Geographic Variation in Camouflage Specialization by a Decorator Crab

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ABSTRACT: In North Carolina, the decorator crab *Libinia dubia* camouflages almost exclusively with the chemically noxious alga *Dictyota menstrualis*. By placing this alga on its carapace, the crab behaviorally sequesters the defensive chemicals of the plant and gains protection from omnivorous consumers. However, *Dictyota* is absent north of North Carolina, whereas *Libinia* occurs as far north as New England. Crabs from three northern locations where *Dictyota* is absent (Rhode Island, Connecticut, and New Jersey) camouflaged to match their environment, rather than selectively accumulating any one species. When *D. menstrualis* was offered to crabs from northern sites, they did not distinguish between it and other seaweeds for camouflage, whereas crabs from Alabama and two locations in North Carolina used *D. menstrualis* almost exclusively. In addition, in winter and spring, when *Dictyota* was seasonally absent in North Carolina, *Libinia* selectively camouflaged with the sun sponge *Hymeniacidon heliophila*, which was chemically unpalatable to local fishes. Thus, southern crabs were consistent specialists on chemically defended species for camouflage, while northern crabs were more generalized. The geographic shift in crab behavior away from specialization coincides with a reported decrease in both total predation pressure and the frequency of omnivorous consumers. These shifts in the nature and intensity of predation pressure may favor different camouflage strategies (generalist vs. specialist), contributing to the observed geographic differences in camouflage behavior.

Keywords: decorator crabs, geographic comparison, intraspecific variation, local specialization, plant-herbivore interactions, seaweeds.

It has been argued that the ecological and evolutionary importance of positive interactions among species has been underappreciated by most biologists (Kareiva and Bertness 1997). While many factors likely contribute to this bias (Boucher et al. 1982; Bertness and Callaway 1994), part of the reason for the modest attention given to the role of mutalism and other positive associations may be that the nature and strength of these interactions can be highly variable. Mutualisms that moderate local biotic or abiotic stresses may become commensal, and commensalisms may become antagonistic when those stresses are relaxed (e.g., Palumbi 1985; Hay 1986; Bronstein 1994; Bertness and Leonard 1997; Holzapfel and Mahall 1999; Stachowicz and Hay 1999a). Although many biologists recognize that biotic interactions vary in outcome with local conditions, few studies examine how these changes may alter species' behaviors and evolution over geographic scales. Such studies of geographic variation may serve as a "lens" through which many important ecological and evolutionary questions can be profitably examined (Travis 1996).

As an example, geographic variation in the outcome of interspecific interactions is thought to be important to the evolution of specialization (Thompson 1994). Studies of plant-insect interactions have demonstrated that conspecific populations differ in the extent to which they specialize; some populations become highly specialized for the interactions as others remain or become less specialized (e.g., Janzen 1973; Rickson 1977; Whitham 1983; Abrahamson et al. 1989; Steiner and Whitehead 1990; Tauber et al. 1995). In particular, populations that fall outside the geographic range of the other species may exhibit few of the morphological or behavioral traits that enhance the association (Janzen 1973; Rickson 1977). While it is easy to envision how this scenario may apply for associations involving poorly dispersed organisms or physically separated populations, local adaptation is predicted to be far less common in marine systems because they are generally more open and because larval and adult stages of many species disperse widely (Jablonski 1986; Scheltema 1986; Palumbi 1992). Although

geographic differences in allozyme frequencies or mito-chondrial DNA sequences within species have been demonstrated in a variety of marine invertebrates with pelagic larvae (e.g., Avise 1992), geographic variation in behavioral traits relevant to the outcome of interspecific interactions is poorly known.

Specialized positive associations are known among many marine invertebrates with pelagic dispersal phases (Steneck 1982; Glynn 1987; Littler et al. 1995; Stachowicz and Hay 1999*a*, 1999*c*). These specialized positive interactions may be critical to the maintenance of marine communities through their positive effects on producers of biogenic structure such as corals or calcified seaweeds (Glynn 1987; Littler et al. 1995; Stachowicz and Hay 1996, 1999*a*). Could local specialization play a role in the origin and maintenance of these commensal and mutualistic associations, or does the high dispersal potential of these marine species preclude such responses to local selection? Just as the study of geographic variation in host-plant preferences has increased our understanding of the basis of the evolution of specialization and coevolution among insects and plants (e.g., Thompson 1994; Abrahamson and Weis 1997), a fuller understanding of variation in specialized marine interactions could enhance our ability to predict the circumstances under which these associations arise and come to play an important role in marine communities.

In this study, we examine spatial and temporal variation in the associational defense employed by the decorator crab *Libinia dubia* along the east coast of the United States. In North Carolina, *Libinia* is known to enter into a specialized association with the chemically noxious seaweed *Dictyota menstrualis* (Stachowicz and Hay 1999*c*). In this association, the crab escapes predation by placing the alga on its carapace as camouflage, behaviorally sequestering the alga's defensive chemicals. However, the crab and alga do not have completely overlapping ranges, and it is currently unknown whether crabs outside the range of the preferred host specialize on other defended algae, generalize in an attempt to blend into the background, or cease decorating altogether. Our results demonstrate that although all populations of *Libinia* do camouflage with seaweeds or sessile invertebrates, the nature and specificity of camouflage preferences differ greatly between northern and southern populations in the western North Atlantic. Because these behavioral shifts are coincident with both quantitative and qualitative latitudinal gradients in predation pressure, we suggest that local differences in selection by predators may contribute to these differences in behavior.

