analyses of variance (ANOVA) with the statistical package SPSS 12 (SPSS, Chicago, IL, USA). Density for each species at a site was estimated as the mean of the densities from each of the three sampling times (with density at each sampling time estimated as the mean of the replicate quadrats at that site). Occasionally, some locations could not be sampled because of adverse weather conditions, and data for any sites that had fewer than two sampling times were omitted. Densities were log-transformed before analysis to satisfy the assumptions of ANOVA. For this mixed model ANOVA, a standard F-ratio was 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).

To test for changes in the mean size as the species approached their range limits, we performed linear regression analyses on

untransformed data using the SYSTAT 10 (Systat Software, Chicago, IL, USA) statistical package. For *M. marginalba* and *A. pyramidalis*, we plotted the weighted mean size from the three sampling times against distance (measured along the coastline) from the range limit, whereas for *T. rosea*, we analysed these patterns of the weighted mean size for juvenile recruits (<3-mm aperture length) and adults (≥3-mm aperture length) separately (Denley 1981).

To look for evidence of pulses of recruits, indicated by the presence of small individuals, size-frequency distributions from the three sampling times were combined (following examination at each sampling time to ensure that size structures were similar). For the two gastropod species, each location appeared to have a unimodal distribution and it was impossible to distinguish among cohorts (see Results); therefore, no further analysis was performed. For *T. rosea*, however, cohort analysis was carried out by 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. To test for a significant change in the frequency of recruitment towards the range limit of *T. rosea*, we then plotted the number of cohorts at each location against distance from the range limit and carried out a linear regression analysis on untransformed data using SYSTAT 10.

Results

Patterns of abundance

The abundance of *M. marginalba*, *A. pyramidalis* and *T. rosea* varied substantially across the study region along the south-eastern coast of Australia. Densities for all three species were dramatically and significantly smaller within Sector 4, at the southern range limit, than in Sectors 1–3, closer to the middle of the species' ranges (Fig. 2; Table 1). Mean densities were 8–100-fold greater in Sectors 1–3, ranging from 24.3 to 41.9 individuals per quadrat for *M. marginalba*, from 6.3 to 18.1 individuals per quadrat for *A. pyramidalis*, and from 74.6 to 134.4 individuals per quadrat for *T. rosea*, than in Sector 4 of the range limit, where mean densities were only 0.4, 0.6 and 16.4 individuals per quadrat, respectively, for the three species (Fig. 2). *T. rosea* exhibited a gradual pattern of decline in density towards the range limit from Sector 1 to Sector 4; the densities of the two gastropods, *M. marginalba* and *A. pyramidalis*, followed the same general pattern, although abundances were greatest in Sector 2 and there was an abrupt decline in Sector 4 at the range limit.

Densities also varied substantially among locations within sectors for all three species, although differences among locations were statistically significant only for *T. rosea* (Fig. 2; Table 1). For all species, the magnitude of variation in densities among locations within sectors was generally the same across all sectors, reflecting considerable variability among sites (Fig. 2). Indeed, for *T. rosea*, locations only 10 km apart differed in density by up to 180-fold (Fig. 2). Furthermore, at least one location within Sector 1 for each species had a similar mean density to a location in Sector 3, or in the case of *T. rosea*, Sector 4.

Patterns of size and recruitment

The size-frequency distributions of the two gastropods did not show any distinguishable changes in patterns among locations towards the range limit (Fig. 3). Each location appeared to have a unimodal distribution, and it was thus impossible to distinguish among cohorts (Fig. 3). In addition, at most locations, individuals were not small enough to be categorised as recruits. Mean size decreased slightly towards the range limit for *M. marginalba*, and increased slightly for *A. pyramidalis*; however, was not significantly related to distance from the range limit for either species (*M. marginalba*: $r^2 = 0.03$, $P = 0.55$, $n = 16$; *A. pyramidalis*: $r^2 = 0.09$, $P = 0.29$, $n = 16$).

