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***“The evolution of marine herbivores in response to algal secondary metabolites”***

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Interactions between macrophytes and marine herbivores play central roles in regulating and structuring nearshore communities, biodiversity and their cycling of nutrients and materials, and can determine the success of human introductions and poleward expansion of seaweeds due to a warming ocean (Lubchenco and Gaines 1981; Schiel and Foster 1985; Hay and Fenical 1988; Duffy and Hay 2001; Steneck et al. 2002; Stachowicz et al. 2007; Ling et al. 2008; Poore et al. 2012; Verges et al. 2015). These impacts occur despite the fact that marine herbivores face profound challenges when feeding on seaweeds. Although seaweeds are generally of higher quality food than terrestrial plants they are among the low quality producers in marine ecosystems (Cebrian and Lartique 2004). Seaweeds contain low levels of nitrogen relative to herbivore tissues, produce physical structures (e.g., crusts and calcification) that make the algae tough and more difficult to digest, and contain an arsenal of secondary metabolites that deter herbivores (Mattson 1980; Littler and Littler 1980; Paul 1992; Paul et al. 2001; Targett and Arnold 2001; Amsler and Fairhead 2006).

In response to seaweed defenses, herbivores employ multiple strategies (termed “herbivore offenses” Karban and Agrawal 2002) that allow them to tolerate or avoid poorer-quality foods. Offensive traits are determined from the herbivores’ point of view and represent their evolutionary solutions to the challenges of feeding on structurally and chemically-defended seaweeds (Jormalainen 2015; Sotka et al. 2008, 2009). In this chapter, we outline our current understanding of the evolution of herbivore offenses, with a focus principally on responses to algal chemical defenses. We briefly outline the spatial and temporal variation in seaweed defenses, highlight the range of herbivore responses to seaweed defenses, and review the evidence for their genetic basis and ecological constraints on herbivore responses. We end with a review of micro- and macroevolutionary patterns in herbivore offenses documented to date.

**1. Variation in seaweed defensive traits**

Variation in defensive traits of aquatic macrophytes is a precondition for the evolution of feeding preferences and locally varying selection for herbivore tolerance. This variation occurs in different scales, from within plant variation among different tissues (Van Alstyne et al. 2001a; Pavia and Toth 2008; Jormalainen and Honkanen 2008) to variation among genotypes (e.g. Tomas et al. 2011; Wright et al. 2004; Jormalainen et al. 2011), populations (e.g., Hemmi and Jormalainen 2004b; Koivikko et al. 2008) and species (Paul et al. 2001; Rasher et al. 2013). In addition, chemical defenses are notoriously plastic, and are known to vary across individuals in response to local abiotic environments (reviewed in Amsler and Fairhead 2006; Jormalainen and Honkanen 2008) and the induction of chemical defenses following damage (reviewed in Toth and Pavia 2007; Pavia and Toth 2008).

The net result of both within- and between- species variation is that macrophyte assemblages will consistently differ with respect to the frequency and strength of defenses they harbor. Assemblages that are exposed to intensive and persistent herbivory will likely have greater numbers of chemically-defended species and genotypes, relative to assemblages with lower herbivory (e.g., Pennings et al. 2002). Differences in the mean palatability of multi-seaweed assemblages have been tested only rarely. For example, Thornber and Stachowicz (2008) offered intertidal and subtidal pairs of closely related species to intertidal and subtidal consumers, testing the notion that subtidal species will have greater herbivory pressure than intertidal species. Their results did not find a general intertidal gradient in palatability, nor in morphological or chemical defenses. Other gradients in mean palatability across macrophyte assemblages that have been tested are across biogeographic gradients (among hemispheres or between tropical and temperate latitudes), but these are discussed in more detail in the context of macroevolutionary patterns (see Section 5.).

**2. Herbivore offensive traits**

In response to spatial and temporal variation in seaweed chemical defenses, herbivores employ a range of behavioral, physiological and morphological adaptations, collectively known as herbivore offenses (Karban and Agrawal 2002). These represent their evolutionary solutions to the challenges of feeding on structurally and chemically-defended seaweeds (Sotka et al. 2009). Our focus here is principally on responses to chemical defenses (i.e., herbivore feeding behavior and physiology). Herbivore adaptations that evolved primarily to cope with seaweed structural defenses in crustaceans (Jormalainen 2015), mollusks (Steneck and Watling 1982; Padilla 1985) and herbivorous fish (Horn and Messer 1992; Horn and Ferry-Graham 2006) have been reviewed elsewhere.

