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Sex-biased dispersal depends on the spatial scale in a tube-building amphipod

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ABSTRACT: Behavioral differences between males and females can lead to sex-biased dispersal (SBD), and tube-building amphipods are good model organisms to study this process. Depending on the species, males or females have a different affinity to their tubes, and one sex may be more mobile than the other. This distinct dispersal behavior and the scales at which it occurs are not fully understood. Here, we tested the SBD hypothesis at different spatial scales in *Cymadusa filosa* using direct and indirect approaches. We conducted laboratory (small scale) and field experiments (local scale), and molecular analyses (local and large scale). Laboratory experiments indicated male-biased dispersal over small scales (cm), whereas over local scales (m), field experiments showed similar colonization rates of previously cleaned fronds for both males and females, suggesting no SBD. A higher proportion of juveniles than expected had colonized these fronds, suggesting that juveniles have higher dispersal rates than adults. Also, neighboring individuals were not more genetically related than spatially distant individuals. Over large scales (km), molecular analyses did not indicate SBD, and there were no differences in genetic structure between sexes. Our results showed that SBD depends on the spatial scale. Combining different approaches, we showed that the dispersal of males and females over local and large scales is sufficient to cause a lack of genetic differentiation within each sex, despite small-scale SBD.

KEY WORDS: *Cymadusa filosa* · Peracarida · Mesograzer · Dispersal · Tube-building behavior · Microsatellites · Colonization

1. INTRODUCTION

Dispersal plays a central role in understanding species ecology and evolution (Bowler & Benton 2005). This process is defined by the movement of an individual from one site to another, followed by a reproduction event at the new site (Ronce 2007). This definition addresses the individual movement, which directly affects population dynamics and distribution, and the possibility of mating encounters, promoting gene flow and affecting the genetic structure (Cayuela et al. 2018). In a particular type of dispersal known as sex-biased dispersal (SBD), males and females present contrasting behaviors that lead to different dispersal patterns (Perrin & Mazalov 2000, Li & Kokko 2019a): a philopatric (non-dispersing) sex and a dispersing sex. These differences in mobility have consequences for ecological and evolutionary dynamics (Trochet et al. 2016, Li & Kokko 2019b). Previous studies on SBD have focused on terrestrial

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vertebrates, and thus this phenomenon is poorly explored for marine organisms, especially invertebrates (Trochet et al. 2016).

The study of SBD commonly relies on 2 different approaches. Direct approaches (e.g. manipulative experiments, tracking, and mark–release–recapture techniques in the field) may precisely identify the dispersing sex (Hutchings & Gerber 2002, Beirinckx et al. 2006). However, such methodologies may be challenging when studying marine invertebrate taxa because these organisms can be small and cryptic, and their dispersal commonly includes a planktonic larval phase. Contrastingly, indirect approaches consist of molecular analyses, which may infer SBD, given its potential to leave a genetic signature on species genetic structure (Prugnolle & De Meeus 2002). Usually, indirect approaches compare nuclear DNA and mitochondrial DNA markers, indicating male-biased dispersal when markers show discordant results (Prugnolle & De Meeus 2002). Due to maternal inheritance of the mitochondrial DNA, this marker only indicates the female genealogy. Discordant patterns between maternally and bi-parentally inherited markers might therefore indicate dispersal differences between sexes. Bi-parentally inherited markers, such as microsatellites, are also used to detect male- and female-biased dispersal (Goudet et al. 2002, Durand et al. 2019). These approaches are often used to investigate SBD in marine organisms because they do not require the movements of an individual to be fully tracked (Driggers et al. 2014, Roycroft et al. 2019). To better evaluate SBD, direct and indirect approaches should be combined when possible (Lawson Handley & Perrin 2007).

Tube-building amphipods are good model organisms for the study of SBD by integrating direct and indirect methods. These animals have direct development, no larval phase, and are commonly found in shallow waters and rocky shores (Duffy & Hay 2000, Hamilton et al. 2006, Bueno et al. 2016). The tube-building trait is found in species from the superfamilies Corophioidea, Synopioidea, Photoidea, Caprelloidea, and Aoroidea (Lowry & Myers 2013, Serejo & Siqueira 2018). Usually, pereopods 3 and 4 have silk-producing glands (Kronenberger et al. 2012, Lowry & Myers 2013). The 'amphipod silk' is used to build sand or seaweed tubes that are then inhabited by these animals (Dixon & Moore 1997, Cerda et al. 2010, Poore et al. 2018). Adults (males and females) and juveniles construct tubes occupied by a single individual except during reproductive events, when mating pairs share the same tube, or when juveniles born in the progenitor's tube remain there for days (Borowsky 1983, Appadoo & Myers 2003).

Tube-building amphipods are less mobile than non-tubiculous species (Duffy & Hay 1994), but mobility may vary among tubiculous species (McDonald & Bingham 2010, Beermann & Franke 2012). Males and females of tube-dwelling amphipods might show differences in affinity to their tubes, with males being more mobile than females and frequently found outside the tubes, searching for mates (Borowsky 1983, 1985a,b, Shillaker & Moore 1987, Mattson & Cedhagen 1989, McCurdy et al. 2000). Females of many species seem to have lower mobility because they do not actively search for males. In contrast, there are also cases where females are found outside tubes more frequently than males (Stevens et al. 2006, Bringloe et al. 2013). The distinct dispersal behavior and its consequences are still not fully understood, and we lack studies combining direct and indirect approaches.

