Old Dominion University
ODU Digital Commons

Biological Sciences Faculty Publications

Biological Sciences

2013

Ontogenetic Shifts in Resource Allocation: Colour Change and Allometric Growth of Defensive and Reproductive Structures in the Caribbean Spiny Lobster Panulirus argus

Joshua R. Anderson

Angelo J. Spadaro
Old Dominion University

J. Antonio Baeza
Old Dominion University

Donald C. Behringer

Follow this and additional works at: https://digitalcommons.odu.edu/biology_fac_pubs

Part of the Ecology and Evolutionary Biology Commons, and the Marine Biology Commons

Ontogenetic shifts in resource allocation: colour change and allometric growth of defensive and reproductive structures in the Caribbean spiny lobster *Panulirus argus*

JOSHUA R. ANDERSON[1,2], ANGELO J. SPADARO[3], J. ANTONIO BAEZA[3,4,5]* and DONALD C. BEHRINGER[1,2]

[1]*School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program, University of Florida, Gainesville, FL 32653, USA*
[2]*Emerging Pathogens Institute, University of Florida, Gainesville, FL 32611, USA*
[3]*Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA*
[4]*Smithsonian Marine Station at Fort Pierce, 701 Seaway Drive, Fort Pierce, FL 34949, USA*
[5]*Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile*

Resource allocation theory predicts a disproportionately large allocation of resources to defensive structures during early ontogeny in organisms that are subject to more intense predation at smaller than at larger body sizes. We tested this prediction on the Caribbean spiny lobster *Panulirus argus*, which exhibits a negative relationship between predation risk and body size with a high natural mortality of smaller individuals. Independent allometric growth analyses demonstrated that numerous defensive structures (e.g. orbital horns, segments supporting the antenna, the tail fan) display negative allometric growth throughout ontogeny. We interpret these findings as lobsters investing disproportionately more resources to defensive structures when small to improve survivorship. Similarly, we observed an ontogenetic shift in lobster colour pattern; small individuals (< 23 mm carapace length) that inhabit nursery grounds (preferably among red algae) displayed a disruptive pattern (camouflage), whereas larger juveniles displayed a bicolour pigmentation typical of adult lobsters. This shift in colour pattern further suggests that small lobsters employ cryptic coloration throughout their asocial algal stage. However, this cryptic coloration offers no advantage when lobsters grow larger and start dwelling in crevices. Other structures linked to reproduction (e.g. female pleopods and male pereopods) experienced either isometric or positive allometric growth throughout ontogeny. Our results support one of the main predictions of resource allocation theory and demonstrate ontogenetic shifts in defensive structures and coloration concomitantly with changes in lobster mortality risk mediated by size-dependent predation risk. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **108**, 87–98.

ADDITIONAL KEYWORDS: crustacea – defence – marine – predation – size-dependent.

INTRODUCTION

'If under changed conditions of life a structure, before useful, becomes less useful, its diminution will be favoured, for it will profit the individual not to have its nutriment wasted in building up a useless structure' (Darwin, 1872).

The concept of resource allocation is at the core of evolutionary theory (Pianka, 1976; Charnov, 1982; Van Noordwijk & Jong, 1986; Boggs, 1992). It predicts the optimal allocation of resources to particular functions (e.g. growth, reproduction, foraging and defence) along with shifts in resource distribution depending upon varying intrinsic (e.g. age and size) or extrinsic (e.g. environmental and social) conditions

*Corresponding author. E-mail: baezaa@si.edu

(Roff, 1992; Stearns, 1992). Organisms that exhibit ontogenetic shifts in habitat preference and experience differing ecological pressures (e.g. predation) during their lifetime are well-suited for exploring the principles of optimal resource allocation.

Predation is one of the most important sources of mortality that affects prey behaviour (Werner *et al.*, 1983; Lima & Lawrence, 1990), morphology (Pigliucci, 2001; Relyea, 2005), and physiology (Appleton & Palmer, 1988; Stibor, 1992; Leong & Pawlik, 2010). Several empirical studies have provided examples of impressive strategies for coping with predation risk. For example, marine sponges increase the production of chemical deterrents when under a high risk of predation (Leong & Pawlik, 2010). Freshwater crustaceans (*Daphnia hyalina*) are known to speed up sexual maturity in environments with intense predatory cues (Stibor, 1992). Lastly, many species are capable of mimicking the colour characteristics (e.g. cryptic camouflage) of their surrounding habitat in the presence of potential predators (Stuart-Fox & Moussalli, 2009). Each of these strategies includes shifts in resource allocation.

The intensity of predation may also change throughout the life of the organism. A commonly reported pattern for both marine and terrestrial invertebrates is a decrease in predation risk with increasing body size (Herrnkind & Butler, 1986; Persson *et al.*, 1996). In situations where predation risk decreases through ontogeny, individuals are expected to allocate more resources to defensive structures and behaviours when small and to diminish resource allocation to defence with increasing body size. This lifetime shift in resource allocation to defensive strategies is expected to increase survivorship (Pigliucci, 2001; Relyea, 2005), and various studies in marine invertebrate support this principle by reporting ontogenetic changes in body proportions or coloration during ontogeny (Hartnoll, 1965, 1974; Palma & Steneck, 2001; Berke & Woodin, 2008; Baeza & Asorey, 2012). Importantly, most work on the relationship between resource allocation and predation risk has been conducted on short-term inducible defences (Stibor, 1992; Leong & Pawlik, 2010). In turn, although the notion that resource allocation to defensive strategies should be the greatest during early life is widely accepted, it has rarely been explored empirically. Indeed, ontogenetic shifts in morphological traits that diminish predation risk is one of the least explored aspects of predator-induced defences (Relyea, 2005).

Concomitantly with diminished allocation to defence, individuals are expected to increase resources devoted to body structures related to reproduction with increasing body size. Theoretically, body structures relevant for searching, guarding or choosing sexual partners should become positively allometric, and possibly sexually dimorphic, at the onset of sexual maturity (Crawford & De Smidt, 1922; Lipcius *et al.*, 1983). The exaggeration of body parts relevant for reproduction immediately before or at the onset of sexual maturity is considered an adaptation for increasing reproductive output (e.g. in females) or mating success (e.g. in males) allowing individuals to optimize fitness over their lifetime (Dean, 1981; Stearns, 1992).

The Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) is an ideal model for testing size-dependent resource allocation to defensive and reproductive structures (Smith & Herrnkind, 1992; Booth & Phillips, 1994; Herrnkind *et al.*, 1997). A diverse suite of predators has been recognized for this species, including sharks (Smith & Herrnkind, 1992; Mintz *et al.*, 1994), rays (Eggleston *et al.*, 1990; Smith & Herrnkind, 1992), teleost fishes (Mintz *et al.*, 1994; Briones-Fourzán, Pérez-Ortiz & Lozano-Álvarez, 2006), and invertebrates (Smith & Herrnkind, 1992; Mintz *et al.*, 1994; Berger & Butler, 2001). These predators typically target juveniles up to approximately 60 mm carapace length (CL) (Herrnkind & Butler, 1986), although the smallest juveniles (< 35 mm CL) are most vulnerable (Eggleston *et al.*, 1990), clearly indicating a size-dependent predation risk for *P. argus*. To maximize fitness, *P. argus* individuals are expected to invest heavily in features that serve in defence (i.e. coloration, body parts, behaviours) when they are small and decrease this allocation as body size increases and predation rate decreases. Importantly, the main antipredator mechanism of spiny lobsters is probably overall body size because, as body size increases, gape limitation reduces the number of possible predators (Persson *et al.*, 1996; Nilsson & Bronmark, 2000). Experiments have demonstrated that survivorship of small juveniles (5–15 mm CL) increased when tethered apart from one another (Butler, Herrnkind & Hunt, 1997), animals of intermediate body size (30–35 mm CL) experience equal predation when tethered together or alone (Childress & Herrnkind, 2001), although animals > 45 mm CL experience reduced predation when paired with other conspecifics (Eggleston *et al.*, 1990; Eggleston, Lipcius & Miller, 1992; Butler, MacDiarmid & Booth, 1999). This suggests that lobsters should allocate considerable energy to defence at body sizes < 40 mm CL because increases in body size and group living do not translate to survival benefits (i.e. decreased predation) until individuals become larger than approximately 40 mm CL (Zimmer-Faust & Spanier, 1987; Smith & Herrnkind, 1992).

Some defensive mechanisms that could be paramount to the survival of *P. argus* juveniles include the development of body structures for detecting predators (antennules: Zimmer-Faust, Tyre & Case, 1985;

Berger & Butler, 2001), for deterring predators (antennae and spines: Zimmer-Faust *et al.*, 1985; Briones-Fourzán *et al.*, 2006), and for escaping predators (abdomen musculature and tail fan: Nauen & Shadwick, 2001). All these defensive structures should experience negative allometry in lobsters as they decrease in vulnerability with increasing body size. Furthermore, with the reduction in allocation to defence, lobsters are expected to augment allocation to body structures relevant for reproduction with increasing body size. Body structures such as pleopods in females (i.e. that help protecting embryos from abrasion; Crawford & De Smidt, 1922) and the second pereopods in males (i.e. that might help males to grasp females during mating; Lipcius *et al.*, 1983; D. C. Behringer, pers. observ.) should display positive allometric growth in *P. argus*.

In the present study, we test the hypothesis that traits under strong natural selection by predators should be negatively allometric in the spiny lobster *P. argus* because small individuals are at greater risk than large conspecifics. In turn, traits that are under strong sexual selection should be positively allometric at approximately the size of sexual maturity in *P. argus*. To test our predictions, a series of measurements were taken from the Caribbean spiny lobster: (1) to determine relative growth of several defensive and reproductive structures across a broad range of lobster sizes (10–130 mm CL) and (2) to explore the existence of different ontogenetic phases characterized by differing allometric scaling of body parts and shifts in coloration.

MATERIAL AND METHODS

COLLECTION AND MEASUREMENT OF SPECIMENS

Specimens of *P. argus* were collected between July and November 2010 near Long Key, Florida, USA (N24°49′26″; W80°48′48″). Juveniles < 14 mm CL were captured from benthic recruitment collectors deployed within Florida Bay (for habitat description, see Behringer & Butler, 2006). Individuals > 14 mm CL were collected by hand from natural lobster dens (e.g. sponges, small coral heads, and substrate crevices) in hard-bottom habitat or from patch reefs on the ocean side of Long Key. The largest specimens (> 90 mm CL) were retrieved from commercial fishers who captured them in Florida Bay and the ocean side of Long Key. After field collection, lobsters were processed alive on board research vessels, dockside from commercial fishers, or at the Goshen College Marine Laboratory on Long Key.

Male and female lobsters were distinguished by the presence (males) or absence (females) of gonopores on the coxae of the fifth pereopods. Subsequently, the

measurements taken from each lobster were: carapace length (measured dorsally from the midpoint of the eyestalks to the distal carapace margin), abdomen length (AbL) and abdomen width (AbW, measured at the level of the first abdominal segment), antenna width (AW, at the base) and antenna length (AL), external flagellum of the right antennule length (AnnL), third right antennal segment width (A3W) and length (A3L), right eye horn basal width (HW) and horn length (HL), second walking leg (pereopod) total length (2PL) and width (2PW, at the base of the merus), and telson width (TW) and length (TL) (Fig. 1). Only intact antennae were measured. Almost invariably, the length of the right antenna was measured unless it was missing or broken, in which case the length of the left antenna was measured. Specimens < 14 mm CL were measured using a graduated ocular micrometer on a stereomicroscope (precision = 0.025 mm), whereas specimens > 14 mm CL were measured using a SPI 2000 series dial calliper (Swiss Precision Instruments) (precision = 0.1 mm). One of three distinct colour patterns was recorded for each lobster; disruptive, intermediate, and bicolour (see below).

ALLOMETRIC GROWTH AND COLOUR PATTERN IN *P. ARGUS*

We determined whether the morphological structures measured grew proportionally (linearly) with a unit of increase in body size in male and female *P. argus*. All of the dimensions studied were unidimensional; thus, the relationship between body size (CL) and the length or width of each structure of interest was evaluated using the allometric model $y = ax^b$ (Hartnoll, 1978). The slope *b* of the log-log least-squares linear regression represents positive allometric ($b > 1$) or negative allometric ($b < 1$) growth of the structure relative to body size (Hartnoll, 1978). To assess deviations from linearity, a *t*-test was used to determine whether the observed slope *b* deviated significantly from the expected slope of unity ($b = 1$).

