Seasonal Differences In Egg Size In Three Species Of Crabs From A Tropical Upwelling Zone

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Abstract

Egg size and offspring size are fundamentally important aspects of the life histories of all animals. However, the impact of environmental conditions on intraspecific variation in egg size of marine invertebrates is poorly documented. Here we followed 3 species of intertidal crabs *Xanthodius sternberghii, Petrolisthes armatus,* and *Clibanarius albidigitus* to understand how seasonal environmental variation in temperature and salinity associated with seasonal upwelling impacts egg size. Ovigerous females of both *Petrolisthes armatus* and *Clibanarius albidigitus* were found year round, while *Xanthodius sternberghii* has a limited reproductive season, with ovigerous females found only between November and February. In all three species, more than half of the variation in egg size was attributable to variation among broods from different females. Eggs collected during the dry, upwelling season were significantly larger than those collected during the wet, non-upwelling season. Multiple regression analysis showed that average egg size from each brood was significantly negatively correlated with temperature for all three species. Egg size was also negatively correlated with salinity in *Petrolisthes armatus* when we controlled for temperature. Overall these results support the idea that changes in environmental temperature caused by seasonal upwelling play a significant role in generating seasonal differences in egg size.

Keywords: Panama, salinity, hermit crab, Xanthidae, porcelain crab, phenotypic plasticity, offspring size, temperature size rule.

Introduction

Egg size and offspring size are fundamentally important aspects of the life histories of all animal species (Bernardo 1996). Among marine invertebrates attention to offspring size has focused primarily on interspecific differences. However, it is becoming increasingly evident that intraspecific variation in offspring size may be influenced in significant ways by environmental conditions (Atkinson et al. 2001; Moran & McAlister 2009). Laboratory experiments have shown that egg size and offspring size in many marine invertebrates are influenced by temperature, following the offspring temperature size rule, with smaller eggs and offspring produced at higher temperatures and larger eggs and offspring produced at cooler temperatures (Atkinson et al. 2001; Collin & Salazar 2010; Collin 2012). Some field observations seem to support this pattern as well. For example, in decapod crustaceans that reproduce year round, eggs are often smaller in the summer compared to other times of the year (*Crangon*: Urzúa et al. 2012; *Sesarma*: de Arruda Leme 2006; *Alpheus*: Pavanelli et al. 2010). Likewise, intertidal gastropods show larger offspring sizes when temperatures are cooler (Collin & Ochoa 2016).

Temperature is not the only environmental factor that seems to induce plasticity in egg size or offspring size. Salinity has also been linked to egg size in some crustaceans (Gimenez & Anger 2001; Moran & McAlister 2009). The negative relationship between salinity and egg size may be due to osmotic uptake of water by the eggs at low salinities (Moran & McAlister 2009), but in some cases the larger eggs produced under lower salinities also produce larger hatchlings (Gimenez & Anger 2001) suggesting that this difference in egg size reflects differences in energy content. Maternal nutrition has also been linked to variation in egg size in a number of aquatic invertebrates, with females provided more resources generally producing larger eggs or offspring (Qian & Chia 1991; de Jong-Westman et al. 1995; Guisande & Harris 1995; George 1996; Kirk 1997).

Overall, however, few publications investigate the environmental factors that may influence egg size and offspring size in the field in any group of marine invertebrates. This knowledge gap is unfortunate as propagule size and quality may have significant carry-over effects on larval and juvenile growth and survival (Marshall et al. 2003; Marshall & Keough 2005). In addition, seasonal variation in offspring quality could interact with the documented effects of seasonal variation in oceanographic conditions and direction of surface currents to influence the spatial distribution of larvae and recruits of differing qualities (Wing et al. 1995; 1998; Connolly et al. 2001; Narváez, et al. 2006; Queiroga et al. 2007).