SBD can be a scale-dependent phenomenon (Gauffre et al. 2009, Li et al. 2019), particularly for tube-building species living on host algae along rocky shores. For these animals, there are 3 distinct hierarchical spatial scales: small, local, and large. The small scale represents individual dispersal at the level of the individual's size, along with limited distances (cm). Some of the amphipod traits may be associated with limitations on dispersal over small scales. For instance, these amphipods are considered to present low mobility compared to other marine species due to their small size, direct development (Gunnill 1982, Hay et al. 1988, Christie et al. 1998), and juveniles recruiting near their parents (Thiel & Vásquez 2000). These traits may also affect dispersal over local scales (m) along the rocky shore. Amphipods exhibit patchy distributions in this environment (Tanaka & Leite 2003), with dispersal among patches being potentially influenced by differential sex mobility over small scales. It is known that individuals might be transported by drifting (Miller et al. 2007, Bringloe et al. 2013). Thus, if one sex is more mobile over small scales (i.e. moves between algae more frequently), it has a higher chance of being transported over local distances. Finally, large scales represent the movement of individuals among rocky shores (km). Even though amphipods are direct developers, long-distance dispersal may be mediated by rafting (Haye et al. 2012), i.e. passive transport of organisms on items floating on the ocean surface (Thiel & Gutow 2005). Over large scales, males and females have the same chances of being transported by rafting, which reduces the probability of SBD at this scale.

Here, we used *Cymadusa filosa* Savigny, 1816, a tube-building amphipod species, to explore dispersal at distinct spatial scales combining direct and indirect approaches. Ultimately, we tested whether dispersal in *C. filosa* is sex-biased at different scales. To confirm that sexes present different mobility over small scales, we performed behavioral tube-occupancy experiments to define male and female behavior. Over local scales, field colonization experiments and molecular analyses using microsatellites were conducted to evaluate dispersal rates and genetic relatedness for each sex. Finally, we investigated the dispersal of each sex over large scales (among sites) using microsatellites. Specifically, we tested the following hypotheses: (1) over the small scale of SBD, one of the sexes will show lower fidelity to their tubes and subsequently show higher mobility than the other sex; (2) the sex with the higher mobility will be more likely to colonize new habitats than the other sex, resulting in more significant genetic variation seen in the more mobile sex (local-scale SBD); and (3) sex does not influence large-scale SBD.

2. MATERIALS AND METHODS

2.1. Study system

The tube-dwelling amphipod *Cymadusa filosa* (Fig. 1) is a marine herbivore commonly found inhabiting many macrophyte species in tropical and warm-temperate shallow waters (LeCroy 2002, Peart 2004, Serejo & Siqueira 2018). On rocky shores, this amphipod inhabits macroalgae and constructs tubes by binding algal blades and other small particles using silk (Appadoo & Myers 2003, Machado et al. 2019a). Newly born juveniles use their silk to build tubes using only fecal pellets and detritus. Often, the tube is occupied by a single individual. However, tube-sharing occurs between sexually mature males and females for copulation or between females and offspring (Appadoo & Myers 2003). Like other small marine herbivores, *C. filosa* uses algal hosts as both food and habitat (Duffy & Hay 1991, Lasley-Rasher et al. 2011, Machado et al. 2019b). Although this herbivore is a generalist feeder, thus able to feed and potentially occur on various macroalgae, its abundance on algal hosts is strongly determined by predation pressure (Machado et al. 2019b). Selecting *C. filosa* as a model organism had additional benefits because it can be successfully raised under laboratory conditions and it can also rapidly colonize new algal patches, which allows laboratory and field experiments with this tube-dwelling amphipod (Bueno & Leite 2019, Machado et al. 2019a).

2.2. Laboratory experiment — small-scale SBD

To test if the level of mobility of *C. filosa* varies between sexes over small scales, we conducted a laboratory experiment using adult males and non-ovigerous females (mean ± SD length: males = 14.8 ± 1.7 mm; females = 15.1 ± 1.7 mm). We used the frequency of amphipods that moved between 2 algal pieces to measure mobility over a small spatial scale (cm). Observations were conducted over 96 h. Ovigerous females were not included in the analysis to avoid the effects of offspring brooding on female behavior. In this experiment, the brown seaweed

