

Influence of seasonal environmental variation on the reproduction of four tropical marine gastropods

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ABSTRACT: The 2 main hypotheses put forward to explain seasonal timing of marine invertebrate reproduction hinge on variation in temperature and phytoplankton. Seasonal upwelling in the tropical eastern Pacific provides an ideal system in which to test these ideas. During the non-upwelling season, the Bay of Panama is warmer, less saline and less productive than during the upwelling season. We followed egg deposition of 4 intertidal gastropod species — *Littoraria variegata*, *Cerithideopsis californica* var. *valida*, *Crepidula* cf. *marginalis* and *Natica chemnitzii* — to determine if these seasonal environmental differences are associated with variation in reproductive intensity or offspring size. The species from the mangroves, *L. variegata* and *C. californica*, produced fewer egg masses during the dry season. The slipper limpet *C. cf. marginalis* was more likely to brood during the dry season. Egg masses from the moon snail *N. chemnitzii* showed no difference in abundance between the seasons. Shell length at hatching, an estimate of per offspring maternal investment, was larger during the dry season for *C. californica* and *C. cf. marginalis* but did not differ across the seasons for *L. variegata*. Hatching size in the moon snail was bimodal during the dry season, but both offspring size classes showed increased offspring size in the dry season compared to the wet season. Three of the 4 species show patterns in offspring size consistent with the offspring temperature–size rule, while seasonal cycles in reproductive intensity are likely driven by other factors such as adult food availability or desiccation stress.

KEY WORDS: Littorinid · Life histories · Reproduction · Upwelling · Maternal investment

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INTRODUCTION

The 2 main hypotheses that have been put forward to explain seasonal timing of reproduction are based on variation in temperature and phytoplankton (e.g. Orton 1920, Thorson 1950, Bauer 1992). One hypothesis posits that reproduction is temperature dependent, promoting broad reproductive seasons or year-round reproduction where temperatures are high and vary little (i.e. the tropics) and sharply defined seasons where temperatures show marked seasonal variation. The second posits that reproduction is driven by availability of phytoplankton, the food supply of feeding larvae, and that reproduction is more seasonal when phytoplankton blooms are more intense and seasonal. In those species with extended

reproductive seasons, the intensity of reproduction and the quality of offspring produced may also be influenced by variation in temperature and food availability.

Seasonal timing of reproduction

The pattern of seasonal reproduction is well documented in many temperate marine organisms, and significant effort has focused on determining if temperature, larval food availability or other cues determine reproductive periods (e.g. Olive 1992, 1995, Reitzel et al. 2004). Detailed studies of shallow water marine invertebrates have shown that seasonal reproduction can be triggered by, or linked to, seasonal

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increases in temperature (Byrne 1990, Waddy & Aiken 1992) and sudden temperature changes (Bonardelli et al. 1996) as well as a variety of other cues, some of which may be correlated with temperature. These include phytoplankton blooms (Himmelman 1975, Starr et al. 1993, 1994), photoperiod (Byrne 1990, Waddy & Aiken 1992, Bingham 1997, Wangenstein et al. 2013), upwelling (Ventura et al. 1997) and rough seas related to downwelling (Shanks 1998, Bueno et al. 2010). In other temperate species, protracted reproductive seasons may last virtually year round (e.g. Chaparro et al. 2005).

This view of the importance of temperature and productivity in shaping seasonal patterns of reproduction is based primarily on data from temperate systems. The data available for tropical marine invertebrates are focused on reef invertebrates, especially corals, and show a somewhat different pattern (Babcock et al. 1992). Extreme annual cycles are apparent in a number of marine invertebrates that participate in single large annual mass spawning events (Harrison et al. 1984, Richmond & Hunter 1990, Babcock et al. 1992) or species that reproduce only during short windows (e.g. gorgonians [Rossi & Gili 2009], sea anemones [Scott & Harrison 2007], sea urchins [Bronstein & Loya 2015]). The timing of these events may be closely linked to ensuring fertilization success. Numerous other tropical species reproduce multiple times during the year, either continuously through the year (e.g. sea urchins [Lessios 1984], shrimps [Bauer 1989], hermit crabs [Varadarajan & Subramoniam 1982], other crustaceans [Goodbody 1965, Kerr et al. 2014a], brittlestars [Mladenov 1983]) or during a protracted reproductive season (e.g. *Echinometra vanbrunti* [Lessios 1991], *Haliotis asinina* [Singhagraiwan & Doi 1992, Capinpin et al. 1998]). Yet others range from year-round reproduction to broadly seasonal as latitude increases (Pearse 1968, Terossi et al. 2010). When seasonality is evident, reproduction often occurs during the warmest part of the year, despite the moderate seasonal differences in temperature experienced by most tropical locations. As is the case in temperate regions, other physical conditions may also vary seasonally in conjunction with temperature, but little is known about their impact on reproduction in tropical invertebrates.

Seasonal variation in offspring size or quality

In temperate species with protracted reproductive seasons or year-round reproduction, offspring size

may vary seasonally in response to temperature. Offspring size has been demonstrated to vary inversely with temperature in laboratory studies for numerous ectotherms, including marine invertebrates (Atkinson et al. 2001, Moran & McAlister 2009, Collin & Salazar 2010, Collin 2012). This is known as the offspring temperature–size rule (Atkinson et al. 2001). Data from field-collected animals also support this pattern. In temperate and subtropical decapod crustaceans that reproduce year round, eggs are often smaller in the summer compared to other times of the year (e.g. *Crangon* [Urzúa et al. 2012], *Sesarma* [de Arruda Leme 2006], *Alpheus* [Pavanelli et al. 2010]). In decapod species with seasonal reproduction, egg size is often larger at the cooler start of the reproductive season than later in the season (e.g. Bas et al. 2007, Fischer et al. 2009). This pattern is roughly consistent with an inverse correlation between temperature and offspring size, although numerous other environmental factors vary with temperature and cannot be ruled out in field studies. Maternal condition and food availability can also play a role in offspring size. Females in better condition or with better access to resources generally produce larger eggs or better-quality offspring (Qian & Chia 1991, de Jong-Westman et al. 1995, Guisande & Harris 1995, George 1996, Kirk 1997, but see Qian 1994 for the opposite pattern). Eggs may therefore be larger early in the reproductive season, before female resources have become depleted from producing multiple clutches (e.g. Bas et al. 2007, 2008, Fischer et al. 2009, Gebauer et al. 2013, Vázquez et al. 2013).

We studied 4 common species of intertidal gastropods to determine how the intensity of reproduction and offspring size vary seasonally on the Pacific coast of Panama. The Bay of Panama experiences upwelling during the dry season (January to mid-May), when offshore winds drive upwelling of cool, nutrient-rich waters. Using this seasonal variation, we planned to test 2 alternative hypotheses regarding the intensity of reproduction: (1) reproduction occurs primarily during the warm, non-upwelling season (consistent with reproduction tracking warm temperatures) versus (2) reproduction occurs primarily during the highly productive upwelling season (consistent with reproduction timed to coincide with increased larval food availability). We also tested 2 non-exclusive hypotheses regarding intraspecific variation in offspring size: (3) offspring are larger when females experience cooler environmental temperatures (consistent with the offspring temperature–size rule) and (4) offspring are larger when maternal food availability is greater.

