Supply-side biogeography: geographic patterns of settlement and early mortality for a barnacle approaching its range limit

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ABSTRACT: Species range limits are often associated with reduced adult densities, and this may reflect the failure of a particular life-history stage. For benthic marine invertebrates, settlement is a time of great mortality that strongly influences adult population structure, at least at local spatial scales. In south-eastern Australia we determined that adult abundance of the intertidal barnacle *Tesseropora rosea* declines over a 450 km region of rocky shore from the middle to the southern limit of its range, and we tested the hypothesis that this biogeographic pattern reflects variations in the production, settlement, or early post-settlement mortality of larvae or adult mortality. Sampling at 2 sites on 11 rocky shores in this region over 2 yr revealed that none of the life-history stages or demographic processes displayed a latitudinal gradient or a clear decline towards the south, and settlement and adult mortality were highly variable among locations. Indeed local variation in early life-history processes and adult mortality appears to dictate regional variability and observed latitudinal patterns of adult abundance of *T. rosea*, but longer term studies spanning at least a decade may determine if storage from one strong year in recruitment can set patterns of adult abundance.

KEY WORDS: Abundant-centre hypothesis · Early post-settlement mortality · *Tesseropora rosea* · Adult mortality · Geographic distribution · Latitudinal gradient

INTRODUCTION

Biogeographic theory predicts that the abundance of a species is generally greatest at the centre of its range and least at its edges (Brown 1984, Caughley et al. 1988, Sagarin & Gaines 2002a,b). This 'abundant-centre hypothesis' has been supported for many species of terrestrial plants, with adult abundance declining towards their geographic range limits because physiological stress reduces reproductive output and survival (Pigott & Huntley 1981, Parsons 1991, Woodward 1997, Dorken & Eckert 2001, Jump & Woodward 2003, Mathews & Bonser 2005). As for terrestrial plants, many benthic marine invertebrates have sessile adults and dispersive propagules and, consequently, their geographic patterns of abundance might be expected to conform to abundant-centre distributions as a result of decreased larval supply and increased

early post-settlement mortality of larvae from the centres to the edges of their range (Zacherl et al. 2003, Bahn et al. 2006, Gilman 2006a,b, Sanford et al. 2006). Dispersal in the ocean and recruitment variability into the benthic habitat is potentially much greater for benthic invertebrates than for most plants. However, the relatively few studies to date indicate that geographic patterns of adult abundance for benthic marine invertebrates generally do not reflect abundant-centre distributions (Sagarin & Gaines 2002a).

For many benthic marine invertebrates with sessile adults and dispersive larvae, recruitment is a key demographic process structuring adult populations (Connell 1985, Gaines & Roughgarden 1985, Minchinton & Scheibling 1991, Caley et al. 1996, Hunt & Scheibling 1997). Recruitment integrates the arrival, settlement and early post-settlement mortality of larvae (Thorson 1950, Keough & Downes 1982) and,

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although these supply-side processes are often highly variable in space and time (see Underwood & Fairweather 1989, Caley et al. 1996, Hunt & Scheibling 1997), they sometimes reflect latitudinal gradients of temperature, currents, wave exposure and nutrient availability in the ocean (Connolly & Roughgarden 1998, Connolly et al. 2001, Zacherl et al. 2003, Sanford et al. 2006). Consequently, the geographic distribution of benthic marine invertebrates, particularly as a species approaches its range limit, may be strongly influenced by latitudinal gradients in the supply and early life history of larvae. Alternatively, processes operating at more local scales in the post-recruitment environment (e.g. storm events, habitat, microclimates, predation) could override larger scale patterns of recruitment that might determine geographic patterns in adult abundance (Helmuth 1998). Measuring settlement and early post-settlement mortality of benthic marine invertebrates is often difficult, however, because larvae are small and often die soon after settlement. Few studies have measured these early life-history processes simultaneously across large geographic scales (but see Caffey 1985, Connolly et al. 2001, Hughes et al. 2002), but such studies can yield important insights into the processes setting the range limits of species.

Along the linear coastline of south-eastern Australia, there is great potential for the population size of sessile marine invertebrates with planktonically dispersing larvae to decline with increasing latitude. First, the unidirectional East Australian Current (EAC) runs north to south along the east coast of Australia, and then weakens and deflects away from the coast at the south-eastern corner of the mainland (Knox 1963, Huyer et al. 1988, O'Hara & Poore 2000, Oke & Middleton 2001, Roughan & Middleton 2004). Second, seawater and air temperatures decline with the transition from subtropical to temperate regions with increasing latitude. Together, these latitudinal variations in oceanographic conditions and potential physiological stresses in the benthic habitat are predicted to reduce the fecundity of adults, increase the early post-settlement mortality of early juveniles and diminish reliability in the supply of larvae from northern to southern populations (Murray-Jones & Ayre 1997, Hidas et al. 2007). Indeed, due to the absence of small individuals in southern locations, Hidas et al. (in press) suggest recruitment events are less frequent for the intertidal barnacle *Tesseropora rosea* (Krauss) towards its southern range limit.

