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Adaptive specialization and constraint in morphological defences of planktonic larvae

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Abstract

1. Morphological defences of plankton can include armour, spines and coloration. Spines defend from gape-limited fish predators, while pigmentation increases visibility to fishes but defends from ultraviolet radiation (UVR).
2. Planktonic crab larvae (zoeae) exhibit inter- and intraspecific variability in the lengths of defensive spines, extent of pigmentation and body size. The determinants of this variability and the relationships among these traits are largely unknown.
3. Larvae may employ generalized defences against the dual threats of UVR and predation or specialized defences against their primary threat, with an unknown role of allometric or phylogenetic constraints. Generalization would result in longer spines compensating for the increased predation risk imposed by darker pigments, while specialization would lead to more investment in either defence from predation (long spines) or UVR (dark pigments), at the expense of the other trait.
4. We examined (a) the relationship between spine lengths and pigmentation, (b) the scaling of spine lengths with body size, and (c) phylogenetic constraint in spine lengths, pigmentation, and body size, among and within 21 species of laboratory-hatched and 23 species of field-collected crab larvae from Panama and California.
5. We found a negative relationship between spine length and pigmentation among species from laboratory and field. Within species, we found a marginally significant negative relationship among field-collected larvae.
6. Spine lengths showed positive allometric scaling with carapace length, while spine and carapace lengths, but not pigmentation, had significant phylogenetic signals.
7. The negative relationship we observed between pigmentation and spine length supports our defence specialization hypothesis.
8. Positive allometric scaling of spine lengths means larger larvae are better defended from predators, which may indicate that larvae face greater predation risk as they grow larger.
9. Phylogenetic constraint may have arisen because related species encounter similar predation threats. Conversely, phylogenetic constraint in the evolution of spine lengths may induce convergent behaviours resulting in related species facing similar predation threats.

10. Our results improve understanding of the evolution of the larval morphology of crabs, morphological defences in the plankton and evolutionary responses of morphology to multiple spatially segregated selective forces.

KEYWORDS

allometry, coloration, comparative phylogenetics, crab, marine, predation, ultraviolet radiation, zoea

1 | INTRODUCTION

Morphological defences can take a number of forms. Common examples include the hard armour plating of armadillos (Superina & Loughry, 2012), crustacean carapaces (Fryer, 1968), sharp porcupine quills (Quick, 1953) and *Daphnia* (water flea) spines (Dodson, 1984). In addition, pigmentation may camouflage from predators (Merilaita, Scott-Samuel, & Cuthill, 2017) or defend from ultraviolet radiation (Bandaranayake, 2006). These features are common in terrestrial, aquatic and marine habitats, although the optimal defence may vary with habitat type. For example, while terrestrial camouflage often involves some form of pigmentation to match backgrounds or confuse predators, the best camouflage in aquatic and marine habitats is often transparency or the lack of pigmentation (Johnsen, 2001; McFall-Ngai, 1990; Stevens & Merilaita, 2009).

Morphological defences often have costs. Armadillos carrying a heavy carapace move (and thus feed) slowly and must spend most of their active time feeding (Superina & Loughry, 2012). Spines grown by *Daphnia* in the presence of predators slow growth in the rest of the body and delay reproductive maturity (Riessen & Sprules, 1990). Transparent camouflage in marine and aquatic plankton increases mortality from ultraviolet radiation (Bashevkin, Christy, & Morgan, 2019b; Hairston, 1976; Morgan & Christy, 1996).

Morphological defences vary considerably both within and among species. Some of this variation may be related to the environment. *Daphnia* grow long spines in the presence of predator cues (Krueger & Dodson, 1981) and copepods maintain transparency in lakes with low UVR and high fish predation risk but increase pigmentation when conditions are reversed (Hairston, 1976; Hansson, Hylander, & Sommaruga, 2007; Hylander, Souza, Balseiro, Modenutti, & Hansson, 2012). Morphological variation can also be driven by differences in genetics, maternal investment or other factors resulting in a range of morphologies in a common environment (Monteiro et al., 2000). Variation in offspring size within broods, among broods and among species would influence the size and thereby efficacy of morphological defences such as spines. The effect of this size variation would strongly depend on the nature of the scaling of the defensive feature with body size. Positive allometry would confer disproportionately greater predator defence with larger body size while negative allometry, as is found in *Daphnia* (Lampert & Wolf, 1986; Smakulska & Górnjak, 2004), would confer disproportionately greater predator defence to smaller body sizes. Furthermore, the optimal spine length would depend on the size distribution of gape-limited predators.

Like *Daphnia*, larval crabs have defensive spines that deter gape-limited predators such as fishes (Morgan, 1987, 1989, 1990). Larval crabs are also pigmented to reduce UVR damage but these pigments may increase susceptibility to visual predators, such as fishes (Bashevkin et al., 2019b; Morgan & Christy, 1996; Bashevkin, Christy, & Morgan, in review). Both pigmentation and spine length show considerable variation among species of crabs, as well as some variation within species. Some variability in spine length may be related to the level of predation risk in larval habitats (Morgan, 1990), but we do not yet know whether spine lengths are related to pigmentation, how spine lengths scale with body size or how constrained these traits may be by phylogeny (i.e. are these traits free to evolve or are they constrained by their evolutionary history to be similar to related species?).

Better knowledge of the drivers of morphological variability in larval crabs will improve our understanding of crab larval distributions, survival, and dispersal and, more generally, the evolution of morphological defences. Understanding the adaptive benefits of morphological features can help identify sources of selection on larvae of understudied species based on their morphology. Since UVR and visual predation are both vertically stratified threats concentrated in the upper surface of the water column, a better understanding of the traits affecting vulnerability to these sources of mortality could improve understanding of larval vertical distributions that determine horizontal dispersal (Morgan, 2014; Queiroga & Blanton, 2005). Defining the scaling relationship of spine lengths with body size will help us understand how changing ocean conditions altering body sizes (Bashevkin et al., in press) may also impact predator defence. A phylogenetically controlled analysis of these morphological defences will improve our understanding of their evolution and constraints on adaptation to shifting threats.