MATERIALS AND METHODS

Four abundant species of intertidal snails (*Crepidula* cf. *marginalis*, *Littoraria variegata*, *Cerithideopsis californica* var. *valida* and *Natica chemnitzii*; Fig. 1, Table 1) were surveyed between October 2012 and August 2015 to determine if reproduction and offspring size vary seasonally.

Study sites and environmental data

The Bay of Panama experiences 2 distinct seasons. The non-upwelling season corresponds to cooler air temperature during the rainy season from mid-May to December. The upwelling season corresponds to warmer air temperatures during the dry season, which is dominated by northeasterly trade winds and

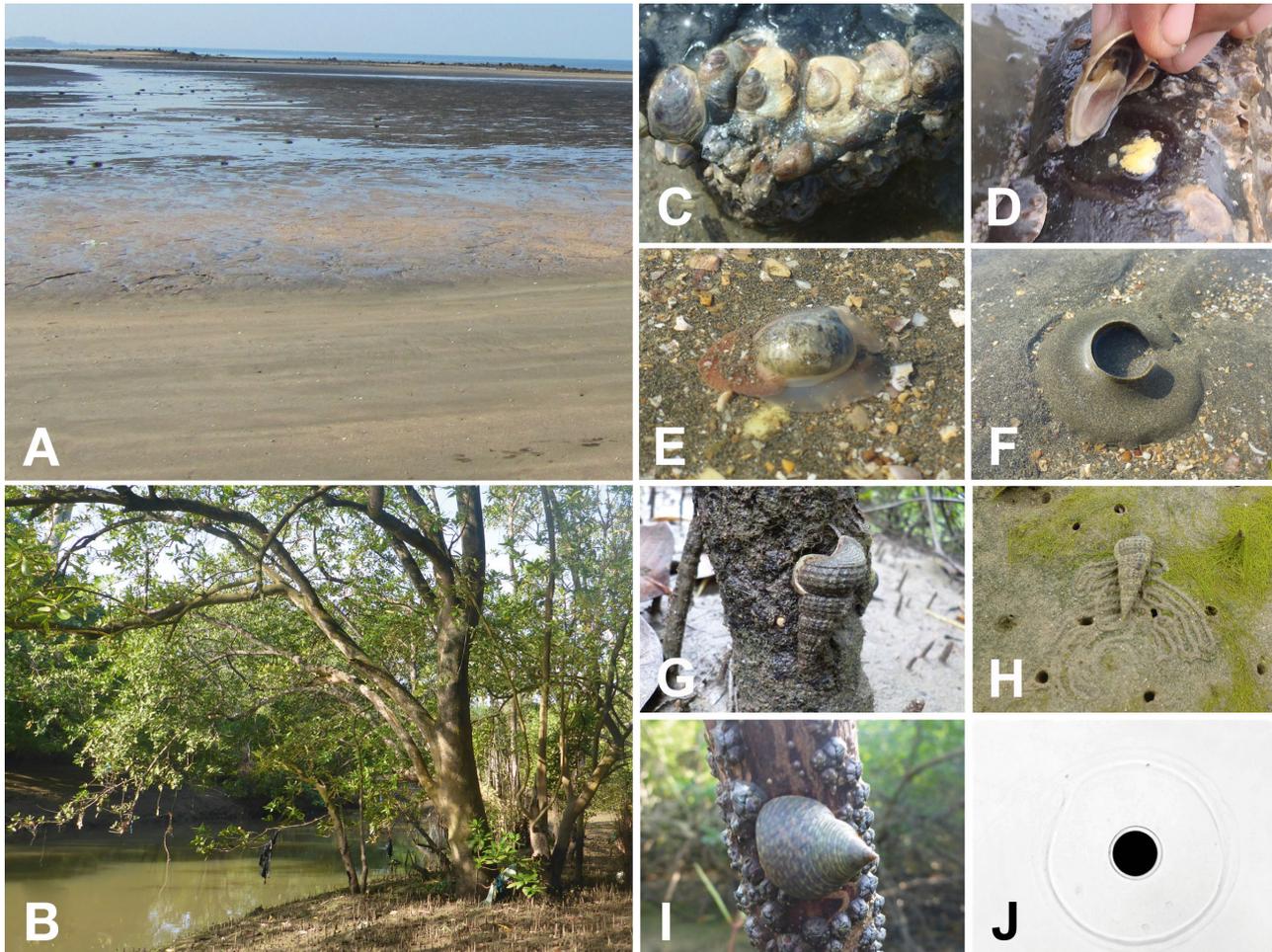


Fig. 1. Habitats, study species and their eggs. (A) Beach. (B) Mangrove forest. (C,D) *Crepidula* cf. *marginalis* and a brooded egg mass. (E,F) *Natica chemnitzii* and an egg mass. (G,H) *Cerithideopsis californica* and an egg mass. (I,J) *Littoraria variegata* and an egg capsule

Table 1. Summary of the characteristics of the 4 study species

Species	Trophic mode	Adult habitat	Embryo habitat
<i>Littoraria variegata</i>	Grazer	Mangrove trunks	Pelagic
<i>Cerithideopsis californica</i>	Grazer	Mangrove trunks or mud	Mangrove mud
<i>Crepidula</i> cf. <i>marginalis</i>	Filter feeder	Intertidal under rocks	Intertidal under rocks
<i>Natica chemnitzii</i>	Predator	Intertidal in sand	Intertidal on sand

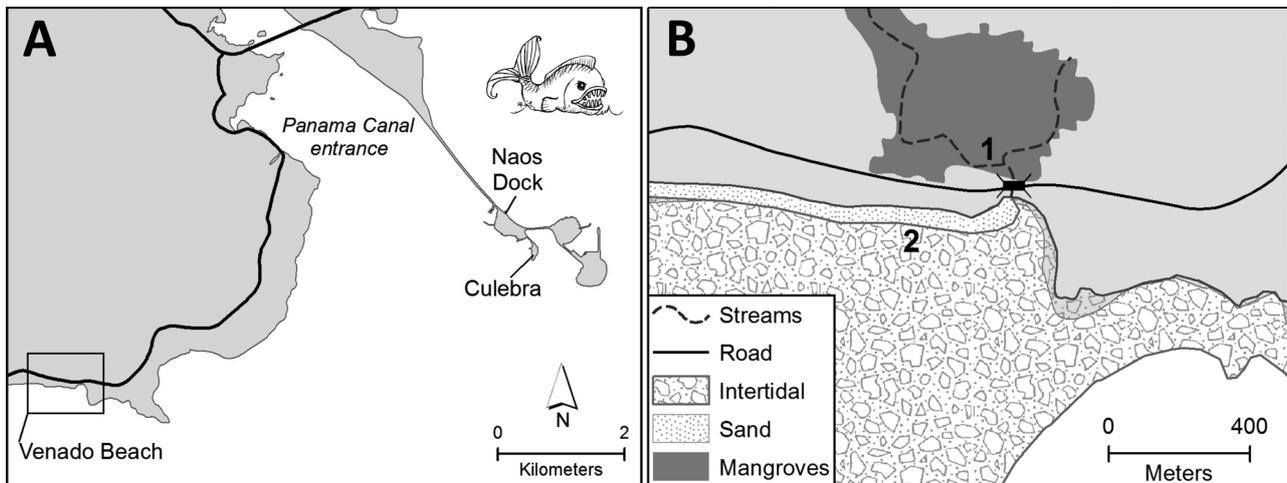


Fig. 2. Sites on the southern coast of Panama, west of Panama City. (A) Spatial relationships between Playa Venado 8.892° N, 79.597° W, Naos Laboratories 8.915° N, 79.533° W and Punta Culebra. (B) Study site at Playa Venado. 1 = mangrove site; 2 = sandy and rocky site

which lasts from December until mid-May. The Bay of Panama is a large, shallow embayment, and upwelling during the dry season dramatically decreases surface sea temperature, increases nutrients and phytoplankton and zooplankton biomass in the surface waters (Smayda 1963, D’Croz & Robertson 1997), increases the frequency of hydromedusa blooms (Miglietta et al. 2008), and alters the rates of predation risk in the plankton (Kerr et al. 2014b,c).

