



FEATURE ARTICLE

# Abundance and active patch selection modulate reproductive connectivity and fitness of pea crabs living on sand dollars

Juliana A. Souza<sup>1,2,\*</sup>, Augusto A. V. Flores<sup>1,2</sup>

<sup>1</sup>Department of Biology, Faculty of Philosophy, Sciences and Letters of Ribeirão Preto, University of São Paulo, Ribeirão Preto, 14040-901, Brazil

<sup>2</sup>Center for Marine Biology, University of São Paulo, São Sebastião, 11612-109, Brazil

**ABSTRACT:** Connectivity is paramount for population stability, but the mechanisms underlying the distribution of populated patches and how they affect reproductive connectivity and individual fitness remain elusive. Here, we mapped the distribution of sand dollars *Encope emarginata* as habitat patches for obligate-commensal pea crabs *Dissodactylus crinitichelis*, at several sites in Brazil. At occupied patches, we assessed whole-crab population structure and the fitness of ovigerous females. By doing so, we obtained population snapshots under varying environmental conditions that portrayed the natural variation of connectivity and fitness in the region. While sand dollar supply did not limit the size of crab populations, overall crab abundance limited reproductive connectivity and the potential for offspring production. However, except for cases where connectivity was extremely low and high, active crab aggregations enhanced reproductive potential despite the overall random distribution of sand dollars. Crab interactions within hosts, likely controlled by larger females, added to reproductive connectivity by increasing the frequency of mating pairs. Differently from the population-level case, effects of crab abundance on individual fitness were dual and only detectable when abundance was lowest (positive) or highest (negative), so that fitness remained high at intermediate crab abundance, decreasing when it became either too low (e.g. Allee effects) or too high (e.g. energetic costs of intraspecific competition).



An overturned sand dollar *Encope emarginata*, showing the natural position of a commensal pinnotherid crab *Dissodactylus crinitichelis*

Photo: Alvaro E. Migotto

**KEY WORDS:** *Dissodactylus crinitichelis* · *Encope emarginata* · Metapopulation dynamics · Benthic ecology · Commensalism · Chemical attraction · Spatial distribution · Pinnotheridae

## 1. INTRODUCTION

Environmental heterogeneity is commonplace in virtually all terrestrial and aquatic habitats, profoundly affecting the abundance and distribution of species (Stein et al. 2014). Key ecological resources,

\*Corresponding author: julias@usp.br

mostly food and shelter (Bertness & Grosholz 1985, Elzinga et al. 2007, Chamaillé-Jammes et al. 2008), are usually found in discrete habitat patches where individuals aggregate and closely interact, thus forming local populations. At spatial scales large enough to include several such patches, populations typically show a consistent structure, which persists over time through individual migrations connecting populated habitat patches (Hanski 1998, van Nouhuys 2009), as defined by the metapopulation concept (van Nouhuys 2009). Connectivity may relieve intraspecific competition locally (Britton 1989, Nowicki and Vrabec 2011), and in some cases prevent density from decreasing beyond critical thresholds at marginal subpopulations (Fahrig & Merriam 1985, Almany et al. 2009). However, dispersal among occupied patches and colonization of new areas (Stacey et al. 1997, Hanski et al. 2004) can yield high mortality rates, as individuals need to travel over unsuitable habitat where food supply is very limited (Fryxell & Sinclair 1988, Lampert 1989) or predation risk is very high (Wiens 1976, Rodríguez et al. 2001).

Despite the relatively well documented role of connectivity on the overall abundance and stability of animal populations (Hansson 1991, Hanski 1998), little is known about how individual dispersal may affect the spatial arrangement of occupied habitat patches, and how it may affect the rate of conspecific interactions. Mating interactions are particularly relevant, as several populations may be restrained by negative density-dependent effects (e.g. Allee effects; Stephens et al. 1999, Courchamp et al. 2008), in which overall offspring production is limited by the scarcity of encounters among potential mates (Boukal & Berec 2002, Breedveld & Fitze 2015). Therefore, individual dispersal among populated habitat patches may greatly contribute to overall population connectivity and reproductive output. Here we address the effects of reproductive population connectivity, i.e. the dispersal of individuals among subpopulations that survive and reproduce (Pineda et al. 2007), henceforth 'reproductive connectivity', on both the population and the individual level (i.e. fitness). To our knowledge, those effects remain largely unknown (but see e.g. Vandewoestijne et al. 2008 for a study on butterflies, and Matesanz et al. 2015 on baby's breath plants). At the population level, estimates of reproductive connectivity can rely on the intuitive prediction that more frequent migrations will increase reproductive output by increasing encounter rates between potential mates. At the individual level, however, reproductive performance may decrease when population density surpasses an

optimal threshold. This could be the case for species that exploit very specific and small habitat patches, as they are often territorial (Emlen & Oring 1977, Fischer & Fiedler 2001, Ambrosio & Baeza 2016) and face strong intraspecific competition (Weiner 1988, Allen et al. 2008).

Large-scale patterns of reproductive output may be modulated by connectivity, which in the case of marine benthic invertebrates may be viewed as a combined result of processes operating at 2 different spatial scales. Most species undergo a life cycle with the release of free-swimming larvae that usually spend days to weeks in the water column and disperse over distances of a few to tens of km (Shanks 2009). While most studies have emphasized large-scale connectivity through larval dispersal (e.g. Kritzer & Sale 2006, Fobert et al. 2019), less attention has been paid to smaller-scale connectivity involving the movements of adults, which can be complex and underlie important ecological processes (González-Gurriarán et al. 1998, Pittman & McAlpine 2001, Fogarty & Botsford 2006). Post-settlement spatial processes in decapod crustaceans may include foraging movements away from shelters within a given home range, but also larger-scale migrations to avoid unfavorable conditions or exploit different resources (Pittman & McAlpine 2001). Enduring directional migrations often promote the concentration of high numbers of reproductively active adults at temporary habitats where food is abundant (Pittman & McAlpine 2001, Thiel et al. 2003).

To address this topic, we focused on populations of the pea crabs *Dissodactylus crinitichelis* Moreira, 1901, living on sand dollars *Encope emarginata* (Leske, 1778). These crabs are obligatorily associated with sand dollars, so that crab population structure at any given host is likely controlled by classic metapopulation dynamics. Sand dollars provide a hard substrate and food resources for these crabs (Baeza & Hernáez 2015) and constitute island habitats amidst the unsuitable sandy seabed. Crab subpopulations are confined to sand dollar hosts most of the time, but adult connectivity takes place through eventual crab dispersals. The tight relationship with sand dollar hosts shapes the mating systems of pea crabs (Baeza & Thiel 2007), since these species are reportedly promiscuous and frequently switch hosts in order to maximize mating encounters (Thiel et al. 2003, Alves et al. 2017). Pea crab males appear to be more active than females (De Bruyn et al. 2009, Baeza & Hernáez 2015), engaging in simple mate searches (Correa & Thiel 2003, Alves et al. 2017). Chemical cues released by healthy sand dollars, the crabs they host, or

a combination of both, can be used by migrating individuals searching for mates (Souza et al. 2019). On the other hand, females are larger than males (Ambrosio & Baeza 2016, Alves et al. 2017) and markedly territorial (Ambrosio & Baeza 2016), probably guarding sand dollars and expelling any crabs from their host. Still, there is no evidence of durable pair bonds or monogamy, so that females may benefit from mating with multiple mates (McDermott 2006), as they can use sperm from up to 6 different males in a single brood (Jossart et al. 2014). Therefore, restricted access to males may greatly restrain the potential for egg production owing to sperm limitation (e.g. Rondeau & Sainte-Marie 2001, Pardo et al. 2017). The carrying capacity of sand dollars is apparently restricted to 4 adult crabs, with density-dependent processes regulating migration rates to an alternative host (Alves et al. 2017).

