REVIEWS AND SYNTHESES

Local adaptation in host use among marine invertebrates

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Abstract

The study of interactions between small invertebrates and their larger plant and animal hosts has a long tradition. One persistent theme within this literature is that spatially-segregated populations of terrestrial and freshwater invertebrates commonly adapt to local hosts across their geographic ranges. Marine examples are rare, which leaves the impression that marine populations are less likely to adapt to locally abundant hosts and more likely to evolve generalized or phenotypically-plastic strategies. Here, I review a short but growing list of marine invertebrates that appear to display local adaptation in host use. As expected, most of the marine examples are brooded animals with weak dispersal potential. However, some species with pelagically dispersed larvae have apparently adapted to local hosts. This surprising result is consistent with recent evidence that pelagically-dispersed larvae are not always broadly dispersed, that strong selective pressures maintain local differences in host use, or both. The presence of host-mediated adaptation in the sea alters predictions on how marine communities respond to disturbance, supports the notion that marine consumer-prey interactions can coevolve, and indicates that hosts play fundamental roles in the differentiation and perhaps speciation of small marine invertebrates.

Keywords

Coevolution, geographic variation, host use, larval dispersal, local adaptation, selection.

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INTRODUCTION

Population-level differences in phenotypic traits have been the research focus of evolutionary ecologists since and including the studies of Charles Darwin (e.g. Levins 1968; Mayr 1970; Futuyma & Moreno 1988; Moran 1992; Schluter 2001; Via 2001). Recent contributions to this rich tradition focus on the pattern and process of local adaptation – that is, when local genotypes have higher relative fitness on local habitats relative to genotypes from alternative habitats (Kawecki & Ebert 2005). One primary motivation for these studies is to describe the central roles that local adaptation play in the formation and maintenance of species boundaries (Via 2001). Local adaptation is also responsible for extant patterns in the distribution, abundance and ecological roles of organisms (Fox & Morrow 1981; Mopper & Strauss 1998), helps to maintain genetic variation within and among populations, and can serve to predict responses of populations to natural or anthropogenic disturbance (Frankham & Kingsolver 2004).

The literature on local adaptation has been dominated by terrestrial and aquatic examples and contain few marine examples. Consequently, there is a lingering perception that populations in the sea rarely locally adapt, and are more likely to evolve generalized or phenotypically-plastic strategies in response to spatial heterogeneity in habitat (Warner 1997). In part, this may reflect the reality of most marine populations. There is tremendous phenotypic plasticity within species of marine organisms in thermal stress response (Hochachka & Somero 2002), the feeding preferences of marine consumers (Palmer 1984; Pennings 1990; Clements & Choat 1993; Cronin & Hay 1996; Thacker *et al.* 1997), the anti-consumer defenses of invertebrates and seaweeds (Hay 1996; Lively *et al.* 2000; Trossell & Etter 2001), and the reproductive strategies of fishes and invertebrates (Warner 1997), among other ecologically-important traits.

Further, the notion that marine populations rarely locally adapt to their environment is consistent with traditional views of oceanic dispersal. Most marine organisms spawn their larvae into the water column (Thorson 1950), where

they must feed and float for days, weeks or months before becoming competent to settle. During this time, the marine larvae could potentially be entrained within currents for 10s to 100s of kilometres before returning to the shoreline. The evolutionary consequences of dispersal over broad spatial scales are clear; dispersal homogenizes genetic differences that may have been generated by local selection and instead favours the evolution of generalism and plasticity (Levins 1968; Sultan & Spencer 2002). Contrast this scenario with the situation for terrestrial plants, in which seed dispersal is 'long' when it exceeds 100 m (e.g. Cain *et al.* 2000) and the spatial scales by which local adaptation will be allowed to proceed is far reduced.

However, more recent evidence indicates that the realized dispersal distances can be far more restricted than the life history of the organism would predict (see review by Swearer *et al.* 2002). The exact degrees of spatial spread are undoubtedly species-specific, and will depend on local oceanographic circulation patterns, the local ecology of the animal, the behaviour of their larvae and the local availability of suitable habitat (Shanks 1995; Cowen *et al.* 2000; Armsworth *et al.* 2001; Largier 2003; Sotka *et al.* 2004). These dynamics make generalization difficult, but there appears to be growing consensus that marine dispersal is more restricted spatially and more geographically variable than a spawning life-history would simplistically predict. Such restricted dispersal predicts that marine populations are more likely to adapt to local environmental conditions than previously thought. If true, then the relative dearth of marine local adaptation may not reflect reality in the sea. Instead, it is possible that marine evolutionary ecologists have not pursued local adaptation with as much vigour as researchers of terrestrial and aquatic systems.

One potentially fruitful place to look for local adaptation is among invertebrates that utilize larger biotic hosts. Populations of terrestrial and freshwater invertebrates commonly adapt to locally distinct hosts across their geographic ranges. Larger plants and animals exert strong selection on the feeding habits, life-histories and morphology of smaller invertebrates, most dramatically among herbivorous insects (Thompson 1994). These pressures often result in the evolution of genetic differences among populations in preferences for locally abundant host species (Fox & Morrow 1981). Thus, by analogy, local adaptation should be common among marine invertebrates that are 'insect-like' (c.f. Hay *et al.* 1987) – that is, amphipods, isopods, worms, and crabs that are small relative to their hosts, and utilize their hosts for both food and shelter.

Here, I review historically neglected and recently published studies of marine populations that have locally adapted in response to their biotic hosts. What emerges is a growing appreciation among marine evolutionary ecologists that local adaptation of marine populations is more common than currently acknowledged or predicted by theory.

MARINE EXAMPLES OF LOCAL ADAPTATION TO BIOTIC HOSTS

Demonstrating a pattern of local adaptation requires estimating fitnesses of several subpopulations (or demes) from distinct habitats using reciprocal field transplants or common garden experiments. The empirical prediction is that local populations display higher relative fitness within local habitats relative to populations from alternative habitats and that these population-level differences are genetically mediated. However, describing the signals of local adaptation is merely the first step, and a complete understanding of local adaptation requires studying its underlying evolutionary processes, including the 'ecological factors responsible for divergent natural selection, traits under selection and their genetic architecture, gene flow, and processes affecting immigrants (such as heterosis or outbreeding depression)' (see Kawecki & Ebert 2005 for review). For example, the direction and magnitude of ongoing gene flow among populations is a crucial element of demonstrating local adaptation because local adaptation requires restricted gene flow via low passive dispersal or active habitat choices (Kawecki & Ebert 2005). In part, this is because the pattern of local adaptation could arise from genetic drift or population history rather than natural selection. Further, if gene flow is broad, then low-fitness genotypes may recruit from alternative habitats in each generation and genetic differences among populations will only be maintained by purifying selection. In such cases, the system is best characterized as a balanced polymorphism within a panmictic population (for *Mytilus* mussels, see Hilbish 1996; for *Semibalanus balanoides* barnacles, see Schmidt & Rand 1999) rather locally adapted subpopulations.

