

Abundance of *Tesseropora rosea* at the margins of its biogeographic range is closely linked to recruitment, but not fecundity

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ABSTRACT: For benthic marine invertebrates with planktonic larvae, adult abundance at the species' range limit may depend on local fecundity, and recruitment from central, source populations. We tested the importance of these processes using a hierarchical design at multiple spatial scales (from tens to hundreds of kilometres) to assess relationships between patterns of adult abundance, fecundity and recruitment in the rocky intertidal barnacle *Tesseropora rosea*, approaching its geographical range limit on the southeast coast of Australia. Across the 600 km region, adult abundance, recruitment and fecundity all declined towards the range limit, but only adult abundance and recruitment were positively correlated, suggesting that recruitment is negatively affected at the range limit and that recruitment plays a significant role in setting the geographical patterns of abundance of *T. rosea*. In contrast, at smaller spatial scales within this region, adult abundance and recruitment varied by up to 15- and 100-fold, respectively, among some locations only tens of kilometres apart, and no obvious patterns in adult-recruit relationships were revealed towards the range limit. Local patterns of abundance and life-cycle relationships do not, therefore, translate to biogeographic scales, but investigation at this multitude of spatial scales helps to identify the defining processes that account for spatial variation and determine population structure towards the range limits of benthic marine invertebrates.

KEY WORDS: Larval supply · Adult abundance · Intertidal barnacles · Supply side ecology · Recruitment

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INTRODUCTION

Ecologists have long sought to understand the factors and processes that determine the abundance distribution and range limits of organisms (Grinnell 1917, Hutchins 1947). In recent years, several studies (Sagarin & Gaines 2002b, Gilman 2005, Hidas et al. 2010) have tested the applicability of the abundant-centre hypothesis, which predicts that the abundance of a species is greatest at the centre of its geographical range, to benthic marine invertebrates.

The little empirical evidence supporting this type of distribution in marine habitats has highlighted the need to understand how the different life-cycle stages of benthic marine invertebrates interact at various spatial scales to determine adult abundance across the geographical range and at the range limit (Sagarin & Gaines 2002a, Sagarin et al. 2006).

For many benthic marine invertebrates that have a planktonic larval stage, adult abundances at a local scale can be determined by patterns of larval recruitment (Connell 1985, Gaines & Roughgarden 1985,

Minchinton & Scheibling 1991). Because planktonic larvae disperse mostly passively with oceanic currents (Pechenik 1999, Kinlan & Gaines 2003), dominant surface currents are expected to cause the downstream accumulation of larvae originating from productive source populations within the middle of the range. If there were no environmental factors influencing post-settlement survival of recruits or adults at smaller spatial scales approaching the range limit, then this should lead to an increase in adult abundance towards the downstream range limit (Gaylord & Gaines 2000). Empirical studies assessing large-scale patterns of recruitment for benthic marine invertebrates approaching their range limits have shown a decline in recruit density gradually towards, or abruptly at, the range limit (Broitman et al. 2008, Herbert et al. 2009); decreased recruitment frequency at the range limit (Zacherl et al. 2003, Lima et al. 2006, Hidas et al. 2010); or no changes in recruitment patterns towards the range limit (Broitman et al. 2008, Lathlean et al. 2010). Assessing these variations in recruitment, and their relationship with adult abundance and fecundity at smaller spatial scales approaching the range limit, is necessary to understand the variable outcomes in patterns of abundance at geographical scales (Fowler-Walker et al. 2005).

Aside from the effects of oceanic currents, recruitment across the ranges of benthic marine invertebrates also partially depends on the intensity and success of larval production (i.e. fecundity; Hughes 1990). Fecundity, however, may decline towards the range limit due to changes in air or sea surface temperature (Hughes et al. 2000, Ramirez Llodra 2002) or food availability (Ramirez Llodra 2002), particularly along the latitudinal distribution of many intertidal species (Lewis 1986), and thus may lead to a decrease in recruitment and adult abundance towards the range limit for species whose larvae are locally retained. The only previous large-scale study that has explored adult–fecundity–recruitment relationships of benthic marine invertebrates focused on broadcast spawning corals on the Great Barrier Reef in Australia (Hughes et al. 2000). For these species, adult abundance and recruitment were not correlated at either small or large spatial scales, but 72% of the variation in recruitment was explained by the fecundity of the adults at large spatial scales. This result is likely to reflect the highly lim-

ited dispersal and low degree of population connectivity of at least some coral species (Ayre & Hughes 2000).