Fig. 1. A male (♂) and a female (♀) specimen of *Cymadusa filosa*

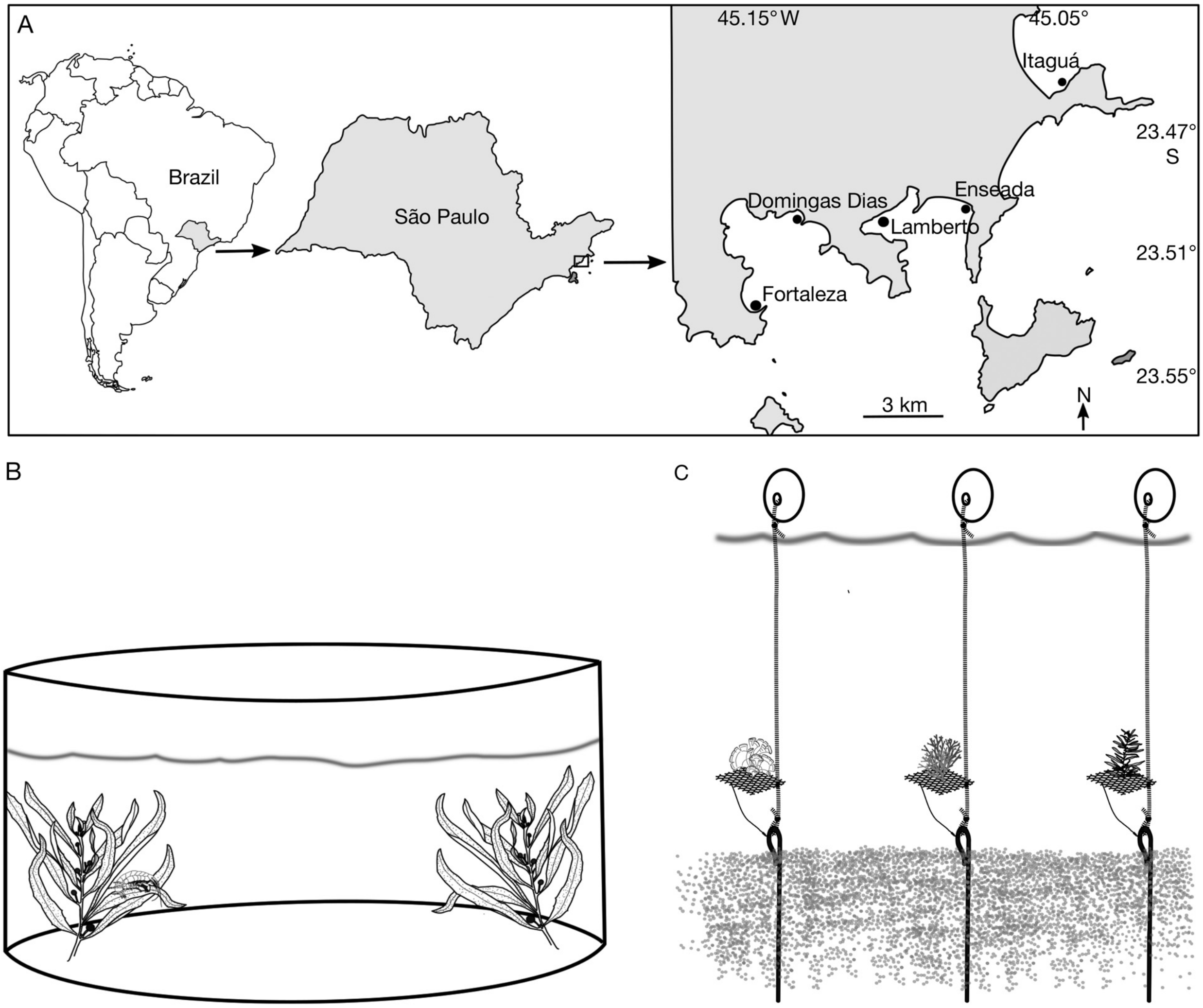

Fig. 2. (A) Study sites in Ubatuba, southeastern Brazil. (B) Petri dish setup used in the male and female *Cymadusa filosa* mobility experiment (for details of the experiment, see Section 2.2). (C) Field experiment underwater (for details of the experiment, see Section 2.3)

Sargassum sp. was offered as food and substratum to *C. filosa*. We could not identify the *Sargassum* at the species level due to taxonomic uncertainty on species from the South Atlantic (Coimbra 2006). Amphipods were collected at Fortaleza Beach, southeastern Brazil (23° 31′ S, 45° 09′ W), and maintained in laboratory cultures. The cultures were kept in tanks with seawater with an air pump and aerator, under a 12:12 h photoperiod, and at a temperature of 22°C. The amphipods used in the experiment were obtained from cultures in the laboratory. Seaweeds were collected at the same site and kept in the laboratory for approximately 5 d before the experiment.

Each experimental unit (n = 17 per sex) consisted of a cylindrical cup with seawater (height = 6 cm, diameter = 10 cm, volume = ~400 ml), 2 apical portions (~8 cm thallus length) of *Sargassum* sp. placed at opposite sides of the cup, and 1 adult amphipod (Fig. 2B). Experimental units were maintained with seawater under a 12:12 h photoperiod and at a temperature of 22°C. Based on previous tests, we offered each amphipod a quantity of seaweed greater than they should be able to consume during the experiment. The location of the first constructed tube was registered 2 h after adding the amphipods to the cups. Algal pieces were examined every 12 h. We considered that the amphipod did not move if it was on the same algal piece as it was during the previous observation. Otherwise, it was considered that the amphipod moved from one algal piece to the other. The change between algal pieces was considered a proxy for mobility.

For the laboratory experiment, we compared the mobility level between males and females of *C. filosa* using generalized estimating equations (GEEs) with a binomial distribution. This approach accounts for data with dependence structure, such as repeated measurement data (Quinn & Keough 2002, Zuur et al. 2009, Pekár & Brabec 2018). For the analysis, we considered the change between algal pieces (0 or 1, binary variable) as the response variable, sex (male and female) as a fixed factor, and individuals (each one with a unique identification) as a grouping variable. An exchangeable correlation structure was used to account for repeated observations over time. The choice of such a correlation structure over other possibilities (e.g. autoregressive) was supported by quasi-likelihood under the independence model information criterion calculated from the 'MESS' package in R (Ekstrøm 2020). The Wald test was used to test the significance of the factor 'sex'. The GEE was performed using the 'geepack' package (Yan 2002, Yan & Fine 2004, Højsgaard et al. 2006) in R 3.6.3 (R Core Team 2020). Trials in which a dead amphipod was found at the end of the experiment (1 out of 17 males) or in which the amphipod joined the 2 algal pieces (1 out of 17 females) were excluded from the analysis because, in these cases, it was impossible to determine the movement between algal pieces. Also, replicates in which the amphipod consumed one of the algal pieces entirely (1 out of 17 females) were not considered for analysis, as a change towards the unconsumed algal piece could represent foraging rather than the level of mobility of this individual.

2.3. Field experiment — local-scale SBD

To test if males and females of *C. filosa* differ in their potential to disperse in the field, we performed a field experiment at Fortaleza Beach in March 2019. We considered the colonization of defaunated seaweeds by male and female *C. filosa* as a dispersal proxy over a local scale (m). The seaweeds *Sargassum* sp., *Dichotomaria marginata* (J. Ellis & Solander) Lamarck, and *Padina gymnospora* (Kützing) were randomly collected in the subtidal zone (1 to 2 m depth) at the study area and carried to the laboratory in thermal boxes. These were the most abundant algae species (Machado et al. 2019a, Peres et al. 2019). In the laboratory, seaweeds were cleaned in seawater to remove associated organisms (e.g. fauna and epiphytes). Each experimental unit (n = 5 per algal species) consisted of 1 algal frond tied to a plastic screen (1 cm mesh size; 10 cm × 10 cm area) with adjustable plastic clamps and a string. In the field, by using adjustable plastic clamps, each experimental unit was attached to a rope with a fishing float and an iron stick buried in the sediment (Fig. 2C). The experiment was set up during low tide at 1.5 m depth. The experimental unit remained underwater, with the fishing float at the surface. Replicates were kept about 50 cm from the rocky shore and at least 1 m from each other. The field experiment ran for 4 d, allowing for the recolonization of defaunated algal fronds by associated mobile fauna (Taylor 1998, Tanaka & Leite 2004).