Here we investigate whether a latitudinal gradient of recruitment drives the adult population structure of the intertidal barnacle *Tesseropora rosea*, a species that disperses via planktonic larvae and, furthermore, shows adult abundances consistent with an abundant-

centre distribution, with declines from the middle to the southern limit of its range at the south-eastern corner of mainland Australia (Hidas et al. in press). The only study to have assessed the large-scale patterns of settlement and early post-settlement mortality for *T. rosea* found no latitudinal trends in recruitment; however, only populations within the middle of its geographic range were examined (Caffey 1985). We measured the fecundity of adults and the settlement and early post-settlement mortality of larvae (i.e. recruitment) for a cohort of *T. rosea* on rocky intertidal shores spanning 450 km of coastline to determine how geographic variation in these demographic processes was related to the patterns of abundance of individuals within the cohort surviving to adulthood at the end of that year. We predicted that a combination of reduced larval production, settlement and increased early post-settlement mortality of larvae from north to south accounts for the latitudinal decline in the abundance of *T. rosea* adults as they approach their southern range limit. We also monitored the recruitment into and mortality of adult populations for 2 yr, to determine how local or geographic variation in these processes might account for the latitudinal gradient in population size.

MATERIALS AND METHODS

Study region and species. We monitored the production, settlement and early post-settlement mortality of larvae and the mortality of adults of the intertidal barnacle *Tesseropora rosea* from February 2007 to December 2008 in mid-shore regions at 2 sites on 11 rocky shores along the south-eastern coast of Australia. Rocky shore locations extended from Garie Beach, south of Sydney, New South Wales (34° 09′ S, 151° 04′ E), in the middle of the geographic range of *T. rosea*, to Mallacoota, Victoria (37° 34′ S, 149° 45′ E), at its southern range limit (Bennett & Pope 1953, Edgar 2008) (Fig. 1). Occasionally, individuals of *T. rosea* are found in central Victoria (Jones 1990), but they do not persist, probably due to colder environmental conditions. The rocky shores were selected to have the same rock type (sandstone), degree of wave exposure (moderate to exposed), slope (gradually sloping platforms) and aspect (facing east to southeast) to ensure abiotic conditions such as substratum, hydrodynamic processes and exposure to sunlight remained equivalent amongst locations. *In situ* data loggers (Onset TidbiT v2 Temp logger), recording air and water temperatures every 10 min, were deployed within the mid-shore region at both Garie Beach and Mallacoota (i.e. the most northern and southern locations, respectively) and confirmed that a temperature gradient exists across the study region, with the maximum (air: 50.8°C; water:
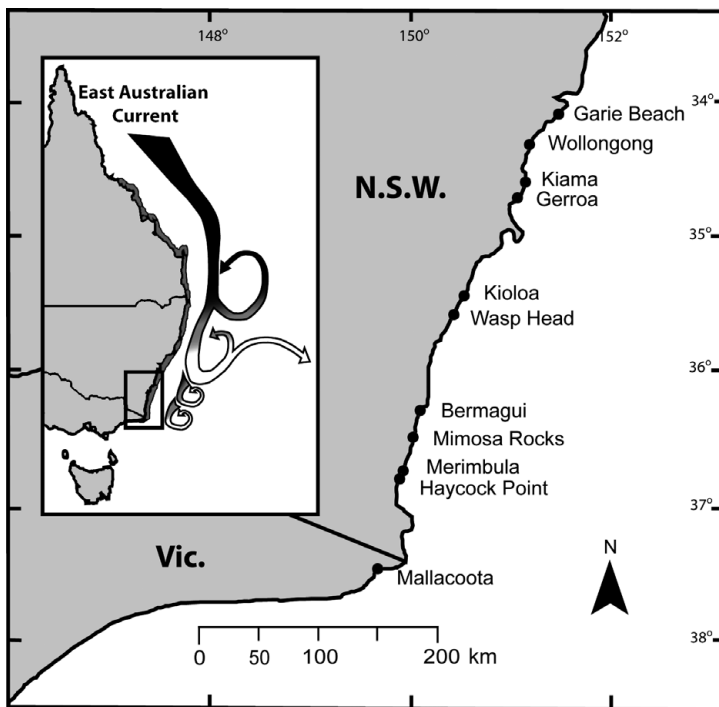
Fig. 1. Coast of south-eastern Australia showing sampling locations separated by 10 to 80 km. Inset shows the geographic range of *Tesseropora rosea* (shaded area) and the Eastern Australian Current, with shading from black to white representing strong to weak influence

26.4°C) and minimum (air: 5°C; water: 14.2°C) temperatures at Garie Beach being greater than the maximum (air: 42.3°C; water: 22.4°C) and minimum (air: 3.8°C; water: 12.3°C) temperatures at Mallacoota recorded continuously between December 2007 and December 2008.

