

Decorating behavior begins immediately after metamorphosis in the decorator crab *Oregonia gracilis*

Steven R. Hein^{1,2,3,*}, Molly W. Jacobs^{1,2}

¹Biology Department, McDaniel College, 2 College Hill, Westminster, Maryland 21157, USA

²Friday Harbor Laboratories, University of Washington, 620 University Rd, Friday Harbor, Washington 98250, USA

³Present address: Department of Biology, Miami University, 700 East High St, Oxford, Ohio 45056, USA

ABSTRACT: Behavioral transitions during metamorphosis are critically important for juvenile survival, but often poorly studied relative to morphological and habitat transitions. We used manipulative laboratory experiments paired with scanning electron microscopy imaging to examine the ontogeny of a specific behavior (decorating behavior) during and after metamorphosis in the decorator crab *Oregonia gracilis*. We found that the hooked setae required for decoration were absent in the megalopa stage, but present in the first instar juvenile stage. The onset of decorating behavior was tightly coupled with this morphological transition: megalopae did not decorate, but first instar juveniles began active decoration immediately. Megalopae and early instar juvenile *O. gracilis* both displayed strong habitat selection behavior, likely driven by the availability of decorating materials and plentiful hiding places. We also observed an ontogenetic change in decorating behavior between early instar juveniles and adults: first instar juveniles actively decorated with organic debris, rather than any of the offered materials commonly used by sub-adults and adults. Organic debris may be easier for the small juveniles to handle and retain, it may provide better camouflage in microhabitats commonly used by juveniles, or it may act as a partial food cache. The ontogeny of decorating behavior is a useful system for exploring how behavior, morphology, and habitat transitions can be coordinated by *O. gracilis* during metamorphosis.

KEY WORDS: Metamorphosis · Larval transitions · Decoration · Decapoda · *Oregonia*

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INTRODUCTION

Metamorphosis in most organisms is associated with a sharp morphological transition from larval to adult body plan, and an ecological transition from the larval to the adult habitat. Metamorphosing organisms also must undergo behavioral transitions, from larval to adult behaviors, but these are rarely studied directly as part of the metamorphic process. For example, behavioral transitions are mentioned in only 2 of 14 definitions of metamorphosis submitted by a panel of experts at a metamorphosis symposium

(Bishop et al. 2006). Behaviors are closely linked to morphology and habitat, but the morphological, habitat, and behavioral transitions of metamorphosis may or may not be tightly coupled with one another. The behavioral transition from swimming to crawling in the sea hare *Aplysia californica*, for example, is tightly coupled with the habitat transition from the plankton to the benthos, while the transition from behaviors associated with ciliary feeding to behaviors associated with radular feeding is tightly coupled with the loss of the velum—a morphological transition (Kriegstein et al. 1974). The coupling between

behavioral, morphological, and ecological transitions has been studied most extensively in insects (e.g. Consoulas et al. 2000, Ainsley et al. 2008) and some vertebrates (e.g. Hourdry et al. 1996, Touchon et al. 2013).

Metamorphic shifts in morphology and habitat occur rapidly and simultaneously for most marine invertebrates with complex life histories (Hadfield 2000, Heyland & Moroz 2006). Decapod crustaceans are unique in that they undergo a major morphological transition (from larval form to decapodid form) followed by a gradual habitat transition during the decapodid stage (Anger 2006), and a much more subtle morphological transition from decapodid to juvenile. Thus, in decapods it is possible to test whether major behavioral transitions are closely associated with morphological transitions, habitat transitions, or neither (e.g. Brodie 1999). Here, we study the ontogeny of a specific adult behavior (decorating behavior) in the decorator crab *Oregonia gracilis* Dana 1851.

Decorating behavior occurs when animals actively adorn their bodies with foreign matter (Berke et al. 2006, Ruxton & Stevens 2015). Decorating behavior can be observed in a broad range of organisms, including echinoderms (Richner & Milinski 2000), annelids (Berke & Woodin 2008a), and arthropods (Brandt & Mahsberg 2002, Berke & Woodin 2008b, 2009, Guinot & Wicksten 2015). Some of the best-known decorating arthropods belong to the family Majoidea, commonly known as decorator crabs. These crabs actively decorate themselves by selecting a piece of material from their environment and rubbing it against their exoskeletons using their chelae. The material is held onto the crab by structures known as hooked setae (Berke & Woodin 2009, Guinot & Wicksten 2015). The presence and density of hooked setae directly correlates with the degree of decorating behavior displayed by a given species, which varies greatly both inter- and intra-specifically across this diverse group of crabs (Hultgren & Stachowicz 2009).