Ultraviolet radiation at relevant field intensities has substantial lethal and sublethal effects on marine organisms, including larval crabs (Bancroft, Baker, & Blaustein, 2007; Bashevkin et al., 2019b). While visual predation and UVR are both concentrated in surface waters, visual fish predation is more intense in shallow nearshore habitats with high productivity (Morgan, 1986, 1990) and UVR is more intense in clear offshore waters with low productivity (Tedetti & Sempéré, 2006). This vertical overlap but horizontal segregation of threats suggests that crab larvae may employ either defence generalization or specialization. If larvae are generalizing and adopting the best defence from both threats, pigmented larvae would morphologically compensate for increased predation risk by growing longer spines, resulting in a positive relationship between these

traits. Conversely, if larvae are specializing, larvae would invest more energy in either long spines or dark pigments at the expense of the other trait because of finite energy budgets, resulting in a negative relationship between these traits. In generalization, the relationship between spine length and pigmentation is driven by compensation, while in specialization, it is driven by energetic trade-offs (Figure 1). We expect to find defence generalization since some overlap in these two threats is unavoidable. However, phylogenetic or allometric constraints may complicate the attainment of optimal defences by restricting the capacity of species to evolve optimal spine lengths or pigmentations. In this study, we examined the relationship between larval spine length and pigmentation, the allometric scaling of larval spine length with larval body size, and phylogenetic signal (an indication of phylogenetic constraint) in these traits. We investigated inter- and intraspecific patterns among 23 species types of field-collected larvae and 21 species of laboratory-hatched larvae.

2 | MATERIALS AND METHODS

2.1 | Sample locations

Crab larvae were collected at the Punta Galeta Marine Laboratory (9.403035°, -79.861027°) and the Bocas del Toro Research Station (9.351659°, -82.256612°) on the Caribbean coast of Panama, the Naos Marine Laboratory (8.917468°, -79.532621°) on the Pacific coast of Panama, and Bodega Harbor, California, USA (38.317119°, -123.056745°).

2.2 | Field-collected larvae

Crab larvae were collected from the plankton at Galeta and Naos by pumping raw seawater with a Marathon SL160 5.5 HP

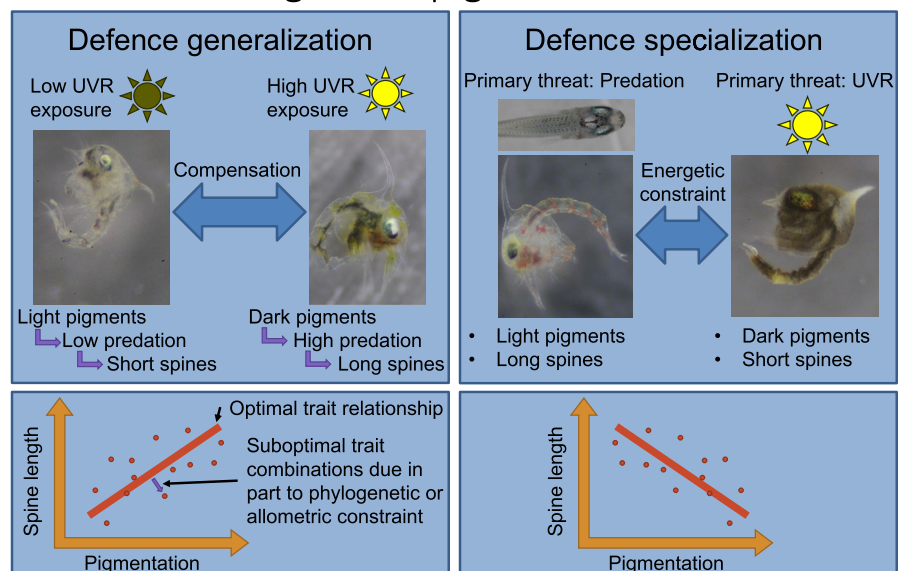
centrifugal pump at 30 m³/h into a 333 µm-mesh plankton net for 10–20 min per sample. Plankton was collected on four sampling dates each at Naos and Galeta. Samples were collected at the surface (1 m deep) and near the bottom (10–20 m deep) and then transported to the laboratory where crab larvae were immediately isolated, photographed and identified (Table S3). When samples were too large for all larvae to be photographed within the span of a few hours, larvae were haphazardly sampled and photographed. Only actively swimming larvae were used in these analyses since moribund larvae have contracted chromatophores. Because no key exists for crab larvae of the Tropical East Pacific or the Caribbean, field-collected larvae could not be identified to species. However, they were identified to family and genus when possible and grouped into species types based on common features used to identify zoeae, including the lengths and shapes of antennae, antennules, and spines; telson shape and exospines; pigmentation; and size. Larval stage was identified by maxilliped setae count and pleopod stage.

2.3 | Laboratory-hatched larvae

Gravid crabs were collected from terrestrial, intertidal and shallow subtidal habitats at Galeta and Bocas del Toro and from intertidal and shallow subtidal habits in Bodega Harbor. These adults were identified to species using Rathbun (1918, 1925, 1930), Klompmaker, Portell, Klier, Prueter, and Tucker (2015), Abele (1976, 1992) and Crane (1975). At Galeta and Bocas del Toro, crabs were held individually until they released larvae in containers surrounded by flowing seawater at ambient temperatures. Each crab was checked for freshly hatched larvae and its water was changed every morning. In Bodega Bay, *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* were held individually in flowing

Hypothesized relationships between spine length and pigmentation

FIGURE 1 Hypothesized relationships between crab larval pigmentation and spine length. Under the defence generalization hypothesis, species exposed to high ultraviolet radiation (UVR) would evolve dark defensive pigments, thereby increasing visibility to visual fish predators, thus selecting for longer spines. Under the defence specialization hypothesis, energetic constraints force a trade-off whereby species adapt to the primary threat they face, evolving either dark pigments to defend from UVR or long spines to defend from fish predators



seawater and checked daily for larvae. *Romaleon antennarium* and *Pugettia producta* were each held in large tanks (~190 L) with flowing seawater containing multiple individuals and larvae were collected the day they were released in large swarms that may have come from multiple mothers. A total of 1,601 first stage zoea larvae were measured (see below) from 84 hatches and 21 species. Whenever possible, 20 larvae were measured from each of at least five hatches per species but only 1–2 hatches were obtained for eight species (Table S2).