The Bay of Panama and several other regions along the tropical Pacific coast of the Americas experience strong seasonal upwelling. Winds passing westward over low-lying land generate regions of upwelling in the Bay of Panama (Panama), the Gulf of Tehuantepec (Mexico), and the Gulf of Papagayo (Costa Rica) (Li et al. 2012). In the Bay of Panama, upwelling occurs between January and the end of April or early May. It is associated with dramatic decreases in sea surface temperature, increased salinities, increased nutrients, phytoplankton and zooplankton biomass in the surface waters (D'Croz & Robertson 1997; Smayda 1963), increased frequency of hydromedusa blooms (Miglietta et al. 2008), and altered rates of predation risk in the plankton (Kerr et al. 2014a,b). Upwelling also impacts the reproduction of marine invertebrates and fishes in the region. Previous work has shown that during the dry, upwelling season in the Bay of Panama 6 of 8 reef fishes studied produce larger eggs (Robertson & Collin 2015), and 3 of 4 intertidal snails studied produce larger hatchlings (Collin & Ochoa 2016) than during the wet season. Although causality was not demonstrated directly in these field studies, both results were consistent with the hypothesis that temperature, rather than salinity or productivity drives seasonal variation in offspring size.

To determine how seasonal environmental changes associated with upwelling impact egg size in intertidal crabs we followed three species, the hermit crab *Clibanarius albidigitus* Nobili, 1901, the rubble crab *Xanthodius sternberghii* Stimpson, 1859, and the porcelain crab *Petrolisthes armatus* (Gibbes, 1850) in the intertidal around the Pacific entrance to the Panama Canal. These species are abundant members of rocky intertidal and shallow subtidal communities along the Pacific coast of Central America, where they experience seasonal upwelling over significant portions of their ranges. Examining three co-occurring species from different families, with different natural histories we hoped to uncover generalizable relationships between environmental conditions and offspring size.

Materials and Methods

This study was conducted around Naos Island (8.917N, 79.533W) between December 2013 and January 2017. Naos Island is part of the rocky causeway at the Pacific entrance to the Panama Canal. The initial field site was located on the north coast of Naos Island, but obliteration of this site by rocky fill as part of an expansion of the causeway necessitated a relocation of our collecting site to the west side of the island in 2015. Obliteration of this new site by additional fill ended the study. Environmental temperatures under the rocks where the crabs occur at low tide were measured with Thermochron ibutton data loggers (Maxim Embedded Datasystems) with ± 0.5°C accuracy, 0.06°C resolution and set to record every 5 minutes, which were wrapped in plastic and secured to the rocks (Kerr et al. 2012). Subtidal water temperature was measured with HOBO Stow-Away TidbiT and HOBO Water Temperature Pro V2 instruments (Onset Computer Corporation) with an accuracy of 0.25°C at 2m on the Naos Island dock, on the north side of the island, until they were stolen in August 2015, in the seawater system intake at the Smithsonian Tropical Research Institute's Naos Island Laboratories, and at 12-meters depth offshore at Isla Taboguilla. Hobo measurements were taken every 30 minutes. Measurements were averaged for each month over the sampling period (Figure 1). Salinity was measured with a VitalSine SR-6 refractometer with 1 ppt gradations twice daily from water in the Naos Laboratory. At the beginning of the study this water was drawn from 2-3m depth near the Naos dock, adjacent to the initial collecting site. At the time when our collecting site had to be moved to the western side of the island, the seawater intake was also moved to this side. Therefore, throughout the study, salinity was measured from water collected from less than 200m from our collection sites.

The three intertidal crab species used in this study overlap in habitat and geographic range. The rubble crab *Xanthodius sternberghii* (Xanthidae) ranges from Magdalena Bay, Mexico to Paita, Peru (Hendrickx 1995). They live under rocks, and previous studies in Panama have shown that they release larvae following a semilunar cycle (Christy 1986). We used this as a guide to collect animals at the time the cycle where eggs were expected to be in an early stage of development. The porcelain crab *Petrolisthes armatus* (Porcellanidae) has an extremely large range, which includes the Caribbean as well as the tropical eastern Pacific (Haig 1960; Gore et al. 1976; Werding et al. 2003). *P. armatus* occurs in the lower intertidal, under stones, in oyster and mussel beds, among mangrove roots, and on dock pilings (Haig 1960). This species reproduces year round on the Pacific coast of Costa Rica (Díaz-Ferguson & Vargas-Zamora 2001; Wehrtmann et al. 2011) and was therefore expected to reproduce year round in Panama. Reproduction does not follow a semi-lunar cycle (Christy 1986). The hermit crab *Clibanarius albidigitus* (Diogenidae) ranges from Puerto Peñasco, Mexico to Paita, Peru (Hendrickx 1995).

Previous studies with this species in Panama have shown that they reproduce year round (Bertness 1981a). All three of these species are abundant under rocks at our study sites in the mid-intertidal.