Visual examination of the relationship between body size to second pereopod width, antennule length, and antenna length in the two sexes suggested ontogenetic shifts in growth rate (two differing growth rates), which has been demonstrated in several crustaceans (Hartnoll, 1965). To confirm that these shifts were occurring in only these anatomical features, a modified analysis similar to that described by Sampedro *et al.* (1999) and Baeza & Asorey (2012) was performed using SAS software (SAS Institute). First, a principal components analysis (PCA; using PROC PRINCOMP) between variable pairs was conducted to determine the number of ontogenetic phases. Subsequently, a clustering analysis (*K*-means;
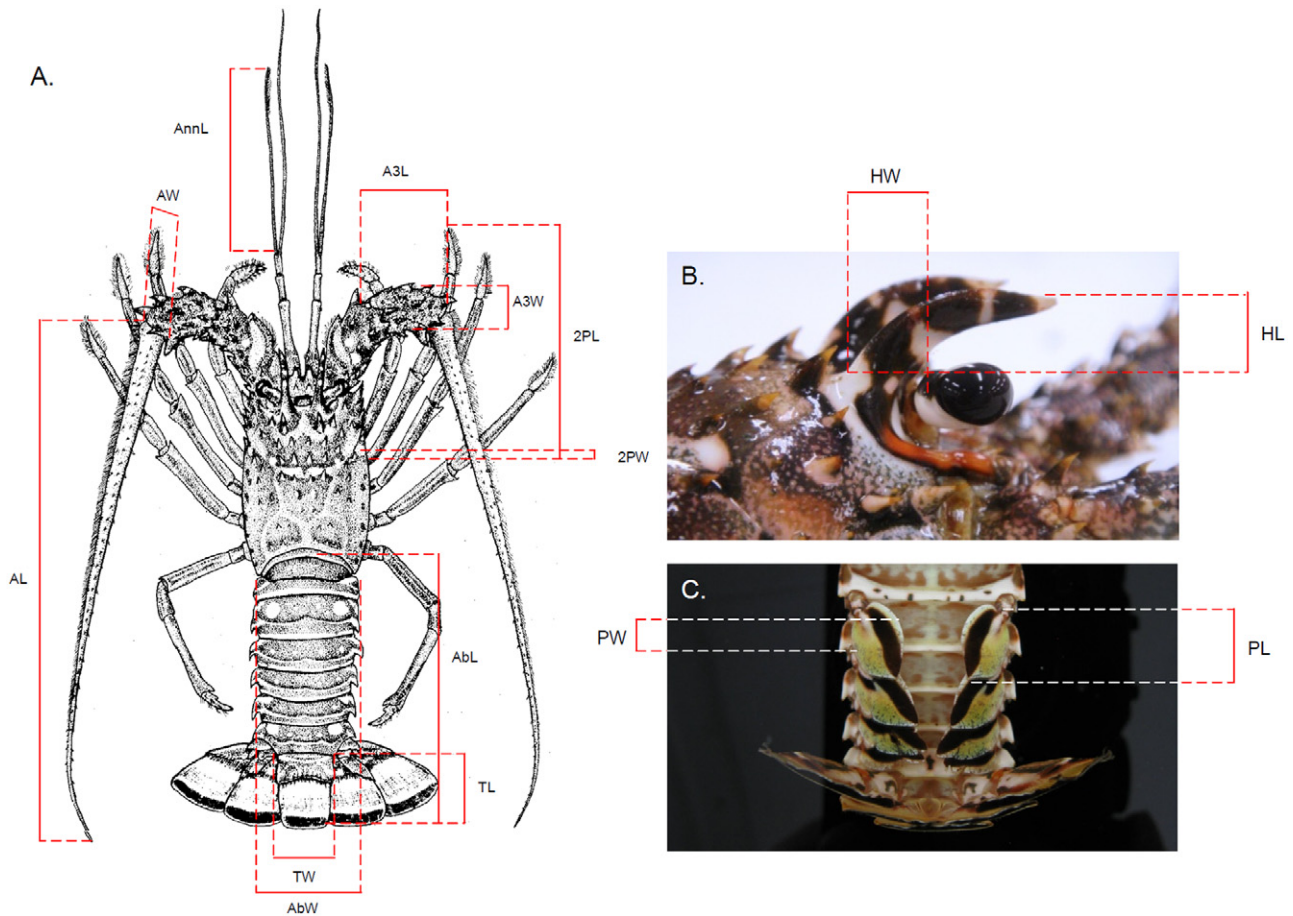
Figure 1. Measurements used during the experiment. A, dorsal view of measurements: antenna width (AW), antenna length (AL), antenna third segment length (A3L), antenna third segment width (A3W), antennule length (AnnL), telson width (TW), telson length (TL), abdominal width (AbW), abdominal length (AbL), second pereopod length (2PL), and second pereopod width (2PW). B, lateral view of the horn length (HL) and horn width (HW) measurements. C, ventral view of pleopod width (PW) and pleopod length (PL) measurements.

using PROC FASTCLUS) was performed to assign growth phases to the different groups predetermined by the PCA. For this analysis, the maximum number of clusters was set at 2 based on the results of the PCA ($N_{clusters} = 2$). Finally, a bivariate linear discriminant analysis (using PROC DISCRIM) was conducted to cross-validate our results. This analysis permitted us to classify each lobster into a discrete ontogenetic phase previously identified by the PCA and clustering analyses, with CL treated as the independent variable.

If the above analyses indicated strong ontogenetic shifts in resource allocation, denoted by discontinuities (transitional point) between differing slopes, then this discontinuity was calculated using the protocol developed by Lovett & Felder (1989). In brief, the data were visually divided into two subsets by their differing slopes, with the hypothesized transitional point bisecting the subsets. Two separate regressions

(using PROC REG) were used for each subset (with CL always the independent variable) repetitively, with the transitional point shifting by 0.5 mm CL between each run of the two regressions. The transitional point was defined as the resulting lowest combined sum of square residuals (SSR) of the two subset regressions. This transitional point was the midpoint of the size range over which resource allocation shifts with ontogenetic phase (Lovett & Felder, 1989). Second pereopod width, antennule length, and antenna length in males and females were analysed in this fashion because they appeared to have a distinct transition point between two growth rates (see results).

Lastly, we observed three distinct colour patterns (see above) that appeared to shift with ontogeny and estimated the size at which the colour pattern changed using a logistic regression analysis in SYSTAT (2002). The shift from one ontogenetic

© 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, **108**, 87–98

pigmentation phase to another was defined as the size (CL) at which the probability of an individual exhibiting a bicolour pattern was 0.5 (Wilson & Hardy, 2002).

RESULTS

A total of 74 males and 77 females were used for the analysis of allometric growth. A positive correlation between body size (CL) and the length and width of numerous structures was detected in the two sexes (Table 1). These structures differed in the extent of allometry, with a few exceptions. In both sexes, telson width and length, antenna width, third antennal segment width and length, post-orbital horn width and length, and abdomen width and length all experienced negative allometric growth; the slope of the relationship between CL and each of these structures was significantly < 1 ($P < 0.0001$ in all cases) (Fig. 2A, B, C, D, E, F, Table 1). One anatomical feature that differed in allometric status between males and females was the first pleopod, both in terms of length and width. In males, pleopod length was isometric ($b = 1.03$, $P = 0.0627$) (Fig. 2F) and width was negatively allometric ($b = 0.93$, $P < 0.0001$) (Fig. 2E). By contrast, pleopod length ($b = 1.20$, $P < 0.0001$)

(Fig. 2F) and width ($b = 1.09$, $P < 0.0001$) (Fig. 2E) were positively allometric in females. The length of the second pereopod was the only anatomical feature to be positively allometric in both males ($b = 1.12$, $P < 0.0001$) and females ($b = 1.06$, $P < 0.0001$) (Table 1).