The attachment of decorating materials in majoids is generally considered to play a role in predation reduction by acting as camouflage (crypsis), as a chemical deterrent, or both (Hultgren & Stachowicz 2008, 2011, Guinot & Wicksten 2015). Tethering experiments have provided evidence that decorating can reduce predation rates on decorated crabs vs. non-decorated crabs by as much as 50% (Thanh et al. 2003, Hultgren & Stachowicz 2008). A large number of decorator crab species are also known to attach material containing chemicals that many common

local predators find distasteful or unpalatable (reviewed in Hultgren & Stachowicz 2011). For example, in the southern portion of its range, *Libinia dubia* has been shown to decorate itself with up to 75% *Dictyota menstrualis*, an alga that local omnivorous fish do not eat, even though *D. menstrualis* only represents 6% of the local algal community (Stachowicz & Hay 2000). In addition, some decorator crabs eat their decorations during periods of food stress, although food caching is generally not considered to be a primary function of decoration behavior (Kilar & Lou 1986, Woods & McLay 1994a, Hultgren & Stachowicz 2011).

It is likely that decorating comes at a cost, and indeed energetic cost has been proposed as a major factor constraining the evolution of decorating behavior across phyla (Berke et al. 2006, Ruxton & Stevens 2015). Decorating requires energy expenditure to add decorations, and then additional energy to carry them around, although the relative costs of adding vs. carrying decorations are largely unknown. Adult *O. gracilis* crabs with decorations experienced more weight loss than undecorated crabs in a starvation experiment (Berke & Woodin 2008b). An energetic trade-off between decorating and chelae growth has also been proposed to explain the sexually dimorphic ontogenetic shift in decorating observed in adult *O. gracilis*: female crabs continue to decorate extensively as adults, but adult males exhibit reduced decoration while growing larger chelae (Berke & Woodin 2008b).

Many crab species display high selectivity in their decorating material choices, often choosing only certain materials when there are large numbers of possible choices available (Woods & McLay 1994b, Stachowicz & Hay 1999, Hultgren & Stachowicz 2008, Vasconcelos et al. 2009). *Inachus phalangium*, a species of decorator crab from the Mediterranean Sea and the northeastern Atlantic, is even selective regarding where exactly on its body it attaches certain materials (Rorandelli et al. 2007). This high selectivity suggests that crabs gain a fitness advantage from attaching the correct decorations, in the correct amounts, at the correct locations on their body. Although selectivity has not been examined in *O. gracilis*, adults and sub-adults decorate extensively with a large variety of sessile organisms, including bryozoans, hydroids, and sponges (Stevens 1913, Berke & Woodin 2009).

The onset of decorating behavior in early juveniles has not, to our knowledge, been characterized in any crab species. Ruxton & Stevens (2015) predicted that the cost of decoration might be less for small-

bodied organisms, suggesting that decorating behavior is likely to begin early in juvenile life. While adult and sub-adult *O. gracilis* are thought to rely primarily on the visual crypsis provided by their decorations for protection from predation (Berke et al. 2006), decapodids have been shown to select habitats that reduce their vulnerability to predation by providing a large number of suitable hiding places (Botero & Atema 1982, Herrnkind & Butler 1986, Fernandez et al. 1993, Moksnes 2002). As juvenile crabs grow, their ability to hide should decrease and their reliance on visual crypsis should increase.

We designed a series of manipulative laboratory experiments paired with scanning electron microscopy in order to investigate behavioral and morphological transitions during the early life stages of *O. gracilis*. Specifically, we asked: (1) When in the ontogeny of *O. gracilis* do hooked setae appear (in other words, when does morphology allow decorating)? (2) Is the onset of active decoration (behavioral transition) tightly coupled to the appearance of hooked setae (morphological transition)? We hypothesized that hooked setae and decorating behaviors could appear as early as the megalopa stage (the time of first contact with the benthos), but were more likely in early juvenile stages.

We were unsure whether decorating behavior would be present, minimal, or absent in early instar juveniles, but we wanted to explore the relationship between early decorating behaviors and habitat preference. Therefore, we designed a series of decoration and habitat choice laboratory experiments to ask: (3) Do the earliest decorating stages demonstrate preference amongst decorating materials? (4) Do megalopae or early instar juveniles display habitat selectivity? We hypothesized that if juveniles did not decorate, then habitat selection should be strongly influenced by the availability of suitable hiding places, but that if they did decorate, habitat selection might also be driven by the availability of materials used in decoration.