Here we examine adult–fecundity–recruitment relationships at a hierarchy of spatial scales (from tens to hundreds of kilometres) across the southern third of the geographical range of the intertidal rocky shore barnacle *Tessieropora rosea*, on the southeast coast of Australia (Edgar 1997, Hidas et al. 2007). The adult abundance of this species declines steeply from Sydney, New South Wales, to its southern range limit at Cape Conran in eastern Victoria (Fig. 1; Hidas et al. 2010), its larvae spend up to 5 wk in the plankton (Wisely & Blick 1964, Caffey 1985), and the recruit stage of the life cycle is easily recognisable. During the larval phase, its distribution is likely to be influenced by the warm temperate East Australian Current (EAC), which flows predominantly southwards along much of the eastern coast of Australia (Ridgway & Dunn 2003). The current partially deflects away from the coast at approximately the latitude of Sydney, and partially continues southwards as a

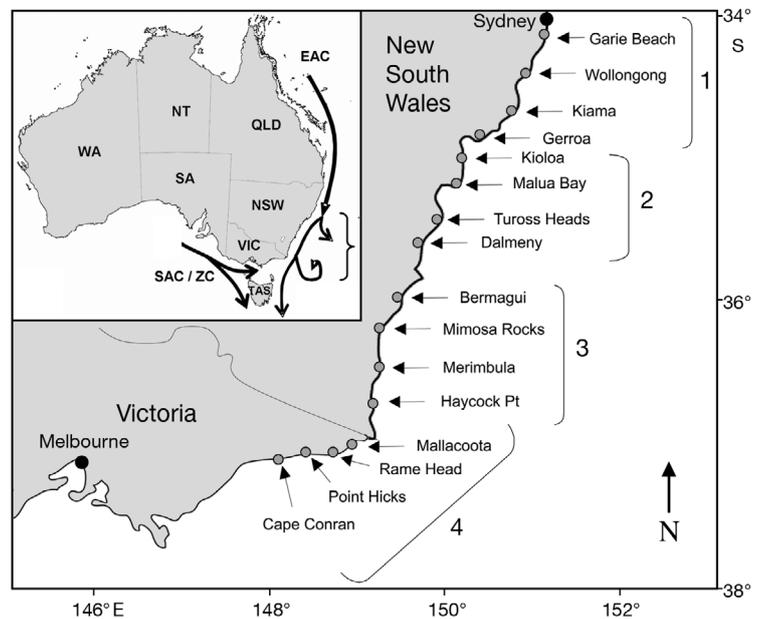


Fig. 1. Southeast coast of Australia, showing the 4 sectors (brackets 1 to 4) and corresponding 16 locations used to assess the adult abundance, fecundity, sexual maturity and recruitment of *Tessieropora rosea* along the southern third of its distributional range, from Garie Beach near Sydney, New South Wales (NSW), to Cape Conran, Victoria (VIC). Inset: Australia with its major states and territories (QLD: Queensland, TAS: Tasmania, SA: South Australia, WA: Western Australia, NT: Northern Territory). The bracket identifies the location of the larger map. Flow patterns of the southward flowing East Australian Current (EAC) and eastward flowing Zeehan Current (ZC) are also shown

weaker current, forming occasional coastal eddies as it reaches the southeast corner of Australia (Fig. 1; Ridgway & Dunn 2003). West of this point, sea surface temperatures change dramatically by up to 5°C compared with conditions to the north (Knox 1963, Ridgway & Dunn 2003), and for 300 km west of Cape Conran, rocky shore habitat is mostly unavailable, except for 1 isolated rocky patch (Fig. 1, Hidas et al. 2007). As a consequence of these complex hydrological, climatic and topographic conditions and the high dispersal potential of the species, we expect significant small-scale (over tens of kilometres) variation in demographic processes across the southern third of the species' range, which may also be reflected by a disparity in small-scale adult and recruit relationships. At large scales (over hundreds of kilometres), however, we expect to see a decrease in fecundity resulting from decreasing air or sea surface temperatures, a decline in recruit abundance resulting from the potential re-circulation of larvae by coastal eddies upstream, and as a result, despite the high dispersal potential of this species, a significant link between adult abundance, fecundity and recruitment.