Methods

Organisms and Study Sites

The decorator crab *Libinia dubia* (Decapoda, Majidae) occurs from the Gulf of Mexico to southern New England in sounds and saltier estuaries (Williams 1984). As with several other species of majid crabs (e.g., Kilar and Lou 1986), juveniles of the species "decorate" their carapace with materials from the surrounding environment, presumably as a defense against predators. Juveniles in North Carolina selectively camouflage with the chemically noxious seaweed *Dictyota menstrualis*; crabs decorated with this alga experience less predation in the field than crabs decorated with a common seaweed that is not chemically defended from omnivorous consumers (Stachowicz and Hay 1999*c*). The crabs prefer *D. menstrualis* over all other seaweeds, and this preference is cued by the diterpene alcohol dictyol E (Stachowicz and Hay 1999*c*), a metabolite specific to *D. menstrualis* that deters feeding by omnivorous fishes (Hay et al. 1987, 1988; Cronin and Hay 1996), which prey on both seaweeds and crustaceans. This alga occurs from southern Virginia south to the Gulf of Mexico and throughout the Caribbean (Schneider and Searles 1991). Thus, although the two species co-occur over a large portion of their range, northern populations of *Libinia* do not co-occur with *Dictyota*.

We collected *Libinia* from six locations along the east coast of the United States: Mobile Bay, Alabama (30°13′N, 68°02′W); Mitchell Village, North Carolina (34°44′N, 76°50′W); Drum Shoal, North Carolina (34°43′N, 76°45′W); Little Egg Harbor and Great Bay, New Jersey (39°30′N, 74°20′W); Noank, Connecticut (41°19′N, 72°59′W); and Narragansett, Rhode Island (41°25′N, 71°27′W). The Alabama site, at the inlet to Mobile Bay, was deeper (5.0 m) and more turbid than any of the other sites, and it supported few sessile benthic organisms. The North Carolina sites were shoals comprised of a series of sea grass and algal beds, ranging in depth from 0.5 to 1.0 m in Bogue Sound, North Carolina, near the University of North Carolina's Institute of Marine Sciences. The New Jersey sites, near the Rutgers University Marine Station in Tuckerton, New Jersey, consisted of algal flats that ranged in depth from 1.5 to 2.0 m. The Connecticut site was at the former University of Connecticut Marine Lab in Noank and consisted primarily of invertebrate-encrusted pilings and rocks that ranged in depth from just subsurface to 3.0 m. The Rhode Island site was located adjacent to the Narragansett town pier, in 1.0–2.5 m deep water with algal-covered gravel and cobbles. All water depths are heights above the bottom at low tide. A more detailed characterization of the sessile benthos of these sites is given in the "Results."

Geographic Variation in Crab Behavior

We assessed which materials *Libinia* selects for camouflage in the field by collecting crabs at different sites and comparing the composition and wet mass of their camouflage with the wet mass of seaweeds and sessile invertebrates available at each site. We could not assess camouflage preferences in the field in Alabama because crabs collected there had no camouflage and the site lacked sessile benthos that might have served as material for camouflage. However, decorated crabs have been collected at this site during other times of the year (K. Heck and J. Valentine, personal communication), so we did use individuals from this site in laboratory camouflage-preference assays (see below). At the Mitchell Village site in North Carolina, we collected crabs by manually dragging a net (0.5-cm mesh size) through sea grass beds. The total area searched was ~100 × 10 m. Crabs were returned to the lab, where camouflage material was removed, blotted dry with a paper towel, and weighed to the nearest 1 mg. We estimated the availability of camouflage materials by collecting and weighing (wet) all seaweeds and sessile invertebrates in haphazardly located 1.0-m^2 quadrats ($N = 10$) from the site where the crabs were collected. In New Jersey, water depth and muddy sediments prohibited manual deployment of a net, so we collected crabs in a 1.0-m beam trawl (0.5-cm mesh size) dragged behind a boat at 5 km h^{-1} for 2 min. The total area sampled per trawl was thus ~167 m^2, and a total of 10 trawls were made. Algae and sessile invertebrates from each trawl were collected, sorted, and weighed (wet) to determine the relative availability of these for camouflage. Crabs at both the Connecticut and Rhode Island sites were sufficiently abundant to be collected by scuba divers. All crabs in haphazardly located 1.0-m^2 quadrats were collected along with the benthic flora and fauna within the quadrat. At each site, we compared the relative abundance of each sessile organism in the field with its relative abundance as camouflage (percentage of total wet mass) using unpaired *t*-tests. Arcsine transformations were used to achieve homogeneity of variances where necessary, and where these transformations were unsuccessful, nonparametric Mann-Whitney *U*-tests were employed. Surveys were performed at all sites during late summer (August–September).

Crabs collected from all sites were transported to the Institute of Marine Sciences in Morehead City, North Carolina, where we assessed their feeding and camouflage preferences by offering them a simultaneous choice of the same eight species of seaweeds. All the seaweeds used occur in shallow waters of North Carolina in the early summer through at least late fall: the green alga *Ulva rigida*; the brown algae *Sargassum filapendula*, *Padina gymnospora*, *D. menstrualis*, and *Dictyota ciliolata*; and the red algae *Hyp-*

nea musciformis, *Chondria dasyphylla*, and *Gracilaria tikvahiae*. We stripped each crab of existing camouflage and placed it in a 0.5-L bowl ($N = 6$–19 for each population) with four 1-cm-diameter holes to allow for flow-through seawater. Each bowl with a crab held a 150 ± 25–mg piece (blotted wet mass) of all eight seaweed species (i.e., a choice assay). As a control for changes in seaweed mass unrelated to herbivory or camouflaging, identical bowls without crabs contained same-sized pieces of the same species of seaweed. Within each replicate, treatment and control pieces of algae were taken from the same algal thallus. After 38–42 h, each piece of alga was blotted dry with a paper towel and reweighed; camouflage was then removed from crabs and weighed. Assays were conducted during late summer and early fall (August–October).