We used distribution maps (see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m721p001\\_supp.pdf](http://www.int-res.com/articles/suppl/m721p001_supp.pdf)) at 9 different sites along a 16 km long coastline (Fig. 1) to address 4 research questions. (1) We investigated the distribution patterns of pea crabs among potential sand dollar hosts. Given that chemical attraction is known to mediate this associa-

tion, we hypothesized that the subsets of occupied sand dollars are more aggregated than whole sand dollar populations, making migrations among potential hosts more likely. (2) We assessed the population structure of crabs at occupied sand dollars to elucidate possible mechanisms underlying the formation of non-random distribution patterns. According to previous information on size sexual dimorphism and behavior patterns, we anticipated a higher frequency of sand dollars hosting a heterosexual pair, and a lower frequency of sand dollars bearing 2 or more adult females, as agonistic interactions among them may be intense. (3) We used connectivity metrics based on the incidence function model (IFM; Moilanen & Nieminen 2002) to verify whether site-specific combinations of spatial distribution patterns and crab structure correlate to differences in reproductive connectivity between vacant and occupied sand dollars. We hypothesized that behaviorally driven aggregation patterns ultimately enhance reproductive connectivity. Finally (4), we tested whether the accessibility of females to searching males may disrupt the fitness of the former, by assessing deviations from expected reproductive outputs. Based on the possible roles of Allee effects and intraspecific com-

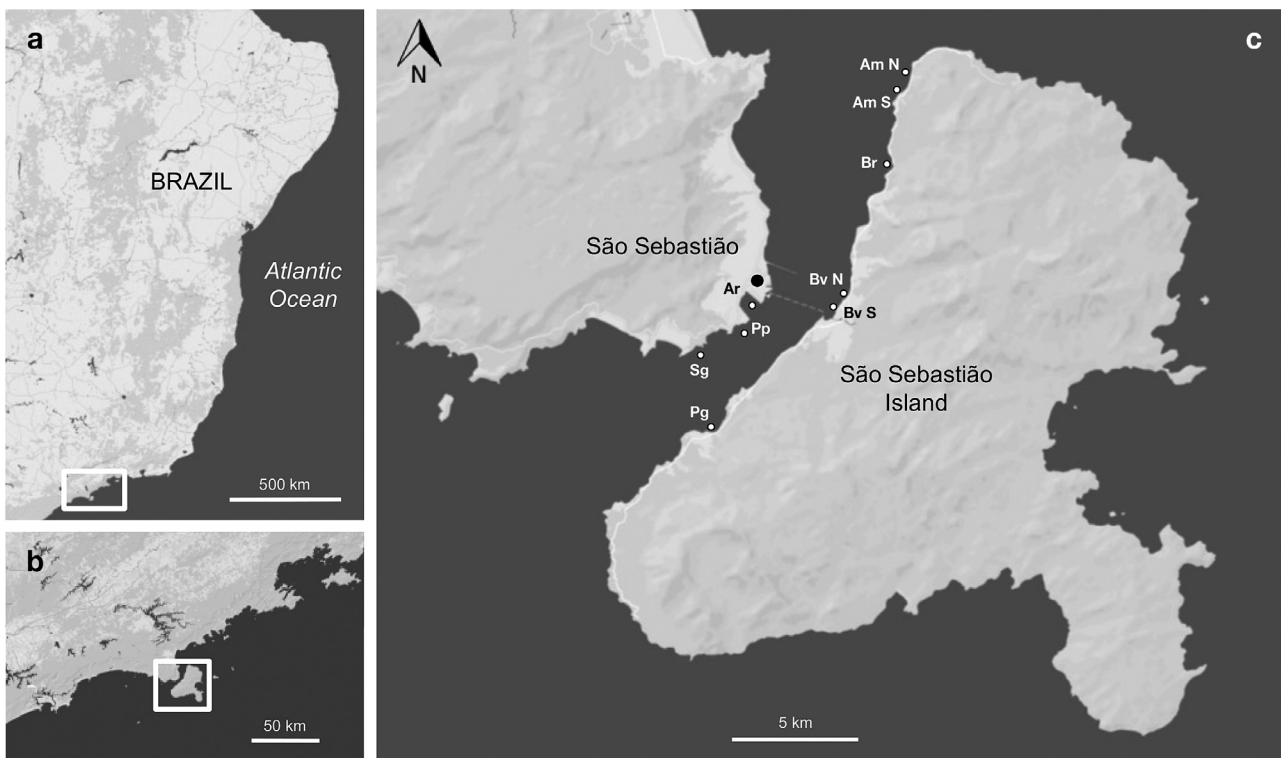


Fig. 1. (a) Northern and central coast of Brazil, (b) the northern coast of São Paulo State and (c) the São Sebastião Channel, showing the position of sampling sites: Armação North (Am N), Armação South (Am S), Barreiros (Br), Barra Velha North (Bv N), Barra Velha South (Bv S), Araçá (Ar), Praia Preta (Pp), Saco Grande (Sg) and Praia Grande (Pg)

petition, we expected that effects on female fitness would change from positive to negative with increasing reproductive connectivity.

## 2. MATERIALS AND METHODS

### 2.1. Study sites, fieldwork and laboratory procedures

We conducted this study along the São Sebastião Channel (SSC), in the State of São Paulo, Brazil (Fig. 1), located in the warm-temperate/subtropical SW Atlantic where sea surface temperature is seasonal, with monthly averages varying from 21°C in winter to 27°C in summer (Wainer & Taschetto 2008). Data retrieved from an oceanographic buoy deployed outside of the Centre for Marine Biology of the University of São Paulo (SP, Brazil; <https://simcosta.furg.br/home>), for the period encompassing this study, further describes this seasonal pattern (Supplementary Fig. S2). Other important physical variables did not show a clear seasonal trend, but there was a long-term increase in oxygen concentration (but still around saturation levels), possibly related to a decrease in salinity, as observed during the first 18 mo of the series (Supplementary Fig. S2). The hydrodynamics of the SSC influence the transport and deposition of sediments along the channel (Netto et al. 2005, Pires-Vanin et al. 2013), with the prevalence of fine sand and clay along the continental margin (Netto et al. 2005).

We established 9 sites for this study, with depths ranging from 2 to 8 m: Armação North (Am N), Armação South (Am S), Barreiros (Ba), Barra Velha North (Bv N), Barra Velha South (Bv S), Araçá (Ar), Praia Preta (Pp), Saco Grande (Sg) and Praia Grande (Pg; Fig. 1c). Fieldwork consisted of obtaining distribution maps of sand dollars and the crabs they host (Fig. S1). At each site, divers first delimited a 15 × 15 m square area with marked ropes. Two pairs of divers then scanned the whole area using parallel leading ropes and a gridded 1 × 1 m PVC quadrat, allowing a coordinate precision of 0.25 m, to define sand dollar positions. Each sand dollar was checked for the presence of adult *Dissodactylus crinitichelis* crabs (carapace width, CW, larger than 3.0 mm), which were removed from hosts and placed in separate labeled Eppendorf tubes; sand dollars were then left at the same spot. Patch size (i.e. sand dollar area) was not measured because there is no significant correlation between the diameter of sand dollars *Encope emarginata* and the number of *D. crinitichelis* crabs they host (Guilherme

et al. 2015). Fieldwork was undertaken in January 2019 (at sites Sg, Pp, Bv N), April 2019 (Ba), July 2019 (Pg), August 2019 (Am N), November 2019 (Ar), January 2020 (Bv S) and March 2020 (Am S), and ovigerous females were always present in samples, indicating continuous reproductive activity (but still possibly following a seasonal cycle, as reported for the warm-temperate congener *D. mellitae*; Bell & Stancyk 1983, George & Boone 2003). In the laboratory, all crabs were sexed and measured (CW to the nearest 0.1 mm), and the eggs of all ovigerous females were counted under a dissecting microscope. Based on the work of Bell & Stancyk (1983) on *D. mellitae*, clutch size, in terms of egg numbers, was not expected to change over the seasonal cycle.

### 2.2. Numerical and statistical analyses

#### 2.2.1. Correlations among sand dollar and crab population parameters

A collinearity matrix for the variables (1) host abundance (abundance of sand dollars), (2) occupancy ratio (proportion of sand dollars hosting crabs), (3) crab abundance (total number of crabs sampled), (4) proportion of female crabs and (5) host demand (crab abundance / host abundance) was calculated for a better understanding of the relationships between crabs and their hosts, and also to select the candidate independent variables that might affect crab connectivity and its potential influence on individual fitness (see Section 2.2.5).

#### 2.2.2. Spatial distributions of sand dollars

For each site map, we developed a matrix of distances between all sand dollars using ImageJ 1.x software (Schneider et al. 2012), and calculated  $\Delta R$ , i.e. the difference between the observed ( $R_o$ ) and the expected ( $R_e$ ) average nearest-neighbor distance of sand dollars for a random distribution, and the respective standard error of this difference ( $S_{R_i}$  Krebs 1999).  $R_e$  was corrected for the absence of boundary strips. Separate 95% confidence intervals (CIs) around  $\Delta R$  estimates were calculated for the distribution of all sand dollars, and the subset of sand dollars hosting an adult crab population. Cases where CIs included 0 indicated random spatial distributions, and cases where CIs spanned only positive or only negative values indicated uniform and clumped distributions, respectively. For sand dollars

hosting crabs, uniform distributions would support crab repulsion through interference competition, while clumped distributions would favor connectivity and the formation of adult crab aggregations.

### 2.2.3. Population structure of crabs

The number of adult crabs populating sand dollars is often low (Alves et al. 2017), so that all combinations of males and females can be easily listed. Here, this number varied from 0 to 3, and therefore the population structure in any given occupied sand dollar necessarily fell in 1 out of only 9 possibilities (i.e. from 1 male [1M] to 3 females [3F]). The expected frequencies of all 9 possible combinations were calculated in 2 steps. First, we determined the expected frequency,  $g(k, \lambda)$ , of sand dollars occupied by 1, 2 and 3 crabs, regardless of their sex, using a zero-truncated Poisson ( $P$ ) distribution (Johnson et al. 2005):

$$g(k, \lambda) = P(x = k | x > 0) = \frac{\lambda^k}{(e^\lambda - 1)k!} \quad (1)$$

where  $k$  is population size (number of crabs, from 1 to 3), and  $\lambda$  is the average estimate of the number of crabs per sand dollar, using the whole sample (including unoccupied sand dollars).