The size-frequency distribution of *T. rosea* showed some evidence for fewer very small and very large individuals at locations near its range limit (Fig. 3). There was, however, no significant relationship between the mean size (for all individuals) and distance from the range limit ($r^2 = 0.11$, $P = 0.26$, $n = 16$). When the mean sizes of recruits (<3 mm) and adults (≥3 mm) were plotted separately against the distance from the range limit, there was a significant increase towards the range limit for the mean size of recruits ($r^2 = 0.49$, $P = 0.01$, $n = 16$) and a decrease for the mean size of adults, although this relationship was not significant ($r^2 = 0.25$, $P = 0.07$, $n = 16$). Cohort analysis revealed that the number of age classes of *T. rosea* at each location decreased significantly towards the range limit ($r^2 = 0.37$, $P = 0.02$, $n = 16$), with three or four cohorts identified at locations in the northern sectors, but only two or three predominant cohorts at locations in the most southerly sector at the range limit for this species (Fig. 3).

Discussion

Surprisingly, large-scale patterns of abundance among sectors for the intertidal, rocky-shore barnacle, *Tesseropora rosea*, provided evidence for an abundant-centre distribution in the southern third of its geographical range along the south-eastern coast of Australia. Although the abundances of the two intertidal, rocky-shore gastropods, *Morula marginalba* and *Afrolittorina pyramidalis*, also declined dramatically at their range limits, there was no evidence of a gradual decline in abundance towards the range limit, as would be expected for an abundant-centre distribution (Brown 1984; Sagarin and Gaines 2002a). Furthermore, for all three species, smaller-scale patterns of abundance among locations did not appear to be a simple function of position within the range, because, in some cases, there were large variations in abundance among locations only tens of kilometres apart. Therefore, the processes determining the abundances of these species are likely to vary considerably towards, and sharply at, their southern range limit. Moreover, the predictability of the abundances of each species varied with scale at which the abundance was assessed. Sagarin and Gaines (2002b) and Gilman (2005) found similarly large variations in the large- and small-scale patterns of abundance along the geographical ranges of 13 rocky-shore, intertidal marine invertebrates on the western coast of the USA.

