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Effects of habitat quality on abundance, size and growth of mussel recruits

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Abstract Recruitment of mussels is a complex process with the successful arrival of individuals hinging on the availability of suitable habitats. We examined the effects of adult mussels as settlement habitat and the degree to which the suitability of habitat they offer is species-specific by comparing the recruitment success of intertidal mussels. We hypothesised that mussel recruitment and early growth are dictated by the quality of habitat offered by conspecifics adults.

We used a unique experimental arena on the south coast of South Africa, where *Mytilus galloprovincialis* and two lineages of *Perna perna* co-exist. Treatments were based on the translocation of individuals of *M. galloprovincialis*, western- and eastern lineage of *P. perna* to a single site, where artificial beds were created and sampled monthly over one year. Recruit's number, their sizes and growth were greater within beds of the western lineage of *Perna* than eastern lineage or *Mytilus* beds. The results clearly demonstrate that the quality of settlement habitat offered by adult beds differs among adult lineages/species and affects rates of settlement and the early growth of recruits. This effect extends to the intraspecific level; we found

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greater differences in density and growth of recruits between lineages of *Perna* than between either lineage and *M. galloprovincialis*.

**Keywords** Microhabitats · Mussel species · Recruitment · Range edges · Conspecifics

Introduction

Conceptually, the geographic limit of a species' distribution represents the point where the species cannot balance recruitment and mortality, reflecting the effects of both physical and biological factors (Godsoe et al., 2017; Angert et al., 2020). While understanding the role of physiological limitation in setting distributional limits is often the first consideration for investigations of species distributions (Kroeker & Sanford, 2022), the importance of recruitment success is less well understood. Recruitment is a determinant factor influencing population increase or decrease and depends on a number of biotic and environmental factors (Roughgarden et al., 1988). Populations can be either closed or open in terms of recruitment, and for species with highly dispersive propagules (Cowen et al., 2000), this is strongly regulated by the physical parameters influencing dispersal (Haye et al., 2014; Weidberg et al., 2018). Furthermore, such factors can operate at a wide variety of spatial and temporal scales (Gaines & Roughgarden, 1985; Kinlan et al., 2005). The regulation of recruit dispersal is particularly complex for benthic marine organisms with planktonic propagules and effective dispersal is a function of the duration of planktonic life as well as hydrodynamics (Jenkins et al., 2000; Shanks, 2009). For shallow water and intertidal animals, hydrodynamic effects operate at scales ranging from hundreds of kilometres to centimetres (Keith et al., 2011). In addition to delivery to habitable areas, successful recruitment depends on the presence of suitable settlement habitat (Pinsky et al., 2012), for example soft versus hard substratum (Herbert & Hawkins, 2006). In many cases, larvae are chemically attracted to adult populations and for habitat-forming organisms such as many sedentary filter-feeders, the adults themselves act as a settlement site (Navarrete & Castilla, 1990; Jenkins, 2005; Tamburri et al., 2007).

We examined the degree to which the suitability of settlement habitat offered by the adults of ecological

engineers is species-specific by comparing recruitment success among one invasive species of intertidal mussel and two distinct genetic lineages of a native mussel species. The native mussel *Perna perna* is a warm-temperate to subtropical species that exists as distinct eastern and western genetic lineages (referred to here for convenience as species) along the coast of South Africa (Zardi et al., 2007a, b, 2011; Ntuli et al., 2020). The two lineages have different evolutionary histories and different temperature tolerances. The eastern lineage exhibits better survival at high air temperatures (Nicastro et al., submitted), and western lineage individuals translocated to the subtropical east coast suffer higher mortality than eastern lineage individuals with no difference between lineages when translocated to the west (Zardi et al., 2011). The two lineages do, however, co-exist over approximately 200 km of shoreline (Zardi et al., 2007b). The second species is the temperate invasive Mediterranean mussel, *Mytilus galloprovincialis*, which dominates mussel populations on the west coast of the country and extends around the Cape of Good Hope as far east as the region of overlap of the two lineages of *P. perna* (Zardi et al., 2018; Fig. 1). Biogeographic transition zones appear to act as barriers to the spread of *M. galloprovincialis* and, while small individuals can be found farther east than the overlap zone, they are extremely rare and the distributional limits of the species within South Africa have been stable for decades (Ma et al., 2021). Over much of the south coast, the western lineage of *P. perna* and *M. galloprovincialis* co-exist, *P. perna* dominating the lower mussel zone and *M. galloprovincialis* the upper, with mixed beds in the middle (Bownes & McQuaid, 2006). This reflects the outcome of complex interactions involving competition and facilitation (Rius & McQuaid, 2006, 2009; McQuaid et al. 2015). Although Bayne (1964) hypothesised that larval mussels settle first onto macroalgae and later undergo detachment and secondary relocation to adult mussel beds, this seems not to be the case for *P. perna* (Lasiak & Barnard, 1995; Erlandsson & McQuaid, 2004; Reaugh et al., 2007). Rather, this species recruits directly onto adult beds, suffering a high degree of cannibalism by adults in the process (Porri et al., 2008a). There are well known differences in the conditions within beds of different mussel species (Helmuth, 1999; Cole, 2010), and in our case these include the density of byssal threads and the degree to which adults exhibit gaping behaviour (i.e. a periodic closure and opening of the shell), which differ between

Fig. 1 Distributional ranges of *Perna* lineages (western and eastern) and *M. galloprovincialis* and sampling sites on the South African coastline. Arrows indicate translocation of individuals of mussels from Nature Valley (NV), i.e. western *Perna* lineage and *M. galloprovincialis*; and from Port St Johns (PJ), i.e. eastern *Perna* lineage, to Old Woman's River (OW; dashed square). Modified figure from Nicastro et al. (2020)
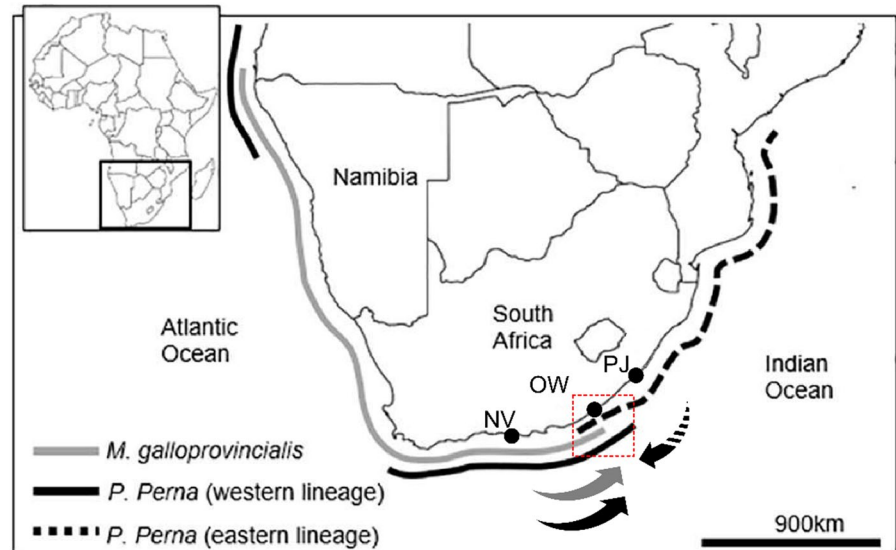
P. perna and *M. galloprovincialis* and also between the two lineages of *Perna* (Nicastro et al., 2010a, b, 2012). Gaping behaviour decreases in the order *P. perna* eastern lineage > *P. perna* western lineage > *M. galloprovincialis* and results in a reduction in body temperature through evaporative cooling, but at the cost of water loss. Gaping also results in higher humidity within mussel beds, influencing the structure and composition of the infaunal community (Nicastro et al., 2020).

