

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

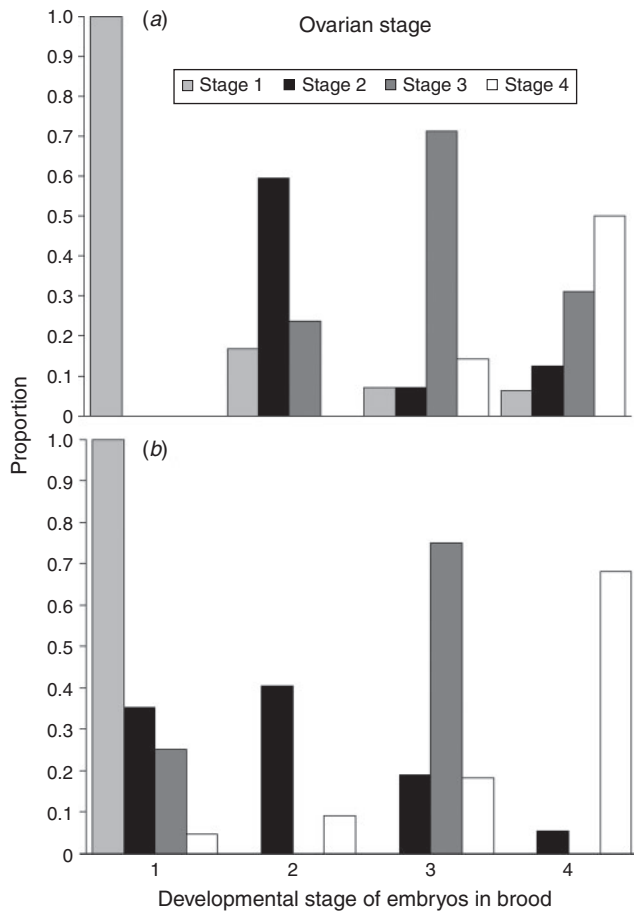


Fig. 6. Ovarian developmental condition of *Ambidexter symmetricus* females incubating embryos of different developmental stages for 2010 (a) and 2011 (b).

Table 3. Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sex × 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 × N	F × Y	M × N	M × Y
F × N		<0.001	<0.001	0.262
F × Y	***		<0.001	0.506
M × N	***	***		<0.001
M × Y	–	–	***	

date × sex (Tukey–Kramer  $P = 0.003$ , Table 5). There was also a significant relationship in 2011 between sex × presence of a parasite (Tukey–Kramer  $P = <0.001$ , Table 6), sample date and × presence of a parasite (Tukey–Kramer  $P < 0.001$ , Table 7), and sample date × 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 × 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 × N	F × Y	M × N	M × Y
F × N		0.979	<0.001	0.579
F × Y	–		<0.001	0.772
M × N	***	***		<0.001
M × 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  $CL_{50\%}$  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  $CL_{50\%}$  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 × sex on *Ambidexter symmetricus* carapace length (mm) in 2010**F, 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 × F	AG × M	JL × F	JL × M	JN × F	JN × M	MY × F	MY × M	MJ × F	MJ × M
AG × F		0.531	1.000	0.981	1.000	0.988	<0.001	0.006	0.771	0.999
AG × M	–		0.374	0.995	0.252	0.966	<0.001	<0.001	0.017	0.931
JL × F	–	–		0.459	1.000	0.313	<0.001	<0.001	0.358	0.885
JL × M	–	–	–		0.337	1.000	<0.001	<0.001	0.007	1.000
JN × F	–	–	–	–		0.022	<0.001	<0.001	0.335	0.681
JN × M	–	–	–	–	*		<0.001	<0.001	0.001	1.000
MY × F	***	***	***	***	***	***		0.996	0.004	<0.001
MY × M	**	***	***	***	***	***	–		0.069	<0.001
MJ × F	–	*	–	**	–	**	**	–		<0.001
MJ × M	–	–	–	–	–	–	***	***	***	

**Table 6. Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sample × sex on *Ambidexter symmetricus* carapace length (mm) in 2011**F, 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 × F	AP × M	AG × F	AG × M	JN × F	JN × M	MY × F	MY × M	OC × F	OC × M	SP × F	SP × M
AP × F		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
AP × M	***		0.162	<0.001	<0.001	<0.001	0.721	0.005	<0.001	0.007	<0.001	<0.001
AG × F	***	–		0.289	1.000	0.980	0.987	1.000	0.999	1.000	0.105	0.047
AG × M	***	***	–		0.231	0.962	0.035	0.511	0.932	0.735	1.000	1.000
JN × F	***	***	–	–		0.473	0.894	1.000	0.939	1.000	<0.001	<0.001
JN × M	***	***	–	–	–		0.048	0.970	1.000	0.999	0.379	0.129
MY × F	***	–	–	*	–	*		0.385	0.284	0.873	<0.001	<0.001
MY × M	***	**	–	–	–	–	–		0.999	1.000	0.049	0.006
OC × F	***	***	–	–	–	–	–	–		0.997	0.371	0.160
OC × M	***	**	–	–	–	–	–	–	–		0.273	0.037
SP × F	***	***	–	–	***	–	***	*	–	–		0.999
SP × M	***	***	*	–	***	–	***	**	–	*	–	

**Table 7. Tukey–Kramer *post hoc* interactions of Least Square Means for effect of sample × parasite presence on *Ambidexter symmetricus* carapace length (mm) in 2010**N, 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 × N	AG × Y	JL × N	JL × Y	JN × N	JN × Y	MY × N	MY × Y	MJ × N	MJ × Y
AG × N		1.000	1.000	0.656	0.938	0.810	1.000	<0.001	0.242	0.644
AG × Y	–		1.000	0.996	1.000	1.000	1.000	<0.001	0.997	0.990
JL × N	–	–		0.344	0.506	0.406	1.000	<0.001	0.004	0.449
JL × Y	–	–	–		0.970	1.000	0.162	<0.001	1.000	1.000
JN × N	–	–	–	–		0.999	0.007	<0.001	0.315	0.953
JN × Y	–	–	–	–	–		0.055	<0.001	0.998	0.998
MY × N	–	–	–	–	**	–		<0.001	<0.001	0.249
MY × Y	***	***	***	***	***	***	***		<0.001	<0.001
MJ × N	–	–	**	–	–	–	***	***		1.000
MJ × 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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