The south-eastern coast of Australia has both a spatially and temporally variable marine environment, which may influence the abundance patterns of our study species. Most importantly, the EAC deflects eastwards just north of Sydney, and only
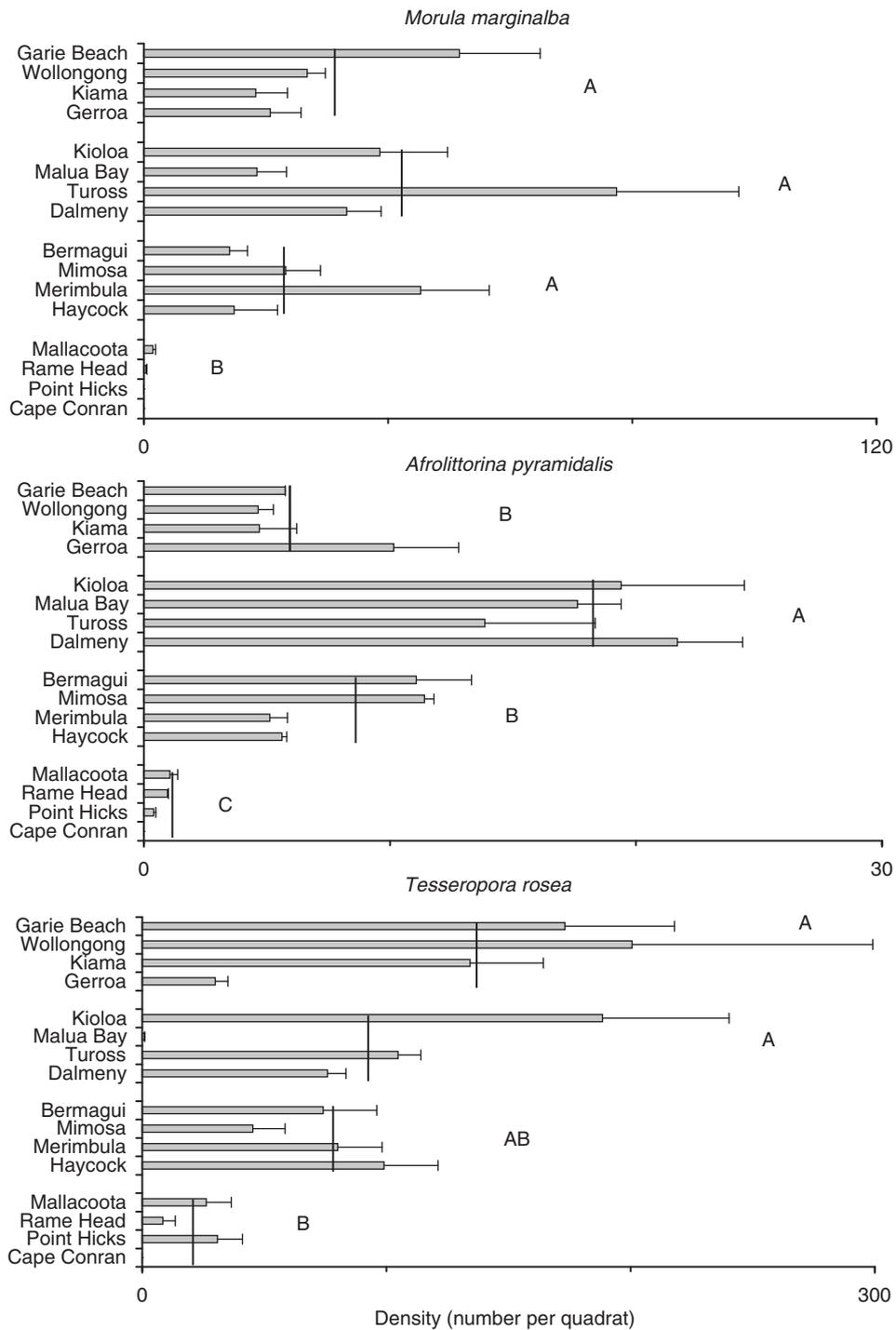
Fig. 2. Mean (+s.e.) densities of the three rocky-shore, intertidal marine invertebrate species, *Morula margin-alba*, *Afrolittorina pyramidalis* and *Tesseropora rosea*, at 16 locations from Garie Beach, New South Wales, to their southern range limits at Cape Conran, Victoria, on the south-eastern coast of Australia (see Fig. 1) between May 2005 and January 2006. Thick vertical lines indicate mean densities per sector for each species. For each panel, letters above bars indicate significant differences (according to Tukey's *post hoc* tests) in densities among sectors for that species. Note the different scales on *x*-axes.

Table 1. Mixed model, nested analyses of variance of the densities of three rocky-shore, intertidal marine invertebrates, *Morula marginalba*, *Afrolittorina pyramidalis* and *Tesseropora rosea*, on the south-eastern coast of Australia
The significance of the nested random factor is indicated (Wald Z test)

Species	Parameter	d.f.	SS	F	Wald Z	P
M. marginalba	Sector	3	15.225	12.38		0.001
	Location (sector)	10	6.462		1.33	0.183
	Residual	28				
A. pyramidalis	Sector	3	13.329	40.34		0.000
	Location (sector)	12	2.526		1.57	0.116
	Residual	32				
T. rosea	Sector	3	2.716	5.28		0.017
	Location (sector)	11	30.046		2.20	0.028
	Residual	30				

a fraction of it continues southwards as a weaker current, forming powerful anti-cyclonic eddies along its path (Ridgway and Godfrey 1997), which have a strong potential to influence the shoreline abundance of adults and distribution of species with planktonic larvae (Gaylord and Gaines 2000). Although the size-frequency distribution patterns of *M. marginalba* and *A. pyramidalis* did not reveal any significant changes in recruitment from north to south, the peaks in the abundances for these species in Sector 2 of our study region, on the mid-southern coast of NSW, coincide with the location of offshore eddies, which are likely to have the potential in some seasons and years to recirculate larvae of these species back to their shores of origin. The size-frequency patterns of the barnacle *T. rosea*, however, gave evidence of more successful recent recruitment events at northern locations approaching the middle of the species range. As predicted, recruitment events for this species may thus be less frequent, or survival of recruits may be decreased, towards the south, possibly due to the decreased reliability of the EAC for dispersal from north to south (Murray-Jones and Ayre 1997; Sherman *et al.* 2008). This hypothesis would be consistent with the results of Caffey (1985), who examined recruitment of *T. rosea* in the middle of its geographical distribution, and found more frequent recruitment events at more northern locations along the NSW coast than in the south.