*2a. Herbivore behavior*

Despite the prevalence of generalism among marine herbivores, choosiness among seaweed species (e.g. Duffy and Hay 1991; Pennings et al. 1993; Poore et al. 2000; Cruz-Rivera and Hay 2000a; Jormalainen et al. 2001a; Raubenheimer et al. 2005; Taylor and Brown 2006; Crawley and Hyndes 2007) and among tissues within individuals (e.g. Pavia et al. 2002; Taylor et al. 2002; Honkanen et al. 2002) is ubiquitous and well documented. These feeding preferences can be mediated by nutritive quality and secondary metabolites and by non-nutritional factors such as habitat choice (especially for mesograzers). It is, however, worth noting that evolution of feeding specialization through selection for food utilization ability or through selection for habitat are not mutually exclusive but rather act together: the associations of small mesograzers with their seaweed hosts may well be initially driven by predation avoidance but the association as such will then select for better host use ability (Hay et al. 1989; Hay et al. 1990b; Duffy and Hay 1991).

Several kinds of evidence imply that secondary chemicals play a major role in feeding preferences. First, induced resistance of macroalgae, which is typically measured by feeding bio-assays, often covaries with the increasing contents of secondary metabolites. Second, bioassay-guided fractionation of herbivore-deterrent extracts has provided ample evidence for the role of a wide variety of both polar and lipid soluble macroalgal secondary metabolites on feeding preferences (Pennings et al. 1999; Becerro et al. 2001; Taylor et al. 2003; Kubanek et al. 2004; Van Alstyne et al. 2006; Enge et al. 2012; reviewed in Paul et al. 2001 and Van Alstyne et al. 2001). Third, field observations have demonstrated that macrophyte susceptibility to grazing negatively covaries with the contents of their secondary metabolites (Steinberg 1984; Jormalainen and Ramsay 2009).

Although most marine herbivores display feeding choices among alternate diets, analyses of their gut contents commonly indicate a diverse resource base. Some species actively maintain a mixed diet, with evidence that individuals feed at greater rates on macrophytes that were not encountered previously (e.g., the amphipod *Peramphithoe parmerong,* Poore and Hill 2006; the sea urchin *Strongylocentrotus droebachiensis*, Lyons and Scheibling 2007; and the opisthobranch *Dolabella auricularia,* Pennings et al. 1993). In many mesograzers, diet changes with ontogeny thus giving rise to life-history dietary generalism (e.g. Hemmi and Jormalainen 2004a; Hultgren and Stachowicz 2010; Williamson and Steinberg 2012).

The benefit of mixing diets is that it broadens the available resource base, and provides the herbivore equal if not better fitness than when reared on a single species diet (e.g., Pennings et al. 1993; Cruz-Rivera and Hay 2000a,b 2001; Hemmi and Jormalainen 2004a; Vesakoski et al. 2008; Aquilino et al. 2012; see review in Stachowicz et al. 2007 and Lefcheck et al. 2013). A prominent mechanistic hypothesis is that this dietary generalism dilutes plant toxins by adding less toxic species or species containing toxins that are dealt with a different kind of absorbance limitation or detoxification pathway (e.g., Barreiro et al. 2007; Sotka and Gantz 2013). Mixing diets is also thought to allow herbivores to balance their nutrient intake. In practice, both nutrients and secondary metabolites occur simultaneously within macrophyte tissue and it can be difficult to disentangle their independent and interactive effects on feeding behavior and herbivore fitness (Forbey et al. 2013).

Decorating behavior by majoidean crabs (Hultgren and Stachowicz 2011) represents another offensive behavior, as decoration can co-opt plant chemical defenses for the herbivore’s own protection from larger consumers (Stachowicz and Hay 2000; Cruz-Rivera 2001; Rorandelli et al. 2007; Vasconcelos et al. 2009). As an example, the chemically-rich *Dictyota* minimizes predation rates by omnivorous pinfishes on juveniles of the crab *Libinia dubia* because fishes avoid consuming the diterpene compounds of *Dictyota* (Stachowicz and Hay 1999). In most cases, the chemically-defended alga used as protection décor is a low preference food (see also Amsler et al. 1999 for an urchin example).

