Source populations in coastal crabs: parameters affecting egg production

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ABSTRACT: Benthic marine invertebrates may form metapopulations connected via propagule dispersal. Conservation efforts often target potential source coastlines to indirectly benefit areas depending on allochthonous offspring production. Besides population density, adult size structure, sex ratio, brooding frequency and the proportion of breeding individuals may significantly influence the reproductive output of benthic populations, but these effects have seldom been tested. We used rocky shore crabs to assess the spatial variability of such parameters at relevant scales for conservation purposes and to test their consistency over 2 consecutive years; we then used the data to address whether bottom-up processes or biological interactions might explain the patterns observed. We decomposed egg production rates into their components for the 2 most abundant brachyuran species inhabiting the intertidal rocky habitat. Adult density and brooding frequency varied consistently among shores for both species and largely explained the overall spatial trends of egg production. Temporally consistent patterns also included among-shore differences in the size of ovigerous females of the grapsid *Pachygrapsus transversus* and between-bay differences in the fecundity of the spider crab *Epialtus brasiliensis*. Sex ratio was remarkably constant in both. We found no positive or negative correlations between adult density and brooding frequency to support either the existence of a component Allee effect (lack of mate encounters) or an effect of intra-specific competition. Likewise, shore-specific potential growth in *P. transversus* does not negatively correlate with frequency of ovigerous individuals, as would be expected under a critical balance between these 2 processes. The patterns observed suggest that bottom-up drivers may best explain spatial trends in the reproductive output of these species.

KEY WORDS: Reproductive traits · Spatial structure · Source areas · Adult benthic populations · Marine conservation

INTRODUCTION

Historically, the spatial scales at which ecologists usually addressed population dynamics tended to increase from local interactions affecting focal populations, largely explained by competition and predation, to large-scale processes, including the occasional interchange of individuals among isolated habitat patches, which is currently examined in the light of metapopulation theory (Hixon et al. 2002). In this latter scenario, the concept of source–sink dynamics was introduced to distinguish between habitats in which offspring production supersedes mortality, and emigration to other areas is expected (sources), and habitats in which self recruitment is insufficient to balance mortality, and thus the input of allochthonous individuals (sinks) is required (Pulliam 1988). In sink habitats, juveniles may either fail to develop into adults (Macpherson et al. 1997) or reproductive output of adults may be insufficient to replenish the population (Kreuzer & Huntly 2003). Identifying the demographic and reproductive parameters consistently limiting off-

spring production is therefore a necessary step in understanding the mechanisms controlling population dynamics.

Benthic stages of marine invertebrates with an indirect life cycle, colonizing hard substrata such as rocky shores, are likely to be distributed in a complex spatial arrangement (Johnson 2006). Potential benthic habitat for these animals is often patchy, reflecting the discontinuous distribution of hard bottoms along coastline distances at which connectivity via larval dispersal is thought to take place. A source–sink metapopulation model could explain population dynamics in these systems (Roughgarden & Iwasa 1986), in which the location of sink populations would be determined by the interaction between the potential of larval dispersal, which depends on larval duration and behaviour, and the oceanographic conditions prevailing over the shelf and at the coast (Largier 2003, Aiken et al. 2007). Ultimate source populations are very difficult to identify because the fate of their offspring while in the plankton is almost always unknown. Potential sources are commonly defined instead (e.g. Dethier et al. 2003, Harding et al. 2005). Estimates of egg production or larval release may be used to measure reproductive output, and, hence, the potential of a given population to contribute to a pelagic larval pool. Habitat spots of high offspring production should be identified and protected to achieve major conservation goals (Crowder et al. 2000).

Adult population density, although a very important factor, should not be viewed *a priori* as a predictor of reproductive output, because limited resources may cause a drastic decrease in offspring production (Branch 1984, Beck 1995), for instance, due to markedly restrained growth of breeding individuals (Branch 1975, Wenngren & Ólafsson 2002). Because fecundity is often a function of parental size, usually increasing as a cubic power of a linear size dimension (Jensen 1958, Hines 1982), intraspecific competition may thus indirectly affect egg production. The amount of energy allocated to gonads and mating may also be affected by intra-specific competition. Regardless of size, individuals may also be affected by competition, which can reduce per capita fecundity and/or brooding frequency (Branch 1975, Spight & Emlen 1976, Keller 1983). In large mobile consumers, another possible outcome of competition is size-dependent shelter shortage, leading to a lethal indirect effect and a demographic bottleneck (Beck 1997).

Identifying potential source populations from sampling benthic stages must therefore combine estimates of population density and structure with measurements of egg production. Despite a large list of contributions on both topics separately, joint analyses to produce profiles of egg production in decapod crustaceans at the population level have rarely been reported (but see Dugan et al. 1991, Wenner & Dugan 1991). The repro-

ductive biology of brachyuran crabs has been well documented, enabling the establishment of reasonable assumptions supporting the present study. Females produce egg clutches constrained in size due to the internal volume available to the development of gonads (Hines 1982, 1992). Usually, when oocytes become fully mature, they are all extruded during oviposition, and embryo development is synchronous through incubation. In some cases, however, distorted sex ratios caused by male-biased fisheries may result in relatively large numbers of sperm-depleted males, which are incapable of fertilizing all of the oocytes. Sperm limitation may thus lead to gonad resorption or egg loss soon after extrusion (Rondeau & Sainte-Marie 2001, Hines et al. 2003, Sato et al. 2005). Natural differences in sex ratios among undisturbed populations, e.g. emerging from different predation rates on males and females (Ribeiro et al. 2003), may render similar scenarios.

Intertidal grapsid crabs often become mature while still young-of-the-year, when they attain roughly a third of the size of the largest individuals (Flores & Negreiros-Fransozo 1999, Flores & Paula 2002a), thus maintaining moulting and reproductive activities throughout adulthood. Majoids, on the other hand obligatorily undergo anecdysis, i.e. they cease moulting and thus growth after reaching maturity (Hartnoll 1969). As a result, the size span of mature crabs is only due to the variable juvenile growth of individuals that survive to adulthood, and, therefore, size and age are not necessarily well correlated. Moreover, grapsids are prone to shift their diet according to the availability of potential food resources (Kennish 1997, Cannicci et al. 2007), while spider crabs are more specialized and may only explore a very narrow niche (Hines 1992). Therefore, different reproductive parameters, and the extent to which they can vary under natural conditions, may differ considerably in these brachyuran groups.