To calculate net mass loss for each algal species due to crab feeding, we corrected for mass changes unrelated to herbivory using the formula $(T_i × [C_f/C_i]) - (T_f + D)$, where T_i and T_f are the initial and final masses of the seaweed portion in the container with a crab, C_i and C_f are the initial and final masses of the seaweed portion in the paired-control container, and D is the amount of the seaweed used as camouflage. Crabs never consumed, or used as camouflage, 100% of any of the choices, so use of an alga as camouflage did not make that alga unavailable for consumption, and vice versa. We used one-way ANOVA to assess whether the total amount of algae used for feeding or decoration differed among sites, then assessed whether crabs within a site made choices among the various algal species offered for food and decoration using the nonparametric Friedman's two-way test on ranked data.

Seasonal Variation in Decoration in North Carolina

During the cooler months (January–May), the upright, macroscopic form of *D. menstrualis* used by *Libinia* for camouflage is absent from North Carolina, although the species persists microscopically (Richardson 1979). Field and laboratory decoration preferences of *Libinia* from the Mitchell Village site were assessed during this period to gain insight into whether these crabs are inherent specialists or whether they revert to more generalized behavior when their preferred camouflage is unavailable. Field and lab methods were identical to those for the geographic survey described previously. The dominant sessile-benthic organisms at this time of year included the sun sponge *Hymeniacidon heliophila*; the bryozoan *Bugula neritina*; and the seaweeds *Hypnea*, *Gracilaria*, *Ulva*, and *Agardhiella subulata*.

Because crabs selectively accumulated *Hymeniacidon* in these cooler months and because previous work has demonstrated that selective decoration with *Dictyota* provides
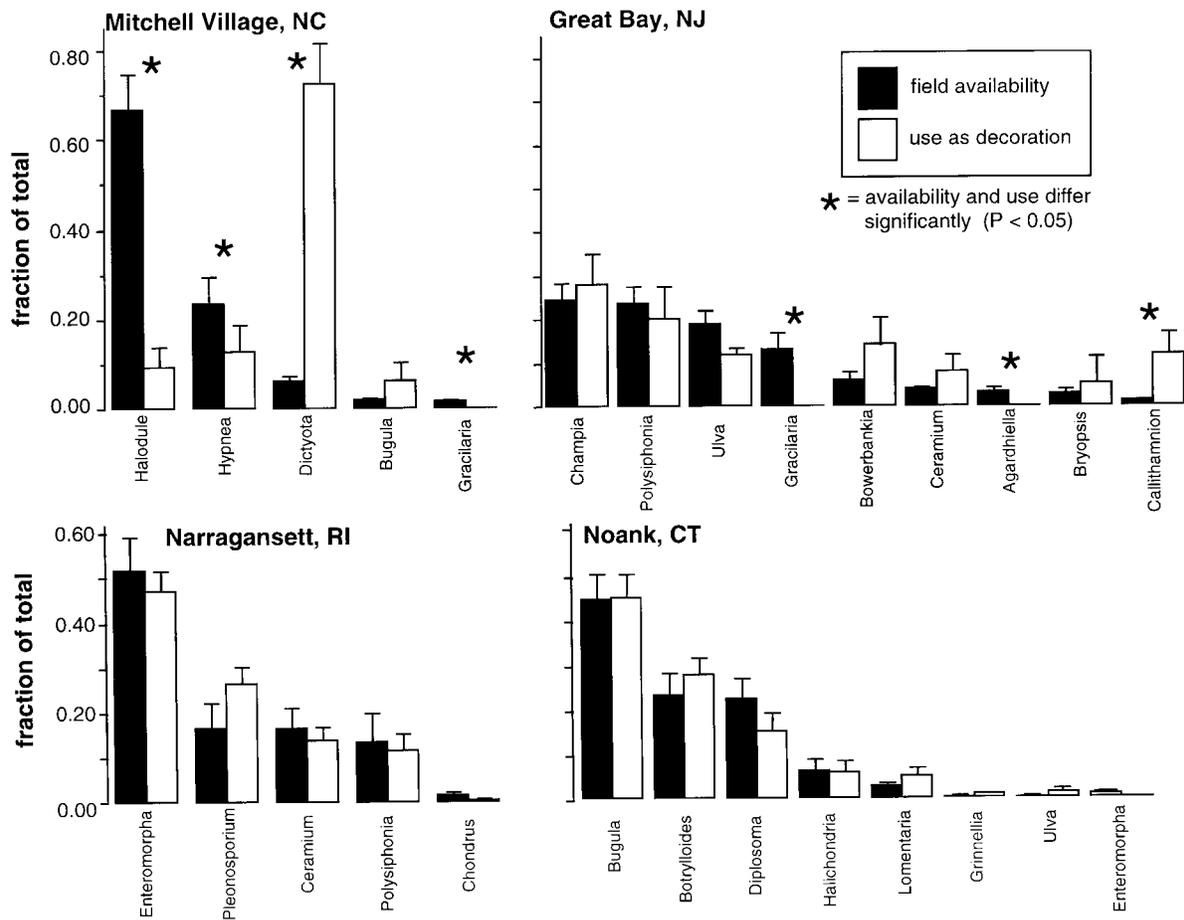
Figure 1: Camouflage availability (*black bars*) and use (*white bars*) by juvenile *Libinia dubia* at three locations north of the known range of *Dictyota menstrualis* (Rhode Island, Connecticut, and New Jersey) and one location within the range of this alga (North Carolina). Values are mean relative abundances, and error bars represent 1 SE. Statistically significant differences in the relative abundance of availability and use ($P < .05$, unpaired *t*-tests or Mann-Whitney *U*-test) are indicated by an asterisk.

a refuge from predation due to its chemical unpalatability (Stachowicz and Hay 1999*c*), we examined *Hymeniacidon* to see if it also might be chemically deterrent to potential crab predators. We compared pinfish consumption of bite-sized pieces of sponge, artificial food pellets containing sponge extracts at natural concentration, and control artificial food pellets. Detailed procedure for extraction and bioassay can be found in Stachowicz and Lindquist (1997).