MATERIALS AND METHODS

We examined the adult abundance, fecundity, sexual maturity and recruitment of the barnacle *Tessieropora rosea* along 600 km of coastline, from Garie Beach near Sydney (34° 10' S, 151° 04' E) to Cape Conran in Victoria (37° 08' S, 148° 07' E; Fig. 1), which constitutes approximately the southern third of the geographical range of the species (Edgar 1997, Hidas et al. 2007). *T. rosea* is found on exposed emergent rock platforms in the mid-shore of the intertidal zone (Caffey 1985, Edgar 1997). This species is hermaphroditic, adults cross-fertilise with their nearest neighbours, and multiple broods are likely produced per breeding season as mature adults almost always contain distinct batches of embryos at different developmental stages (J. Lathlean pers. comm.). Mature larvae are released into the water column predominantly from January to April (Wisely & Blick 1964), but also sporadically throughout the year (Caffey 1985, Egan & Anderson 1988).

To assess spatial changes in adult abundance, recruitment, sexual maturity and fecundity from small to large spatial scales (i.e. from tens to hundreds of kilometres) towards the range limit, we surveyed at 3 different spatial scales using a hierarchical sampling design, with 4 fixed sectors each covering

70 to 110 km of coastline, 4 locations within each sector and 3 sites at each location (Fig. 1). To ensure that temporal variation did not influence spatial variation, we sampled 4 times during a 12 mo period: May and September 2005, and January and May 2006. Sectors were separated by 30 to 100 km, locations by 10 to 50 km, and sites by 0 to 50 m. Sites were approximately 30 m alongshore and of variable intertidal extent (from 6 to 50 m). Sectors 1 to 4 represented regions farthest from and closest to the range limit, respectively, although sectors 1, 2 and 3 were all considered to be within the interior of the range of the species, while sector 4 was at the range limit (Fig. 1). Locations and sites accessible from land were randomly selected, although spaced apart at minimum distances indicated above to cover the geographical range along the coast, and chosen to have the same physical characteristics. Locations were positioned on moderately exposed headlands facing the open ocean, with a platform slope <30°, but most were gradually sloping rock platforms. Rock type varied naturally between siltstone/sandstone (n = 13), granite (n = 2) and basalt (n = 1), but this variation was not systematic towards the range limit and therefore results were not spatially confounded in this way.

To estimate spatial variation in the abundance of adults and recruits, we counted adults (≥ 3 mm aperture length) and recruits (<3 mm aperture length; Wisely & Blick 1964, Lathlean et al. 2010) within 20 haphazardly placed 0.15 × 0.15 m photoquadrats site⁻¹. To quantify levels of sexual maturity and fecundity of *Tessieropora rosea* at each location, we haphazardly collected samples of 20 to 60 (depending on availability) adults and determined the proportion of these displaying gonads (i.e. sexually mature) and ready-to-release mature larvae (i.e. fecund, as indicated by orange or brown embryos with obvious eyed nauplii; Wisely & Blick 1964), respectively.

We used restricted maximum likelihood (REML; Patterson & Thompson 1971) analysis (SPSS 20; IBM) to test for differences in the mean densities of adults and recruits among sectors (entered as a fixed factor), and among locations within sectors (entered as a random factor) along the southern distributional range of *Tessieropora rosea* for the time period between May 2005 and May 2006. Adult and recruit density data for each site at each location for each of the 4 sampling times (when available) was obtained and entered into the analysis by taking the mean of the 20 photoquadrats. Missing data for some sites for some sampling times, corresponding to days when sampling could not be carried out, rendered our analysis

unbalanced, and therefore, conventional mixed model analysis of variance (ANOVA) was not appropriate. Time was added into the analysis as a fixed factor blocking term to ensure that spatial patterns were not confounded by temporal variation. Data were log transformed, as a Kolmogorov-Smirnov test indicated that they did not satisfy the assumptions of a normal distribution. Pairwise comparisons between each pair of sectors and each pair of sampling times were carried out through Bonferroni *post hoc* tests. REML analyses generate 2 test statistics: a standard *F*-ratio for the fixed factor, and a Wald-Z value for the nested random factor. Denominator variances in the *F*-tests do not necessarily have a whole number for the degrees of freedom, because they are estimated by approximate methods.

To test for differences in the proportions of sexually mature and fecund individuals of *Tesseropora rosea* among sectors (entered as a fixed effect) and among locations within sectors (entered as a random effect) at the 4 different sampling times (entered as a fixed effect), we used generalised linear mixed models in GenStat 14.1 (VSN International), using a binomial distribution with a logit link. Data were entered into the analysis as the numbers of individuals with and without gonads per location for sexual maturity, and the numbers of individuals with and without mature embryos per location for fecundity, for each of the 4 sampling times.