The brachyuran crabs used in the present study were the common grapsid *Pachygrapsus transversus* Gibbes, which is distributed over most of the intertidal zone, and the spider crab *Epialtus brasiliensis* Dana, which lives in association with *Sargassum* spp., over the lower intertidal and shallow subtidal. Unlike other crab species, which are concentrated in microhabitats characteristic of only a few sites, such as many xanthoids and pinnotherids, *P. transversus* and *E. brasiliensis* are very abundant on rocky shores along the coastlines of south-eastern Brazil. Both species reproduce year-round, with a higher frequency of breeding females during summer (Negreiros-Fransozo et al. 1994, Flores & Negreiros-Fransozo 1998, authors' unpubl. data). For *P. transversus*, juvenile recruitment is highest in winter and crabs grow to maturity by late summer (Flores & Negreiros-Fransozo 1999). For *E. brasiliensis*, the first juvenile stages are more abun-

dant during autumn (authors' unpubl. data) and no information is yet available on their age at maturity. These brachyurans are probably among the most important consumers in the rocky intertidal along the south-eastern Brazilian coast. Since keystone predators such as seastars (Paine 1966) and large gastropods (Navarrete & Castilla 2003) are absent from the system, *P. transversus* becomes one of the main potential sources of top-down control of benthic assemblages of sessile invertebrates and algae. *E. brasiliensis* is the dominant brachyuran associated with the algal canopy of the infralittoral fringe, and, thus, is probably an important energetic link between this vegetated zone and neighbouring habitats.

In the present study, we examined spatial and temporal variations in egg production, based on estimates of demographic and reproductive variables, and assessed the relative importance of such parameters in several populations of *Pachygrapsus transversus* and *Epialtus brasiliensis* along a sub-tropical coastline. We compared the relative importance of basic population parameters (density, sex ratio, frequency and size of breeding females) and size-adjusted fecundity in determining the rate of offspring production, by assessing their overall variability across 6 populations of each crab species. For each species and measured parameter, spatial comparisons considered shore (in kilometres) and bay (in 10s of kilometres) scales, and temporal variation was tested by sampling over 2 consecutive years. Spatially consistent patterns are defined here as among-shore or between-bay variability, of any given parameter, that persisted over time. Traits exhibiting consistent variation were thus considered the best candidates to determine the spatial structure of reproductive output in these crabs. The interplay among fecundity, relative frequency and the size structure of ovigerous females was used to test a possible trade-off between growth and reproductive investment in the optimization of offspring production. Although not covering spatial scales at which season length and temperature drive profound changes in the reproductive biology of benthic invertebrates, the present study focused on the identification of relevant variables affecting egg production over a geographic range in which connectivity due to larval dispersal is most probable, and therefore of special interest for the management of stretches of coastline to the order of a few to several 10s of kilometres in length.

MATERIALS AND METHODS

Study area. Fieldwork was undertaken in Ubatuba, São Paulo, southeast Brazil, over a coastline of approximately 30 km, encompassing 2 different embayments: Fortaleza and Flamengo Bays. The sampled coastal

system is mostly marine, but rainfall may cause dilution to 30 PSU. Within each bay, 3 different rocky shores were selected for sampling (Fig. 1), without any other concern than making ground access as easy as possible, and assuring that distance between neighbouring sites was kept to the order of kilometres. The available sampling area on these shores consisted of a coastline belt 90 to 410 m long and 2 to 15 m wide, depending on the slope. Tides are semidiurnal and their range is small (ca. 1.5 m during spring tides). Common features of the intertidal zone at the sampled shores are the presence of a chthamalid barnacle cover (*Chtamalus bisinuatus* Pilsbry) along the upper midlittoral, variable cover of mytilid bivalves (*Brachidontes* spp.) and coronuloid barnacles (*Tetraclita stalactifera* [Lamarck]) at the lower midlittoral, and a mixed-algal zone dominated by *Sargassum* spp., which extends from the infralittoral fringe down to a depth of 1 to 2 m (Eston et al. 1986, Paula 1988, Skinner & Coutinho 2002).

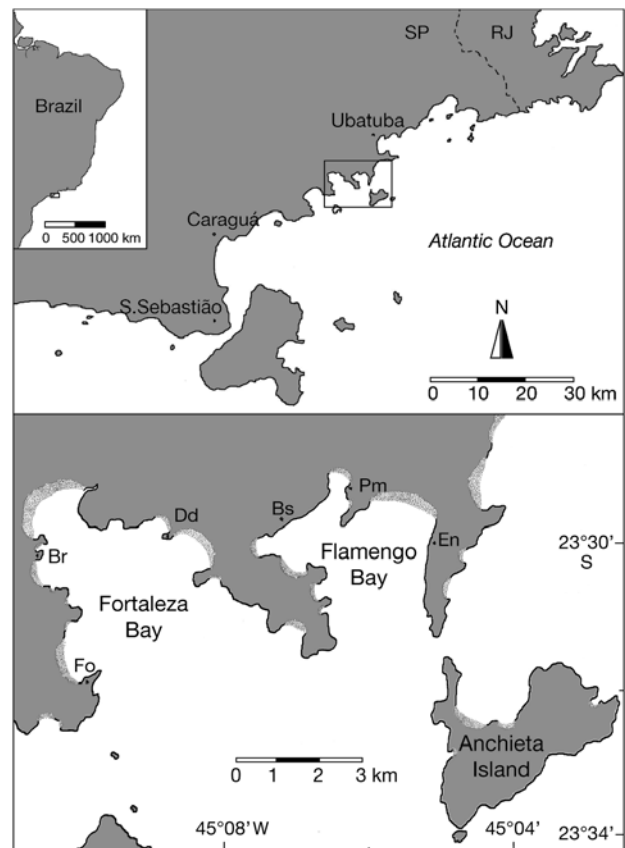**Fieldwork.** Regular visits to the study shores were undertaken from January 2005 to December 2006 to

Fig. 1. Map of the study region showing the location of sampled bays and respective shores. Lower panel is an enlargement of the enclosed area in the upper panel. Stippled coastlines represent sandy areas. Fo: Ponta da Fortaleza; Br: Bravinha; Dd: Domingas Dias; Bs: Base; Pm: Perequê Mirim; En: Enseada

obtain estimates of adult density, sex ratio, and average size, fecundity and proportion of ovigerous females relative to all adult females, at least once every 2 mo at all shores. All fieldwork was carried out at nocturnal low water during spring tides, when sampling efficiency is highest for both species. Sampling encompassed the whole coastline at the different shores, and therefore estimates of all measured variables are likely to be representative of all populations.