Results

Geographic Variation in Specialization

Libinia dubia from New Jersey, Connecticut, and Rhode Island exhibited few strong camouflage preferences in the field, while those from North Carolina exhibited a strong preference (fig. 1). In the summer, Mitchell Village, North

Carolina, crabs preferentially accumulated *Dictyota menstrualis*, which on average made up 75% of their total camouflage, despite the fact that *Dictyota* made up only 6% of the total wet mass of available camouflage material in the field (significantly different by paired *t*-test, $P < .0001$). It was the dominant species used by 11 out of 14 individuals. These crabs avoided decorating with seaweeds like *Hypnea* and *Gracilaria* ($P < .0001$ and $P = .030$, respectively) that are palatable to omnivorous fishes (Hay et al. 1987, 1988; Stachowicz and Hay 1999*a*, 1999*c*) and used the bryozoan *Bugula neritina* infrequently, but in proportion to its availability ($P = .354$). They also avoided camouflaging with the sea grass *Halodule*, the most abundant potential camouflage material in the field (fig. 1; $P < .0001$). There was no significant correlation between the availability of a camouflage material and its use by crabs from North Carolina ($N = 5$, $r = -0.20$, $P = .775$).

While crabs from North Carolina preferentially decorated with one alga that was relatively rare, crabs from more northern populations camouflaged to match their surroundings. For crabs from each of the northern populations, the average amount of each species used for decoration was positively correlated with its abundance in the field (Rhode Island: $N = 5$, $r = 0.90$, $P = .010$; Connecticut: $N = 6$, $r = 0.97$, $P < .0001$; New Jersey: $N = 9$, $r = 0.67$, $P = .045$). In New Jersey, six of the nine seaweeds or invertebrates co-occurring with *Libinia* were used for camouflage in proportions not different from their field abundance ($P > .05$, fig. 1). Two species (*Gracilaria tikvahiae* and *Agardhiella subulata*) were avoided relative to their abundance in the field ($P = .002$ and $P = .007$, respectively). These two species were never used as camouflage, possibly because their thalli were relatively broad and thick and may not fit among the hooked setae that hold camouflage on a crab's carapace. Only one species (*Callithamnion corymbosum*) in New Jersey was used more frequently by crabs than its abundance in the field would predict ($P = .028$). However, we probably undersampled the relative availability of this alga in the field. Individuals of this species are small, and most of them may have passed through the mesh in our trawl. Regardless, this species made up on average only 12% of the total camouflage and was never the most abundant camouflage material on an individual crab. In both Rhode Island and Connecticut, *Libinia* used all species in proportions not different from their availability ($P > .05$; fig. 1). At Noank, Connecticut, both the benthic community and the composition of the crabs' camouflage were dominated by colonial invertebrates, particularly the bryozoan *Bugula turrita*, the ascidians *Botrylloides diegensis*, and *Diplosoma macdonaldi*. In Rhode Island, both crabs' carapaces and the substrate supported a community of ephemeral green and filamentous red algae, dominated by *Enteromorpha intestinalis*, *Pleonosporium borreri*, and species in the genera *Ceramium* and *Polysiphonia*, which were not distinguished to the species level.

Crabs from different sites did not differ in the total mass of camouflage used in laboratory choice assays (one-way ANOVA, $F = 1.42$, df $= 5, 80$, $P = .225$), but the composition of this camouflage differed dramatically among populations (fig. 2). *Dictyota menstrualis* made up most of the camouflage on crabs from the two North Carolina sites and from Alabama (76%, 83%, and 82%, respectively) but was used significantly less frequently by crabs from New Jersey (32%), Connecticut (12%), and Rhode Island (13%; one-way ANOVA on the percentage of the total camouflage comprised by *Dictyota*: $F = 17.8$, df $= 5, 80$, $P < .0001$; means comparisons made using the Tukey-Kramer procedure). Seaweeds other than *D. menstrualis* were used only rarely by North Carolina and Alabama crabs. In con-

trast, analysis of decoration preferences among crabs within northern populations showed that New Jersey crabs used *Hypnea musciformis* and *Dictyota ciliolata* at levels not different from *D. menstrualis* (26% and 40%, respectively, $P > .05$, Friedman's test; fig. 2). Connecticut crabs preferred *Hypnea* over *D. menstrualis*; Rhode Island crabs preferred *Ulva* to *D. menstrualis* ($P < .05$, Friedman's test; fig. 2). Thus, the variation in decoration behavior appeared to have a geographic basis; crabs from North Carolina and Alabama sites strongly preferred *D. menstrualis* for camouflage over all other species, whereas crabs from outside the range of this alga used other species just as readily (or even more readily) than they used *D. menstrualis*. Crabs from all sites generally rejected *Gracilaria*, *Padina*, and *Sargassum* as decoration during the summer months.

Crabs from all sites showed distinct feeding preferences among algal species (fig. 3). These differences were statistically significant ($P < .0001$, Friedman's test) for all sites where replication was adequate to allow analyses. For Mobile Bay, the number of crabs ($N = 6$) was lower than the number of choices offered (eight species of seaweed), precluding statistical analysis. *Hypnea* and *Ulva* were readily eaten by crabs from all sites. *Gracilaria* was heavily consumed by North Carolina and Rhode Island crabs, whereas *Chondria* ranked more highly among Connecticut, New Jersey, and Alabama crabs. *Libinia* from both sites in North Carolina showed similar overall trends but a reversal of preference among the two most preferred algae (*Ulva* and *Hypnea*). Although all populations exhibited feeding preferences, there were no clear geographic differences in preferences: *D. menstrualis* was low preference and *H. musciformis* was relatively high preference for all populations.