Finally, we used simple correlation analyses (SPSS 20; IBM) to test for relationships between recruit and adult densities of *Tesseropora rosea* across the 600 km study region (based on mean values at locations), and across sectors (based on mean values at sites). Additionally, using the same methodology, we assessed the relationships between the proportion of adults with larvae (fecundity) and recruit densities,

and between the proportion of adults with larvae (fecundity) and adult densities of *T. rosea*, based on mean values for each location across the study region. Recruit density data were initially transformed, but this did not result in a better fit for any of the relationships tested, and hence results are presented as untransformed data. To allow for the time lag between larval release and settlement, relationships between densities of adults and recruits, and between the proportions of adults with larvae and densities of recruits were examined by correlating the means of the May and September 2005, and January 2006 adult densities and their proportions of larvae at each location, with the means of the September 2005, and January and May 2006 recruit densities at each location.

RESULTS

Patterns of adult abundance, recruitment and fecundity

The mean densities of adult *Tesseropora rosea*, pooled over the 4 sampling times from May 2005 to May 2006, were 7- to 15-fold higher within sectors 1, 2 and 3 in the middle of the range, with values ranging from 14 to 30 adults per quadrat, than within sector 4 at the species' range limit where on average only 3 adults were present per quadrat (Fig. 2a). There appeared to be a stepwise decline in adult density towards the range limit (Fig. 2a), with sectors 2 and 3 having considerably lower densities than sector 1. However, adult density only differed significantly between sector 1 and the range limit sector 4 (Fig. 2a, Table 1). There was significant temporal variation in adult densities between September 2005

Table 1. *Tesseropora rosea*. Restricted maximum likelihood (REML) analysis of the adult and recruit densities among 4 fixed sectors and 16 nested, random locations on the southeast coast of Australia. Time has been added as a fixed blocking term. The denominator variances in the *F*-tests do not necessarily have a whole number for the degrees of freedom, because they have been estimated by approximate methods. The significance of the nested random factor is indicated by the p-value associated with the Wald Z

Variable	Fixed effects					Covariances of random effects				
	Source	Numerator df	Denominator df	<i>F</i>	p	Parameter	Estimate	SE	Wald Z	p
Adult density	Sector	3	11.684	5.474	0.014	Location(Sector)	0.628	0.282	2.228	0.026
	Time	3	113.062	2.945	0.036	Site(Location[Sector])	0.037	0.047	0.782	0.434
						Residual	0.406	0.054	7.464	
Recruit density	Sector	3	11.611	4.216	0.031	Location(Sector)	1.101	0.502	2.194	0.028
	Time	3	124.794	4.203	0.007	Site(Location[Sector])	0.061	0.076	0.799	0.425
						Residual	0.872	0.111	7.850	

