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Justin A. Lathlean
University of Wollongong, justinl@uow.edu.au

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

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

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Abstract

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Disciplines

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

Justin A. Lathlean*, David J. Ayre and Todd E. Minchinton

Institute for Conservation Biology & School of Biological Sciences

University of Wollongong, New South Wales 2522, Australia

*Corresponding author, Justin A. Lathlean: jl887@uow.edu.au

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 southeast 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 two sites on 11 rocky shores in this region over two years revealed that none of the life history stages or demographic processes displayed a latitudinal gradient or clear decline towards the south, and settlement and adult mortality were highly variable among locations. Indeed local variation in the 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.

Keywords

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 and Gaines, 2002a; Sagarin and Gaines, 2002b). 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 and Huntley, 1981; Parsons, 1991; Woodward, 1997; Dorken and Eckert, 2001; Jump and Woodward, 2003; Mathews and 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; Gilman, 2006b; 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 and 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 and Roughgarden, 1985; Minchinton and Scheibling, 1991; Caley *et al.*, 1996; Hunt and Scheibling, 1997). Recruitment integrates the arrival, settlement and early post-settlement mortality of larvae (Thorson, 1950; Keough and Downes, 1982) and, although these supply-side processes are often highly variable in space and time (see

Underwood and Fairweather, 1989; Caley *et al.*, 1996; Hunt and Scheibling, 1997), they sometimes reflect latitudinal gradients of temperature, currents, wave exposure and nutrient availability in the ocean (Connolly and 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 of 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 southeast 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 southeast corner of the mainland (Knox, 1963; Huyer *et al.*, 1988; O'Hara and Poore, 2000; Oke and Middleton, 2001; Roughan and 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 fecundity of adults, increase early post-settlement mortality of early juveniles and diminish reliability in the supply of larvae from northern to southern populations (Murray-Jones and 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 adult population structure for the intertidal barnacle *Tesseropora rosea*, a species that disperses via planktonic larvae and with adult abundances indicative of an abundant centre distribution, with declines from the middle to the southern limit of its range at the southeast corner of mainland Australia (Hidas *et al.*, in press). The only study to have assessed large-scale patterns of settlement and early post-settlement mortality for *T. rosea* found no latitudinal trends in recruitment, but only populations within the middle of its geographic range were examined (Caffey, 1985). We measured fecundity of adults and 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 were 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 for two years recruitment into and mortality of adult populations to determine how local or geographic variation in these processes might account for the latitudinal gradient in population size.

METHODS

Study region and species

We monitored the production, settlement, and early post-settlement mortality of larvae and mortality of adults of the intertidal barnacle *Tessieropora rosea* from February 2007 to December 2008 in mid shore regions at 2 sites on 11 rocky shores along the southeast coast of Australia. Rocky shore locations extended from Garie Beach south of Sydney, New South Wales (34°09'S, 151°04'E), within the middle of the geographic range of *T. rosea*, to Mallacoota, Victoria (37°34'S, 149°45'E), at its southern range limit (Bennett and 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 (50.8°C) and minimum (5°C) air temperatures at Garie Beach being greater than the maximum (42.3°C) and minimum (3.8°C) air temperatures at Mallacoota recorded continuously between December 2007 and December 2008.

Adult *T. rosea* are hermaphroditic planktivores that release planktotrophic larvae predominantly from January to June with the larvae estimated to remain within the

water column for approximately 13 days (Wisely and Blick, 1964; Anderson and Buckle, 1983; Egan and Anderson, 1988). Although larval settlement may occur throughout the year, the vast majority settle between January and July with two 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 two to three months 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 and Anderson, 1988). Embryos are internally fertilised and 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-IV) (Anderson, 1969; see further details below).

Sampling design and variables

At each rocky shore location, we established two sites that extended 30 m alongshore and were separated by 10 to 30 m. At each site, 30, 10 cm × 10 cm permanent quadrats were randomly located within the mid shore region characteristically dominated by *T. 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 m 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 unpublished data). We photographed each quadrat monthly (February to July 2007) during the main period of settlement for *T. 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 week old) could not always be distinguished from recently settled individuals of the barnacle *Catomerus polymerus*, but *Catomerus polymerus* recruits (individuals greater than 1 month 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 one of three treatments: ‘releared’ quadrats, were cleared of all *T. rosea* at each sampling time and used to estimate settlement, ‘cumulative’ quadrats, which were cleared initially and then allowed to accumulate *T. rosea* recruits and used to estimate recruitment, and ‘untouched’ quadrats, which were not cleared at any time and 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 Caffey (1985) such that we did not alternatively clear quadrats once every 2-months. In doing so we were able to estimate the percentage of recruits surviving for more than 2-