There are few well-documented examples of local adaptation to biotic hosts among marine and estuarine species. I searched for articles in the Aquatic Sciences and Fisheries Abstracts, BIOSIS and ISI's Science Citation Index using the key words 'geographic variation' or 'local adaptation' and 'marine' or 'estuarine'. I did not include systems in which populations locally adapt to the abiotic environment (e.g. temperature and salinity: see Powers & Schulte 1998; Johannesson 2003). In addition, responses to human-induced perturbations of the marine environment, including pollution (e.g. Nacci *et al.* 1999) or increases in hypoxic events (e.g. Decker *et al.* 2003) were removed. Although examples of microscopic parasites of fishes and large invertebrates are available (e.g. *Doridicola* copepods on sea anemones, Lønning & Vader 1984; isopods on barnacles, Blower & Roughgarden 1988; *Perkinsus marinas*

protozoan on oysters, Bushek & Allen 1996; digenean parasites on fish, Sasal *et al.* 2000), many of these studies are descriptive and will require further genetic treatments, experimental manipulations or both.

In all, I identified at least eight marine systems that have quantified patterns consistent with local adaptation to host use by macroinvertebrates (Table 1). Common garden experiments were used to quantify fitness differences among subpopulations in four of these systems; interestingly, not one marine system has utilized a reciprocal field transplant to quantify differential fitnesses on alternative habitats (for an example of reciprocal field transplant, see Fawcett 1984). Several lines of indirect evidence support the pattern of local adaptation for other examples. Three of the eight examples are consumers on their hosts, and the remaining five are commensal with larger hosts. Below, I highlight aspects of the natural history and evidence for local adaptation within each system.

The predatory whelk *Nucella canaliculata*

Along the rocky intertidal of the north-eastern Pacific coastline, the predatory whelk *Nucella canaliculata* consumes sessile barnacles and blue mussels in the genus *Mytilus*. Across the broad geographic range of the whelk (> 1500 km from Vancouver Island to central California), there is tremendous spatial variation in the relative abundances of available prey. In particular, the bay mussel *Mytilus trossulus* – which is the preferred prey of *N. canaliculata* – is very common in Oregon and Washington and rare along the central California coastline. Sanford *et al.* (2003) found that in the absence of the preferred prey, central California populations of *N. canaliculata* feed more often on the less-preferred, thick-shelled *M. californianus* than do the Oregon and Washington whelks. This geographic variation in propensity to feed on *M. californianus* was consistent among both field-collected and laboratory-raised populations of *N. canaliculata*, suggesting that the variation has a genetic basis. What is remarkable is that even when field-collected populations from Oregon were isolated with *M. californianus* for a year, the whelks still were unable or unwilling to feed on the mussel. This suggests that these predatory whelks cannot or do not shift feeding preferences towards alternative prey within an individuals' lifetime, a finding that runs counter to the tremendous phenotypic plasticity in feeding preferences among a number of other, mostly herbivorous molluscan consumers (see Williams & Walker 1999).

The authors also report data from DNA sequences at a mitochondrial locus to confirm that populations of this direct developer exchange very low gene flow. This allows selection to alter feeding behaviour unimpeded by the homogenizing influence of strong gene flow. However, as

Table 1 A summary of probable examples of local adaptation in host use among marine invertebrates

Animal	Consumes host?	Hosts	Life history	Experimental evidence	Generation assayed	Evidence for gene flow	Reference
Ampithoe longimana, amphipod	Yes	Seaweeds	Brooder	Common garden	Field-collected and Laboratory-reared	COI and ITS sequences	Sotka & Hay (2002); Sotka *et al.* (2003)
Elysia viridis, sea slug	Yes	Seaweeds	Spawner	Common garden	Field-collected and Laboratory-reared†	No	Trowbridge & Todd (2001)
Eogammarus confervicolus, amphipods	No	Seaweed, Mud, Wood	Brooder	Common garden	Field-collected and Laboratory-reared	RFLPs	Stanhope *et al.* (1992a,b), Stanhope *et al.* (1993)
Libinia dubia, decorator crab	No	Seaweeds	Spawner	N/A	Field-collected	No	Stachowicz & Hay (2000)
Nucella canaliculata, whelk	Yes	Mussels, Barnacles	Brooder	Common garden	Field-collected and Laboratory-reared	COI sequences	Sanford *et al.* (2003)
Pinnotheres novaezelandiae, pea crabs	No	Mussels	Spawner	N/A	Field-collected	Allozyme	Stevens (1990a,b)
Spirobis borealis, polychaete	No	Seaweeds	Spawner	N/A	Field-collected†	No	Doyle (1975); Mackay & Doyle (1978)
Synalpheus brooksi, snapping shrimp	No*	Sponges	Brooder	N/A	Field-collected†	Allozyme differences	Duffy (1996a,b)

*May consume host tissue (E. Duffy, pers. comm.).
†Includes larvae of field-collected adults.

Sanford *et al.* (2003) point out, the exact mode of such selection is untested. The hypothesis posited by the authors suggests that higher preference for *M. californianus* in central California is maintained by regional differences in prey availability, which in turn was generated by regional differences in recruitment (Connolly *et al.* 2001). That is, the preferred prey of the whelks (i.e. *M. trossulus*) is rare in central California but is abundant in Oregon; consequently, selection will favour individuals that consume the less preferred *M. californianus* in central California. This seems plausible, but it also is an incomplete explanation because of the uncertain roles played by *M. californianus* among Oregon and California whelks. For example, does the whelk respond evolutionarily to *M. californianus* because the mussel provides food to whelks that would otherwise starve in California? Does *M. californianus* provide whelks protection from larger consumers (e.g. crabs, fishes, octopi), and does that protection become more valuable in California because predation risk is greater relative to Oregon coastlines? Or, does *M. californianus* simply provide protection from abiotic forces (e.g. temperature, desiccation or wave stress) that are not provided by other co-occurring species? In any case, it is amazing that strong geographic variation in feeding preferences have gone previously unrecognized in this whelk, given that it is a central player within one of the most intensively studied marine ecosystems in the literature.

The herbivorous amphipod *Ampithoe longimana*

In estuaries of the south-eastern Atlantic coastline of North America, the herbivorous amphipod *Ampithoe longimana* readily consumes tropical brown seaweeds in the genus *Dictyota* (Duffy & Hay 1994). However, the tropical *Dictyota* is unavailable to more northerly populations (i.e. amphipods from Virginia to Maine). In a series of laboratory-based experiments with transplanted populations, southern populations of *A. longimana* that are sympatric with *Dictyota* displayed stronger feeding preference for *Dictyota* than populations that are north of *Dictyota*'s geographic endpoint (Sotka & Hay 2002; Sotka *et al.* 2003). Bioassay-guided fractionation showed that southern populations were more tolerant of the diterpene alcohols produced by *Dictyota* than were northern populations (Sotka & Hay 2002). Further, the offspring of southern mothers had higher relative fitness when raised on *Dictyota* than did those of northern mothers. These geographic differences in feeding behaviour and performance are genetically mediated, since the patterns were maintained even after 5+ generations were reared on a variety of green and red seaweeds (Sotka *et al.* 2003; Sotka 2003).