After 4 d, algal fronds were collected and stored in fabric bags (0.2 mm mesh size) for faunal retention. Samples were transported to the laboratory, frozen, and then washed in fresh water to remove the associated fauna. Individuals of *C. filosa* were identified, and the number of males and females per sample was counted. The sex determination of *C. filosa* was based on secondary sexual traits. Males present genital papilla and a striking difference in size between gnathopods 1 and 2, while females have oostegites. Individuals with no secondary sexual traits were considered juveniles.

To evaluate the potential source of males and females of *C. filosa* colonizing the defaunated algal fronds of the field experiment, we sampled the algal bed at the study area monthly during the summer (December 2018, January and February 2019). At each sampling event, 3 fronds of *Sargassum* sp., *D. marginata*, and *P. gymnospora* were collected randomly from the subtidal rocky shore (n = 9 per algal species) and stored in fabric bags (0.2 mm mesh size) for faunal retention. The same procedures described above for samples from the field experiment were applied to determine the sex ratio of *C. filosa* in the algal bed.

A chi-squared test was used to evaluate if observed ratios (male:female or juvenile:adult) deviated from specific expected ratios for amphipods in algal beds and in the colonization experiment. We tested the null hypothesis for amphipods from the algal bed that the sex ratio does not deviate from 1:1. For amphipods in the colonization experiment, we tested the null hypothesis that the sex ratio does not deviate from that found on the algal bed, since the number of males and females colonizing the defaunated algal fronds would depend on the stock of such amphipods on the algal bed. In this case, any deviation in the sex ratio of *C. filosa* from the colonization experiment compared to the sex ratio found on the algal bed could indicate differences in dispersal levels between males and females of this amphipod. Due to the high occurrence of juveniles (see Section 3), we also tested if the ability of *C. filosa* to colonize defaunated algal patches differed between juveniles and adults. We used the chi-squared test to compare the ratio between juveniles and adults in the colonization experiment (i.e. observed ratio) based on that found on the algal bed (i.e. expected ratio). Amphipods were deposited at the Zoology Museum of the State University of Campinas (ZUEC) (ZUEC-CRU 4373 to 4384).

2.4. Molecular analyses — local- and large-scale SBD

Molecular analyses were performed with individuals of *C. filosa* collected on 5 different rocky shores located in Ubatuba, São Paulo, Brazil: Fortaleza; Domingas Dias (23° 30′ S, 45° 08′ W); Enseada (23° 29′ S, 45° 05′ W); Lamberto (23° 30′ S, 45° 07′ W); and Itaguá (23° 27′ S, 45° 03′ W) (Fig. 2A). We tested sex-biased dispersal within (local scale) and among (large scale) locations, enabling us to evaluate dispersal at both scales. At each location, we sampled 40 fronds of each of the 3 most abundant macroalgae species in the subtidal zone: *Sargassum* sp., *D. marginata*, and *P. gymnospora*. It is essential to note that algal species does not affect the genetic structure of the same *C. filosa* populations (Peres et al. 2019). All algal species were collected at depths of 1 to 2 m by snorkeling. In total, we collected 120 fronds per location to maximize our chances of obtaining a sufficient number of males and females for the analyses. Each frond was collected from the rocky bottom by scraping. Fronds were then enclosed in individual plastic bags before transportation to the laboratory. Even if some amphipods escaped during this process and not all individuals were collected, this would not affect molecular analyses. Because we were interested in the precise position of each animal and its distance to other individuals on a local scale, every collected frond was assigned to an (x,y) coordinate. We used a measuring tape to establish a fixed horizontal transect along with the total extent of the rocky shore to define our x-axis. Each collected frond was then assigned a y-coordinate using the perpendicular distance from the frond position to the horizontal fixed x-axis, also determined using a measuring tape. The maximum x-value was 65 m, and the maximum y-value was 28 m. In the laboratory, we examined all fronds for *C. filosa* individuals. Every specimen had its exact position on the rocky shore defined and its sex determined. All individuals were preserved in 100 % ethanol and stored at −20°C.

A total of 123 males and 249 females of *C. filosa* were included in the genetic analysis (Table 1). Genomic DNA was extracted from all individuals following a modified salt-extraction protocol, according to Aljanabi & Martinez (1997). All amphipods were genotyped at 10 polymorphic microsatellite loci (for details on primers and PCR amplification, see Peres et al. 2018). All analyses were performed using male and female datasets. We estimated F_{IS} (Weir & Cockerham 1984) and compared it between sexes. This index represents heterozygote deficiency in local populations; we expect the dispersing sex to have higher values because local populations will consist of local individuals and immigrants from other populations. As a result of selecting individuals from 2 different gene pools, there will be a sign of heterozygotic deficit caused by the Wahlund effect. We also assessed relatedness ($2F_{ST}$ / [$1 + F_{IT}$]) of individuals (Queller & Goodnight 1989), which is expected to be higher in the philopatric sex. F_{ST} (Weir & Cockerham 1984) was used as an estimator of population differentiation and is also expected to be higher in the philopatric sex. All calculations were performed in FSTAT ver. 2.9.3.2 (Goudet 1995), and statistical significance was assessed using 10 000 randomizations. Population differentiation was also investigated by conducting a principal coordinate analysis (PCO) and pairwise-F_{ST} among locations using GeneAlEx 6.5 (Peakall & Smouse 2006, 2012). Significance for pairwise-F_{ST} was assessed with 9999 permutations, followed by the Bonferroni correction (Rice 1989).