Crabs were collected once a month, during the same point in the tidal amplitude cycle between the end of November 2013 and January 2017. When females with early stage embryos (>90% yolk) were collected, the eggs were removed from the crab and photographed alive, individually, on the day of collection. We only photographed early stage embryos to control for the possibility that egg size changes over development. We used a Nikon E600 compound microscope with a ProgRes C14 Plus (Jenoptik) digital camera. A stage micrometer was photographed at the same magnification as the eggs (100X) and at the same high resolution prior to photographing the eggs from each brood individually. Lighting was adjusted so that the photographs of the opaque eggs appeared to be monochrome although the photographs were captured in color. If few early stage eggs were found, we sampled again either within 4 days of the original collecting date or at the same point during the next tidal amplitude cycle (i.e., 14 days later). The photographs were measured with ImageJ using the ShapeDiscriptor plug-in and the egg volume was calculated from the measures of the major and minor axes following the standard equation of the volume of a spheroid = 4/3*pi*(major axis/2)*(minor axis/s)^2. Size of ovigerous females was measured with calipers as carapace width for *X. sternberghii* and *P. armatus*. *C. albidigitus* inhabiting *Planaxis* sp. shells were used exclusively, and length of the host shell which is an approximate measure of size and available space for embryos was recorded. Since observations during the first 18 months suggested that reproduction in *X. sternberghii* was unexpectedly seasonal, during the subsequent part of the study, we also recorded the number and size of the ovigerous females relative to the total number of crabs encountered. As the focus of this study was on environmental influences on offspring size, and not on components of yield (i.e., trade-offs between clutch frequency, clutch size, and offspring size) we did not document clutch size.

All statistics were conducted in JMP version 12.2.0. A nested ANOVA of egg volume was conducted with season and site as factors, the interaction between site and season, and female as a random effect nested within site and season. The statistical effect of "female" encompasses variation due to maternal size and/or condition, genetic differences among females, and potential variation due to trade-offs between egg size and clutch size (see Collin 2010 for a more detailed discussion). To understand if egg size correlates with temperature and/or salinity we used multiple regression analysis, regressing average egg size for each female on the average temperature and average salinity measured during the week prior to the date her eggs were collected. Significant interactions were examined using the profiler function in JMP which generates profile traces. These are the predicted responses of the dependent variable to one of the independent variables when the values of the other independent variables are held constant. When interactions between continuous variables are significant it is a useful way of visualizing the interaction. This allows the user to determine, for example, the slope and confidence intervals of the relationship between egg size and temperature when salinity is held at 33ppt compared to when salinity is held at 35ppt. Finally, logistic regression was used to determine if female size and season influenced the probability that a crab was ovigerous.

Results

Environmental Conditions - As has been reported elsewhere for various habitats and locations around Panama City, both salinity and temperature showed strong seasonal patterns (Figure 1) (D'Croz & Robertson 1997; Robertson et al. 2009; Robertson & Collin 2015; Collin & Ochoa 2016). During the wet season, temperatures offshore at the seawater intake, on the dock and under the intertidal rocks where the crabs live were higher than during the dry season. All of the nearshore temperatures were very similar. The seawater also showed higher salinities during the dry season compared to the rainy season (Figure 1).

Egg Size - A total of 3092 early stage eggs were photographed and measured from 151 broods of *X. sternberghii*, 3836 from 196 broods of *P. armatus*, and 2985 from 147 broods of *C. albidigitus*. The population mean of the average egg volume for each female was 0.010 mm^3 (s.d. = 0.00084 mm^3; range 0.0083 - 0.014 mm^3) for *X. sternberghii*, 0.039 mm^3 (s.d. = 0.0099 mm^3; 0.025-0.068 mm^3) for *P. armatus*, and 0.020 mm^3 (s.d. = 0.0020 mm^3; 0.015-0.026 mm^3) for *C. albidigitus*.

Egg volume was larger during the dry season than the wet season in all three species (Figure 2). Analysis of variance of the effects of season, site, their interaction and the nested random effect of female showed that more than half the variance in egg volume for each species was attributable to variation among the females (Table 1). In *P. armatus* and *C. albidigitus* egg size was significantly larger during the dry season than the wet season and there was no significant effect of site and no significant interaction between site and season (Figure 2; Table 1). In *X. sternberghii* site, season, and their interaction all had significant effects on egg volume. Eggs were significantly larger during the dry season than the wet season, and egg size during the dry season differed significantly between the two sites but did not differ during the wet season (Table 1; Figure 2). In these analyses samples from May were scored as wet season samples, as the salinity and water temperature for May were more similar to the rest of the wet season than the dry season (Figure 1). However, scoring the May samples as belonging to the dry season (as the eggs may have developed in the ovary during the dry season) did not alter the significance or direction of the effect of season on egg size.