Predators of amphipods strongly select for high preference for *Dictyota* among southern amphipod populations (i.e. in North Carolina: Duffy & Hay 1994). *Dictyota* dominates local plant communities in the south-eastern US during times of the year when omnivorous fishes and urchins are abundant because *Dictyota* contains a variety of diterpene alcohols that deter large omnivores. *Ampithoe longimana* is one of the few herbivores that eat this chemically-rich seaweed, and consequently, the amphipods' populations increase in abundance while other small herbivores that cannot tolerate its secondary defenses go locally extinct (Duffy & Hay 1994). In contrast, the evolutionary forces that maintain low preference for *Dictyota* among northern populations are unknown. There might be a fitness cost to maintaining high *Dictyota* tolerance when *Dictyota* is absent. A comparison of mitochondrial and nuclear DNA sequence data and population-level tolerance for *Dictyota* suggests that geographic shift in feeding behaviour occurs in areas where the neutrally-evolving loci do not shift (Sotka *et al.* 2003), suggesting that selection operates to increase tolerance for *Dictyota* in North Carolina and decrease tolerance for *Dictyota* among more northerly populations. High preference for *Dictyota* may be energetically expensive (Sotka & Hay 2002; Cruz-Rivera & Hay 2003) or may lower an individuals' ability to utilize other seaweeds as hosts. Alternatively, it is possible that the random accumulation of deleterious alleles (i.e. genetic drift) could have degraded tolerance for *Dictyota* among these northernmost populations to current levels. In general, the physiological and behavioural consequences of tolerating and consuming secondary metabolites are poorly known for most marine consumers (Targett & Arnold 2001; Paul & Puglisi 2004), and the experimental manipulation of locally adapted *A. longimana* populations may reveal valuable clues.

The herbivorous sea slug *Elysia viridis*

Along the shorelines of Scotland, populations of the herbivorous sea slug *Elysia viridis* can be found abundantly on two green seaweeds; the native *Cladophora ruprestis* and the recently (< 50 years) introduced *Codium fragile* spp. *tomentosoides* (hereafter *C. fragile*). In an admirable series of logistically-difficult assays, Trowbridge & Todd (2001) were able to demonstrate that *E. viridis* did not simply include the introduced *C. fragile* into its diet, but rather that a subpopulation have undergone a 'host-switch' onto the introduced *C. fragile* within the last 50 years. Adult sea slugs from *Cladophora* and from *C. fragile* will strongly prefer their recent host relative to the alternative. The authors also collected batches of eggs that were attached to introduced *C. fragile* fronds and raised the emerged larvae for a month in the laboratory. Although these sea slug larvae metamorphosed on both native and introduced hosts, neither postlarvae nor adults were able to grow on the native *Cladophora* although they were able to feed and grow on the introduced *C. fragile*. If these ecological differences among

individuals are genetically mediated, such local adaptation would be particularly striking for an animal with tremendous potential for broad dispersal (i.e. *E. viridis* larvae are planktonic for over 30 days).

Unfortunately, as pointed by the authors, 'it is not yet known whether the constraints (on the diet change) are based on genetic differences or on irreversible host-induced changes triggered by parental diet' (Trowbridge & Todd 2001, p. 235). Although it seems likely that genetic differences do account for the host-switch, acclimation or conditioning to hosts operating during an early life stage is also consistent with their results. The genetic component could be assessed experimentally by directly comparing the fitness of *Cladophora*-associated and *C. fragile* spp. *tomentosoides*-associated offspring on the alternative diets, a test that was not performed for (presumably) logistical reasons. Another line of evidence for the genetic basis of this apparent host switch could come from an examination of patterns of gene flow from neutral, and quickly evolving molecular markers such as microsatellites. In addition, it would be useful to know the selective forces that drive the host-switch (e.g. minimizing loss to enemies or abiotic forces, competition, or food quality).

The estuarine amphipod *Eogammarus confervicolus*

There are five other examples of invertebrates that have evolved strong local preferences for larger host plants and animals, but that do not consume their hosts with regularity (i.e. are commensals). One of the most thoroughly studied examples of local adaptation to marine biotic habitats centres on the estuarine amphipod *Eogammarus confervicolus* in coastal British Columbia. Subpopulations of the gammaridean amphipod associated with three distinct habitats that occur within 100s of metres of each other: a bank of marshes dominated by *Carex lyngbyei* rhizomes, a mudflat covered with wood from logged trees, and a mudflat covered with the seaweeds *Fucus distichus* and *Pelvetia fastigiata*. Demographic surveys indicated the population dynamics were independent across habitats, suggesting few demographic connections (Stanhope & Levings 1985). A series of choice assays with field-collected and laboratory-reared individuals revealed that subpopulations strongly preferred the habitat in which they were raised and that these preferences were genetically-based (Stanhope *et al.* 1992a,b).

Several restriction fragment length polymorphisms (or RFLPs) confirmed the demographic separation of the populations and generated a historical context in which these habitat preferences evolved (Stanhope *et al.* 1993). Across three independent estuaries, *Fucus*-preferring populations were more similar to each other than to any of the bank- or wood-preferring populations. This finding is consistent with the notion that *Fucus*-preferring populations arose in allopatry from the others and subsequently invaded each estuary. In addition, there were less profound but significant RFLP differences between wood-preferring and bank-preferring populations within two independent estuaries. Interestingly, the timing of this ecological differentiation can be ascertained because high densities of the timber swamped the estuaries only after the onset of commercial logging at the turn of the 20th century. Consequently, the authors argue that the genetically-driven local preferences for wood habitats arose in less than 150 generations.

The authors suggest that mating preferences appear to play a substantial role in maintaining local habitat preferences in *E. confervicolus*, as is predicted by several models of sympatric speciation (Via 2001). Mature adults are strongly attracted to a water-borne chemical produced by females raised from within the male's natal environment, indicating that the pheromone is metabolized by the female using local substrates (Stanhope *et al.* 1992a). However, other selective forces that may also operate to maintain local differences in host use have not been tested. The authors suggest that local host preferences may be important in preventing loss when flooding tide enters the estuary, yet it is also possible that evolving local preferences minimizes loss to enemies. In any case, the authors suggest that similar habitat differentiation occurs among other gammaridean amphipods, leading them to conclude that 'polygenically controlled shifts in habitat preference may not be that uncommon in gammaridean amphipods' (Stanhope *et al.* 1993, pp. 109–110).

The polychaete *Spirobis borealis*

Along the shorelines of Nova Scotia, the sessile polychaete *Spirobris borealis* lives in a calcareous shell glued to the surfaces of brown seaweeds in one of two genera (*Fucus* or *Ascophyllum*). These surfaces apparently do not provide equivalent fitness for the filter-feeding worms: evidence from a field survey suggests that *Fucus* species provide greater fitness to *Spirobis* worms relative to *Ascophyllum* species (Doyle 1975; Mackay & Doyle 1978). The authors suggest that these fitness differences arise because worms can more readily adhere to the rough surfaces of *Fucus* fronds than to smooth *Ascophyllum* fronds, and that such adhesion minimizes loss to wave action.

