

Size-related habitat shifts facilitated by positive preference induction in a marine kelp crab

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Individual variation in habitat use has important ecological and evolutionary consequences. Here, we combine developmental and functional approaches to study habitat use in *Pugettia producta*, a marine crab that sequesters pigments from the algae it inhabits and consumes to camouflage with different colored algal habitats. *Pugettia* from different habitats differ in size and color; individuals living in red intertidal algae are small and red, whereas crabs in amber-colored kelp forests are larger and more amber. We examine the developmental causes (effects of size and experience) and the functional consequences (growth and mortality rates) of size-specific habitat use in *Pugettia*. We demonstrate that positive preference induction may be a mechanism facilitating size-specific habitat use: prior feeding experience with kelp (in the field or laboratory) increases habitat preferences for kelp but only for larger crabs. Habitat use also has important fitness consequences; small red crabs grow equally fast on both kelp and red algae but suffer much higher mortality in kelp; large red crabs grow faster on kelp diets relative to red algae but experience only marginally higher mortality in kelp. Thus, habitat-specific mortality rates may explain the use of intertidal red algal habitats by small crabs, whereas reduced growth of large crabs on red algae may help trigger shifts to subtidal kelp habitats. Size-specific functional consequences of habitat use may select for developmental processes—such as positive preference induction—that facilitate shifts in habitat use in *Pugettia* and other phenotypically plastic organisms that shift habitats through ontogeny. **Key words:** habitat selection, kelp forest, ontogenetic habitat shift, positive preference induction, *Pugettia producta*, size. [*Behav Ecol* 21:329–336 (2010)]

Individual variation in habitat use has important ecological and evolutionary consequences for a species (Polis 1984; Werner and Gilliam 1984; Bernays and Graham 1988; Bolnick et al. 2003; Stamps 2003). Habitat selection, like other components of behavior, can be approached from either a proximate or an ultimate perspective, that is, by studying “how” an animal selects habitats and/or “why” (in terms of fitness) an animal may ultimately make such choices (Tinbergen 1963; Krebs and Davies 1997). In a proximal sense, animals may choose habitats by cueing on stimuli such as color, habitat architecture, temperature, predator presence, and other factors (Holbrook and Schmitt 1988; Hacker and Steneck 1990; Lima and Dill 1990; Hacker and Madin 1991; Childress and Herrnkind 2001; Garcia et al. 2004; Ahnesjö and Forsman 2006). Habitat choices of animals may also be influenced by developmental processes such as ontogenetic changes in behavior or physiology (Childress and Herrnkind 1996, 2001; Williamson et al. 2004; Freeman 2006) and the effects of learning and experience (Jermy 1987; Bernays and Weiss 1996; Davis and Stamps 2004; Botello and Krug 2006; Poore and Hill 2006). Ultimately, where an animal chooses to live is shaped by the fitness consequences—including growth, mortality, and mating success—of living in different habitats (Werner and Gilliam 1984; Bernays and Graham 1988; Dahlgren and Eggleston 2000).

Combined examination of both the proximate and ultimate causes of habitat choice has resulted in fundamental advances in our understanding of the ecology and evolution of these behaviors. For example, determining both the plant chemical

cues used in habitat selection and the fitness consequences of those choices has led to a more satisfactory explanation of the evolution of host specialization in phytophagous insects and herbivorous crustaceans (Price et al. 1980; Hay et al. 1987; Bernays 1988; Bernays and Graham 1988; Stachowicz and Hay 1999). Similarly, examining both the developmental causes and the functional consequences of habitat preferences can elucidate how developmental processes may be favored by selection to drive individual variation in habitat use (Stamps 2003).

Many animals undergo ontogenetic (size-related) habitat shifts (Polis 1984; Werner and Gilliam 1984). However, much of the research on ontogenetic habitat shifts has focused on the functional consequences of habitat use rather than on understanding exactly how such behavioral decisions and shifts are made. For example, many studies have tested adaptive models of ontogenetic niche shifts (e.g., Werner and Gilliam 1984), but few of these have concurrently examined the developmental mechanisms that cause these changes in behavior (Werner and Hall 1988; Gosselin 1997; Dahlgren and Eggleston 2000; Ide 2009; but see Williamson et al. 2004). Here, we examine both the developmental causes and the functional consequences of size-related behavioral shifts in habitat use in the marine crab *Pugettia producta*.

Pugettia producta, commonly known as the kelp crab, inhabits and consumes several different species of algae along the United States west coast. As it grows, *Pugettia* typically changes color to maintain camouflage as it moves to different algal habitats by sequestering pigments from algae into its developing cuticle (Hines 1982; Iampietro 1999; Hultgren and Stachowicz 2008). Smaller, red individuals are typically found in intertidal red algae and shallow subtidal red algae closer to shore, whereas larger, more amber-colored individuals are found in the fronds of amber-colored giant kelp *Macrocystis pyrifera* (hereafter “kelp”), where they typically breed (Hines 1982; Wicksten and Bostick 1983; Iampietro 1999; Hultgren and Stachowicz 2008). As the smallest crabs are typically only

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Received 18 March 2009; revised 15 October 2009; accepted 9 December 2009.

found in red algae, *Pugettia* are thought to undergo an ontogenetic habitat shift from red algae to kelp (Hines 1982). Predation intensity is often higher in subtidal habitats (such as kelp forests) relative to intertidal habitats (Connell 1972; Menge 1978), and one functional explanation for ontogenetic habitat shifts in *Pugettia* is that larger individuals more successfully avoid predators (and grow faster) on kelp than small individuals. Differences in size among habitats could also occur if crabs settle equally in both habitats but grow faster and to larger sizes in kelp forests. Investigating size-specific growth and mortality rates in this system can help to distinguish between these different scenarios.