2.4 | Morphological measurements

Since some species of crab larvae expand their chromatophores in light (e.g. Pautsch, 1967), individuals were placed under a lamp for at least 30 min before photographs were taken. Freshly released laboratory-hatched larvae and field-collected larvae were photographed using the same methods. Larvae were photographed through a dissecting microscope at 45× with a Canon EOS Rebel T3 Digital SLR Camera fitted with a microscope adapter. Live larvae were photographed individually on depression slides against a white and black background while illuminated from above with white LED lights. Larvae were photographed from the lateral view while still.

The proportion of pigment cover was quantified from the photographs against a white background using the image analysis program IMAGEJ through the Fiji platform (Schindelin et al., 2012). Images were first converted to binary format, transforming the pigmentation to black and the transparent areas to white. The black (pigment) surface area was then measured in this binary image. The larval surface area was obtained by tracing larvae in IMAGEJ, and the proportion of pigment cover was calculated by dividing the pigmented area by larval surface area. A pilot experiment with *P. crassipes* larvae demonstrated no effect of different overhead lighting conditions during photograph capture on the percent cover calculation by this method. This approach to quantifying pigmentation is the same as that used by Bashevkin et al. (2019b; in review) and very similar to the approach described by Siegenthaler, Mondal, and Benvenuto (2017) used to study background matching in shrimp (Siegenthaler, Mastin, Dufaut, Mondal, & Benvenuto, 2018). This approach was superior in speed, accuracy and precision to traditional methods of measuring chromatophore size that rank size by an index from 1 to 5 (Siegenthaler et al., 2017).

The carapace and spine lengths of larvae were measured from the photographs against a black background that better highlighted the carapace boundaries (Figure 1). Two metrics of spine length were used in this study: total spine length, the sum of all spine lengths and rostral–dorsal length, the straight-line length from the tip of the most ventral spine tip (rostral spine or antenna, whichever was longer) to the dorsal spine tip, corresponding to the minimum gape width needed to consume these larvae.

The rostral spine, dorsal spine and antennal lengths were measured with a straight line from base to tip. The antennae were not measured on field-collected larvae since this feature did not show up well in those photographs. Carapace length was measured from

the anterior margin between the eyes to the posterior margin at the base of the abdomen. Carapace height was measured from the base of the rostral spine to the base of the dorsal spine. Rostral–dorsal length was measured as the distance from the tip of the dorsal spine to the tip of either the antenna or rostral spine, whichever was longer. Rostral–dorsal length was not directly measured for field-collected larvae since some larvae were too large for the rostral–dorsal length to fit into one photograph. Instead, rostral–dorsal length was estimated for field-collected larvae as the sum of the rostral spine length, carapace height and dorsal spine length. Total spine length was calculated as the sum of the dorsal spine length, rostral spine length and antennal length (for laboratory-hatched larvae; Figure 2).

2.5 | Statistical analyses

All statistical analyses were conducted in R (R Core Team, 2019). Analyses of the relationships between spine length and pigmentation were conducted with the Bayesian statistical analysis package BRMS (Bürkner, 2017). Bayesian methods were utilized because their flexibility enabled us to best account for the complex random effects structure of our data collected at multiple levels of biological organization with phylogenetic corrections (Bolker et al., 2009; Gelman et al., 2013; McElreath, 2015). Best-fit models were selected after model comparison with kfold validation using the package LOO (Vehtari, Gelman, & Gabry, 2017). For each model, predictors were centred and standardized, and the diagnostics and posterior predictive checks were thoroughly inspected before proceeding. Statistical significance of parameters was confirmed by 95% confidence intervals that did not overlap 0, corresponding to $p < .05$.

The relationship between total spine length and pigment cover for field-collected larvae was analysed with a linear mixed model (LMM) with spine length as the response variable. Total spine length was $\log(x + 1)$ transformed to fit a normal distribution. We included random intercepts for larval stage nested within species type. Adding a random intercept for family as a form of phylogenetic correction did not improve the model so it was not included in the final model.

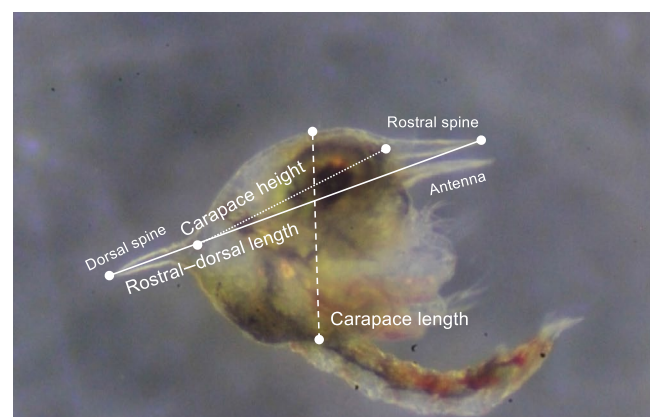


FIGURE 2 Morphological features measured in this study, superimposed on a *Grapsus grapsus* first stage zoea larva

Fixed effects were included for the average pigment proportion for each species and stage (species pigmentation), the offset of individual pigment proportion from the average (individual pigmentation), and carapace length. The best model had no interactions. Including a fixed effect for sampling location (Galeta or Naos) worsened the model and had no significant effect so it was excluded. The relationship between rostral–dorsal length and pigment cover was analysed with the same model, substituting log-transformed rostral–dorsal length as the response variable.