Second, we determined the share of each sexual combination, within each population size, based on the binomial distribution:

$$f(n, k, p) = \binom{k}{n} p^n (1 - p)^{k-n} \quad (2)$$

where  $n$  is the number of males,  $p$  is the estimated proportion of males, and  $(1 - p)$  is the estimated proportion of females. The resulting null model thus assumes a random distribution of crabs among occupied sand dollars and independent occurrence of males and females.

Overall departures from expected values were examined using a chi-squared goodness-of-fit test for the whole dataset and for each site separately. We then tested (1) whether females are less likely than males to share their host with crabs of the same sex, and (2) whether the frequency of sand dollars hosting a sexual pair is higher than could be assumed by chance. For the first hypothesis, we tested the dependence of 'sex' (male, female) and 'number of individuals' ( $1, >1$ ) in  $2 \times 2$  contingency tables, and for the second hypothesis, we ran a goodness-of-fit test for the subset of sand dollars hosting 2 or 3 crabs, to assess whether the formation of heterosexual pairs is more frequent than expected. In both cases, we

used the chi-squared statistic when expected frequencies were all  $\geq 5$ , and the Fisher exact test when this condition could not be met. Critical p-values were adjusted using the Bonferroni correction for multiple comparisons.

### 2.2.4. Connectivity estimates for hosting reproductive populations

We tested whether the potential for hosting a reproductive population (i.e. subpopulations hosting at least 1 mating pair) differed between empty and occupied sand dollars. Increased reproductive connectivity of occupied sand dollars would be a result of successful crab migrations from one host to another, reducing the average distance between potential mates. For that, we used a connectivity measure based on the IFM, following the recommendations of Moilanen & Nieminen (2002). We assumed that individual crab movements would usually not exceed 2.5 m away from the focal sand dollar, as this was the travel distance reported by Telford (1978) for individuals of this same species over 24 h. Only potential hosts within a 2.5 m buffer radius were thus considered to comprise the metapopulation around any given focal sand dollar. Reproductive connectivity estimates ( $C_i$ ) aimed to measure the likelihood of sexual pairings, assuming that the reproductive value of each crab is inversely related to (1) the distance from the focal sand dollar and (2) the proportion of its sex within the buffer radius, and were calculated as:

$$C_i = \sum_{j=1}^n \exp(-d_{ij}) \times 2(n_{mj}\hat{p}_f + n_{fj}\hat{p}_m) \quad (3)$$

where  $n$  is the number of occupied sand dollars within the metapopulation,  $d_{ij}$  is the distance of the reference sand dollar  $j$  to the focal sand dollar  $i$ ,  $n_{mj}$  and  $n_{fj}$  are the number of males and females on the reference sand dollar, and  $\hat{p}_m$  and  $\hat{p}_f$  are the proportion of males and females in the potentially interacting crab metapopulation, respectively. When focal sand dollars were close to margins and the buffer radius partially lay outside of the sampling square area, connectivity estimates were corrected proportionally. Reproductive connectivity values were converted to z-scores ( $z_c$ ), separately for each site, and compared between empty and occupied sand dollars using the Mann-Whitney  $U$ -test procedure, owing to several cases of strong right skewness. Because sample size was in most cases large ( $n > 20$ ), p-values were computed for  $U$  statistics using the normal distribution approximation ( $z_u$ ). Aligned to the expecta-

tions explained above (see Section 2.2.2), occupied sand dollars would be less connected in the case of crab repulsion through agonistic interactions, but more connected if interactions ultimately lead to the proximity of potentially mating pairs.

### 2.2.5. Connectivity estimates on individual fitness

For individual fitness estimates, we focused only on sand dollars hosting ovigerous females. The goal here was to estimate how often focal breeding females would be accessed by searching males within the buffer radius, and then test the correlation between this connectivity measure and a proxy of fitness based on fecundity (i.e. percent departure from expected egg numbers). We anticipated that female reproductive output would be highest when searching males were not so numerous as to compete with females for resources, but also not so low as to reduce mating frequency to the point of sperm limitation (Rondeau & Sainte-Marie 2001, Pardo et al. 2017). Connectivity here was calculated using the same rationale above, but accounting only for the number of potential mates and their distance to focal ovigerous females:

$$C_i = \sum_{j=1}^n \exp(-d_{ij}) \times (n_{mj}) \quad (4)$$

Estimates of fitness were developed by fitting the allometric model to size vs. fecundity data (e.g. Somers 1991) for each site separately, and then measuring the relative residual (in %) of each fecundity estimate from its expected value. A negative correlation between connectivity and fitness (i.e. a negative slope,  $b_f < 0$ ) would suggest that searching males would negatively impact females, such as through exploitative competition, while a positive one ( $b_f > 0$ ) would indicate that mating opportunities are scarce, so that an increased frequency of male accesses ultimately leads to enhanced female fitness by increasing offspring size.

### 2.2.6. Overall relationships of host and crab population parameters on connectivity and its effects on individual fitness

The sand dollar and crab variables examined for collinearities (see Section 2.2.1), except for 'occupancy ratio', which was related to 2 other predictor variables (see Section 3), were used here as independent variables in stepwise backward multiple

regression analyses to indicate potential processes underlying site-to-site differences in the aggregation index ( $R_o/R_e$ ) and reproductive connectivity of occupied sand dollars ( $ZC_{occ}$ , calculated from average  $C_i$  values at each site), and on the effects of female connectivity, as their access to searching males, on individual fitness ( $b_f$ ).

## 3. RESULTS

### 3.1. Correlations among sand dollar and crab population parameters

Most overall variables of crab and sand dollar populations were not significantly correlated (Table 1). Interestingly, there was no correlation between host and crab abundance, and the only significant associations were those between host abundance and occupancy ratio (negatively), and between host demand (n crabs / n sand dollars) and occupancy ratio (positively, Table 1). In other words, these results suggest that host abundance has no significant effects on overall crab abundance (i.e. no habitat limitation), so that with an increasing number of available hosts, the share of occupied ones decreases. However, when the demand for hosts increases, there might be more frequent spillover to empty neighboring patches, increasing the overall share of occupied sand dollars.

### 3.2. Spatial distributions of sand dollars

At all sampled sites, except for Ba and Ar, the spatial distribution of the subset of occupied sand dollars clearly differed from the distribution of the whole sand dollar population (Fig. 2; Fig. S1). Except for Ar, whole sand dollar population distributions were random, while the subsets of occupied sand dollars were always clearly clumped (Fig. 2). Sand dollars hosting crabs were typically 0.3 to 0.5 m closer to their nearest neighbor compared to expected distances for random positions, except for Bv S and Bv N, where occupied sand dollars were even more aggregated, 0.9 to 1.3 m closer than expected, respectively. Bv N was the site with the lowest proportion of occupied hosts (0.059; Table S1). Likewise, Bv S ranked next lowest in the proportion of occupied patches (0.118). Bv N and Bv S both had high abundances of sand dollars (1.7 and 1.3 m<sup>-2</sup>, respectively), similar to Am N and Am S, which had the highest abundances of sand

Table 1. Collinearity matrix for overall population parameters of pea crabs *Disodactylus crinitichelis* and their sand dollar hosts *Encope emarginata*. Correlation coefficients in **bold** indicate statistical significance ( $p < 0.05$ ). Host demand was calculated as the number of crabs divided by the number of sand dollars

Parameter	Mean	SD	(1)	(2)	(3)	(4)	(5)
(1) Host abundance	229.22	160.50	–				
(2) Occupancy ratio	0.34	0.19	<b>-0.74</b>	–			
(3) Crab abundance	72.00	49.19	-0.36	0.56	–		
(4) Proportion of females	0.47	0.12	0.27	-0.20	-0.36	–	
(5) Host demand	0.44	0.27	-0.61	<b>0.67</b>	0.32	-0.41	–

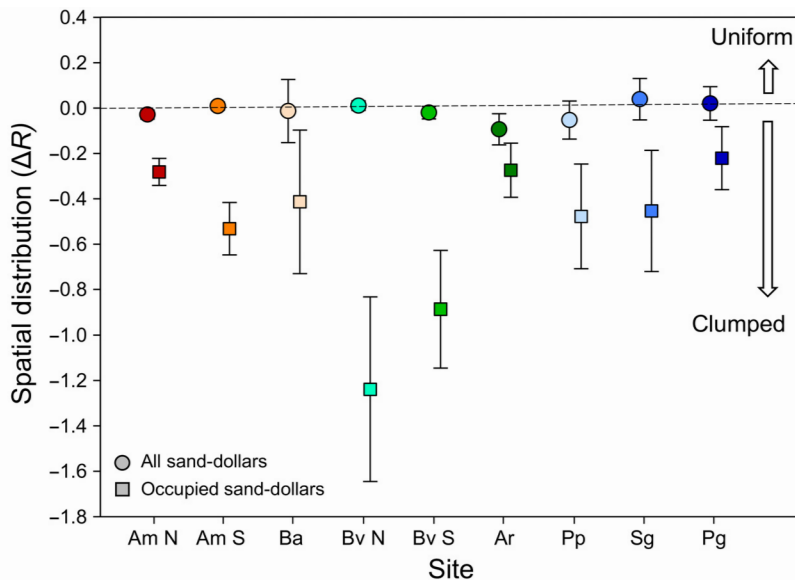


Fig. 2. Spatial distributions of sand dollars at sampling sites: average differences, in meters, between observed ( $R_o$ ) and expected ( $R_e$ , for a random pattern) nearest-neighbor distances for all individuals, and for only those hosting crab populations at each sampling site. At  $\Delta R = 0$  populations, marked with a dashed line, distributions are distributed at random. Error bars are 95% CIs. See Fig. 1 for site abbreviations

dollars (1.8 and 2.1  $m^{-2}$ , respectively) and the fourth and third lowest proportion of occupied patches (0.345 and 0.160, respectively).