MATERIALS AND METHODS

Specimen collection and care. All *Oregonia gracilis* megalopae included in these experiments were collected opportunistically during the day, or at night by night lighting, from the docks at the University of Washington Friday Harbor Labs (FHL), Friday Harbor, WA, USA (60° 32' 43" N, 123° 00' 44" W) between 10 June and 3 August 2012. We identified individuals

to species level based on the arrangement of carapace spines (Shanks 2001). Juveniles were either raised from captured megalopae, or wild-caught from docks by searching through attached tires or ropes. Wild-caught individuals were determined to be either first or second instar juveniles by comparing carapace sizes to those of known-age lab-reared individuals. We also collected decorating material (erect bryozoans: *Scrupocellaria* spp. and *Tricellaria* spp.; sponges: *Mycale* spp.; red algae [hereafter referred to as algae]) from the FHL dock. Megalopae were held in mesh bottom ice cube trays or mesh bottom PVC pipes in a flow-through aquarium continuously circulated with fresh seawater and fed live *Artemia* nauplii daily (Léger et al. 1986). Juveniles reared in the laboratory were held in the same conditions and offered *Artemia* nauplii, freeze dried *Artemia*, and red algae as food. Wild-caught juveniles were used in experiments the same day and released immediately thereafter, and were not offered any food.

Morphological characterization. We used a scanning electron microscope (SEM) (Jeol JCM-5000 Neoscope) to examine carapace morphology of megalopae and first-instar juveniles. Under a dissecting microscope 3 megalopae and 5 first-instar juveniles were dissected, and their carapaces were placed on SEM stubs and allowed 3 to 4 days to air dry before any SEM microscopy work. Prior to imaging, the specimens were sputter coated with gold-palladium. Images were taken under a high vacuum setting at 15 kV.

Megalopae habitat selection. We tested active habitat selection by megalopae ($n = 21$), using a cross-shaped arena divided into 5 equal areas measuring $7.5 \times 7.5 \times 5$ cm each (Fig. 1). A 2.5 cm tall piece of wide-mouthed mesh separated each of the 4 outer chambers of the cross from the center area. The mesh prevented the habitat materials from floating freely around the arena, but was large enough to allow megalopae and juveniles to move through completely unobstructed. We frequently observed megalopae and juveniles moving through or over the mesh fencing without any hindrance (S. R. Hein pers. obs.). The ground space and up to top of the 2.5 cm mesh fence of each of the outer chambers (Fig. 1) was filled completely with either (1) sponges (*Mycale* spp.); (2) erect branching bryozoans (*Scrupocellaria* spp. and *Tricellaria* spp.); (3) red algae; or (4) a mix of all 3 materials. We selected these materials based on their abundance on the FHL docks, and because juvenile *O. gracilis* and other similarly sized crabs were observed amongst them. These materials are also

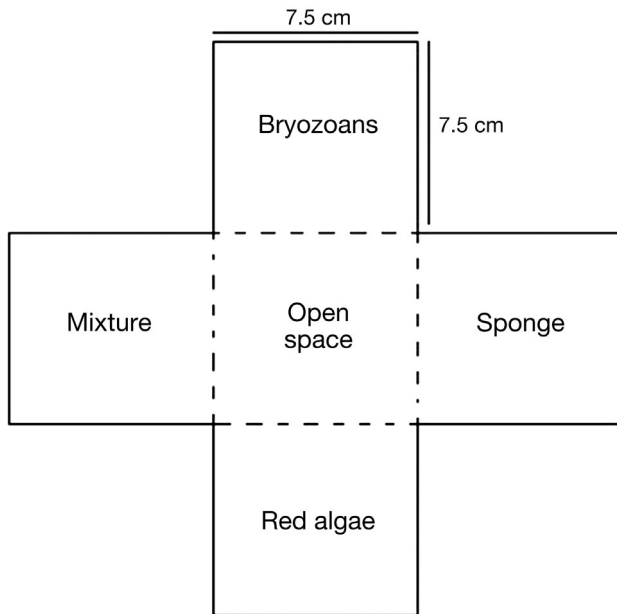


Fig. 1. Schematic of the cross-shaped arena used in the megalopae and juvenile *Oregonia gracilis* habitat selection experiments. Dotted lines represent mesh borders (2.5 cm tall) between habitat chambers. Windows covered with fine micron mesh were made on the bottom of each chamber in juvenile trials to allow fresh water to circulate

commonly found as decorations on adults (Stevens 1913, Berke & Woodin 2008b, S. R. Hein & J. Odierno pers. obs.). The center area of the arena was kept free of any material. The arena was filled to the top with seawater and kept in a water bath to maintain constant temperature (11–14°C).

