

# Reproductive pattern and sexual system of the nocturnal seagrass shrimp *Ambidexter symmetricus* (Decapoda: Caridea: Processidae) in a Florida bay

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**Abstract.** The purpose of the current study was to analyse the reproductive ecology and sexual system in *Ambidexter symmetricus* (Processidae), a nocturnal seagrass shrimp. This work was conducted in St Joseph Bay, Florida, in May–August 2010 and April–October 2011. The sex ratio in *A. symmetricus* and the presence of juvenile females supported the hypothesis of a gonochoric sexual system. Breeding in the population occurred seasonally from April until September. Successive spawning of individual females was shown by the presence of late-stage (prespawning) ovaries in females that were brooding late-stage (near hatching) embryos. Female *A. symmetricus* were generally larger and more abundant than males. Male *A. symmetricus* with parasites exhibited gigantism. Because of seasonal differences in recruitment and growth, body size varied with time of year, with larger (overwintered) individuals collected in April and May, and smaller more recently recruited individuals more abundant in September and October. The population biology of this species is similar to many other warm-temperate, shallow-water carideans, thus supporting hypotheses about latitudinal variation in breeding and recruitment in marine benthic invertebrates.

**Additional keywords:** breeding, gonochory, latitudinal variation, sex ratio, spawning.

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## Introduction

Reproductive patterns in marine invertebrates, including crustaceans, may differ according to environmental conditions and latitude (Thorson 1950; Bauer 1992; Marshall *et al.* 2012). Crustaceans in shallow-water tropical habitats generally reproduce year-round, with shorter breeding seasons in populations and species farther away from the tropics (Thorson 1950; Sastry 1983). Breeding seasons in marine invertebrates, including crustaceans, have long been known to be correlated with latitude because of latitudinal variation in factors such as water temperature, nutrient cycling, and plankton production (larval food) (Thorson 1950; Bauer 1992, 2004; Marshall *et al.* 2012). Population dynamics and life-history traits may be understood in many species by examining relationships among breeding patterns, recruitment, and growth in organisms sampled during the course of annual cycles (Ridley and Thompson 1985; Ramirez Llodra 2002).

Caridean shrimps are important faunal components of temperate and tropical seagrass meadow ecosystems (e.g. Kikuchi 1962, 1966; Bauer 1985, 1989, 2004; De Grave *et al.* 2006). Considerable temporal variation in breeding patterns occurs in caridean species. Species may reproduce year-round or seasonally, and may reproduce just once (semelparous) or repeatedly (iteroparous) during the breeding season. On an individual basis, shrimps may reproduce continuously (successive spawns)

during the breeding season (Bauer 1989, 1991, 2004; Bauer and VanHoy 1996).

Although many carideans are gonochoristic, numerous species are sequential hermaphrodites (Bauer 2000; Chiba 2007). Gonochoristic shrimps spend their entire lives either as functional males or females. Sequential hermaphrodites start out their reproductive life in one sex, and then change to the opposite sex over time (Ghiselin 1969). In carideans, hermaphroditic sexual systems are mainly protandric, in which individuals develop first as males, and then change to females (Warner 1975; Bauer 2000, 2004; Chiba 2007; Baeza 2010; Baeza and Piantoni 2010). Less common is protandric simultaneous hermaphroditism, in which individuals first go through a male phase before changing to a simultaneous hermaphrodite with a mainly female phenotype (Bauer 2000; Baeza 2009).

Analysis of sex ratios may allow tests of hypotheses about the sexual system (gonochory or hermaphroditism) in caridean shrimps, which can then be examined more carefully with population structure, sexual morphology, and experimental evidence (Bauer 2004; Espinoza-Fuenzalida *et al.* 2008; Baeza and Piantoni 2010; Bauer and Conner 2012). Sex ratios of populations may vary considerably among and between species. In shallow-water benthic organisms, sex ratios are influenced by life-history traits such as size at sexual maturity, adult life-span,

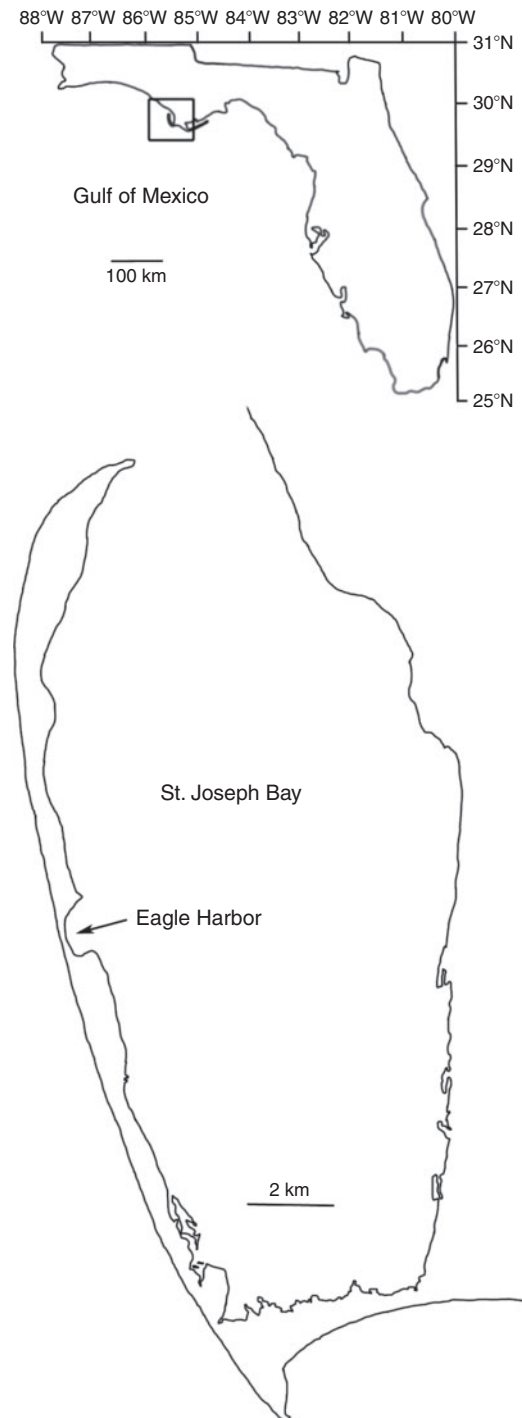
frequency of reproduction, differential mortality between sexes, migration and sex-change (Wenner 1972; Emlen and Oring 1977).