Independent of size, any crabs that migrate from red algae to kelp will initially be mismatched in color, posing a problem for the evolution of ontogenetic shifts. Color change occurs only when crabs molt, and there is a time lag of 14–40 days (the mean time between molts) between when a crab migrates to a new habitat and when it molts to match the habitat (Hultgren and Stachowicz 2008). This temporary camouflage mismatch has fitness consequences: red crabs in amber-colored kelp forests suffer much higher rates of mortality than amber crabs (Hultgren and Stachowicz 2008). Investigating the effects of size and prior habitat experience on habitat preferences could help to explain how preferences for kelp develop despite the camouflage mismatch that occurs when red crabs migrate from intertidal to kelp habitats. For example, larger crabs may have stronger intrinsic habitat preferences for kelp or may be more likely to experience (and learn to prefer) kelp habitats in the field. In this study, we use surveys, field experiments, and laboratory assays to examine how *P. producta* size and prior experience shape the habitat preferences, growth, and mortality of crabs living in intertidal red algae and subtidal kelp habitats.

MATERIALS AND METHODS

Size distributions among habitats

To examine differences in *P. producta* size among different habitats, we conducted field surveys in 3 macroalgal habitats in and around Bodega Bay, CA (long 123°02'13"W, lat 38°18'21"N) during summer 2004 and 2005, when all 3 habitat types were abundant. These surveys are extensively described elsewhere (Hultgren and Stachowicz 2008); briefly, the 3 sampled habitats were 1) intertidal red algae (0 to 1-m depth, dominated by red algae); 2) subtidal red algae (1 to 8-m depth, dominated by red algae); and 3) subtidal kelp forests composed of the amber-colored giant kelp *M. pyrifera* (referred to here as kelp), which occasionally had an understory of subtidal red algae. Intertidal habitats were surveyed at 2 sites adjacent to Bodega Marine Laboratory, and subtidal red and kelp habitats were surveyed at 2 sites in Bodega Harbor, using randomly placed quadrats (subtidal and intertidal red algae habitats) or entire plants (kelp habitats), in which we measured the carapace width (CW) of each crab (total intertidal red $n = 59$, subtidal red $n = 19$, amber kelp $n = 73$).

As size data among the 3 habitats were nonnormal (despite various transformations), we used 2 methods to examine differences in size among habitats. First, to examine differences in size among habitats while incorporating secondary variables (site and year effects), we implemented permutational multivariate analyses of variance (PERMANOVA) using the program DISTLM (Anderson 2004). We coded data as the number of crabs in 13 equally spaced size classes, used the program XMATRIX (Anderson 2003) to code design matrices incorporating main (habitat) and secondary (site, year) variables, and performed 9999 permutations of raw data to

obtain P values using the Bray–Curtis dissimilarity index. Initial multivariate analyses detected no significant effects of site (analyzed within each habitat type; permutation $P > 0.549$), so we tested whether there were effects of habitat, year, or habitat \times year interactions on crab size using PERMANOVA. Second, to examine pairwise differences in size among habitats, we pooled all crabs from all sites and years (within a habitat type) and used nonparametric Kruskal–Wallis tests (JMP 5.1, SAS Institute, Cary, NC) and Kruskal–Wallis post hoc tests (Conover 1999).

Effects of crab size and experience on habitat preference

To investigate whether differences in habitat preference between large and small crabs could have created or maintained the differences in size we saw between habitats (see Results), we conducted 3 separate habitat selection experiments to assess the presence, and cause, of individual differences in habitat preference. All 3 experiments were conducted in outdoor mesocosms (treated as individual replicates) that were supplied with filtered flow-through seawater at $\sim 45 \text{ l} \cdot \text{min}^{-1}$ and covered with netting to approximate the filtered light conditions typical of algal habitats in the field. Mesocosms were 400 l (1-m diameter, 0.5-m deep) and allowed kelp to float to the surface and mimic the vertical structure of kelp in the field. Equal masses of both “habitats” (pieces of red algae and kelp) took up similar cubic volume, so we standardized habitat availability by mass (50–150 g of each habitat depending on crab size or $\sim 0.35 \text{ g habitat} / \text{cm CW}$) in each mesocosm, using fishing weights to anchor algae to the bottom. Crabs did not prefer any particular side of the mesocosm in the absence of algal habitats, and habitats were placed in random orientations equidistant (10 cm) from the center. At the beginning of each experiment, one crab was placed in the center of each mesocosm, allowed to acclimate for 4 h, and then observed every 6 h, twice each day and night. During observations, both habitats were gently probed to check for crabs, and night observations were conducted with a flashlight that only transmitted red light (crabs are unaffected by red light) to minimize disturbance. Crabs spent most of their time on algae (97% of all observations), and at least 77% of individual crabs switched habitats at some point during the experiment. Experiments I and III were run for 48 h each in 3–5 experimental blocks, and experiment II was run for 24 h in 6 blocks (crabs made similar habitat selections during each 24-h period of experiments I and III).