Adult *Tesseropora rosea* are hermaphroditic and brood plantivorous larvae that are released predominantly from January to June, with the larvae estimated to remain within the water column for approximately 13 d (Wisely & Blick 1964, Anderson & Buckle 1983, Egan & Anderson 1988). Although larval settlement may occur throughout the year, the vast majority settle between January and July with 2 peaks, one during January and February and then a second during May and June, with the peak in January to February generally being more prominent at northern locations, and vice versa for more southern locations (Caffey 1985). We found that recently settled *T. rosea* grow quickly and become reproductively mature 2 to 3 mo after settlement, with some individuals with aperture lengths as small as 1.5 mm possessing either gonads or mature or developing embryos (but see Egan & Anderson 1988). Fertilization is internal and larvae are brooded within the mantle cavity until they are ready to be released. Mature embryos are recognised as eyed

nauplii (Embryo Stage V) (Anderson 1969). From our observations embryo development in the mantle cavity is relatively synchronised so that the majority of embryos reach maturity at approximately the same time. We therefore scored individuals as being mature, if eyed nauplii were present in the mantle cavity, or developing, if embryos were present but immature (Stages II to IV) (Anderson 1969; see further details below).

Sampling design and variables. At each rocky shore location, we established 2 sites that extended 30 m alongshore and were separated by 10 to 30 m. At each site, 30 permanent quadrats of 10 × 10 cm were randomly located within the mid-shore region characteristically dominated by *Tesseropora rosea* (0 to 1.6 m above the mean low water mark of neap tides: MLWN). Quadrats were positioned on horizontal to slightly sloping surfaces and separated by 0.5 to 1 m. A stainless steel screw was drilled into the centre of each quadrat to ensure that they could be accurately resampled over time.

We tracked individual barnacles in these 30 quadrats over time using digital photographs taken with a high-resolution digital camera (Fujifilm S9600), and comparisons of *in situ* counts and photographs showed this method to be accurate (Lathlean unpubl. data). We photographed each quadrat monthly (February to July 2007) during the main period of settlement for *Tesseropora rosea* (see Wisely & Blick 1964, Caffey 1985), then approximately quarterly until December 2008 (i.e. August and December 2007; February, May, August and December 2008). Recently settled *T. rosea* (individuals <1 wk old) could not always be distinguished from recently settled individuals of the barnacle *Catomerus polymerus*, but *C. polymerus* recruits (individuals >1 mo old) were rarely observed, and constituted <1% of the total number of barnacle recruits; therefore, any misidentification is unlikely to influence results.

Geographic patterns of demography and population structure. During 2007, settlement, recruitment and adult density at each site were determined in separate quadrats, with 10 of the 30 quadrats randomly assigned to 1 of 3 treatments: 'recleared' quadrats were cleared of all *Tesseropora rosea* at each sampling time and used to estimate settlement, 'cumulative' quadrats were cleared initially and then allowed to accumulate *T. rosea* recruits and were used to estimate recruitment and 'untouched' quadrats were not cleared at any time and were used to estimate adult density (see details below). From these estimates of

abundance, mortality at each life-history stage (early post-settlement mortality, post-recruitment mortality, adult mortality) was calculated (see details below). This approach differed somewhat from that used by Caffey (1985) in that we did not alternatively clear quadrats once every 2 mo. In doing so we were able to estimate the percentage of recruits surviving for >2 mo and assess the likelihood that these recruits reach reproductive maturity and contribute to the size of the adult population.

Settlement at a site was estimated by counting the number of recently settled *Tesseropora rosea*, as well as any empty tests from recent deaths of settlers, in the 10 'recleared' quadrats. To ensure that we counted only recently settled individuals, recleared quadrats were cleared of all organisms at the start of the study in February 2007 and then again after each census. A metal brush was also used to remove any existing layer of biofilm within these recleared quadrats at each census. This may have caused us to potentially underestimate settlement, as settlement increases with the amount and age of biofilm (Qian et al. 2003, Thiyagarajan et al. 2006; but see Olivier et al. 2000), but was necessary to remove any confounding effects of increased amounts of biofilm within southern locations where adult densities were lower. Therefore, because we sampled only once per month, our 'settlers' could be 1 to 30 d old. Undoubtedly, at this sampling frequency we missed some individuals that settled and died before they could be counted, and this could have resulted in an underestimation of the absolute magnitude of settlement and early mortality (see Minchinton & Scheibling 1993). Nevertheless, Caffey (1985) found that for this species this frequency suitably differentiated settlement from recruitment. Settlement at a site was calculated as the sum of the number of *T. rosea* that settled in each of the 10 recleared quadrats for all months between February and December 2007.