Caridean shrimps are often a dominant faunal group in seagrass beds and include carnivorous and herbivorous species (Heck 1977; Saloman 1979; Gore *et al.* 1981; García Raso *et al.* 2006; Unsworth *et al.* 2007). Shrimps are an important link between primary production and higher trophic levels (Kikuchi 1966; De Grave *et al.* 2006; Unsworth *et al.* 2007). Studies using nocturnal sampling have shown that carideans of the family Processidae may be abundant in seagrass meadows (Kikuchi 1962, 1966; Leber 1983; Bauer 1985; De Grave *et al.* 2006). However, fairly little is known about their life history and population dynamics.

Caridean shrimps are often infected by isopod parasites in the family Bopyridae. Bopyrids are ectoparasites, attaching within the branchial chamber or under the abdomen of their hosts (O'Brien and Van Wyk 1985; Markham 1986). These parasites do not kill their hosts as a requirement for development (Anderson and May 1978) but often castrate them (Baudoin 1975; Beck 1979; O'Brien and Van Wyk 1985). Bopyrid parasites may cause gigantism in their hosts (Ebert *et al.* 2004; Hall *et al.* 2007). *Urobopyrus processae* is a bopyrid with a cosmopolitan distribution known to infect members of the family Processidae (Markham 1985, 1986).

*Ambidexter symmetricus* is a processid shrimp that inhabits seagrass meadows in tropical and subtropical waters (Manning and Chace 1971; Saloman 1979). This species has an ampho-American distribution, from Florida to Santa Catarina, Brazil, including the Gulf of Mexico, in the Atlantic; and along the western coasts of California and Mexico in the eastern Pacific (Manning and Chace 1971; Abele 1972; Ríos and Carvacho 1982; Christoffersen 1998). This species has been shown to be an important component of seagrass habitats in the north-eastern Gulf of Mexico (Greening and Livingston 1982; Leber 1983). It is more abundant in warmer months, with the highest abundances during the spring and summer, and appears to decline in fall and winter collections (Leber 1983), similar to *Hayashidonus japonicus* (Kikuchi 1962, 1966). Food habits are carnivorous, feeding on polychaetes, amphipods, and other shrimps, similar to *Processa edulis edulis* (Guerao 1993) and *Processa bermudensis* (Leber 1983). *A. symmetricus* buries in soft substrates during the day, and emerges at night to feed (Barba *et al.* 2005; pers. obs.). This feeding and burying behaviour is consistent with other members of Processidae (Kikuchi 1962; Noël 1973, 1976; Leber 1983; Bauer 1985; Guerao 1993). Molting and mating occurs at night as in *P. edulis edulis* (Noël 1976; J.A. Rasch, pers. obs.).

Our overall objective in the present study was to analyse the population structure, infer the sexual system, and investigate the reproductive ecology of *A. symmetricus*. We tested the hypotheses that reproduction in female *A. symmetricus* was continuous on both the population and individual levels. We also tested the hypothesis of a gonochoric sexual system in *A. symmetricus* based on seasonal variation in sex ratios. Our final objective was to analyse factors that may influence *A. symmetricus* size, including sex, sample date, and the presence of a parasite.



**Fig. 1.** Map of the study site, Eagle Harbor in St Joseph Peninsular State Park, which is part of St Joseph Bay in Florida.

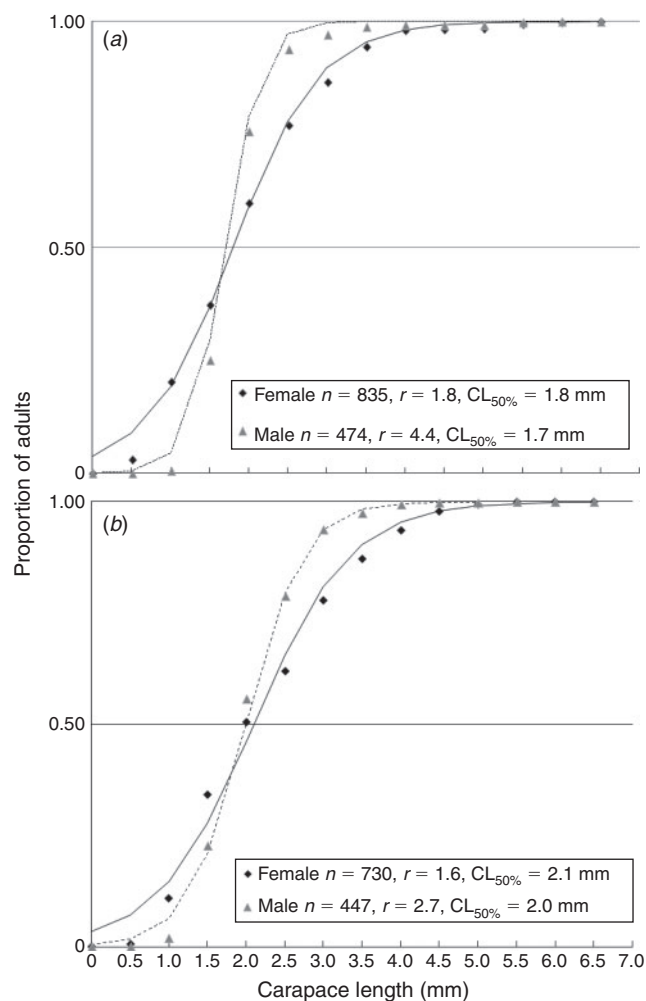
## Materials and methods

### Study area

A sampling site was established in the north-eastern Gulf of Mexico in Eagle Harbor of St Joseph Bay, Florida, within St Joseph Peninsular State Park (29°46'3.94"N, 85°24'12.22"W) (Fig. 1). This area is composed of shallow seagrass beds that are a

**Table 1.** Samples sizes of *Ambidexter symmetricus* males, total females (Total Fem), females with ovaries (Fem Ov), females with embryos (Fem Em), and total number of shrimps with a carapace length >2.00 mm per sample collected in 2010 and 2011

Year	Sample	Male	Total Fem	Fem Ov	Fem Em	Total $n > 2.00$
2010	May	140	147	6	8	287
	May–June	83	141	52	47	224
	June	93	145	33	30	238
	July	25	76	10	11	101
	August	14	15	3	3	29
2011	April	64	80	42	47	144
	May	50	81	11	10	131
	June	36	57	23	18	93
	July	0	0	0	0	0
	August	14	15	6	7	29
	September	66	102	21	9	168
	October	115	146	0	1	261



**Fig. 2.** Sexual maturity of *Ambidexter symmetricus*, based on the  $CL_{50\%}$  (carapace length) of females and males sampled in 2010 (a) and 2011 (b).