Our aim was to test whether mussel bed identity affects the abundance, size and growth of mussel recruits, in a region where each species approaches the geographic limits of its adult distribution. To do this, we set up artificial mussel beds by translocating individuals from populations at the centre of each species/lineage distribution to a single site at the overlapping range edges. We then destructively sampled artificial beds on a monthly basis to measure the numbers and sizes of recruits. Additionally, this allowed us to test for a preference of settlers for conspecific adults.

Methods

Study site

The study site occurs in an overlap zone where *M. galloprovincialis* and both lineages of *P. perna* have co-existed as healthy populations, showing regular

recruitment and reproduction at the study site for over 15 years (Robinson et al., 2005; Rius & McQuaid, 2006). Artificial mussel beds were deployed at Old Woman's River (hereafter OW) on the warm-temperate south coast of South Africa (Fig. 1). Shores at OW are mostly flat rock, with gently sloping sandstone platforms and uniform topography (Nicastro et al., 2020). OW is situated within the contact area of the two genetic lineages of *P. perna* (Zardi et al., 2007b, 2011; Ntuli et al., 2020), where individuals from both eastern and western lineages as well as *M. galloprovincialis* naturally co-occur as range edges populations (Fig. 1).

Thermal conditions at OW

To characterise intertidal thermal conditions at OW, three temperatures loggers were deployed roughly 10 m apart within the experimental area ($\leq 0.1°C$ precision, $\leq 0.2°C$ accuracy, and $0.5°C$ temperature resolution; Envlogger, ElectricBlue CRL, Portugal). Loggers were set to record temperatures hourly and were deployed to capture thermal conditions experienced by translocated mussels (see below) during the study period of June 2019 to September 2020. We calculated the effective shore level (ESL), which is an estimate of the height where loggers were placed (Harley & Helmuth, 2003; Gilman et al., 2006). To calculate the mean ESL and its standard deviation (SD), we identified all sudden drops ($\geq 16.5°C/h$) in

temperature during incoming tides, corresponding to the moment when loggers are immersed with cold sea water, and retrieved corresponding tide levels from published tables (Gilman et al., 2006). We used a threshold of 16.5°C/h, which corresponds to a drop of 5.5°C in 20 min, to avoid false positives (Gilman et al., 2006). Using the estimated ESL along with predicted tide levels (hourly predictions at East London, c. 80 km distant, were obtained from the South African Navy), we defined periods of submergence when tide levels > mean ESL and emergence when tide levels < mean ESL. Note that the ESL can vary daily due to surge and wave exposure and predicted tide levels may not match perfectly realised ones due to the effects of winds, atmospheric pressure, or shore topography (Gilman et al., 2006). To avoid the risk of misidentifying periods of emergence or submergence given these sources of uncertainty, we excluded all temperature data that occurred when tide levels fell within the following buffer zone: mean ESL (− SD) < tide levels < mean ESL (+ SD). After hourly temperatures were attributed to periods of submergence or emergence, we calculated monthly temperature means, SDs, minima and maxima, over the study period.

Translocated mussel beds

A manipulative experiment was set up as described by Nicastro et al. (2020). The experimental design consisted of three treatments: (1) 100% western lineage *P. perna* (hereafter western *Perna* bed), (2) 100% eastern lineage *P. perna* (hereafter eastern *Perna* bed), and (3) 100% *M. galloprovincialis* (hereafter *Mytilus* bed). In late-August 2019, individuals of *P. perna* were collected from one of two locations outside the overlap zone, as described by Zardi et al. (2007a, b) to ensure pure genetic lineages, i.e. Port St Johns (PJ, eastern lineage; Fig. 1) and Nature's Valley (NV, western lineage; Fig. 1). Since *M. galloprovincialis* occurs at low numbers at OWR compared to *P. perna* abundance (Nicastro et al., 2020; Ma et al., 2021), individuals of the former were collected at the same locations as the western lineage of *P. perna*, NV (Fig. 1). After collection, mussels were acclimated in tanks in a controlled environment room set at 20°C (± 0.5°C) for 12 h before deployment in the field. Individuals were carefully scrubbed and cleaned of fouling organisms.

Each treatment consisted of mussels (3–5 cm in shell length) placed in 15 × 15 cm metal frames, secured by large washers and screws into rawl plugs in pre-drilled holes. Each quadrat had 100% mussel cover (i.e. $n = 30$ individuals) representing the natural density of mussel patches at OW (McQuaid & Mostert, 2010). To eliminate possible effects of zonation, each artificial mussel bed was placed in a flat area cleared at the mid-shore levels 60–100 cm from the nearest natural patch, where individuals of *P. perna* and *M. galloprovincialis* are mixed in the intertidal zone (Bownes & McQuaid, 2006). To avoid loss of mussels due to wave action or storm events, each quadrat was covered by a strong plastic mesh (16 mm mesh size). The number of mussels was checked every month for one-year period with mesh replacement every 3 months to avoid biofouling effects on all quadrats (e.g. Ulvales growth; first change of meshes made in December 2019). Mortality of translocated adults was < 20% for all treatments with nonsignificant effects among treatments ($P > 0.05$).

Density and size of recruits on different mussel beds

To evaluate the number and size of recruits of *P. perna* (hereafter *Perna* recruits) and *M. galloprovincialis* (hereafter *Mytilus* recruits), artificial mussel beds (number of replicates = 5) of each experimental treatment (i.e. western *Perna* bed, eastern *Perna* bed and *Mytilus* bed) were sampled by collecting the whole metal frame monthly for 12-month period starting September 2019 ($n = 60$ per treatment), with the exception between April and July 2020. This was because of the South African government declaring a National State of Disaster and a rigorous lockdown due to the Severe Acute Respiratory Syndrome Coronavirus-2 (SARS-CoV-2) pandemic, making it impossible to sample during those months.