Both males and females displayed a constant growth rate relationship with CL in all the above measurements. By contrast, PCA and clustering analyses demonstrated the existence of a relationship between CL and second pereopod width, antennule length, and antenna length in the two sexes that included two growth phases separated by a small transitional CL range (Figs 3, 4). For the second pereopod width, the transitional point between ontogenetic phases occurred at 27.80 mm CL in males (Fig. 3C) and 25.5 mm CL in females (Fig. 4C). During the first ontogenetic phase, all lobsters exhibited negative allometric growth of the second pereopod width (both sexes: $P < 0.0001$). However, growth became isometric during the second growth phase (both sexes: $P < 0.05$). During the first ontogenetic phase, lobsters of the two sexes exhibited positive allometric growth of antennule length (females $b = 1.45$, $P < 0.0001$: males $b = 1.43$, $P < 0.0001$), although the same structure was negatively allometric during the

Table 1. Relative growth of selected structures in male and female *Panulirus argus*

	Males				Females		
	r^2	b (SE$_s$)	P		r^2	b (SE$_s$)	P
Negative allometry							
Antennae width	0.985	0.77 (0.011)	**< 0.0001**	Antennae width	0.980	0.77 (0.013)	**< 0.0001**
Third segment length	0.991	0.83 (0.010)	**< 0.0001**	Third segment length	0.990	0.82 (0.009)	**< 0.0001**
Third segment width	0.994	0.77 (0.007)	**< 0.0001**	Third segment width	0.991	0.78 (0.009)	**< 0.0001**
Horn length	0.981	0.90 (0.015)	**< 0.0001**	Horn length	0.973	0.90 (0.017)	**< 0.0001**
Horn width	0.973	0.78 (0.017)	**< 0.0001**	Horn width	0.974	0.79 (0.015)	**< 0.0001**
Telson width	0.958	0.92 (0.023)	**0.0004**	Telson width	0.997	0.92 (0.006)	**< 0.0001**
Telson length	0.992	0.82 (0.009)	**0.0004**	Telson length	0.992	0.88 (0.009)	**< 0.0001**
Abdomen width	0.995	0.95 (0.008)	**< 0.0001**	Abdomen width	0.995	0.94 (0.007)	**< 0.0001**
Abdomen length	0.995	0.97 (0.008)	**0.0001**	Abdomen length	0.995	0.95 (0.008)	**< 0.0001**
Pleopod width	0.981	0.93 (0.016)	**< 0.0001**				
Isometry							
Pleopod length	0.984	1.03 (0.015)	0.0627	–	–	–	–
Positive allometry							
Second pereopod length	0.993	1.12 (0.012)	**< 0.0001**	Pleopod width	0.983	1.09 (0.017)	**< 0.0001**
				Pleopod length	0.990	1.20 (0.014)	**< 0.0001**
				Second pereopod length	0.993	1.06 (0.010)	**< 0.0001**

The regression equations for each structure dimension versus CL (using $\log_{10} - \log_{10}$ transformed data) and associated coefficients of determination (r^2), slope (b) along with standard error of the slopes (SE$_s$), allometric status, and P-values used to test for significant departures from isometry are shown. Significant P-values are shown in bold.
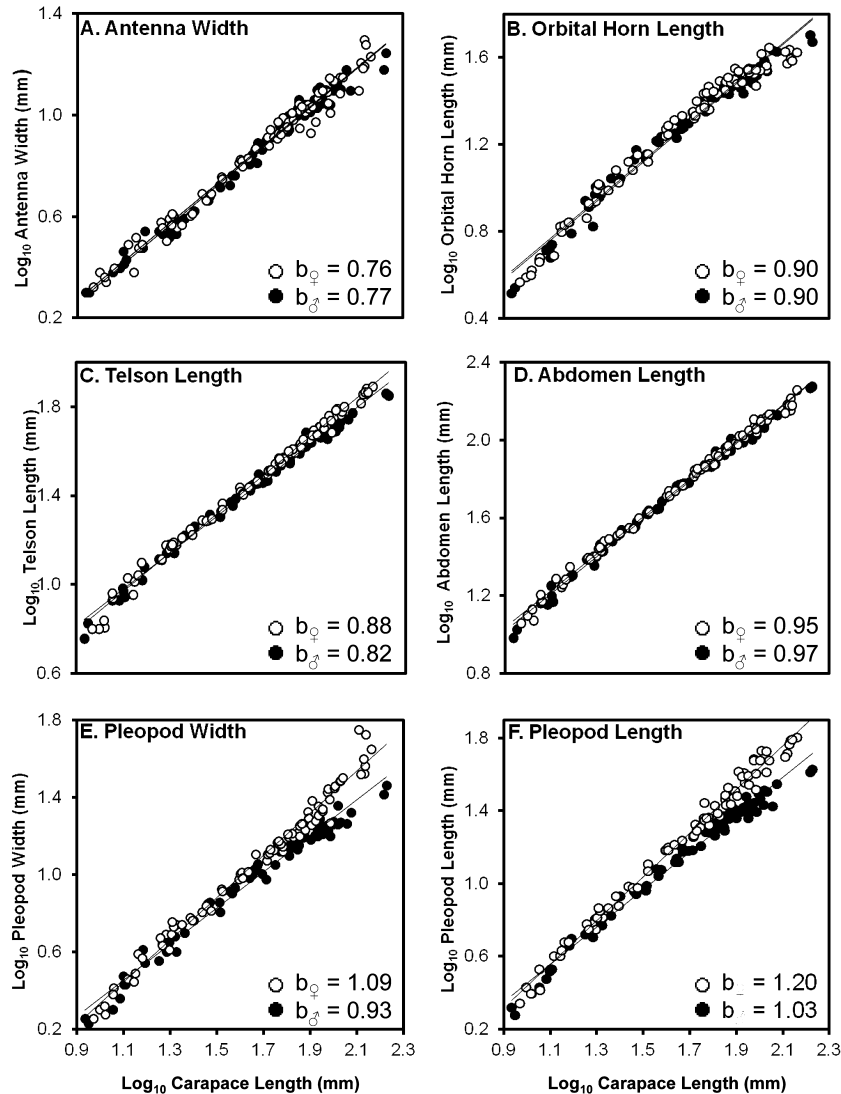
Figure 2. Allometric growth of different morphological traits featuring a single ontogenetic growth phase in both sexes of the spiny lobster *Panulirus argus*. The different graphs show the $\log_{10}$ of the antenna width (A), orbital horn length (B), telson length (C), abdomen length (D), pleopod width (E), and pleopod length (F) as a function of the $\log_{10}$ of the carapace length. Black (•) and white (○) circles denote males and females along with their corresponding slope (*b*).

second ontogenetic stage both in males and females ($b_{females} = 0.68$, $P < 0.0001$: $b_{males} = 0.86$, $P < 0.0001$). Total SSR was minimized for antennule length when the transitional point was 27.80 mm CL in males (Fig. 3B) and 35.30 mm CL in females (Fig. 4B). Total SSR was minimized for antenna length when the transitional point was 26.85 mm CL in females and 63.95 mm CL in males. In males, antenna length before the transitional point displayed negative allometric growth ($b = 0.96$, $P < 0.0001$), after which no correlation between CL and antenna length existed ($b = 0.13$, $P = 0.1608$) (Fig. 3A). In turn, female antenna length before the transitional point displayed positive allometric growth ($b = 1.35$, $P < 0.0001$), after

which growth was negatively allometric ($b = 0.61$, $P < 0.0001$) (Fig. 4A).