For populations of *Pachygrapsus transversus*, all the above estimates, except density, were gathered by visual scrutiny of the rock surface following Flores & Paula (2002a). Crabs were collected during 1 nocturnal low-tide period with the use of head lamps, which increased efficiency. At this time, foraging activity was maximum and crabs could be readily captured, measured, sexed and released. Due to its high mobility and use of inaccessible habitat, such as deep crevices, density estimates were obtained using a different sampling protocol. Because time-consuming marking–recapture techniques were needed (Petersen method; Krebs 1989) density records, at each shore, were only obtained twice for *P. transversus* (December 2005 to January 2006 and October to November 2006). Four transversal transects, 15 m wide, were randomly allocated at each shore, from which adult crabs (carapace width >7.0 mm) were captured by 2 trained people, marked on their carapace with quick-dry metallic ink and released close to their initial positions. Searches stopped when unmarked crabs were no longer found over a period of 10 to 15 min at any given transect. Second visits were conducted 2 d after the first captures, which is long enough to allow re-mixing of crabs within the sampling population and still short enough to avoid a significant bias of density estimates due to moulting. At each shore and sampling period, an average (±SD) of 281 ± 140 crabs were captured and marked during the first visit, and 334 ± 156 were captured during the second visit, of which 58 ± 44 were recaptures. At each transect, the area of the intertidal habitat used by *P. transversus* was estimated by multiplying the transect width (15 m) by the average of 5 measurements of the shore height, perpendicular to the coastline, between the upper limits of the mixed red algal fringe and the dense chthamalid cover. Such measurements were regularly spaced at 3 m intervals, thus covering the whole transect width. Transect sampling areas averaged 81.4 ± 26.4 m². For each transect, abundance was calculated using the correction proposed by Seber (1982):

$$\hat{N} = \frac{(M+1)(C+1)}{R+1} - 1 \qquad (1)$$

where $\hat{N}$ is the estimate of the number of crabs, M is the number of individuals marked in the first sample,

C is the total of individuals captured in the second sample and R is the number of individuals in the second sample that were found marked. Density values were calculated as the estimate of the number of individuals at a given transect divided by its area. Density estimates, from each transect and year, were considered replicate values in statistical analyses (see below).

In order to measure fecundity in *Pachygrapsus transversus* populations, 28 ovigerous females were selected at each shore, during each of 3 different breeding seasons (early 2005, late 2005, late 2006). Those crabs were randomly removed from the pool of individuals examined during regular nocturnal surveys and were immediately separated in individual sealed plastic bags. For any given season and shore, the examined ovigerous crab pool was obtained from 2 consecutive sampling dates.

Populations of the spider crab *Epialtus brasiliensis* were sampled by removing four ~1 kg samples of *Sargassum* spp. during each visit, randomly collected along the shore. These samples were brought to the laboratory and frozen.

Laboratory procedures. In order to estimate size-specific fecundity, ovigerous *Pachygrapsus transversus* females were measured and their eggs were detached from pleopods, suspended in seawater and sub-sampled, following Flores & Paula (2002b).

In the case of *Epialtus brasiliensis*, the algal material was thawed and broken into little pieces; these were vigorously washed in a large plastic bucket. The contents remaining after washing were then sieved through a 0.5 mm mesh and placed in a white plastic tray, covered with a 1 cm water layer, on which a grid was drawn to facilitate sorting out the animals. Crabs were placed in labelled small plastic bags and returned to the freezer. All specimens were measured and sexed under a dissecting microscope provided with a micrometric ocular. Juveniles were easily distinguished from adults based on the morphology of chelipeds in males and abdominal morphology in females. In this species, fecundity is much lower and could be estimated by direct counting. Since mechanical procedures to sort the samples cause backward flapping of the abdomen in some females, and hence egg loss, only crabs retaining the natural abdominal position, i.e. tightly fit to the sternum forming a brood chamber, were used for fecundity estimates. A total of 30 ovigerous females per shore and year were available for analyses.

Numerical and statistical analyses. In the present study we used the ovigerous ratio as a proxy for brooding frequency, because spatial differences of average temperature, a factor strongly affecting incubation period (Wear 1974), remained almost null during a

period of 71 d (8 April to 18 June 2004) among 4 sites spanning the study region (Fortaleza: 24.60°C; Domingas Dias: 24.39°C; Base: 24.90°C; Enseada: 24.43°C, as retrieved from continuous readings of temperature recorders installed at 1 m depth). These relative estimates of brooding frequency were combined with the remaining variables to produce estimates of egg production.

Adult density was calculated as individuals per surface area for *Pachygrapsus transversus* and individuals per canopy wet weight for *Epialtus brasiliensis*. For the former, the sampling procedure excluded juveniles *a priori*. For the latter, juveniles could be readily identified in samples and were removed from analyses. Sex ratio stands for the number of adult females divided by the total number of adult females and males. The relative frequency of ovigerous crabs was calculated as their proportion among adult females. In order to remove the effect of size, a fecundity index (FI) was computed as:

$$FI = NE/CW^b \qquad (2)$$

where NE is the number of eggs, CW stands for carapace width and b is the allometric constant obtained from estimating size-specific fecundity relationships (Somers 1991) for each species separately, using all ovigerous females across shores and years.

Replicate measures of adult sex ratios, sizes of ovigerous females and their relative frequencies were obtained every 2 mo for each shore, thus enabling both spatial (between bays and among shores) and temporal (inter-annual) comparisons. In the case of adult *Pachygrapsus transversus* density, sampling took place on only 2 occasions, and data from transects for each shore were considered as replicate observations. The fecundity data for *Epialtus brasiliensis* were grouped within years (2005, 2006), while specific sampling for ovigerous *P. transversus* was undertaken during 3 different seasons, as explained above. The overall relative egg production was first compared among sites. For this, overall estimates at each site were obtained by multiplying the estimates for each parameter, and then dividing this product by the highest value recorded among all sampled sites. More detailed spatial analyses and the temporal consistency of the examined traits were carried out using a specific ANOVA model. In these analyses, 3 factors were considered to test for spatial and temporal consistency of reproductive traits: 'year', with 2 levels concerning inter-annual variability, except for the *P. transversus* fecundity index, in which 3 breeding seasons were included: 'bay', with 2 levels (Fortaleza and Flamengo); and 'shore', as a random factor nested in 'bay', with 3 levels corresponding to the shores sampled. Six replicates were used for analyses involving frequency and size of

ovigerous females and adult sex ratios. Four replicates were used to examine adult *P. transversus* density, corresponding to random transversal sectors sampled at each shore. Samples of *Sargassum* spp. were all regarded as independent observations, and therefore 24 replicates were included to analyse adult *E. brasiliensis* density. The fecundity estimate for each examined female was considered an independent value, totalling 28 replicate observations for each breeding season in *P. transversus*, and 30 replicates each year for *E. brasiliensis*. The Cochran's procedure was used to test homogeneity of variances. Homoscedasticity was verified in all cases, except for the *E. brasiliensis* density data. In this case, the square-root transformation did not solve the issue, but the analysis was run anyway since replication was very high, thus preserving the strength of this procedure (Underwood 1997). When needed, the Student-Newman-Keuls (SNK) test was used for *a posteriori* comparisons. The outcomes of analyses testing fecundity and adult density differences could not be directly compared between species because point estimates (density) or variability during only a part of the breeding season (fecundity index) were used in the analyses for *P. transversus*.