We began each trial by placing a 4 cm diameter PVC cage in the center of the arena and introducing a single megalopa into the cage. We allowed the megalopa 2 min in the cage to acclimate to the arena, and then slowly lifted the cage to release the megalopa. We recorded the location of the megalopa every minute for 20 min and whether the individual was swimming or in contact with a habitat. After the trial was terminated the megalopa was removed from the arena. The arena was rotated 90° between each of the 21 trials to avoid bias from any unknown exterior directional cues. Juveniles that molted from the megalopae used in this experiment were excluded from any future behavioral testing. After a brief exploratory period the majority of the megalopae selected a habitat and remained there for the remainder of the trial, allowing us to assign each megalopa a specific choice. We tested the hypothesis that megalopae would display a habitat preference for one specific habitat over the other choices using a chi-square analysis.

Juvenile habitat selection. Juveniles were slower and more cryptic than megalopae, and so we altered the cross-shaped arena (Fig. 1) by adding windows with fine mesh covering to the bottom and side. This permitted water flow through the chamber from the surrounding water bath, allowing us to maintain the juveniles for longer trials. The outer chambers of the arena were filled with sponges, bryozoans, red algae, and a mixture as described above. Freshly captured first or second instar juvenile *O. gracilis* ($n = 20$) were carefully cleaned of pre-existing decoration using a variety of tools including paint brushes, fine forceps, and floppy forceps (S. K. Berke pers. comm.), before being placed in the center of the arena for 2 min in a PVC cage for acclimation. After 24 h in the arena at a natural light cycle, we recorded the location of the juvenile. Two individuals were found dead and therefore excluded from the analysis. We used a chi-square test to determine whether juveniles demonstrated habitat selectivity.

Juvenile decoration preferences. In the same flow-through aquarium as previously described, lab-reared first instar juveniles (24–48 h post metamorphosis) ($n = 24$) were placed individually in 6 cm tall (5 cm diameter) vertically oriented PVC pipe cages with a fine mesh screen bottom. The mesh bottom allowed free flow of the circulating seawater into and out of the cage. Of the 24 juveniles, 19 received 3 cm³ of one of the materials used in the habitat experiments to act as decorating materials: either the bryozoans; sponges; red algae; or an equal mixture of all 3 materials. The 5 other juveniles were offered nothing, to act as controls. However, the particulate organic debris found freely floating in the circulating seawater was still available to the control treatment. The crabs were allowed 72 h at a natural light cycle to decorate. After 72 h the crabs were removed and photographed under a dissecting microscope using a Canon Rebel Tli camera. After visually identifying accumulated decorating materials on the crabs, we quantified the surface area of each material using ImageJ photographic analysis software (Rasband 1997–2015). At the conclusion of the experiment, we found that most juveniles decorated with unidentifiable organic debris instead of with the offered materials (see 'Results'). Data were transformed by log ($x+1$) to normalize distributions and homogenize variances. We used a repeated measures analysis of variance in JMP 12.0 to compare decoration with debris vs. decoration with other materials, with decorating treatment included as a blocking variable.

Chelae ablation control experiment. To determine whether material accumulation on the carapaces of