Sampled mussel beds were preserved in ethanol, then washed and separated through a 0.5 mm mesh sieve. While the recruits of *Mytilus* and *Perna* can be differentiated morphologically (Bownes et al., 2008), it was not possible to separate recruits of the two lineages of *Perna*. Therefore, recruits were only identified as *Perna* or *Mytilus*. All recruits of mussels > 0.5 mm length in each replicate were identified, counted and measured (to the nearest 0.1 mm) under a binocular microscope (× 5 magnification).

Growth patterns of *P. perna* recruits

Growth estimates were not possible for *Mytilus* recruits due the low numbers found. Therefore, we focused on estimating growth rates for *Perna* recruits. Von Bertalanffy growth (VBG) curves were fitted to the length-frequency data for *Perna* recruits for each experimental translocation, following the methods described in Mildenberger et al. (2017). As we focus on growth patterns of mussels before adulthood in the present study, we excluded all data for animals > 15 mm in maximum length from our length-frequency dataset prior to curve fitting because individuals of *P. perna* can reach sexual maturity at approximately that size (Kaehler & McQuaid, 1999; McQuaid & Lindsay, 2000). The VBG parameters were estimated from the original equation:

$$L_t = L_\infty \left(1 - e\left[-K\left(t - t_0 \right) \right] \right),$$

where L_t is the length at time t, L_∞ is the theoretical maximum length that species would reach, the K parameter is a growth coefficient estimating how fast the individual approaches L_∞ and t_0 is the theoretical age at zero length. Note that the parameter t_0 is referred to as t_{anchor} and describes the fraction of the year (defined between 0 and 1) where annually repeating growth curves cross length equal to zero (see Mildenberger et al., 2017 for details). In other words, t_{anchor} can be interpreted as the recruitment time because growth is related to time rather than age in this context. For instance, if $t_{anchor} = 0.25$, it suggests that eggs were theoretically fertilised on the 1st of April.

The TropFishR package was used to estimate von Bertalanffy parameters in the CRAN R project environment (R Core Team 2019, v4.0.1; Mildenberger et al., 2017), which is applicable to any species with length–frequency data for estimations of growth rates (see Schwamborn et al., 2019; Barbosa et al., 2021 for details). Following Mildenberger et al. (2017), we obtained a first estimation of L_∞ and its confidence interval using the Powell–Wetherall approach (Wetherall et al., 1987). Then, we used the Electronical LEngth-Frequency ANalysis (ELEFAN) method with a genetic algorithm to refine estimates of t_{anchor}, L_∞ and K (Taylor & Mildenberger, 2017). To ensure that the best solution was achieved (after visual examination of the optimisation process), we ran the Genetic Algorithm with the following settings: length-frequency data restructured with moving average = 9, population size = 1,000, maximum number of generations = 1,000, maximum number of generations without improvement = 500, probability of mutation in the parent gene = decreasing over the generations with an initial probability of 0.5 and a limiting probability of 0.1 (Mildenberger et al., 2017; Taylor & Mildenberger, 2017; see also help of the function ELEFAN_GA in the R package for further details on the parameters). As information on L_∞ and K is already available from the literature (max $L_\infty = 117.44$ mm and min $K = 0.31$ from McQuaid & Lindsay, 2000), we restricted the search for L_∞ within 5 and 117.5 mm and for K within 0.3 and 3. We obtained confidence intervals for t_{anchor}, L_∞ and K using the Jack Knife technique, which is a resampling method with replacement to estimate the variance (Quenouille, 1956; Tukey, 1958), as recommended by Mildenberger et al. (2017).

Data analyses

To determine whether density and size (maximum length) of *Perna* and *Mytilus* recruits differed among experimental treatments (i.e. western *Perna* bed, eastern *Perna* bed and *Mytilus* bed), generalised linear model (GLM) analyses were performed for each dependent variable.

The GLM for density of recruits was performed using Gaussian (link 'identity') and including two fixed factors: (1) experimental treatment (i.e. the artificial beds), with three levels: western bed, eastern bed and *Mytilus* bed; and (2) Species, with two levels: *Perna* and *Mytilus*. Size frequency distributions of *Perna* and *Mytilus* recruits were compared among experimental treatments using pairwise Kolmogorov–Smirnov tests ($\alpha < 0.05$). An additional GLM was made by including Season (i.e. spring, summer, autumn and winter) as a fixed factor for each dependent variable using Poisson (link 'log') family error for density and Gamma (link 'identity') family error for size of recruits, respectively.

For model selection, we used backward method whereby interactions and single terms were removed sequentially, one at a time. Then, models were compared and ranked by using the corrected Akaike Information Criterion (AIC_c), which evaluates the quality of the fit that penalises for overfitting too

many parameters, with a correction to account for finite sample size (Akaike, 1974; Burnham & Anderson, 2002). The lowest AIC_c value was compared with other models using the differences between AIC_c scores (i.e. ΔAIC_c). Models with $\Delta AIC_c < 2$ were considered as competitive and, for the sake of parsimony, the model with the least number of parameters was retained. Diagnostic plots (i.e. histograms of residuals and residuals vs. linear predictor) to evaluate both model fitness and statistical assumptions of residuals were used (Zuur et al., 2010). For each response variable, when interaction terms were significant ($\alpha < 0.05$), Tukey post hoc tests were carried out for multiple pairwise comparisons. All statistical analyses were made in the CRAN R project environment (R Core Team 2019, v4.0.1). We used the glmmTMB package (i.e. GLMMs using Template Model Builder) to fit both density and size datasets. Tukey's post hoc tests were carried out using the emmeans package [estimated marginal means (least-squares means)].

Results

Thermal conditions at OW

Maximum and minimum air temperatures were recorded during emergence time and were between 8.3 and 48.2°C (mean $= 19.06 \pm 5.5$). In contrast, seawater temperatures during submergence time exhibited a narrower range (i.e. between 12.5 and 22.8°C, mean $= 17.4 \pm 1.6$). Higher temperatures during emergence time were seen between September 2019 and March 2020, with the highest variability in January and February 2020 (Fig. 2). Conversely, lower and less variables temperatures were recorded between July and August 2019 at the same time before the 1st collection of experimental beds (September 2019; Fig. 2).

Density and size of recruits on different mussel beds

Comparison with earlier studies is difficult because of differences in experimental design, but recruitment of *Mytilus* was unexpectedly low. Numbers of recruits were an order of magnitude lower for *Mytilus* than *Perna* across all months and all treatments (Fig. 1SI). *Mytilus* beds showed no effect of treatment on recruit densities, while for *Perna* beds there was a clear treatment effect (Fig. 3); numbers of recruits were greater in beds of the western *Perna* than in the other two treatments, i.e. eastern *Perna* bed and *Mytilus* bed ($AIC_c = 1765.66$, GLM output, Treatment × Species: Estimate $= 6.82$, SE $= 1.87$, t-value $= 3.65$, $P < 0.05$; Tukey post hoc test, $P < 0.05$).