### 3.3. Population structure of crabs

The number of adult crabs on sand dollars ranged between 1 and 3, with a much higher frequency of sand dollars hosting a single crab (75.4%), compared to those hosting 2 (22.8%) or 3 (1.8%, Fig. 3). The overall sex ratio departed from the 1:1 ratio ( $\chi^2 = 7.13$ ,  $p = 0.008$ ), with a higher proportion of males (0.55) than females (0.45, Fig. 3). From all possible combinations of males and females for any given sand dollar, only 2 were not observed in the field (1 male plus

2 females [1M2F] and 3 females [3F]). The most obvious deviations from theoretical frequencies, assuming random distribution of crabs among occupied sand dollars and independent occurrence of males and females, were a lower frequency of solitary males and females, a much higher frequency of sand dollars hosting a heterosexual pair (1M1F) and a much lower frequency of sand dollars occupied by 2 females (2F; Fig. 3). The inset in Fig. 3 groups the different combinations that allowed for the testing of our hypothesis (2) that a higher frequency of sand dollars hosting heterosexual pairs, and a lower frequency of 2 or more adult females sharing a same host, are expected. Results show that (i) males were more likely than females to coexist with other individuals of the same sex ( $\chi^2 = 15.69$ ,  $p < 0.01$ ), and (ii) among all sand dollars populated by 2 or 3 crabs, those hosting at least 1 male and 1 female (\*M\*F) were more frequent than expected by chance ( $\chi^2 = 38.21$ ,  $p < 0.01$ ).

The same predictions were tested at all sites separately, but test power was restrained by low sample size (number of crabs). Even so, departures followed the same directions when detected (Fig. S3). Result (i) (see paragraph above) was held at Ar ( $\chi^2 = 7.97$ ,  $p < 0.01$ ; Fig. S3f), and result (ii) was supported at Am N ( $\chi^2 = 20.65$ ,  $p < 0.01$ ; Fig. S3a), Ba ( $\chi^2 = 6.93$ ,  $p < 0.01$ ; Fig. S3c), Pp ( $\chi^2 = 8.01$ ,  $p < 0.01$ ; Fig. S3g) and Pg ( $\chi^2 = 10.26$ ,  $p < 0.05$ ; Fig. S3i). Likewise, at all sites where the sex ratio differed significantly from 1:1, males outnumbered females. This was the case at Am S (relative frequency of males [ $f_\sigma$ ] = 0.70,  $\chi^2 = 13.76$ ,  $p < 0.01$ ; Fig. S3b), Ar ( $f_\sigma = 0.66$ ,  $\chi^2 = 10.57$ ,  $p < 0.001$ ; Fig. S3f) and Pg ( $f_\sigma = 0.61$ ,  $\chi^2 = 3.85$ ,  $p < 0.05$ ; Fig. S3i).

### 3.4. Connectivity estimates for hosting reproductive populations

In most cases, reproductive connectivity was higher for occupied sand dollars compared to unoccupied ones (Fig. 4). This difference was statistically significant at 5 sites, Am S ( $z_u = 3.33$ ,  $p = 0.0009$ ,

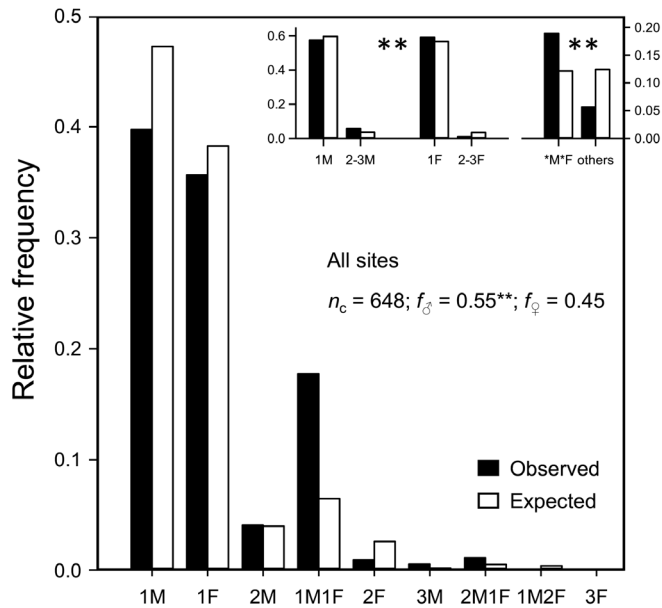


Fig. 3. Overall population structure of pea crabs *Dissodactylus crinitichelis*: frequencies of all observed sexual combinations (M: male; F: female) on single sand dollar hosts *Encope emarginata*. Expected frequencies, assuming random distribution of crabs among occupied sand dollars and independent occurrence of males and females, are given in white and observed frequencies are given in black. Categories are grouped in the inset to test whether females have a lower chance than males to coexist in the same host (left), and whether the occurrence of heterosexual pairs (overall combinations of males and females, \*M\*F) is higher than expected by chance for sand dollars hosting 2 crabs or more (right).  $n_c$ : total number of crabs,  $f_m$ : male relative frequency,  $f_f$ : female relative frequency, ns: non-significant, \*\* $p < 0.01$

Fig. 4b), Bv N ( $z_u = 2.66$ ,  $p = 0.008$ , Fig. 4d), Bv S ( $z_u = 1.99$ ,  $p = 0.047$ , Fig. 4e), Pp ( $z_u = 2.74$ ,  $p = 0.006$ , Fig. 4g) and Pg ( $z_u = 3.56$ ,  $p = 0.0004$ , Fig. 4i). Four of these cases with significant differences between reproductive connectivity of vacant and occupied sand dollars were also among those with the most clumped distributions (Fig. 2: Am S, Bv N, Bv S and Pp). At 2 sites (Am N and Sg), the pattern was inverted (Fig. 4a,h), but differences between occupied and empty sand dollars were not significant. It is interesting to note that connectivity of occupied sand dollars ( $Z_{C_{occ}}$ ) ranked first (Am N) and last (Sg) at those 2 sites (+2.068 and -0.922, respectively; Table S2).

### 3.5. Connectivity estimates on individual fitness

The allometric model fitted size (CW) to fecundity relationships well (Fig. S4, Table S3), except for Am S (Fig. S4b, Table S3), where the size range of

ovigerous females (5.0–6.1 mm) was probably too narrow for a proper analysis. Mean body size (4.8 mm at Am N to 6.9 mm at Bv N; Fig. S4a,d) and average fecundity (233 eggs at Am N to 587 eggs at Bv S; Fig. S4a,e) showed substantial variation across sites. This was also the case for intercepts (0.84–34.50, mean 10.7) and allometric coefficients (1.2–3.3, mean 2.3; Table S3), leading to substantial differences in size-adjusted fecundity, for instance higher at Sg (Fig. S4h) compared to Ba (Fig. S4c).

The relationship between connectivity (i.e. a proxy for the frequency of mating interactions through male searching) and female individual fitness (i.e. the departure from expected fecundity) was highly variable (Fig. 5). In most cases, effects were slight, with slope values ( $b_f$ ) ranging from -5.80 to 8.28 (Table S4), but in 2 cases effects were large and significant ( $p < 0.05$ ), negative at Am N ( $b_f = -20.4$ ,  $r = 0.48$ ; Fig. 5a) and positive at Bv N ( $b_f = 12.1$ ,  $r = 0.74$ ; Fig. 5d).

### 3.6. Overall relationships of host and crab population parameters on connectivity and its effects on individual fitness

The best models explaining the variation in all 3 dependent variables examined (i.e. aggregation index, reproductive connectivity and connectivity effects on individual fitness) included only a single factor (Table 2). In all cases, both the full model and parameter coefficients were significant. Host demand, as the number of crabs per sand dollar, explained 78% of the variation in the aggregation index of occupied sand dollars. Crab abundance explained 93 and 46% of the variation in the reproductive connectivity of occupied sand dollars and the variation in connectivity effects on fitness, respectively. Occupancy ratio was left out of the list of independent variables owing to its correlation with 2 other predictors (Table 1).

The 3 main relationships are plotted in Fig. 6. The positive relationships between host demand and aggregation of occupied sand dollars (Fig. 6a), and between crab abundance and reproductive connectivity (Fig. 6b) are strong and compelling. The negative linear relationship between crab abundance and the effects of connectivity on individual female fitness is weaker, albeit significant. It is interesting to note, however, that the positive effects at Bv N and the negative effects at Am N, which were the only significant trends in Fig. 5, showed up in extreme positions in Fig. 6c.