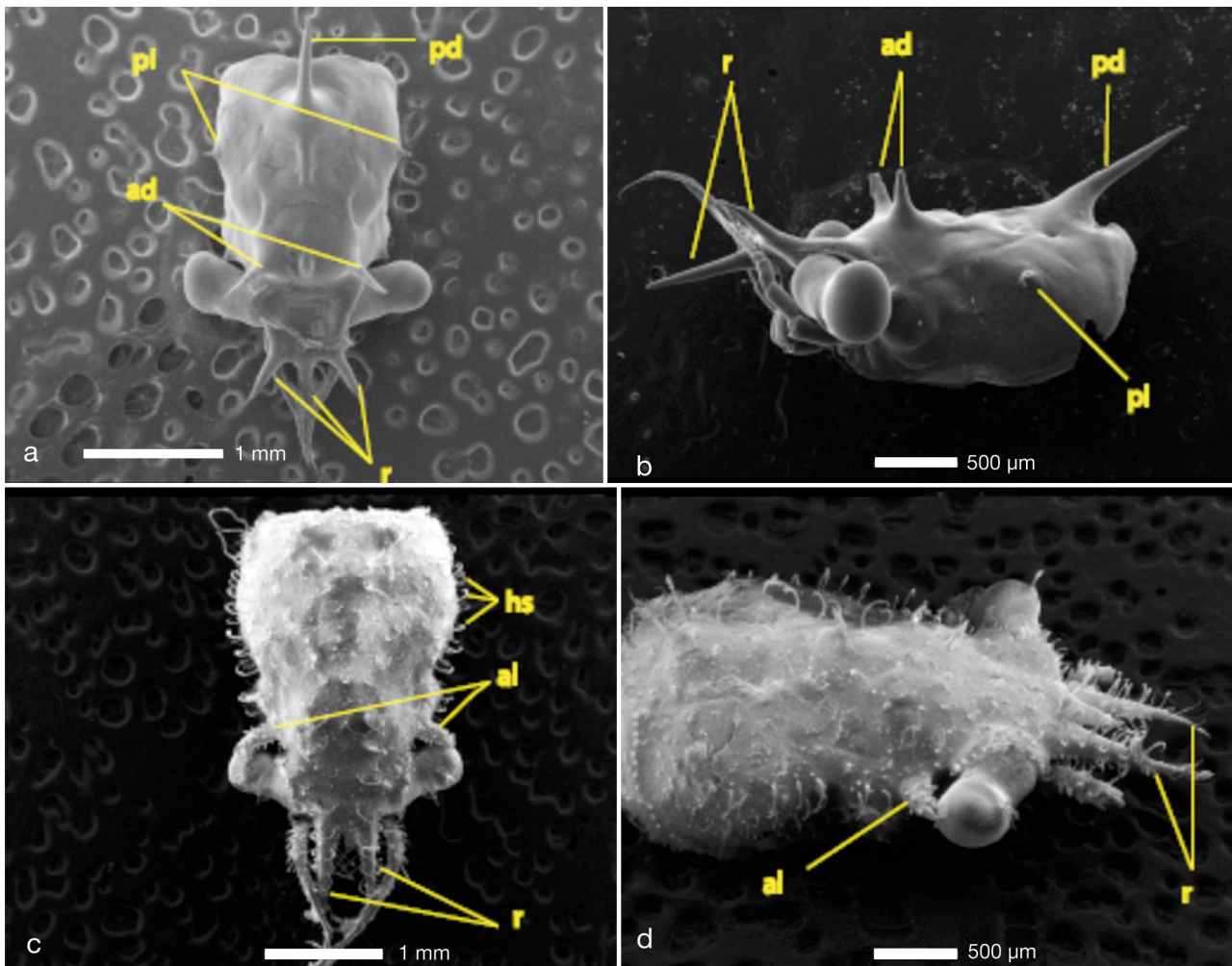


Fig. 2. *Oregonia gracilis*. Scanning electron microscopy images of (a,b) megalopal and (c,d) first instar juvenile carapaces. (a,c) Dorsal, (b) lateral, and (d) dorsolateral views. ad: anterior dorsal spines; al: anterior lateral spines; hs: hooked setae, pd: posterior dorsal spine; pl: posterior lateral spines; r: rostral spines

juvenile crabs was the result of passive attachment or of active decorating behavior, we examined the effects of chelae removal on material accumulations. First or second instar wild-caught juveniles ($n = 22$) were stripped of all decoration under a dissecting microscope as described above and photographed. Crabs were randomly divided into 2 treatments of equal sample size: those with chelae removed (used in decorating behavior) and those with the first pair of walking legs removed (to control for altered behavior due to injury). The crabs were housed in the same PVC cages as described in the decoration preference experiment. Since neither the habitat selection nor decoration preference experiments revealed an effect of decoration treatment on the amount or composition of decoration (see 'Results'), juveniles in this experiment were not offered decorating materi-

als, but the floating organic debris was still available to both treatments. The crabs were left undisturbed for 72 h and then re-photographed. The pre- and post-experiment photographs were analyzed as described above for the identity and surface area of material accumulation using ImageJ (Rasband 1997–2015). Data were transformed by $\log(x+1)$ to normalize distributions. Surface areas of accumulated materials between ablation treatments were compared using Welch's t -test, (Welch 1947, Zimmerman 2004).