Environmental conditions were monitored on Culebra and Naos islands (Fig. 2; Robertson et al. 2009) as part of the Smithsonian Tropical Research

Institute’s environmental monitoring program. Subtidal water temperature was measured with HOBO StowAway TidbiT and HOBO Water Temperature Pro v2 instruments (Onset Computer) with an accuracy of $\pm 0.25^\circ\text{C}$ (Kaufmann & Thompson 2005) at 2 m on the Naos Island dock. Sensors were changed and calibrated biannually. Hourly measurements were averaged for each week over the sampling period (Table 2, Fig. 3). Salinity was measured with a refractometer twice daily from water in the Naos Laboratories seawater system, which is drawn from 2 to 3 m depth near the Naos dock. Air temperature and rela-

Table 2. Summary of environmental data from the Smithsonian Tropical Research Institute’s environmental monitoring program and from iButton data loggers deployed at the study sites. **Bold:** $p < 0.05$ (t -test); one iButton was deployed on the beach, 2 were deployed in the mangrove branches and 2 were deployed in the mangrove mud

	Upwelling	Non-upwelling	Measurement period
Sea temperature ($^\circ\text{C}$)	25.61	28.80	June 2012–July 2015
Air temperature ($^\circ\text{C}$)	27.20	27.26	January 2011–July 2015
Salinity (ppt)	32.06	29.59	January 2011–July 2015
Relative humidity (%)	79.79	88.13	January 2011–July 2015
Temperature, mangrove trees ($^\circ\text{C}$)			October 2013–August 2014
Mean \pm SE	27.8 \pm 0.07	27.3 \pm 0.05	
Mean daily maximum \pm SE	35.2 \pm 0.20	32.9 \pm 0.14	
Mean daily minimum \pm SE	24.0 \pm 0.07	24.7 \pm 0.05	
Temperature, mangrove mud ($^\circ\text{C}$)			September 2013–August 2014
Mean \pm SE	26.9 \pm 0.08	27.6 \pm 0.06	
Mean daily maximum \pm SE	33.1 \pm 0.24	31.6 \pm 0.20	
Mean daily minimum \pm SE	24.2 \pm 0.17	25.6 \pm 0.06	
Temperature, beach ($^\circ\text{C}$)			September 2013–August 2014
Mean \pm SE	26.9 \pm 0.11	29.1 \pm 0.08	
Mean daily maximum \pm SE	35.8 \pm 0.33	35.6 \pm 0.25	
Mean daily minimum \pm SE	23.4 \pm 0.09	25.7 \pm 0.07	

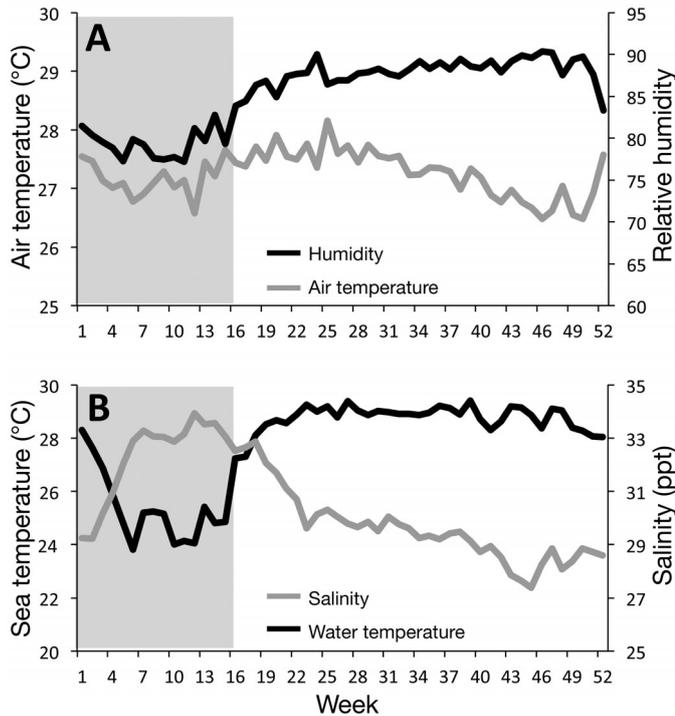


Fig. 3. Seasonal variation in conditions from the Smithsonian Tropical Research Institute's environmental monitoring program. (A) Air temperature and relative humidity at Punta Culebra. (B) Sea temperature and salinity at Isla Naos. Lines connect weekly averages calculated from daily (salinity) or hourly (all other) measurements taken over 3 yr (sea temperature) or 4.5 yr (all other measures). Grey box indicates the dry season during the first 16 wk of the year

tive humidity data were obtained from a weather station on Isla Culebra. These data show a clear increase in salinity and decrease in water temperature during the upwelling season concordant with decreased humidity (Table 2, Fig. 3). Average air temperature shows little seasonal variation, but the range of temperatures is somewhat wider in the dry season due to cooler nights and warmer daytime temperatures.

The 4 snail species were studied in their respective intertidal habitats (see next subsection) at Playa Venado, near the town of Veracruz, 8 km from Naos and Culebra islands. To characterize the thermal environment in the 3 habitats, iButton data loggers were deployed in the intertidal at the site where we sampled each species. We wrapped each iButton in 2 layers of plastic to protect it from the seawater and enclosed it in a small Vexar cage (Kerr et al. 2012). The cages were then attached to the branches of mangrove trees where we found *L. variegata*, secured in the mud at the base of the trees and embedded at the surface of the sediment on the beach.

Study species and methods

Egg masses of the moon snail *N. chemnitzii* and the slipper limpet *C. cf. marginalis* were studied on the beach, which is a mix of muddy sand and rock rubble (Fig. 1A). *N. chemnitzii* produce sand-covered egg collars typical of moon snails, which hatch as small planktotrophic veligers (Fig. 1E,F). These egg collars occur on top of the sand or muddy sand in the high mid-intertidal where adults are also often observed (Figs. 1 & 2). *C. cf. marginalis* are abundant and are attached to the sides of and underneath small rocks, which occur in patches on the beach at the same tidal height as the moon snail egg masses. Slipper limpets brood masses between their neck, propodium and the substrate (Fig. 1C,D). Larvae are planktotrophic, and in the laboratory, under otherwise constant conditions, egg size and hatching size correlate negatively with environmental temperature (Collin 2012).