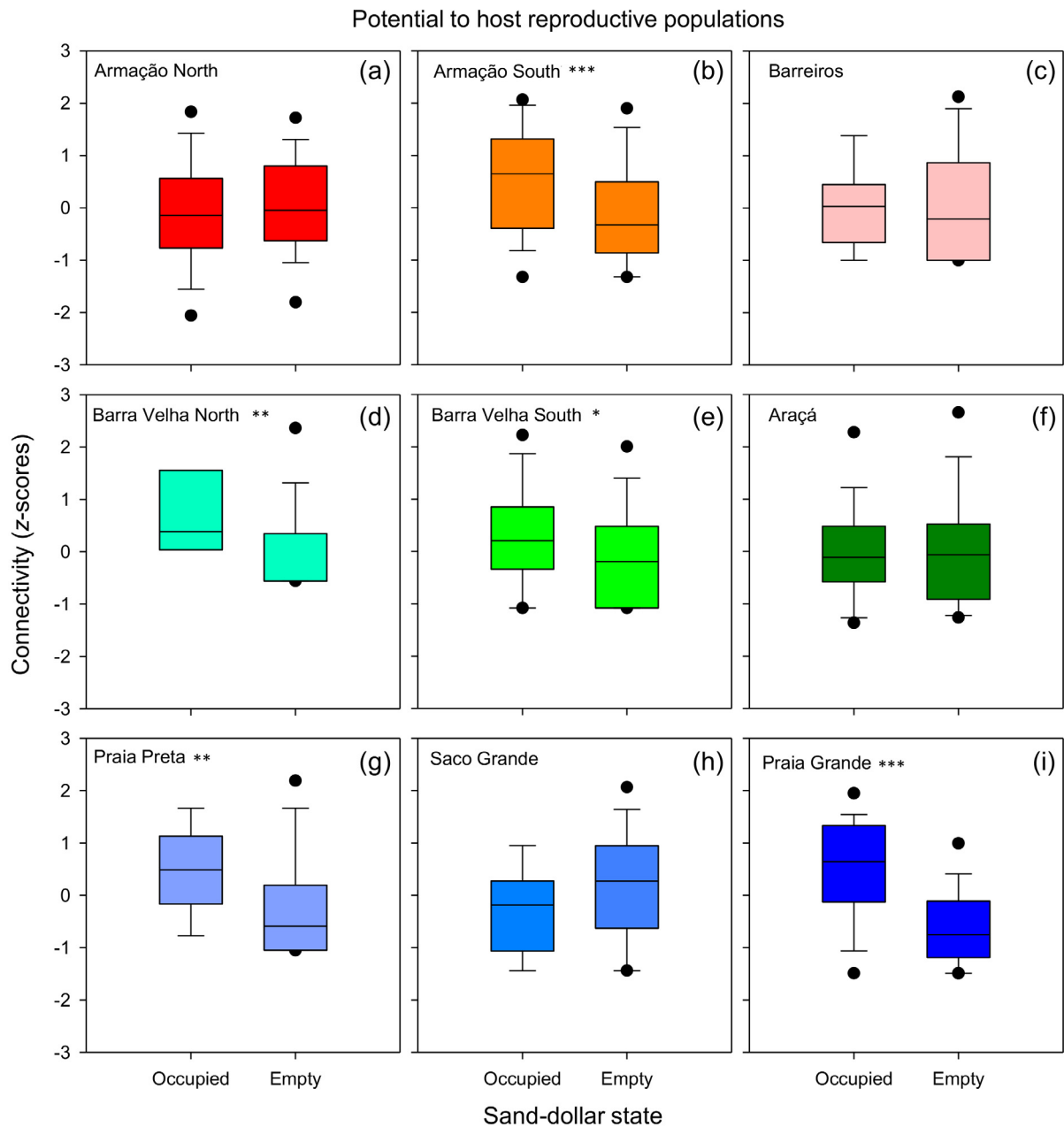


Fig. 4. Connectivity estimates measuring the potential for hosting reproductive populations (male and female coexistence) in empty and occupied sand dollars at the time of sampling in all study areas. Boxes show the median and the interquartile range, whiskers extend to 10th and 90th percentiles, and dots mark the 5th and 95th percentiles. Asterisk codes after site labels indicate statistical differences of connectivity between occupied and empty sand dollars: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.0005$

#### 4. DISCUSSION

Connectivity among discrete population patches, which is a key process in metapopulation dynamics, strongly depends on the spatial distribution of both occupied and vacant habitat patches, as well as dispersal efficiency (e.g. Kool et al. 2013). Here we show that occupied patches tended to be distributed in clusters, in almost all cases contrasting with the over-

arching random distribution of all patches that can be potentially colonized. These results might reflect a combination of early colonization and later adult movements (Pittman & McAlpine 2001), both non-random and known to be driven to a large extent by chemical attraction (Ambrosio & Brooks 2011, Souza et al. 2019). Therefore, any mechanisms involving active habitat selection would thus enhance average connectivity and possibly the persistence of popu-

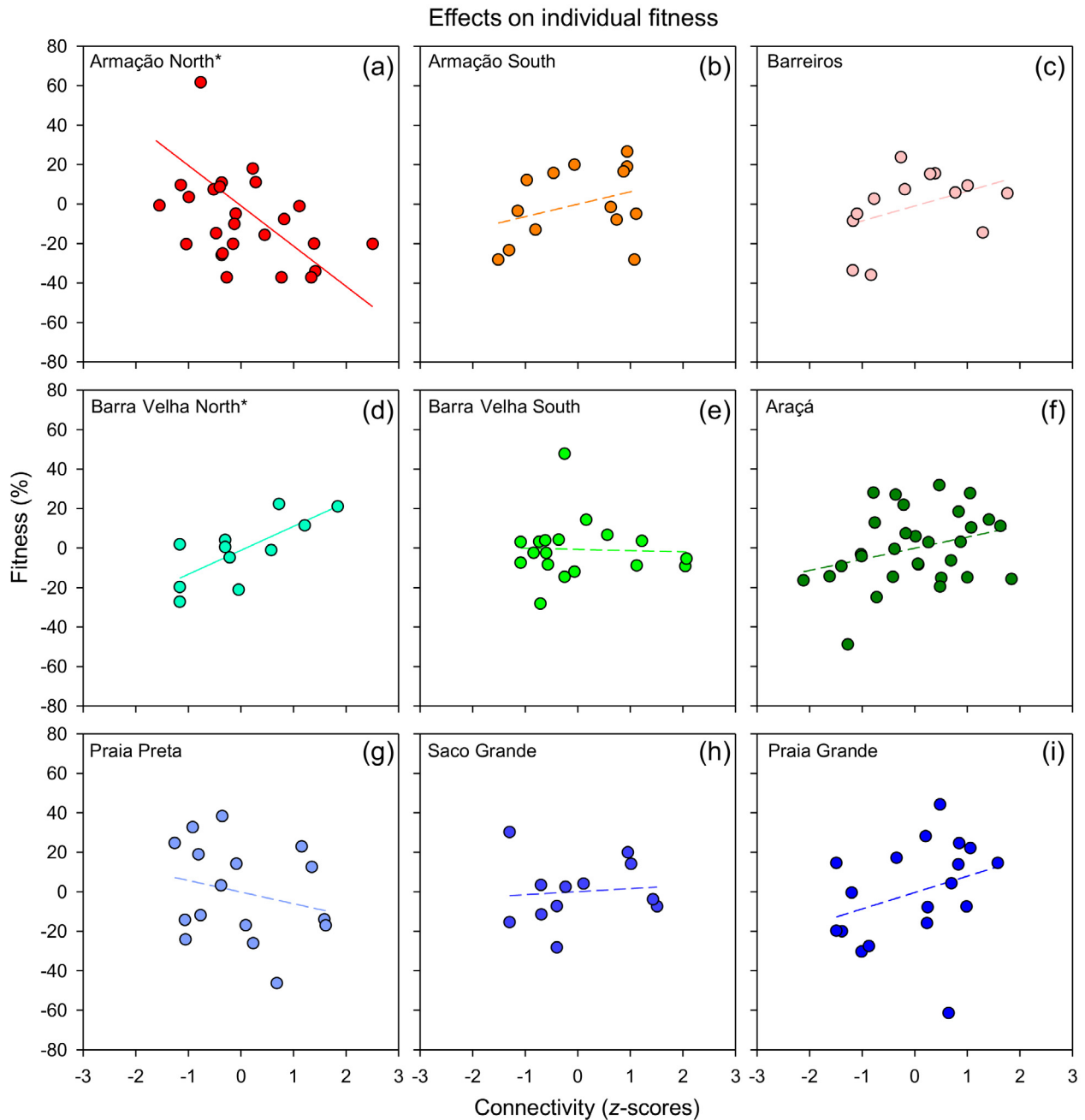


Fig. 5. Relationships between connectivity metrics estimating the frequency of mating interactions and individual female fitness, as percent departures from expected fecundity. Significant relationships ( $*p < 0.05$ ), observed at sites Armação North and Barra Velha North, are shown as solid trend lines. More information on specific regression estimates is given in Table S3

lated patches (Ray et al. 1991, Hanski 1998, Singer & Hanski 2004). This translated into a higher connectivity of occupied patches compared to vacant ones, with likely high encounter rates between males and females at 5 out of the 9 study sites. While gregarious behavior apparently favors reproductive potential at the population level, effects at the individual level appear to be dual. Effects on individuals are gener-

ally weak, but at the sites where overall crab abundance is very high and very low, connectivity effects are respectively negative and positive. The former indicates that crowding likely elicits strong intraspecific competition, possibly for territory (since females prefer to occupy hosts alone or with a male) or mates (since they usually mate with multiple males), ultimately impacting egg production, while the latter