*2b. Physiological adaptations*

After choosing to consume a chemically-rich food, herbivore responses will largely be mediated by their physiological traits, including the length and conditions of the digestive tract (Horn and Messer 1992; Choat and Clements 1998; Targett and Arnold 2001), regulation of absorption and detoxification of the dietary toxins (McLean and Duncan 2006), and sequestration of secondary metabolites from the diet. The detailed physiological mechanisms of how herbivores deal with plant defensive compounds are still relatively poorly known (see Sotka and Whalen 2008, Sotka et al. 2009, Forbey et al. 2013). We briefly outline herbivore traits that respond to seaweed chemical defenses and that may serve as targets of natural selection.

*Gut conditions:* Herbivore gut conditions can modify the potentially harmful effects of brown algal phlorotannins and red algal phenolics. Phlorotannins are not easily absorbed due to their polymeric nature and large size. Their harmful action has conventionally been attributed to their ability to form insoluble precipitates with dietary and endogenous proteins in the gut, thereby preventing nutrient absorption (Stern et al. 1996). On the other hand, as phenolic compounds have high oxidative capacity they may also act as auto-oxidants in the gut causing oxidative damage and cytotoxic effects on gut epithelium (Barbehenn et al. 2005). The protein precipitation reactions require acidic to neutral conditions while oxidation occurs particularly under high pH (Salminen and Karonen 2011). The slightly alkaline nature of the sea water, when reflected in gut environment, may increase the importance of oxidation activity but this still remains to be shown in marine herbivores. Other chemical traits of the gut also mediate phlorotannin effectiveness (surfactants, microbial activity, redox potential; reviewed in Tugwell and Branch 1992; Targett and Arnold 2001), and have the potential to create herbivore offence traits.

*Efflux transporters and detoxification:* The absorption of secondary metabolites through the gut epithelium is mainly based on passive diffusion down a concentration gradient and depends on lipid solubility of the compound, with the more lipophilic compounds permeating membranes more easily (McLean and Duncan 2006). Absorbed compounds can, however, be actively transported back to the gut and excreted into feces (Sorensen and Dearing 2006). Such excretion is based on so-called efflux transporters, permeability glycoproteins and other multidrug-resistance-associated proteins, that pump foreign molecules out of the body into the gut. These are aided by cytochromes P-450 and glutathione s-transferases (GST), which together limit or prevent absorption of secondary metabolites through several, non-exclusive mechanisms (Sorensen and Dearing 2006). While secondary metabolites act as substrates for efflux transporters, their presence or the presence of other diet derived metabolites may either facilitate or inhibit excretion activity of efflux transporters (McLean and Duncan 2006; Forbey et al. 2013).

The occurrence of xenobiotic transporter mechanisms has been frequently demonstrated in aquatic animals (clams, mussels, snails, crabs, shrimps, fish), particularly in the context of organism response to pollutants (Bard 2000). Furthermore, xenobiotic transporter mechanisms in marine consumers can be induced as a response to diet derived toxin substrates (See Kuhajek and Schlenk 2003 for red algal metabolite effects on a chiton; Ame et al. 2009 for cyanotoxin effect on a fish; Whalen et al. 2010 for efflux transporters in predatory gastropods; Huang et al. 2014 for dinoflagellate toxin effects on a mussel). In addition, the activities of biotransformation enzymes have been found to be particularly high in herbivorous fish (P-450s; Stegeman et al. 1997) and sea turtles (GSTs; Richardson et al. 2009), as compared to carnivorous ones, suggesting a role for these enzymes in metabolizing plant derived secondary compounds.