**Table 2.** Sex ratios of *Ambidexter symmetricus* in 0.5-mm size classes of frequency distributions for 2010 and 2011

Year	Size class (CL, mm)	Sex-ratio	$n$	$\chi^2$	$P$	Conclusion
2010	0.50–0.99	0.00	25	–	–	$F > M$
2010	1.00–1.49	0.02	147	135.2	<0.001	$F > M$
2010	1.50–1.99	0.45	258	2.6	0.106	$F = M$
2010	2.00–2.49	0.56	428	6.3	0.012	$F < M$
2010	2.50–2.99	0.37	231	15.1	<0.001	$F > M$
2010	3.00–3.49	0.16	94	43.6	<0.001	$F > M$
2010	3.50–3.99	0.12	74	42.4	<0.001	$F > M$
2010	4.00–4.49	0.03	32	28.1	<0.001	$F > M$
2010	4.50–4.99	0.00	1	–	–	$F > M$
2010	5.00–5.49	0.00	3	–	–	$F > M$
2010	5.50–5.99	0.30	10	1.6	0.206	$F = M$
2010	6.00–6.49	0.25	4	1.0	0.317	$F = M$
2010	6.50–6.99	0.00	2	–	–	$F > M$
2010	All size classes	0.17	1309	99.6	<0.001	$F > M$
2011	0.50–0.99	0.00	5	–	–	$F > M$
2011	1.00–1.49	0.11	83	50.9	<0.001	$F > M$
2011	1.50–1.99	0.35	263	22.5	<0.001	$F > M$
2011	2.00–2.49	0.55	266	2.9	0.086	$F = M$
2011	2.50–2.99	0.55	187	1.9	0.165	$F = M$
2011	3.00–3.49	0.36	184	13.6	0.002	$F > M$
2011	3.50–3.99	0.20	85	30.6	<0.001	$F > M$
2011	4.00–4.49	0.15	54	26.7	<0.001	$F > M$
2011	4.50–4.99	0.06	34	26.5	<0.001	$F > M$
2011	5.00–5.49	0.00	11	–	–	$F > M$
2011	5.50–5.99	0.20	5	1.8	0.180	$F = M$
2011	All size classes	0.23	1177	68.0	<0.001	$F > M$

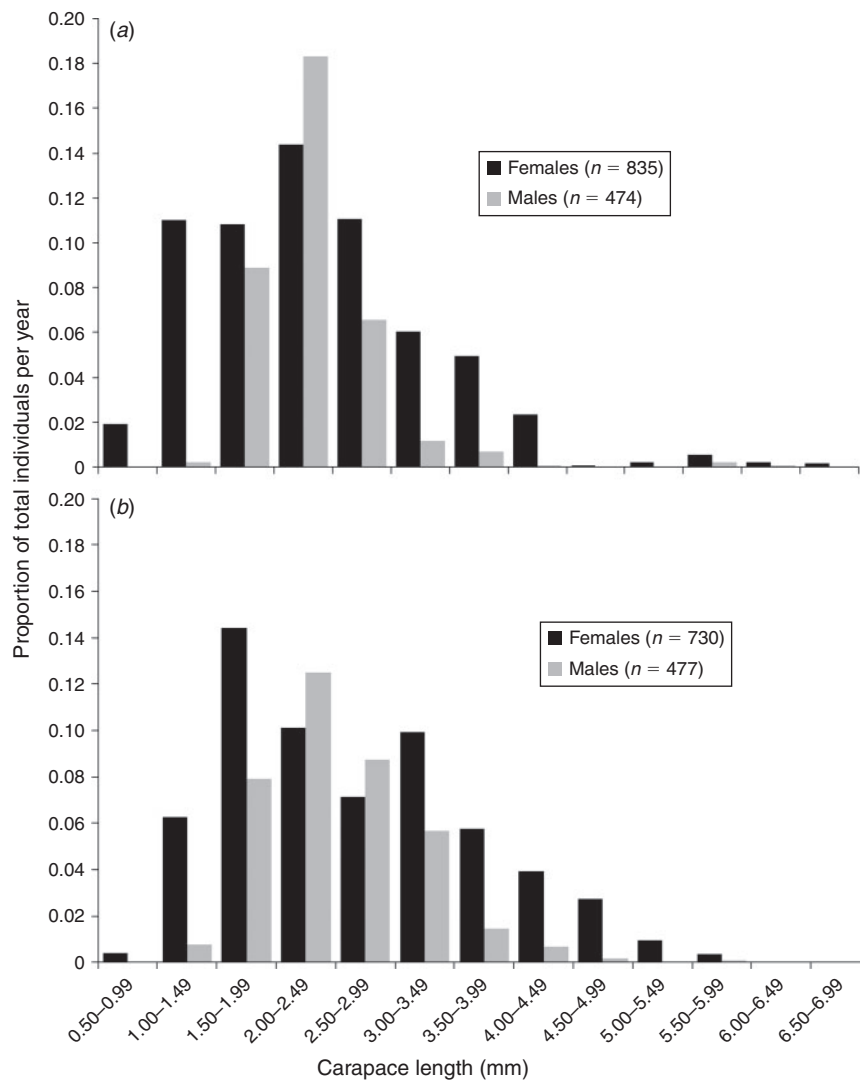
mixture of *Halodule wrightii*, *Thalassia testudinum* and *Syringodium filiforme* over sand (Iverson and Bittaker 1986). Sampling focussed on areas primarily composed of *T. testudinum* as preliminary work determined higher abundances of *Ambidexter symmetricus* in these areas. The depth sampled at this site was from 0.5 to 1.3 m during night low tides.

#### Sampling gear and design

We collected samples at night during low tides in St Joseph Bay using a pushnet with a mouth of  $45 \times 23$  cm, with a 1-mm mesh size. We sampled haphazard distances, which varied with sampler endurance, or filling of the net with plant or other material. We then sorted net samples by hand using headlamps, and all processid shrimps removed were kept in a bucket of ambient seawater before preservation. Sampling was repeated over the course of up to three hours, and was discontinued when conditions became adverse to the safety of the samplers, e.g. rising tide. We also measured salinity and water temperature for each sampling period. *A. symmetricus* were preserved in a solution of 10% formalin (10% formaldehyde, 90% ambient seawater) for transport back to the laboratory.