In experiment I (habitat source), we tested for preference differences between red crabs collected from intertidal red algae (i.e., juvenile habitat) and amber crabs from kelp forests (adult habitat). We also tested for any effects of size on habitat preference. We extensively searched intertidal red algae and kelp forest habitats to collect the widest possible size range of crabs in each habitat ($n = 28/\text{habitat}$, $\text{CW} = 1.2\text{--}5.5 \text{ cm}$) and selected individuals such that the size range and mean size of crabs were similar between habitat source treatments ($F_{1,54} = 0.0045$, $P = 0.95$). Crab color was quantified in all experiments by analyzing standardized photographs on Adobe Photoshop 7.0 using previously described methods (Hultgren and Stachowicz 2008). Briefly, red channel values were used to quantify color, such that amber crabs had higher “color” values (50–100) and red crabs had lower color values (15–40). Crab color differed between habitat type treatments (t -test, $P < 0.0001$; amber crabs had higher color values than red crabs, see “Results”). In this experiment, crabs were offered a choice between kelp (*Macrocystis*) and the red algae *Chondracanthus corymbifera* (hereafter “subtidal red algae”), a dark red alga that has a blade-like morphology similar to

Macrocystis and occurs adjacent to kelp (as an understory species) and in lower intertidal red habitats.

In experiment II (laboratory experience and size), we tested for the effect of prior kelp consumption on habitat preferences of large and small crabs. We attempted to mimic a dietary and habitat shift in *Pugettia* by collecting crabs from juvenile intertidal red algae habitats (typically *Neorhodomela* sp.) and maintaining them in the laboratory for ~30 days in 3 randomly assigned treatments: 1) no change (fed red algae for 30 days), 2) low experience (fed red algae for 26 days, followed by kelp for 4 days), and 3) high experience (fed kelp for 30 days). We crossed these 3 experience treatments with crab size (i.e., large and small). To define large and small crab size categories, we first used survey data to identify crabs in the “transition” size range (i.e., the largest crabs occurring in intertidal red algae and the smallest crabs occurring in kelp forests, Figure 1) and set the boundary between size classes in the middle of this range (large crabs = 1.90–5.18 cm CW, mean \pm 1 standard error [SE] = 2.52 \pm 0.12 cm; small crabs = 0.96–1.86 cm CW, mean = 1.43 \pm 0.47). This resulted in a total of 6 treatments by size combinations ($n = 12$ each). In the habitat selection experiment, crabs were simultaneously offered as habitat the 2 algae used as food in rearing treatments: kelp and red algae, the latter consisting of *Neorhodomela larix* and *Sarcodiotheca gaudichaudii*, 2 species common in intertidal and subtidal red algae habitats that are the most preferred dietary choices for *Pugettia* in feeding trials (Hultgren K, unpublished data).

In experiment III (molt status), we tested whether changes in habitat preference were caused by molt-induced differences in color. Crabs were collected from intertidal red algae and were fed kelp in the laboratory for ~30 days, at which point ~50% of the crabs had molted and were more amber (mean color = 68.44, one way t -test, $P < 0.0001$) than remaining red unmolted crabs (mean color = 30.61). We selected a subset of large (mean CW \pm 1 SE = 2.46 \pm 0.12 cm) unmolted ($n = 19$) and molted ($n = 17$) crabs, such that treatment groups did not differ in size ($F_{1,34} = 1.27$, $P = 0.26$). We offered each crab a choice of kelp (*Macrocystis*) and red algae (a combination of *Chondracanthus* and *Sarcodiotheca*) as habitat.

For each experiment, we measured habitat use using p_{kelp} (proportion of total observations on kelp). Although crabs were often observed feeding on the habitat they used, we were unable to simultaneously measure feeding, and p_{kelp} values reflect both foraging and general habitat preferences. We

examined diel differences by comparing p_{kelp} during day checks versus night checks for each treatment by experiment combination with nonparametric paired Wilcoxon tests.

For experiments I and III, we arcsine transformed p_{kelp} to achieve normality and homogeneity of variance and initially tested whether p_{kelp} varied among treatments using 2-way general linear models (GLMs) with main treatments (habitat source or molt status) and secondary variables (CW and experimental block) using JMP 5.1 (SAS Institute). There were neither any significant effects of block or block by treatment interactions ($P > 0.153$) nor any effects of size ($P > 0.136$) in either experiment, so we removed nonsignificant variables from the analysis and reanalyzed data (Underwood 1981). Data from experiment II (dietary experience by size) violated assumptions of homogeneity of variance and normality, even after various transformations, so we examined kelp habitat use using a generalized linear mixed model (Bolker et al. 2009) implemented using the lme4 package (Bates and Sarkar 2007) on R (R Development Core Team 2008). This method allowed us to include random effects ($n = 6$ blocks) and compare models with different combinations of fixed effects (size, experience, and the size \times experience interaction) using the Akaike information criterion (AIC; Burnham and Anderson 2002). We also ran analyses coding experience into 2 treatments (no experience and experience, the latter including high and low experience treatments). There was no evidence of overdispersion, so we used the Poisson distribution with a LaPlace approximation (Bolker et al. 2009) and compared different models using the AIC_c (a small sample version of AIC).