Table 2. Summary results of stepwise backward multiple regression analyses testing the overall effects of host abundance (abundance of sand dollars), crab abundance, proportion of female crabs, and host demand (crab abundance / host abundance) on the aggregation index and reproductive connectivity of occupied hosts, and on the effects of connectivity on individual fitness (estimated as the slope of connectivity vs. fitness relationships, see Fig. 5). Significance of overall selected models and respective predictors are specified in **bold** ( $p < 0.05$ ). Dashes (–) represent cases in which correlation coefficients were not significant

	Aggregation index ( $R_o/R_e$ )			Reproductive connectivity ( $Z_{C_{occ}}$ )			Connectivity effect on fitness ( $b_f$ )		
	Coefficient	<i>t</i>	<i>p</i>	Coefficient	<i>t</i>	<i>p</i>	Coefficient	<i>t</i>	<i>p</i>
<b>All effects</b>									
Intercept	-2.7316	-2.19	0.094	-1.0990	-1.26	0.276	15.8528	0.80	0.469
Host abundance	0.0000	0.03	0.981	0.0001	0.08	0.939	0.0200	0.86	0.439
Crab abundance	0.0003	0.07	0.944	0.0196	6.81	0.002	-0.1546	-2.35	0.078
Proportion of females	-0.7520	-0.44	0.685	-0.5144	-0.43	0.690	-26.6822	-0.98	0.384
Host demand	2.4835	2.75	0.051	-0.2070	-0.33	0.759	11.2556	0.79	0.476
	Multiple $r^2$	$F_{4,4}$	<i>p</i>	Multiple $r^2$	$F_{4,4}$	<i>p</i>	Multiple $r^2$	$F_{4,4}$	<i>p</i>
	0.794	3.84	0.110	0.936	14.69	0.012	0.657	1.92	0.272
<b>Backward stepwise solution</b>									
Intercept	-3.1183	-11.77	<b>&lt;0.001</b>	-1.4129	-8.20	<b>&lt;0.001</b>	11.3662	2.39	<b>0.048</b>
Host abundance	–	–	–	–	–	–	–	–	–
Crab abundance	–	–	–	0.0196	9.76	<b>&lt;0.001</b>	-0.1353	-2.43	<b>0.045</b>
Prop. Females	–	–	–	–	–	–	–	–	–
Host demand	2.6257	5.01	<b>0.002</b>	–	–	–	–	–	–
	Multiple $r^2$	$F_{1,7}$	<i>p</i>	Multiple $r^2$	$F_{1,7}$	<i>p</i>	Multiple $r^2$	$F_{1,7}$	<i>p</i>
	0.782	25.06	<b>0.002</b>	0.932	95.25	<b>&lt;0.001</b>	0.459	5.93	<b>0.045</b>

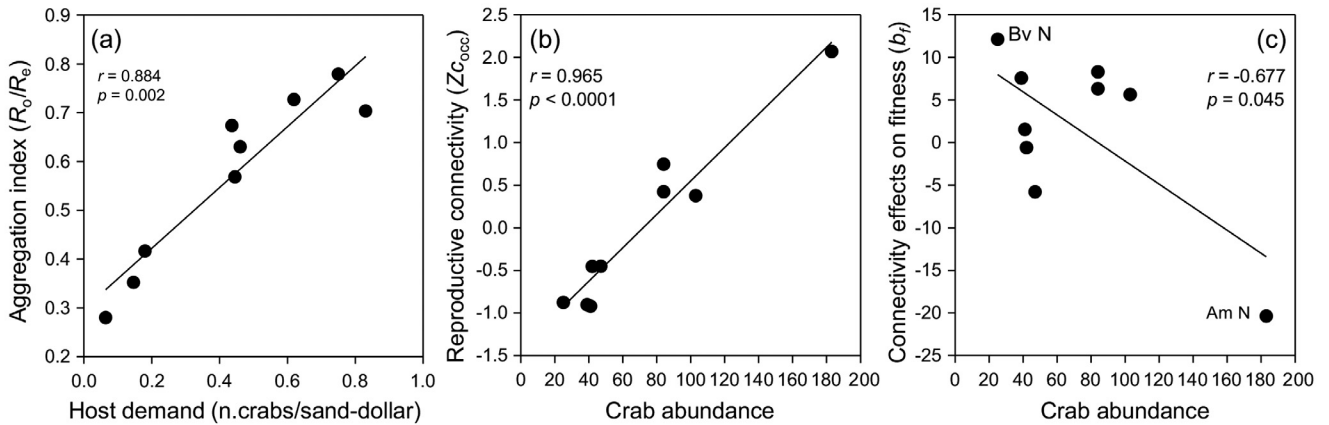


Fig. 6. Linear trends between metrics relating overall population attributes and crab connectivity. (a) Positive relationship between host demand and the aggregation index ( $R_o/R_e$ ) of occupied sand dollars, (b) positive relationship between crab abundance and reproductive connectivity ( $Z_{C_{occ}}$ ) and (c) negative relationship between crab abundance and the effects of connectivity on individual female fitness ( $b_f$ ). The position of sampling sites Barra Velha North (Bv N) and Armação North (Am N), where connectivity to fitness relationships were extreme and significant, are indicated in panel (c)

suggests that infrequent access to potential mates may indeed restrain brood size. Individual fitness is therefore apparently maximized at average crab density.

The aggregation index of occupied hosts was positively correlated to the demand of sand dollars; that is, when the relative number of crabs becomes large,

they tend to cluster in higher numbers in nearby sand dollars, with occupied hosts becoming much closer than expected for a random distribution. Such a distribution pattern may enhance per capita reproductive rate and reduce predation risk (Kareiva 1987, Murdoch & Stewart-Oaten 1989). Most crab dispersals connecting individuals are thus expected to be

mediated by chemical cues, which are known to be very effective even when the concentration of waterborne cues is very low (e.g. Ward et al. 1992, Lecchini et al. 2014). Even when overall crab density is low, the relatively few crabs commuting between potential hosts may successfully cluster around the limited spots already colonized by founding individuals (as observed in Bv N and Bv S). In contrast, when crabs are more abundant and scattered, the concentration of chemical cues is likely above any response threshold over the entire site (as in Ward et al. 1992), and individuals colonize available sand dollars at more variable distances from cue sources, especially when they are in short relative supply (as observed in Ar and Pg). Those chemically driven dynamics may set up an advantageous trade-off for pea crab populations, decreasing crowding within sand dollar hosts when overall crab abundance is exceedingly high, and favoring persistence at sites of low crab abundance by ensuring connectivity at the few spots where the occupancy ratio remains high.

Crab distribution patterns clearly affected reproductive connectivity. Gregarious behaviors are usually associated with adjustments in mating systems (Correa & Thiel 2003), which mediate competitive interactions while maximizing mating success. The frequency of sand dollars with only 1 adult crab, either a male or a female, was lower than expected, while sand dollars hosting a potential mating pair were more frequent than predicted by the null model assuming random distributions and independent occurrence of males and females. This suggests that solitary crabs are prone to leave their hosts to find a potential mate. In addition, the frequency of females (but not males) sharing their hosts with crabs of the same sex was lower than expected, indicating some sort of agonistic behavior that would ensure the winning female a higher mating success (as observed in pipefish, Rosenqvist 1990). This would set a selective pressure for large female size, which is common in pinnotherid species but not in most other brachyuran crabs, in which agonistic behaviors linked to mating and resource guarding are more common in males. In the case of *Dissodactylus crinitichelis*, females attain a size 12% larger than males (Alves et al. 2017), which suggests they play a major role in controlling the population structure within sand dollars.

The combined effects of gregarious behaviors, setting the spatial distribution of occupied sand dollars, and interactions among individuals, determining the population structure at each host, may modulate the reproductive connectivity of each sand dollar. At most sites, crab dispersals and interactions may have

contributed to an increase in potential encounters between males and females, as reproductive connectivity was generally higher for occupied sand dollars compared to unoccupied ones. When reproductive connectivity z-scores were computed for the whole sample instead ( $Z_{c_{occ}}$ ), not separately for each site, we found that the 2 exceptional sites where empty sand dollars were the most connected ones (although without statistical support) were sites where occupied hosts were on average either the least or the most connected. This might suggest that the capacity for crabs to actively reach and colonize more proximate sand dollar hosts, as to increase the chances of male–female interactions, is lower at extreme overall reproductive connectivity. Very low connectivity may lead to an unfavorable combination of (high) distance among potential hosts, (low) crab abundance and (more) unbalanced sex ratio (Sg, Table S2). Very high connectivity may lead to exceptional density of potential hosts (Am S, Table S2), leaving no margin to active improvement of reproductive connectivity through crab movements. Therefore, except for those 2 extreme conditions, active selection of habitat patches may not only contribute to an increased dispersal rate (as host shifts), but also to an increased reproductive output of whole populations through an intensification of encounters between males and females (i.e. effective connectivity, Pineda et al. 2007, Lowe & Allendorf 2010, Robertson et al. 2018). Independently of within-site host occupancy patterns and ratios, the overall reproductive connectivity of crab populations is tightly related to overall crab abundance. This, in turn, is not likely controlled by habitat limitation (i.e. no correlation between overall sand dollar and crab abundance), but probably by other processes such as limited larval settlement, recruitment and benthic mortality.