#### Data collection and analysis

Processid shrimps were collected between May and August of 2010 and between April and October of 2011, weather and low tide permitting. Formalin-preserved *A. symmetricus* were rinsed



**Fig. 3.** Length–frequency distributions of *Ambidexter symmetricus* males and females at St Joseph Bay for 2010 (a) and 2011 (b).

with water before being dehydrated in an ascending ethanol series to 70% ethanol for storage. Species were identified using keys from Manning and Chace (1971), Manning (1991) and Abele and Kim (1986). Carapace length (CL  $\pm$  0.01 mm) was defined as the distance from the posterior edge of the orbit to the posterolateral edge of the carapace and measured using a calibrated ocular micrometer. Sex was determined by examining the second pleopod for the presence or absence of an appendix masculina. Ovigerous condition was ranked on a scale of 1 to 4: 1, individuals with no apparent ovary; 2, oocytes visible filling less than half of the cephalothoracic space above the cardiac stomach; 3, oocytes filling greater than half but not all the cephalothoracic space; and 4, oocytes completely filling the cephalothoracic space (Bauer 1986, 1989). Embryonic condition was defined on the scale of 0–4: 0, embryos absent; 1, embryos present and apparently composed entirely of yolk, 2, embryos present and blastodisc visible but no eyespot present;

3, embryos present with eyespot visible, cephalothorax and abdomen fused; and 4, embryos present and near hatching, with cephalothorax and abdomen separated (Bauer 1986, 1989; 1991). Parasites were recorded as present if an isopod bopyrid parasite was visible within the branchial chamber, or if one side of the carapace was deformed (bulged outward), indicating the shrimp had been infected but parasite lost (Jay 1989). The parasites were all identified as *Urobopyrus processae*, the only documented branchial parasite of processids (Manning and Chace 1971; Noël 1976; Markham 1985).

We composed length–frequency distributions of individuals from monthly collections using 0.5-mm CL size intervals and tested for deviation of a 0.50 sex ratio with a goodness of fit Chi-Square (Wenner 1972). To estimate the parameter of size at sexual maturity, we plotted the relative proportion of females and males in each size class using the logistic function  $y = 1/(1 + e^{-r(CL - CL_{50})})$ . The  $CL_{50\%}$  corresponds to

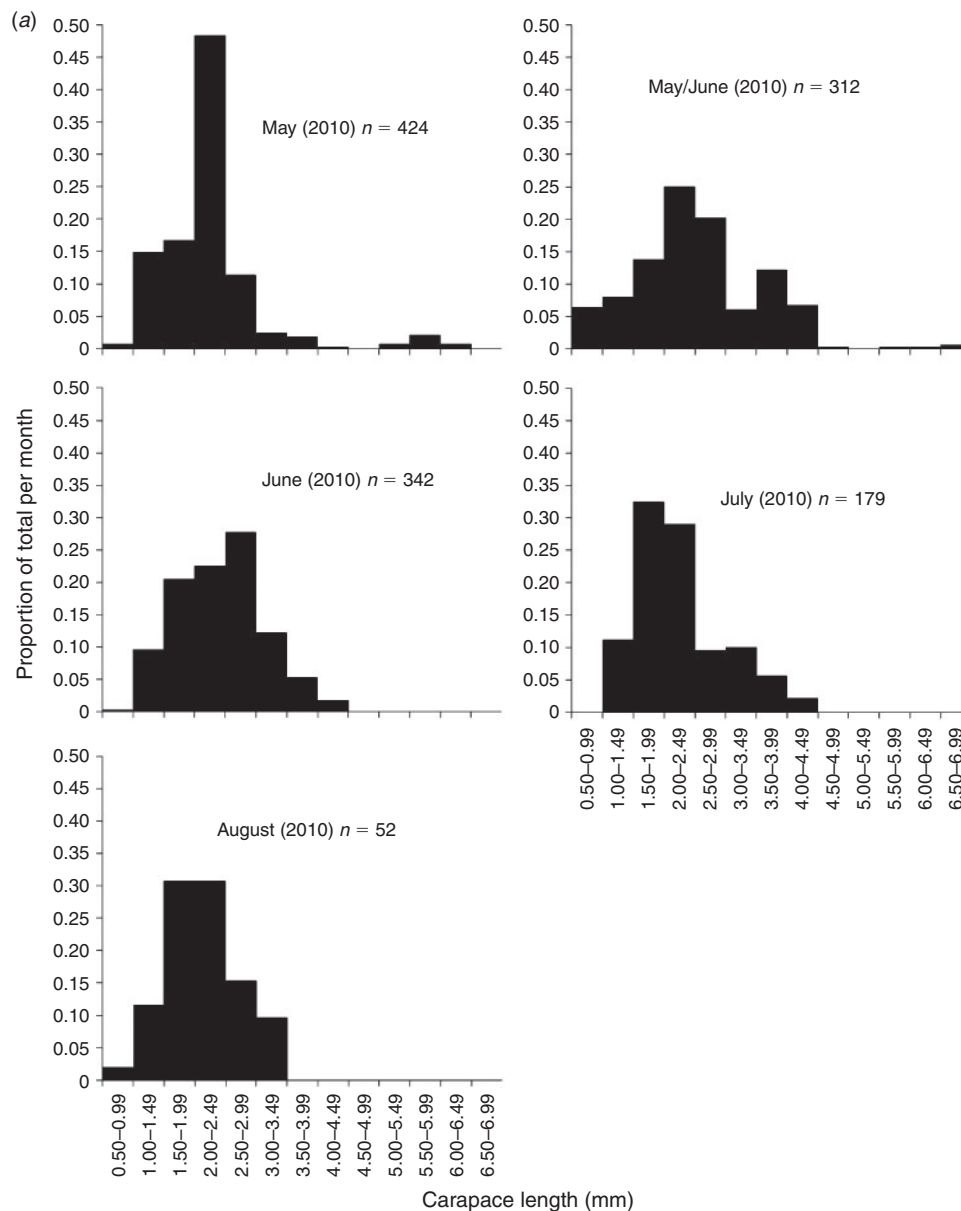


Fig. 4. Length–frequency distributions of *Ambidexter symmetricus* by sample for 2010 (a) and 2011 (b).

the size at which 50% of individuals are considered sexually mature, and  $r$  stands for the slope of the curve (King 1995). We used the least-squares method in Excel 2007 (Microsoft, Redmond, WA, USA) for fitting the data, with individuals in 0.5-mm size-classes (Castilho *et al.* 2007a, 2007b). We used a  $4 \times 4$  contingency table analysis to test the null hypothesis that there is no association between the ovarian and the embryonic condition of female *A. symmetricus* in sampling years 2010 and 2011. A Monte Carlo sampling (10 000 replications) was used to determine distribution-free  $P$  values (Proc FREQ, SAS Institute Inc., Cary, NC). A multifactorial analysis of variance (ANOVA) was used to test for differences in mean CL among individuals by sample date, sex, and parasite presence in a full

factorial design for both years. We ran a Tukey–Kramer *post hoc* test to determine interactions between Least Square Means (SAS Institute Inc. 2013).