A recent survey of mitochondrial DNA-sequence variation in samples of *T. rosea* and *M. marginalba* collected from sites arrayed along the coast from Bermagui in the north to Cape Conran in the south revealed minimal divergence ($\theta = 0$), suggesting that there is a high degree of genetic connectivity among populations of these species along this coast (Ayre *et al.* 2009). Given the predominantly southward flow of the EAC, this implies that populations at the range limits for these species are likely to comprise recruits from upstream 'source' populations (*sensu* Pulliam 1988). This supply of recruits, however, may not always be reliable, given the high variability in the flow of the EAC among years, and among seasons (Ridgway and Godfrey 1997). Indeed, this was reflected by the decline in the number of cohorts on shores near the range limit of *T. rosea*. The size-frequency distribution patterns of *M. marginalba* and *A. pyramidalis*, however, suggested that our sampling did not include a period of recruitment anywhere within the range of

sampling, and thus that recruitment is episodic for these species. Such patterns suggest that edge populations are likely to be limited by successful recruitment because they are more likely to miss pulses of recruitment than are those at the centre. Assessing abundance and size-frequency patterns of our study species through different seasons over multiple years would help confirm this.

Range boundaries of coastal marine species can occur at regions where there are marked changes in near-shore current and oceanographic conditions (Gaylord and Gaines 2000; Wares *et al.* 2001). South of the NSW and Victoria border (Fig. 1), warm temperate waters transported by the EAC from the north meet cool temperate waters derived from western currents (e.g. South Australian and Zeehan Currents) and wind-driven and tidal forcing within Bass Strait (Knox 1963; Ridgway and Godfrey 1997; Ridgway and Condie 2004; Sandery and Kämpf 2007). This region coincides exactly with the range limits, and dramatic decline in abundances, of our three study species, and for *T. rosea*, the disappearance from the shore of very large individuals (Bennett and Pope 1953; Knox 1963; O'Hara and Poore 2000). In addition, coastal geomorphology changes abruptly in this south-eastern corner of the region, with the generally north–south coastline veering to the south-west (Fig. 1), potentially resulting in the offshore transport of larvae. Finally, a five-degree sea-surface temperature difference, which also occurs in this region (Knox 1963; Ridgway and Dunn 2003), may contribute to limiting both the early and long-term survival of individuals of our study species on the shore. This may be particularly true for range-limit populations of *T. rosea* and *M. marginalba*, because their connectivity to populations from Bermagui at more northern locations of the coast (Ayre *et al.* 2009) may potentially render them less able to adapt genetically to 'marginal conditions' at the range edge (Sagarin *et al.* 2006). Assessing post-settlement mortality of recruits and adults from the middle to the limit of the range may be an appropriate future study to investigate this hypothesis.