There were no significant effects on recruit densities of either the main factors Treatment, Species and Seasons or their three-way interaction ($P > 0.05$, Fig. 4). However, there were significant two-way

Fig. 2 Mean (+ SD), minima and maxima of rock temperature at both emergence and submergence times recorded in the experimental area at Old Woman's River between June 2019 and September 2020 ($n = 3$). Grey and black arrows on the *x*-axis indicate thermal conditions before the experiment started, and during the sampling period, respectively
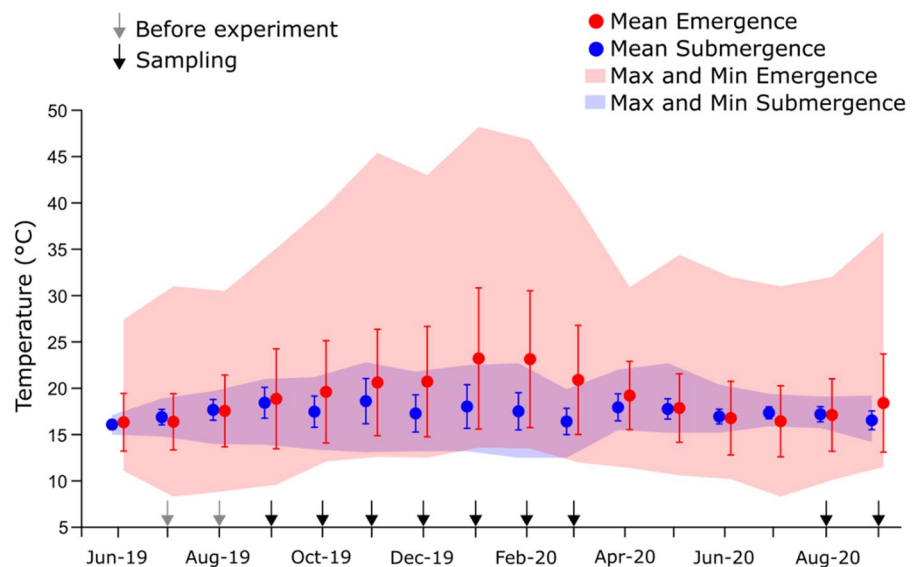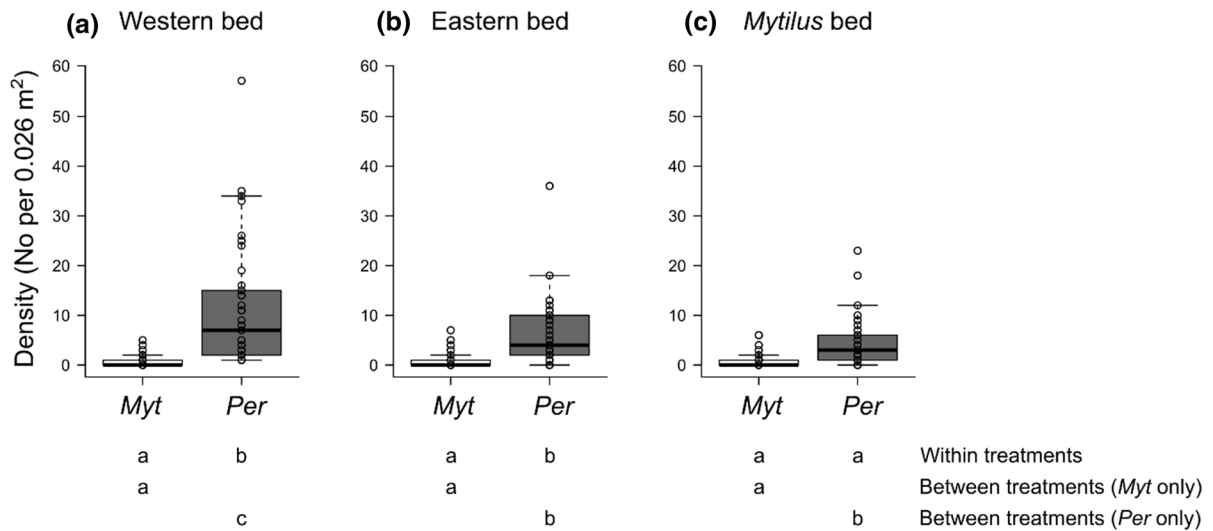
Fig. 3 Boxplot of density (No ind. per 0.026 m²) of recruits per species of mussels (*Myt Mytilus* and *Per Perna*) found in three experimental treatments: western bed (**a**), eastern bed (**b**) and *Mytilus* bed (**c**) between September 2019 and August 2020. Letters indicate significant differences found within and among treatments (Tukey post hoc test; $P < 0.05$). Lines extending from the boxes (whiskers) indicate minimum and maximum values excluding outliers, which are above the whiskers. Horizontal black lines inside boxes indicate the median values of each group. From those lines, the first and third quartiles on boxes (lower and upper quartiles, respectively) are the median of the lower and upper half of the dataset, respectively

interactions between the factors: Treatment × Species, Season × Species, and Treatment × Season (AICc = 1,523.86; $P < 0.05$; Table 1S). The significant interaction between Treatment × Species reflects the low numbers of *Mytilus* recruits across treatments (GLM output: Estimated = 1.15, SE = 0.25, z-value = 4.52, $P < 0.05$). The interaction between Season × Species was due to differences between species in the seasonality of recruitment (Fig. 4; GLM output: Estimated = − 1.04, SE = 0.35, z-value = − 2.92, $P = 0.003$). Recruitment of mussel species showed differences between summer and spring (Fig. 4; Table 1S, Tukey's post hoc test, $P < 0.05$) with *Perna* recruits showing the highest peak into the western beds in summer between January and February 2021 (Fig. 4a–c; Fig. 1SI). Density *Perna* recruits also showed differences between summer and autumn (Table 1S; Tukey's post hoc test, $P < 0.05$) that were not identified for *Mytilus* recruits (Fig. 4). Finally, the interaction between Season and Treatment also indicated differences in density of recruits (GLM output: Estimated = 0.59, SE = 0.24, z-value = 2.42, $P = 0.015$). Recruitment into the western beds was higher during summer than spring (Fig. 4a; Table 1S, Tukey's post hoc test, $P < 0.05$).

For eastern beds, higher recruitment was recorded during summer and winter (June–August; Fig. 1SI) than spring and autumn (Fig. 4b, Tukey's post hoc test, $P < 0.05$). Density of recruits of mussels did not show a clear seasonal pattern in *Mytilus* beds (Fig. 4c).