Egg size was not significantly correlated with maternal shell size in *C. albidigitus* (r^2 = 0.01; N = 99; p = 0.33) or maternal size in *X. sternberghii* (r^2 = 0.01; N =128; p = 0.20), and maternal size did not differ between the seasons (p > 0.4). The eggs of *P. armatus* increased significantly with maternal size but maternal size explained very little of the overall variation in egg size (r^2 = 0.05; N = 157; p = 0.005).

The average egg size for each female was negatively correlated with average temperature for the week before the eggs were collected for all three species (Table 2; Figures 3 & 4). Egg size of *Petrolisthes armatus* also significantly decreased with increasing salinities and there was a significant interaction between temperature and salinity (Table 2; Figure 4). Examination of the interaction using the profiler in JMP showed that the decrease in egg size with increasing salinity is steeper at low temperatures and almost flat at high temperatures (Figure 4). In addition, the decrease in egg size with temperature is steeper at low salinities than at high salinities.

Monthly sampling between December 2015 and January 2017 showed that, as expected, *C. albidigitus* and *P. armatus* reproduce throughout the year (Figure 5). The proportion of the total sampled crabs brooding ranged between 2% and 50% for *C. albidigitus* and between 16% and 47% for *P. armatus*. In contrast *X. sternberghii* showed a distinct seasonal pattern in reproduction with significant numbers of ovigerous females found only from November to February (Figure 4). This pattern was consistent in the winters of 2014, 2015 and 2016. Logistic regression showed that female carapace width did not predict the likelihood that a female was ovigerous for *P. armatus* or *X. sternberghii* (χ^2 = 2.80; N = 1472; p = 0.09 and χ^2 = 0.44; N =

1843; p = 0.51, respectively). For *C. albidigitus* however shell length significantly contributed to the likelihood that the crab was ovigerous ($\chi^2 = 7.86$; N = 1875; p = 0.005).

Discussion

In temperate regions, the reproduction of marine invertebrates closely tracks seasonal variation in environmental conditions. In particular, reproduction is often associated with the warmest times of the year or with spring increases in temperature. Despite minimal seasonal variation in temperature, reproduction in tropical species may also coincide with warmer part of the year. However, little is known about how offspring of marine organisms are influenced by temperature or other environmental conditions. This may be relevant, not only in regions like the Bay of Panama with strong seasonal upwelling zones, but also at the higher latitude margins of these species ranges, like the Gulf of California, which may also experience strong seasonal patterns in temperature (Roden 1964).

In the Bay of Panama some species of small shallow-water fishes and several intertidal snails reduce or suppress reproduction during the dry, upwelling season (Robertson 1990; Collin & Ochoa 2016; Collin et al. 2017). Two species of sea urchins *Echinometra vanbrunti* and *Diadema mexicanum* show a somewhat different pattern with gonad indices suggesting that reproduction is reduced or suppressed between October and April, including both the wettest part of the wet season and the entire upwelling season (Lessios 1981). In contrast, a number of other invertebrates reproduce year round, including some fiddler crabs (Kerr et al. 2012), the intertidal sand dollar *Melita stokes* (Dexter 1977), the high intertidal isopod *Excirolana braziliensis* (Cardoso & Defeo 2003), and 3 species of hermit crabs, including *C. albidigitus* (Bertness 1981a). In addition, *Callinectes arcuatus* reproduces all year round but shows a distinct peak in reproduction during the upwelling season in the Gulf of Nicoya, Costa Rica (DeVries et al. 1983). We provide additional data that the porcelain crab *P. armatus* reproduces year round and that the xanthid, *X. sternberghii* has an unusual reproductive season spanning only the last 2 months of the wet season and the first 2 months of the upwelling season. Overall it is clear that, although a number of species (mostly fish and snails) repress reproduction during the upwelling season, an equal number have been shown to reproduce all year round or to have reproductive seasons that do not coincide clearly with the dry or the wet season.