Our results suggest that crab migrations and host shifts may also affect individual fitness. However, strong effects were limited to 2 out of the 9 cases examined, when potential encounter rates were either unusually high or low. Again, crab abundance is apparently the most relevant variable, since connectivity effects on fitness were strong only at the sites where crab abundance was the highest (Am N) and the lowest (Bv N). Although seasonality may have played an important role on fecundity variation among sites, we still found a relationship between population connectivity and individual fitness of females. Also, both Am N and Bv N were sampled during the summer of 2020, suggesting that the significant (and opposite) trends at those sites were not an outcome of seasonality. In Am N, the effect was

negative and very strong ( $b_f = -20.4$ ), with less connected females producing broods 20% above the expected size (with 1 individual reaching >60%), and more connected females producing broods nearly 40% smaller than expected. Given the wide variation in fitness and the higher number of observations below 0% (Fig. 5a), the trend suggests that most females may be facing strong intraspecific competition which may affect egg production. This result is consistent with previous studies suggesting that interference competition and crowding may cause a decline in reproductive success (Rinkevich & Loya 1985, Weinberg 1985, Allen et al. 2008). In contrast, the effect of reproductive connectivity was positive in Bv N. Although significant, the effect in this case was not so strong ( $b_f = +12.1$ ), with fitness varying within a slightly narrower range (-25% to +20%) and observations more symmetrically distributed around 0% (Fig. 5d). This result is consistent with sperm limitation caused by restricted access to suitable mates (e.g. Rondeau & Sainte-Marie 2001, Pardo et al. 2017), which may lead females to mate more frequently (Alonzo & Pizzari 2013). We caution that the observed differences are likely a result of processes that take place in very particular conditions, not necessarily reflecting any spatially consistent structure. Sites were surveyed only once, not controlling for any possible temporal effects within the breeding season such as those caused by temperature changes, or the dynamics of breeding cohorts.

Altogether, these results indicate that habitat supply is not limiting the size of pea crab populations in the study area, but crab abundance, in turn, is clearly restraining reproductive connectivity and thus the potential for offspring production. However, except for extreme cases of low and high connectivity, patterns of crab aggregations and eventual within-host interactions greatly enhance the reproductive potential, given the natural spatial distribution of sand dollars. This may be key for the long-term stability of small crab populations scattered in sparse sand dollar hosts. Contrary to the reproductive potential of whole crab populations, crab abundance has a dual indirect influence on individual fitness through contrasting connectivity effects. Individual fitness, measured as the percent deviation from expected egg production, is probably maximum at intermediate crab densities, not too low as to limit mate encounters, and thus sperm transfer, but also not too high as to impose severe interspecific competition in the confined host habitat.

It is important to highlight that our results are based on samples obtained at random sites within the São Sebastião Channel, and at different times,

with the aim of capturing large environmental variability and set natural ranges of reproductive connectivity and individual (female) fitness. It is likely that the frequency of searching behaviors, and effective migrations from one host to another, vary considerably at different spatial and temporal scales (underlying, for instance, the marked seasonal differences in pea crab distributions reported by George & Boone 2003). Identifying the environmental drivers that ultimately modulate the redistribution of individuals among habitat patches, and assessing the impacts of any processes precluding optimal spatial arrangements maximizing fitness, are promising avenues of future research.

*Acknowledgements.* This work was supported by FAPESP (as an MSc fellowship to J.A.S., grant number 2018/25562-5), and CNPq (as a grant for research productivity to A.A.V.F., #301601/2018-6) and hosted by the Faculty of Philosophy, Science and Letters at Ribeirão Preto and the Center for Marine Biology (CEBIMar) of the University of São Paulo (USP). We are grateful to Andreia S. Freire (Federal University of Santa Catarina), Jussara M. M. Lemos (Federal University of Pará), Sidney F. Gouveia (Federal University of Sergipe) and 2 anonymous reviewers for their criticism and suggestions on an early manuscript draft. Ligia Luz (PhD student at the CEBIMar/USP) retrieved and formatted the oceanographic data used to characterize our sampling area. We also thank the graduate students and staff at the CEBIMar for their assistance in field work, especially Carla B. Pavone, Eduardo Honuma and Joseilto M. de Oliveira. This is a contribution of the Research Centre for Marine Biodiversity of the University of São Paulo (NPBiomar/USP).

#### LITERATURE CITED

- ✦ Allen RM, Buckley YM, Marshall DJ (2008) Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am Nat* 171:225–237
- ✦ Almany GR, Connolly SR, Heath DD, Hogan JD, Jones GP, McCook LJ, Williamson DH (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339–351
- ✦ Alonzo SH, Pizzari T (2013) Selection on female remating interval is influenced by male sperm competition strategies and ejaculate characteristics. *Philos Trans R Soc B* 368:20120044
- ✦ Alves DFR, Hirose GL, Barros-Alves SP, Baeza JA (2017) The mating system of the symbiotic pea-crab *Dissodactylus crinitichelis* (Brachyura, Pinnotheridae): monogamy or promiscuity? *Mar Biol* 164:200
- ✦ Ambrosio LJ, Baeza JA (2016) Territoriality and conflict avoidance explain asociality (solitariness) of the endosymbiotic pea crab *Tunicotheres moseri*. *PLOS ONE* 11: e0148285
- ✦ Ambrosio LJ, Brooks WR (2011) Recognition and use of ascidian hosts, and mate acquisition by the symbiotic pea crab *Tunicotheres moseri* (Rathbun, 1918): the role of chemical, visual and tactile cues. *Symbiosis* 53:53–61