The relationship between total spine length and pigment cover for laboratory-hatched larvae was analysed with a LMM with spine length as the response variable. We included random intercepts for each hatch of larvae (i.e. a group of siblings) and each species. To account for phylogenetic relatedness among species, the species random intercept covariance matrix was constrained to the covariance matrix of species relatedness from the phylogenetic tree (Appendix S1), as described in the ‘Estimating Phylogenetic Multilevel Models with BRMS’ vignette included with the BRMS package (Bürkner, 2017). This is the same method used by Bashevkin et al. (2019b) to account for phylogeny. Total spine length was log-transformed to fit a normal distribution. Fixed effects were included for the average

pigmentation of each species (species pigmentation), the offset of the average pigmentation of each hatch from the species average (hatch pigmentation), the offset of the individual's pigmentation from the average hatch pigment cover (individual pigmentation), the carapace length to control for size and all interactions up to 3-way. The relationship between rostral–dorsal length and pigment cover was analysed with the same model, substituting log-transformed rostral–dorsal length as the response variable.

The presence and strength of allometric scaling of spine lengths with carapace length in laboratory-hatched species was analysed with standardized (reduced) major axis regression. Intraspecific relationships were analysed with the R package *SMATR* (Warton, Duursma, Falster, & Taskinen, 2012), while interspecific data were analysed with the *phyl.RMA* function from the *PHYTOOLS* package (Revell, 2011) to account for phylogeny. Size-corrected phylogenetic residuals for Figure 3 were calculated with the *phyl.resid* function from *PHYTOOLS*. Phylogenetic signal (the correlation of each trait with patterns of phylogenetic relatedness) was estimated for pigment proportion cover, total spine length, carapace length and rostral–dorsal length while incorporating intraspecific variation using *PHYTOOLS*.

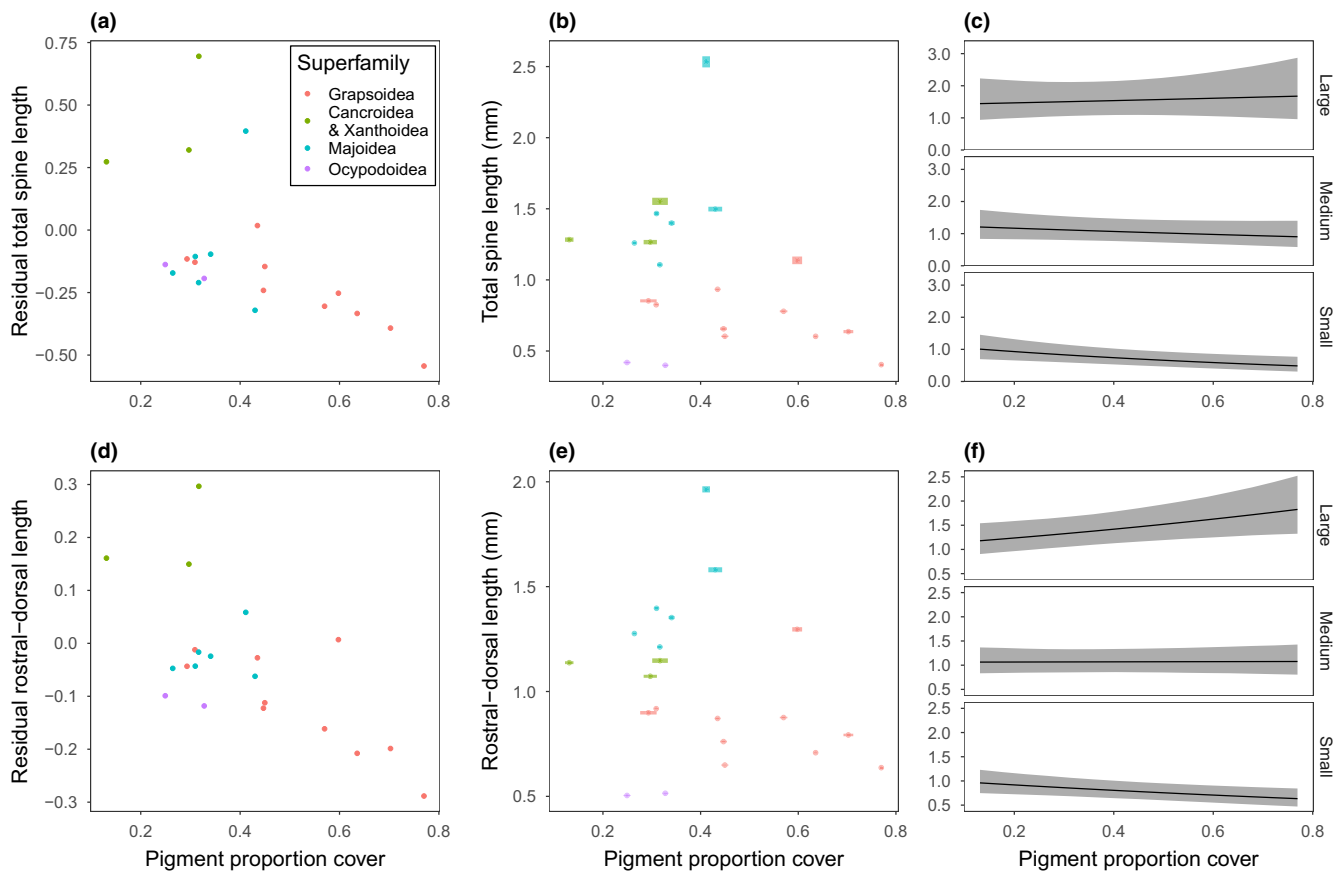


FIGURE 3 Interspecific relationship between pigmentation and total spine length or rostral–dorsal length among 21 species of laboratory-hatched crab larvae. (a,d) Residual values are derived from a phylogenetic regression of spine length against carapace length and thus represent spine lengths without the influence of phylogeny or larval size. (b,e) Mean trait values for each species with standard errors represented by rectangular boxes. (c,f) Linear relationships and 95% confidence intervals for larvae with small (0.26 mm), medium (0.62 mm) or large (0.97 mm) carapace lengths, derived from a Bayesian mixed model. Response variables were log-transformed for analysis but plotted in their raw form to facilitate data interpretation

3 | RESULTS

3.1 | Field-collected larvae

Overall, 98 crab larvae were photographed with intact spines and pigments. Fifty-one larvae were analysed from Naos and 47 from Galeta, representing 23 unique species types and 32 unique species-larval stage combinations (Table S1).