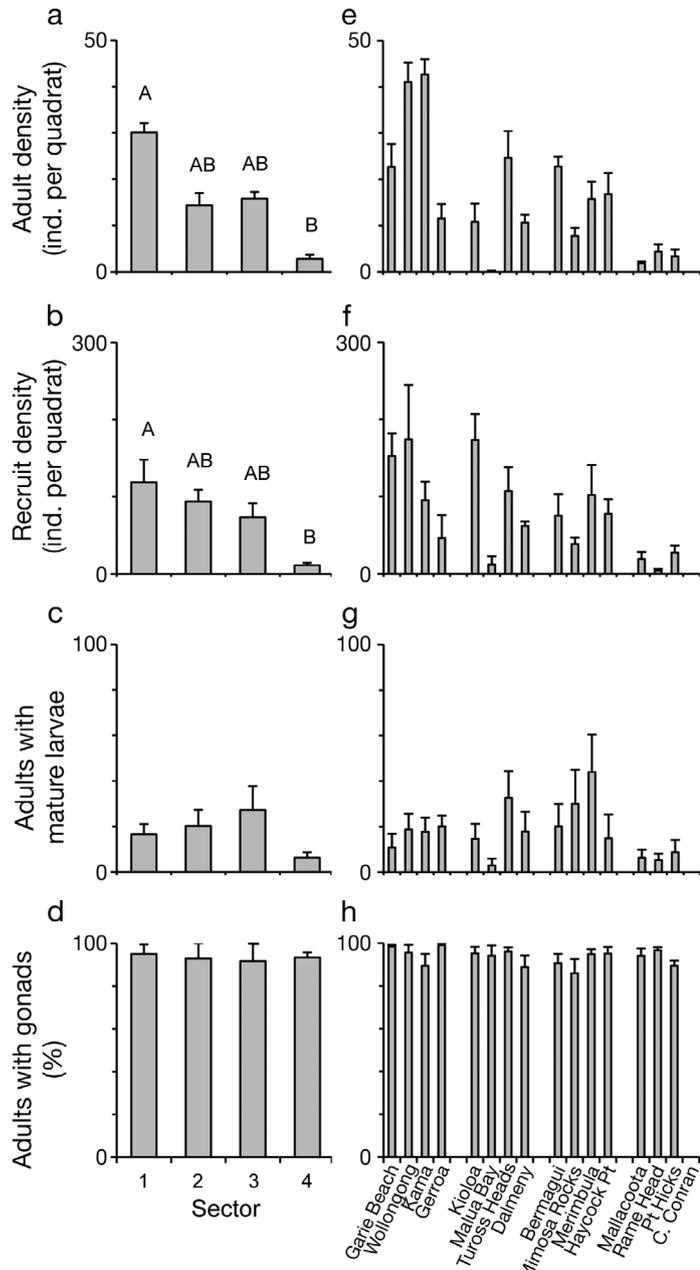


Fig. 2. *Tesseropora rosea*. (a,e) Adult and (b,f) recruit densities, and percentages of adults with (c,g) gonads and (d,h) mature larvae across 4 sectors and corresponding 16 locations, along the southern third of its distributional range from Garie Beach near Sydney, New South Wales, to Cape Conran, Victoria, on the southeast coast of Australia, between May 2005 and May 2006. All means + SE. Within each graph, sectors marked by different letters are significantly different from one another

and January 2006 (Table 1), and significant spatial variation among locations within sectors (Table 1), particularly in sectors 1 and 2 where densities varied between 4- and 100-fold among some locations, respectively (Fig. 2e).

The mean densities of recruits, pooled over the 4 sampling times, mirrored the variation in adult densities across the 4 sectors (Fig. 2b). Mean density displayed a non-significant decline across sectors 1, 2 and 3, from 119 to 73 recruits quadrat⁻¹, and was significantly lowest at the range limit within sector 4, where we detected only 11 recruits quadrat⁻¹ (Fig. 2b, Table 1). Similar to adult density, recruit density varied significantly among locations within sectors (Table 1), particularly in sector 2 where densities varied 15-fold between some locations (Fig. 2f), as well as between sampling times, namely between January and May 2006 (Table 1).

Interestingly, we found little evidence of variation in sexual maturity across sectors. The mean proportions of adults with gonads were consistently high (95–100%) within all 4 sectors (Fig. 2d), and there was little variation among locations within sectors (Fig. 2h). Indeed, results of the generalised linear mixed model analysis showed no significant changes in sexual maturity across space (Table 2). There were, however, changes in sexual maturity across time (Table 2; Wald test, $p < 0.001$). Fecundity, in contrast, showed a decreasing trend towards the range limit, with a mean of only 6% of individuals containing mature embryos in sector 4, compared to 17, 20 and 27% within sectors 1, 2 and 3, respectively (Fig. 2c,g). These proportions, however, varied significantly among sampling times (Table 3), and there was thus a significant interaction between sector and time (Wald test, $p < 0.001$). There were no significant differences in fecundity among sectors in May 2005 and January 2006, whereas in September 2005, the proportion of fecund individuals was significantly greater in sector 3 than in other sectors, and in May 2006, the proportions of fecund individuals were significantly greater in sector 3 than in sector 1 and significantly lower in sector 4 than all other sectors (Table 3).

Table 2. *Tesseropora rosea*. Predicted probabilities from a generalised linear mixed model analysis, for encountering sexually mature adults (i.e. possessing gonads) at each of 4 sectors (1 = farthest from, 4 = nearest to the range limit) for each of 4 sampling times (1 = May 2005, 2 = September 2005, 3 = January 2006, 4 = May 2006), along the southern third of the species' distributional range on the southeast coast of Australia

Time	Sector			
	1	2	3	4
1	0.9704	0.9273	0.9301	0.9825
2	1.0000	1.0000	0.9935	0.9479
3	0.9821	0.9405	0.8767	0.9066
4	0.8974	0.8605	0.8812	0.9052