Recruitment at a site was estimated in the 10 'cumulative' quadrats. These quadrats were cleared of all organisms once, in February 2007, and then settling barnacles were allowed to accumulate for the entire 2 yr sampling period. Recruitment at a site was calculated by summing the peak, or maximal, number of *Tesseropora rosea* recruits (i.e. individuals >30 d old) recorded within each of the 10 cumulative quadrats at any sampling interval between February and December 2007. Early post-settlement mortality was calculated as the percentage difference between settlement and recruitment. Likewise, post-recruitment mortality was calculated as the percentage difference between recruitment and the number of *T. rosea* remaining within cumulative quadrats in December 2007.

Adult density at a site was calculated as the sum of the number of *Tesseropora rosea* adults (i.e. individuals

with an aperture length of >1.5 mm) within each of the 10 untouched quadrats in December 2007. Maximal adult density at a site was calculated as the sum of the maximal number of *T. rosea* adults recorded within each of the 10 untouched quadrats between February and December 2007. Adult mortality at a site was calculated as the percentage difference between 'maximal' adult density and adult density in December 2007.

Following the methods of Egan & Anderson (1988), the potential for larval production at each location was determined by quantifying the percentage of adults with developing (creamy to bright yellow coloured embryos) or mature, ready-to-spawn (i.e. brown-eyed nauplii) larvae over time (Wisely & Blick 1964, Egan & Anderson 1988). Quantitative assessment of fecundity proved difficult because mantle cavities were often damaged when adults were prised from the substratum for examination. We collected at least 40 adult *Tesseropora rosea* (i.e. individuals with an aperture length of >1.5 mm) once per month during the main breeding season (i.e. February to July 2007), then again in August and December 2007, from areas outside the permanent quadrats and spread across both sites at each location. Adults were preserved, transported to the laboratory and the presence of developing larvae was assessed using a dissecting microscope. The proportion of adults at each location with either mature or developing larvae was calculated for all adults sampled over the entire year.

Changes to population structure. We monitored latitudinal changes in population structure by comparing densities of *Tesseropora rosea* within both the cumulative and untouched quadrats at each site at the beginning of the sampling period in February 2007 and again in both December 2007 and 2008. This allowed us to determine whether recruitment processes (i.e. settlement and post-settlement mortality within cumulative quadrats) would return each population to its former abundance, or whether the adult population abundance initially observed persists through time (i.e. untouched quadrats).

Statistical analysis. We expected substantial variation among quadrats at a site, and, given that our aim here was to determine how demographic and population parameters varied with latitude, we pooled densities of settlers, recruits and adults among recleared, cumulative and untouched quadrats, respectively, to yield 1 estimate of each for each site (i.e. n = 2 sites location^{-1}). Due to extreme weather events and ephemeral algae or sand obscuring quadrats, we were unable to sample all sites in each month. For the months when sites were covered by sand, we assumed new settlers and recruits would have died, and, therefore, we assigned values of zero for such months (and subsequent observations showed that this was gener-

ally the case). For months when sites could not be sampled due to bad weather or were obscured by algae, we excluded such months and sampled as previously described for the following months. This did not occur often, with only 7.8% of the sites not being sampled during the entire 2 yr sampling period. Larval production, settlement, recruitment, early post-settlement mortality, post-recruitment mortality, adult mortality and adult densities were correlated with latitude to test for the presence of latitudinal gradients.

We used 1-way ANOVAs to test for heterogeneity of (1) settlement, (2) recruitment, (3) early post-settlement mortality, (4) early post-recruitment mortality, (5) adult mortality and (6) adult density across the 11 locations. Where significant differences were found, a Student-Neuman-Keuls (SNK) test was used to determine which locations had significantly different settlement, recruitment, early post-settlement mortality, post-recruitment mortality, adult mortality, or adult densities. We confirmed that the data were approximately normally distributed and showed equal variance using the Shapiro-Wilks' and Cochran's test, respectively.

RESULTS

Geographic patterns of demography

The vast majority of adult *Tesseropora rosea* brooded developing and mature embryos at all locations throughout the range, but the proportion of adults with eyed nauplii did not vary across the geographic range or show any significant relationship to latitude (r^2 = 0.052, n = 10, p = 0.501; Fig. 2a).