3.1.1 | Total spine length

Total spine length was positively correlated with carapace length (Figure S1, Table S3), negatively correlated with pigmentation among species (species pigmentation; Figure S1, Table S3) and marginally negatively correlated with pigmentation within species (individual pigmentation; marginal $R^2 = .54$, Figure S2, Table S3).

3.1.2 | Rostral-dorsal length

Rostral-dorsal length was positively correlated with carapace length and negatively correlated with pigmentation among species (species pigmentation; marginal $R^2 = .65$, Figure S1, Table S3). Within species, however, there was no relationship between rostral-dorsal length and individual pigmentation (Figure S2, Table S3).

Negative relationships between spine length and pigmentation were evident as larvae moulted and grew as illustrated by Grapsid1, the only species type with four zoeal stages represented (Figure S2).

3.2 | Laboratory-hatched larvae

3.2.1 | Total spine length

Among laboratory-hatched species, total spine length was positively correlated with carapace length and negatively correlated interspecifically with pigmentation (species pigmentation; marginal $R^2 = .25$, Figure 3, Table S3). There was also an interaction between species pigmentation and carapace length: the negative relationship was strong for smaller larvae and nonexistent for species with larger larvae (Figure 3, Table S3). One species, *P. producta*, was a strong outlier with spines over 150% of the length of the next closest species but with intermediate pigment coverage. For the intraspecific comparisons, hatch pigmentation (the average pigmentation of each hatch of sibling larvae) and individual pigmentation interacted with carapace length but with very low effect sizes (parameter estimates = 0.01) and otherwise had no effect on total spine length (Figure S3, Table S3).

3.2.2 | Rostral-dorsal length

Similarly, rostral-dorsal length was positively correlated with carapace length and negatively correlated interspecifically with pigmentation (species pigmentation; marginal $R^2 = .18$; Figure 3, Table S3).

There was also an interaction between species pigmentation and carapace length: the relationship between species pigmentation and rostral-dorsal length was negative for species with small larvae and positive for species with large larvae (Figure 3, Table S3). Neither hatch nor individual pigmentation had any effects on rostral-dorsal length (Figure S3, Table S3).

3.2.3 | Allometric scaling

In almost all cases, both total spine length and rostral-dorsal length exhibited positive allometric scaling with carapace length ($p < .05$, Figure 4, Table S4), indicating that larger larvae may be better defended from gape-limited predators. Negative allometry was detected for a few species but all of these R^2 were $\leq .01$ except for *Cardisoma guanhumi* with $R^2 = .11$ (Figure 4, Table S4, Figure S4). In all intraspecific allometric analyses, R^2 were low, never exceeding .5 (Figure 4, Table S4, Figure S4). Allometric slopes for rostral-dorsal length were much less variable and generally clustered around 2 (Figure 4). In interspecific comparisons, spine lengths were strongly related to carapace length (Figure 5) and the allometric slopes were positive, with values of 3.59 ($R^2 = .54$, $p < .0001$) and 2.46 ($R^2 = .78$, $p < .0001$) for total spine length and rostral-dorsal length respectively (Figure 4, Table S4).

3.2.4 | Phylogenetic signal

There was a phylogenetic signal in total spine length ($\lambda = 1.04$, $p < .0001$), rostral-dorsal length ($\lambda = 1.04$, $p < .0001$) and carapace length ($\lambda = 1.04$, $p < .0001$), but not in pigment proportion ($\lambda = 0.39$, $p = .15$; Figure 6). Pigmentation had the most intraspecific variability relative to the interspecific variability generally encompassing a range of 0.25, followed by total spine length (range ~ 0.5 mm), rostral-dorsal length (range ~ 0.25 mm) and lastly carapace length (range ~ 0.2 mm; Figure 6).

4 | DISCUSSION

We expected to find a positive relationship between pigmentation and spine length. Because dark pigmentation increases visual predation risk for zooplankton (Hairston, 1979; Luecke & O'Brien, 1981; Utne-Palm, 1999) and spines protect from the same predators (Morgan, 1987, 1989, 1990), we expected pigmented larvae to exhibit defence generalization and compensate for increased predation risk by growing longer spines. Contrary to our expectations, we found evidence for defence specialization in crab larvae (Figure 1). We detected a predominantly negative relationship between larval spine length and pigmentation cover in crab larvae, although this relationship varied with larval size for laboratory-hatched larvae. Furthermore, we found that predator defence increased with body size: spine length exhibited positive allometric scaling with carapace length intraspecifically and even more strongly interspecifically. We observed a slight