Perna recruits showed right-skewed size distributions across all experimental treatments, while the size distribution of *Mytilus* recruits showed less clear structure (Fig. 5). Neither species showed an effect of treatment on its size distribution (Table 1). However, *Perna* and *Mytilus* recruits showed different size distributions in western and eastern beds, with *Perna* recruits being generally larger (Fig. 5; Table 1).

There were no significant effects on recruit size of the three factors: Experimental Treatment, Species and Season or their three-way interaction ($P > 0.05$; Fig. 6a–c). However, there were significant two-way interactions between the factors: Treatment × Season, and Species × Season (AICc = 6,202.11; $P < 0.05$). The Treatment × Season interaction (GLM output: Estimate = 2.30, SE = 1.15, t-value = 1.98, $P = 0.047$) indicated that mussel recruits were larger in western bed than eastern bed or *Mytilus* bed in summer (Fig. 6a–c; Table 2S, Tukey's post hoc test, $P < 0.05$),
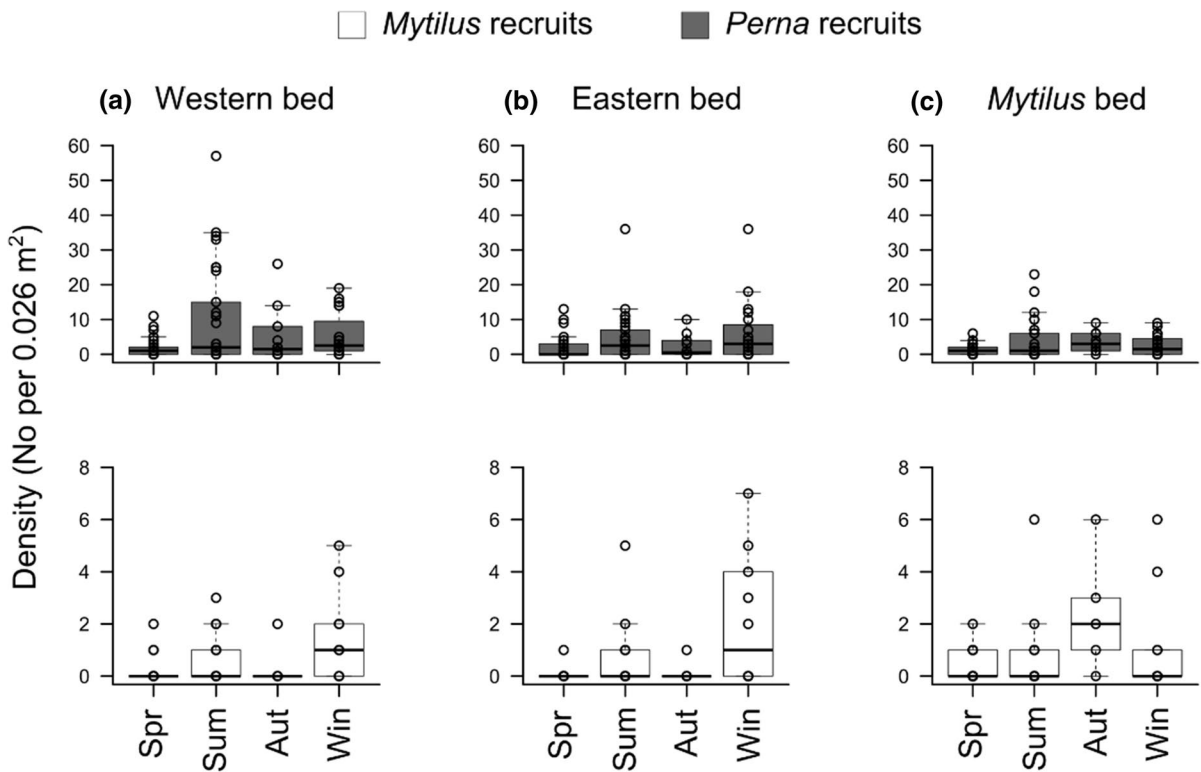
Fig. 4 Boxplot of density (No. ind. per 0.026 m^2) of *Mytilus* and *Perna* recruits recorded in three experimental treatments: western bed (**a**), eastern bed (**b**) and *Mytilus* bed (**c**) between September 2019 and August 2020 at each season: *Spr* Spring (September–November), *Sum* Summer (December–February), *Aut* Autumn (March–May), *Win* Winter (June–August). *Note* April–June 2020 = COVID restrictions. See Table 1S for Tukey post hoc test; $P < 0.05$

with greater maximum length recorded in February 2020 (Fig. 2SI). The interaction Species × Season interaction (GLM output: Estimated = 8.28, SE = 2.99, t-value = 2.76, P = 0.005) indicated that the size of *Perna* recruits differed between autumn and winter (Fig. 6a–c; Table 2S, Tukey's post hoc test, P < 0.05).

Growth of recruits at each experimental bed

VBG curves were fitted to length-frequency data for *Perna* recruits in all three treatments (Fig. 7). The VBG parameters such L_∞ and K (growth coefficient) tended to differ (Table 2), and it was clear that after one year of growth, recruits could be ranked by size according to treatment, i.e. western *Perna* bed > *Mytilus* bed > eastern *Perna* bed, indicating that the growth of *Perna* recruits differed among treatments (Fig. 7; Table 2).

Discussion

For benthic marine animals with planktonic larvae, the processes regulating settlement from the water column into the benthos are extremely important to population dynamics and can be under strong selective pressure (Roughgarden et al., 1988). It has been suggested that the initial life stages of sessile marine organisms prefer conspecifics as settlement sites (Tamburri et al., 2007), and other studies have found a preference of settling mussel larvae for conspecific adults (Mörtl & Rothhaupt, 2003; Sardiña et al., 2009), though manipulative field experiments of *Perna* and *Mytilus* revealed little attraction of larvae to conspecific adults (Porri et al., 2007). Here, we found a preference of *Perna* settlers for western conspecifics beds, with no such effect for *Mytilus* settlers. *Mytilus* and *Perna* tend to reproduce at different times (Zardi et al., 2007a), and the overall numbers of *Mytilus* recruits were extremely low, generally an order of

Table 1 Comparison of size frequency distributions of recruits of *Perna* and *Mytilus* recorded at three different experimental treatments: western bed (western *Perna*), eastern bed (eastern *Perna*) and *Mytilus* bed between September 2019 and August 2020 (see Fig. 5)

Recruit	Treatment	D value	P value
Perna	Western bed vs. Eastern bed	0.138	0.878
Perna	Western bed vs. *Mytilus* bed	0.250	0.210
Perna	Eastern bed vs. *Mytilus* bed	0.194	0.504
Mytilus	Western bed vs. Eastern bed	0.083	0.999
Mytilus	Western bed vs. *Mytilus* bed	0.194	0.504
Mytilus	Eastern bed vs. *Mytilus* bed	0.138	0.878
Perna vs. *Mytilus*	Western bed	0.444	**0.001**
Perna vs. *Mytilus*	Eastern bed	0.444	**0.001**
Perna vs. *Mytilus*	*Mytilus* bed	0.166	0.699