L. variegata and *C. californica* were studied in the high intertidal in the mangrove forest composed of *Avicennia germinans*, *A. bicolor*, *Laguncularia racemosa* and *Rhizophora* sp. along a creek that flows onto the eastern part of the beach (Figs. 1B & 2). *L. variegata* live on the trunks and lower branches of mangrove trees. They produce pelagic capsules that each contain a single egg which develops into a small planktotrophic veliger (Fig. 1I,J). *C. californica* inhabit the trunks and, during low tides, the mudflat at the base of the mangroves and deposit gelatinous egg strings on the surface of the mud (Fig. 1G,H; Miura et al. 2011).

To determine if the intensity of reproduction differs between upwelling and non-upwelling seasons, we surveyed the abundance of egg masses for 10 mo starting in the wet season of 2013, covering the dry season of early 2014 and extending into the wet season of 2014. Masses of *N. chemnitzii* were also counted for 3 mo in the dry season and early wet season of 2013. Because reproduction follows a fortnightly tidal amplitude cycle and reproductive intensity varies in a complex way among cycles in these species (R. Collin et al. unpubl.), we quantified reproductive intensity in different ways based on the idiosyncrasies of each species.

For *L. variegata*, 15 to 30 female *Littoraria* were collected 1 to 2 times a week. They were maintained in Falcon tubes half filled with seawater for up to a week (but generally not more than 4–5 d) in the laboratory. Every day, the water was emptied from the tubes and the presence or absence of egg capsules was reported. Because the number of individuals collected varied somewhat, the average percent of cap-

tive animals releasing larvae per day was calculated for each 2 wk cycle from one half moon to the next. Data were collected between early October 2013 and the end of August 2014, with a break between December 20, 2013, and January 20, 2014.

For *C. cf. marginalis*, every Monday, Wednesday and Friday, 10 to 20 large (>9 mm) *C. cf. marginalis* that were paired with a male were removed from the rocks and measured with calipers, and the presence or absence of a brood was recorded. This species does not show a pronounced 2 wk cycle, so the total percent brooding was calculated for each season. Reproduction of *Crepidula* was followed between November 2013 to the end of August 2014, with a break between December 20, 2013, and January 17, 2014. Because *C. cf. marginalis* are protandrous hermaphrodites and we could not determine sex in the field, we used size as a proxy for sex. However, size at sex change can vary with social and environmental conditions (Mérot & Collin 2012a,b). We therefore used logistic regression to account for any effects of size on the probability that a snail would be brooding.

For *N. chemnitzii*, every Monday, Wednesday and Friday, we placed three 100 × 2 m band transects perpendicular to the coast in the same 3 locations in the zone where *Natica* egg masses occur. All the masses in each transect were counted. Individual masses could not be tracked, but the total number of masses counted in each 2 wk cycle was used for analysis.

For *C. californica*, three 1 × 1 m permanent quadrats were installed on the mud at the base of mangrove trees. Every Monday, Wednesday and Friday, we marked each new egg mass with labeled sticks and counted the total number of masses produced in each 2 wk cycle. Data were collected between November 2013 and August 2014, with a break between December 20, 2013, and January 17, 2014.

To determine if offspring size, a proxy for maternal investment per offspring, differed between the upwelling and non-upwelling season, shell lengths of hatchlings of each species were measured from multiple masses during 4 mo of upwelling (January–April) and 4 mo of non-upwelling (June, August, October and early December) in 2012 to 2014 for *N. chemnitzii* and in 2013 to 2015 for the other 3 species. Egg masses (*Cerithideopsis* and *Natica*) or reproductive females (*Crepidula*) were collected and maintained outside at ambient temperatures, semi-submerged in cups in the Naos Laboratories outdoor seawater system. Cups were checked twice a day for hatchlings. For *Littoraria*, the capsules that were released in the Falcon tubes in the study of reproductive intensity (see this subsection) were maintained

in petri dishes in filtered water in incubators at 28°C and monitored daily until they hatched. Larvae were fixed in ethanol and photographed under a compound microscope, and shell length was measured in ImageJ following Collin (2012).

All analyses were conducted in JMP v11. Two sample comparison tests, either *t*-tests or Kruskal-Wallis tests, were used to compare reproductive intensity between the wet and dry seasons. Nested restricted maximum likelihood analyses of variance or covariance were used to analyze the effects of season on offspring size. Factors included mother (dam) as a random effect nested within month and month nested within season. Maternal shell length, which was available for *Littoraria* and *Crepidula* only, was included as a covariate.

RESULTS

Seasonal environmental differences

Physical conditions in the shallow margin of the Bay of Panama differ between the wet and dry seasons (Fig. 3, Table 2), similarly to what has been previously reported for sites further offshore (Smayda 1963, D’Croz & Robertson 1997, Robertson & Collin 2015) as well as on open sandy beaches (Kerr et al. 2014a). Temperature loggers placed in the intertidal where the snails live showed that each habitat was influenced somewhat differently by seasonal variation in air temperature and water temperature (Fig. 4, Table 2). As expected, the beach site showed the greatest influence of sea temperature; average temperatures were significantly cooler during the upwelling season ($26.9 \pm 0.11^\circ\text{C}$, mean \pm SE) than during the non-upwelling season ($29.1 \pm 0.08^\circ\text{C}$). The average daily minima were cooler during the upwelling season than during the non-upwelling season, but the average daily maxima did not differ. The mangrove branches and mangrove mud also showed significant differences in temperature between the upwelling and non-upwelling seasons. In both habitats, temperatures were less variable in the wet (non-upwelling) season, with significantly cooler average maximum temperatures and warmer average minimum temperatures (Table 2, Fig. 4). However, they showed contrasting patterns in overall average temperatures. In the mangrove branches, the average air temperature was slightly higher ($27.8 \pm 0.07^\circ\text{C}$) in the dry (upwelling) season than in the wet (non-upwelling) season ($27.3 \pm 0.05^\circ\text{C}$), while the average temperature in the mud below the mangroves was cooler in the dry (up-

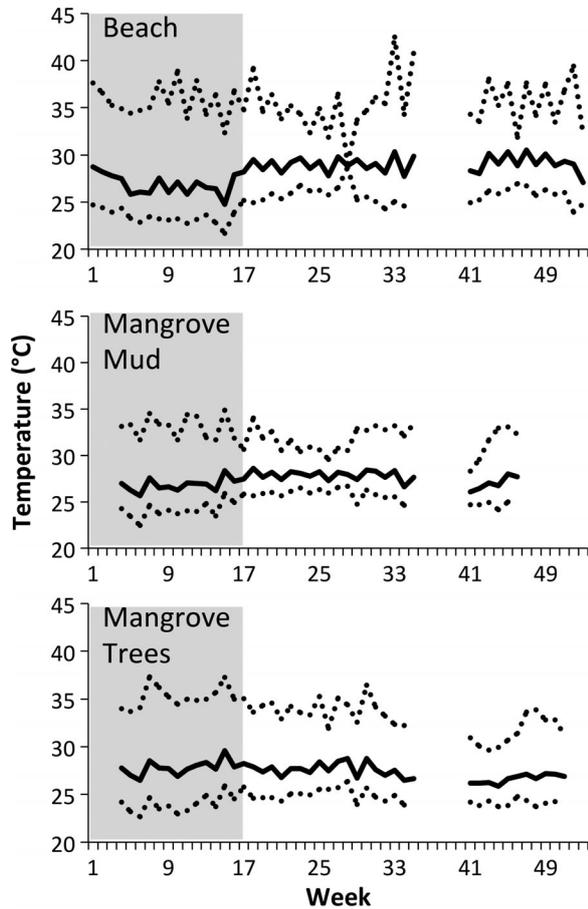


Fig. 4. Seasonal variation in temperature recorded with iButton data loggers in the 3 environments where the snails were collected. Solid lines indicate weekly mean temperatures, and dotted lines indicate weekly averages of the daily maximum and minimum temperatures. Grey box indicates the dry season: the first 16 wk of the year

welling) season ($26.9 \pm 0.08^\circ\text{C}$) than in the wet (non-upwelling) season ($27.6 \pm 0.06^\circ\text{C}$).