Positive and negative linear correlations between adult density and reproductive traits varying consistently over time at the shore scale were tested to indicate whether component Allee effects (Berec et al. 2006) or intra-specific competition, respectively, might take place at the shore spatial scale. In *Pachygrapsus transversus*, the data indicated spatial differences in the size of breeding females. Extreme percentiles (P_2 and P_{98}) in overall size-frequency distributions of ovigerous females at each shore, not their shape, were regarded as indices of absolute growth. Their difference ($P_{98} - P_2$) may reflect the potential growth after reaching maturity in this grapsid species, and its correlation with relevant reproductive parameters was tested in order to advance possible trade-offs between reproductive output and growth.

RESULTS

Size structure and size-specific fecundity

Size-specific fecundity trends in these species followed the patterns repeatedly reported for brachyuran crabs. The allometric model fit overall fecundity data for *Pachygrapsus transversus* ($r_{pt} = 0.92$) and *Epialtus brasiliensis* ($r_{eb} = 0.45$) (p < 0.0001 in both cases), but slope values were significantly <3.00 ($b_{pt} = 2.67$; $b_{eb} = 1.47$; p < 0.0001 in both cases), which is the expected value under the isometric condition. The average

(±SD) number of eggs was 6647 ± 4375 for *Pachygrapsus transversus* and 175 ± 71 for *Epialtus brasiliensis*. Slope estimates were used to calculate the fecundity index for each crab, allowing comparisons of clutch size among crabs of varying size.

Although we lacked valid measurements of juvenile recruitment and adult mortality, a detailed description of the population structure of these species at the sampled shores was used to aid the interpretation of results on the spatial variability of adult density and average size of breeding females. For both species, the population structure varied among the sampled shores, more markedly for *Pachygrapsus transversus*; bimodal distributions were evident at Enseada and Domingas Dias, they appeared to be present at Bravinha and Base, while unimodal distributions were observed at Ponta da Fortaleza and Perequê, left-skewed in the latter (Fig. 2). In this species, the early modal group included juveniles and adults in all populations. In the case of *Epialtus brasiliensis*, all populations were composed predominantly of 2 modal groups, with clear segregation between juveniles and adults (Fig. 3).
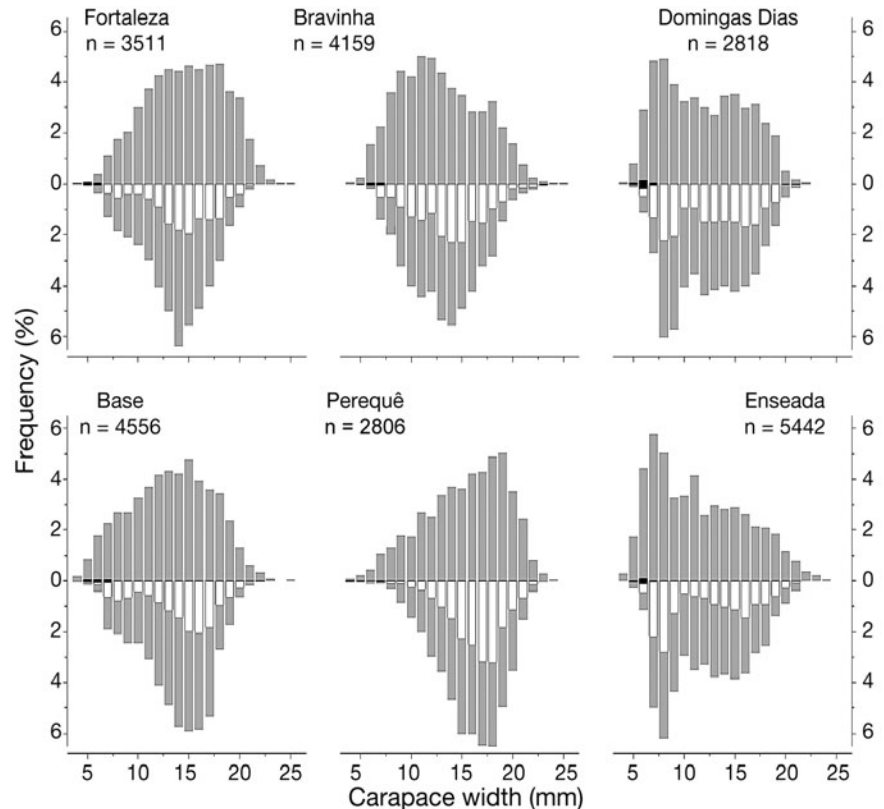

Fig. 2. *Pachygrapsus transversus*. Overall size-frequency distributions for the sampled populations. Males are shown above the origin, and females, below. Individuals too small to be sexed are shown in black, and ovigerous females, in white

Overall shore-specific estimates of reproductive parameters

Overall among-shore variations of measured parameters allowed a first appraisal of the relative importance of each variable determining reproductive output in these crab populations. Coefficients of variation were calculated to allow comparisons among parameters with very different average values. The higher the coefficient of variation for a given parameter, the more it accounts for among-shore differences of overall egg production. Exploratory analyses of the data revealed relatively high variation of average values of the tested parameters at the shore-specific spatial scale (Table 1). As expected, the coefficient of variation was highest for adult density (42.6 to 43.7%), but rather large variability was also found in different reproductive parameters, mainly the relative frequency of ovigerous females (9.4 to 28.7%), their fecundity index (*Epialtus brasiliensis*: 10.0%) and size (*Pachygrapsus transversus*: 9.1%). As a result, ranks of point estimates of over-

all egg production are not coincident with ranks in adult density, suggesting the importance of other variables further determining the reproductive output of populations, which varied, on average, by 33.1% for *P. transversus* and 53.5% for *E. brasiliensis*.