For all experiments, we examined if crabs in a treatment preferred one habitat over another by testing if p_{kelp} was significantly different from 0.5 (the null expectation; $p_{\text{kelp}} > 0.5$ indicates a preference for kelp, $p_{\text{kelp}} < 0.5$ indicates a preference for red algae).

Functional consequences of habitat shifts on mortality and growth

To examine how size may influence the relative advantages of living in intertidal red algae or kelp, we measured size-specific rates of *Pugettia* mortality and growth in these different habitats. As we were most interested in any size-based advantages of migrating to kelp before crabs changed color (i.e., how habitat shifts might initially occur in the field), we used large red and small red crabs from juvenile red algae habitats in experiments to quantify growth rates (in the laboratory, feeding on either intertidal red algae or kelp) and mortality rates (in the field, using tethering experiments). We also present data on growth rates from a smaller experiment comparing growth of amber crabs on intertidal red algae or kelp. These experiments were also designed to see if size-related differences in growth and mortality (rather than ontogenetic habitat shifts) could explain differences in size among habitats (e.g., higher mortality of large crabs in intertidal red algae and of small crabs in kelp and/or higher growth for all crabs on kelp). Size classes of crabs were defined as in the habitat choice experiments (large mean CW \pm 1 SE = 2.31 \pm 0.06 cm, small = 1.32 \pm 0.04 cm).

We calculated growth rates by feeding crabs a diet of either kelp (*Macrocystis*) or intertidal red algae (*Neorhodomela* and *Sarcodiotheca* sp.) consumed in the field and used in habitat selection experiments (large crabs $n = 15$ –17, small crabs $n = 29$ –33). Growth experiments were conducted in outdoor flow-through seawater systems in 2 different years (2004 and 2007) that were treated as experimental blocks. Although abiotic or biotic factors (such as temperature or predation risk) can

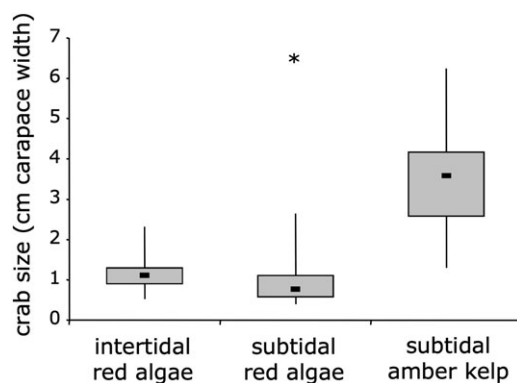


Figure 1
Boxplots of *Pugettia* size (cm CW) in different habitats. Horizontal line indicates median size, box shows 50% confidence intervals, and whiskers indicate maximum and minimum size of individuals in each habitat. Asterisk (*) indicates significant differences in size among habitats (PERMANOVA).

modify the effect of diet on growth in the field, we could not measure growth rates on unconstrained crabs in the field for this study as it is extremely difficult to track tagged individuals after they molt (Hines 1982). Crabs were individually maintained in 3-l plastic buckets and fed their assigned diet ad libitum for 70–100 days, or until each individual crab had molted. We estimated relative growth rate using the following formula: $\ln(CW_e \cdot CW_s^{-1}) \cdot (\text{days to molt})^{-1}$, where CW_s = start CW, CW_e = CW after one molt; crabs that molted during the first week of the experiment were not used in the analysis. Among treatment groups, growth rates were normally distributed and had similar variance, so we performed a 3-way GLM with size (large or small), habitat (i.e., diet; kelp or intertidal red algae), and year (block) as factors and tested all interactions using JMP 5.1 (SAS Institute). There were no significant block or block by main treatment interactions ($P > 0.094$), so we removed all block effects from the analysis and reanalyzed data.

We also compared growth rates on kelp or intertidal red algae for amber crabs (kelp $n = 11$, red $n = 8$) using data from another experiment run in summer 2003. Crabs spanned the small-large size range (range = 1.5–3.4 cm CW, mean ± 1 SE = 2.27 ± 0.141 cm), but experiments were otherwise identical to those conducted in 2004 and 2007. Growth data were not normally distributed, so we compared growth rates between habitats using Mann–Whitney U tests.