In locations in which *Fucus* and *Ascophyllum* species are equally abundant, the *Spirobis* larvae are found on *Fucus* and only rarely on *Ascophyllum*. In coves that are dominated by *Ascophyllum*, *Spirobis* is found readily on *Ascophyllum*. A series of laboratory-based assays revealed that these local differences in seaweed abundance translate to population-level differences in larval settlement preferences. In particular, the short-lived (< 24-h) lecithotrophic larvae of adults that were collected from *Ascophyllum*-dominated or

Fucus- and *Ascophyllum*-dominated coves preferred *Ascophyllum* and *Fucus*, respectively. A clear genetic basis of larval preference was revealed from an analysis of full-sib families. However, the researchers apparently neglected to rear a generation under similar conditions in order to confirm that the population-level differences among field-collected juveniles are genetically mediated.

Interestingly, there is also an interaction between population source and other larval behaviours. *Spirobis* larvae from coves dominated by *Ascophyllum* settle more quickly and more gregariously than larvae from other coves. The authors suggest, although do not test experimentally, that this pattern may be the consequence of selection in the *Ascophyllum*-dominated habitat for minimizing error in delaying settlement. By their reasoning, larvae should not delay settlement in order to find *Fucus* in an *Ascophyllum*-dominated cove, because this delay will risk loss to rushing tidal currents. Alternatively, it is also possible that gregariousness provides an unknown selective advantage to larvae in the *Ascophyllum*-dominated environment because of the increased likelihood of encountering mates.

The decorator crab *Libinia dubia*

In estuaries of the south-eastern US coastline, juveniles of the decorator crab *Libinia dubia* place the chemically rich seaweed *Dictyota menstrualis* onto their carapace and thereby reduce their attractiveness to larger fishes (Stachowicz & Hay 1999). As with the herbivorous amphipod *A. longimana* described earlier, this behavioural response of *L. dubia* populations to *D. menstrualis* is mediated by the secondary chemistry produced by the seaweed. The specialized decorating behaviour should not be characterized as 'camouflage', because the relative abundance of *Dictyota* on the animal far exceeds the density of the seaweed in surrounding habitats. Rather, the crab is using the diterpene alcohols produced by *Dictyota* as a chemically-based shield from omnivorous fishes that avoid consuming *Dictyota*.

In areas in central and northern US estuaries, the tropical *Dictyota* is unavailable. Field surveys indicated that these northern crab populations 'camouflage' their carapaces with a generalized array of seaweeds at concentrations that mirror the natural abundances of seaweeds in the surrounding environment (Stachowicz & Hay 2000). When field-collected animals were transplanted to the laboratory and offered a choice of eight seaweeds, the southern animals only decorated with *Dictyota* while the northern animals indiscriminately decorated with a variety of seaweeds. As stated by the authors, this 'geographic shift in crab behaviour away from specialization coincides with a reported decrease in both total predation pressure and the frequency of omnivorous consumers' (Stachowicz & Hay 2000, p. 59). However, as the authors recognize, there is no evidence on whether the geographic variation in *Dictyota* decorating behaviour has a genetic basis. It seems likely because, as the authors argue, naïve crabs that rely on learning to use *Dictyota* would be quickly consumed in the predator-rich southern habitats. Further evidence for a hardwired preference comes from Mobile Bay, Alabama, whose decorator crabs displayed strong preference for *D. menstrualis* despite the absence of *Dictyota* in the region.

The pea crab *Pinnotheres novaezelandiae*

Pea crabs (i.e. the 120+ members of the decapod family Pinnotheridae) closely associate with a wide variety of invertebrate hosts, and have been recorded from mantle cavities of bivalves, the oral surfaces of sand dollars, the anal passages of sea cucumbers, and the sediment tubes constructed by burrowing polychaetes and shrimps (Ricketts *et al.* 1985). Several of these pea crab species are considered generalists that occur on a number of different hosts across their range. However, work by Stevens and colleagues on the pea crab *Pinnotheres novaezelandiae* from New Zealand shores, suggests that presumably 'generalist' species may in fact be composed of several local subpopulations that specialize on distinct hosts. Adult *P. novaezelandiae* have been found within 15 hosts, but primarily from three bivalve species (the green-lip mussel *Perna canaliculus*, the blue mussel *M. edulis aoteanus* and the cockle *Chione stutchburyi*). When adult crabs were removed from the hosts and offered exudates from alternate hosts, the crabs responded most strongly to their original host. When crabs were forced to live in alternate hosts for 4 weeks, this conditioning tended to lower, although not completely eliminate sensitivity for the original host. This suggests that either there is a genetic basis to the host preference by adults or that the host chemistry is imprinted on the individual at an early age (Stevens 1990a).

Genetic differences in host preference may eventually lead to differences in gene flow between subpopulations within different hosts. An examination of the frequencies of 15 allozyme loci from a number of *P. novaezelandiae* populations suggests that such host-race differentiation has already begun (Stevens 1990b). There were far greater genetic differences between host-associated sub-populations relative to either individual localities (i.e. < 10 km) or regions (10s–100s of kilometres apart). At the same time, host-differentiation occurred in multiple, but not all, estuaries, suggesting that these host associations did not arise by chance and that the differentiation reflects host races rather than separate species or sub-species. *Pinnotheres novaezelandiae* seems a useful system for understanding the interaction of widespread gene flow and local selection because the pelagic larvae of this pinnotherid stay in the water column for weeks rather than days.

The snapping shrimp *Synalpheus brooksi*

On coral reefs of the Caribbean coastline of Panama, the snapping shrimp *Synalpheus brooksi* occurs within two sponge species, *Agelas clathrodes* and *Spheciospongia vesparium*. Field surveys consistently indicated that the demography of shrimps from each host sponge were distinct: shrimp colonies from *A. clathrodes* were more dense, had fewer mature females, and were more heavily parasitized by branchial bopyrid isopods than were colonies from *S. vesparium*. A series of laboratory-based assays using field-collected adults from three spatially segregated reefs (1–3 km apart) indicate strong host preference for the shrimps' original hosts (Duffy 1992, 1996a,b).

These differences in host preference are reflected in an analysis of allozyme loci (Duffy 1996a). There were strong differences in allozyme frequencies among shrimps from different reefs regardless of host origin, which likely results from the highly reduced dispersal, short generation time and reasonably high fecundity of this brooding crustacean. In addition, there were significant frequency differences between host-specific colonies on two of the three reefs, suggesting very little demographic exchange between colonies. One of the forces that may help maintain such local differences in host affinity is the intersexual aggression which is common to this and other alphid shrimps. Signs of incompatibility between sexes were recorded when shrimp snapped at each other (as befitting their name), faced each other in a standoff, or when one shrimp moved rapidly away from the other. In laboratory-based assays, shrimps from colonies that were the most divergent genetically (as measured by allozymes) displayed the greatest amount of behavioural incompatibility between sexes.

One of the outstanding questions includes to what degree the host and mate preferences in this system are genetically mediated. Within a single generation, host preferences and intersexual aggression will result in the exclusion of individuals from other sponges whether the behaviours are genetically wired or plastic. But distinguishing these alternatives is central to the question of whether sponge-specific colonies will eventually speciate. That the host races have not yet diverged may reflect the plastic nature of the host and mate preferences (Duffy 1996a).