Temporal and spatial variability of tested variables

Verifying whether or not the measured parameters varied consistently over the sampling period at the examined spatial scales may indicate their importance for setting differences over the long term. The overall variation among the shores shown above would not necessarily reflect coherent spatial differences through time, but, in this case, parameters showing a large coefficient of variation (Table 1) also exhibited persistent spatial trends. The statistical model used for this purpose allowed testing of not only the significance of variation between bays and among shores within bays, but also their consistency over 2 consecutive years. Significant second-order interactions between spatial sources of variation ('shore [bay]' or 'bay') and time (year) would indicate non-consistent trends. Results are summarized in Table 2.
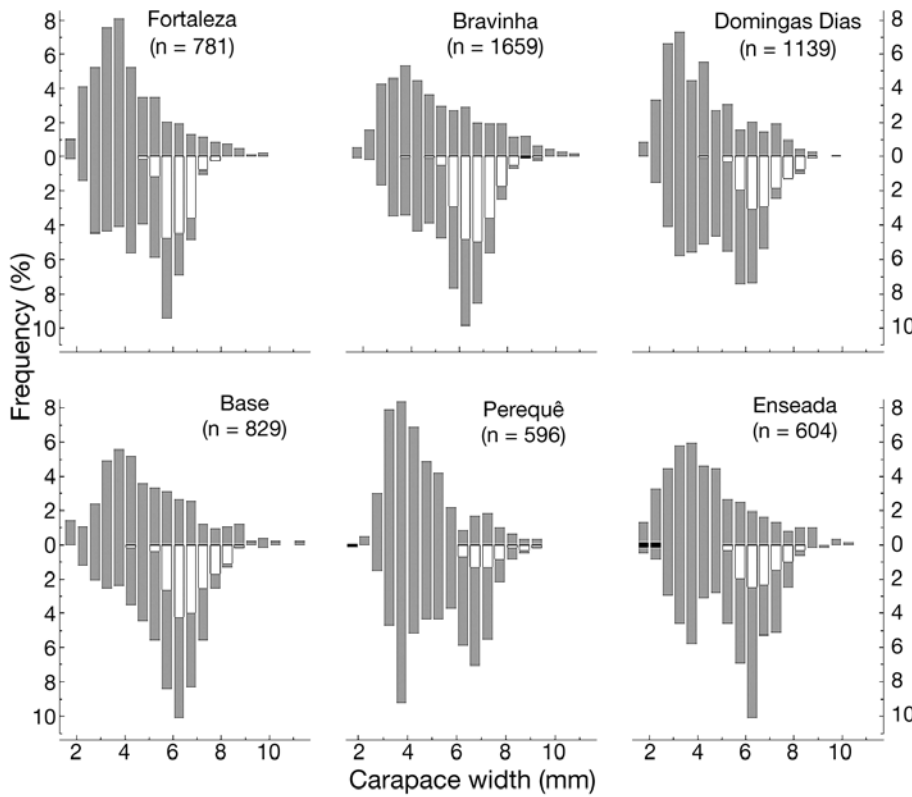
Fig. 3. *Epialtus brasiliensis*. Overall size-frequency distributions for the sampled populations. Details as in Fig. 2

For both species, adult density was a shore-specific feature. In spite of large error margins around marking–recapture density estimates (95% confidence intervals usually spanning 40 to 45% of point estimates), differences among shores were observed for *Pachygrapsus transversus* in Flamengo Bay, namely a much higher crab density at Base than at the other sites (Fig. 4a). For *Epialtus brasiliensis*, shore differences of similar magnitude were found within each bay (Fig. 4b) and more frequently rendered statistical significance due to larger sample size.

The ratio of ovigerous females varied consistently among shores in these 2 species, and also between the sampled embayments in the case of *Epialtus brasiliensis*. In this species, consistent spatial differences of the ovigerous ratio accompanied inter-annual variability (almost 2-fold; Fig. 5a). Spatial contrasts were particularly high (up to 160%) despite an overall

Table 1. *Pachygrapsus transversus*, *Epialtus brasiliensis*. Average shore-specific values for the variables examined. Adult density is expressed as ind. m^{-2} for *P. transversus* (over the shore surface) and ind. kg^{-1} for *E. brasiliensis* (within *Sargassum* spp. samples). Sex-ratio values stand for the proportion of adult females relative to all adults. Ovigerous ratio was calculated as the proportion of brooding individuals relative to the adult female population. Average size is expressed in mm, and fecundity indices were determined as indicated in 'Materials and methods'. For any given variable, relative numbers (parentheses) correspond to the estimates obtained at each shore divided by the highest value recorded. The overall relative egg production at each site was obtained by first multiplying the estimates for each parameter and then calculating relative values as above. CV: coefficient of variation, calculated from overall average values at each shore; shore labels as in Fig. 1

	Adult density		Sex ratio		Ovigerous females Ratio		Average size		Fecundity index		Overall relative egg production
Pachygrapsus transversus											
Pf	4.31	(0.61)	0.47	(0.90)	0.30	(0.91)	13.84	(0.89)	4.64	(0.88)	0.67
Br	2.47	(0.35)	0.48	(0.92)	0.33	(1.00)	13.61	(0.87)	5.21	(0.98)	0.47
Dd	4.26	(0.60)	0.50	(0.96)	0.30	(0.91)	12.37	(0.79)	5.29	(1.00)	0.71
Bs	7.05	(1.00)	0.48	(0.92)	0.26	(0.79)	13.11	(0.84)	5.06	(0.96)	1.00
Pm	2.37	(0.34)	0.52	(1.00)	0.28	(0.85)	15.59	(1.00)	5.14	(0.97)	0.47
En	3.62	(0.51)	0.48	(0.92)	0.26	(0.79)	12.32	(0.79)	5.02	(0.95)	0.48
CV	42.6		3.8		9.4		9.1		4.3		33.0
Epialtus brasiliensis											
Pf	2.72	(0.37)	0.81	(0.93)	0.65	(1.00)	6.21	(0.92)	10.74	(0.82)	0.40
Br	7.34	(1.00)	0.81	(0.93)	0.59	(0.91)	6.59	(0.97)	10.30	(0.79)	1.00
Dd	4.63	(0.63)	0.83	(0.95)	0.53	(0.82)	5.95	(0.88)	10.29	(0.79)	0.53
Bs	4.22	(0.57)	0.87	(1.00)	0.47	(0.72)	6.63	(0.98)	12.14	(0.93)	0.59
Pm	2.41	(0.33)	0.86	(0.99)	0.41	(0.63)	6.78	(1.00)	13.03	(1.00)	0.32
En	3.34	(0.46)	0.79	(0.91)	0.26	(0.40)	6.71	(0.99)	12.08	(0.93)	0.23
CV	43.7		3.8		28.7		4.9		10.0		53.3