Seasonal Variation in Specialization

In the late spring, before *Dictyota*'s becoming apparent in North Carolina grass beds, *Libinia* preferentially decorated with the sun sponge *Hymeniacidon heliophila* (fig. 4), although the crabs' preference for this species was not as strong as for *Dictyota* in the summer (fig. 1). This sponge made up only 6% of organisms in the field yet made up 46% of *Libinia*'s camouflage ($P < .0001$, unpaired *t*-test). *Libinia* also frequently decorated with *Hypnea* (25%) and *Ceramium* (13%), but both these seaweeds were used in proportions that did not differ from their abundance in the field (fig. 4). In contrast, the green alga *Ulva* was strongly avoided, as it made up <1% of the total camouflage but made up 33% of the mass of organisms found in the field. In lab assays in which crabs were given equal amounts of six species as potential decorating materials, the sun sponge made up 67% of the total camouflage,
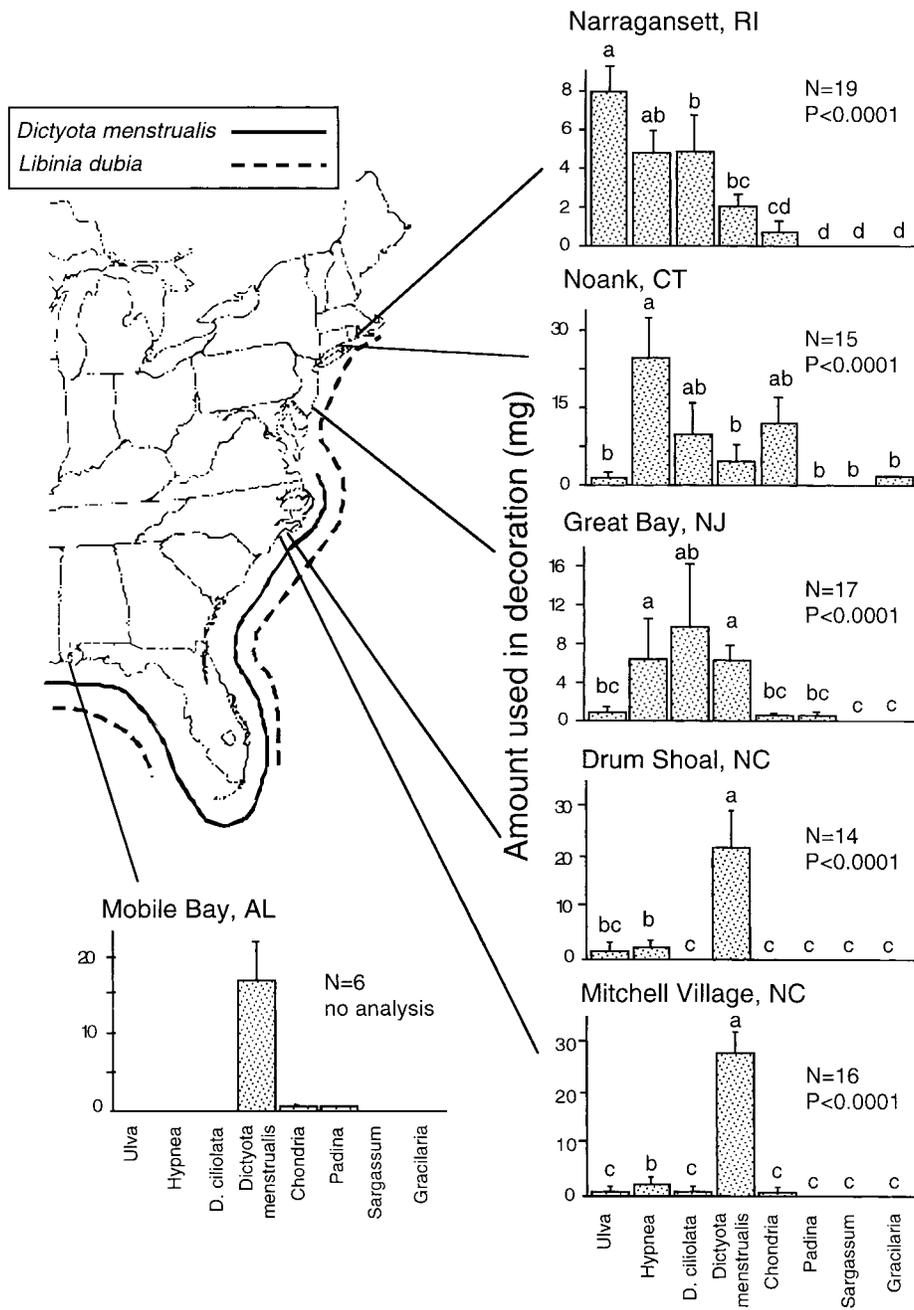
Figure 2: Use of North Carolina seaweeds for camouflage ($\overline{X}$ + 1 SE) by *Libinia dubia* from six locations along the east coast of the United States. The range of occurrence of *L. dubia* and *Dictyota menstrualis* are given for comparison. Statistical analyses were by the Friedman's test; letters indicate significant ($P < .05$) differences among species in use for camouflage. Analyses not done for Mobile Bay population due to insufficient replication relative to the number of algal choices.