Three different colour patterns were observed in lobsters of both sexes (Fig. 5). Small lobsters (7.6–17.4 mm CL) displayed a combination of an apparent disruptive coloration and camouflage characterized by alternating white and red–brown bands on the pereopods along with a pale yellow medial band running dorsally down the length of the body, which was otherwise dark brown or green in coloration (Fig. 5). Lobsters as small as 17.2 mm CL (but often larger than 24.2 mm CL) displayed a second 'bicolour' pattern typically observed in large juveniles and adults, characterized by alternating longitudinal
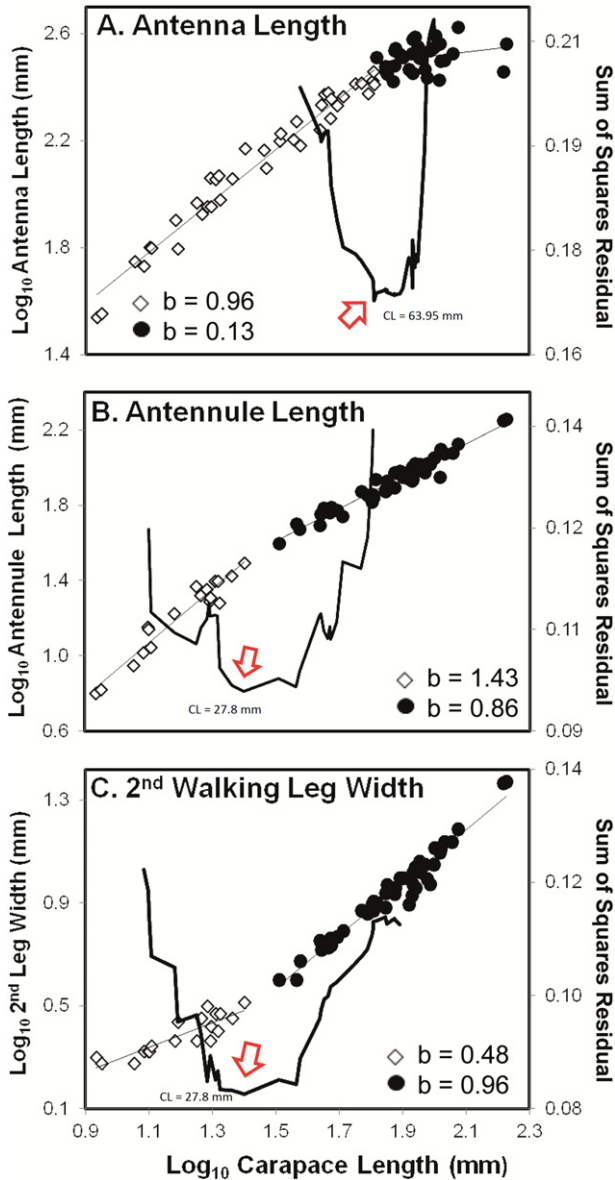
Figure 3. Allometric growth plots for three morphological structures in male *Panulirus argus*. Log$_{10}$ antenna length (A), antennule length (B), and second walking leg width (C) as a function of log$_{10}$ of the carapace length are shown. First growth phase (◇) and second growth phase (●) along with their corresponding slope (*b*) are shown. The bold line is the combined sum of squared residuals of the regressions depicting the two separate data point clusters. The red arrow indicates the lowest combined sum of square of residuals; the inflection point separating the two different growth phases (corresponding CL noted).

stripes of yellow and turquoise on the pereopods, a red or rust coloured carapace and abdomen that blended with white or pale yellow on the lateral surfaces, and also featuring distinctive and well

defined dorsal whitish spots on the abdomen (Fig. 5). The third 'intermediate' colour pattern, observed in lobsters 10.4–24.2 mm CL, represented a blend of the coloration typically observed in the smallest lobsters and the 'bicolour' pattern typical of the large lobsters. The magnitude of blending between the two colour patterns was typically size-dependent (Fig. 5). These are general patterns with natural variability in the precise colours. Logistic regressions indicated that the CL at which 50% of lobsters shifted from the first colour pattern (disruptive) to the 'bicolour' pattern was 22.86 mm for males (95% confidence interval = 18.43–27.39 mm CL) and 22.33 mm for females (95% confidence interval = 17.24–27.19 mm CL) (Fig. 5).

DISCUSSION

The present study demonstrates that several defensive structures in *P. argus* experience negative allometric growth, which agrees with the theoretical considerations and predictions (Roff, 1992; Stearns, 1992) suggesting that, at their smallest and most vulnerable stage, lobsters should devote resources disproportionately to structures that improve their defensive capabilities. In turn, with increasing body size and a diminishing suite of potential predators, fewer resources are allocated to the development of defensive structures. Concomitant with a decreased allocation to defensive structures, lobsters appear to allocate additional resources to traits relevant for reproduction (e.g. pleopod width and length in females, second pereopod length in males) with increasing body size. Our results support predictions central to resource allocation and life-history theory indicating that ontogenetic shifts in resource allocation (i.e. to defensive and reproductive structures) represent an adaptation in organisms inhabiting environments in which conditions (e.g. predation risk) change during lifetime.