*Sequestration of secondary metabolites*: Sequestration of secondary metabolites from the diet and distributing them among tissues is an offensive trait used by many species of opisthobranch mollusks. Such sequestration of secondary metabolites from food algae is understood as a diet-derived chemical defense mechanism (reviewed in Avila 1995; Ginsburg and Paul 2001; Rogers et al. 2002; Marin and Ros 2004; Baumgartner et al. 2009). The compounds sequestered from algae include mono-, di-, tri- and sesquiterpenoids, steroids, halogenated furanones, nitrogenated compounds, and phenolics (Avila 1995). Known algal hosts include mainly red and green algae, but also some brown algae and cyanobacteria (Avila 1995).

The detailed physiological mechanisms how the sequestered chemicals are chosen and transported are poorly known, but the alga-feeding ophistobranchs store defensive metabolites in various epidermal, subepithelial and specific glandular structures (Wägele et al. 2006). In addition, algal metabolites have been found in mucous and opaline secretions, egg masses and in the defensive ink sprayed towards attacking predator (Avila 1995; Rogers et al. 2000; Johnson et al. 2006). Absorbed algal metabolites are either transported and used as such or biotransformed to novel defensive compounds. For example, certain sacoglossan species transform caulerpenyne from green algae into more toxic oxytoxins (Marin and Ros 2004). The occurrence of algal metabolites in the tegument, mucous secretions and ink highlight their antipredator function although they may have other functions such as acting as antimicrobial compounds. Accumulation of compounds in glands may have initially been a way to excrete and avoid autotoxicity of dietary chemicals, which have then evolved to a defensive mechanism (Wägele et al. 2006). There is recent evidence to suggest that other marine herbivores may gain protection from fish predation after consuming chemically defended algae (the herbivorous amphipod *Paradexamine fissicauda* consuming the red alga *Plocamium cartilagineum*, Amsler et al. 2013). It is not yet known whether this protection derives from active sequestration of metabolites or passive accumulation of dietary metabolites.

**3. Potential for herbivore adaptation**

In order for herbivore behavior and physiology to evolve in response to plant secondary metabolites, there must be fitness consequences of consuming metabolites, and a heritable basis to variation in herbivore traits must exist. Here, we review the evidence for each.

*3a. Fitness consequences*

Fitness consequences of consuming macrophyte secondary metabolites are relatively poorly known, given the large number of studies that effects of metabolites on herbivore feeding behavior (Section 2, above). Most fitness studies using marine herbivores isolate individuals with whole tissue from macrophyte species (e.g., Arrontes 1990; Duffy and Hay 1991; Poore and Steinberg 1999; Jormalainen et al. 2001; Sotka and Hay 2002; Taylor and Brown 2006). Relatively few studies have established that variation in fitness across macrophytes is due to variation in the identity and concentration of secondary metabolites. Similarly, there are few studies that have considered the fitness consequences to herbivores of intraspecific variation in secondary metabolites (e.g., Taylor et al. 2003; Toth et al. 2005, Haavisto et al. 2010) despite the fact that such variation is common (Section 1, above).

The fitness consequences of consuming brown algal phlorotannins has mixed effects on herbivorous fish, urchins, gastropods and crustaceans (reviewed by Targett and Arnold 2001; Amsler 2006). Assimilation efficiency and growth decline with increasing phlorotannin concentrations for some herbivores (e.g., the isopod *Idotea baltica*, Jormalainen et al. 2005; the fish *Xiphister mucosus*, Boetcher and Targett 1993), while other herbivores are unaffected (e.g., urchins and gastropods of south-eastern Australia, Steinberg and Van Altena, 1992) or display enhanced performance on diets rich in phlorotannins (the amphipod *Ampithoe valida*, Kubanek et al. 2004).

In most studies using non-polar metabolites, herbivore fitness generally declines with increasing concentrations of metabolites. For non-polar metabolites, Schnitzler et al. (2001) demonstrated that survival of the amphipod *Ampithoe longimana* was reduced by the inclusion of dithiepanone and 9-oxo acid from the brown alga *Dictyopteris membranacea*. Diterpene alchohols from the brown alga *Dictyota menstrualis* reduced growth, survival and fecundity of four species of amphipod, but enhanced survival of the isopod *Paracerceis caudata*, and effects were modified by the nutritional quality of the diets in some cases (Cruz-Rivera and Hay 2003).

Thus, while the body of evidence remains relatively weak, the strong impacts of metabolites on herbivore behavior and at least in some cases, on fitness, indicates that metabolites can be a selective agent on herbivore response.