Finally, changes in habitat availability, such as natural variations in rock type and associated changes in habitat structure, may limit the supply, survival or persistence of recruits of our study species at their range limits (Gaston 2003). The range limit of our three species also corresponds to the northern limit of a biogeographical barrier for rocky-shore,
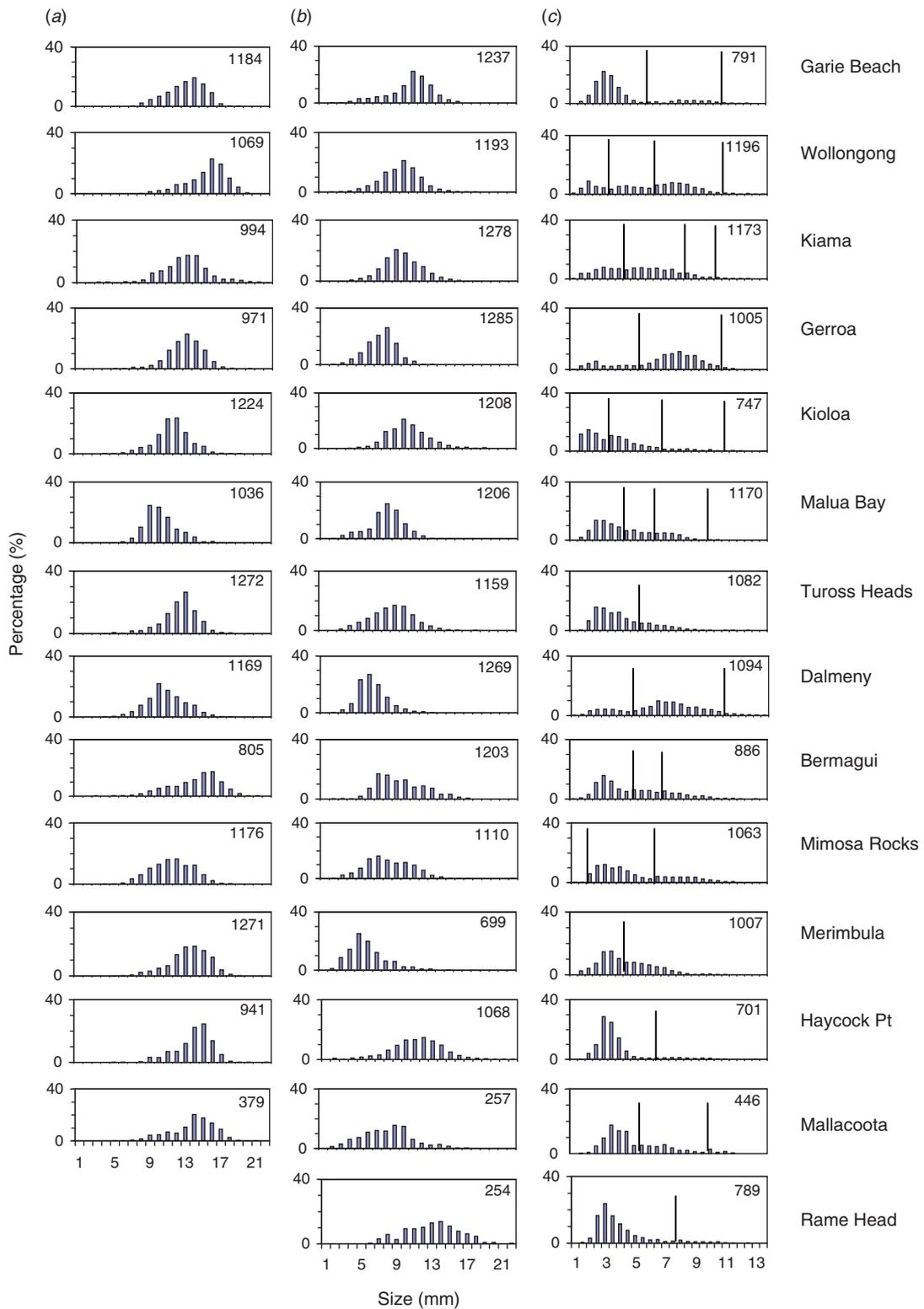
Fig. 3. Size-frequency distributions of the three rocky-shore, intertidal marine invertebrate species, (*a*) *M. marginalba*, (*b*) *A. pyramidalis* and (*c*) *T. rosea*, between May 2005 and January 2006 at 13 locations from Garie Beach, New South Wales, to near their southern range limits at Rame Head, Victoria. Numbers in top right-hand corner show sample sizes. Two range limit locations, Point Hicks and Cape Conran (see Fig. 1), are not included here, because insufficient numbers of individuals were available at these locations. Vertical lines separate cohorts.

intertidal marine species (Hidas *et al.* 2007; Ayre *et al.* 2009), composed of a 300-km stretch of sandy shore (Ninety Mile Beach) and mangrove forest (between Cape Conran and Wilsons Promontory; Fig. 1), separating the nearest natural rocky intertidal habitats. Between the border of NSW and Victoria, and the northern limit of the biogeographical barrier (Mallacoota to Cape Conran, Fig. 1), the generally flat, wide, sandstone rocky platforms of southern NSW are replaced at several locations by steep, granite slopes (E. Hidas, pers. obs.). This change in potential habitat suitability, followed south by the Ninety Mile Beach biogeographical barrier, may reduce the ability of the species to colonise more southern locations. Although all three study species have planktonic larvae that spend up to a few weeks in the water column (Wisely and Blick 1964; Underwood 1974; Caffey 1985), recent genetic investigations into the connectivity of populations of rocky, intertidal marine species across the Ninety Mile Beach biogeographical barrier have revealed that degree of population connectivity across this barrier is not related to the mode of larval dispersal, but rather, to flexibility in habitat utilisation (Ayre *et al.* 2009).