We examined mortality rates by tethering large red and small red *Pugettia* in adult (kelp) and juvenile (intertidal red algae) habitats in August 2007. Tethering experiments were conducted at the same intertidal and subtidal locations used in size surveys. For each experiment, red *Pugettia* were collected from the intertidal, classified as either large or small (using the size classes defined in habitat selection and growth experiments), randomly assigned to kelp forest habitats (large $n = 25$, small $n = 27$) or red intertidal habitats (large $n = 26$, small $n = 34$), and tethered with 8-lb braided fishing line (Spiderwire, Spirit Lake, IA) to eyebolts at mean low water (in the red intertidal among *Neorhodomela* and *Sarcodiotheca* sp.) or kelp stipes (in subtidal kelp forests) using cable ties. Crabs were checked daily, and we calculated mean mortality rates for each size habitat treatment by averaging the scores of each individual (survived = 0, consumed = 1) daily over the course of the experiment. Preliminary studies using this method indicated that unconsumed crabs could remain effectively tethered for >2 weeks in the field. Although tethering experiments may overestimate overall mortality rates, we use them here to examine relative differences in mortality between habitats and furthermore minimized experimental artifacts unrelated to these differences (Peterson and Black 1994) by only scoring crabs as eaten if pieces of the crab's carapace remained on the tether. This produced a conservative measure of mortality designed to minimize differences in tether efficacy between habitats (e.g., longer periods of submergence in subtidal kelp) or among crabs of different sizes (e.g., increased escape abilities for larger crabs). Data were nonnormally distributed, so we analyzed mortality differences between habitats separately for large and small size classes using Mann–Whitney U tests.

RESULTS

Size differences among habitats

Pugettia differed in size among habitats (multivariate PERMANOVA; habitat pseudo $F = 12.375$, permutation $P < 0.0001$, Figure 1), increasing in size in kelp compared with red algae, as reported in previous studies (Hines 1982; Iampietro 1999). There also were significant effects of year ($F = 4.648$, $P = 0.0002$) on crab size but no year \times habitat

effects ($F = 0.842$, $P = 0.616$). Significant effects of year may be due to differences in the number of crabs sampled from each habitat type in different years, as there were no differences in crab size among years when analyzed within each habitat type ($P > 0.159$). There were also significant differences in size among habitats when we coded size as a continuous variable (Kruskal–Wallis test, $\chi^2 = 104.885$, degrees of freedom [df] = 2, $P < 0.0001$). Crabs from kelp were significantly larger than crabs from subtidal red algae (Kruskal–Wallis post hoc test, $P < 0.05$) and intertidal red algae ($P < 0.05$), whereas crabs from subtidal and intertidal red habitats did not differ in size ($P > 0.05$).

Individual variation in habitat use

In experiment I (habitat source), crabs from kelp habitat spent more time on kelp than did crabs from red intertidal habitat ($F_{1,54} = 9.055$, $P = 0.004$; Figure 2). Interestingly, there were no effects of crab size ($F = 0.002$, $P = 0.963$) and no crab size by source interactions ($F = 0.195$, $P = 0.660$)—that is, the largest crabs from red algae did not have stronger preferences for kelp than smaller crabs (p_{kelp} never varied as a function of size in linear models; red intertidal habitat source $P = 0.653$, slope = -0.0002 , $R^2 = 0.007$; kelp habitat source $P = 0.7306$, slope = 0.5643 , $R^2 = 0.0046$). Crabs preferred the habitat source they were collected from: amber crabs from the kelp habitat source preferred kelp ($p_{\text{kelp}} > 0.5$, 2-tailed $P = 0.021$; Figure 2), whereas red crabs from intertidal habitat preferred red algae ($p_{\text{kelp}} < 0.5$, $P = 0.017$; Figure 2).

In experiment II, there was support for effects of both size and dietary experience (Figure 3). The confidence set of

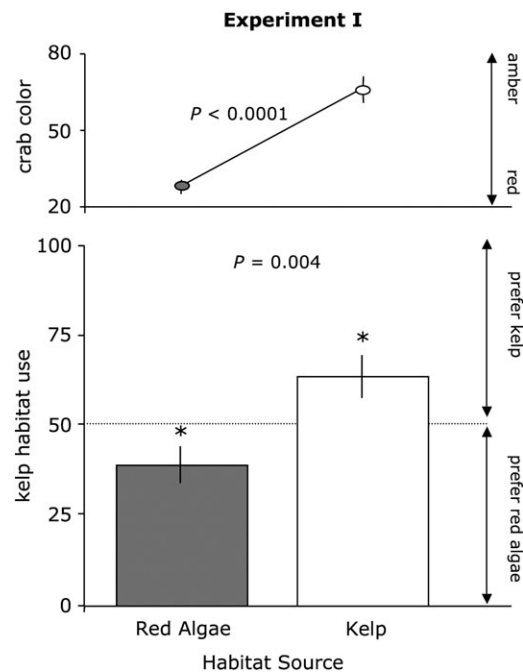


Figure 2

Crab color (top panel, mean ± 1 SE) and kelp habitat use (percentage of observations on kelp habitat, mean ± 1 SE) by crabs from intertidal red algae habitat source and kelp habitat source. P values indicate whether there are significant differences in crab color (t -test) or kelp habitat use (GLM) between treatments; dashed line in bottom panel indicates null expectation of habitat use (50%); asterisks (*) indicate significant preferences for kelp (means falling above the line) or for intertidal red algae (means falling below the line).