D Kolmogorov–Smirnov statistic

$P < 0.05$ in bold

magnitude lower than *Perna* recruits. Nevertheless, this does not affect the interpretation of intraspecific effects of treatment, and we interpret the findings as a clear indication that the quality of settlement habitat offered by adult mussels influences larval recruitment and growth. Beds of adult *Mytilus* and the two lineages of *Perna* all differ from one another in terms of the mean numbers of byssal threads and the degree of shell gaping that they exhibit. These two aspects of their biology will influence the quality of habitat they offer to settlers and recruits in terms of both architectural complexity and humidity through evaporative water loss. While we cannot separate the influence on recruit numbers of settlement rate versus post-settlement mortality, the net effect is obvious; recruit abundances, sizes and growth were all greatest in western *Perna* beds.

The two lineages of *Perna* have different evolutionary backgrounds, having separated before the closure of the Tethys Sea and migrated independently down the east and the west coast of the African continent, with the study area representing a zone of secondary contact between them (Cunha et al., 2014). The situation is now made more complicated by the eastward expansion of the invasive *Mytilus* from the west coast

of South Africa, reaching an apparently stable eastern limit in the study area (Robinson et al., 2005). All three have co-existed for around 20 years at the study site, where they exhibit healthy populations with regular reproduction and recruitment (Robinson et al., 2005; Rius & McQuaid, 2006). The within-shore and alongshore distributions of the three are set by complex interactions between their biological interactions and abiotic conditions (Mcquaid et al., 2015). Using a completely different experimental design, Porri et al. (2007) found no evidence of conspecific attraction of recruits to conspecific adults under field conditions, and their results indirectly corroborate our interpretation of the present results. Porri et al. (2007) used two approaches, one involving the use of plastic scouring pads as settlement sites placed among adult mussel beds. This tests for coarse attraction of larvae to adults, with larvae potentially settling in the proximity of conspecific adults. The second approach involved placing adults in bags anchored to the shore and tested the possibility of larvae being attracted to individual conspecific adults. Neither approach tests the effects of the structure of habitat formed by adults. In combination with our data, this indicates that chemical attraction to conspecifics is weak or non-existent, and that larvae are attracted to, trapped by, or survive better in the more benign or architecturally complex habitats provided by *Perna* beds.

Habitat conditions affecting mussel recruitment success

The physical and biological characteristics of a habitat may influence species interactions (Bulleri et al., 2006, 2016), for example, interactions between *Perna* and *Mytilus* can be competitive or facilitative depending on position on the shore (Rius & McQuaid, 2009). Our species differ in two aspects likely to affect recruitment success. First, gaping of the shells by mussels reflects the species' tolerance of anaerobic conditions and results in water loss and evaporative cooling as side effects (Nicastro et al., 2010b). This affects levels of humidity and temperatures inside adult beds (Zardi et al., 2015; Lathlean et al., 2016) with consequences for associated infauna assemblages (Nicastro et al., 2010b, 2020) and potentially the success of mussel recruitment. *Mytilus* is highly tolerant of anaerobiosis and does not exhibit gaping, while *Perna*, particularly the eastern lineage, gapes

Fig. 5 Frequency (proportion) of sizes of *Mytilus* and *Perna* recruits (maximum length, in 1 mm classes) recorded in three experimental treatments: western bed (**a**), eastern bed (**b**) and *Mytilus* bed (**c**) between September 2019 and August 2020 (see also Table 1)
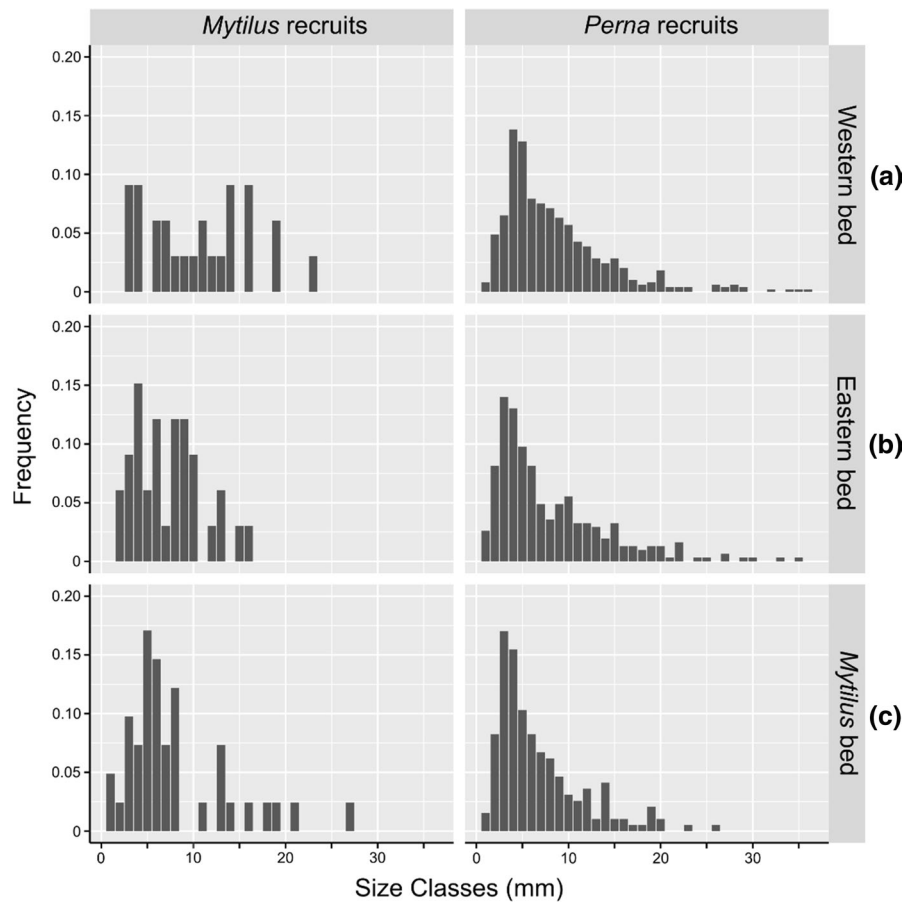
frequently (Nicastro et al., 2010b). The gaping behaviour of *Perna* has such a marked effect on temperature stress that it can even benefit adjacent *Mytilus* by leading to reduced body temperatures (Lathlean et al., 2016). Secondly, *Perna* and *Mytilus* differ in the approach they take to coping with the stress of wave action (Zardi et al., 2008). For both species, adult mortality through wave action is greater on the open coast than under more sheltered conditions, but *Perna* essentially adopts a 'resistance' strategy, relying on strong attachment through the production of large numbers of byssal threads (Zardi et al., 2006, 2008). In contrast, *Mytilus* adopts essentially a resilience strategy, exhibiting less strong attachment, with roughly 20% fewer byssal threads than *Perna* (Zardi et al., 2006), and higher mortality under wave stress, but higher mobility that allows individuals to reposition themselves when neighbours are lost (Nicastro et al., 2008). Thus, the two species differ in the average number of byssal threads produced by adults, but