Settlement at most locations was typically derived from single, large pulses of larvae settling on shore sporadically from late summer to late autumn. Indeed, although not significantly different, densities of settlers varied greatly between sites at a location and by more than an order of magnitude among locations ($F_{10,11}$ = 2.37, p = 0.086), and there was no significant relationship between settlement and latitude (r^2 = 0.013, n = 21, p = 0.613; Fig. 2b).

There was great early post-settlement mortality at all locations, with an average of 79.4% of newly settled *Tesseropora rosea* dying by December 2007 (Fig. 2c), and, as for settlement, no latitudinal decline in early post-settlement mortality was detected (r^2 = 0.005, n = 21, p = 0.752). Densities of recruits varied significantly among locations ($F_{10,11}$ = 3.20, p = 0.035), with an SNK test indicating that the number of recruits at Mimosa Rocks was greater than that at all other locations (Fig. 2d). Interestingly, recruitment of *T. rosea* was largely reflective of settlement, as locations that received large numbers of settlers generally had a
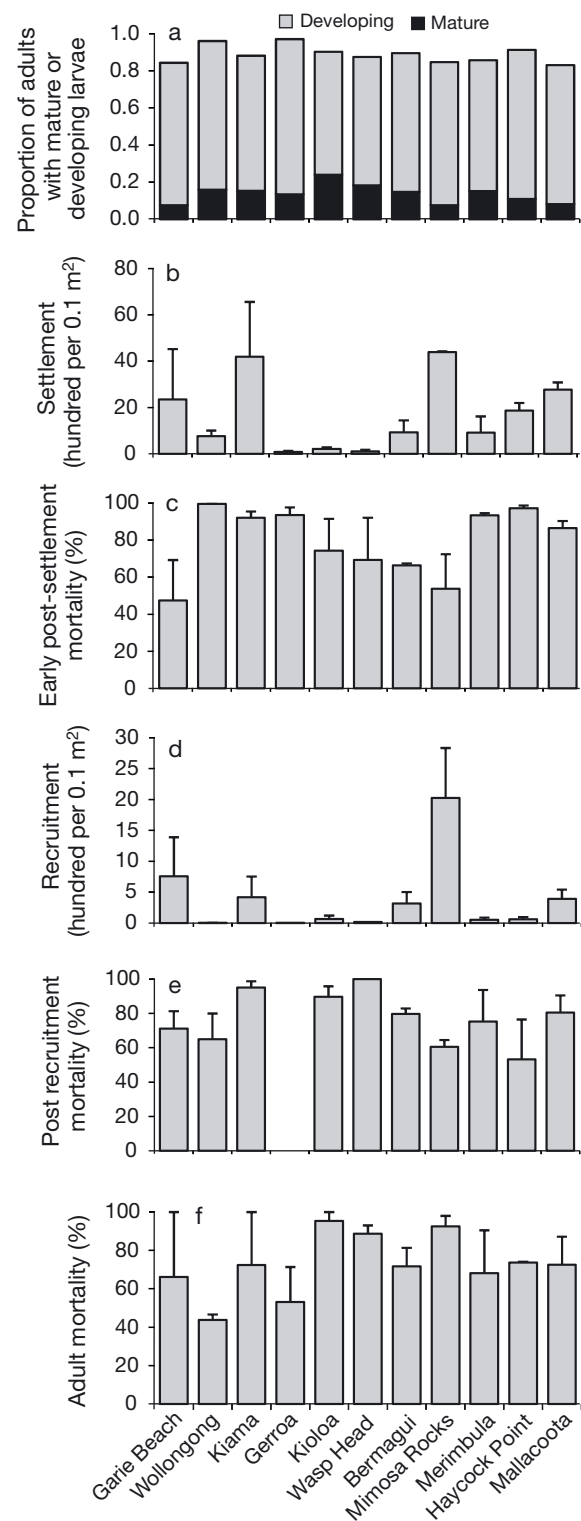

Fig. 2. *Tesseropora rosea.* Latitudinal variation in (a) proportion of adults with either mature or developing larvae, (b) mean settlement, (c) mean percentage mortality of recently settled individuals, (d) mean recruitment, (e) mean post-recruitment mortality and (f) mean percentage adult mortality during 2007. Error bars represent standard errors due to variation between pairs of sites at each location

larger number of recruits. For example, Mimosa Rocks received the greatest number of settlers and subsequently had the greatest number of recruits (Fig. 2b,d). Additionally, though not as great as early post-settlement mortality, post-recruitment mortality was also great and varied significantly among locations ($F_{10,11}$ = 5.86, p = 0.004), with an average of 70% of recruits dying by December 2007, with a SNK test finding substantially lower mortality at Gerroa, Haycock Point and Mimosa Rocks (Fig. 2e).