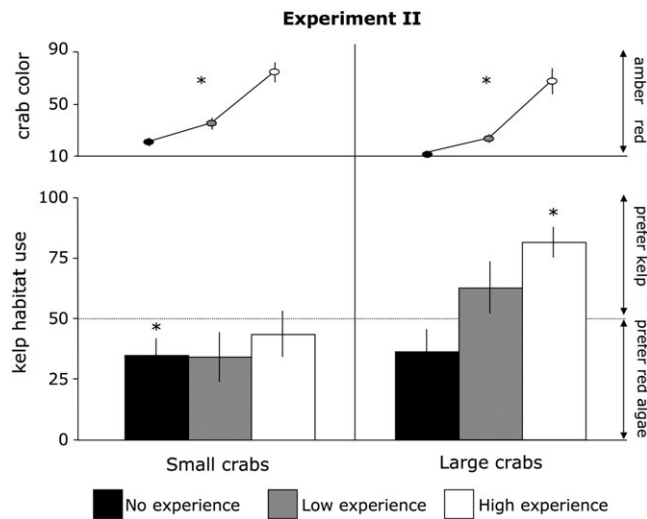


Figure 3
Crab color (top panels, mean \pm 1 SE) and kelp habitat use (percentage of observations on kelp habitat, mean \pm 1 SE) by small and large crabs across 3 experience treatments. For crab color, asterisks indicate significant differences in color as a result of treatment (Kruskal–Wallis test; see text for additional details). For habitat use, dashed line and asterisks as in Figure 2.

candidate models (models with AIC_c within 10% of the best model) all included random block effects (but no block by main effect interactions), and included models with size only ($AIC_c = 47.54$), size and dietary experience ($AIC_c = 47.57$), dietary experience only ($AIC_c = 50.20$), and a size \times dietary experience interaction ($AIC_c = 50.89$). There was stronger support (lower AIC_c values) for a size \times dietary experience interaction if we categorized experience into 2 treatments (crabs with no experience and crabs with high or low experience); the confidence set included models with experience and size ($AIC_c = 46.38$), a size \times dietary interaction ($AIC_c = 47.20$), size only ($AIC_c = 47.54$), and experience only ($AIC_c = 49.08$). When we tested preferences of individual treatment groups (size \times experience) to assess the form of the possible interaction between factors, we found that dietary experience with kelp significantly increased preference for kelp only for large crabs in the high experience treatment (30 days of feeding on kelp; $p_{\text{kelp}} > 0.5$, $P = 0.002$, Wilcoxon signed-rank test). Small crabs in the no experience treatment (30 days of red algae) preferred red algae ($p_{\text{kelp}} < 0.5$, $P = 0.027$), and crabs in all other treatments preferred neither kelp nor red algae (Figure 3).

Because crabs in experiment II differed in the amount of kelp they consumed between treatments (and some crabs molted during treatment periods), there were significant differences in crab color as a function of dietary experience (large and small crabs pooled, Kruskal–Wallis $\chi^2 = 33.831$, $df = 2$, $P < 0.0001$; Figure 3). Crabs in the no experience treatments were more red (mean color = 72.12) than crabs in the low experience and high experience treatments (Kruskal–Wallis post hoc test, $P < 0.05$). Longer duration of experience with kelp (30 days vs. 4 days) also resulted in crabs that were on average more amber in color ($P < 0.05$), primarily because a greater number of crabs molted amber in 30 days experience treatments.

In experiment III (molt status), crabs of different molt status (i.e., color) but with equal experience feeding on kelp did not differ in their preferences for kelp ($F_{1,34} = 0.455$, $P = 0.504$; Figure 4). As was seen in experiment II, crabs with 30 days of

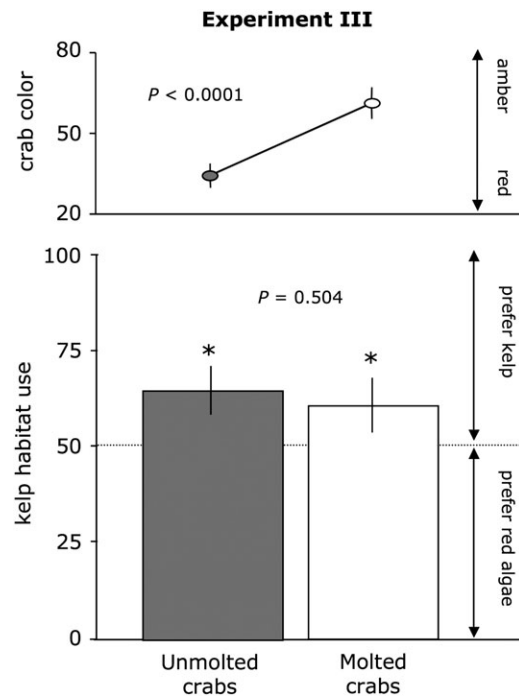


Figure 4
Crab color (top panel, mean \pm 1 SE) and kelp habitat use (percentage of observations on kelp habitat, mean \pm 1 SE) as a result of molt status. P values (top and bottom panels), dashed line, and asterisks (bottom panel) as in Figure 2.

experience feeding on kelp (whether they were molted or unmolted) preferred kelp over subtidal red algae (pooled across both treatments: 2-tailed $P = 0.006$, $N = 36$), even though molted crabs were more amber than unmolted crabs (t -test, $P < 0.0001$; Figure 4). Crab size did not affect preference for kelp ($P = 0.136$), presumably because crabs were all in the “large” size class. Thus, on balance, the habitat choice experiments point to an important role of prior experience in determining crab preference for kelp and that effects of other variables (size, color) are driven in part by differences in experience among groups.