Table 3. *Tesseropora rosea*. Predicted probabilities from a generalised linear mixed model analysis, for encountering fecund adults (i.e. possessing mature larvae) at each of 4 sectors. Code see Table 2 heading

Time	Sector			
	1	2	3	4
1	0.0966	0.1683	0.0641	0.0595
2	0.0507	0.0272	0.3908	0.0540
3	0.2262	0.2044	0.0975	0.1539
4	0.2433	0.3038	0.4964	0.0108

Adult–fecundity–recruit relationships

Across the entire 600 km region, adult and recruit densities were positively correlated, with 38% of the variance in adult density explained by variation in recruit density (Fig. 3a). In contrast, fecundity was not significantly correlated with either the densities of adults or recruits (Figs. 3b,c). Indeed, several locations within the middle of the range with low proportions of fecund adults still had high densities of adults and recruits (Figs. 3b,c). Within sectors, densities of recruits and adults were only significantly correlated within sector 2 (Fig. 3e), while in sectors 1, 3 and the range limit sector 4 (Figs. 3d,f,g, respectively), these relationships showed no significant patterns.

DISCUSSION

Our hierarchical survey of populations of the intertidal barnacle *Tesseropora rosea* revealed a dramatic decline in adult and recruit densities at locations towards the southern range limit on the southeast coast of Australia. Across the 600 km region, patterns of recruitment were positively correlated with variations in the number of adults, but they were not significantly correlated with variations in the proportions of sexually mature or fecund adults, at each location. This contrasts with the outcome of the study by Hughes et al. (2000), who examined these relationships for corals at the centre of their geographical ranges on Australia's Great Barrier Reef, in which fecundity and recruitment were strongly positively associated at large spatial scales. The difference between our study and that of Hughes et al. (2000) may be due to the more widespread dispersal of *T. rosea* compared to coral species (Ayre et al. 2009), which may increase the scale at which fecundity and recruitment are related. Alternatively, in the study by Hughes et al. (2000), coral recruits were only identified to family or genus

level, which may have confounded species-specific relationships. Our results suggest that either dispersal is limited, or some biotic or abiotic factor affects negatively the recruitment stage of the life cycle of *T. rosea* as it approaches its southern range limit on the south-east coast of Australia.

In contrast to the positive relationship between adult and recruit densities of *Tesseropora rosea* across our 600 km study area, smaller-scale adult–recruit relationships were only evident within 1 of our 4 sectors. This disparity between adult and recruit densities at smaller spatial scales is not surprising, given the long larval stage of the species (Wisely & Blick 1964, Caffey 1985) and the potential for widespread dispersal provided by the predominantly southward-flowing EAC (Ridgway & Dunn 2003). Indeed, we were surprised to find a positive relationship between adults and recruits within 1 of the sectors positioned in the middle of our study area. This result suggests that adult–recruit relationships are not influenced by position within the geographical range but rather, by more local processes. This was also evident from the large differences in adult and recruit densities among some locations positioned only tens of kilometres apart. Small-scale natural variations in abiotic and biotic conditions at each location, such as the density of already existing populations and their effects on food and habitat availability (Connell 1985, Minchinton & Scheibling 1991), temperature (Helmuth et al. 2002), predation and competition (Denley & Underwood 1979) as well as the effects of currents and wave action specific to platforms (Connell 1985, Gaines & Roughgarden 1985) have been shown to influence adult abundance, and small-scale adult–recruit relationships of marine intertidal invertebrates. While every effort was made to choose study locations with comparable physical attributes, conditions inevitably varied among platforms independent of latitude and proximity to the range limit, thus influencing populations at a local scale.

An abrupt decline in recruit abundance at range limit locations of *Tesseropora rosea* was observed, which may have several possible explanations. If local populations of *T. rosea* at the range limit are dependent on the supply of larvae from source populations upstream, which is possible considering the high degree of genetic connectivity among populations of *T. rosea* and other taxa along the coasts of southern New South Wales and eastern Victoria (Ayre et al. 2009), then the weakening of the EAC and the occasional formation of coastal eddies on the southeast corner of Australia may fail to transport lar-