Intensity of reproduction

Reproductive intensity was greater in the dry season (January–April) than in the wet season (May–December) for 1 of the 4 species, was greater in the wet season for 2 species, and showed no seasonal difference for the fourth species (Table 3).

Average reproductive intensity per period in *Littoraria variegata* was greater in the wet season than in the dry season (Kruskal-Wallis test: $p = 0.04$; $N_{\text{dry}} = 6$; $N_{\text{wet}} = 11$; $\chi^2 = 4.48$; $df = 1$). The maximum percentage of females releasing on any single day during each period was also greater in the wet season (Kruskal-Wallis test: $\chi^2 = 4.48$; $N_{\text{dry}} = 6$; $N_{\text{wet}} = 11$; $df = 1$; $p = 0.034$). The overall maximum percent releasing on a

Table 3. Observations of changes in temperature and food availability during upwelling relative to non-upwelling and the predicted and observed changes in reproductive intensity (hypotheses 1 and 2) and offspring size (hypotheses 3 and 4). +: greater during upwelling; -: smaller during upwelling; =: does not differ between seasons

	Hypothesis 1 ^a		Hypothesis 2 ^b		Observed change
	Maternal temperature (°C)	Predicted change in reproductive intensity	Larval food	Predicted change in reproductive intensity	
<i>Littoraria variegata</i>	+0.5	+	+	+	-
<i>Cerithideopsis californica</i>	+0.5	+	+	+	-
<i>Crepidula cf. marginalis</i>	-2.2	-	+	+	+
<i>Natica chemnitzii</i>	-2.2	-	+	+	=
	Hypothesis 3 ^c		Hypothesis 4 ^d		Observed change
	Maternal temperature (°C)	Predicted change in offspring size	Maternal food	Predicted change in offspring size	
<i>L. variegata</i>	+0.5	-	-	-	=
<i>C. californica</i>	+0.5	-	-	-	+
<i>C. cf. marginalis</i>	-2.2	+	+	+	+
<i>N. chemnitzii</i>	-2.2	+	=	=	+

^aReproduction occurs primarily during the warm, non-upwelling season (consistent with reproduction tracking warm temperatures)
^bReproduction occurs primarily during the highly productive upwelling season (consistent with reproduction timed to coincide with increased larval food availability)
^cOffspring are larger when females experience cooler environmental temperatures (consistent with the offspring temperature-size rule)
^dOffspring are larger when maternal food availability is greater

single day was 22 % in the dry season and 86 % in the wet season.

Reproductive intensity in *Cerithideopsis californica* was also greater during the wet season. There were significantly fewer masses deposited per 2 wk cycle during the dry season, with an average of 48.75 cycle⁻¹ (range: 27–95; SE = 7.99; N = 8), compared to the wet season, with an average of 96.25 cycle⁻¹ (range: 38–157; SE = 16.12; N = 8) (*t*-test: *p* = 0.019; *df* = 1; *F* = 6.97).

Crepidula cf. marginalis collected during the dry season were more likely to be brooding (62.9%) than were those collected during the wet season (51.6%) (G-test: $\chi^2 = 28.9$; *p* < 0.0001; N = 2378). Logistic regression showed that there was no interaction between shell length and season on the likelihood that a snail was brooding (*p* = 0.075; *r*² = 0.06; N = 2378), but the probability that a snail was brooding increased with shell length (*p* < 0.0001) and was greater in the dry season than in the wet season (*p* < 0.0001).

Table 4. ANOVA and ANCOVA tables showing the effects of season, sampling month, female and female size on hatching size of the 4 gastropod species. **Bold:** *p* < 0.05

	df	F	p	%var
<i>Littoraria variegata</i>				
Season	1	1.44	0.24	
Month [Season]	6	1.31	0.26	
Female [Month] Random				66.18
Female Length	1	4.83	0.03	
Model fit: <i>r</i> ² = 0.68; N = 2236				
<i>Cerithideopsis californica</i>				
Season	1	32.34	<0.0001	
Month [Season]	6	9.45	<0.0001	
Female [Month] Random				47.93
Model fit: <i>r</i> ² = 0.57; N = 4558				
<i>Crepidula cf. marginalis</i>				
Season	1	22.53	<0.0001	
Month [Season]	6	5.74	<0.0001	
Female [Month] Random				62.95
Female Length	1	0.00	0.99	
Model fit: <i>r</i> ² = 0.68; N = 4670				
<i>Natica chemnitzii</i> (large eggs)				
Season	1	21.19	<0.0001	
Month [Season]	3	10.72	<0.0001	
Female [Month] Random				32.90
Model fit: <i>r</i> ² = 0.40; N = 4340				
<i>N. chemnitzii</i> (small eggs)				
Season	1	97.42	<0.0001	
Month [Season]	6	8.61	<0.0001	
Female [month, season] Random				51.62
Model fit: <i>r</i> ² = 0.65; N = 8011				

The average number of masses of *Natica chemnitzii* observed on the beach during each 2 wk period did not differ significantly between the wet (104.7 cycle⁻¹; range 26–205) and dry (102.7 cycle⁻¹; range 40–261) seasons (Kruskal-Wallis $\chi^2 = 0.48$; N_{dry} = 13; N_{wet} = 11; *df* = 1; *p* = 0.49).

Offspring size

In all of the species studied here, 30 to 65 % of the variation in hatching size was due to the random effect of dam nested within month (Table 4, Figs. 5 & 6). In *Littoraria*, there was no significant effect of season or month nested within season on hatching size (Table 4, Fig. 5). In *Cerithideopsis* and *Crepidula*, there was a significant effect of both season and month nested within season (Table 4, Figs. 5 & 6). In both species, hatching size was significantly larger