In the case of *X. sternberghii*, the observed reproductive season suggests a role of short photoperiod in inducting reproduction. A relationship between reproduction and photoperiod occurs in other crabs, but in these cases long photoperiods coincident with warmer temperatures usually induce reproduction (e.g., *Pachygrapsus transversus*: Flores & Negreiros-Fransozo 1998; *Goniopsis cruentata*: Cobo & Fransozo 2003). Experimental work with echinoderms has shown that reproduction may be controlled by photoperiod and that both long days and short days may trigger reproduction (Pearse & Eernisse 1982; Pearse & Beauchamp 1986; McClintock & Watts 1990). If reproduction of *X. sternberghii* is indeed linked to photoperiod, their reproductive season should be longer at higher latitudes.

Seasonal differences in offspring size, with larger offspring produced during the upwelling season, occur in the majority of animals in which this has been studied, including the 3 crabs examined here. Three species of gastropods also show monthly increases in hatching size as the upwelling season progresses, followed by a sudden decrease in size at the beginning of the wet season between April and June (Collin & Ochoa 2016). Because a number of environmental factors differ between the upwelling and non-upwelling seasons, it is difficult to unambiguously attribute causation to this pattern. However, the following three lines of evidence suggest that temperature plays a major role in determining egg size. In the three crab species studied here, the average size of eggs with <90% yolk (< 4 days after ovulation, see Garcia-Guerrero & Hendrickx 2005 and Turra & Leite 2007 which provide development schedules for development at cooler temperatures than the present study) was negatively correlated with temperature experienced over the 7 days prior to collection. Increased offspring size associated with the cooler temperatures experienced during upwelling is consistent with the effect of temperature predicted by the offspring temperature size rule (i.e., the almost ubiquitous decrease in egg size or offspring size with increasing temperature; see Atkinson et al. 2001). Finally, larger egg size during upwelling is the opposite of that expected if salinity, the other major abiotic difference between upwelling and non-upwelling seasons, influences egg size. When salinity influences egg size, eggs are larger at lower salinities (Moran & McAlister 2009). Therefore, if salinity was a major factor influencing egg size in the field, the crabs in the Bay of Panama would have produced larger eggs during the wet season, the opposite of the pattern we observed.

The other major difference between upwelling and non-upwelling seasons is the increased ocean productivity and plankton abundance during upwelling. Increased maternal nutrition can result in larger eggs or offspring in marine invertebrates (Qian & Chia 1991; de

Jong-Westman et al. 1995; Guisande & Harris 1995; George 1996; Kirk 1997). However, a direct link between increased productivity during upwelling and increased maternal nutrition has yet to be demonstrated. *Petrolistes armatus* is a suspension feeder, and therefore likely has increased access to food during upwelling, although most of the diet of related species include significant amounts of benthic microalgae, as well as phytoplankton (Zimba et al. 2016). *Clibanarius albidigitus* is a deposit feeder, and *Xanthodius sternberghii* is a predator. It is not clear how the upwelling and non-upwelling seasons may influence the nutritional status of these species. It seems intuitively appealing that benthic microalgae might increase during the nutrient-rich upwelling season, but detritus and nutrients may also increase in these shoreline habitats due to increased run-off during the wet season. It is unknown how upwelling effects availability of *X. sternberghii* prey.

Potential trade-offs or covariances between clutch frequency, clutch size, and egg size could also impact egg size, either independent of seasonal environmental differences, or they could mediate the effect of seasonal environmental differences on egg size. Little is known about the relationship between these factors and the impact of environmental conditions on these relationships in the species studied here. The short duration of development in most tropical species, combined with the relatively high percentages of brooding crabs recovered in this study suggest that in all 3 species females reproduce multiple times during the year. In general, clutch size increases with maternal size in most decapods, although this relationship can be complicated by the relationship between body size and host shell size in hermit crabs. This has been demonstrated clearly in C. *albidigitus*, where clutch size increases with body size in shell-limited females, but not in shell-unlimited females (Bertness 1981b). Clutch size can also be significantly impacted by embryo loss during development. *P. armatus* females can have lost as much as 25% of the embryos by the time they reach the end of Stage 2 (Wehrtmann et al. 2012), making it difficult to detect subtle trade-offs between egg size and number. Such high rates of egg loss are common in other crabs and make the original clutch size a poor predictor of realized reproductive output (Figueiredo et al. 2008). Clutch size in crabs can also vary with population and latitude (e.g., Wehrtmann et al. 2011 for *P. armatus*; Lardes and Castillo 2001) and across seasons (e.g., Bas et al. 2007). For example, in the grapsoid *Chasmagnathus granulatus* clutch size and egg biomass are positively correlated across the reproductive season (Bas et al. 2007). Untangling how these complex and poorly documented covariances between female body size, clutch frequency, and clutch size are influenced by seasonal changes in environmental conditions and how this contributes to the observed seasonal differences in egg size would be an important contribution of understanding the life histories of these species.