Adult mortality was substantial at all locations, with on average 72.5% of adult barnacles dying during 2007 (Fig. 2f). Nevertheless, adult mortality was highly variable between sites and not significantly different among locations ($F_{10,11}$ = 0.857, p = 0.953), being greatest at Kioloa (95.3%) and least at Wollongong (43.7%). Similar to larval production, settlement, early post-settlement mortality, recruitment and post-recruitment mortality, no latitudinal gradient was found for adult mortality (r^2 = 0.07, df = 21, p = 0.231).

Changes to population structure

There was a significant linear relationship between the density of adult *Tesseropora rosea* and latitude at the start of sampling in February 2007, with adult abundance in untouched quadrats declining substantially from the middle to the edge of its range (r^2 = 0.36, n = 21, p = 0.003; Fig. 3). But, as a result of the consistently high and variable early post-settlement mortality post-recruitment mortality and adult mortality, by the end of sampling in December 2008 there was no latitudinal gradient in adult abundance within either untouched (r^2 = 0.17, n = 21, p = 0.054) or cumulative quadrats (r^2 = 0.028, n = 21, p = 0.455), suggesting the original latitudinal decline in adult abundance neither persists nor becomes re-established in time (Fig. 3). Indeed, there were no latitudinal patterns for any demographic process examined, with local variability in adult mortality appearing to drive geographic patterns of adult abundance.

DISCUSSION

At the start of the study, populations of the rocky shore barnacle *Tesseropora rosea* displayed abundant-centre patterns of geographic distribution (see also Hidas et al. in press), with an inverse relationship between density and latitude from the middle to the southern limits of its range. Contrary to expectations, however, we detected no latitudinal gradients in the key demographic processes expected to contribute to
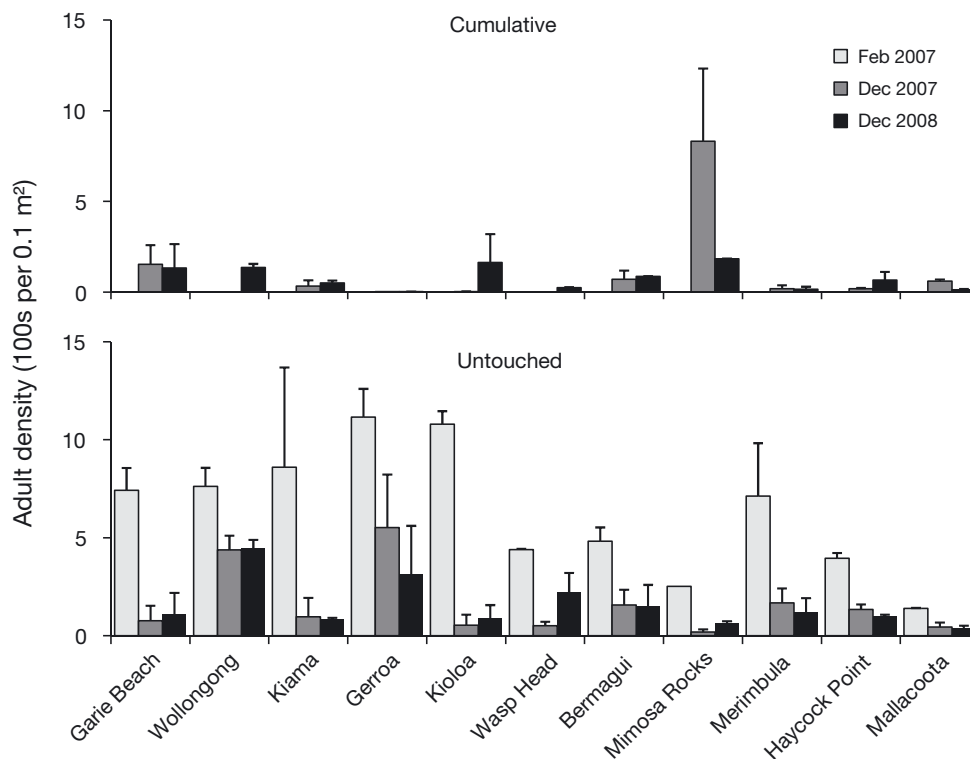

Fig. 3. *Tesseropora rosea*. Latitudinal variation in density for both cumulative and untouched treatments in February and December 2007 and December 2008. Error bars represent standard errors due to variation between pairs of sites at each location

this pattern, including larval production, settlement, early post-settlement mortality, or recruitment. Indeed, it appears that variations in recruitment and adult mortality due to local forces might make the greatest contribution to geographic patterns of abundance and apparent latitudinal trends.