significantly more than any other species (Friedman's test multiple comparisons, $P < .05$; fig. 5). Crabs also decorated with *Hypnea* and *Gracilaria* in the lab but did so in much lower amounts (20% and 12%, respectively). The sun sponge was chemically unpalatable to fishes ($P < .0001$; fig. 6), suggesting that the crabs' preference for this animal as decoration when *Dictyota* is absent may be a consequence of its chemical unpalatability to potential crab predators.
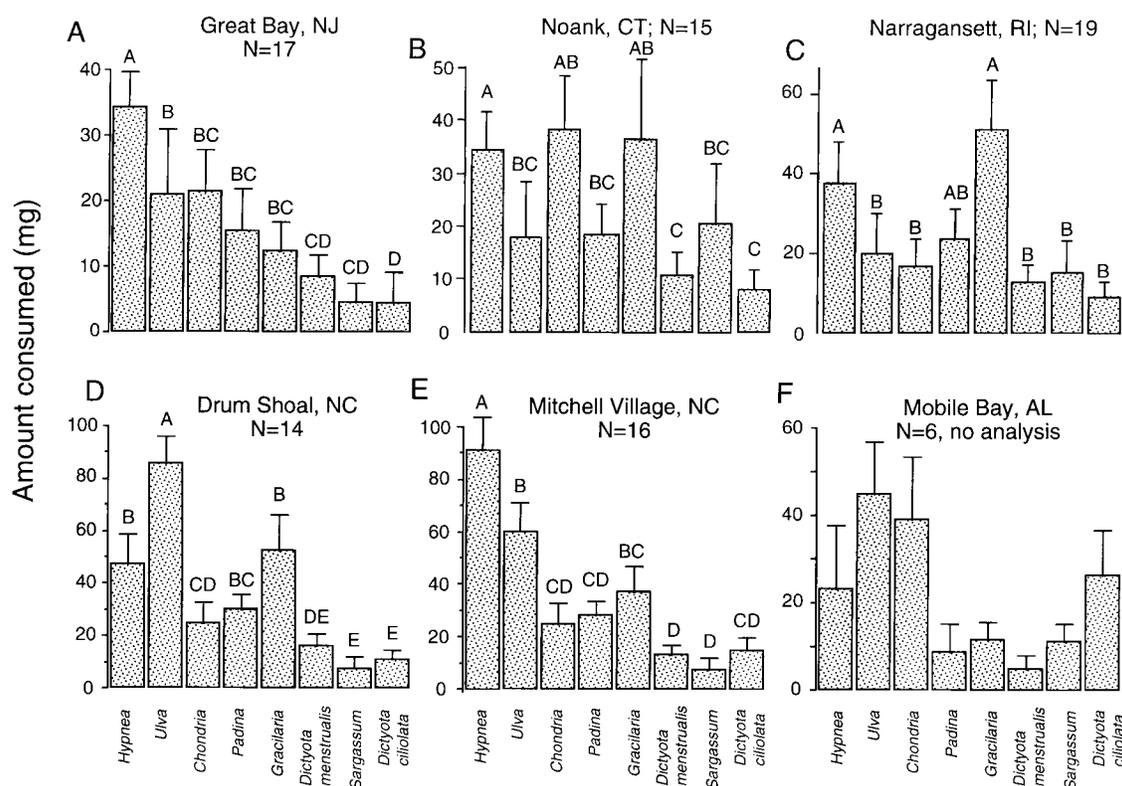
Figure 3: Use of North Carolina seaweeds for food by *Libinia dubia* from six locations along the east coast of the United States. Statistics and symbols are as in figure 2.

Discussion

Despite the fact that *Libinia* has a planktonic larval phase that could promote homogeneity within the species, our results demonstrate significant geographic variation in the decoration behavior of this crab. Where *Dictyota menstrualis* occurs (North Carolina and Alabama), crabs strongly prefer this alga for camouflage, whereas crabs collected outside the range of this alga (Rhode Island, Connecticut, New Jersey) use most camouflage materials in proportion to their abundance in the field. This is not simply a facultative shift in behavior from specialist to generalist due to the absence of the preferred species. When crabs from northern sites were offered *D. menstrualis*, they did not prefer it over other algae, including those like *Hypnea* and *Ulva* that are palatable to potential crab predators. Further, when *Dictyota* became seasonally unavailable in North Carolina, crabs there specialized on another chemically defended organism for camouflage (the sun sponge *Hymeniacidon heliophila*; figs. 4, 6). Unfortunately, we were unable to determine whether the defensive metabolites from the sponge also stimulate camou-

flaging by crabs because these compounds are water soluble (fig. 6) and would dissolve from test surfaces before crabs could make a choice. Regardless, it appears that the northern populations are differentiated from the Alabama and North Carolina populations with respect to camouflage behavior; southern populations consistently decorate with chemically defended materials, whereas northern crabs adopt a strategy of background matching.

Although among-population differences in preference for *Dictyota* could be the result of learning or past experience, this seems unlikely because mistakes during the learning process would greatly increase mortality (Stachowicz and Hay 1999*c*), and crabs from the turbid waters of Mobile Bay, Alabama, did not have direct contact with *D. menstrualis*, yet they still exhibited extreme preference for this alga when offered it in choice assays (fig. 2), suggesting that the preference is "hardwired" among southern populations and not induced by the presence of *Dictyota*. However, our data are only suggestive of genetic differentiation as a mechanism for the observed differences in behavior between geographic regions. More conclusive
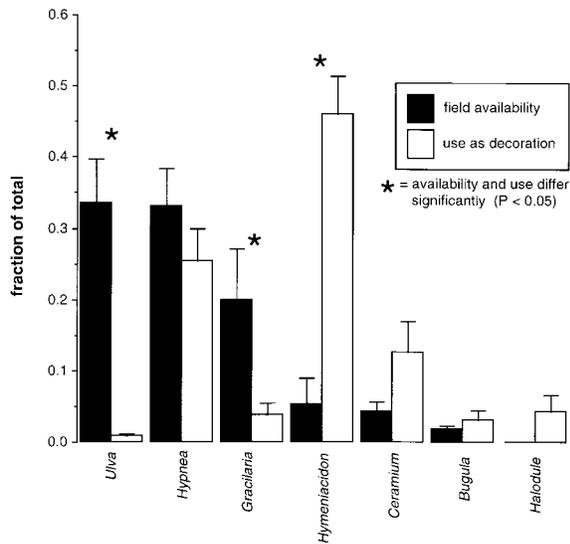
Figure 4: Field decoration patterns of *Libinia dubia* at Mitchell Village, North Carolina, in May, before *Dictyota menstrualis* became apparent in these habitats. Analyses and symbols as in figure 1.

support would require raising crabs from several different populations in the presence and absence of *D. menstrualis*, then assessing decorating preferences among the offspring. Such experiments have been conducted with herbivorous amphipods and show a genetic link to algal preferences based in part on plant chemistry (E. Sotka and M. Hay, unpublished data).