After pooling all data from experiments I–III, we detected a modest increase in crab use of kelp habitat at night relative to day (mean increase = 14.3%, Wilcoxon signed-rank test $P < 0.001$; data not shown).

Consequences of size-dependent habitat use on growth and mortality rates

In growth assays, crabs differed in relative growth rate as a function of both their initial size and whether they were fed kelp versus red algae (2-way GLM, $F_{3,90} = 5.830$, $P = 0.001$; Figure 5a). In addition to main effects of diet ($P = 0.002$) and size ($P = 0.027$), there was a diet by size interaction ($P = 0.025$) because large red crabs grew nearly twice as fast on kelp diets relative to red algae diets (Tukey test, $P < 0.05$), whereas small crabs grew equally on both diets ($P > 0.05$). In separate experiments specifically comparing growth on kelp versus intertidal red algae diets for amber crabs (2003), amber crabs consuming kelp grew significantly faster than those consuming red algae (Mann–Whitney U test $Z = -2.023$, $df = 1$, $P = 0.043$; Figure 5b).

In tethering experiments, small red crabs had significantly higher mortality rates in a subtidal kelp forest relative to intertidal red algae habitat (Mann–Whitney U test, $Z = 2.922$,

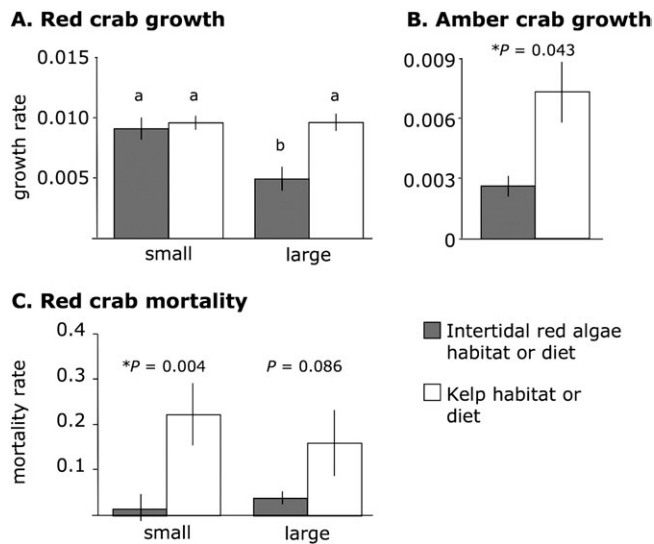


Figure 5
Red crab (A) and amber crab (B) growth rate on different diets ($\ln(CW_e \cdot CW_s^{-1}) \cdot (\text{days to molt})^{-1}$, least-squared mean \pm 1 SE), and (C) red crab mortality in different habitats (mean mortality \pm 1 SE more than 48 h). In (A), means with different letters are significantly different using Tukey post hoc tests; In (B, C), P values indicate whether there are significant differences between treatments (Mann–Whitney U tests; asterisks indicate significant differences).

$P = 0.004$, Figure 5c). Large red crabs differed only marginally (but not significantly) in mortality rate among habitats ($Z = 0.083$, $P = 0.086$; Figure 5c).

DISCUSSION

Our study suggests that size-related differences in habitat use in *P. producta* are not simply a result of differential mortality and growth in different habitats. Instead, our data support the idea that size-related differences in habitat use are driven by a flexible ontogenetic shift in habitat preference from red algae to kelp, facilitated by size-specific preference induction for kelp. This shift has positive functional consequences for *Pugettia*, in terms of mortality and growth.

Developmental causes

Habitat selection experiments revealed that habitat preferences in *Pugettia* were influenced by size and experience. Experiment I demonstrated that individuals preferred the habitat from which they were collected, regardless of size, suggesting habitat use is maintained by individual differences in habitat preference. Experiment II indicated that habitat preferences for kelp could be experimentally induced by dietary experience with kelp but only for large crabs. Large crabs reared on kelp for 30 days preferred kelp habitat, but experience did not affect habitat preferences of small crabs, despite the fact that many small crabs had molted amber and were well-matched with kelp habitat. Experiment III (molt-ing) demonstrated that positive effects of experience on preference for kelp were not due solely to the changing color of crabs fed kelp, as large crabs with similar experience (30 days of feeding on kelp) preferred kelp, regardless of whether they had molted to become amber color or not. Thus, there is no evidence that the crabs actually assess their environment and/or own color visually then act to minimize mismatch.

Together these data are consistent with positive preference induction—increases in use of a habitat or diet as a result of prior experience (also known as “ingestive conditioning” or “induced preference”)—as a mechanism influencing habitat selection. For example, in some phytophagous insects, early experience feeding on a certain host plant can induce specific dietary preferences for that plant (Jermy et al. 1968; Jermy 1987). Field data suggest this mechanism could be responsible for the size-specific patterns of *Pugettia* habitat use in the field. Although the distance a crab may have to travel from the intertidal to the middle of kelp forest can range from 10 to 100s of meters, red algae and kelp habitats often grade together, and gut content data show *Pugettia* from red algae habitat often feed on drift kelp swept into the intertidal (Hines 1982; Iampietro 1999). Furthermore, short-term mark-recapture experiments (<1 week) have demonstrated that larger *Pugettia* typically moved more (up to 40 m) than smaller *Pugettia* (10 m; Hines 1982), indicating that large *Pugettia* from red algae are more likely to experience kelp habitats while foraging than are small *Pugettia*. This, combined with our demonstration that only large individuals develop an induced preference for kelp, can help explain why only large crabs are found in kelp habitats.