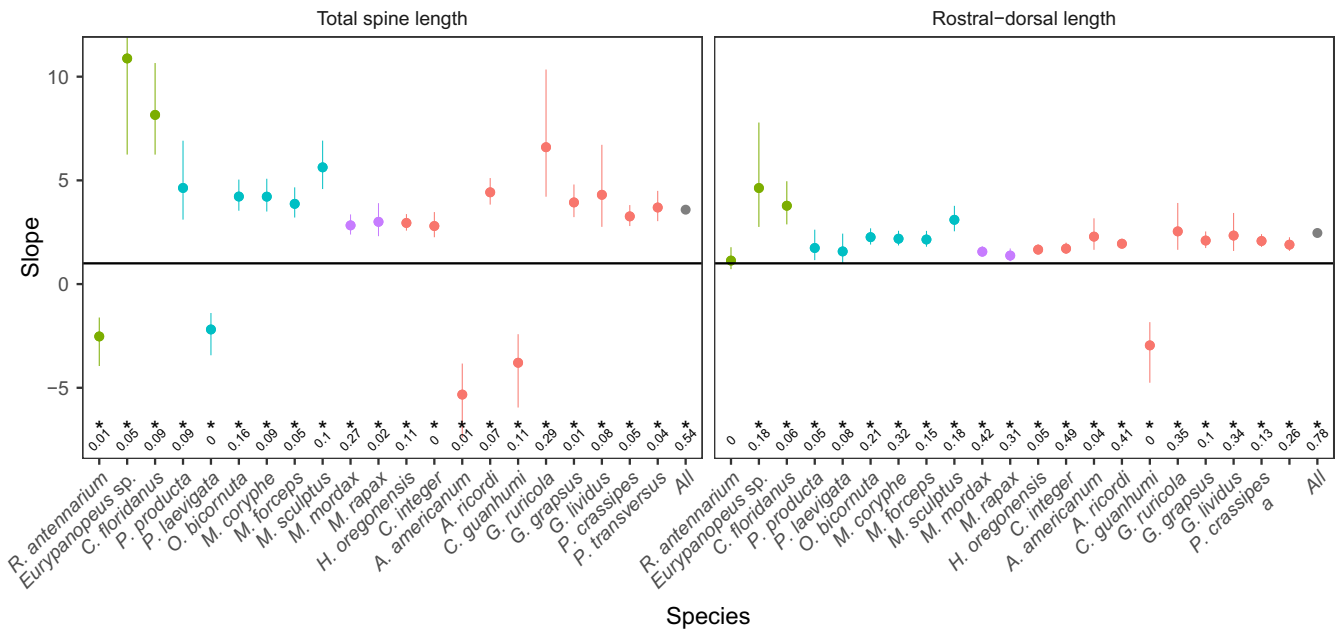


FIGURE 4 Slopes of the relationships between carapace length and total spine length or rostral-dorsal length. The interspecific relationships are represented as 'All'. Stars indicate the slope is significantly different from 1 at $p < .05$ and numbers indicate the R^2 . Colours represent superfamily (green = Xanthoidea & Cancroidea, teal = Majoidea, purple = Ocypodoidea, red = Grapsoidea). Slopes were calculated with the standardized (reduced) major axis method. Error bars on individual species points represent standard errors

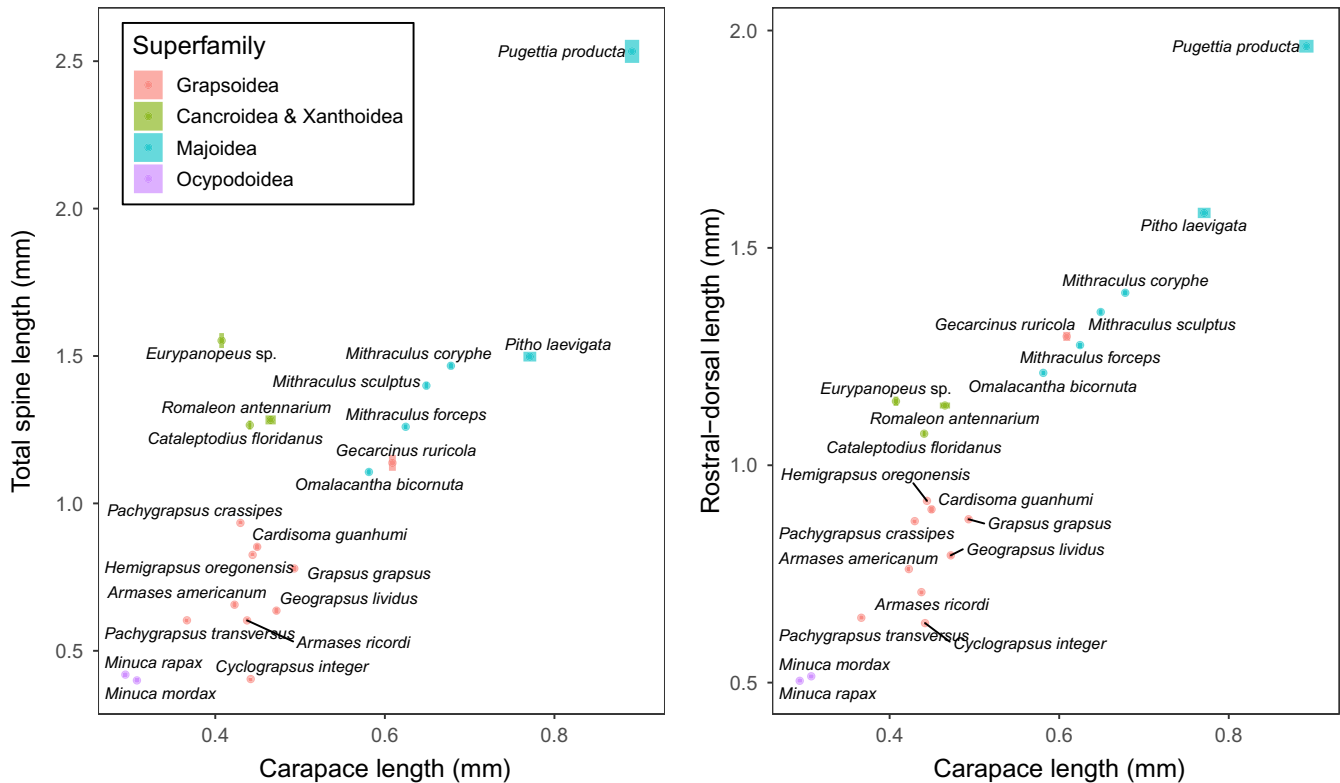


FIGURE 5 Interspecific scaling of total spine length and rostral-dorsal length with carapace length among 21 species of laboratory-hatched crab larvae

positive relationship between rostral-dorsal length and pigmentation among large laboratory-hatched larvae, but the relationship was negative in most other analyses and not significant in a few

analyses. Lastly, spine and carapace length were phylogenetically constrained, while pigmentation had no phylogenetic signal and may more readily evolve to changing threats.