in addition, eastern *Perna* adults produce more byssal threads than western *Perna* adults (Zardi et al., 2015), and this will affect the architectural complexity of the habitat as experienced by settlers and recruits. The larvae of *Perna* produce a mucous thread immediately before settlement (Petrone et al., 2008; Wilkens et al., 2012; Rusk et al., 2017) and in the turbulent environment of the intertidal this seems to result in larvae attaching to substrata in accordance with the likelihood of entanglement, though in the laboratory older recruits (9–10 mm) are more likely to crawl towards adults using the foot (Erlandsson et al., 2008; Porri et al., 2016). In situ comparisons of settlement rates among various potential substrata indicates that mussel larvae settle most commonly on more complex substrata; in that case macroalgae were preferred to adult mussel beds (McQuaid & Lindsay, 2005), highlighting the relevance of architecture to settlement rates. Indeed, the importance of complexity and the provision of more attachment points and spatial
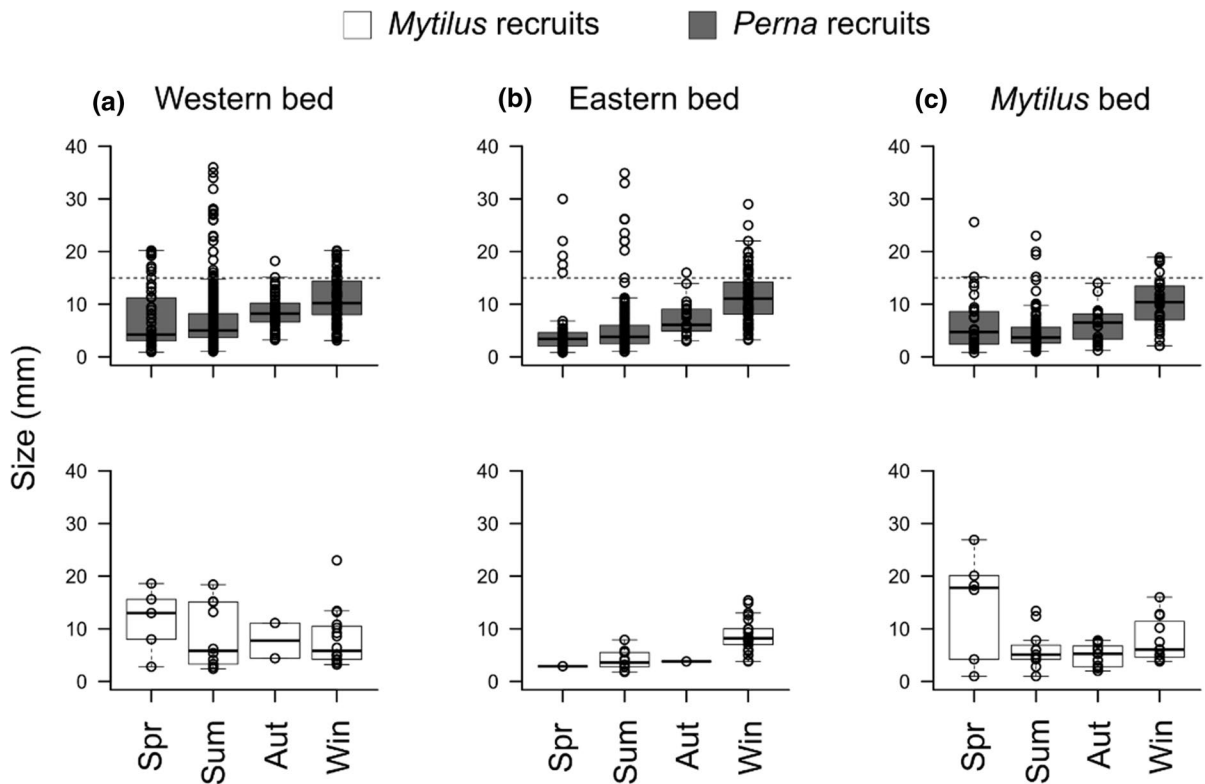
Fig. 6 Boxplot of sizes (mm) of *Mytilus* and *Perna* recruits recorded in three experimental treatments: western bed (**a**), eastern bed (**b**) and *Mytilus* bed (**c**) between September 2019 and August 2020 at each season: *Spr* Spring (September–November), *Sum* Summer (December–February), *Aut* Autumn (March–May), *Win* Winter (June–August). Horizontal dotted line in plots for *Perna* recruits indicates 15 mm in maximum length for those individuals used to build VBG curves (see Fig. 7; Table 2 for details). *Note* April–June 2020 = COVID restrictions. See also Table 2S for Tukey post hoc test; $P < 0.05$

Table 2 Comparison of von Bertalanffy growth (VBG) parameters L_∞, K and t_{anchor} estimated for recruits of *Perna* recorded at each experimental treatment (western bed, eastern bed and *Mytilus* bed) between September 2019 and September 2020

Treatment	VGB parameter [lower CI, upper CI]		
	L_∞	K (year^{-1})	t_{anchor}
Western bed	15.25 [15.25, 17.49]	2.37 [0.84, 2.38]	0.93 [0.66, 0.93]
Eastern bed	15.50 [15.16, 17.30]	1.02 [0.37, 1.10]	0.79 [0.40, 0.83]
Mytilus bed	19.39 [16.42, 20.75]	1.09 [0.43, 1.20]	0.88 [0.62, 0.90]

The VBG curves are indicated in Fig. 7

L_∞ (mm) theoretical maximum length that species can reach, K (year^{-1}) measurement of the rate at which the maximum size can be reached, t_{anchor} fraction of the year at zero length, *CI* confidence intervals

refuges for recruits has been highlighted for other mussels species such as *Mytilus edulis* (McGrath et al., 1988; Christensen et al., 2015).