## Results

We collected a total of 2486 *Ambidexter symmetricus* for the present study, 1309 in 2010 and 1177 in 2011. *A. symmetricus* collected in 2010 and 2011 ranged in CL from 0.79 to 6.50 mm. The smallest female *A. symmetricus* carrying embryos had a CL of 1.86 mm, and the next smallest a CL of 3.18 mm. The smallest female *A. symmetricus* with a developing ovary had a CL of 2.20 mm. Complete development of an appendix masculina was

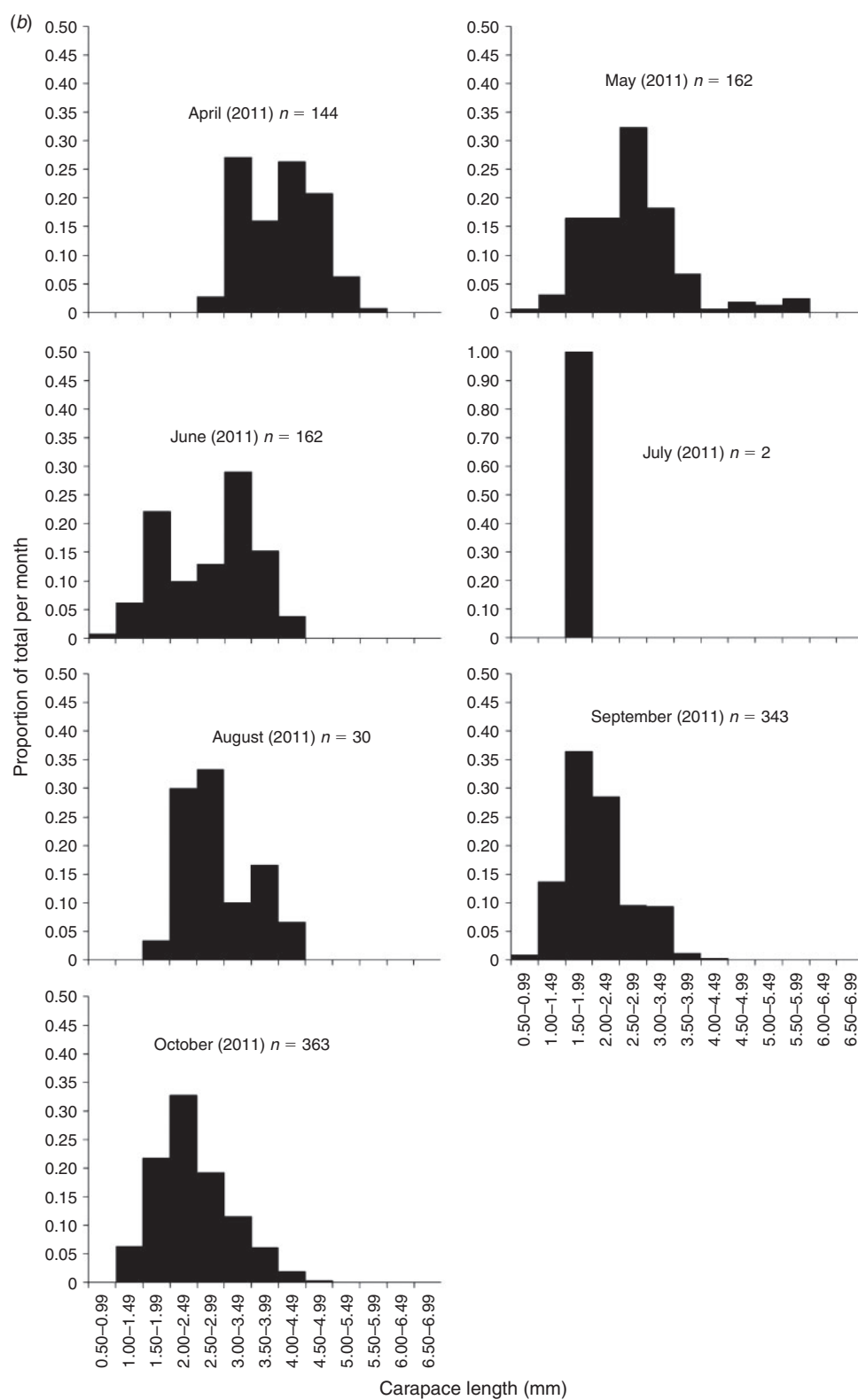


Fig. 4. (Continued).