Regardless of the causes of seasonal variation in reproduction and in propagule size, these differences could have important consequences for the population dynamics of marine organisms. Seasonal differences in surface currents associated with offshore winds mean that small differences in reproductive season could impact the direction of dispersal and successful arrival habitats suitable for metamorphosis and settlement. In species that reproduce year round, seasonal variation in propagule quality combined with seasonal changes in surface currents could result in differences in the quality of larvae dispersing in different directions (Gebauer et al. 2010). If carryover effects are important (Marshall et al. 2003; Marshall & Keough 2005), this could result in geographic differences in juvenile growth and survival.

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Table 1: Nested Analysis of variance of egg volume in the three species of crabs testing for effects of season, site, and their interaction, while accounting for the random effect of the mother.

	Factor	**df**	**F-Ratio**	**p**	**% variance explained**
Clibanarius albidigitus					
	Season	1	7.09	**0.009**	
	Site	1	1.41	0.23	
	Season X Site	1	3.84	**0.05**	
	Female [Site, Season] Random				70.60
N= 2985; r^2 =0.75					
Petrolisthes armatus					
	Season	1	31.38	**<0.0001**	
	Site	1	0.03	0.86	
	Season X Site	1	2.34	0.12	
	Female [Site, Season] Random				85.95
N= 3836; r^2 =0.88					
Xanthodius sternberghii					
	Season	1	80.85	**<0.0001**	
	Site	1	17.11	**<0.0001**	
	Season X Site	1	11.57	**0.0009**	
	Female [Site, Season] Random				52.62
N=3092; r^2 =0.64					

Table 2: Results from multiple regression analysis of average egg size for each date on the temperature and salinity averaged over the 7 days prior to the day the eggs were collected.

	Source	df	F-Ratio	p
Clibanarius albidigitus *				
	Temperature	1	10.91	**0.0012**
	Salinity	1	0.32	0.3
N = 147; r^2 = 0.32				
Petrolisthes armatus				
	Temperature	1	33.06	**<0.0001**
	Salinity	1	11.60	**0.0008**
	Temperature X Salinity	1	9.96	**0.0019**
N = 186; r^2 = 0.18				
Xanthodius sternberghii *				
	Temperature	1	27.00	**<0.0001**
	Salinity	1	2.18	0.14
N = 150; r^2 = 0.28				

* The interaction term was not significant with p>0.05 and was therefore removed from the analysis.

Figure Legends

Figure 1: The seasonal patterns in temperature and salinity recorded during the study period. Dry, upwelling seasons are indicated by the grey boxes.

Figure 2: Bargraphs showing the monthly average egg volume (left) and average seasonal egg volume (right) for the 3 species of crabs. Data from the dry, upwelling season are shown with white bars and those from the wet season are shown with black bars. There was a significant difference between seasons in all three species (Table 1). Error bars indicate standard errors.

Figure 3: Regression of average egg volume for each female on temperature averaged over the 7 days prior to egg collection for *Clibanarius albidigitus* and *Xanthodius sternberghii*. Both relationships were significant in the multiple regression analysis (Table 2).

Figure 4: Profiler traces, showing the significant effect of the interaction between temperature and salinity on egg size in *Petrolisthes armatus* (Table 2). Egg size decreases with increasing temperature at all salinities. Egg size increases with salinity only at lower temperatures and is not affected by salinity at higher temperatures. Solid line shows the mean and dashed line shows the confidence limits.

Figure 5: The percentage of ovigerous crabs in collections made between December 2015 and January 2017. Percentages of ovigerous *Petrolisthes armatus* and *Clibanarius albidigitus* were calculated from the total number of crabs collected and percentages of ovigerous *Xanthodius sternberghii* were calculated from the total number of females collected. White bars indicate the dry, upwelling season; black bars indicate the wet season.