These points led us to expect higher recruit numbers on beds of *Perna* east than *Perna* west, but unexpectedly, we found the reverse. While the key driver for this result is unknown, one other difference between our species may be relevant; as sedentary filter-feeders, adult mussels can exert considerable consumption pressure on larvae attempting to settle into existing beds (Alfaro, 2006). The effect is particularly strong during receding tides, and

Fig. 7 Von Bertalanffy growth (VBG) curves fitted to length-frequency data for recruits of *Perna* recorded at three different experimental treatments: western bed (**a**), eastern bed (**b**) and *Mytilus* (**c**) between September 2019 and August 2020. Horizontal dotted lines are the expected length reached of mussel recruits after 1 year. See Table 2 for parameters of each VBG curve
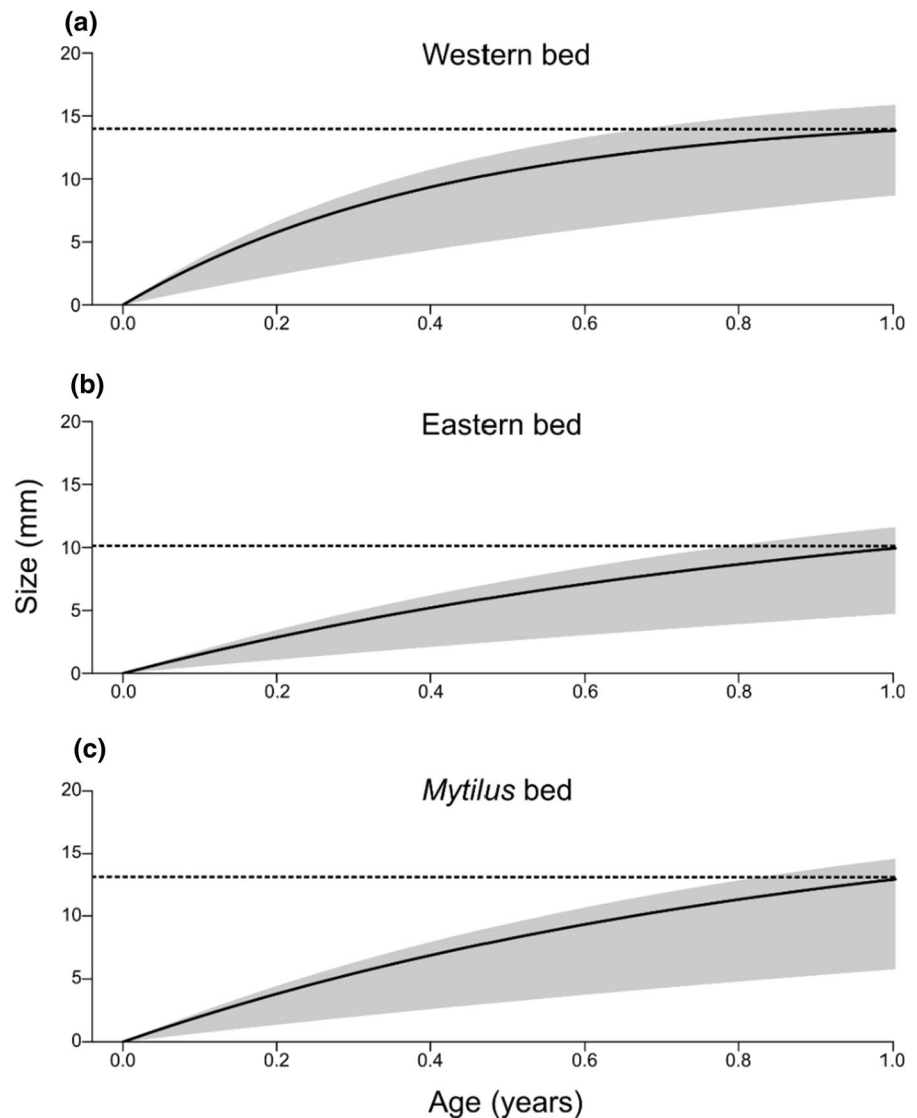
larviphagy by adults can remove nearly 80% of larvae before they can find refuge among the byssal threads of the adults (Porri et al., 2008a). Porri et al. (2008a) also found that adults of *Mytilus* can exhibit stronger predation pressure on early mussel stages than adults of *Perna* and this presumably reflects rates of filtration. While there are no comparisons of filtration rate between *Mytilus* and *P. perna*, mussel species are known to differ in their filtering efficiencies and *M. galloprovincialis* is known to show higher clearance rates than *Perna canaliculus* (Wright et al., 1982; Gardner, 2002). The study by Porri et al. (2008a) involved only the western adults of *Perna* and, as the two lineages of *Perna* have not

been compared with one another; differences in the efficiency which they filter out larvae could theoretically help explain our findings.

Growth rates of mussel recruits

Growth of mussels can be estimated using several different approaches and its estimations are highly variable, with local conditions, particularly of water flow, having a strong influence (Gomes et al., 2018; Barbosa et al., 2021). For example, McQuaid & Lindsay (2000) used three complementary techniques to demonstrate faster growth rates on exposed than sheltered shores, but smaller within-shore scales, are

also important. McQuaid & Mostert (2010) reduced adult growth rates by roughly 30% by experimentally manipulating water flow at centimetre scales in the field. In both cases, this seems to operate through the supply of food. The models in this study indicate that, after one year of growth, recruits of *Perna* clearly attain larger sizes in beds of the western lineage of conspecifics than in other beds. Our results differ from those of Bulleri et al. (2006) who experimentally manipulated the habitat-forming macroalga *Codium fragile*. They found that recruit numbers were greater in areas where the alga was present than in areas where it had been removed, but with no difference in recruit growth rates. Whether our finding of dissimilar growth rates of recruits among different adult mussel beds is related to food or to abiotic conditions is unclear, but one possibility is that differences among species in filtration efficiency or pseudo faeces production by adults may affect the availability of food to recruits, and thus their growth rates.

Conclusions

On scales of 100 m, hydrodynamics in the nearshore environment are particularly powerful and complex, resulting in preferential delivery of more larvae to some sites than others (Porri et al., 2008b). At smaller scales, there is evidence of an ontogenetic shift in how primary and secondary mussel settlers are attracted to biofilm and conspecifics (Von Der Meden et al., 2010). In our study, we could not differentiate between the effects of settlement and post-settlement mortality. Recruits were not only more abundant on beds of western *Perna* than other treatments; they are also expected to reach larger sizes after recruitment according to the modelled growth, suggesting that western *Perna* provides a particularly favourable post-settlement environment at the study site.

Beds of adult mussels form critical habitats for the settlement and recruitment of earlier ontogenetic stages. Overall, however, our results indicate that the quality of habitat that adults offer differs among species and, importantly, even between different genetic lineages of the same species. Comparing with earlier studies on chemical attraction of larvae to conspecifics, our data clearly indicate that larval preference for one lineage of *Perna* reflects differences in the architectural complexity of adult beds and the influence of gaping behaviour on creating more benign conditions within those beds.

Data availability All data and material generated during the present study are available from the corresponding author upon request.

Declarations

Conflict of interest The authors declare that there are no competing interests.

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