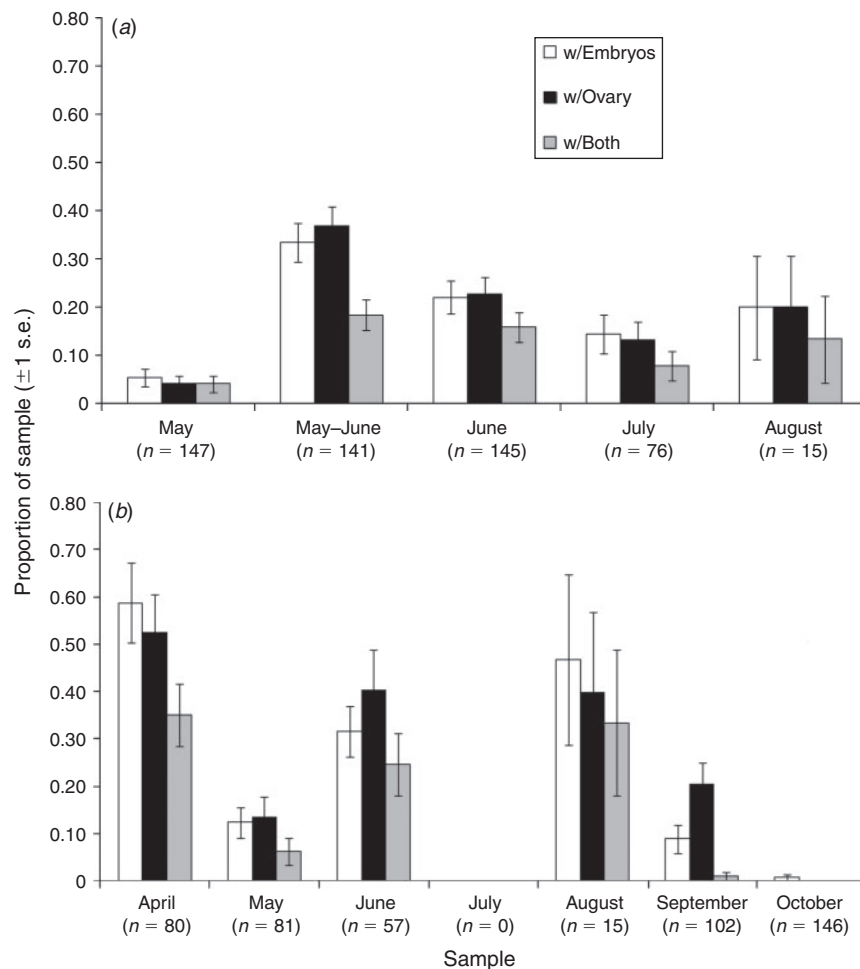


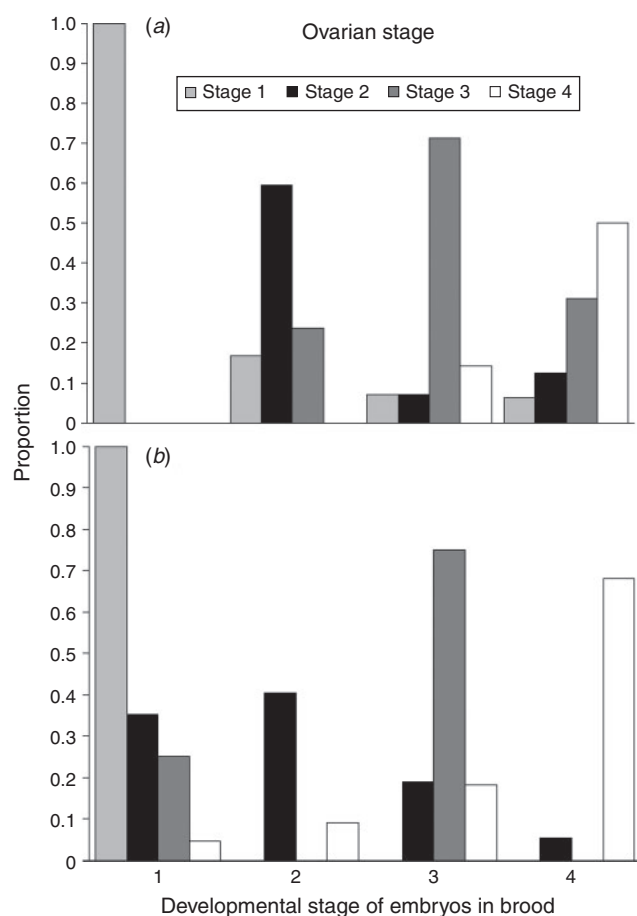
Fig. 5. Proportion of reproductive *Ambidexter symmetricus* females in samples of females of reproductive size (>2.0 mm) for 2010 (a) and 2011 (b).

attained in males between 1.80 and 2.00 mm CL (Table 1, Fig. 2). Thus, some of the individuals in the smaller two size-classes may have been juvenile males indistinguishable from juvenile females (Table 2, Fig. 3). The  $CL_{50\%}$  for females was 1.8 mm (2010) and 2.1 mm (2011), whereas for males  $CL_{50\%}$  was 1.7 (2010) and 2.0 (2011). Goodness of fit Chi-Square comparisons of sex ratios by 0.5-mm size classes (Table 2) showed a trend of significantly more females in most size-classes than males. There were both females and males in most size classes, both large and small (Fig. 3). Size-frequency distributions by month showed population changes over the course of the year. Smaller individuals appeared in the length–frequency distribution in greater abundances in later months in 2010 and 2011, with a loss of larger individuals present in April and May compared with the frequency distributions in August, September, and October (Fig. 4).

Females were reproductive seasonally from April to September (Fig. 5). Females with developing ovaries were not found in October, when only one female was carrying embryos, indicating the end of the breeding season. During the breeding season, most females carrying embryos showed prespawning ovaries

(Fig. 6), indicating a posthatching molt, mating, and spawning, the usual pattern in caridean species with continuous reproduction on an individual basis (successive spawning) (Bauer 2004). We tested and rejected the null hypothesis of no relationship between degree of ovarian and degree of embryonic development in *A. symmetricus* females. Females brooding late-stage embryos had late-stage developing ovaries, whereas females brooding early-stage embryos had undeveloped ovaries, or early-stage developing ovaries in both 2010 ( $\chi^2_9 = 122.45$ ,  $n = 101$ ,  $P_{\text{exact}} < 0.001$ ) and 2011 ( $\chi^2_9 = 100.85$ ,  $n = 92$ ,  $P_{\text{exact}} < 0.001$ ).

We performed a multifactorial ANOVA to examine the interactions of month, sex, and parasite presence in individuals larger than 2.00 mm CL in 2010 and 2011. A carapace length of 2.00 mm was the lower size limit, as secondary sexual characters may not have been visible before this size. Significant relationships were found between full-cross factors in both 2010 ( $F_{15,863} = 20.81$ ,  $P < 0.001$ ) and 2011 ( $F_{18,807} = 63.68$ ,  $P < 0.001$ ). In 2010 there was a significant relationship between sex  $\times$  presence of a parasite (Tukey–Kramer  $P = 0.028$ , Table 3), the sample date  $\times$  presence of a parasite (Tukey–Kramer  $P < 0.001$ , Table 4), and sample



**Fig. 6.** Ovarian developmental condition of *Ambidexter symmetricus* females incubating embryos of different developmental stages for 2010 (a) and 2011 (b).