MARINE PATTERNS OF LOCAL ADAPTATION IN HOST USE

Although the list of locally adapted marine populations is relatively short, some interesting trends are emerging. First, at least two pelagically dispersed animals have locally adapted to distinct hosts (*P. novaezelandiae* and *L. dubia*, and perhaps *Elysia viridis*), indicating that a spawning life-history does not preclude local adaptation to biotic hosts in

the sea. Two hypotheses may help explain how these marine spawners locally specialize. It is possible that dispersal occurs on a much finer spatial scale than is the geographic shift in host abundance. This is probably true for the decorator crab *L. dubia*, which display shifts in decoration across spatial scales of 100s of kilometres and a major biogeographic shift in seaweed availability. However, the shifts in host preference occur on very local scales in the other two examples (i.e. within the same estuary for the pea crab *P. novaezelandiae* and within 10s of kilometres in the sea slug *E. viridis*; both have larval duration of several weeks). These patterns suggest a second hypothesis, namely that strong selection (see section on *Mechanisms of selection*) may operate to maintain local differences in host usage despite the potential dispersal from other locations and hosts.

It seems highly unlikely that these three animals will be the only pelagically-dispersed species that display local adaptation to marine hosts, and marine evolutionary ecologists are only beginning to recognize and explore such intraspecific variation. However, at the same time, it is undeniable that most marine invertebrates have the potential to broadly disperse (Thorson 1950), and it seems likely that this tendency must be realized in many cases. Although the hypothesis awaits testing, the relatively broad dispersal of many marine larvae might indicate that the frequency of local adaptation to marine biota will not match the frequencies displayed within terrestrial and aquatic systems.

Second, and not surprisingly, brooded and lecithotrophic offspring dominate the list of locally adapted species. These life-histories tend to result in reduced dispersal and gene flow relative to animals with pelagically dispersed larvae (Behrens Yamada 1989; Bohonak 1999), which increases the opportunity for local adaptation to biotic hosts on extremely local scales. The importance of brooded animals to future progress in the field cannot be underestimated because of the ease with which marine researchers raise and cross their offspring.

Third, several marine consumers (the amphipod *A. longimana*, the whelk *N. canaliculata*, and perhaps *Elysia viridis*) are able to adapt to local prey communities. This contrasts strongly with most of the marine literature, which attributes variation in feeding behaviour to ontogeny, the consumers' recent history, prey availability or prey quality, rather than genetic differences among individuals or populations (see reviews by Hay 1996; Stachowicz 2001; Sotka 2003; Paul & Puglisi 2004). Current results suggest that the response of local populations to natural and anthropogenic shifts in prey communities might be phenotypic and genetic (Trowbridge 2004). It would be useful to know whether such local evolution is more likely among marine herbivores or carnivores. In terrestrial systems, local adaptation to biotic hosts appears to be a rarely-violated rule among insects that feed on plants (Fox &

Morrow 1981). Reflecting this high incidence of local adaptation, herbivorous insects also tend to have significantly higher speciation rates than do carnivorous insects (Mitter *et al.* 1988). To test this hypothesis for marine organisms, biologists will need to overcome current taxonomic uncertainties and a general dearth of information on the feeding ecology of small consumers across their geographic ranges.

Finally, several of these case studies confirm that chemicals play central roles in mediating interactions between invertebrates and their host organisms. It is well understood that biochemicals cue settlement choices by larvae, the feeding choices of consumers, and the mate and habitat choices of commensals (Crisp 1974; Pawlik 1992; Stachowicz 2001; Paul & Puglisi 2004). The presence of chemical mediation among locally adapted populations indicates that chemical signals and responses may evolve across small spatial distances and on microevolutionary timescales. In a review of sibling species in the sea, Knowlton (1993) concluded that 'the dominant role of chemical recognition systems is perhaps the biggest obstacle to recognizing species boundaries'. Similarly, we may not recognize many other local adaptations because host choices are mediated by chemistry, rather than visually-obvious traits.

MECHANISMS OF SELECTION

It is clear from this review that we lack empirical data for most examples on the selective mechanisms that may drive local evolution in host use. However, the examples do suggest that populations might locally adapt to hosts because preferring local hosts minimizes predation rates, minimizes genetically-based tradeoffs, and/or maximizes the opportunity to encounter mates. As a side note, although we normally think that habitat heterogeneity will favour either phenotypic plasticity or local adaptation (e.g. Sultan & Spencer 2002), researchers should be aware that the strength of phenotypic plasticity itself may be under local selection and the mechanisms of natural selection will thus take other forms.

Selection to avoid enemies can drive genetic differences on microevolutionary timescales. In the case of *L. dubia* and *A. longimana*, there is experimental evidence that population-level variation in habitat choices mediate susceptibility to predators (see also Fawcett 1984). The chemically-rich seaweed *Dictyota* provides these animals a measure of protection from their omnivorous consumers, thereby selecting for strong preference for *Dictyota* as a host. Predator-avoidance behaviours play a significant role in the ecology of virtually all small invertebrates (Hay & Fenical 1988), and has been cited as being a central force underlying the microevolution of several terrestrial insects (Brown *et al.* 1995; Feder 1995; Hufbauer & Via 1999).

In addition, selection to minimize morphologically-based tradeoffs might be a powerful force for generating local genetic differentiation among marine populations. Molluscan grazers (e.g. limpets and slugs) produce feeding morphologies that efficiently utilize one type of seaweed (e.g. tough, leathery tissues) but inefficiently remove other types of seaweeds (e.g. filamentous or flexible tissues: Padilla 1985). As a consequence of this trade-off, populations reared on one host can have lower growth or can starve when on alternate hosts. It is likely, although not demonstrated, that morphological-based tradeoffs play a role in the local patterns in host use among the herbivorous sea slug *Elysia viridis* and the predatory whelk *N. canaliculata*.

On the other hand, there has been far less attention played to the roles that chemically-based tradeoffs may play in the local evolution of marine consumers. On a macroevolutionary scale, a small number of studies suggests that species that are able to tolerate the chemical defenses of one seaweed also tolerate the chemical defenses produced by other seaweeds (e.g. Steinberg *et al.* 1995; Cronin *et al.* 1997). Further, the vast majority of marine herbivores are generalists that feed on a wide range of available seaweeds (Hay & Fenical 1988). Both of these patterns are consistent with the absence of strong chemically-mediated tradeoffs. However, such between-species comparisons are far less convincing than are tests for tradeoffs between individuals and populations within a single species (Poore & Steinberg 2001; Sotka *et al.* 2003).

Finally, selection to find a proper mate can help to maintain local adaptation because mating encounters are far more likely when mate location is predictably linked with specific habitats (see Via 2001). The putative link between habitat and mating choices, termed the 'rendezvous host' hypothesis, has empirical support among mite and aphid species with poor mobility (Bush & Smith 1998; Hawthorne & Via 2001), and there is tremendous opportunity to understand its roles among marine populations. This force may be a primary driver of the local adaptation of commensal species who might be less concerned with the morphological and chemical traits of their hosts than are consumers.

ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF LOCAL ADAPTATION TO PREY

The pattern and process of local adaptation by consumers to their prey have several consequences for the way in which biologists think about marine biodiversity. On ecological timescales, local adaptation alters predictions about how marine communities will respond to natural or human-induced perturbations. A clear example comes from Sanford *et al.* (2003), which showed that *N. canaliculata* drills *M. californianus* far more frequently on California

shorelines than on the Oregon shoreline. When California and Oregon whelks were isolated with transplanted mussels in the field, the California whelks readily consumed *c.* 20% of the mussels while the Oregon whelks did not eat a single individual (Sanford *et al.* 2003). Consequently, the authors speculate that if the current keystone predator on mussels – the seastar *Pisaster ochraceus* – disappeared, California whelk populations that voraciously consumed mussels could functionally fill the *Pisaster* niche, while Oregon whelk populations would not be able to replace *Pisaster* predation. Thus, in this case, predicting how communities will respond to potential disturbances requires information on the genetic capacity of local consumers.