We performed comparisons on the assignment index mean (mAIc) and on variance (vAIc) between males and females (Favre et al. 1997, Mossman & Waser 1999, Goudet et al. 2002). AIs determine the probability of an individual being assigned to the population from where it was sampled or being assigned as an immigrant. The sex with the lower mAIc and higher vAIc represents the one that is probably migrating among populations. These analyses were performed using FSTAT ver. 2.9.3.2 (Goudet

Table 1. Number of individuals of *Cymadusa filosa* from each location used for genetic analysis

Location	Females	Males
Itaguá	69	43
Enseada	36	7
Lamberto	39	19
Domingas Dias	67	35
Fortaleza	38	19
Total	249	123

1995) and GeneAlEx 6.5 (Peakall & Smouse 2006, 2012). We decided to use both software programs because FSTAT allows the input of missing genotypes (i.e. not all 10 microsatellites scored for an individual), while GeneAlEx does not allow missing values (i.e. it excludes these individuals).

We conducted a genetic autocorrelation analysis to detect local-scale genetic structure at each location using male and female datasets separately (Peakall et al. 2003, Banks & Peakall 2012). This analysis combines pairwise genetic distance and spatial data for all individual pairs at a specific location and generates an r coefficient ranging from −1 to 1 for each predetermined distance class. Here, we used 1 m interval distance classes, which means that an r coefficient was generated for all individuals that were less than 1 m apart, followed by iterations every 1 m (1, 2, 3, … m) until the entire spatial area was covered. The error associated with the r coefficient was calculated with 9999 bootstraps; we also estimated the 95 % confidence interval with 9999 permutations, testing for r = 0. The philopatric sex is expected to show higher r coefficients outside the 95 % confidence interval and error bars not containing 0 within the range.

3. RESULTS

3.1. Laboratory experiment — small-scale SBD

Males changed between algal pieces more often than females (GEE, correlation parameter = 0.095 ± 0.056 [SE]; Wald test, $\chi^2 = 4.44$, df = 1, p = 0.035). During the experiment, 13 males (of 16) relocated to the other algal piece at least once, while only 7 females (of 15) explored a novel habitat. During every observation period, we noted a higher proportion of males changing between algal pieces than females, except for the last observation (96 h) (Fig. 3).

3.2. Field experiment — local-scale SBD

A total of 202 individuals of *Cymadusa filosa* were found in the algal bed (34 males, 29 females, and 139 juveniles). The sex ratio of *C. filosa* observed on the algal bed did not deviate from the expected 1:1 (male:female) ($\chi^2 = 0.40$, df = 1, p = 0.529). In the colonization experiment, 308 individuals of *C. filosa* (38 males, 39 females, and 231 juveniles) were found on the experimental thalli. The sex ratio of *C. filosa* from the colonization experiment (1:1.03) did not deviate from the expected 1:0.85 (male: female ratio, based on the algal bed) ($\chi^2 = 0.66$, df = 1, p = 0.416), suggesting that males and females have similar capabilities of dispersal and colonization of novel habitats. Juveniles were more abundant than adults in both the algal bed and in the colonization experiments (juvenile:adult ratio = 1:0.45 for the algal bed and 1:0.33 for the experiment). Furthermore, juveniles were found in the colonization experiment in a higher proportion than expected (i.e. juvenile:adult ratio in the algal bed) ($\chi^2 = 5.50$, df = 1, p = 0.019), suggesting that juveniles have higher dispersal rates than adults.

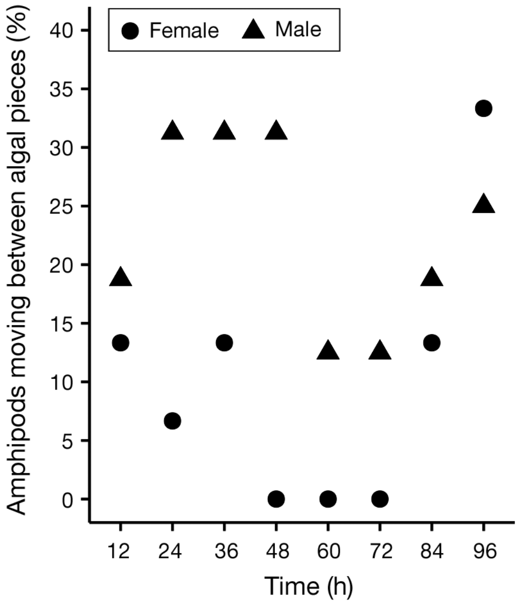

Fig. 3. Percentage of male (▲) and female (●) *Cymadusa filosa* changing between algal pieces every 12 h throughout a 96 h laboratory experiment

3.3. Genetic analyses — local- and large-scale SBD

There were no significant differences between males and females for F_{ST}, mAIc, and vAIc estimates, but we found a difference between F_{IS} values (Table 2,

Table 2. FSTAT results of assignment index mean (mAIc) and variance (vAIc), *F*-statistics, and relatedness (r) for each sex of *Cymadusa filosa*. **Bold** indicates significance (p < 0.05)

	F_{IS}	F_{ST}	r	mAIc	vAIc
Female	0.0183	0.0247	0.0475	0.04353	5.52061
Male	0.0872	0.0203	0.0368	−0.08882	5.12992
p	**0.0443**	0.6637	0.5683	0.5986	0.7930

Fig. 4). PCO showed no differences between male and female genetic structure (Fig. 5), with the *x*- and *y*-axes explaining, respectively, 12.35 and 9.97% of the variation for females and 12.69 and 11.31% for males. Pairwise-F_{ST} values represent low levels of population differentiation (Table 3). Moreover, genetic autocorrelation did not show signs of sex-biased dispersal for any sex at any location in our distance classes (see Fig. A1 in the Appendix).