*3b. Genetic variation*

The potential for selection by secondary metabolites to engender evolutionary change depends on heritability of herbivore traits. The feeding behaviors and traits closely associated with fitness of several mesograzers are known to be heritable. The growth and feeding preferences of the amphipod *Amphithoe longimana* when feedingon chemically rich *Dictyota* vary significantly among full-sib families (Duffy and Hay 1991; Sotka et al. 2003), while preference for the palatable red *Hypnea musciformis* did not vary. Hybrids of *A. longimana* populations with high versus low preference for *Dictyota* had intermediate levels of preference, indicating that *Dictyota* preference was likely an autogenic and quantitative trait (Sotka 2003). In the isopod *Idotea baltica*, growth rate was highly heritable when raised on diets that vary in breadth (the brown alga *Fucus* *vesiculosus* alone vs *F. vesiculosus* and its epiphyte *Pilayella littoralis*) and nutrient enrichment of those diets (Hemmi and Jormalainen 2004a). For the amphipod *Peramphithoe parmerong*, survival on a poor quality host, the brown alga *Padina crassa*, varies significantly among full-sib families, while there was no evidence of heritable variation for performance on the high quality *Sargassum linearifolium* (Poore and Steinberg 2001).

Specific genetic markers have been associated with feeding preference for seaweeds in the amphipod *Gammarus palustris*. The frequency of different isozymes of the amylase varies with feeding preferences for two species of green algae (Borowsky et al. 1985). The isozymes differ in their efficiency in metabolizing the principal starches within each food, and amphipods preferred to consume the alga for which they had the most appropriate isozyme.

Genetic variation of feeding preference can manifest itself as individual specialization (Araújo et al. 2011). Within populations of two generalist marine herbivores, relatively specialized individuals are known to differ in their feeding behavior. Individuals of the sacoglossan *Elysia viridis* preferred green algal hosts similar to the one from which they collected, but subsequent growth was independent of the original host (Baumgartner et al. 2014). In a more extreme example of individual specialization, individuals of the sacoglossan *Placida dendritica* do not survive when switched from their original green algal host to species consumed by other individuals of this herbivore (Trowbridge 1991). Other tests for individual specialization have found that feeding preferences were strongly influenced by recent diet and a rather weak effect of feeding canalization by individuals (Poore and Hill 2006). The role, if any, of seaweed chemical defenses in mediating the individual specialization of these examples was not reported.

While the studies are relatively few in number, especially in contrast to the extensive research with terrestrial insect herbivores (e.g., Futuyma and Peterson 1985), they do indicate considerable heritable variation in feeding behavior or performance within populations of marine herbivores. Further testing of the genetic basis to macrophyte use, however, is required to better predict evolutionary responses to secondary metabolites. In particular, we have no knowledge of possible trade-offs in performance among diets (an important concept underlying models of dietary specialization (Dethier 1954; Via 1984), or trade-offs between diet choice and other traits relating to fitness. Testing for negative genetic correlations among suites of traits is required to establish whether such trade-offs may constrain responses to directional selection on tolerance to metabolites (see Section 5a).

*3c. Constraints on evolution*

Herbivore behavior and physiology may respond strongly to macrophyte secondary metabolites, but their interaction does not occur in a vacuum. The dynamics of herbivore populations depend on other ecological factors that vary spatially and temporally and that can profoundly alter an herbivore’s interaction with macrophytes. We cover three factors that have garnered much attention: competition with other herbivores, predation risk and interactions with gut microbiota.

One long-standing hypothesis for the evolution of feeding preferences is that herbivores will specialize or evolve greater feeding preferences for plants that minimize competition with other herbivores (Strong et al. 1984). Such competition can play a role in determining marine herbivore density and host use. For example, Best et al. (2013) showed that the number of coexisting species in a community of grazing amphipods increased with the diversity of their feeding traits, although it seems likely that these mesograzers are competing for sheltered habitats, rather than for food (Best and Stachowicz 2014). A meta-analysis of the strength of competition over ecosystems and trophic levels, found statistically significant intermediate-sized effects of competition in marine herbivorous mollusks and echinoderms (Gurevitch et al. 1992). Competition for food may occur periodically during mass occurrences of herbivores, e.g. echinoderms (Estes et al. 2004), amphipods (Tegner and Dayton 1991) and isopods (Engkvist et al. 2000), during which the host availability has been seriously depleted. However, under most conditions, marine grazers are rarely food-limited because seaweeds typically have high primary production, and herbivores tend to be very generalized in their feeding preferences and opportunistically feed on animal tissue or dead, decomposed or allochthonous material (e.g. Pennings et al. 2000; Norderhaug et al. 2003; Lastra et al. 2010).