Although the majority of traits examined in the present study (12 of 15) displayed a single growth phase through ontogeny, other structures (e.g. antennules and antenna) experienced substantial shifts in relative growth. These shifts occurred over a narrow body size range indicating the existence of more than a single ontogenetic phase in *P. argus*. Shifts in resource allocation during ontogeny are well-documented around the onset of sexual maturity in other crustaceans (Hartnoll, 1965, 1974; Baeza & Asorey, 2012), such as in various spider crabs (family Majidae) for which morphometric analyses of secondary sexual characteristics have identified two or three ontogenetic stages (Hartnoll, 1965, 1974; Finney & Abele, 1981; Berke & Woodin, 2008). In these species, males display a greater positive allometric growth of
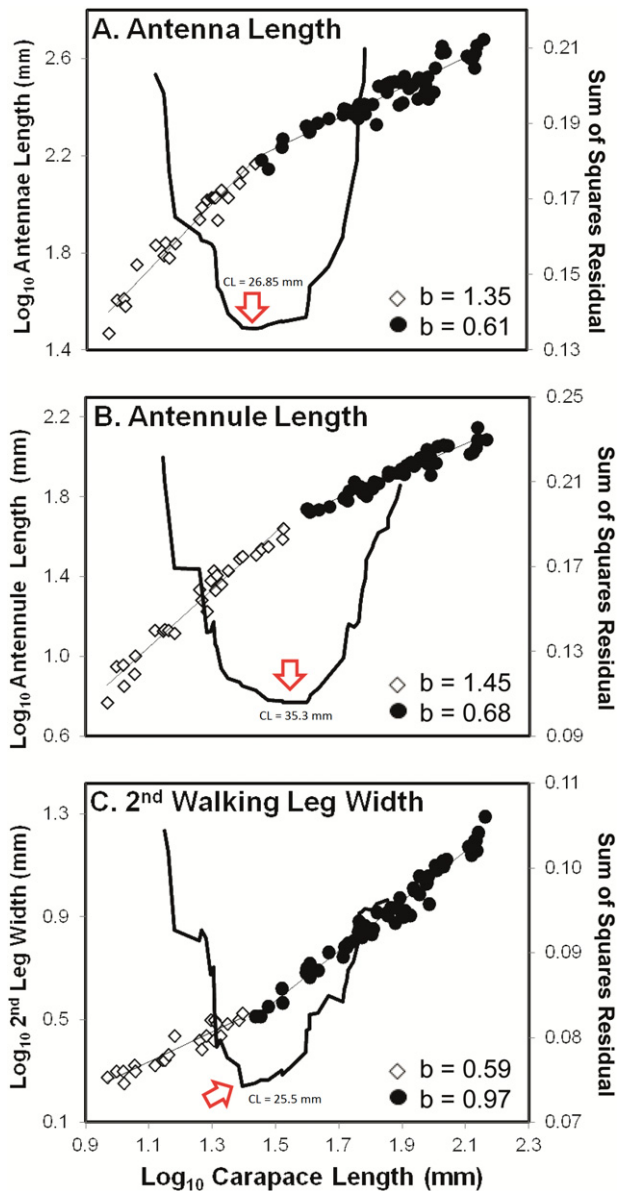
Figure 4. Allometric growth plots for three morphological structures in female *Panulirus argus*. Log$_{10}$ antenna length (A), antennule length (B), and second walking leg width (C) as a function of log$_{10}$ of the carapace length are shown. First growth phase (◊) and second growth phase (●) along with their corresponding slope (*b*) are shown. The bold line is the combined sum of squared residual of the two regressions depicting the two separate data point clusters, with the red arrow indicating the lowest combined residual sum of squares; the inflection point separating the two different growth phases (corresponding CL noted).

their chelipeds (claws) relative to body size after the pubertal moult compared to before the pubertal molt (Hartnoll, 1974; Finney & Abele, 1981). Similarly, in the male squat lobster *Munida rugosa*, allometric

growth of the chelipeds is greater after the pubertal moult, whereas females experience an increase in the relative growth of the abdomen after the pubertal moult (Claverie & Smith, 2009).

However, the body size at which *P. argus* shifts from one ontogenetic stage to another did not correlate with the onset of maturity, estimated at 76.2 mm CL in the Florida Keys (Crawford & De Smidt, 1922). Our results indicated ontogenetic shifts in the growth rate at 35.30 mm CL in females and 27.80 mm CL in males for antennules; 26.85 mm CL in females and 63.95 mm CL in males for antenna length; and at 25.5 mm CL in females and 27.80 mm CL in males for the second pereopod width. Unlike maturity estimates, most of these transitional points correlate more closely with a shift from the asocial algae-dwelling stage to a gregarious crevice-dwelling stage in *P. argus*, previously reported at 17–25 mm CL (Marx & Herrnkind, 1985; Childress & Herrnkind, 1996). Thus, although the emergence of the juveniles from algae occurs at approximately 17–25 mm CL, the actual benefits of increased body size and sociality are not realized until > 45 mm CL (Eggleston *et al.*, 1990, 1992). This shift in ontogenetic phase at small body size agrees with the notion that lobster should allocate considerable resources to defensive structures during this early vulnerable life period in which defensive structures are crucial for survival. In turn, when the body size of lobsters approaches 45 mm CL, larger defensive structures (e.g. antenna) may be unnecessary as predation risk decreases. At this point, allocation of resources to defence diminishes and lobsters invest more in reproductive traits to prepare for sexual maturity.

In addition to changes in body structures, the coloration of *P. argus* also varied through ontogeny. Ontogenetic shifts in camouflage/crypsis have been reported for a few other marine crustaceans (Palma & Steneck, 2001; Berke & Woodin, 2008; Hultgren & Stachowicz, 2009). Small lobsters exhibited a rusty-red colour pattern with a light dorsal medial band spanning the length of the carapace and abdomen making them more difficult to distinguish from red algae (*Laurencia* spp.), comprising their preferred nursery habitat (Marx & Herrnkind, 1985; Behringer *et al.*, 2009). Medial bands (or spots) similar to those observed on small algal-dwelling *P. argus* visually obscure the body form of other marine invertebrates (e.g. breaking down their bilateral symmetry), decreasing the likelihood of visual detection by potential predators (Merilaita, 1998; Cuthill *et al.*, 2005). By contrast, lobsters larger than 24.2 mm CL invariably displayed the typical bicolour pattern known for larger *P. argus* (Crawford & De Smidt, 1922; Humann & DeLoach, 2002). This shift in coloration also corresponds well to the size (17–25 mm CL) at which early
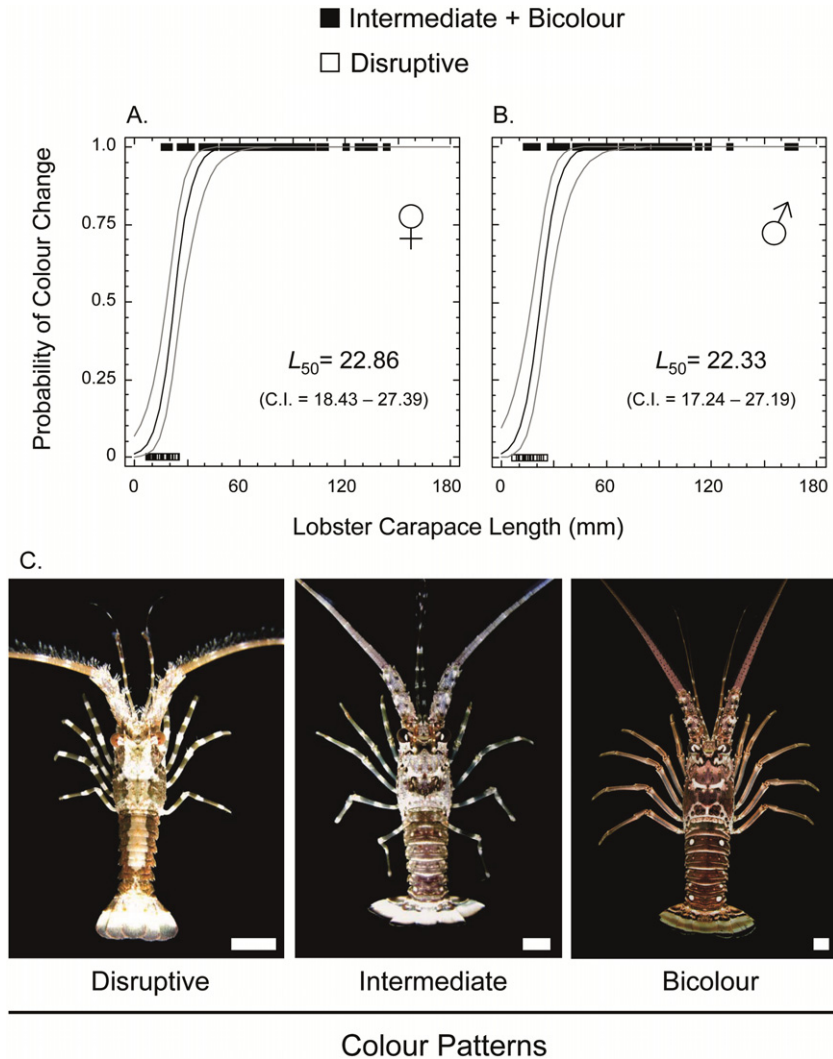
Figure 5. The relationship between carapace length and the probability of change from the disruptive coloration phase (■) to the bicolour phase (□) in females (A) and males (B) of *Panulirus argus*. White squares (□) denote the disruptive colour pattern and black squares (■) denote the intermediate and 'bicolour' colour pattern. C, the three different colour pattern observed in *P. argus*. From left to right: disruptive, intermediate, and 'bicolour' colour patterns. Scale bars = 10 mm.