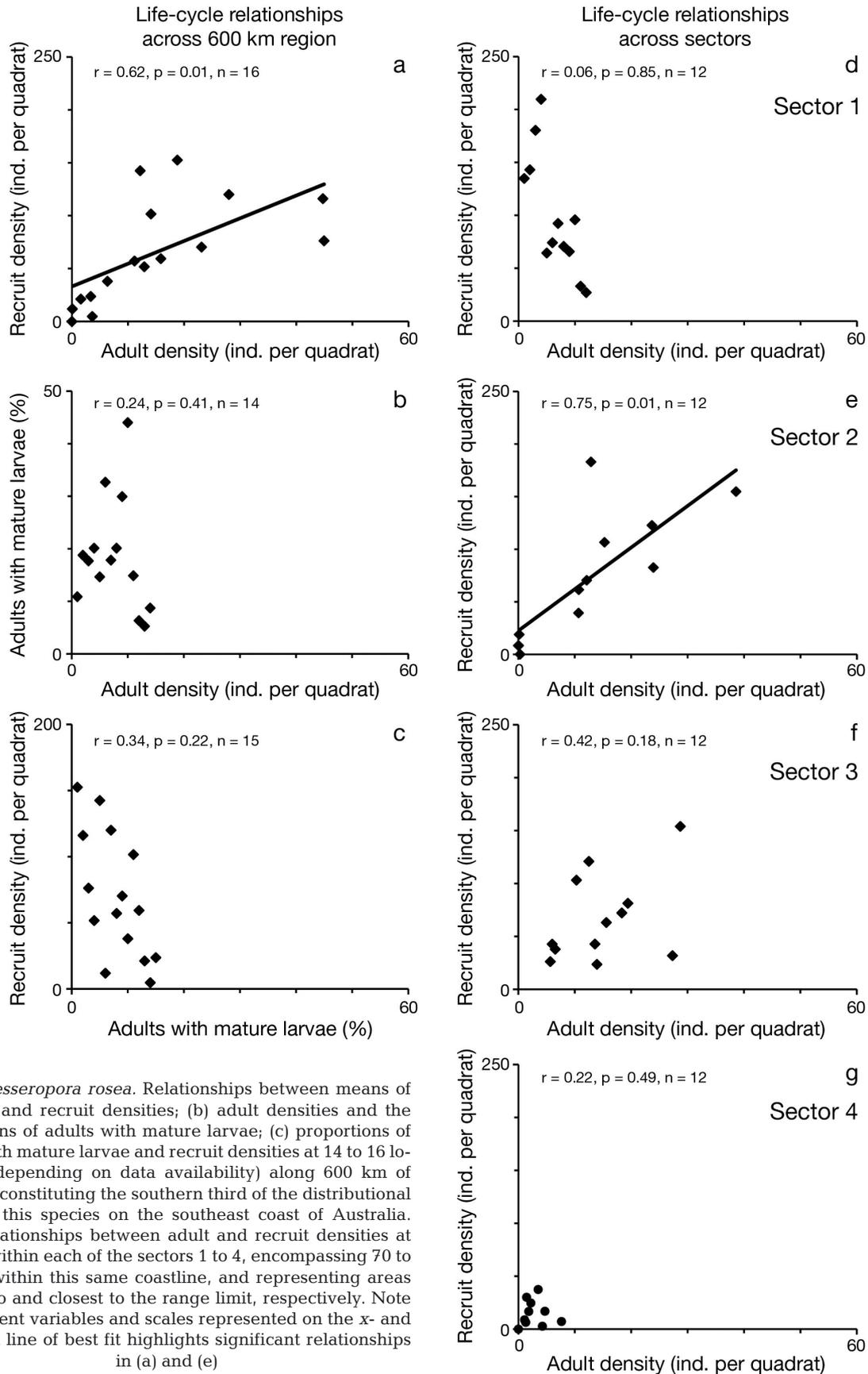


Fig. 3. *Tesseropora rosea*. Relationships between means of (a) adult and recruit densities; (b) adult densities and the proportions of adults with mature larvae; (c) proportions of adults with mature larvae and recruit densities at 14 to 16 locations (depending on data availability) along 600 km of coastline constituting the southern third of the distributional range of this species on the southeast coast of Australia. (d–g) Relationships between adult and recruit densities at 12 sites within each of the sectors 1 to 4, encompassing 70 to 100 km within this same coastline, and representing areas farthest to and closest to the range limit, respectively. Note the different variables and scales represented on the x- and y-axes. A line of best fit highlights significant relationships in (a) and (e)

vae in large enough numbers downstream, or may re-circulate larvae back to, or close to, their shores of origin (Murray-Jones & Ayre 1997, Ridgway & Dunn 2003). Indeed, analyses of size-frequency distributions of *T. rosea* along the same stretch of coast appeared to point towards less frequent or temporally variable recruitment at the range limit (Hidas et al. 2010). The influence of less frequent recruitment events at range limit locations on the southward distribution of the species may also be exacerbated by the predominantly unsuitable rocky shore habitat for 300 km westwards of Cape Conran (Hidas et al. 2007), which may limit the further southward extension of the species (Lewis 1986). An investigation into the latitudinal changes in larval abundance of *T. rosea* as it approaches its southern range limit would help to confirm these hypotheses.