- Baeza JA, Hernáez P (2015) Population distribution, sexual dimorphism, and reproductive parameters in the crab *Pinnixa valdiviensis* Rathbun, 1907 (Decapoda: Pinnotheridae), a symbiont of the ghost shrimp *Callinectes garthi* (Retamal, 1975) in the Southeastern Pacific. *J Crustac Biol* 35:68–75
- Baeza JA, Thiel M (2007) The mating system of symbiotic crustaceans: a conceptual model based on optimality and ecological constraints. In: Duffy JE, Thiel M (eds) *Evolutionary ecology of social and sexual systems: crustaceans as model organisms*. Oxford University Press, New York, NY, p 250–267
- Bell JL, Stancyk SE (1983) Population dynamics and reproduction of *Dissodactylus mellitae* (Brachyura: Pinnotheridae) on its sand dollar host *Mellita quinquesperforata* (Echinodermata). *Mar Ecol Prog Ser* 13:141–149
- Bertness MD, Grosholz E (1985) Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* 67:192–204
- Boukal DS, Berec L (2002) Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters. *J Theor Biol* 218:375–394
- Breedveld MC, Fitze PS (2015) A matter of time: delayed mate encounter postpones mating window initiation and reduces the strength of female choosiness. *Behav Ecol Sociobiol* 69:533–541
- Britton NF (1989) Aggregation and the competitive exclusion principle. *J Theor Biol* 136:57–66
- Chamailé-Jammes S, Fritz H, Valeix M, Murindagomo F, Clobert J (2008) Resource variability, aggregation, and direct density dependence in an open context: the local regulation of an African elephant population. *J Anim Ecol* 77:135–144
- Correa C, Thiel M (2003) Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Rev Chil Hist Nat* 76:187–203
- Courchamp F, Berec L, Gascoigne J (2008) *Allee effects in ecology and conservation*. Oxford University Press, New York, NY
- De Bruyn C, Rigaud T, David B, De Ridder C (2009) Symbiosis between the pea crab *Dissodactylus primitivus* and its echinoid host *Meoma ventricosa*: potential consequences for the crab mating system. *Mar Ecol Prog Ser* 375: 173–183
- Elzinga JA, Van Nouhuys S, Van Leeuwen DJ, Biere A (2007) Distribution and colonization ability of three parasitoids and their herbivorous host in a fragmented landscape. *Basic Appl Ecol* 8:75–88
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Fahrig L, Merriam G (1985) Habitat patch connectivity and population survival. *Ecology* 66:1762–1768
- Fischer K, Fiedler K (2001) Resource-based territoriality in the butterfly *Lycaena hippothoe* and environmentally induced behavioural shifts. *Anim Behav* 61:723–732
- Fobert EK, Treml EA, Swearer SE (2019) Dispersal and population connectivity are phenotype dependent in a marine metapopulation. *Proc R Soc B* 286:20191104
- Fogarty MJ, Botsford LW (2006) Metapopulation dynamics of coastal decapods. In: Kritzer JP, Sale PF (eds) *Marine metapopulations*. Elsevier-Academic Press, Amsterdam, p 271–319
- Fryxell JM, Sinclair ARE (1988) Causes and consequences of dispersal by large herbivores. *Trends Ecol Evol* 3:237–241
- George SB, Boone S (2003) The ectosymbiont crab *Dissodactylus mellitae*–sand dollar *Mellita isometra* relationship. *J Exp Mar Biol Ecol* 294:235–255
- González-Gurriarán E, Fernández L, Freire J, Muiño R (1998) Mating and role of seminal receptacles in the reproductive biology of the spider crab *Maja squinado* (Decapoda, Majidae). *J Exp Mar Biol Ecol* 220:269–285
- Guilherme PD, Brustolin MC, Bueno MDL (2015) Distribution patterns of ectosymbiont crabs and their sand dollar hosts in a subtropical estuarine sandflat. *Rev Biol Trop* 63:209–220
- Hanski I (1998) Metapopulation dynamics. *Nature* 396:41–49
- Hanski I, Erälahti C, Kankare M, Ovaskainen O, Sirén H (2004) Variation in dispersal propensity among individuals maintained by landscape structure. *Ecol Lett* 7: 958–966
- Hansson L (1991) Dispersal and connectivity in metapopulations. *Biol J Linn Soc* 42:89–103
- Johnson NL, Kemp AW, Kotz S (2005) *Univariate discrete distributions* (3<sup>rd</sup> edn). Wiley-Interscience, Hoboken, NJ
- Jossart Q, Wattier RA, Kastally C, Aron S, David B, De Ridder C, Rigaud T (2014) Genetic evidence confirms polygamous mating system in a crustacean parasite with multiple hosts. *PLOS ONE* 9:e90680
- Kareiva P (1987) Habitat fragmentation and the stability of predator–prey interactions. *Nature* 326:388–390
- Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspectives. *Landsc Ecol* 28:165–185
- Krebs CJ (1999) *Ecological methodology* (2nd edn). Benjamin/Cummings, Menlo Park, CA
- Kritzer JP, Sale PF (2006) The metapopulation ecology of coral reef fishes. In: Kritzer JP, Sale PF (eds) *Marine metapopulations*. Elsevier-Academic Press, Amsterdam, p 31–67
- Lampert W (1989) The adaptive significance of diel vertical dispersal of zooplankton. *Funct Ecol* 3:21–27
- Lecchini D, Miura T, Lecellier G, Banaigs B, Nakamura Y (2014) Transmission distance of chemical cues from coral habitats: implications for marine larval settlement in context of reef degradation. *Mar Biol* 161:1677–1686
- Lowe WH, Allendorf FW (2010) What can genetics tell us about population connectivity? *Mol Ecol* 19:3038–3051
- Matesanz S, Gómez-Fernández A, Alcocer I, Escudero A (2015) Fragment size does not matter when you are well connected: effects of fragmentation on fitness of coexisting gypsophiles. *Plant Biol* 17:1047–1056
- McDermott JJ (2006) The biology of *Austinia gorei* (Manning & Felder, 1989) (Decapoda, Brachyura, Pinnotheridae) symbiotic in the burrows of intertidal ghost shrimp (Decapoda, Thalassinidea, Callinassidae) in Miami, Florida. *Crustaceana* 79:345–361
- Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. *Ecology* 83:1131–1145
- Murdoch WW, Stewart-Oaten A (1989) Aggregation by parasitoids and predators: effects on equilibrium and stability. *Am Nat* 134:288–310
- Netto LF, Hadel VF, Tiago CG (2005) Echinodermata from São Sebastião Channel (São Paulo, Brazil). *Rev Biol Trop* 53:207–218
- Nowicki P, Vrabec V (2011) Evidence for positive density-dependent dispersal in butterfly metapopulations. *Oecologia* 167:657–665
- Pardo LM, Riveros MP, Fuentes JP, Pinochet R, Cardenas C, Sainte-Marie B (2017) High fishing intensity reduces females' sperm reserve and brood fecundity in a eu-

- brachyuran crab subject to sex- and size-biased harvest. *Sci Rep* 74:2459–2469
- ✦ Pineda J, Hare JA, Sponaugle SU (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20:22–39
- ✦ Pires-Vanin AMS, Arasaki E, Muniz P (2013) Spatial pattern of benthic macrofauna in a sub-tropical shelf, São Sebastião Channel, southeastern Brazil. *Lat Am J Aquat Res* 41:42–56
- ✦ Pittman SJ, McAlpine CA (2001) Movements of marine fish and decapod crustaceans: process, theory and application. *Adv Mar Biol* 44:205–294
- ✦ Ray C, Gilpin M, Smith AT (1991) The effect of conspecific attraction on metapopulation dynamics. *Biol J Linn Soc* 42:123–134
- ✦ Rinkevich B, Loya Y (1985) Intraspecific competition in a reef coral: effects on growth and reproduction. *Oecologia* 66:100–105
- ✦ Robertson EP, Fletcher RJ Jr, Cattau CE, Udell BJ, Reichert BE, Austin JD, Valle D (2018) Isolating the roles of movement and reproduction on effective connectivity alters conservation priorities for an endangered bird. *Proc Natl Acad Sci USA* 115:8591–8596
- ✦ Rodríguez A, Andrén H, Jansson G (2001) Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* 95:383–396
- ✦ Rondeau A, Sainte-Marie B (2001) Variable mate-guarding time and sperm allocation by male snow crabs (*Chionoecetes opilio*) in response to sexual competition, and their impact on the mating success of females. *Biol Bull (Woods Hole)* 201:204–217
- ✦ Rosenqvist G (1990) Male mate choice and female–female competition for mates in the pipefish *Nerophis ophidion*. *Anim Behav* 39:1110–1115
- ✦ Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9: 671–675
- ✦ Shanks AL (2009) Pelagic larval duration and dispersal distance revisited. *Biol Bull (Woods Hole)* 216:373–385
- Singer MC, Hanski I (2004) Dispersal behavior and evolutionary metapopulation dynamics. In: Ehrlich PR, Hanski I (eds) *On the wings of checkerspot: a model system for population biology*. Oxford University Press, New York, NY, p 181–198
- Somers KM (1991) Characterizing size-specific fecundity in crustaceans. In: Wenner A, Kuris A (eds) *Crustacean egg production*. Balkema AA, Rotterdam, p 357–378
- ✦ Souza JA, Barroso D, Hirose GL (2019) Chemical recognition in the symbiotic pea crab *Dissodactylus crinitichelis* (Crustacea: Decapoda: Pinnotheridae): host and conspecific cues. *J Exp Mar Biol Ecol* 511:108–112
- Stacey PB, Taper ML, Johnson VA (1997) Migration within metapopulations: the impact upon local population dynamics. In: Hanski I, Gilpin ME (eds) *Metapopulation biology. Ecology, genetics, and evolution*. Academic Press, San Diego, CA, p 267–291
- ✦ Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol Lett* 17:866–880
- ✦ Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect? *Oikos* 87:185–190
- Telford M (1978) Distribution of two species of *Dissodactylus* (Brachyura: Pinnotheridae) among their echinoid host populations in Barbados. *Bull Mar Sci* 28:651–658
- Thiel M, Zander A, Baeza JA (2003) Movements of the symbiotic crab *Liopetrolisthes mitra* between its host sea urchin *Tetrapygus niger*. *Bull Mar Sci* 72:89–101
- van Nouhuys S (2009) Metapopulation ecology. In: *Encyclopedia of life sciences*. John Wiley & Sons, Chichester, p 1–9
- ✦ Vandewoestijne S, Shtickzelle N, Baguette M (2008) Positive correlation between genetic diversity and fitness in a large, well-connected metapopulation. *BMC Biol* 6:46
- Wainer I, Taschetto AS (2008) Climatologia dos parâmetros de superfície marinha da região sudeste da costa brasileira: ênfase na região de São Sebastião. In: Pires-Vanin AMS (ed) *Oceanografia de um ecossistema subtropical: Plataforma de São Sebastião, SP*. Editora da Universidade de São Paulo, São Paulo, p 41–57
- ✦ Ward JE, Cassell HK, MacDonald BA (1992) Chemoreception in the sea scallop *Placopecten magellanicus* (Gmelin). I. Stimulatory effects of phytoplankton metabolites on clearance and ingestion rates. *J Exp Mar Biol Ecol* 163:235–250
- ✦ Weinberg JR (1985) Factors regulating population dynamics of the marine bivalve *Gemma gemma*: intraspecific competition and salinity. *Mar Biol* 86:173–182
- Weiner J (1988) The influence of competition on plant reproduction. In: Lovett JD, Doust LL (eds) *Plant reproductive ecology: patterns and strategies*. Oxford University Press, New York, NY, p 228–245
- ✦ Wiens JA (1976) Population responses to patchy environments. *Annu Rev Ecol Evol Syst* 7:81–120

Editorial responsibility: Romuald Lipcius,  
Gloucester Point, Virginia, USA  
Reviewed by: E. Ocampo and 1 anonymous referee

Submitted: March 10, 2023  
Accepted: August 9, 2023  
Proofs received from author(s): October 16, 2023