In contrast to the marked cline in decoration preferences, there are few geographic differences in choice of plants for food, as *Libinia* from all sites exhibit generalized feeding preferences for several red and green seaweeds. Avoidance of brown algae as food by *Libinia* is most likely due to the production of chemical feeding deterrents by these species (Stachowicz and Hay 1999*a*, 1999*b*), although the leathery texture of some brown algae (e.g., *Sargassum*) could also play a role. We did not address the reasons for the limited differences among populations in food choice, but intraspecific variability in both herbivore preference and seaweed chemical composition (nutritional value, defensive chemicals) may play a role (Renaud et al. 1990; Cronin and Hay 1996).

Association of Geographic Variation in Decoration with Variation in Predation Pressure

Because specialization by *Libinia* on *D. menstrualis* allows the crab to significantly reduce susceptibility to predation in the field (Stachowicz and Hay 1999*c*), it seems plausible that geographic variation in this behavior could be due to

coincident variation in predation pressure. A decrease in predation pressure with increasing size through ontogeny may explain why adult *Libinia* do not decorate (Stachowicz and Hay 1999*c*) and why other animals abandon antipredator tactics as they grow in size (e.g., Pennings 1990). Predation pressure on marine invertebrates generally declines with increasing latitude (Bertness et al. 1981; Menge and Lubchenco 1981), and more specifically, predation rates on crabs are lower in the northern portion of the range of *Libinia dubia* than further south (Heck and Wilson 1987). Although current predation regimes may not be representative of historical selection pressures due to reductions in predator abundance from overfishing, the consequences of such reductions in predation intensity have been documented in both temperate and tropical habitats (Carpenter 1984; Hay 1984; Witman and Sebens 1992). Thus, while overfishing may have reduced the absolute level of predation on crabs, the latitudinal gradient in predation pressure has probably existed historically and could have contributed to the geographic differences in crab behavior. This seems particularly likely given the correspondence between latitudinal gradients in predation pressure and the prevalence of prey defenses in other species (Bertness et al. 1981; Coley and Aide 1990; Bolser and Hay 1996).

In addition to latitudinal differences in the overall intensity of predation by fishes, predation pressure changes
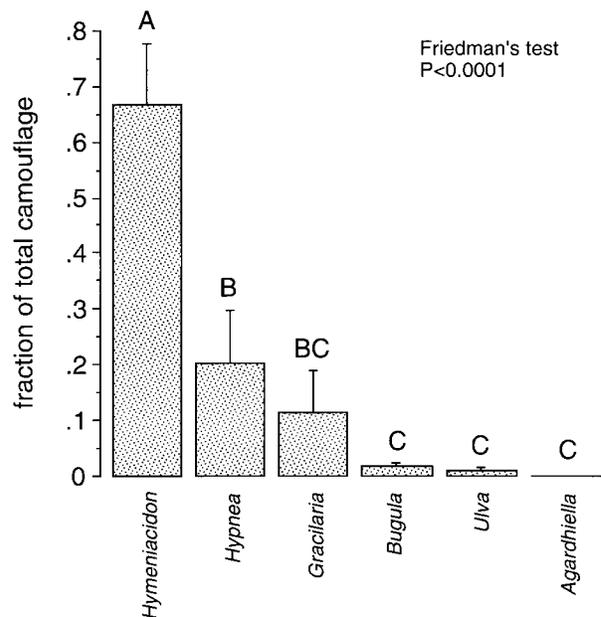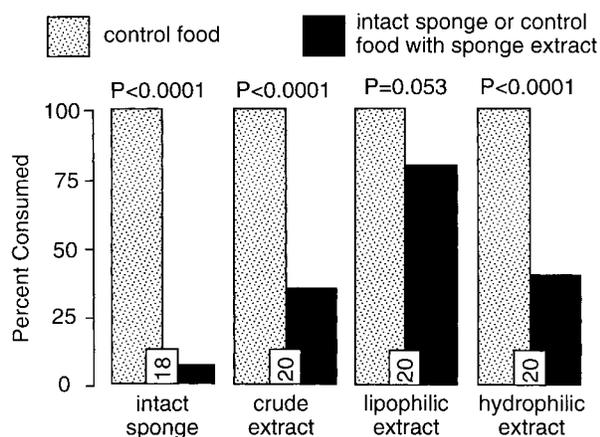

Figure 5: Laboratory decoration choices of *Libinia dubia* among potential items available in the late spring, before *Dictyota* became apparent in these habitats. Statistics and symbols are as in figure 2.