**Table 3.** Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sex  $\times$  parasite presence on *Ambidexter symmetricus* carapace length (mm) in 2010

F, female; M, male; N, no parasite; Y, parasite present; –,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$

	F $\times$ N	F $\times$ Y	M $\times$ N	M $\times$ Y
F $\times$ N		<0.001	<0.001	0.262
F $\times$ Y	***		<0.001	0.506
M $\times$ N	***	***		<0.001
M $\times$ Y	–	–	***	

date  $\times$  sex (Tukey–Kramer  $P = 0.003$ , Table 5). There was also a significant relationship in 2011 between sex  $\times$  presence of a parasite (Tukey–Kramer  $P < 0.001$ , Table 6), sample date and  $\times$  presence of a parasite (Tukey–Kramer  $P < 0.001$ , Table 7), and sample date  $\times$  sex (Tukey–Kramer  $P < 0.001$ , Table 8).

## Discussion

Females of *Ambidexter symmetricus* produced successive broods, developing new sets of oocytes in their ovaries while

**Table 4.** Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sex  $\times$  parasite presence on *Ambidexter symmetricus* carapace length (mm) in 2011

F, female; M, male; N, no parasite; Y, parasite present; –,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$

	F $\times$ N	F $\times$ Y	M $\times$ N	M $\times$ Y
F $\times$ N		0.979	<0.001	0.579
F $\times$ Y	–		<0.001	0.772
M $\times$ N	***	***		<0.001
M $\times$ Y	–	–	***	

brooding embryos from a previous spawn, indicating a new spawn will occur after hatching of the incubated embryos, as in many caridean species (Bauer 2004). On the population level, reproduction of *A. symmetricus* that we examined from a subtropical (warm temperate) habitat in the Gulf of Mexico, was seasonal (from April to September). The processids *Processa bermudensis* and *Processa riveroi* reproduce year round both on an individual and population level in tropical populations (Bauer 1989). The seasonality of population-level reproduction is consistent with that of two other processid species, *Processa edulis edulis* (Labat and Noël 1987; temperate) and *Haya-shidonus japonicus* (Kikuchi 1962; subtropical), suggesting a latitudinal effect on reproductive periodicity for processid shrimps, with a shorter breeding season with increasing latitude. Temperature, as well as other factors such as plankton productivity (larval food), varies with latitude and influences the length of the breeding season of these shrimps as in many other invertebrates (Thorson 1950; Sastry 1983; Bauer 1992; Lardies and Castilla 2001; Marshall *et al.* 2012). Individual females can reproduce continuously, but as populations move away from the tropics this continuous reproduction becomes limited by season on the population level (Kikuchi 1962; Labat and Noël 1987; Bauer 1991). A similar reproductive pattern occurs in other carideans (Bauer 2004) as well as dendrobranchiate shrimps (Castilho *et al.* 2007a, 2007b, 2008). This pattern appears in marine invertebrates in general (Collin and Salazar 2010; Marshall *et al.* 2012).

The CL<sub>50%</sub> calculated from our data indicates that ~50% of both male and female *A. symmetricus* reach sexual maturity at 1.7 and 2.1 mm respectively. This result was supported by observational data showing that females in general developed ovaries at a CL slightly above 2.0 mm and that secondary sexual characters were fully developed in both sexes at approximately this size. A statistic such as CL<sub>50%</sub> is important to show trends in the size that individuals in the population become reproductive (Pardo *et al.* 2009), and allows for comparisons in reproductive traits among related species or species from similar latitudes (King 1995). For example, populations of *Artemesia longinaris* from Brazil and Argentina showed the predicted latitudinal differences in female size at maturity (Castilho *et al.* 2007b). Our samples showed small variations from year to year, suggesting fluctuation in abiotic or biotic factors influence reproduction (Pardo *et al.* 2009). Similar deviations were seen in *A. longinaris*, and influencing factors were suggested to be caused by yearly variation in water temperature and primary production



**Table 5.** Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sample  $\times$  sex on *Ambidexter symmetricus* carapace length (mm) in 2010F, female; M, male; AG, August; JL, July; JN, June; MY, May; MJ, end of May–beginning of June; –,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ 

	AG $\times$ F	AG $\times$ M	JL $\times$ F	JL $\times$ M	JN $\times$ F	JN $\times$ M	MY $\times$ F	MY $\times$ M	MJ $\times$ F	MJ $\times$ M
AG $\times$ F		0.531	1.000	0.981	1.000	0.988	<0.001	0.006	0.771	0.999
AG $\times$ M	–		0.374	0.995	0.252	0.966	<0.001	<0.001	0.017	0.931
JL $\times$ F	–	–		0.459	1.000	0.313	<0.001	<0.001	0.358	0.885
JL $\times$ M	–	–	–		0.337	1.000	<0.001	<0.001	0.007	1.000
JN $\times$ F	–	–	–	–		0.022	<0.001	<0.001	0.335	0.681
JN $\times$ M	–	–	–	–	*		<0.001	<0.001	0.001	1.000
MY $\times$ F	***	***	***	***	***	***		0.996	0.004	<0.001
MY $\times$ M	**	***	***	***	***	***	–		0.069	<0.001
MJ $\times$ F	–	*	–	**	–	***	**	–		<0.001
MJ $\times$ M	–	–	–	–	–	–	***	***	***	

**Table 6.** Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sample  $\times$  sex on *Ambidexter symmetricus* carapace length (mm) in 2011F, female; M, male; AP, April; AG, August; JN, June; MY, May; OC, October; SP, September; –,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ 

	AP $\times$ F	AP $\times$ M	AG $\times$ F	AG $\times$ M	JN $\times$ F	JN $\times$ M	MY $\times$ F	MY $\times$ M	OC $\times$ F	OC $\times$ M	SP $\times$ F	SP $\times$ M
AP $\times$ F		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
AP $\times$ M	***		0.162	<0.001	<0.001	<0.001	0.721	0.005	<0.001	0.007	<0.001	<0.001
AG $\times$ F	***	–		0.289	1.000	0.980	0.987	1.000	0.999	1.000	0.105	0.047
AG $\times$ M	***	***	–		0.231	0.962	0.035	0.511	0.932	0.735	1.000	1.000
JN $\times$ F	***	***	–	–		0.473	0.894	1.000	0.939	1.000	<0.001	<0.001
JN $\times$ M	***	***	–	–	–		0.048	0.970	1.000	0.999	0.379	0.129
MY $\times$ F	***	–	–	*	–	*		0.385	0.284	0.873	<0.001	<0.001
MY $\times$ M	***	**	–	–	–	–	–		0.999	1.000	0.049	0.006
OC $\times$ F	***	***	–	–	–	–	–	–		0.997	0.371	0.160
OC $\times$ M	***	**	–	–	–	–	–	–	–		0.273	0.037
SP $\times$ F	***	***	–	–	***	–	***	*	–	–		0.999
SP $\times$ M	***	***	*	–	***	–	***	**	–	*	–	