On evolutionary timescales, the presence of locally adapted consumers raises the possibility of coevolution among marine consumers and their prey populations. Under this scenario, consumer populations evolve high preference for local prey and alters prey fitness. In response, the prey population responds evolutionarily to resist these consumers, thereby generating 'co-evolutionary hotspots' (Thompson 1994). This review outlined two (and perhaps three) examples of consumers that evolve in response to their prey, and in each case, prey fitness has at least the possibility of being altered by these consumer adaptations. For example, populations of the sea slug *Elysia viridis* with high preferences for introduced *Codium* species can drive the local extinction of the seaweed (Trowbridge 2002, 2004). Similarly, the amphipod *A. longimana* can shift seaweed communities in North Carolina from phaeophyte-dominated to rhodophyte-dominated in the course of a few weeks when released from their fish predators (Duffy & Hay 2000), and as described earlier, the whelk *N. canaliculata* readily consumes *M. californianus* in California.

One challenge that remains for these and other consumer-prey interactions is to understand when and where prey populations respond evolutionarily to their consumers. Diffuse coevolutionary cycles have been proposed for marine seaweed – herbivore dynamics in Australasia (Steinberg *et al.* 1995) and for gastropod predator – molluscan prey interactions in the Pacific (Vermeij 1994). The support for these assertions has largely come from differences among species (or higher taxa). Within-species genetic responses of marine prey to their predators are relatively unknown. It is known that molluscan prey (Trossell & Etter 2001) and seaweeds (Van Alstyne 1988; Pavia & Toth 2000; Sotka *et al.* 2002) commonly respond plastically to consumer attack, so determining their genetic responses might be problematic. Interestingly, seaweed populations are known to differ in palatability to their herbivores (e.g. Bolser & Hay 1996; Taylor *et al.* 2003), but we have little information on the ecological genetics of seaweed defenses and in particular, on whether an evolutionary response is possible (but see Wright *et al.* 2004). Coevolution is a complicated process even among the best described and well understood interactions between terrestrial plants and their insect herbivores (Bergelson *et al.* 2001). This terrestrial complexity suggests that such coevolutionary studies in marine systems will be similarly exciting but contentious (Hughes & Glidden 1991).

CONCLUSION

The study of the ecology of marine biotic interactions is undergoing a fundamental shift in perspective. The traditional focus on how *species* interact is slowly being replaced by a focus on how *individuals* and *populations* interact, and on the ecological mechanisms that generate and maintain variation in biotic interactions across a species' geographic range. One mechanism that generates such geographic variation is the adaptation of populations to their local biotic communities. A survey of the marine literature reveals a small but growing list of macroinvertebrates that locally adapt to larger hosts. The spatial scales over which local adaptation occurred varied; in some cases, local adaptation occurred between populations separated by 10s to 100s of kilometres and in at least one case, differentiation occurred within 200 m. The case studies were dominated by animals with brooded or lecithotrophic larvae, and represented commensal, herbivorous and carnivorous lifestyles. The evolutionary mechanisms underlying local adaptation in host use are generally poorly documented, but it is likely that locally distinct host preferences evolve when these preferences minimize loss to enemies, minimize feeding-based tradeoffs, and/or maximize opportunities for mating.

The survey also revealed that a life-history that includes a pelagically-dispersed larval stage did not preclude the evolution of local genetic differences. This surprising result may reflect recent evidence from other sources that pelagically-dispersed larvae are not spread across huge spatial distances, or it may reflect the strong selective pressures to maintain local differences in host use. In any case, these marine results generally suggest that broad dispersal potential will not inevitably preclude the evolution of local ecological differences.

REFERENCES

Armsworth, P.R., James, M.K. & Bode, L. (2001). When to press on or turn back: dispersal strategies for reef fish larvae. *Am. Nat.*, 157, 434.

Behrens Yamada, S. (1989). Are direct developers more locally adapted than planktonic developers? *Mar. Biol.*, 103, 403–411.

Bergelson, J., Dwyer, G. & Emerson, J. (2001). Models and data on plant enemy coevolution. *Annu. Rev. Genet.*, 35, 469–499.

Blower, S.M. & Roughgarden, J. (1988). Parasitic castration: Host species preferences, size-selectivity and spatial heterogeneity. *Oecologia*, 75, 512–515.

Bohonak, A.J. (1999). Dispersal, gene flow, and population structure. *Q. Rev. Biol.*, 74, 21–45.

Bolser, R.C. & Hay, M.E. (1996). Are tropical plants better defended? Palatability and defenses of temperate vs. tropical seaweeds. *Ecology (Washington, DC)*, 77, 2269–2286.

Brown, J., Abrahamson, W., Packer, R. & Way, P. (1995). The role of natural-enemy escape in a gallmaker host-plant shift. *Oecologia*, 104, 52–60.

Bush, G.L. & Smith, J.J. (1998). The genetics and ecology of sympatric speciation: A case study. *Res. Popul. Ecol.*, 40, 175–187.

Bushek, D. & Allen, S.K. (1996). Host-parasite interactions among broadly distributed populations of the eastern oyster *Crassostrea virginica* and the protozoan *Perkinsus marinas*. *Mar. Ecol.-Progr. Ser.*, 139, 127–141.

Cain, M., Milligan, B. & Strand, A. (2000). Long-distance seed dispersal in plant populations. *Am. J. Bot.*, 87, 1217–1227.

Clements, K. & Choat, J. (1993). Influence of season, ontogeny and tide on the diet of the temperate marine herbivorous fish *Odax pullus* (Odacidae). *Mar. Biol.*, 117, 213–220.

Connolly, S.R., Menge, B.A. & Roughgarden, J. (2001). A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology*, 82, 1799–1813.

Cowen, R.K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B. & Olson, D.B. (2000). Connectivity of marine populations: Open or closed? *Science*, 287, 857.

Crisp, D. (1974). Factors influencing the settlement of marine invertebrate larvae. In: *Chemoreception in Marine Organisms* (ed. Grant, P. & Mackie, A.). Academic Press, New York, pp. 177–265.

Cronin, G. & Hay, M.E. (1996). Susceptibility to herbivores depends on recent history of both the plant and animal. *Ecology (Washington, DC)*, 77, 1531–1543.

Cronin, G., Paul, V., Hay, M.E. & Fenical, W. (1997). Are tropical herbivores more resistant than temperate herbivores to seaweed chemical defenses? Diterpenoid metabolites from *Dictyota acutiloba* as feeding deterrents for tropical vs. temperate fishes and urchins. *J. Chem. Ecol.*, 23, 289–302.

Cruz-Rivera, E. & Hay, M.E. (2003). Prey nutritional quality interacts with chemical defenses to affect consumer feeding and fitness. *Ecol. Monogr.*, 73, 483–506.