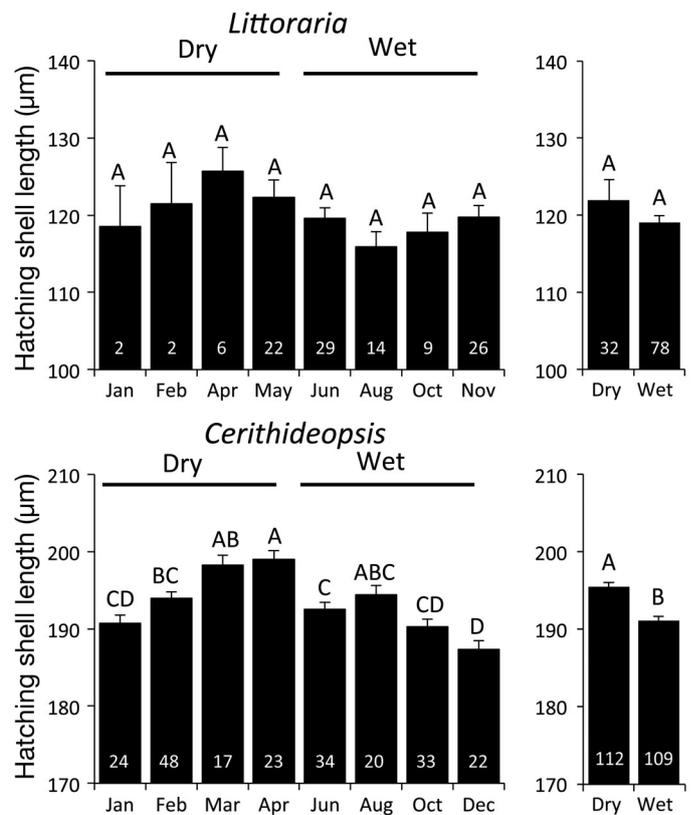


Fig. 5. Variation in hatching size in the 2 species from the mangroves. Bars show the least square means, and lines show the standard errors of the means from ANCOVA and ANOVA models with month (left) nested within season (right) and female treated as a random effect nested within month. Bars linked with the same letter do not differ significantly in post hoc Tukey's HSD test. Numbers at the base of the bars give the number of females for each month

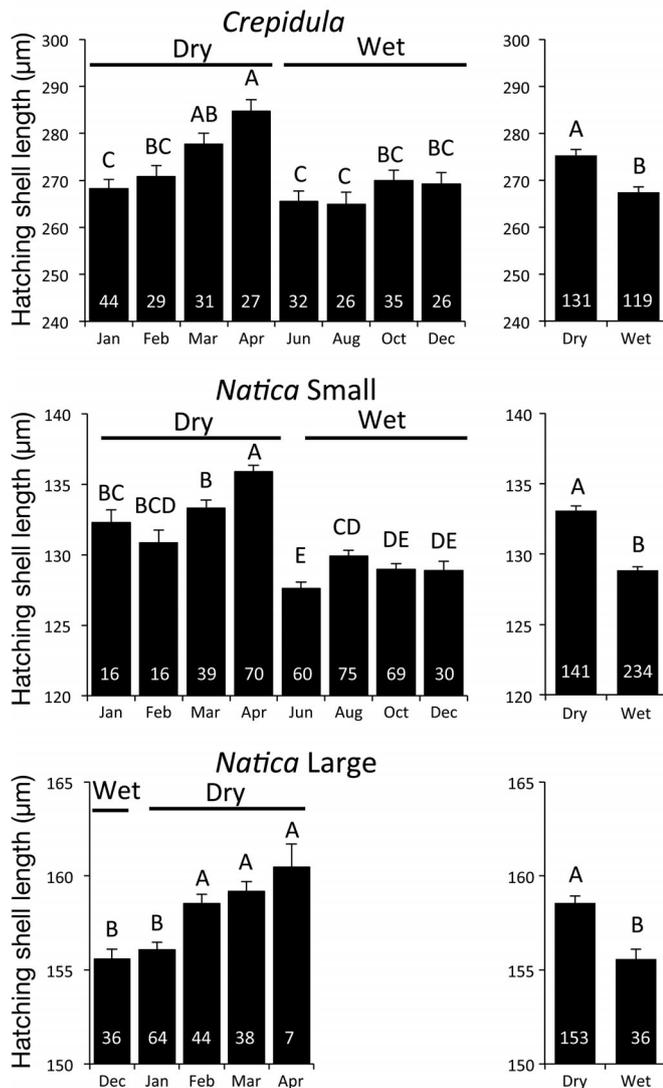


Fig. 6. Variation in hatching size in the 2 species from the beach. Further details as in Fig. 5. *Natica chemnitzii* masses were separated into 2 groups based on bimodal hatching size

during the dry season than during the wet season. The differences in average sizes between the seasons were small: 4.3 µm in *Cerithideopsis* and 7.9 µm in *Crepidula*. In addition, monthly patterns showed an increase in hatching size as the dry season progressed in both species but no clear pattern during the wet season (Table 4, Figs. 5 & 6).

The situation for the *N. chemnitzii* egg masses is more complicated. Although the masses were similar in appearance and collected from the same 3 transects each month, the hatching size was bimodal from December through April (Fig. 7). Each egg mass produced hatchlings whose size fit into only one of the peaks in the overall size distribution (Fig. 7). This pattern is consistent with the presence of 2 species,

one of which reproduces only between December and April and another which reproduces all year. Alternately, these different hatching sizes might represent hatching size plasticity that is triggered only during part of the year. Analysis of clutches with small hatchlings showed a similar pattern to the hatchlings from *Crepidula* (Fig. 6). There was a significant effect of both season and month nested within season (Table 4), with hatchlings on average 4.24 µm larger in the dry season. Hatchlings also increased in size as the dry season progressed (Fig. 6). For the egg masses with large hatchlings, hatching size was also larger in the dry season than in the wet season (early December only), and hatching size increased as the dry season progressed (Table 4, Fig. 6).

DISCUSSION

Is seasonal reproduction related to warm environmental temperatures or increased larval food supply?

The small but distinct seasonal environmental cycles in the intertidal of the Bay of Panama were reflected by seasonal cycles in reproductive intensity in 3 of the 4 snails studied here. However, increased reproductive output is not associated with increased temperatures experienced by the adults, and only in *Crepidula cf. marginalis* is reproduction greater when larval food supply is expected to be higher (Table 3). In fact, the results reported here are most consistent with the idea that reproductive intensity tracks adult food supply and that reduced relative humidity and desiccation stress experienced by snails in the mangroves inhibit reproduction.

The 2 mangrove species, *Cerithideopsis californica* and *Littoraria variegata*, showed large reductions in the number of egg masses or capsules produced during the dry (upwelling) season compared to the wet season. *Littoraria* and *Cerithideopsis* snails are virtually never submerged as adults. *Littoraria* snails usually spend their lives grazing on the branches and in the canopy and move down to the water only to release their egg capsules (Alfaro 2008). *Cerithideopsis* usually spend high tides in vegetation above the waterline but descend to the mud at the base of the vegetation to graze on diatoms on the mud flats during low tide (McGuinness 1994). Like the *Littoraria*, they avoid submersion but deposit their egg masses in areas of the mudflats where the masses are submerged daily. Therefore, the air temperature recorded in the mangrove branches reflects the envi-