The present study supports the mounting evidence (Sagarin and Gaines 2002*b*; Gilman 2005; Sagarin *et al.* 2006) that the abundant-centre hypothesis is too simplistic a model to predict the abundance distributions of planktonically developing benthic marine invertebrates. Our results indicate that abundances of rocky-shore, intertidal invertebrate species are highly variable and perhaps unpredictable across the range, and that their recruitment can be extremely patchy and episodic. This finding is important when considering the sizes and spacing of coastal marine reserves (Shanks *et al.* 2003) and the impacts of climate change on the current patterns and potential range extensions of intertidal rocky-shore invertebrates (Sagarin *et al.* 1999; Zacherl *et al.* 2003; Lima *et al.* 2006; Pitt *et al.* 2010) along the south-eastern coast of Australia.

Acknowledgements

References

Andrewartha, H. G., and Birch, L. C. (1954). 'The Distribution and Abundance of Animals.' (University of Chicago Press: Chicago, IL.)

Ayre, D. J., Minchinton, T. E., and Perrin, C. (2009). Does life history predict past and current connectivity for rocky intertidal invertebrates across a marine biogeographic barrier? *Molecular Ecology* **18**, 1887–1903. doi:10.1111/J.1365-294X.2009.04127.X

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. doi:10.1071/MF9530105

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *American Naturalist* **124**, 255–279. doi:10.1086/284267

Brown, J. H., Mehlman, D. W., and Stevens, G. C. (1995). Spatial variation in abundance. *Ecology* **76**, 2028–2043. doi:10.2307/1941678

Caffey, H. M. (1985). Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* **55**, 313–332. doi:10.2307/1942580

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., *et al.* (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**, 477–500. doi:10.1146/ANNUREV.ECOLSYS.27.1.477

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. doi:10.2307/5092

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**, 511–529. doi:10.1093/MOLLUS/63.4.511

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**, 145–169. doi:10.1016/0022-0981(94)90111-2

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

Eckert, G. L. (2003). Effects of the planktonic period on marine population fluctuations. *Ecology* **84**, 372–383. doi:10.1890/0012-9658(2003)084[0372:EOTPPO]2.0.CO;2

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

Fairweather, P. G. (1988). Movements of intertidal whelks (*Morula marginalba* and *Thais orbita*) in relation to availability of prey and shelter. *Marine Biology* **100**, 63–68. doi:10.1007/BF00392955

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 Sciences, USA* **82**, 3707–3711. doi:10.1073/PNAS.82.11.3707

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

Gaylord, B., and Gaines, S. D. (2000). Temperature or transport? Range limits in marine species mediated solely by flow. *American Naturalist* **155**, 769–789. doi:10.1086/303357

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**, 1239–1251. doi:10.1890/0012-9658(2002)083[1239:APBMOM]2.0.CO;2

Gilman, S. E. (2005). A test of Brown's principle in the intertidal limpet *Collisella scabra* (Gould, 1846). *Journal of Biogeography* **32**, 1583–1589. doi:10.1111/J.1365-2699.2005.01274.X

Grinnell, J. (1917). Field tests of theories concerning distribution control. *American Naturalist* **51**, 115–128. doi:10.1086/279591

Harding, J. P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. *Journal of the Marine Biological Association of the United Kingdom* **28**, 141–153. doi:10.1017/S0025315400055259

Hidas, E. Z., Costa, T. L., Ayre, D. J., and Minchinton, T. E. (2007). Is the species composition of rocky intertidal invertebrates across a biogeographic barrier in southeast Australia related to their potential for dispersal? *Marine and Freshwater Research* **58**, 835–842.