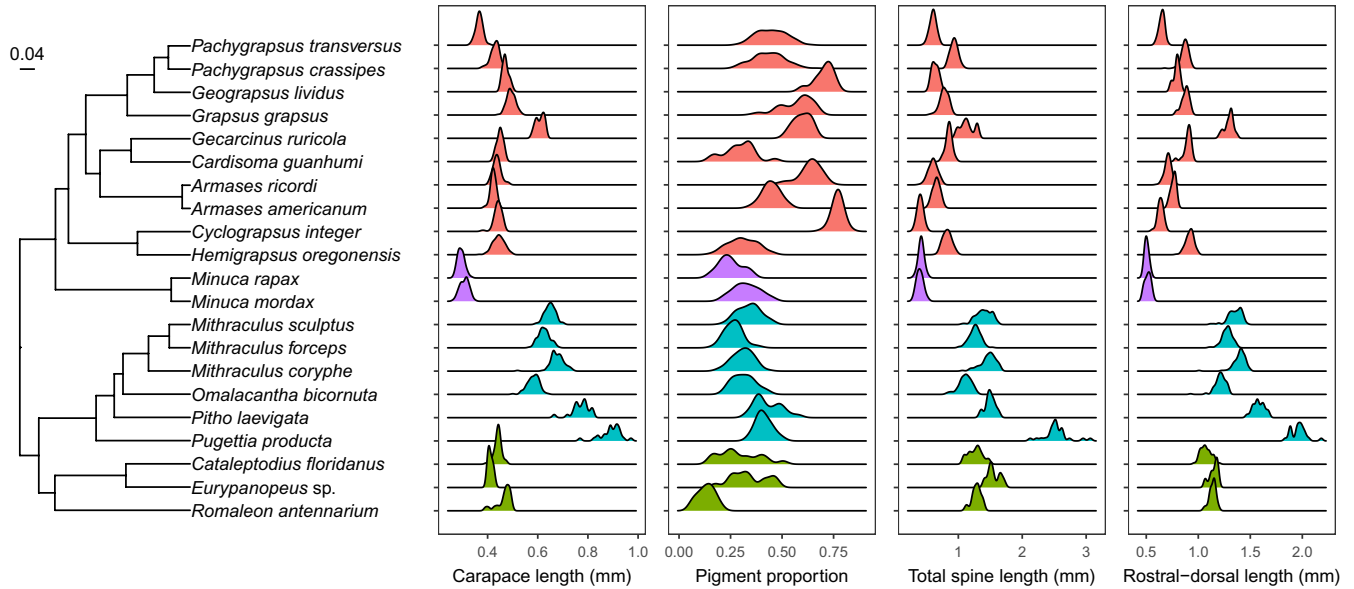


FIGURE 6 Phylogeny of laboratory-hatched study species and density plots of larval carapace length, pigment proportion cover, total spine length and rostral-dorsal length. Colours represent superfamily (red = Grapsoidea, purple = Ocyropodoidea, teal = Majoidea, green = Xanthoidea & Cancroidea). Carapace length ($\lambda = 1.04$, $p < .0001$), total spine length ($\lambda = 1.04$, $p < .0001$) and rostral-dorsal length ($\lambda = 1.04$, $p < .0001$), but not pigmentation ($\lambda = 0.39$, $p = .15$), had a significant phylogenetic signal. In constructing the phylogeny, genetic sequences from *Gecarcinus lateralis* and *Pitho lherminieri* were used in place of *Gecarcinus ruricola* and *Pitho laevigata*, respectively. *Armases americanum* was added to a random position within the *Armases* genus. See Table S2 for sample sizes

The unexpected negative relationships we discovered between pigmentation and spine lengths could indicate that species are specializing in either predator avoidance or UVR defence (Figure 1). In addition, defence specialization may imply that spines are costlier or visibility from dark pigments is less important than assumed. In larval dragonflies of the genus *Leucorrhinia*, dark abdominal pigments are negatively correlated with defensive spines (Walker & Corbet, 1975) that are thought to deter fish predators (Johansson & Mikolajewski, 2008). Freshwater holoplankton often specialize in defending from predators or UVR depending on which is stronger in the lake they occupy (Hairston, 1976; Rautio & Korhola, 2002). Furthermore, a mesocosm study has shown that even in the presence of both threats copepods can prioritize one over another (Hylander, Larsson, & Hansson, 2009). In our crab larvae, species with short spines and dark pigments would be well protected from UVR but susceptible to visual gape-limited predators like fishes. These species may occupy surface or offshore waters with intense UVR or more often encounter predators that neither feed visually nor are gape-limited (e.g. most invertebrate predators or large filter feeding vertebrates; Bashevkin & Morgan, in press). On the other hand, species with long spines and light pigmentation would be susceptible to UVR but well protected from visual gape-limited predators. These species may occupy depths or habitats with strong predation pressure from fishes and possibly less intense UVR. This could include depths just below damaging UVR in pelagic waters or nearshore turbid areas, where UVR attenuates quickly but fish are plentiful.

Alternatively, pigmentation of crab larvae may not be strongly related to visual predation risk. In a companion study, we found that reef silversides only preferentially consumed more pigmented larvae

over less pigmented larvae in the rare circumstances when UVR was absent and sun intensity was strong (Bashevkin, et al., in review). These conditions are unlikely to exactly occur in nature, but the closest match would be sunny days in deeper water. Visual predation may not be directly related to proportional cover by visible pigmentation, in which case we would expect only an energetic trade-off between investment in spines or pigments, resulting in the negative relationship we observed.

The different relationships between spine length and pigmentation observed among species with large larvae are likely due to the influence of the large majoid larvae. Within Majoidea, there appears to be a positive relationship between pigmentation and spine length (Figure 3), but more species are needed to investigate this intrafamilial relationship. Except for *P. producta*, the other temperate species (*P. crassipes*, *H. oregonensis*, *R. antennarium*) fit into the negative relationship well with above-average spine lengths but lower pigmentation compared to their closest tropical relatives (Figure 3). Lower pigmentation may be related to the lower UVR risk at temperate latitudes (Vasilkov et al., 2001). *Pugettia producta* had the longest spines and tied with *Pitho laevigata* for the darkest pigmentation among the majoids.