Decker, M.B., Breitburg, D.L. & Marcus, N.H. (2003). Geographical differences in behavioral responses to hypoxia: Local adaptation to an anthropogenic stressor? *Ecol. Appl.*, 13, 1104–1109.

Doyle, R. (1975). Settlement of planktonic larvae: a theory of habitat selection in varying environments. *Am. Nat.*, 109, 113–126.

Duffy, J.E. (1992). Host use patterns and demography ion a guild of tropical sponge-dwelling shrimps. *Mar. Ecol. Progr. Ser.*, 90, 127–138.

Duffy, J.E. (1996a). Resource-associated population subdivision in a symbiotic coral-reef shrimp. *Evolution*, 50, 360–373.

Duffy, J.E. (1996b). Species boundaries, specialization, and the radiation of sponge-dwelling alpheid shrimp. *Biol. J. Linn. Soc.*, 58, 307–324.

Duffy, J.E. & Hay, M.E. (1994). Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology*, 75, 1304–1319.

Duffy, J.E. & Hay, M.E. (2000). Strong impacts of grazing amphipods on the organization of a benthic community. *Ecol. Monogr.*, 70, 237–263.

Fawcett, M. (1984). Local and latitudinal variation in predation on an herbivorous marine snail. *Ecology*, 65, 1214–1230.

Feder, J. (1995). The effects of parasitoids on sympatric host races of *Rhagoletis pomonella* (Diptera: Tephritidae). *Ecology*, 76, 801–813.

Fox, L. & Morrow, P. (1981). Specialization: species property or local phenomenon? *Science*, 211.

Frankham, R. & Kingsolver, J. (2004). Responses to environmental change: adaptation or extinction. In: *Evolutionary Conservation Biology* (ed. Ferriere, R., Dieckmann, U. & Couvet, D.). Cambridge University Press, Cambridge, pp. 85–100.

Futuyma, D. & Moreno, G. (1988). The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.*, 19.

Hawthorne, D. & Via, S. (2001). Genetic linkage of ecological specialization and reproductive isolation in pea aphids. *Nature*, 412, 904–907.

Hay, M.E. (1996). Marine chemical ecology: what's known and what's next? *J. Exp. Mar. Biol. Ecol.*, 200, 103–134.

Hay, M.E. & Fenical, W. (1988). Marine plant–herbivore interactions: the ecology of chemical defense. *Ann. Rev. Ecol. Syst.*, 19, 111–146.

Hay, M.E., Duffy, J.E., Pfister, C.A. & Fenical, W. (1987). Chemical defense against different marine herbivores: are amphipods insect equivalents? *Ecology*, 68, 1567–1580.

Hilbish, T.J. (1996). Population genetics of marine species: The interaction of natural selection and historically differentiated populations. *J. Exp. Mar. Biol. Ecol.*, 200, 67–83.

Hochachka, P.W. & Somero, G. (2002). *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*. Oxford University Press, Oxford, New York.

Hufbauer, R. & Via, S. (1999). Evolution of an aphid-parasitoid interaction: variation in resistance to parasitism among aphid populations specialized on different plants. *Evolution*, 53, 1435–1445.

Hughes, R. & Glidden, C. (1991). Marine plants and their herbivores: coevolutionary myth and precarious mutualisms. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.*, 333, 231–239.

Johannesson, K. (2003). Evolution in *Littorina*: ecology matters. *J. Sea Res.*, 49, 107–117.

Kawecki, T.J. & Ebert, D. (2005). Conceptual issues in local adaptation. *Ecol. Lett.*, in press.

Knowlton, N. (1993). Sibling species in the sea. *Ann. Rev. Ecol. Syst.*, 24, 189–216.

Lønning, S. & Vader, W. (1984). Sibling species of *Doridicola* (Copepoda: Lichomolgidae) from California sea anemones: biology and host specificity. *J. Exp. Mar. Biol. Ecol.*, 77, 99–135.

Largier, J. (2003). Considerations in estimating larval dispersal distances from oceanographic data. *Ecol. Appl.*, 13, S71–S89.

Levins, R. (1968). *Evolution in Changing Environments*. Princeton University Press, Princeton, NJ.

Lively, C.M., Hazel, W.N., Schellenberger, M.J. & Michelson, K.S. (2000). Predator-induced defense: variation for inducibility in an intertidal barnacle. *Ecology (Washington, DC)*, 81, 1240–1247.

Mackay, T. & Doyle, R. (1978). An ecological genetic analysis of the settling behavior of a marine polychaete: I. Probability of settlement and gregarious behavior. *Heredity*, 40, 1–12.

Mayr, E. (1970). *Populations, Species and Evolution: An Abridgment of Animal Species and Evolution*. Harvard University Press, Cambridge, MA.

Mitter, C., Farrell, B. & Wiegmann, B. (1988). The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *Am. Nat.*, 132, 107–128.

Mopper, S. & Strauss, S. (1998). *Genetic Structure and Local Adaptation in Natural Insect Populations: Effects of Ecology, Life History and Behavior*. Chapman and Hall, New York.

Moran, N. (1992). The evolutionary maintenance of alternative phenotypes. *Am. Nat.*, 139.

Nacci, D., Coiro, L., Champlin, D., Jayaraman, S., McKinney, R., Gleason, T. *et al.* (1999). Adaptations of wild populations of the estuarine fish *Fundulus heteroclitus* to persistent environmental conditions. *Mar. Biol.*, 134, 9–17.

Padilla, D. (1985). Structural resistance of algae to herbivores. *Mar. Biol.*, 90, 103–109.

Palmer, A. (1984). Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. *Oecologia*, 62, 162–192.

Paul, V. & Puglisi, M.P. (2004). Chemical mediation of interactions among marine organisms. *Nat. Prod. Rep.*, 21, 189–209.

Pavia, H. & Toth, G. (2000). Inducible chemical resistance to herbivory in the brown seaweed *Ascophyllum nodosum*. *Ecology*, 81, 3212–3225.

Pawlik, J. (1992). Chemical ecology of the settlement of benthic marine invertebrates. *Oceanogr. Mar. Biol.: Annu. Rev.*, 30, 273–335.

Pennings, S. (1990). Size-related shifts in herbivory: specialization in the sea hare *Aplysia californica* Cooper. *J. Exp. Mar. Biol. Ecol.*, 142, 192–200.

Poore, A.G.B. & Steinberg, P.D. (2001). Host-plant adaptation in an herbivorous marine amphipod: Genetic potential not realized in field populations. *Evolution*, 55, 68–80.

Powers, D.A. & Schulte, P. (1998). Evolutionary adaptations of gene structure and expression in natural populations in relations to a changing environment: a multidisciplinary approach to address the million-year saga of a small fish. *J. Exp. Zool.*, 282, 71–94.

Ricketts, E.F., Calvin, J. & Hedgepeth, J.W. (1985). *Between Pacific Tides*. Stanford University Press, Stanford, CA.

Sanford, E., Roth, M.S., Johns, G.C., Wares, J.P. & Somero, G.N. (2003). Local selection and latitudinal variation in a marine predator-prey interaction. *Science*, 300, 1135–1137.