RESULTS

Morphological characteristics of megalopae. *Oregonia gracilis* megalopal carapace characteristics

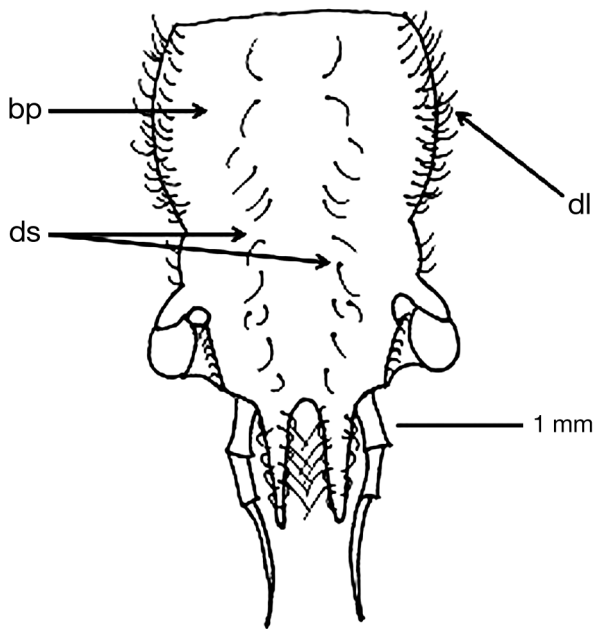


Fig. 3. Layout of hooked setae on carapace of *Oregonia gracilis* first instar juvenile. ds: dorsal setae; bp: barren patch; dl: dense lateral setae patches

were consistent with previous descriptions by Shanks (2001). We found no hooked setae on megalopae (Fig. 2a,b), which showed carapaces having 3 rostral spines: 1 long center spine pointing in a slightly ventral direction and 2 shorter, dorsally angled lateral spines (Fig. 2a,b). Located directly posterior to the eyestalks were 2 anterior dorsal spines (Fig. 2b), while 2 small lateral spines were located towards the posterior end of the carapace (Fig. 2a). These lateral spines are key taxonomic characters for *O. gracilis* megalopae (Shanks 2001). A long posterior dorsal spine pointed to the back.

Morphological characteristics of juveniles. The carapaces of the first instar juveniles were distinctly different from those of the megalopae. The rostrum featured 2 spines angled away from one another in a 'Y' shape (Fig. 2c,d). All dorsal spines as well as the small lateral posterior spines observed in megalopae were absent and there were only 2 anterior lateral spines located directly posterior to the eyestalks (Fig. 2c). Hooked setae were present and laid out in the same characteristic bilaterally symmetric manner on all of the 5 individuals examined. Starting at the tip of the rostral spines, a row of hooked setae ran across the dorsal surface of the carapace, ending at the back (Figs. 2c,d & 3). No setae were located in-between the dorsal rows. On each side of the rows, there was a large patch that was barren of hooked setae (Figs. 2c,d & 3). However, on the lateral sides of

Table 1. Number of *Oregonia gracilis* megalopae and juveniles that selected each of the habitats offered in the experiments. *O. gracilis* were offered byrzoans, sponges and algae in the mixture treatment

	Bryo- zoans	Spon- ges	Algae	Mix- ture	χ^2	p
Megalopae	12	5	1	3	13.10	0.0044
Juveniles	11	4	1	2	13.56	0.0036

the carapace there were dense patches of hooked setae consisting of many rows (Figs. 2c,d & 3). Hooked setae also covered all surfaces of the rostral spines (Figs. 2c,d & 3).

Megalopal habitat selection. Immediately after release into the arena the megalopae displayed exploratory behavior, swimming in circles around the open center portion of the arena and coming into physical contact with a number of surfaces. By minute 3, 18 of the 21 megalopae had selected one of the chambers and remained there for the duration of the trial. The remaining 3 megalopae selected a chamber and remained there for 5 to 7 min before moving to a second chamber where they remained for the duration of the trial. Megalopae strongly preferred branching bryozoans over the other 3 offered habitats (Table 1).

Juvenile habitat selection. In contrast to the megalopae, juveniles remained motionless in the center of the arena for at least 15 to 20 min after their release. However, casual observations over the course of the 24 h trial period revealed the same individuals were observed in different areas of the arena, suggesting that they explored the available habitats. We did not quantify movement during the trial period because it was not always possible to find the small crabs without completely removing the substrates and disrupting the trials. As with the megalopae, juveniles displayed a strong preference for bryozoans (Table 1).

Juvenile decoration preference. After 72 h all juveniles accumulated material on their bodies, particularly along the sides of the carapace where the hooked setae were the densest. However, very few of the juveniles decorated themselves with any of the offered materials (bryozoans, algae, or sponges). The majority of the attached material was the unidentifiable organic debris found in the water column of the flowing seawater ($F_{1,14} = 5.777$, $p < 0.0001$, Fig. 4). There was no effect of decoration treatment on the amount or the composition of the decorations ($F_{4,14} = 0.347$, $p = 0.348$).