months 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 *T. rosea*, as well as any empty tests from recent deaths of settlers, in the 10 'releared' quadrats. To ensure that we counted only recently settled individuals, releared 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 releared 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 days 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 and 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 releared 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-year sampling period. Recruitment at a site was

calculated by summing the peak, or maximal, number of *T. rosea* recruits (i.e. individuals >30 days 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 *T. rosea* adults (i.e. individuals with an aperture length >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 and 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 *T. rosea* (i.e. individuals with an aperture length > 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 *T. 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 one estimate of each for each site (i.e. $n = 2$ sites per location). 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 that month (and subsequent observations showed that this was generally the case). For months when sites could not be sampled due to bad weather or were obscured by algae, we excluded that site for that month and

sampled as previously described in the following month. This did not occur often, with only 7.8% of sites not sampled during the entire 2-year 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 performed one-way ANOVA on (i) settlement, (ii) recruitment, (iii) early post-settlement mortality, (iv) early post-recruitment mortality, (v) adult mortality, and (vi) adult density for the 11 locations. Where significant differences were found, a Student Newman-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 data were approximately normally distributed and with equal variance using the Shapiro-Wilks and Cochran's test respectively.

RESULTS

Geographic patterns of demography

The vast majority of adult *T. 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 *T. 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 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 larger number of recruits. For example, Mimosa Rocks received the greatest number of settlers and subsequently had the greatest number of recruits (Fig. 2b and 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 ($r^2 = 0.07$, d.f. = 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 declining substantially from the middle to the edge of its range ($r^2 = 0.36$, $n = 21$, $P = 0.003$) (Fig. 3c). 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. 3b and e). 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 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 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 *T. 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 and 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 and 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 receiving 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 *T. 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, is influencing local populations at the southern range limit of *T. rosea*.

Early post-settlement mortality of *T. 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-year period when compared to similar studies undertaken over shorter sampling periods (Denley and Underwood, 1979; Caffey, 1985; Jernakoff, 1985; Otway and Underwood, 1987). For example, Otway & Underwood (1987) found adult mortality of *T. rosea* to vary between only 14% and 18% over 13-months, while Jernakoff and Fairweather (1985) found adult mortality to vary between 0.5% and 2.5% over a 3-month 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 and Scheibling, 1997). For *T. rosea* specifically the major causes of early post-

settlement mortality are algal growth, ‘bulldozing’ by grazing limpets and intraspecific competition (Denley and 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, 1984; Moran, 1985). However, whether predation by *M. marginalba* and *D. orbita* continues to influence populations over large spatial scales has yet to be answered. In addition, it is unlikely that interspecific competition between *T. rosea* and *Catomerus polymerus*, another intertidal barnacle more commonly found within southern parts of Australia, contributed to the high levels of early post-settlement mortality and adult mortality of *T. rosea* documented within this study as (i) larval settlement between these two species occur at different times of the year (Wisely and Blick, 1964), (ii) *C. polymerus* abundance was generally low and (iii) free-space did not appear to be a limiting factor within 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 southeast coast of Australia (Roughan and Middleton, 2004) and geographical variation in topographic features that assist in retaining larvae (Jenkins and Hawkins,

2003; Mace and Morgan, 2006). However, since many oceanographic studies have revealed only weak upwelling along this coast (Roughan and 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 and 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; Emler and Sadro, 2006) of larvae. Therefore, local processes may be equally important as regional processes in setting patterns of adult abundance and potentially the geographic distribution and southern range limit of *T. 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 *T. 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 four 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 southeast coast of Australia (Short and 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-years (Caffey, 1985). Consequently the high adult mortality detected in this 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 years 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 southeast 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 this study. Such large recruitment events appear common for *T. rosea* and might lock in latitudinal patterns of adult abundance for the lifespan of the species, which can be 10 years (Denley, 1981;

Caffey, 1985). Only massive mortality such as observed in the present study might disrupt such geographic trends. Clearly longer-term observations are needed in both cases; importantly, however, 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 at a local scale (e.g. recruitment, mortality, natural disturbance), scale might be more important in setting geographic patterns of distributions than differences in larval supply, settlement and early mortality with latitude.

Conclusion

The latitudinal decline in adult abundance of *T. 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 (i) large-scale patterns of larval production, settlement, early post-settlement and adult mortality during a single year dictate demographic patterns for numerous years, or (ii) 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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FIGURE CAPTIONS

Figure 1. Map showing the coast of south eastern Australia and sampling locations separated by 10 to 80km. The inset map shows the geographic range of *T. rosea* (shaded area) and the Eastern Australian Current with shading black to white representing strong to weak influence.

Figure 2. Latitudinal variation in the (a) proportion of adult *T. rosea* with either mature or developing larvae; (b) mean settlement; (c) mean percentage mortality of recently settled *T. rosea*, (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.

Figure 3. Latitudinal variation in the density of *T. rosea* 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.