Table 2. *Pachygrapsus transversus, Epialtus brasiliensis.* Summary results of ANOVA analyses testing spatial and temporal consistency of measured reproductive parameters. Data were square-root transformed in the case of *Epialtus* adult density. NS: not significant; *p < 0.05; **p < 0.01; ***p < 0.001

| | Adult density | | | Sex ratio | | | Ovigerous individuals | | | | | | | | |
| | | | | | | | Ratio | | | Size | | | Fecundity index | | |
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Pachygrapsus transversus															
Year	1	0.02	NS	1	0.44	NS	1	4.21	NS	1	0.03	NS	2	5.54	*
Bay	1	0.19	NS	1	0.91	NS	1	8.03	*	1	0.14	NS	1	0.06	NS
Shore (Bay)	4	6.36	***	4	1.04	NS	4	0.09	NS	4	10.28	***	4	2.17	NS
Year × Bay	1	0.21	NS	1	2.04	NS	1	1.27	NS	1	0.14	NS	2	0.14	NS
Year × Shore (Bay)	4	1.05	NS	4	0.31	NS	4	0.20	NS	4	2.00	NS	8	3.68	***
Residual	36			60			60			60			486		
Cochran's C	0.183	NS		0.148	NS		0.125	NS		0.158	NS		0.100	NS	
Epialtus brasiliensis															
Year	1	0.02	NS	1	0.52	NS	1	30.61	**	1	0.03	NS	1	0.01	NS
Bay	1	0.97	NS	1	0.77	NS	1	8.47	*	1	5.79	NS	1	33.58	***
Shore (Bay)	4	9.12	***	4	0.66	NS	4	2.98	*	4	2.08	NS	4	0.70	NS
Year × Bay	1	0.01	NS	1	3.06	NS	1	0.80	NS	1	1.62	NS	1	3.77	NS
Year × Shore (Bay)	4	1.07	NS	4	0.37	NS	4	1.10	NS	4	0.45	NS	4	2.14	NS
Residual	276			60			60			60			348		
Cochran's C	0.169	p < 0.05		0.200	NS		0.181	NS		0.259	NS		0.121	NS	

very large inter-annual increase in the ovigerous ratio from 2005 to 2006, which remained consistent across sampling sites, since second-order interactions were not significant (Table 2). A higher ovigerous frequency was observed in Fortaleza Bay, where no among-shore differences were found, compared to Flamengo Bay, where the proportion of females carrying eggs at Base and Perequê was significantly higher than at Enseada (Fig. 5b). In the case of *Pachygrapsus transversus*, no temporal differences were observed and significant
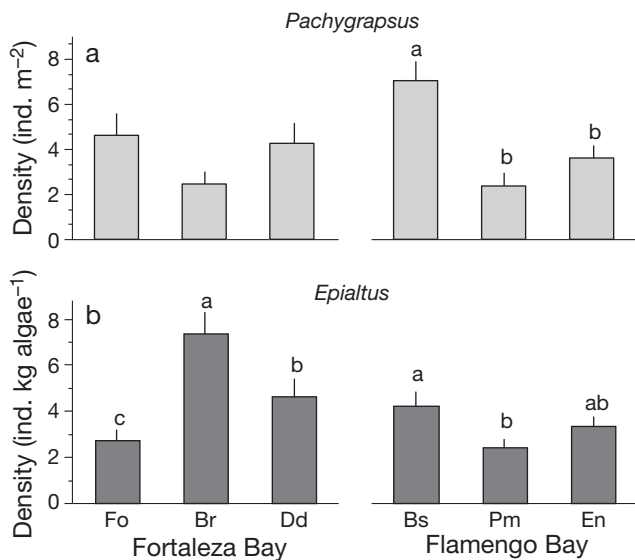

Fig. 4. *Pachygrapsus transversus, Epialtus brasiliensis.* Among-shore differences of adult density for (a) *P. transversus* and (b) *E. brasiliensis.* Data are means ± SE. Values of bars sharing the same letter are not statistically different (Student-Newman-Keuls [SNK] tests; p > 0.05). Shore labels as in Fig. 1
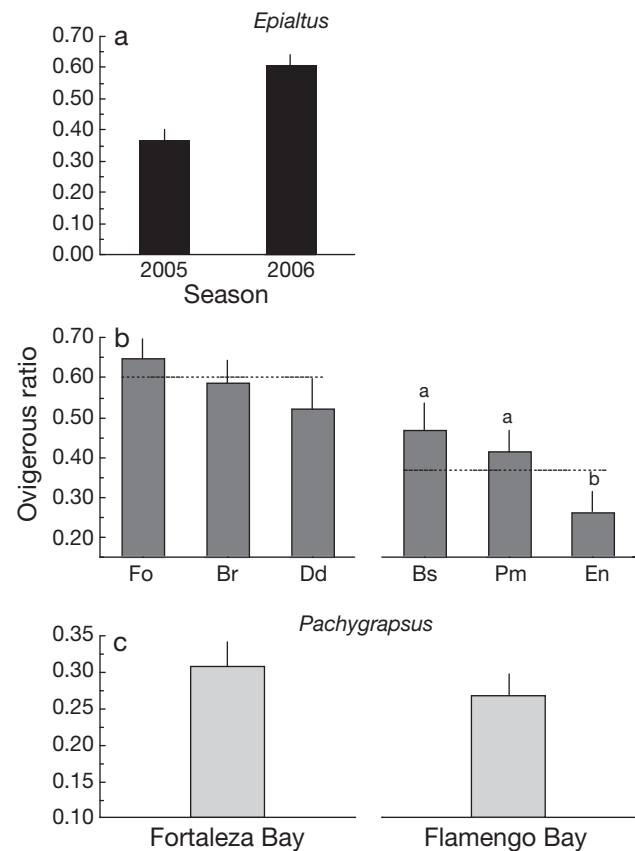

Fig. 5. *Epialtus brasiliensis, Pachygrapsus transversus.* (a) Temporal and (b,c) spatial patterns of the ovigerous ratio. Dashed lines indicate average values at the bay-specific spatial scale for *E. brasiliensis.* Data are means ± SE. Values of bars sharing the same letter are not statistically different (SNK tests; p > 0.05). Shore labels as in Fig. 1

variation, although slighter, is limited to the bay scale (Fig. 5c).

Spatially consistent variability was species specific for other reproductive traits. Size of brooding females varied among shores within each bay for *Pachygrapsus transversus* (Table 2). Brooding females were larger at Ponta da Fortaleza and Bravinha than at Domingas Dias in Fortaleza Bay, and larger at Perequê compared to Base and Enseada in Flamengo Bay (Fig. 6). In the case of *Epialtus brasiliensis*, size variation of ovigerous females was small across shores (Fig. 3), and not statistically significant (Table 2). Fecundity followed a between-bay trend for *E. brasiliensis* (Table 2), with more fecund females at Flamengo, where the average fecundity index was 12.42 compared to 10.44 at Fortaleza, thus corresponding to a difference of 19%. The fecundity index for *P. transversus* is also heterogeneous, but differences are not spatially consistent at the scales tested, at least when results from different seasons are compared (Table 2). No contrasts were observed at Flamengo Bay throughout the study, but were significant for all 3 sampled seasons at Fortaleza Bay. The fecundity index at Ponta da Fortaleza was highest or lowest in different seasons (early 2005 and late 2005, respectively, SNK, $p < 0.05$). During late 2006, the highest fecundity index was recorded at Domingas Dias (SNK, $p < 0.05$).

The sex ratio was remarkably constant over shores, bays and sampled years for both species (Table 2), close to balanced for *Pachygrapsus transversus*, but strongly biased towards females for *Epialtus brasiliensis* (Table 1). Considering the overall record for each species, departures from 1:1 were significant in both cases (*G*-test, $p < 0.001$).