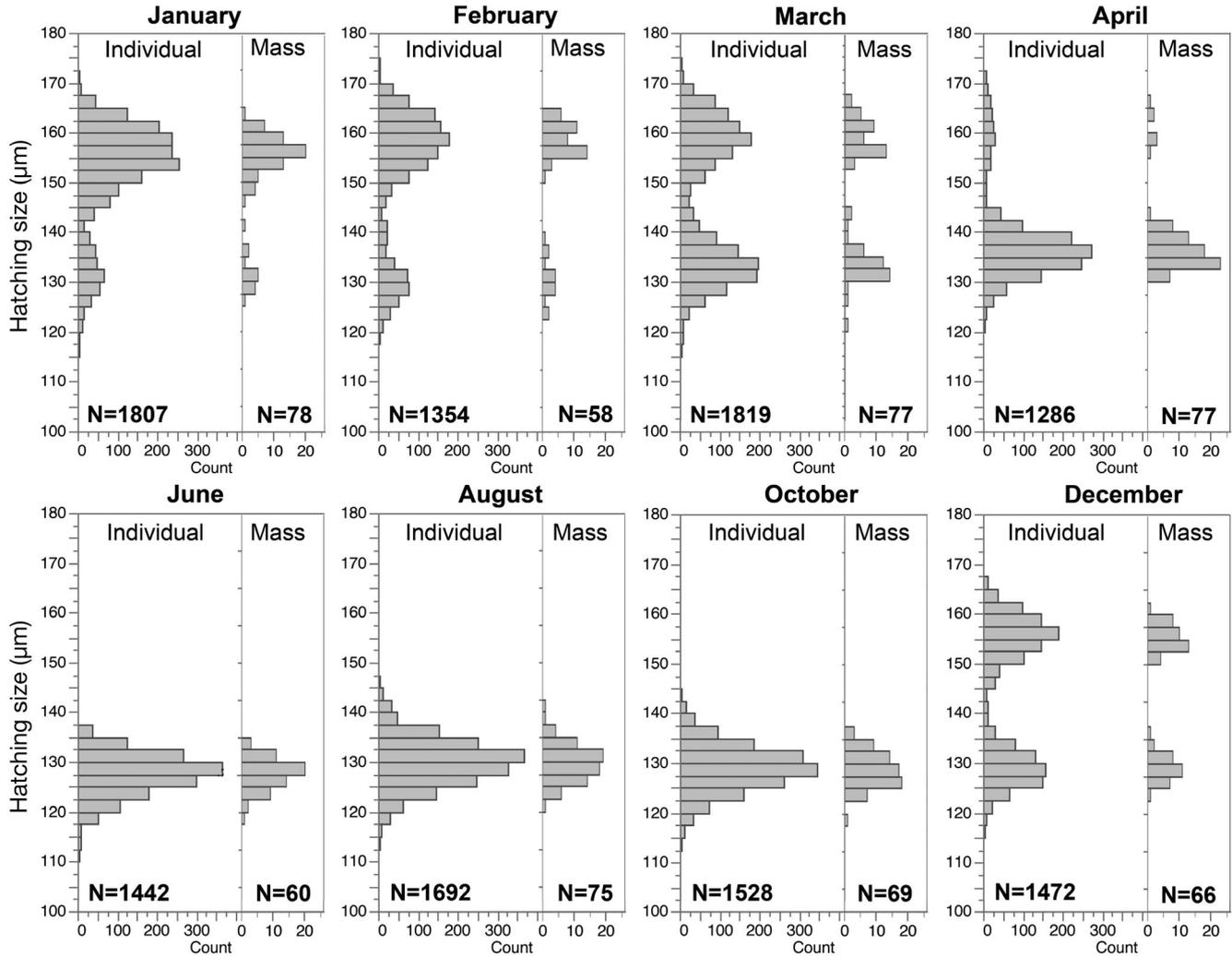


Fig. 7. Distribution of hatching size in larvae of *Natica chemnitzii* by month showing both individual larvae (left) and means from each egg mass (right)

ronmental conditions experienced by the adults of these 2 species, the mangrove mud temperature reflects the temperatures experienced by developing *C. californica*, and ocean temperatures reflect the temperatures experienced by the pelagic capsules of *L. variegata*.

Since the average air temperatures among the mangrove branches were 0.5°C warmer in the dry season compared to the wet season, the seasonal depression of reproduction in the dry season for both of these species is not consistent with the idea that adults favor reproduction when it is warm for them. It is possible that increased maximum temperatures during the dry season cause heat stress, which suppresses reproduction. Panama is roughly in the warmest part of the geographic ranges of both species. *L. variegata* ranges from El Salvador to Peru (Reid 1999), and *C. californica* ranges from southern

California to Panama (Miura et al. 2010). Although no data are available on the impacts of heat stress on reproduction for either species, they may experience heat stress during the dry season. Thermal tolerance data on a variety of *Littoraria* species (but not *L. variegata*) living in mangroves show that heat coma temperatures average 45°C under rapid thermal ramping, with lethal upper thermal limits of 50°C (Marshall et al. 2015). These are above the temperatures recorded in the mangrove branches. One of the iButton canopy sites never exceeded 40°C. The location of the second canopy iButton exceeded 40°C on 8 of the 280 d measured but never exceeded 42°C. *C. californica* is also very tolerant of high temperatures. Experiments with animals from California show no mortality in snails submerged in 40°C seawater for 1 to 4 h and no mortality in animals kept out of water at room temperature and ambient (low)

humidity for up to 10 d (Race 1982). However, tolerance of acute stress may not reflect the conditions under which low levels of chronic stress might influence reproduction.

Reduced humidity during the dry season could be an important factor influencing the seasonal reproductive cycle. Our understanding of the thermal physiology of intertidal molluscs emphasizes the importance of hydration as well as thermal tolerance (McMahon 1990, Jenewein & Gosselin 2013, Rojas et al. 2013). Therefore, heat stress experienced by these snails could be exasperated by desiccation stress during the dry season. A clear reduction in relative humidity was measured above the canopy in Isla Culebra (Fig. 3). The mangrove habitat in Playa Venado is noticeably drier during the dry season; the mud at the base of the trees is dry and firm, sometimes displaying cracks, and the canopy appears somewhat more open. The low humidity and increased air movement as a result of stronger winds during the dry season are also expected to reduce the algal film on the mud and the arboreal algae and fungi that comprise the bulk of the diets of these species (Whitlatch & Obrebski 1980, Lee et al. 2001).

In contrast to the mangrove snails, both beach species maintain high levels of reproduction throughout the year. *Natica chemnitzii* egg masses did not change in abundance between the seasons, although the seasonal changes in offspring size complicate interpretations (see final subsection). An increase in brooding during the dry season was evident in *C. cf. marginalis*. Environmental temperature in the intertidal habitat of this species is cooler during upwelling; therefore, reproduction seems to increase as environmental temperatures decrease. In the laboratory, this species responds to warmer temperatures by reducing the interbrood interval and time to hatching, so that the average percent of the time each female spends brooding remains roughly the same (Collin 2012). This suggests that differences in brood frequency are not likely to drive the increased incidence of brooding females in the dry season. *Crepidula* are minimally selective suspension feeders that consume a wide variety of planktonic microalgae and possibly benthic diatoms but appear to be able to select against sediment and inorganic material (Beninger et al. 2007, Decottignies et al. 2007, Harke et al. 2011, Chaparro et al. 2013). Therefore, the greater abundance and biomass of microalgae in the Bay of Panama during the dry season compared to the wet season (Smayda 1963, see next subsection) suggest that reproductive intensity in this species tracks maternal food availability. The availability of prey for

N. chemnitzii, a drilling predator, is not expected to vary seasonally, and the lack of a pronounced seasonal reproductive cycle is consistent with constant food availability.