The declining abundance of recruits at the range limit could also potentially reflect a decline in fecundity and larval development, particularly if local populations of *Tesseropora rosea* were mostly dependent on local larval recruitment. However, patterns of recruitment and fecundity of *T. rosea* were not significantly correlated across the 600 km study. Fecundity varied considerably over space and time, was interestingly greatest in sector 3 during 2 of the 4 sampling times, and was only significantly lowest at the range limit during 1 of the 4 sampling times. There is faint evidence to suggest, therefore, that fecundity is negatively affected at the range limit, but these results should be interpreted with some caution. Larval maturation may simply be delayed, larvae may fail to mature, or the number of broods of embryos produced or frequency of larval release may be reduced in populations approaching the range limit. Although almost all adults were sexually mature in all locations, fertilisation success may also be reduced at lower densities because a decreased adult density may reduce the probability of encountering a near neighbour (Kent et al. 2003). Furthermore, *T. rosea* is considered to reproduce predominantly from January to April (Wisely & Blick 1964); however, the timing and duration of the reproductive season has been observed to vary among years (Caffey 1985), and may vary with sea surface or air temperature (Knox 1963, Hughes et al. 2000, Ramirez Llodra 2002). For example, intertidal marine invertebrates on the European Atlantic coast have shorter breeding seasons at their northern range limits (Lewis 1986, Burrows et al. 1992). A more detailed study, with a finer measurement of fecundity, such as the weight of egg lamellae or brooded larvae, is required to reveal more subtle effects of the range limit on fecundity.

Finally, recruit abundance may decrease at the range limit because the settlement or survival of larvae may be affected onshore, at range limit locations. A myriad of factors may be influencing larval settlement and survival of *Tesseropora rosea* at its range limit locations, most notably the decline in air and sea temperature (Knox 1963, Ridgway & Dunn 2003, Lathlean et al. 2011), or the presence of potentially competitive or predatory species that do not inhabit shores farther to the north (Hidas et al. 2007, Coulson et al. 2011). Lathlean et al. (2010) did not find any significant differences in percent settlement, early post-settlement mortality, recruitment, post-recruitment mortality or adult mortality among sites between Garie Beach and Mallacoota over 2 yr of rigorous sampling, but their sampling did not extend as far south as the range limit at Cape Conran (Fig. 1).

Our hierarchical sampling collectively suggests that: (1) there is considerable variation in the demography and relationships among life-cycle stages of *Tesseropora rosea* at locations towards its range limit, (2) nevertheless, a declining trend in adult abundance, and a positive relationship between adult abundance and recruitment, is evident towards the range limit, and therefore, (3) the decline in adult abundance is likely due to 1 or a combination of range limit factors affecting the recruitment stage of the life cycle. In the case of *T. rosea*, large-scale processes therefore appear to override the complexities of smaller-scale variation in recruitment towards the range limit (Fowler-Walker et al. 2005). These conclusions are, however, based on a relatively short time-series of data, and recruitment for this species can vary greatly among years (e.g. Caffey 1985), indicating that strong recruitment years could result in different outcomes. The system therefore deserves comparisons of pattern data over a multitude of years, or even decades (Lewis 1986, Mieszowska et al. 2007) before it can be well understood, particularly at a time when the effects of climate change on species' range shifts are increasingly evident (Sagarin et al. 1999, Helmuth et al. 2006, Hawkins et al. 2008, Wetthey et al. 2011). Nevertheless, our results clearly highlight the benefits of investigating processes accounting for spatial variation across a range of scales towards the range limit, to gain greater insight into the factors that set range limits. Genetic data, or the tracking of larvae, may provide the key to identifying the source of recruits and the strength of larval connections between populations within the interior of the range and the range edge. Furthermore, careful assessment of the relationship between the abundance of settlers and consequent

recruits (Connell 1985, Minchinton & Scheibling 1991) may reveal important information about how post-settlement factors and reproductive potential are affected towards the range limit.

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