In general terms, the reproductive traits exhibiting consistent spatial structure were, in order of importance, adult density and ovigerous ratio for both species, followed by adult size in *Pachygrapsus transversus* and the fecundity index in *Epialtus brasiliensis*. The relative magnitudes of variation for such parameters are shown for both species in Fig. 7. Shores scored differently for each species, and the relative weight of the sampled parameters varied as well. Adult density, although the most important variable, was not determinant in setting shore ranks. For instance, the shores with the lowest estimated reproductive potential ranked relatively high in adult density, namely fourth for both *P. transversus* and *E. brasiliensis*. The sites where estimates were the highest differed between species, but, if these shores (Base and Bravinha) are not considered, a slightly decreasing trend is apparent from Ponta da Fortaleza to Enseada, the latter corresponding to the lowest overall reproductive potential.
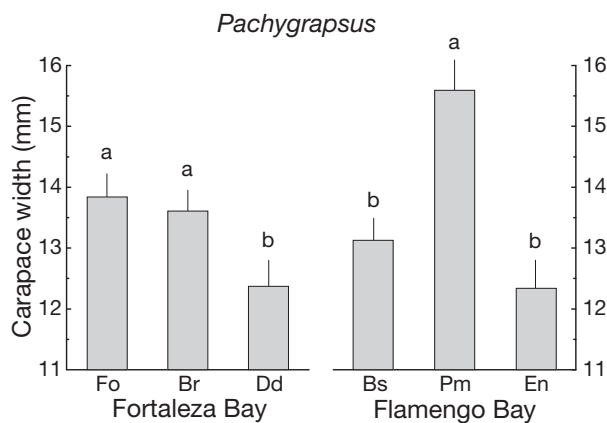

Fig. 6. *Pachygrapsus transversus*. Among-shore differences of the size of breeding females in each sampled bay. Data are means ± SE. Values of bars sharing the same letter are not statistically different (SNK tests; $p > 0.05$). Shore labels as in Fig. 1
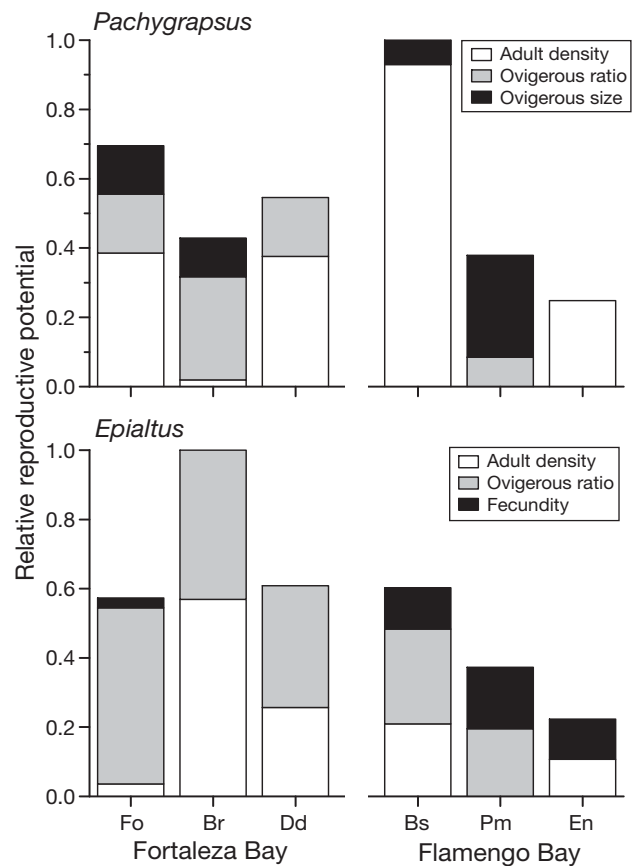

Fig. 7. *Pachygrapsus transversus*, *Epialtus brasiliensis*. Estimated relative reproduction potential of *P. transversus* and *E. brasiliensis* at the sampled shores. Values were calculated directly from the relative average shore-specific values (shown in Table 1) by: (1) subtracting the lower value among shores across each parameter, (2) summing parameter values for each shore, (3) dividing each value, across shores and parameters, by the highest sum obtained in Step 2, and (4) summing again all parameter values for each shore, so that the site with the highest relative reproductive potential scored 1.00. Shore labels as in Fig. 1

Because parameters varying persistently are also those responsible for the bulk of spatial structure, shore ranks in Fig. 7 differ slightly from those shown in Table 1. Yet, these rankings are likely to better reflect average among-shore differences of reproductive potential over time, because the parameters excluded either showed no spatial variability at all, or varied in an unpredictable way.

Density-dependency of shore-consistent traits

Since adult density varied in a persistent way across sites in both species, the correlation between this variable and other shore-consistent traits could suggest the occurrence of self-regulatory processes within these populations. Correlations were run using density and ovigerous ratio estimates averaged for each shore and year for *Epialtus brasiliensis*. In the case of *Pachygrapsus transversus*, size data were pooled for females recorded in late 2005 and late 2006, thus matching the times when density estimates were obtained. *E. brasiliensis* density was not correlated to ovigerous ratio (n = 12, r = 0.20, p > 0.05), and *P. transversus* density was not correlated to average size of breeding females (n = 12, r = −0.19, p > 0.05).

Potential growth versus ovigerous ratio in *Pachygrapsus transversus*

Since reproduction and growth are competing processes, average adult size could conceivably explain the spatial variation of the ovigerous ratio in *Pachygrapsus transversus*. Extreme percentiles (P_2 and P_{98}) in size-frequency distributions of ovigerous females are positively correlated (n = 6, r = 0.82, p < 0.05), suggesting that absolute growth through adulthood is a shore-specific feature. Extremely large percentiles (P_{98}) are also good indicators of average adult size (n = 6, r = 0.88, p < 0.05). Potential growth after maturity ($P_{98} - P_2$) is not correlated to ovigerous ratio (n = 6, r = 0.08, p > 0.05).

DISCUSSION

We have reported a clear spatial structure for the reproductive potential of brachyuran crab populations living on rocky shores. Spatial patterns of measured parameters were mostly evident at the shore scale, but the ovigerous ratio, a proxy of brooding frequency, in both species, and the fecundity index, in *Epialtus brasiliensis*, varied significantly at a larger scale, encompassing the sampled bays. While some demographic

and reproductive variables did not show any spatial or temporal variations, or varied inconsistently, a number of traits did exhibit a persistent spatial pattern. Adult density coupled with brooding frequency largely determined the variability in reproductive potential among sites, and these 2 parameters are likely to be key variables long term.