Another, perhaps more common modifier of the ecology of marine herbivores is predator risk. Herbivores lie between “devil and the great blue sea” (i.e., predators and producers) and their fitness is determined not just by their food utilization ability but also by their ability to avoid predators. Avoiding predation may often be more important than competition for food for their population dynamics, and, consequently, traits related to predation avoidance may be strongly selected for. These involve various behavioral strategies and camouflage (Hacker and Madin 1991; Jormalainen et al. 1995; Merilaita 2001; Hultgren and Stachowicz 2008), but also chemical mediation where algal chemical defenses are used as the herbivore’s antipredator traits: For example, several amphipods use chemically deterrent host algae to build domiciles (Hay et al. 1990a; Sotka et al. 1999; Gutow et al. 2011), and, as discussed above, decorator crabs and opisthobranchs gain protection against predators by using algal metabolites.

Hence, predation may modify the evolutionary outcome of the plant-herbivore interaction: with decreasing grazing pressure, the fitness effects of herbivores on producers diminish (Haavisto and Jormalainen 2014). This implies weaker selection for producer traits while selection for the herbivore traits may remain intense. Variation in predation may therefore contribute not just to the magnitude of grazing but also the evolutionary outcomes of plant-herbivore interactions.

Finally, many herbivores possess obligate or facultative microbial gut symbionts, the effects of which may vary from pathogenic to mutualistic (Dillon and Dillon 2004). In particular, herbivores that feed on low quality diets may rely on microbial symbionts that can contribute to digestion enzymatically and/or provide essential nutrition lacking from the diet. Microbial symbionts may also contribute to the detoxification of diet-derived secondary metabolites either in the gut or in the digestive glands (Engel and Moran 2013; Forbey et al. 2013). Although our knowledge on the gut microbiota and its contribution to digestion in marine herbivores is limited, gut bacteria with digestive activity have been found in isopods, amphipods, decapods, mollusks and echinoderms (reviewed in Harris 1993; Pinn et al. 1997; Klussmann-Kolb and Brodie 1999; Zimmer and Bartholme 2003; Mattila et al. 2014) as well as in vertebrate macrograzers such as fish (reviewed in Clements et al. 2014), marine turtles (Arthur et al. 2014) and dugongs (Nelson et al. 2013). Symbiotic bacteria have also been suggested to play a role also in zooplankton herbivory (Tang et al. 2010). It is, thus, possible that environmental availability of bacteria, or, the diet composition itself, may modify the gut microbiota and its contribution to the host utilization ability. For example, the isopod *Idotea balthica* harbors bacterial symbionts that differ in community composition between populations living in different host assemblages (Mattila et al. 2014). Furthermore, as the digestive contributions of gut microbiota can be seen as an herbivore offense trait, characteristics of gut or digestive glands may evolve to foster certain kinds of gut microbiota. Thus, mutualistic interactions with microbiota can mediate host-use making them a potentially important factor in host-herbivore coevolution.

**4. Microevolution of herbivore offenses**

*4a. Field-collected populations and reciprocal feeding experiments in common-garden*

Marine mesograzers are analogous to terrestrial herbivorous insects in their small size, their intimate interactions with their host plants (for food and shelter), as well as their critical roles in their community as both prey and proficient consumers (Hay et al. 1987; Duffy et al. 2001; Jaschinski and Sommer 2008; Duffy et al. 2015). Terrestrial insects readily evolve population-level differences in host use traits (Thompson 2005), suggesting that marine mesograzers should similarly local adapt. Surprisingly, however, we have relatively few such examples among marine mesograzers (Sotka 2005) despite their potential to evolve (see Section 3) and the spatial variation in the distribution and abundance of seaweeds and their chemical defenses.