Preference induction is common in organisms such as phytophagous insects that (like *Pugettia*) use the same plants for habitat and food (Jermy et al. 1968; Jermy 1987; Papaj and Prokopy 1989), and experience also influences habitat or diet preferences in many marine invertebrates (Hall et al. 1984; Pennings et al. 2000; Baeza and Stotz 2003; Darmaillacq et al. 2004; Poore and Hill 2006). However, the size-specific nature of kelp habitat preference induction in *Pugettia* is relatively unique. One potential proximate mechanism explaining this pattern is differences in habitat architecture. Whereas most red algae used by *Pugettia* in the field is typically bushy and short (with individual fronds typically <20-cm long) and easily accessible to both large and small crabs, giant kelp grows in deeper water and can reach heights of 10–20 m in the field (Hultgren K, personal observation). Small crabs may be less efficient at handling and climbing kelp fronds than large crabs, such that experience with kelp would only increase preference for kelp in large crabs. In one other case of size-specific induction, parasitoid wasps (*Pachycrepoideus vindemiae*) only exhibited positive preference induction for host species with pupae that were of a size that the individual could quickly handle (Morris and Fellowes 2002). Alternatively, the neurophysiological mechanism for forming a preference for kelp may only develop after crabs have reached a certain size or age.

Functional consequences

Regardless of the proximate mechanism that drives the size-dependent preference induction in *Pugettia*, our data on growth and mortality indicate that this behavioral pattern has adaptive functional consequences. Small red crabs experience no growth benefits to feeding on kelp, yet suffer increased predation in kelp; conversely, large crabs suffer only marginally higher predation in kelp forests but grow nearly twice as fast on kelp diets (compared with red algae habitats). Growth differences appear largely driven by consumption rates (large red crabs feeding on kelp had the highest consumption rate of any of the treatment groups), indicating feeding behavior or handling time—rather than higher efficiency of transforming kelp into growth—may drive differences in growth. Size-dependent preference induction may allow small red *Pugettia* to avoid kelp forests (where they experience higher predation risk), whereas allowing larger crabs to shift to kelp forests when they encounter them. Prior work has shown that there are few predation costs incurred

by being mismatched in red algae—small red and amber *Pugettia* are preyed on at similar rates in intertidal red algae habitats (Hultgren and Stachowicz 2008)—suggesting that it is not maladaptive for small crabs to remain in red algae, regardless of whether they had experienced kelp and molted amber.

Data presented here concur with predictions made from adaptive models of ontogenetic habitat shifts (Werner and Gilliam 1984) predicting that individuals should migrate to new habitats at a size at which growth rates are maximized (large crabs grow faster on kelp) and mortality rates are minimized (only small crabs suffer significantly higher mortality on kelp). Although our data demonstrate that large red crabs that migrate to kelp experience some predation risk (there was a trend toward higher predation in kelp habitats; Figure 5c), these predation risks are mitigated once these crabs have consumed enough kelp and molted amber to camouflage with kelp, reducing their predation rates by ~40% (Hultgren and Stachowicz 2008). Large red crabs consumed kelp rapidly (molting occurred in as few as 10 days), and crabs that have molted amber grow faster on kelp relative to red algae, suggesting that short-term costs of the shift pay off in increased growth rates. Additionally, our experiments demonstrated that experience feeding on kelp was correlated with crab color (crabs in kelp experience treatments were more likely to have molted amber; Figure 3). Positive preference induction may indirectly facilitate background matching without use of sensory systems such as color vision, which are limited or absent in most crustaceans (Cronin and Forward 1988; Horch et al. 2002). During this period of mismatch, the tendency for crabs to use kelp more at night than during the day may also help mitigate costs. Additional factors such as reproduction may also help explain why large *Pugettia* prefer kelp habitats; many have noted that *Pugettia* breed in kelp forests (Hines 1982; Wicksten and Bostick 1983), suggesting that reproductive fitness may be higher in kelp forests than intertidal red algae.

Combining the how and why of habitat selection behavior can be complementary, as studies on development of habitat preferences can uncover processes (such as positive preference induction) that underlie individual variation in habitat preferences. Similarly, studies on the functional consequences of habitat use can uncover adaptive advantages that may select for these developmental processes influencing habitat use. Investigating both the developmental factors influencing habitat selection decisions at the individual scale and the functional consequences of living in different habitats are vital to a broader understanding of the causes and consequences of habitat selection in animals.

FUNDING

Center for Population Biology (UC Davis); and National Science Foundation Predoctoral fellowship (to K.M.H.); and National Science Foundation (OCE 03-51778 to J.J.S.).

J. Byrnes, A. Chaudoin, P. Reynolds, R. Coates, J. Ramirez, and M. Young provided assistance in the laboratory and the field for surveys and tethering experiments. Bodega Marine laboratory provided animal care support and mesocosm facilities. This manuscript was greatly improved by suggestions from J. Davis, A. Sih, E. Snell-Rood, and D. Papaj also gave useful comments on earlier versions of the text.

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