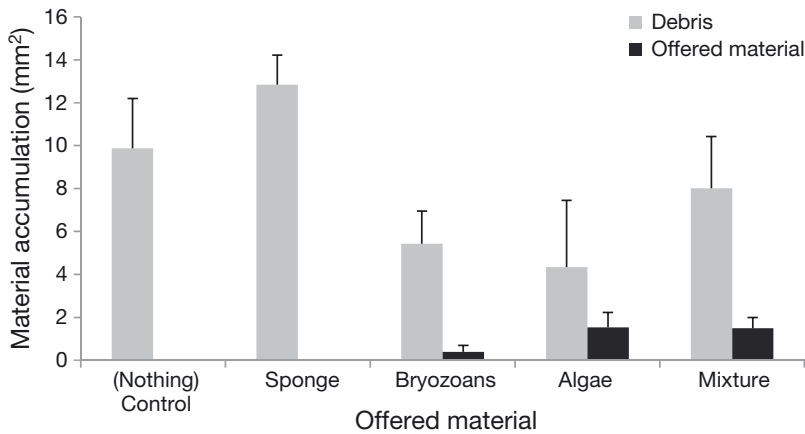


Fig. 4. Mean material accumulation (debris or offered material) on the carapaces of *Oregonia gracilis* juveniles during the juvenile decoration experiment. 'Offered material' refers to bryozoans in the bryozoan treatment, sponges in the sponge treatment, algae in the algae treatment, and all 3 materials in the mixture treatment. Error bars: +1 SE

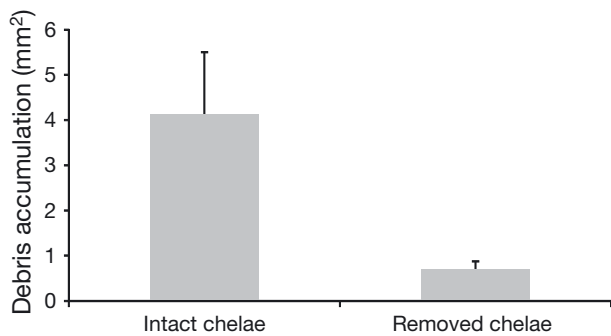


Fig. 5. Mean (+ SE) debris accumulation on the carapaces of *Oregonia gracilis* juveniles as a result of the chelae ablation treatment

Chelae ablation control experiment. We observed crabs with intact chelae holding debris in their chelae and actively rubbing it against themselves, but we did not observe any comparable decorating behavior in the chelae ablation treatment. After 72 h, crabs with intact chelae were heavily decorated with the organic debris found in the flowing seawater, while crabs with ablated chelae displayed little-to-no decoration ($t_{13} = 2.83$, $p = 0.014$, Fig. 5).

DISCUSSION

Metamorphosis is a time of great change and transition for many invertebrates, often marked by drastic and tightly coupled morphological, habitat, and behavioral changes (Hadfield 2000). We found that for the majoid decorator crab *Oregonia gracilis* the

onset of an adult behavior (decorating behavior) is tightly coupled with a morphological shift (the acquisition of hooked setae). However, this morphological shift did not occur as part of the major metamorphic transition from zoea to megalops, but with the more subtle morphological transition from megalops to first instar juvenile.

The onset of decorating behavior has not, to our knowledge, been described in any decorator crab. We found that *O. gracilis* megalopae completely lack the hooked setae required for decorating, and as a result do not decorate. First instar juveniles, however, are profusely covered in hooked setae and decorate extensively. *O. gracilis* megalopae are

active, predatory swimmers, while first instar juveniles are slow and cryptic benthic grazers. Although megalopae spend time in benthic habitats and could hypothetically benefit from the camouflage provided by decorations, the energetic trade-off associated with decorating (Berke & Woodin 2008b) may be too costly for megalopae. It is also possible that decorations are a disadvantage in the plankton, increasing the visibility of the megalopae and reducing their swimming efficiency.

Active decorating began immediately in first instar juveniles, using different materials than adults. The latter decorated with pieces of sponge, algae, bryozoan, or other living organisms from their habitats (Berke & Woodin 2009, S. R. Hein & M. W. Jacobs pers. obs.), while first instar juveniles decorated with pieces of organic debris. There are several possible reasons for this ontogenetic shift in preferred decorating materials.