Despite the overall impression that reproduction is often year round in the tropics, such seasonal changes in the reproduction of tropical marine organisms like those documented here are not uncommon in seasonal tropical environments and may be related to a number of different environmental factors. Some subtidal animals in the Bay of Panama reduce or suppress reproduction during cold upwelling events (Lessios 1981, Robertson 1990). These organisms experience reductions in environmental temperature that are much more severe (5–10°C) than the moderate seasonal changes recorded in the intertidal (0.5–2°C) and appear to conform to the pattern of reproduction tracking warm temperatures. Other environmental factors may also drive seasonality in reproduction in tropical sites. For example, along the coast of India, many marine invertebrates show a seasonal reduction in reproduction during the monsoon season on the west coast (Varadarajan & Subramoniam 1982), while those on the east coast reproduce all year (Pillay & Nair 1971, Varadarajan & Subramoniam 1982). The authors hypothesized that this is the result of a reduction in salinity during the monsoon, as temperature did not differ much between the seasons (Pillay & Nair 1971, Varadarajan & Subramoniam 1982). As only 1 of the 4 gastropods studied here had slightly decreased reproductive intensity in the rainy season, when salinity is reduced in the shallow waters of the Bay of Panama, salinity does not appear to exert such a strong effect at our study site.

Is seasonal variation in offspring size driven by temperature?

Three of the 4 species studied here showed significant seasonal differences in offspring size. In all 3 cases, offspring were slightly larger during the dry (upwelling) season compared to the wet (non-upwelling) season, and size showed a progressive increase during the upwelling season, coincident with progressively decreasing temperatures (Table 2). The beach habitat experienced by 2 of these species is 2.2°C cooler during the dry season than during the wet season. This result is consistent with the offspring temperature–size rule, which predicts a negative relationship between offspring size and the environmental temperatures experienced by the mothers and by the developing eggs. In controlled laboratory

conditions, a constant 5°C difference in temperature produces a 34 µm difference in hatching size in *C. cf. marginalis* (Collin 2012). In the field, where other conditions also vary, we observed an 8 µm increase in hatching size with a 2.2°C decrease in mean seasonal temperature. The small *N. chemnitzii* offspring showed a 4.2 µm increase in hatching size with the same decrease in field temperature. The laboratory experiment with *C. cf. marginalis* also demonstrated that cooler temperatures result in larger eggs, which may account partially or entirely for the difference in offspring size.

Our observations of *C. californica* may not be consistent with the offspring temperature–size rule. *C. californica* adults avoid submersions and therefore likely experience 0.5°C warmer average temperatures during upwelling, yet we recorded a 4.3 µm increase in offspring size. However, we did not track the location of adult snails during this study, and they may have spent more time semi-submerged or on the mud than we expected. This species also deposits its eggs on the mangrove mud, which experiences temperatures 0.7°C cooler during upwelling than during non-upwelling. The mechanisms responsible for the temperature–size rule are not well understood. Therefore, if temperatures experienced during development as well as those experienced by reproductive females during oogenesis influence hatching size, temperature could also explain the seasonal pattern in offspring size. It should also be noted that air temperatures are more variable than water temperatures, and little information is available about the impact of temperature variation on offspring size. Therefore, it is possible that comparisons of average temperatures do not completely capture the aspects of environmental temperatures most relevant to the mechanisms underlying the temperature–size rule.

L. variegata, like *C. californica*, is almost exclusively supra-littoral, but unlike in *C. californica*, we did not detect a seasonal difference in offspring size in *L. variegata*. *L. variegata* is the species for which we had the smallest sample sizes, especially from the dry season, when we recovered eggs from only 2 females in January and February. We included samples from early May, a period approaching the transition between the seasons, as the only samples available from the dry season. Therefore, our failure to detect a significant difference between the seasons is more likely due to a lack of power than a robust demonstration of no difference.

Although a negative relationship between offspring size and temperature has been demonstrated experimentally in a number of marine invertebrates

and appears to be consistent with the results from at least 2 of the species examined here, it is not the only potential explanation for seasonal differences in hatching size. Egg size or offspring size may also increase in response to increased maternal resources. However, although upwelling may increase food availability for *C. cf. marginalis* (see next paragraph), it is not expected to impact food availability for the predatory *N. chemnitzii*, and food availability is expected to decrease during the dry season for the 2 mangrove species. Therefore, only the results from *C. cf. marginalis* are consistent with the predicted effects of maternal resources on egg size.

It is also possible that food availability for the planktotrophic larvae could influence intraspecific variation in offspring size. Seasonal increase in diatom abundance during upwelling underlies a seasonal pattern in algal biomass and chlorophyll (Smayda 1963). Microflagellates, another potential food for gastropod larvae, represent a small portion of the algal biomass but also appear to be more abundant in the Bay of Panama during upwelling compared to non-upwelling (Smayda 1963). Because some microalgal species are more nutritious than others, abundances of broad categories of phytoplankton may be misleading, but it seems likely that food availability does change seasonally for these veligers. Fishes in low-productivity environments are thought to produce larger eggs that, in turn, produce larger hatchlings that are better equipped to survive low food conditions (Cushing 1967, Bagenal 1971). A similar pattern has been observed among some echinoderm species (Lessios 1990). Therefore, it is possible that larval food supply impacts offspring size. However, larvae are hypothesized to be larger when larval food supply is lower, which is opposite to the seasonal pattern we observed in hatching size. It is also not clear how female snails could detect and respond to cues reflecting food availability for their larvae, so this seems to be an unlikely scenario.

In the shallow waters of the Bay of Panama, salinity varies inversely with temperature, and it is therefore possible that salinity plays a role in seasonal variation in offspring size. No information is available on the effects of salinity on marine gastropod egg size or offspring size, but a negative relationship between salinity and egg size has been documented for crustaceans (Giménez & Anger 2001, Moran & McAlister 2009). This is likely due to osmotic uptake of water by the eggs (Moran & McAlister 2009), but in some cases, the larger eggs produced under lower salinities also produce larger hatchlings (Giménez & Anger 2001). Experimental manipulations will be necessary to

demonstrate if different salinities can cause differences in hatching size in these species. Overall, environmental temperature variation seems to match the observed patterns in offspring size more closely than these other factors.

What causes bimodal hatching size in *Natica*?

The seasonally bimodal pattern of offspring size in *N. chemnitzii* is surprising and unusual. This pattern is consistent with the presence of 2 species, one of which reproduces only between December and April and another that reproduces all year. Alternately, these different hatching sizes might represent hatching size plasticity that is triggered by environmental conditions during part of the year. Other than the difference in hatching size, there is little evidence to suggest that the egg masses deposited high in the intertidal belong to 2 species. The egg masses collected throughout the year generally have the same size and shape, they occur in the same transects, and the total number of masses does not change through the year. If there are 2 species that produce similar egg masses in similar locations, it would alter the interpretation of the seasonal pattern in reproductive output but not the pattern in offspring size. The seasonal increase in production of masses by one species would have been exactly compensated for by the seasonal decrease in masses of the other kind, with the changes in frequency happening in December, just prior to the start of the dry season, and in April, just prior to the end of the dry season. We would conclude that one species significantly reduces reproduction during the dry season and the other reproduces exclusively during the dry season. Egg masses of *N. chemnitzii* that produce either large or small offspring show larger offspring during the dry season and an increase in offspring size throughout the dry season (Fig. 6).

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