benthic juvenile lobsters emerge from their nursery habitat (Marx & Herrnkind, 1985; Childress & Herrnkind, 1996). Our results suggests that disruptive coloration no longer results in benefits to lobsters after they reach 17–28 mm CL, emerge from their algae microhabitat, and begin to use crevice dwellings. Similarly, Smith & Herrnkind (1992) found that relative predation considerably decreased with size for the smallest lobsters (5–16 mm CL) but was relatively constant and unrelated to size for transitional lobsters (17–35 mm CL). Nonetheless, whether or not this coloration observed in small lobsters truly decreases predator detection during the algal stage remains to be tested experimentally.

Although many body structures that appear to function in defence experienced negative allometric growth, those relevant to reproduction exhibited positive allometry, which is also in agreement with theoretical considerations (Crawford & De Smidt, 1922; Lipcius *et al*., 1983). Specifically, the width of the pleopods in females and length of the second pereopods in males increased proportionally more with increasing body size. The positive allometric growth of the pleopods presumably facilitates larger clutch sizes in females (Crawford & De Smidt, 1922) and the greater positive growth of the pereopods in males ($b = 1.12$) compared to females ($b = 1.06$) might improve reproductive competitive ability by giving

them larger, stouter legs to grasp reproductive partners (Lipcius *et al*., 1983). Positive allometric growth of both structures is probably only essential after puberty but, to be advantageous at maturity, their size must increase before the onset of sexual maturity. Other studies have shown that, to maximize fitness, a greater proportion of resources are allocated to reproductive features upon or before the animal attaining maturity to achieve the highest possible reproductive output (Snell & King, 1977; Dean, 1981; Stearns, 1992).

Although the present study aimed to test resource allocation theory as an explanation for the differences in the growth patterns of defensive and reproductive structures in the Caribbean spiny lobster, we recognize that there could be other potential explanations for the observed shifts in resource allocation that remain unaddressed. For example, habitat characteristics or restrictions could have a role in driving these allometric growth patterns. The ability to move through the structurally complex red algae might select for a certain body form that might include a streamlined abdomen in algal-dwelling lobsters. Also, the allometric growth of the antenna length was not negative, in disagreement with theoretical expectations. This structure that serves for deterring predators (Zimmer-Faust *et al*., 1985; Briones-Fourzán *et al*., 2006) exhibited positive allometric growth during the first ontogenetic phase. This unexpected increase in allocation to this defensive structure during the ontogeny of *P. argus* is not well understood and should be addressed experimentally. Although alternative explanations for our observations are possible and more experimental work could be carried out, these findings offer a strong explanation for the relative growth patterns observed in *P. argus*.

Panulirus argus has a life history that exposes individuals to a changing suite of habitats, predators, and reproductive challenges. Thus, it is not unexpected that they experience marked shifts in resource allocation through ontogeny. This size-dependent resource allocation should maximize early survival and supports the notion that individuals allocate resources differentially during ontogeny so to optimize lifetime fitness. Trade-offs in resource distribution among sexually-selected (e.g. reproductive) and naturally-selected (e.g. defensive) traits might very well play a pivotal role in the complex life history of *P. argus*, and many other marine invertebrates.

ACKNOWLEDGEMENTS

REFERENCES

Appleton RD, Palmer AR. 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistance shells in marine gastropods. *Proceedings of the National Academy of Science of the United States of America* **85:** 4387–4391.

Baeza JA, Asorey CM. 2012. Testing the role of male-male competition in the evolution of sexual dimorphism: a comparison between two species of porcelain crabs. *Biological Journal of the Linnean Society* **105:** 548–558.

Behringer DC, Butler MJ IV. 2006. Stable isotope analysis of production and trophic relationships in a tropical marine hard-bottom community. *Oecologia* **148:** 334–341.

Behringer DC, Butler MJ IV, Herrnkind WF, Hunt JH, Acosta CA, Sharp WC. 2009. Is seagrass an important nursery habitat for the Caribbean spiny lobster, *Panulirus argus*, in Florida? *New Zealand Journal of Marine and Freshwater Research* **43:** 327–337.

Berger DK, Butler MJ IV. 2001. Octopuses influence den selection by the juvenile Caribbean spiny lobster. *Marine and Freshwater Research* **52:** 1049–1053.

Berke SK, Woodin SA. 2008. Energetic costs, ontogenetic shifts and sexual dimorphism in spider crab decoration. *Functional Ecology* **22:** 1125–1133.

Boggs CL. 1992. Resource allocation: exploring connections between foraging and life history. *Functional Ecology* **6:** 508–518.

Booth JD, Phillips BF. 1994. Early life history of spiny lobster. *Crustaceana* **66:** 271–294.

Briones-Fourzán P, Pérez-Ortiz M, Lozano-Álvarez E. 2006. Defense mechanisms and antipredator behavior in two sympatric species of spiny lobsters, *Panulirus argus* and *P. guttatus*. *Marine Biology* **149:** 227–239.

Butler MJ IV, Herrnkind WF, Hunt JH. 1997. Factors affecting the recruitment of juvenile Caribbean spiny lobsters dwelling in macroalgae. *Bulletin of Marine Sciences* **61:** 3–19.

Butler MJ IV, MacDiarmid AB, Booth JD. 1999. Ontogenetic changes in social aggregation and its adaptive value for spiny lobsters in New Zealand. *Marine Ecology Progress Series* **188:** 179–191.