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**, 665–668.

Kinlan, B. P., and Gaines, S. D. (2003). Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* **84**, 2007–2020. doi:10.1890/01-0622

Knox, G. A. (1963). The biogeography and intertidal ecology of the Australasian coasts. *Oceanography and Marine Biology: An Annual Review* 1, 341–404.

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. doi:10.1111/J.1365-2699.2006.01457.X

Littell, R. C., Milliken, G. A., Stroup, W. W., and Wolfinger, R. D. (1996). 'SAS System for Mixed Models.' (SAS Institute Inc.: Cary, NC.)

Minchinton, T. E., and Scheibling, R. E. (1991). The influence of larval supply and settlement on the population structure of barnacles. *Ecology* 72, 1867–1879. doi:10.2307/1940984

Moran, M. J. (1985). Distribution and dispersion of the predatory intertidal gastropod *Morula marginalba*. *Marine Ecology Progress Series* 22, 41–52. doi:10.3354/MEPS022041

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. doi:10.1016/0022-0981(84)90020-0

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, 83–89. doi:10.1007/S002270050071

O'Hara, T. D., and Poore, G. C. B. (2000). Patterns of distribution of marine echinoderms and decapods. *Journal of Biogeography* 27, 1321–1335. doi:10.1046/J.1365-2699.2000.00499.X

Pitt, N. R., Poloczanska, E. S., and Hobday, A. J. (2010). Climate-driven range changes in Tasmanian intertidal fauna. *Marine and Freshwater Research* 61, 963–970.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist* 132, 652–661. doi:10.1086/284880

Ridgway, K. R., and Condie, S. A. (2004). The 550-km-long boundary flow off western and southern Australia. *Journal of Geophysical Research* 109, C04017. doi:10.1029/2003JC001921

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. doi:10.1016/S0079-6611(03)00004-1

Ridgway, K. R., and Godfrey, J. S. (1997). Seasonal cycle of the East Australian Current. *Journal of Geophysical Research* 102, 22 921–22 936. doi:10.1029/97JC00227

Sagarin, R. D., and Gaines, S. D. (2002*a*). The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters* 5, 137–147. doi:10.1046/J.1461-0248.2002.00297.X

Sagarin, R. D., and Gaines, S. D. (2002*b*). Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography* 29, 985–997. doi:10.1046/J.1365-2699.2002.00705.X

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., 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, 524–530. doi:10.1016/J.TREE.2006.06.008

Sandery, P. A., and Kämpf, J. (2007). Transport timescales for identifying seasonal variation in Bass Strait, south-eastern Australia. *Estuarine, Coastal and Shelf Science* 74, 684–696. doi:10.1016/J.ECSS.2007.05.011

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.

Shanks, A. L., Grantham, B. A., and Carr, M. H. (2003). Propagule dispersal and the size and spacing of marine reserves. *Ecological Applications* 13, 159–169. doi:10.1890/1051-0761(2003)013[0159:PDDATS]2.0.CO;2

Shelford, V. E. (1911). Physiological animal geography. *Journal of Morphology* 22, 551–618. doi:10.1002/JMOR.1050220303

Sherman, C. D. H., Hunt, A., and Ayre, D. J. (2008). Is life history a barrier to dispersal? Contrasting patterns of genetic differentiation along an oceanographically complex coast. *Biological Journal of the Linnean Society. Linnean Society of London* 95, 106–116. doi:10.1111/J.1095-8312.2008.01044.X

Tilburg, C. E., Hurlburt, H. E., O'Brien, J. J., and Shriver, J. F. (2001). The dynamics of the East Australian Current System: The Tasman Front, the East Auckland Current, and the East Cape Current. *Journal of Physical Oceanography* 31, 2917–2943. doi:10.1175/1520-0485(2001)031<2917:TDOTEA>2.0.CO;2

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. doi:10.1071/MF9740063

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, 295–306.

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. doi:10.1071/MF9640162

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 kelleti* (Forbes, 1852). *Journal of Biogeography* 30, 913–924. doi:10.1046/J.1365-2699.2003.00899.X