4. DISCUSSION

Although there are many tube-dwelling amphipod species (Lowry & Myers 2013, Moore & Eastman 2015), little is known about their sex-specific behaviors and dispersal capabilities. Combining manipulative experiments from the laboratory and field with genetic analyses, we provide evidence that the amphipod *Cymadusa filosa* exhibits sex-biased dispersal over small spatial scales but lacks SBD over local and large scales.

4.1. Small-scale SBD — mobility differs between males and females

There are many hypotheses explaining the evolution of SBD, which are based on life-history traits, ecological conditions, and mating systems (Greenwood 1980, Perrin & Mazalov 2000). Tube-building amphipods are prone to SBD over small and local scales due to potential differences in mobility and dispersal between sexes described in some mating observations (Borowsky 1983) and colonization experiments (DeWitt 1987, Munguia et al. 2007). Mating in amphipods is facilitated via pheromone attraction (Borowsky 1984,1985b, Borowsky & Borowsky 1987, Thiel 2010). Usually, females stay in their tubes to molt and mature for reproduction, and males join them in a conjugal tube for copulation (Appadoo & Myers 2003). After mating, it is believed that females (carrying the offspring) remain within the tube while the males leave in search of future partners (Borowsky 1983, Thiel 1999, Drolet & Barbeau 2012). Our laboratory experiments confirmed that changing between tubes (here a proxy for mobility) is more likely in males than females, even in non-mating contexts. Our experiment consisted of single individual trials, and there was no pheromone stimulus for 'cruising male' behavior (Borowsky 1983). Therefore, mobility has to be explained by factors other than reproduction.

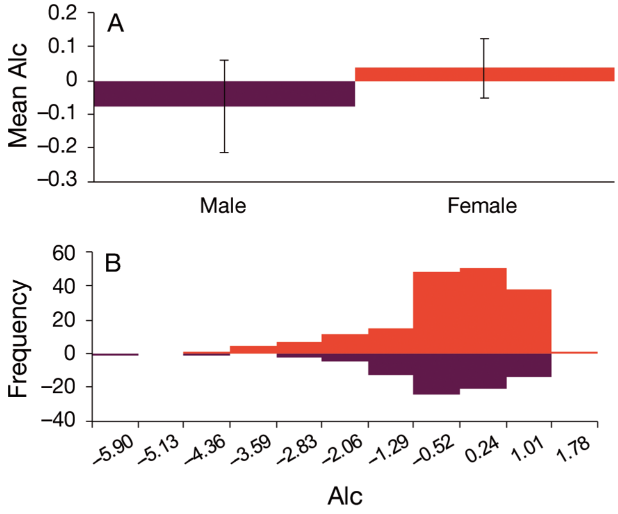

Fig. 4. GenAlEx results of (A) assignment index mean (mAIc) and (B) frequency of distribution of the assignment index (AIc) for female (orange) and male (purple) *Cymadusa filosa*. Vertical bars in (A) represent standard error

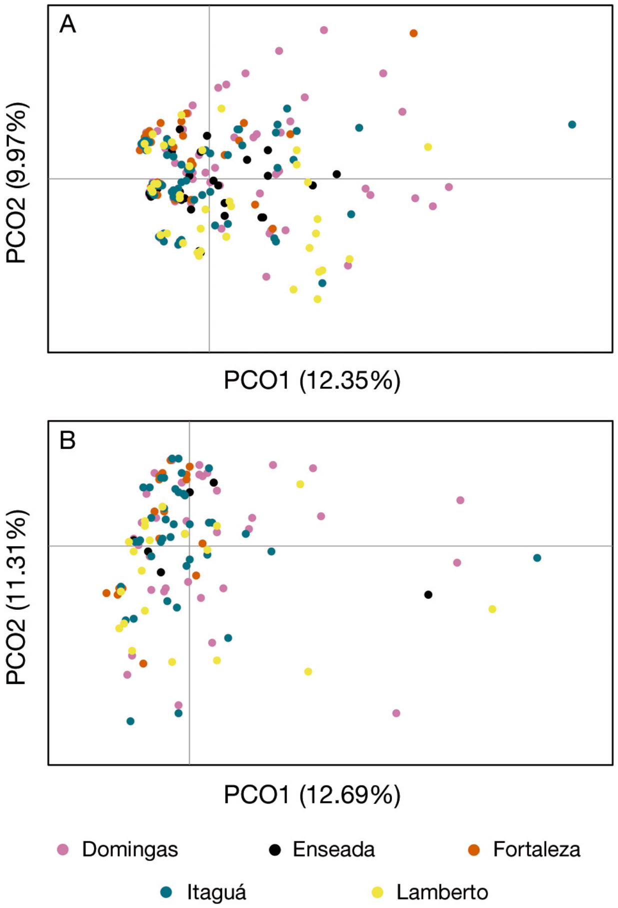

Fig. 5. Principal coordinate analysis (PCO) scatterplots considering the 2 principal coordinates for (A) female and (B) male *Cymadusa filosa*. Gray lines indicate PCO1 and PCO2 axes

Table 3. Pairwise F_{ST} values among populations of *Cymadusa filosa* from different rocky shores. Below diagonal: females; above diagonal: males. No values were significant (at $p < 0.001$ after Bonferroni correction)

	Itaguá	Enseada	Lamberto	Domingas Dias	Fortaleza
Itaguá	–	0.030	0.016	0.019	0.015
Enseada	0.018	–	0.051	0.044	0.046
Lamberto	0.008	0.016	–	0.033	0.028
Domingas Dias	0.021	0.018	0.020	–	0.029
Fortaleza	0.026	0.030	0.026	0.012	–

Space is a limited resource for epibenthic species, such as *C. filosa* and other invertebrates on macroalgae (Angelini et al. 2011). The mobility observed during experiments may be a small-scale mechanism for monitoring nearby resources (López-Sepulcre & Kokko 2005). Due to variation in host shelter (Gutow et al. 2012) and palatability (Cronin & Hay 1996), amphipods may show differential habitat use along distinct regions of a plant (Machado et al. 2015). Some tube-building amphipods, such as *Ampithoe ramondi*, *Erichthonius brasiliensis*, *Jassa falcata*, and *Sunamphitoe femorata*, show aggressiveness towards con- and heterospecifics (Connell 1963, Brawley & Adey 1981, Borowsky 1985a, Cerda et al. 2010), which may indicate a defensive behavior to protect tubes and surroundings. This behavior might even lead to delimited algae-patch territories, with the construction of equally spaced tubes (e.g. Connell 1963), which we also detected in our laboratory culture (S.G.L. Siqueira pers. obs.). *C. filosa* might be a territorial species, whose movement over small distances indicates a patrolling behavior to protect resources (i.e. small algae patches). This behavior is more intense in males, leading to male-biased dispersal when looking at small scales. However, this behavior does not result in genetic signatures over the local scale, as discussed in Section 4.2.