Charnov E. 1982. *The theory of sex allocation*. Princeton, NJ: Princeton University Press.

Childress MJ, Herrnkind WF. 1996. The ontogeny of social behaviour among juvenile Caribbean spiny lobsters. *Animal Behavior* **51:** 675–687.

Childress MJ, Herrnkind WF. 2001. The guide effect influence on the gregariousness of juvenile Caribbean spiny lobsters. *Animal Behaviour* **62:** 465–472.

Claverie T, Smith PI. 2009. Morphological maturity and allometric growth in the squat lobster *Munida rugosa*. *Journal of the Marine Biological Association of the United Kingdom* **89:** 1189–1194.

Crawford DR, De Smidt WJJ. 1922. The spiny lobster, *Panulirus argus*, of southern Florida: its natural history and utilization. *Bulletin of Bureau Fisheries* **38:** 281–310.

Cuthill IC, Stevens M, Sheppard J, Maddocks T, Párraga A, Troscianko TS. 2005. Disruptive coloration and background pattern matching. *Nature* **434:** 72–74.

Darwin C. 1872. *The descent of man and selection in relation to sex*. New York, NY: D. Appleton & Co.

Dean J. 1981. The relationship between lifespan and reproduction in the grasshopper *Melanoplus*. *Oecologia* **48:** 365–368.

Eggleston DB, Lipcius RN, Miller DL. 1992. Artificial shelters and survival of juvenile Caribbean spiny lobster *Panulirus argus*: spatial, habitat, and lobster size effects. *Fishery Bulletin* **90:** 691–702.

Eggleston DB, Lipcius RN, Miller DL, Coba-Cetina L. 1990. Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. *Marine Ecology Progress Series* **62:** 79–88.

Finney WC, Abele LG. 1981. Allometric variation and sexual maturity in the obligate coral commensal, *Trapezia ferruginea* Latreille (Decapoda, Xanthidae). *Crustaceana* **41:** 113–130.

Hartnoll RG. 1965. The biology of spider crabs: a comparison of British and Jamaican species. *Crustaceana* **9:** 1–16.

Hartnoll RG. 1974. Variation in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). *Crustaceana* **27:** 131–136.

Hartnoll RG. 1978. Determination of relative growth in Crustacea. *Crustaceana* **34:** 281–293.

Herrnkind WF, Butler MJ IV. 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. *Marine Ecology Progress Series* **34:** 23–30.

Herrnkind WF, Butler MJ IV, Hunt JH, Childress M. 1997. Role of physical refugia: implications from a mass sponge die-off in a lobster nursery in Florida. *Marine and Freshwater Research* **48:** 759–769.

Hultgren KM, Stachowicz JJ. 2009. Evolution of decoration in Majoid crabs: a comparative phylogenetic analysis of the role of body size and alternative defensive strategies. *American Naturalist* **173:** 566–578.

Humann P, DeLoach N. 2002. *Reef creature identification; Florida, Caribbean, Bahamas*. Jacksonville, FL: New World Publications.

Leong W, Pawlik JP. 2010. Evidence of a resource trade-off between growth and chemical defenses among Caribbean coral reef sponges. *Marine Ecology Progress Series* **406:** 71–78.

Lima SL, Lawrence MD. 1990. Behavioral decision made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68:** 619–640.

Lipcius RN, Edwards ML, Herrnkind WF, Waterman SA. 1983. In situ mating behavior of the spiny lobster *Panulirus argus*. *Journal of Crustacean Biology* **3:** 217–222.

Lovett DL, Felder ME. 1989. Application of regression techniques to studies of relative growth in crustaceans. *Journal of Crustacean Biology* **9:** 529–539.

Marx JM, Herrnkind WF. 1985. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. *Bulletin of Marine Sciences* **36:** 423–431.

Merilaita S. 1998. Crypsis through disruptive coloration in an isopod. *Proceedings of the Royal Society of London Series B, Biological Sciences* **265:** 1059–1064.

Mintz JD, Lipcius RN, Eggleston DB, Seebo MS. 1994. Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location and conspecifics abundance. *Marine Ecology Progress Series* **112:** 255–266.

Nauen JC, Shadwick RE. 2001. The dynamics and scaling of force production during the tail-flip escape response of the California spiny lobster *Panulirus interruptus*. *Journal of Experimental Biology* **204:** 1817–1830.

Nilsson PA, Bronmark C. 2000. Prey vulnerability to a gape-size limited predator: behavioral and morphological impacts on northern pike piscivory. *Oikos* **88:** 539–546.

Palma AT, Steneck RS. 2001. Does variable coloration in juvenile marine crabs reduce risk of visual predation? *Ecology* **82:** 2961–2967.

Persson L, Andersson J, Wahlström E, Eklöv P. 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology* **77:** 900–911.

Pianka ER. 1976. Natural selection of optimal reproductive tactics. *American Zoologist* **15:** 775–784.

Pigliucci M. 2001. *Phenotypic plasticity: beyond nature and nurture*. Baltimore, MD: Johns Hopkins University Press.

Relyea RA. 2005. Constraints on inducible defences. Phylogeny, ontogeny, and phenotypic trade-offs. In: Barbosa P, Castellanos I, eds. *Ecology of predator–prey interactions*. Oxford: Oxford University Press.

Roff D. 1992. *The evolution of life histories: theory and analysis*. New York, NY: Chapman & Hall Printing.

Sampedro MP, Gonzáles-Gurriarán E, Freire J, Muino R. 1999. Morphometry and sexual maturity in the spider crab *Maja squinado* (Decapoda: Majidae) in Galicia, Spain. *Journal of Crustacean Biology* **19:** 578–592.

Smith KN, Herrnkind WF. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. *Journal of Experimental Marine Biology and Ecology* **157:** 3–18.

Snell TW, King CE. 1977. Lifespan and fecundity patterns in rotifers: the cost of reproduction. *Evolution* **31:** 882–890.

Stearns SC. 1992. *The evolution of life histories*. Oxford: Oxford University Press.

Stibor H. 1992. Predator induced life-history shifts in a freshwater cladoceran. *Oecologia* **92:** 162–165.

Stuart-Fox D, Moussalli A. 2009. Camouflage, communication and thermoregulation: lessons from colour changing organisms. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **364:** 463–470.

Van Noordwijk AJ, Jong G. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist* **128:** 137–142.

Werner EE, Gilliam JF, Hal DJ, Mittelbach GG. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* **64:** 1540–1548.

Wilson K, Hardy ICW. 2002. *Sex ratio concepts and research methods*. Cambridge: Cambridge University Press.

Zimmer-Faust RK, Spanier E. 1987. Gregariousness and sociality in spiny lobsters: implications for den habitation. *Journal of Experimental Marine Biology and Ecology* **105:** 57–71.

Zimmer-Faust RK, Tyre JE, Case JF. 1985. Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. *Biological Bulletin* **169:** 106–118.