Larval production was relatively uniform among locations, suggesting that the reduction in seawater and air temperatures towards the southern range limit does not limit the ability of *Tesseropora rosea* to produce larvae. This is perhaps surprising because studies have shown that such differences in seawater temperatures can influence the reproductive ability of benthic marine invertebrates (Brey 1995, Vilchis et al. 2005), and field investigations have detected reduced fecundity at range limits due to changes in seawater temperature (Barber & Blake 1983, Amaro et al. 2005). However, Helmuth et al. (2006) assessed body temperatures of the intertidal mussel *Mytilus californianus* across a latitudinal gradient in sea-surface temperatures and found that body temperatures were often hotter or colder than was predicted from sea-surface temperatures. Consequently, the lack of a latitudinal decline in larval production within the present study may reflect complex interactions between air and sea-surface temperatures. Larval production has also been shown to be directly associated with food availability (Leslie et al. 2005). Therefore, more quantitative sampling of larval production could reveal differences among locations that either experience different air or sea temperatures or food concentrations. Similarly, we expected the reduction in seawater temperatures towards the southern range limit of *T. rosea* to reduce larval settlement and increase early mortality (Gaylord & Gaines 2000, Sprung 2001, Zacherl et al. 2003). Instead, settlement was largely sporadic and unpredictable, with locations separated by hundreds of kilometres simultaneously receiving large pulses of newly settled *T. rosea*, while adjacent locations received relatively few settlers. This supports work by Caffey (1985), who found highly variable settlement of *T. rosea* at large spatial scales and no clear latitudinal trend for this species in the central region of its geographic distribution.

The lack of latitudinal trends in the production and settlement of larvae suggests that populations in the middle and edge of the range receive similar levels of larval supply and settlement success (Hughes et al. 2002). This contrasts with expectations that larval supply would be reduced as *Tesseropora rosea* approaches its southern range limit, due to a combination of reduced larval production and increasingly unreliable larval transport by the East Australian Current from north to south. Indeed, there is no evidence indicating that recruitment limitation, either through limited larval supply and settlement or increased early

mortality, influences local populations at the southern range limit of *T. rosea* (but see Hidas et al. in press).

Early post-settlement mortality of *Tesseropora rosea* was found to be consistently high among all locations and was on average 79%, which is considerably higher than the average of 66.5% detected by Caffey (1985). Likewise, the adult mortality among all locations was extremely high for a 1 yr period when compared to similar studies undertaken over shorter sampling periods (Denley & Underwood 1979, Caffey 1985, Jernakoff 1985, Otway & Underwood 1987). For example, Otway & Underwood (1987) found adult mortality of *T. rosea* to vary between only 14 and 18% over 13 mo, while Jernakoff (1985) found adult mortality to vary between 0.5 and 2.5% over a 3 mo period. Numerous factors such as biological and physical disturbances, physiological stress, predation and competition are known to influence the mortality of newly settled benthic marine invertebrates at small spatial scales (for review see Hunt & Scheibling 1997). For *T. rosea* specifically, the major causes of early postsettlement mortality are algal growth, 'bulldozing' by grazing limpets and intraspecific competition (Denley & Underwood 1979, Underwood et al. 1983, Jernakoff 1985), with the predatory whelks *Morula marginalba* and *Dicathais orbita* being the most likely causes of adult mortality (Underwood et al. 1983, Fairweather et al. 1984, Moran 1985). However, whether predation by *M. marginalba* and *D. orbita* continues to influence populations over large spatial scales has yet to be determined. In addition, it is unlikely that interspecific competition between *T. rosea* and *Catomerus polymerus*, another intertidal barnacle more commonly found in the southern parts of Australia, contributed to the high levels of early post-settlement mortality and adult mortality of *T. rosea* documented in the present study as: (1) larval settlement between these 2 species occurs at different times of the year (Wisely & Blick 1964), (2) *C. polymerus* abundance was generally low and (3) free space did not appear to be a limiting factor in southern locations where densities of *C. polymerus* were somewhat greater. However, further research is required to understand what role, if any, competition between *T. rosea* and *C. polymerus* plays in determining the southern range limit of *T. rosea.*