To our knowledge, the first test of local adaptation in host preference or performance in a marine consumer was with the amphipod *Peramphithoe parmerong* (Poore and Steinberg 2001). Mothers were collected from either *Sargassum linearifolium* or *Padina crassa* individuals within a single bay (meters apart), and from bays in which *P. crassa* did not occur, in southeastern Australia. Despite strong heritable variation in choosing and performing on at least one of the hosts (*P. crassa*)*,* there was no evidence of local adaptation to this host on either spatial scale tested. It is likely that movement among these host plants is too frequent (Poore and Hill 2006) to allow for any differential selection to generate locally adapted demes on these plants.

The first demonstration of geographic variation in feeding preferences comes from *Ampithoe longimana*, an abundant amphipod of estuarine communities along the U.S. Atlantic shoreline*.* In warm-temperate waters of North Carolina, *A. longimana* preferentiallylives and feeds on chemically defended brown seaweeds in the genus *Dictyota*, in large part because diterpene alcohols produced by the genus provides a refuge from consumption by large omnivorous fishes(Duffy and Hay 1991, 1994). *A. longimana* populations sympatric with *Dictyota* more readily consume two species of *Dictyota* and its lipophilic metabolites, and had greater growth and fecundity when reared on *Dictyota,* than did allopatric populations within the colder waters of New England where *Dictyota* does not occur (Sotka and Hay 2002, Sotka *et al.* 2003). It is likely that natural selection, driven largely by omnivorous fish predation pressure, has favored greater feeding preferences for *Dictyota* in warm-water areas where amphipods co-occur with *Dictyota*.

A subsequent study (McCarty and Sotka 2012) tested whether this *A. longimana-Dictyota* interaction represent an exceptional case of local evolution in feeding preference, or alternatively, whether *A. longimana* will locally adapt to any seaweeds that occur at locally high densities. The study found significant regional variation or population-level variation in feeding preferences to seaweed genera that had known chemical defenses (*Dictyota, Caulerpa, Padina, Chondrus* and *Fucus*). In contrast, feeding preference for seaweeds that generally do not produce anti-herbivore metabolites did not differ among herbivore populations (*Acanthophora, Ectocarpus, Gracilaria* and *Hincksia/Feldmannia*). These patterns suggest that while evolution for greater feeding preference of locally important hosts can occur, such evolutionary responses are not uniform across seaweed hosts, and instead seem to depend more on whether the seaweed produces secondary metabolites.

One limitation of the *A. longimana* studies is that populations were compared across large spatial scales (100s of kilometers) that have been separated for 10s or 100s of thousands of generations (Sotka et al. 2003). Thus, it is not clear the extent to which selection or genetic drift may explain geographic variation in feeding patterns. In contrast, the isopod *Idotea balthica* shows geographic variation in juvenile fitness for alternative hosts between populations collected only a few kilometers apart. In the northern Baltic Sea, *I. balthica* occurs in various habitats but prefers *Fucus vesiculosus* as a host plant, a plant that can produce phlorotannins in quantities high enough (e.g., ~15%) to lower isopod growth. As with *A. longimana* on *Dictyota*, the isopod’s preference for *F. vesiculosus* is related to its value as a shelter from visually hunting predatory fish (Jormalainen et al., 2001; Vesakoski et al., 2008). Vesakoski et al. (2009) reared populations, both mothers collected in areas dominated by either *Fucus* or the seagrass *Zostera marina* and their laboratory-born offspring, and showed that while all populations performed best on *Fucus*, isopods from both assemblages performed better with their sympatric dominant host species than did isopods allopatric to this host.

Extending this pattern, Bell and Sotka (2012) compared New England versus Virginia populations (100s of kilometers apart) of *I. balthica* that occur either on *Fucus* versus *Zostera,* respectively. *Fucus vesiculosus* was more readily consumed by northern populations sympatric with *Fucus* than by southern populations allopatric with *Fucus.* This geographic variation in feeding behavior was mediated by both water-soluble and lipophilic secondary metabolites. Similarly, southern *I. balthica* populations occur in habitats that are dominated by seagrasses and *U. linza*, and both hosts were consumed significantly more by southern than northern animals.