4.2. Local-scale SBD — similar rates of colonization and genetic similarity among males and females

Even though we found differences in mobility and tube occupancy over small scales, the field experiment that explored local scales showed males and females colonizing newly available habitats at similar rates. Also, there was no genetic spatial autocorrelation for both sexes, which means that neighboring individuals are not more related than distant individuals from the same rocky shore. Both results suggest that tube-building amphipods are highly mobile animals. Our findings corroborate previous studies demonstrating rapid colonization of habitats by amphipods as well as the absence of genetic differentiation over local scales (Taylor 1998, Poore & Steinberg 2001, Norderhaug et al. 2002, Tanaka & Leite 2004, Bueno & Leite 2019, Peres et al. 2019, Ros et al. 2020). Some field experiments show higher rates of colonizing males (DeWitt 1987) or females (Munguia et al. 2007). Here, we show that both sexes equally colonized defaunated algae.

The difference between small-scale and local-scale dispersal may be explained by drifting in adults. Tidal variation and wave action are critical drivers of coastal community structure (Blamey & Branch 2009), altering the location of an individual through drifting (Miller et al. 2007, Drolet & Barbeau 2012). In this case, we can define drifting as the local transport of individuals due to wave and current actions. For tube-building amphipods, this may be the mechanism that moves animals passively over local scales (Locke & Corey 1989). Although males show less affinity to their tube, this is not enough to skew their drifting rate. Havermans et al. (2007) explored the effects of drifting on dispersal in the amphipod *Jassa herdmani* and found that this species can actively leave its tube, swim to the surface, and be transported through drifting, then sink back to the bottom. Interestingly, the authors did not find differences between sexes performing this behavior. Therefore, this phenomenon may be an essential mechanism of local dispersal despite a tube-dwelling lifestyle (Havermans et al. 2007), and it would explain the similar colonization rates between males and females of *C. filosa*, which would actively leave their tubes and thus be transported by drifting. Colonization experiments of defaunated algae placed 25–400 m from the shore suggested that drifting is the local dispersal mechanism of amphipods (Salovius et al. 2005). These animals did not reach newly available habitats by a stepping-stone dispersal. While stepping-stone local dispersal should be identifiable via genetic analyses (genetic autocorrelation), we could not observe these patterns within our data or within previous studies (Peres et al. 2019).

Field experiments also revealed higher colonization rates by juveniles. Juvenile-biased dispersal has been suggested for some amphipod species (Franz & Mohamed 1989, Thiel 1997, Stevens et al. 2006, Drolet & Barbeau 2012, Beermann 2014, Bueno & Leite 2019, Peres et al. 2019). We are not able to confirm if this is an active or passive process. However, it is known that juveniles are more prone to passive dispersal by drifting because they are easily carried by currents (Franz & Mohamed 1989, Thiel 1997, Drolet & Barbeau 2012) and their tubes might not be as suitable for settling as adult tubes. Instead of binding seaweed blades, juveniles mostly build their tube using fecal pellets and amphipod silk (Appadoo & Myers 2003). Juvenile-biased dispersal can be a strategy to avoid competition in a high-density habitat (Bowler & Benton 2005), such as macroalgae habitats in subtropical environments (Tanaka & Leite 2003, Bueno et al. 2016, 2017, Machado et al. 2019a).

Alternatively, both adults and juveniles can also be passively transported through whole macroalgal dislodgment, followed by local rafting (Martone et al. 2012). The consequences of seaweed rafting are usually discussed from the long-distance dispersal perspective (Thiel & Haye 2006), but it may also be a mechanism to transport animals along the rocky shore over local scales (Miranda & Thiel 2008). Both drifting and rafting may result in males and females reaching new habitats, which might be advantageous in unstable environments such as rocky shores, where macroalgae and other substrates show temporal variation (Bellgrove et al. 2004, Jacobucci et al. 2009).

We expected the male-biased dispersal over small scales (cm) to affect dispersal over local scales (m). That is, males would colonize defaunated algae at a higher rate since they are more mobile than females, and this would be detected by the microsatellite markers, showing genetic relatedness among spatially closer females (hypothesis 2). Our results show that mechanisms acting on local scales (e.g. drifting or local rafting) may be stronger, preventing any signals of genetic differentiation resulting from SBD over a small scale. Juvenile-biased dispersal is more frequent than adult dispersal over local scales, but both mechanisms occur. Adult and juvenile transport, either actively or passively, is probably present throughout the year (Franz & Mohamed 1989, Havermans et al. 2007), leading to genetic homogeneity over local scales.