Sasal, P., Durand, P., Faliex, E. & Morand, S. (2000). Experimental approach to the importance of parasitism in biological conservation. *Mar. Ecol. Progr. Ser.*, 198, 293–302.

Schluter, D. (2001). Ecology and the origin of species. *Trends Ecol. Evol.*, 16, 372–380.

Schmidt, P.S. & Rand, D.M. (1999). Intertidal microhabitat and selection at Mpi: interlocus contrasts in the northern acorn barnacle, *Semibalanus balanoides*. *Evolution*, 53, 135.

Shanks, A. (1995). Mechanisms of cross shelf dispersal of larval invertebrates. In: *Ecology of Marine Invertebrate Larvae* (ed. McEdward, L.). CRC Press, Boca Raton, FL.

Sotka, E.E. (2003). Genetic control of feeding preference in the herbivorous amphipod *Ampithoe longimana*. *Mar. Ecol. Progr. Ser.*, 256, 305–310.

Sotka, E.E. & Hay, M.E. (2002). Geographic variation among herbivore populations in tolerance for a chemically rich seaweed. *Ecology (Washington, DC)*, 83, 2721–2735.

Sotka, E.E., Taylor, R.B. & Hay, M.E. (2002). Tissue-specific induction of resistance to herbivores in a brown seaweed: the importance of direct grazing vs. waterborne signals from grazed neighbors. *J. Exp. Mar. Biol. Ecol.*, 277, 1–12.

Sotka, E.E., Wares, J.P. & Hay, M.E. (2003). Geographic and genetic variation in feeding preference for chemically defended seaweeds. *Evolution*, 57, 2262–2276.

Sotka, E.E., Wares, J.P., Barth, J.B., Grosberg, R.K. & Palumbi, S.R. (2004). Strong genetic clines and geographic variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Mol. Ecol.*, 13, 2143–2156.

Stachowicz, J.J. (2001). Chemical ecology of mobile marine invertebrates: predators and prey, allies and competitors. In: *Marine Chemical Ecology* (ed. Baker, B. & McClintock, K.). CRC Press, Boca Raton, pp. 153–190.

Stachowicz, J.J. & Hay, M.E. (1999). Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores. *Ecology*, 80, 495–509.

Stachowicz, J.J. & Hay, M.E. (2000). Geographic variation in camouflage specialization by a decorator crab. *Am. Nat.*, 156, 59–71.

Stanhope, M.J. & Levings, C. (1985). Growth and production of *Eogammarus confervicolus* (Amphipoda: Anisogammaridae) at a log storage site and in areas of undisturbed habitat within the Squamish estuary, British Columbia. *Can. J. Fish. Aquatic Sci.*, 42, 1733–1740.

Stanhope, M.J., Connelly, M.M. & Hartwick, B. (1992a). Evolution of a crustacean chemical communication channel: behavioral and ecological genetic evidence for a habitat-modified, race-specific pheromone. *J. Chem. Ecol.*, 18, 1871–1887.

Stanhope, M.J., Leighton, B.J. & Hartwick, B. (1992b). Polygenic control of habitat preference and its possible role in sympatric population subdivision in an estuarine crustacean. *Heredity*, 69, 279–288.

Stanhope, M.J., Hartwick, B. & Baillie, D. (1993). Molecular phylogeographic evidence for multiple shifts in habitat preference in the diversification of an amphipod species. *Mol. Ecol.*, 2, 99–112.

Steinberg, P., Estes, J. & Winter, F. (1995). Evolutionary consequences of food chain length in kelp forest communities. *Proc. Natl. Acad. Sci. U. S. A.*, 92, 8145–8148.

Stevens, P. (1990a). Specificity of host recognition of individuals from different host races of symbiotic pea crabs (Decapoda:Pinnotheridae). *J. Exp. Mar. Biol. Ecol.*, 141, 193–207.

Stevens, P.M. (1990b). A genetic analysis of the pea crabs (Decapoda: Pinnotheridae) of New Zealand. I. Patterns of spatial and host-associated genetic structuring in *Pinnotheres novaezelandiae* Filhol. *J. Exp. Mar. Biol. Ecol.*, 141, 195–212.

Sultan, S.E. & Spencer, H.G. (2002). Metapopulation structure favors plasticity over local adaptation. *Am. Nat.*, 160, 271–283.

Swearer, S.E., Shima, J.S., Hellberg, M.E., Thorrold, S.R., Jones, G.P., Robertson, D.R. *et al.* (2002). Evidence of self-recruitment in demersal marine populations. *Bull. Mar. Sci.*, 70, 251.

Targett, N. & Arnold, T. (2001). Effects of secondary metabolites on digestion in marine herbivores. In: *Marine Chemical Ecology* (ed. Baker, B. & McClintock, K.). CRC Press, Boca Raton, pp. 391–411.

Taylor, R.B., Lindquist, N., Kubanek, J. & Hay, M.E. (2003). Intraspecific variation in palatability and defensive chemistry of brown seaweeds: effects on herbivore fitness. *Oecologia (Berlin)*, 136, 412–423.

Thacker, R., Nagle, D. & Paul, V. (1997). Effects of repeated exposures to marine cyanobacterial secondary metabolites on feeding by juvenile rabbitfish and parrotfish. *Mar. Ecol.-Progr. Ser.*, 147, 21–29.

Thompson, J. (1994). *The Coevolutionary Process*. University of Chicago Press, Chicago, IL.

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25, 1–45.

Trossell, G. & Etter, R. (2001). Integrating genetic and environmental forces that shape the evolution of geographic variation in a marine snail. *Genetica*, 112–113, 321–337.

Trowbridge, C.D. (2002). Local elimination of *Codium fragile* ssp. tomentosoides: indirect evidence of sacoglossan herbivory? *J. Mar. Biol. Assoc. U. K.*, 82, 1029–1030.

Trowbridge, C.D. (2004). Emerging associations on marine rocky shores: specialist herbivores on introduced macroalgae. *J. Anim. Ecol.*, 73, 294–308.

Trowbridge, C. & Todd, C. (2001). Host-plant change in marine specialist herbivores: ascoglossan sea slugs on introduced macroalgae. *Ecol. Monogr.*, 71, 219–243.

Van Alstyne, K. (1988). Herbivore grazing increases polyphenolic defenses in the brown alga *Fucus distichus*. *Ecology*, 69, 655–663.

Vermeij, G. (1994). The evolutionary interaction among species: selection, escalation, and coevolution. *Annu. Rev. Ecol. Syst.*, 25, 219–236.

Via, S. (2001). Sympatric speciation in animals: the ugly duckling grows up. *Trends Ecol. Evol.*, 16, 381–390.

Warner, R. (1997). Evolutionary ecology: how to reconcile pelagic dispersal with local adaptation. *Coral Reefs*, 16, S115–S120.

Williams, S. & Walker, D. (1999). Mesoherbivore-macroalgal interactions: feeding ecology of sacoglossan sea slugs (Mollusca, Opisthobranchia) and their effects on their food algae. *Oceanogr. Mar. Biol.: Annu. Rev.*, 37, 87–128.

Wright, J.T., de Nys, R., Poore, A.G.B. & Steinberg, P.D. (2004). Chemical defense in a marine alga: heritability and the potential for selection by herbivores. *Ecology*, 85, 2946–2959.