We detected strong positive allometry in interspecific comparisons and generally weak positive allometry in intraspecific comparisons. Spine length was similarly disproportionately correlated with body size in a previous study comparing the morphology of Dungeness crab *Metacarcinus magister* larvae reared at different temperatures or collected from cold or warm waters (Shirley, Shirley, & Rice, 1987). Our study is the first to identify the relationship under similar environmental conditions and define the slope of this

relationship. In contrast, *Daphnia* spines are negatively allometric with body size, possibly to increase defences of more vulnerable smaller individuals (Lampert & Wolf, 1986; Smakulka & Górnjak, 2004).

Allometry can arise from the genetic architecture underlying growth due to pleiotropy and epistasis (Pavlicev et al., 2008). Physiologically, allometry can result from autonomous growth of body parts, potentially influenced by hormonal communication among organs (Stern & Emlen, 1999). These genetic and physiological drivers of allometry may or may not be refined by selective forces into an adaptive allometric relationship.

An adaptive explanation for positive allometry of spines in crab larvae may be related to shifting predation threats as larvae grow larger. Spines protect from gape-limited predators such as fishes (Morgan, 1989), which selectively consume larger prey in part because of their increased visibility (Confer & Blades, 1975). This preferential consumption of larger prey could result in increased predation risk as crab larvae grow larger, thus selecting for even greater anti-predator defences in larger larvae, resulting in the positive allometry we observed.

Alternatively, the positive allometric relationship we observed may be related to influences of temperature on larval duration and body size. Across and within species, larval duration and body size are both inversely related to temperature (O'Connor et al., 2007; Pettersen, White, Bryson-Richardson, & Marshall, 2019; S. M. Bashevkin, unpublished data), so larvae with larger bodies will spend more time in cold water exposed to predators. Thus, large larvae may compensate for this increased risk by growing disproportionately longer spines (Shirley et al., 1987). Positive allometry also implies that warming ocean conditions (IPCC, 2013) reducing larval body sizes, and thereby disproportionately reducing spine lengths, may increase the instantaneous predation risk of these larvae. As larval duration will also decrease with warming temperatures, there may be no net change in larval mortality. However, other changing ocean conditions such as ocean acidification will increase larval duration (Bashevkin, et al., in press; Gaylord et al., 2015) potentially resulting in an increased predation risk for larval crabs as oceans warm and acidify.

The strong phylogenetic signal we detected in spine lengths indicates that these traits are fairly constrained within clades. Ocypodoids have the shortest spines, and spines are increasingly longer in Grapsoids, Xanthoids and Cancroids, and Majoids. While we are the first to confirm this statistically, it is well known that spination patterns are conserved within families of crab larvae. Spine lengths are often used in dichotomous keys to identify crab larvae. A notable exception to this pattern is pea crabs (superfamily Pinnotheroidea) that show considerable interspecific variation in spination (Marques & Pohle, 1995) along with other atypical traits, such as a parasitic lifestyle as adults and above-average interspecific variation in the number of larval stages (S. M. Bashevkin, unpublished data). Evolutionary constraint in spine lengths could have consequences for the habitats available to larvae. If larvae with short spines are constrained to occupy habitats with fewer predators, as

has been found before (Morgan, 1990), then we may expect larvae of all species within a family to occupy similar larval habitats due to their similar spine lengths. Prey choosing habitat based on their degree of predator defence has been observed before in terrestrial, aquatic and marine systems (Kats, Petranka, & Sih, 1988; Wirsing, Cameron, & Heithaus, 2010). Conversely, the lack of phylogenetic constraint in pigmentation indicates that species can evolve optimal pigmentations relative to the threats they face. Thus, we may not expect related species to occupy habitats with similar UVR threats.

The mechanism of phylogenetic constraint in spine lengths may be related to larval body size since spine lengths were strongly related to carapace length interspecifically. Carapace length showed similar phylogenetic constraint, likely due to offspring provisioning and life-history strategies that are also conserved within families (S. M. Bashevkin, unpublished data). The tight relationship between carapace and spine length may indicate that the optimal spine length increases with a defined relationship to carapace length (we found this slope to be around 2–3), possibly due to the trade-offs among drag (Chia, Buckland-Nicks, & Young, 1984), spine cost (Riessen & Sprules, 1990) and predator defence (Morgan, 1987, 1989, 1990). The lack of phylogenetic constraint in pigmentation may be related to the sources of those pigments. Some, like melanin, are synthesized by the crab but other pigments, like carotenoids, must be obtained from the mother's or larva's diet since animals cannot produce them (Bandaranayake, 2006). Thus, variability in pigmentation could be due to shifts in feeding behaviours or the pigments available in food sources. This could also explain the much higher intraspecific variability of pigmentation relative to spine and carapace lengths.

In conclusion, we found defence specialization (Figure 1) in larval crabs evidenced by a negative correlation between spine lengths and pigmentation, increased predator defence of larger larvae resulting from positive allometric scaling of spine lengths with body size, and phylogenetic constraint in spine and carapace length but not pigmentation. We suggest that larval crabs may be specializing in defending from predators or UVR and this may be related to the habitats they occupy during migrations between adult and larval habitats. Similarly, phylogenetic constraint in spine lengths may indicate that related species with shared life-history traits occupy larval habitats with similar predator threats. Furthermore, positive allometric scaling of spine lengths with body size may result in increased crab larval mortality from predators as larval body size decreases with the expected increase in sea surface temperatures. Our results improve understanding of plankton defensive morphology and morphological evolutionary responses to multiple spatially segregated selective forces.

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AUTHORS' CONTRIBUTIONS

S.M.B., J.H.C. and S.G.M. conceived the study; S.M.B. collected and analysed the data and wrote the manuscript; and J.H.C. and S.G.M. edited the manuscript.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: <http://doi.org/10.5061/dryad.sxksn02z8>, (Bashevkin, Christy, & Morgan, 2019a).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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