Figure 6: Palatability of the intact sponge and of chemical extracts of the sun sponge *Hymeniacidon heliophila* to the pinfish *Lagodon rhomboides*. Statistical analysis was by Fisher's exact test. Sample size (*N*) is given at the base of each pair of bars.

qualitatively with latitude, as the abundance of herbivorous and omnivorous fishes declines in higher-latitude waters (Horn 1989; Ebeling and Hixon 1991). Fishes that consume both seaweeds and mobile invertebrates (including pinfish [*Lagodon rhomboides*], sheepshead [*Archosargus probatocephalus*], and spottail pinfish [*Diplodus holbrookii*]) are abundant in habitats containing *Libinia* in the southern portion of its range but rare or absent north of Chesapeake Bay (Tatham et al. 1984; Stone et al. 1994). Where these omnivores are common, camouflage that matches the background is ineffective at reducing predation on *Libinia* because the background is comprised of seaweeds such as *Hypnea* that are readily consumed by these locally abundant omnivores (Stachowicz and Hay 1999c). In these habitats, camouflage with a chemically defended seaweed is a much more effective means of reducing predation (Stachowicz and Hay 1999c). Because few (if any) of the fishes in the northern habitats we studied perceive seaweeds as food, camouflage that allows the crab to blend into the background cover of benthic vegetation may be sufficient to reduce detection by predators. Seaweed chemical defenses can be effective against carnivores (e.g., Paul and Van Alstyne 1988; Hay et al. 1990a, 1990b), but chemical protection from predation may confer little additional benefit in northern habitats if crabs camouflaged to match the algal background are rarely discovered. Thus, the specialist and generalist strategies may each be favored in different parts of *Libinia*'s geographic range.

Population Subdivision in Libinia

The observed regional differences in crab camouflage strategy may reflect the division of the species into sub-

populations. Although classical life-history theory suggests that localized adaptations are likely to be rare in marine organisms like crabs that typically have long-lived pelagic dispersal phases (e.g., Vance 1973; Scheltema 1986), many organisms do not fit this paradigm (see review in Palumbi 1995). Many factors can contribute to reductions in realized dispersal from the potential dispersal predicted from larval life history. Duration of the planktonic phase of marine invertebrates may be much shorter in the field than in the lab (Olson and MacPherson 1987; Prince et al. 1987; Cronin et al. 1995), which, combined with the short larval period of *L. dubia* in the laboratory (9 d; Sandifer and Van Engel 1971), suggests that realized dispersal of this species could be relatively restricted. In addition, both physical (Bertness and Gaines 1993; Luettich et al. 1999) and behavioral (Cronin and Forward 1986) mechanisms exist that would favor retention of crab larvae in natal estuaries, although it is not known whether these mechanisms operate for *L. dubia*. Furthermore, longer-distance dispersal across Cape Hatteras, North Carolina, may be inhibited by ocean currents that flow toward the cape from the south and the north before turning offshore. Even if crabs from northern populations dispersed to North Carolina, they would likely suffer greater predation than native crabs because they would not specialize on chemically defended species. In a field tethering experiment in North Carolina, juvenile *Libinia* decorated with *Hypnea*, a palatable alga preferred for camouflage by northern crabs in lab assays (fig. 2), were consumed much more frequently than those decorated with *D. menstrualis* (Stachowicz and Hay 1999c). Although crabs could possibly "learn" the specialized behavior, predation would decrease the probability that northern immigrants would survive the learning process and live to sexual maturity in North Carolina relative to residents.

Oceanographic features, reduced larval dispersal, and geographic variation in selection pressure from fishes could all contribute to the observed regional differences in behavior of *Libinia*, but can the relative importance of these factors be distinguished? We suggest that limited larval dispersal because of a brief larval period and reduced transport between areas north and south of Cape Hatteras allows population differentiation in response to differential predation regimes. Furthermore, specialization may be more likely in southern populations because the warmer temperatures characteristic of these habitats speed larval development (Sandifer and Van Engel 1971), increasing the probability that larvae will become competent to settle when still close to their natal habitat. Although further evidence is required, an analogous situation does exist among acorn barnacles, which show localized adaptations to thermal stresses only in bays where flushing rates are low, promoting retention of larvae in natal estuaries and

allowing repeated selection for thermal tolerance in adults over generations (Bertness and Gaines 1993). It seems likely that similar repeated selection over generations would be necessary for the specialized decorating preferences of *Libinia* to evolve.

Differentiation among these possible alternatives for *Libinia* will require integrative studies across levels of biological organization. Genetic comparisons among adult populations and between adults and larval stages using molecular markers may offer some insight as to whether significant dispersal of larvae occurs across the Cape Hatteras biogeographic boundary and whether that dispersal results in the establishment of adults. If northern and southern adult crabs are genetically different but the dispersive larval stages are not, larval transport may be sufficient to promote mixing, and behavioral differences among populations could then be attributed largely to differential postsettlement mortality. The potential for postsettlement predation to maintain differences among populations could be assessed by comparing survival of northern and southern crabs decorated as they choose in tethering experiments at each location. Understanding the subdivision of populations such as this will probably require the integration of investigations at levels from genes to behavior to regional oceanography.

Local Specialization in the Sea

Local specialization for camouflage among the decorator crabs is facilitated by a decoupling of the choice of plants as food and shelter. Crabs place plant "shelter" on their backs as camouflage but need not use these plants as food. For example, *Libinia* in North Carolina uses *Dictyota* for camouflage but avoids consuming this alga (figs. 2, 3). Similarly, other small marine invertebrates exploit plants or sessile animals as refuges from predation but avoid using their host for food (Coen 1988; Duffy 1990, 1993; Hacker and Madin 1990; Stachowicz and Hay 1996, 1999*a*, 1999*c*; Sotka et al. 1999). In contrast, small terrestrial herbivores, like insects, are most often specialized and use the same plant for food and shelter (Strong et al. 1984). Thus, host shifts to avoid competition or predation may involve a trade-off of decreased growth and survival due to poor metabolic adaptation to the new host (e.g., Feder 1995; Abrahamson and Weis 1997). Such trade-offs are absent when the host is not used for food. Host-switching thus carries relatively little cost for many marine invertebrates, suggesting that local specialization could be an important means of coexisting with local predators in the marine environment. When these host-switches involve genetic or behavioral adaptations to better exploit the new host they may be an important means of generating variability and possibly race formation. Adaptation to local hosts may

thus play an evolutionarily important role by facilitating the development, maintenance, and diversification of the growing number of sibling species complexes found in the sea (Buss and Yund 1989; Duffy 1996).

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