4.3. Large-scale SBD — lack of genetic structure among sites

Over large spatial scales, rafting may also promote an absence of genetic structure among sites (Thiel & Haye 2006). Even though we found male-biased dispersal over small scales, this did not lead to SBD when looking at local and large scales. As we expected, both sexes are dispersing among sites, resulting in low levels of population differentiation. Direct-developing species are often considered species with low dispersal ability (Shanks 2009), but there are exceptions (Weersing & Toonen 2009). In the case of our study on amphipods, direct development does not seem to affect dispersal ability on any scale. Although direct developers lack a larval phase, some gastropods, isopods, and amphipods colonize drifting algae (Ingólfsson 1998, Salovius et al. 2005, Miranda & Thiel 2008), and dispersal among sites may occur through rafting. Algae-associated amphipods and isopods might show low genetic differentiation even among distant populations (Thiel & Haye 2006, Nikula et al. 2010, Haye et al. 2012, Grabowski et al. 2019). Thus, rafting seems to be effective in promoting connectivity over larger scales. In our case, we could not identify the *Sargassum* species, but it has pneumatocysts and floats after detachment from the substratum (Britton-Simmons 2004, Thiel & Gutow 2005, Hu et al. 2013, van Hees et al. 2019). This indicates probable occurrence of rafting in the studied region. For other species and locations, specific geographical conditions (currents, barriers) may promote isolation among populations (Luttikhuizen et al. 2019) and lead to speciation (Desiderato et al. 2019).

4.4. Conclusions

We gained a deeper understanding of *C. filosa* dispersal by combining direct and indirect approaches. Direct approaches showed behavioral male-biased dispersal over small scales (laboratory experiment), but different mobility between sexes over this scale did not have consequences on dispersal over local scales (field experiment). Indirect approaches using molecular markers showed no SBD besides the potential for this pattern to emerge due to different mobility between sexes (Perrin & Mazalov 2000). Our results reinforce the importance of integrating more than one source of information and different spatial scales to investigate species dispersal.

Molecular markers have been used to study the dispersal of amphipods and other organisms among sites (Thiel & Haye 2006, Nikula et al. 2010, Grabowski et al. 2019), and less commonly within sites and comparing males and females. Field experiments have shown females (e.g. Munguia et al. 2007), males (e.g. DeWitt 1987), or juveniles as the most dispersing group (e.g. Beermann 2014), although not representing a unique form of dispersal. Nevertheless, little is known about the genetic consequences of these patterns. Given our results, we believe other tube-building amphipods species might show the same pattern we found. Despite different dispersal behavior or recruitment of juveniles closer to the females, the populations will show no genetic signatures of SBD, and no higher genetic relatedness among spatially closer individuals. Behavioral sex- or age-biased dispersal are idiosyncratic and might happen simultaneously. These processes might constrain the emergence of genetic differentiation over small and local scales, while large-scale rafting promotes connectivity among sites.

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Appendix. Additional data

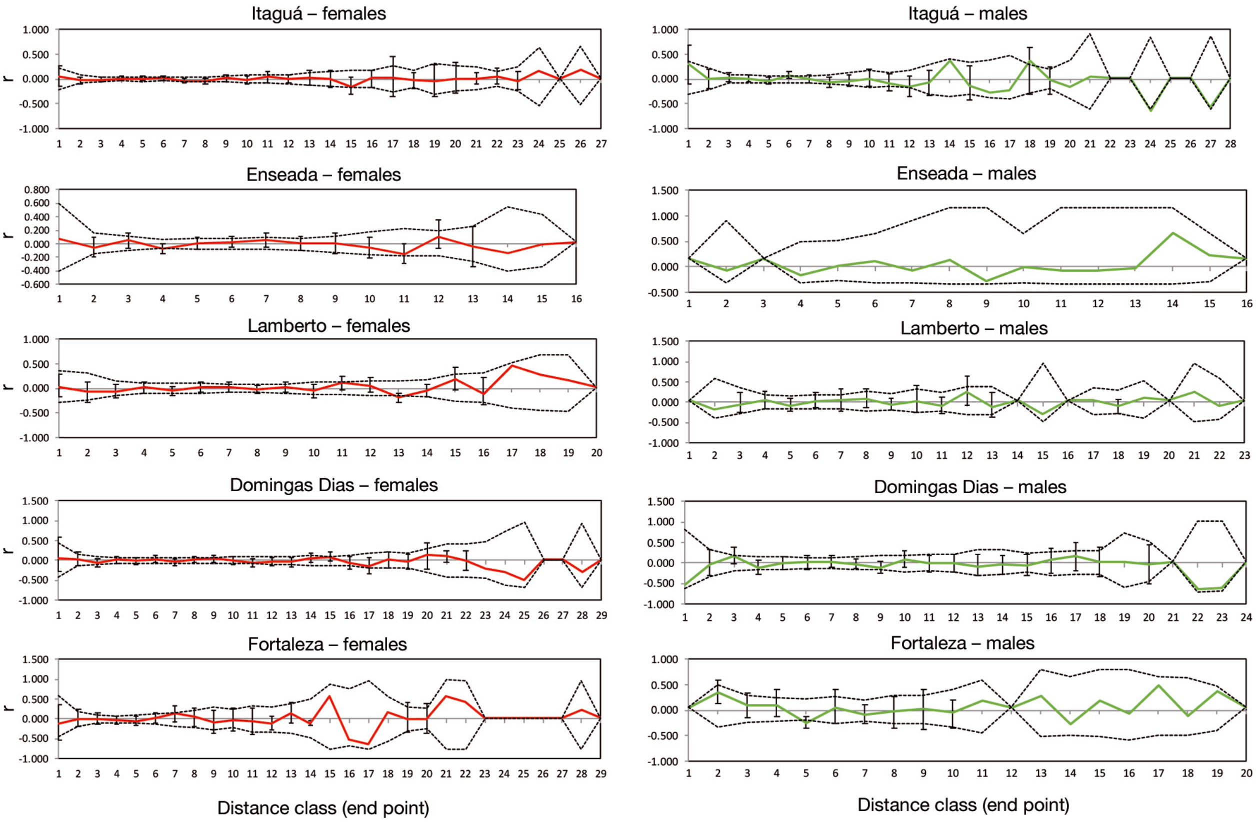

Fig. A1. Results of genetic autocorrelation analysis for female and male *Cymadusa filosa* in each location. Bars represent standard error; dashed lines represent 95% CI, and distance class is represented in meters (m)

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