**Table 7.** Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sample  $\times$  parasite presence on *Ambidexter symmetricus* carapace length (mm) in 2010N, no parasite; Y, parasite present; AG, August; JL, July; JN, June; MY, May; MJ, end of May–beginning of June; –,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ 

	AG $\times$ N	AG $\times$ Y	JL $\times$ N	JL $\times$ Y	JN $\times$ N	JN $\times$ Y	MY $\times$ N	MY $\times$ Y	MJ $\times$ N	MJ $\times$ Y
AG $\times$ N		1.000	1.000	0.656	0.938	0.810	1.000	<0.001	0.242	0.644
AG $\times$ Y	–		1.000	0.996	1.000	1.000	1.000	<0.001	0.997	0.990
JL $\times$ N	–	–		0.344	0.506	0.406	1.000	<0.001	0.004	0.449
JL $\times$ Y	–	–	–		0.970	1.000	0.162	<0.001	1.000	1.000
JN $\times$ N	–	–	–	–		0.999	0.007	<0.001	0.315	0.953
JN $\times$ Y	–	–	–	–	–		0.055	<0.001	0.998	0.998
MY $\times$ N	–	–	–	–	**	–		<0.001	<0.001	0.249
MY $\times$ Y	***	***	***	***	***	***	***		<0.001	<0.001
MJ $\times$ N	–	–	**	–	–	–	***	***		1.000
MJ $\times$ Y	–	–	–	–	–	–	–	***	–	

(Castilho *et al.* 2007b). Information from our study may be important for future modelling of life history parameters (including reproductive traits) in processids and comparisons with other tropical and subtropical caridean species (Ramirez Llodra 2002).

The length–frequency distributions of *A. symmetricus* indicate that females are more abundant than males in the population. The abundance of females and their larger size compared with males suggests that these *A. symmetricus* use a pure search (promiscuous) mating system (Berglund 1981; Wickler and

**Table 8.** Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sample  $\times$  parasite presence on *Ambidexter symmetricus* carapace length (mm) in 2011N, no parasite; Y, parasite present; AP, April; AG, August; JN, June; MY, May; OC, October; SP, September; –,  $P > 0.05$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ 

	AP $\times$ N	AP $\times$ Y	AG $\times$ N	AG $\times$ Y	JN $\times$ N	JN $\times$ Y	MY $\times$ N	MY $\times$ Y	OC $\times$ N	OC $\times$ Y	SP $\times$ N	SP $\times$ Y
AP $\times$ N		0.019	<0.001	0.082	<0.001	<0.001	<0.001	1.000	<0.001	0.916	<0.001	<0.001
AP $\times$ Y	*		<0.001	0.001	<0.001	<0.001	<0.001	0.572	<0.001	0.114	<0.001	<0.001
AG $\times$ N	***	***		1.000	0.802	0.674	1.000	0.001	0.830	0.399	0.014	1.000
AG $\times$ Y	–	***	–		1.000	1.000	1.000	0.492	0.954	0.984	0.521	0.999
JN $\times$ N	***	***	–	–		1.000	0.107	0.031	<0.001	0.906	<0.001	0.900
JN $\times$ Y	***	***	–	–	–		0.111	0.084	<0.001	0.962	<0.001	0.813
MY $\times$ N	***	***	–	–	–	–		<0.001	0.145	0.242	<0.001	1.000
MY $\times$ Y	–	–	**	–	*	–	***		<0.001	0.998	<0.001	0.008
OC $\times$ N	***	***	–	–	***	***	–	***		0.035	0.003	1.000
OC $\times$ Y	–	–	–	–	–	–	–	–	*		0.002	0.377
SP $\times$ N	***	***	*	–	***	***	***	***	**	**		0.952
SP $\times$ Y	***	***	–	–	–	–	–	**	–	–	–	

Seibt 1981) as in most caridean species, in which reproductive males are smaller than reproductive females (Correa and Thiel 2003; Bauer 2004).

The hypothesis of a gonochoristic sexual system for *A. symmetricus* is supported by the sex ratios observed in our samples. There is overlap of juvenile male and female length frequencies in the smaller size classes, indicating that *A. symmetricus* develop into primary males and primary females (Bauer 2004). There was no evidence of previously described sexual systems in carideans in which an individual first develops as a male and then when larger changes to a female (protandry) or female-phase simultaneous hermaphrodite (protandric sequential hermaphroditism) (Bauer 2000; Chiba 2007). In population-samples of purely protandric species, smaller size classes are composed of males whereas larger size classes are primarily female (Bauer 2004). Although protandry has been reported in *Processa edulis edulis* (Noël 1973, 1976), this conclusion is controversial (Bauer and Conner 2012). Thus, sequential hermaphroditism has not been definitively demonstrated in a processid species. The trend of significantly more females than males present in the *A. symmetricus* population sampled suggests differential mortality between the sexes. Increased activity by mature males searching for reproductive females throughout the summer is one conceivable cause for this skewed sex ratio (Willson and Pianka 1963; Berglund 1981; Ridley and Thompson 1985).

Sex, time of year, and parasite presence all had an influence on the size of individuals of *A. symmetricus*. In general, females grew larger than males, and males with parasites suffered from gigantism. However, females with parasites were similar in size to healthy females and infected males. This may be because females are the larger sex, and already grow to the maximum size this species can attain. Large females may not exhibit gigantism when infected because of physiological growth and life-span restraints. However, as males expend fewer energetic resources in producing sperm than females do on eggs, more resources might be directed into somatic growth when males are infected, allowing gigantism to occur (Baudoin 1975). *A. symmetricus* of both sexes were also larger in the spring,

indicating that they were recruits of the previous year which had overwintered. Later in the year, the mean body size of the population decreased as recruitment occurred and smaller individuals entered the population.

Although processids are abundant in some habitats, there is a lack of information about their reproductive biology, population ecology, and evolutionary relationships. The data presented here allow for comparisons of this subtropical population with other subtropical species as well as those from other latitudes and habitats. Our data support the conclusion that females produce successive broods within a limited part of the year (April–September). With possible impacts of oil spills, climate change and overfishing of shrimp predators on abundant seagrass shrimps such as *A. symmetricus*, further insights about such ecologically important species are essential to help management agencies conserve both habitat and species diversity.

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