Our results suggest that spatial variability of adult density, often used as a proxy to assess potential reproductive output of marine populations (e.g. Lipcius et al. 1997, Arnold et al. 1998), largely underlies spatial patterns of egg production in these crab populations. Well-documented local crab aggregations, at a scale of metres or 10s of metres (Colby & Fonseca 1984, Flores et al. 2005), may be more important than density variability at larger scales, blurring eventual patterns along coastlines. In the present study, however, variability among populations inhabiting different shores was found to be quite large and consistent over time. Interestingly, differences did not exist at the larger bay scale, providing important insight into the factors affecting population density in this region.

Larval settlement and juvenile recruitment were repeatedly suggested to be leading processes regulating the size of benthic populations, and spatial scales of their natural variability include the 'shore' scale tested herein (Jenkins et al. 2000, Flores et al. 2002). The extent to which recruitment success affects adult density is inversely related to resource limitation for developing stages. In decapod crustaceans, shelter shortage is particularly important and may often cause a demographic bottleneck at different times during benthic ontogeny (Beck 1995, Halpern 2004). We did not attempt to measure either juvenile recruitment or mortality in the present study, but size-frequency distributions at the sampled shores suggest that both processes shape population structure in the 2 studied species. Bimodal distributions, representing a juvenile recruitment pulse and a less abundant group in which adults prevail, were found for both species. Yet, populations of *Pachygrapsus transversus* at Fortaleza, Bravinha and Perequê, where the first modal group is not obvious, may be strongly recruitment limited. Particularly evident is that ovigerous *P. transversus* are already present in the early modal group in all populations, while ovigerous *Epialtus brasiliensis* are exclusively found in the later modal group. Because the onset of reproductive maturity takes place very early in *P. transversus*, females start reproducing while still vulnerable to high early mortality. This is not the case for *E. brasiliensis*, in which only larger females, in their final anecdysial stage, constitute the breeding population. This explains why the size of adults was very stable in *E. brasiliensis*, but changed considerably, and, consistently, in *P. transversus*.

Since *Pachygrapsus transversus* is the only abundant grapsid species in the study region, intra-specific competition could be a major factor controlling growth rate and therefore average adult size. Yet, adult size and density in the sampled populations were not correlated, suggesting that resource availability may be more important. Sex ratios were markedly constant in both species, implying a very stable mating system. Balanced sex ratios in the case of *P. transversus* indicate that sex-dependent sources of mortality, such as preferential predation for the more conspicuous or active sex (Ribeiro et al. 2003), are doubtful. Biological interactions are therefore unlikely to set any spatial structure of these variables.

Besides adult density, we found that different reproductive parameters vary among populations of these crab species, some of them consistently over at least 2 yr. Whether these spatial patterns remain over longer time scales is an open question, and would involve the outcome of long-term environmental change. Particularly important is that brooding frequency varied consistently at the bay scale for *Pachygrapsus transversus* and at both the bay and the shore scale for *Epialtus brasiliensis*. Even when inter-annual variation of the ovigerous ratio occurred, as observed for the latter species, such a change was similar across sites, indicating that factors driving brooding frequency operate at spatial scales ranging from at least units to 10s of kilometres.

Variability of brood production could be driven by density-dependent processes. Lack of mating encounters, for mobile invertebrates, and low availability of gametes in the water column, in the case of broadcast spawners, may reduce reproductive output of marine animals (Levitan et al. 1992, Stoner & Ray-Culp 2000, Gascoigne & Lipcius 2004), constituting a component Allee effect (sensu Berec et al. 2006) because the fitness of a single individual would decrease as population size also declines. The opposite hypothesis is that the density of crabs may be too high, leading to intraspecific competition for resources reflected in less frequent brooding, as suggested for mud crabs (Henmi 1992). Neither of these hypotheses is supported by our results. Spatially consistent variation of the ovigerous ratio is not related to adult density in *Epialtus brasiliensis*. Such a test would be meaningless for *Pachygrapsus transversus* because among-shore variation of the ovigerous ratio was not significant.

Yet, it is interesting to note that the ovigerous ratio increased at Fortaleza Bay in both species and, for *Epialtus brasiliensis*, the ovigerous ratio actually decreased over a gradient from Ponta da Fortaleza to Enseada. Several environmental factors may follow such a steady trend and therefore may explain spatial variability of brooding frequency. For instance, wave exposure and salinity decline from Fortaleza to Flamengo Bay. These factors may well alter intertidal sessile assemblages and epiphytic cover of *Sargassum* spp. blades, thus changing availability of food resources, which was found to deeply affect brooding rate in calanoid copepods (Runge 1984, Niehoff 2004). Alternatively, water-borne pollutants are more likely to affect intertidal assemblages in Flamengo Bay due to the settlement of a larger human population and the activities of a recreational harbour, the latter potentially causing a drastic reduction of spawning frequency, as observed in mytilid bivalves (Carr & Linden 1984).

Between-species comparisons of fecundity trends are complicated because year-round sampling was not possible for *Pachygrapsus transversus*. Yet, sampling across half a breeding season would target a fraction of 39 to 53% of the ovigerous crabs expected for the whole year (Flores & Negreiros Fransozo 1998), and thus should correspond to a large fraction of the interannual variation. For *Epialtus brasiliensis*, crabs obtained over 3 mo within the main reproductive season represented 41 to 51% of the whole sample. Therefore, although crabs sampled year-round were included in analyses, results will largely reflect what happened in summer. In these 2 species, the fecundity index showed spatial variability, which was apparently inconsistent in the case of *P. transversus*. For this grapsid, the fecundity index seems a very plastic trait, dependent on shore-specific conditions and changing on an infra-seasonal time scale. Consistent betweenbay differences in *E. brasiliensis* fecundity are considerable, approximately 20%, but still much less than what was found for the proportion of ovigerous females. Conversely, higher fecundity was found in populations at Flamengo Bay. Hence, factors affecting fecundity are likely to differ between these crab species and are probably less predictable in *P. transversus*, which lives in a more heterogeneous habitat. The environmental conditions responsible for setting largescale patterns of fecundity and brooding frequency are certainly different for both species, because these parameters followed quite different spatial trends.

Despite the clear importance of adult population density, significant improvements for the correct identification of potential source populations should rely, not only on the analysis of population density and structure, but also on estimates of the capacity of individuals to reproduce. In the case of the crab species examined in the present study, brooding frequency, manifested as the ratio of ovigerous females, varied largely among shores and between bays, deserving special attention. Because we found no support for density-dependent control of reproductive effort, bottom-up control seems a more plausible explanation

for the patterns observed. For both species, the number of broods produced increased in gradients from low to moderate wave exposure and from high to low human impact. Enhanced supply of valuable food resources driven by higher hydrodynamism, or contamination by water-borne pollutants, may both explain the variation in brooding frequency, which proved to be the most important non-demographic component of reproductive output in these crab populations.

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