First, decoration preference in early stage *O. gracilis* may be constrained by the size and strength of their chelae or hooked setae. Early juveniles may not be strong enough to cut or rip some materials, or their setae may not be able to retain them. Decoration is energetically costly (Berke & Woodin 2009), suggesting that crabs choose materials with morphological properties that reduce handling time and improve retention on the hooked setae. Consistent with this hypothesis, previous authors have suggested that adult crabs may select certain decorating materials over others based on their morphological properties (Stachowicz & Hay 2000, Cruz-Rivera 2001, Hultgren et al. 2006). While to our knowledge handling time for decorating materials has not been measured,

prey-handling time does significantly impact prey preference in other species of crabs (Creswell & McLay 1990, Seed & Hughes 1995). The cancrivore crab *Cancer novaezelandiae* appears to optimize handling time per unit of energy intake by selecting specific species and size classes from among a wide range of potential prey items (Creswell & McLay 1990). A similar optimization of energy expenditure per amount of benefit gained by decorating may account for the observed decorating preferences of juvenile *O. gracilis*.

Second, crabs may select decorating materials that maximize their visual crypsis depending on their size. Camouflage in decorator crabs is often thought to work simply by making the crab look less crab-like (Cruz-Rivera 2001). However, it is possible that crabs are using a more advanced form of camouflage, specifically choosing decorating materials to help themselves blend-in based on substrate contrast and configuration or particle size. For example, the cuttlefish *Sepia officinalis* displays uniform coloration on low-contrast or small-particle-size backgrounds, but a highly contrasting disruptive pattern on high-contrast or large-particle-size backgrounds (Barbosa et al. 2008). The benthic substrates occupied by *O. gracilis* adults and juveniles are patchy mosaics. If newly settled juveniles are smaller than the average patch size in their habitat, then it may be advantageous for them to adopt a uniform appearance by decorating with a single item. Adult crabs, by contrast, may blend-in best by selecting a wider variety of items, matching the level of contrast and patch size of their habitat. Although this hypothesis remains to be tested, we did observe that many of the decorations on adult crabs were similar in size to, or larger than, those of the juveniles.

Third, the use of organic debris may facilitate juvenile dispersal because it maximizes camouflage in a wide range of habitats. The camouflage provided by decorating in majoids is considered a form of acquired or plastic camouflaging, which typically allows the animal to exploit a range of habitats (Hultgren & Stachowicz 2008). Crabs frequently undergo an ontogenetic shift in habitat as they age (Hultgren & Stachowicz 2010), even undergoing a post-settlement redistribution as early as the second to ninth instar (Moksnes 2002). In our experiments, organic debris was widely distributed throughout the available habitats. By using this debris, the juvenile crabs may greatly increase the number of habitats with which they blend, facilitating their ability to move between such habitats. The extent of movement between habitats on the scale of days or weeks has

not to our knowledge been quantified for either adult or juvenile *O. gracilis*.

Finally, decorations are generally not considered to be a major source of nutrition in majoids, although some species have been known to eat their decorating materials, particularly in times of starvation (Kilar & Lou 1986, Woods & McLay 1994a). Little is known about the diet of very young decorator crabs, and so we cannot eliminate the possibility that the debris used in decoration also plays a dietary role.

The acquisition of hooked setae and the onset of decorating behavior coincide with the completion of the habitat transition from plankton to benthos. This transition is initiated during the megalopal stage, with one important role of the megalopa being selection of the habitat where the juvenile will live. Consistent with this, *O. gracilis* megalopae and juveniles demonstrated clear and similar habitat preferences. Both stages consistently chose branching bryozoans over any other of the offered choices. Such habitat preference in megalopal and juvenile decorator crabs may be driven by the availability of good shelter from predators (Moksnes 2002), food availability, the availability of decorating materials for camouflage, or some combination of these. Branching bryozoans are structurally complex, offering an abundance of suitable hiding places (Botero & Atema 1982, Fernandez et al. 1993, Moksnes 2002). The bryozoans contained large accumulations of attached particulate organic debris, offering the juvenile crabs a large source of preferred decorating materials immediately after metamorphosis. Finally, amongst the bryozoans were small pieces of algae, detritus, and tiny invertebrates, which are known food items of other majoids (Woods & McLay 1994b, Guinot & Wicksten 2015).

The onset of decorating behavior was coupled with the molt from megalops to juvenile, and first instar juveniles decorated selectively, profusely, and immediately after metamorphosis. These results strongly suggest that early instar juveniles rely on visual crypsis for protection from predation. We also observed an ontogenetic shift in decorating material preference: young juveniles decorated with organic debris, while older crabs decorated with sponges, bryozoans, algae, and other living materials from their environments. We hypothesize that decorating behavior in *O. gracilis* is specifically adapted to maximize protection at different sizes and life stages by favoring different materials; a more detailed ontogenetic series is required to test this hypothesis. The ontogeny of decorating behavior is a useful system for exploring how behavior, morphology, and habitat transitions can be coordinated during metamorphosis.

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*Editorial responsibility: Pei-Yuan Qian,
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