Latitudinal gradients in settlement and recruitment may be attributed to differential coastal upwelling, as increased upwelling reduces larval concentrations within coastal waters and subsequently reduces settlement as more larvae are transported offshore, limiting contact with their preferred substrata (Gaines et al. 1985, Roughgarden et al. 1988, Connolly et al. 2001, Menge et al. 2004). Consequently, the highly variable patterns of settlement detected within the present study could reflect variable upwelling along the south-

eastern coast of Australia (Roughan & Middleton 2004) and geographical variation in topographic features that assist in retaining larvae (Jenkins & Hawkins 2003, Mace & Morgan 2006). However, since many oceanographic studies have revealed only weak up-welling along this coast (Roughan & Middleton 2004), it is unlikely that variable upwelling is the only contributing factor to variable settlement. This highly variable settlement could also suggest that larval physiological condition varies significantly within the study region as recent studies have shown larval condition, which can be determined by variable temperature and food concentrations (Desai & Anil 2004), to strongly influence the settlement (Thiyagarajan et al. 2002, Tremblay et al. 2007) and early post-settlement growth and survival (Thiyagarajan et al. 2005, Emlet & Sadro 2006) of larvae. Therefore, local processes may be equally important as regional processes in setting the patterns of adult abundance and potentially the geographic distribution and southern range limit of *Tesseropora rosea*.

The absence of latitudinal gradients in larval production, settlement, early post-settlement and adult mortality suggest that these life-history processes are not responsible for the latitudinal decline in adult abundance or the southern range limit of *Tesseropora rosea*. However, the exceptionally high mortalities of both recently settled and adult *T. rosea* significantly reduced adult densities such that, by the final census, adult densities no longer declined towards the southern range limit, suggesting an exceptionally large disturbance had occurred, obscuring important relationships. Indeed, the shift from an El Niño to a La Niña pattern during 2007 may have attributed to several atypical oceanographic features, including 4 unusually large consecutive low pressure systems crossing the Tasman Sea in June 2007, causing strong, predominantly southerly swells over the study area, at times in excess of 7 m (Australian Bureau of Meteorology 2007). Increased sand scour caused by such an oceanographic regime would presumably have had a significant impact on large-scale patterns of settlement, early post-settlement and adult mortality of *T. rosea*. Such large southerly swells are seasonally common during winter along the south-eastern coast of Australia (Short & Trenaman 1992). Therefore, *T. rosea* recruits may experience increased mortality during winter each year, with survival favouring earlier settling individuals that managed to reach a specific size. Alternatively, the average life expectancy of adult *T. rosea* is only 4 yr (Caffey 1985), and consequently, the high adult mortality detected in the present study may be reflective of the senescence of a large cohort that gave rise to the initial latitudinal decline in adult abundance simultaneously dying off. However, adult mortality appeared to occur irrespective of size or age, suggesting mortality was high across several cohorts within each location. Regardless, demographic processes operating over 2 yr have greatly influenced the population structure of *T. rosea*, suggesting that infrequent events could potentially have longer lasting impacts than patterns of settlement, early post-settlement and adult mortality combined over numerous years.

Geographic patterns of adult abundance might of course reflect environmental cycles with longer periodicity than most studies, including this one. For example, geographic patterns might develop over time due to changing environmental conditions, such as the prolonged El Niño conditions in south-eastern Australia from 2001 to 2006 (Australian Bureau of Meteorology 2007), influencing demographic processes gradually. Alternatively, observed patterns of decreasing adult abundances with latitude might reflect 'stored' patterns determined by a year of great recruitment combined with different environmental conditions to those observed during the present study. Such large recruitment events appear to be common for *Tesseropora rosea* and might lock in latitudinal patterns of adult abundance for the lifespan of the species, which can be 10 yr (Denley 1981, Caffey 1985). Only massive mortality, such as that observed in the present study, might disrupt such geographic trends. Clearly longer term observations are needed in both cases; importantly, however, the results here indicate that such latitudinal patterns are dynamic. The great variability in settlement and early mortality over geographic scales observed here suggest that, for sessile marine invertebrates with planktonic dispersing larvae, factors that act on a local scale (e.g. recruitment, mortality, natural disturbance) might be more important in setting geographic patterns of distributions than differences in larval supply, settlement and early mortality with latitude.

CONCLUSIONS

The latitudinal decline in adult abundance of *Tesseropora rosea* towards its southern range limit does not appear to be governed by latitudinal gradients in early life-history processes or adult mortalities. Therefore, either processes affecting the life-history stages of *T. rosea* do not influence the abundance at its southern range limit, or these life-history processes must be extremely variable between years such that: (1) large-scale patterns of larval production, settlement, early post-settlement and adult mortality during a single year dictate demographic patterns for numerous years or (2) the combined affect of life-history processes over numerous years determines large-scale demographic variability. Regardless, it is evident that

more long-term, large-scale studies are required to confidently conclude which processes determine the southern range limit of *T. rosea* and the range limits of benthic marine invertebrates in general.

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