A final example is in the urchin *Arbacia punctulata* (Craft et al. 2013). When offered lipophilic extracts from nine subtropical seaweeds, subtropical populations of *Arbacia* consumed significantly more extract from *Dictyota ciliolata, D. pulchella* and *S. zonale* than did cold-temperate populations that are naïve to these subtropical seaweeds*.* Unlike the previous examples, these animals were collected from the field, and thus, the study cannot rule out the possibility that previous experience affected feeding preferences.

All three species for which geographic variation in herbivore offensive traits have been detected are generalists. One consequence is that there must be geographic variation in the preference ranking of foods, as with some terrestrial generalist insects like grasshoppers and some beetles and butterflies (Thompson 2005; Singer 2008). This suggests that polyphagous herbivores are typically composed of populations diverged in their preferences rather than cryptic specialists at the individual or population level as commonly accepted for polyphagous insects (Fox and Morrow 1981; Bolnick et al. 2003; Sword et al. 2005). We propose that microevolutionary shifts in preference ranks are common because they allow generalist herbivores to minimize any fitness or ecological trade-offs that are incurred (Jormalainen et al. 2001a; Sotka and Reynolds 2011), while maintaining the benefits of marine polyphagy (Hay and Steinberg 1992; Stachowicz et al. 2007. see Section 5a below.).

*4b. Selection experiments*

Selection experiments are a powerful approach to understanding evolutionary potential and constraints (Fry 2003). To our knowledge, Sotka and Reynolds (2011) represents the only study that uses a controlled natural-selection experiment to test responses to alternative diets in a marine herbivore. Replicate lines of the polyphagous herbivore *Ampithoe longimana* isolated with only *Dictyota* displayed greater feeding tolerance for *Dictyota* and its secondary metabolites compared to lines isolated on alternative hosts (*Sargassum, Hypnea,* and *Ulva)*. In addition, *Dictyota*-line females become reproductive more quickly when on *Dictyota* than did mixed-seaweed-line females. However, such adaptation appeared to come at a fitness cost when on non-*Dictyota* seaweeds, as mixed-seaweed-lines grew more quickly and produced more eggs when isolated on *Sargassum* and *Ulva* than did *Dictyota*-line individuals. The observed cost does not appear to be symmetrical; that is, a greater cost is incurred when *Dictyota*-adapted individuals are isolated on non-*Dictyota* species, compared to when mixed-seaweed-lines are isolated on *Dictyota*. Fitness costs to when evolving greater preference for *Dictyota* may be strong enough to drive the evolution of specialist feeding preferences for *Dictyota*. That *A. longimana* does not specialize on *Dictyota* may be explained by the seasonal disappearance of the tropically-distributed genus during winter months of North Carolina.

*4c. Novel associations*

Novel associations between herbivores and seaweeds arise when one is introduced accidentally or deliberately. For example, Scottish 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 and Todd (2001) were able to demonstrate that *E. viridis* 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 the 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* even though they were able to feed and grow on the introduced *C. fragile*.

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” (pg. 235 in Trowbridge & Todd 2001). Though it seems likely that genetic differences do account for the host-switch, phenotypic plasticity operating during an early life stage is also consistent with their results. The ecological differences among individuals are particularly striking for an animal with such tremendous potential for broad dispersal (i.e., *E. viridis* larvae are planktonic for over 30 days). It is also unclear the extent to which chemical defenses may underlie these patterns.

It is likely that other examples are present, given that at least 200 seaweeds have been introduced worldwide (Williams and Smith 2007), and chemical defenses have cited in facilitating success of several species (e.g., *Gracilaria vermiculophylla* Hammann et al. 2013, *Fucus evanescens*, Wikström et al. 2006; *Bonnemaisonia hamifera,* Enge et al. 2012; *Caulerpa cylindracea*, Bulleri et al. 2015). It would be interesting to explore the frequency by which local herbivores add invasive seaweeds to their diet with or without evolutionary change.

**5. Macroevolutionary hypotheses of herbivore offenses**

*5a. Generalism in marine herbivores*

The host ranges of most small marine herbivore species remain undescribed. Previous reviews (Hay and Steinberg 1992; Brawley, 1992) have argued that marine herbivores are largely generalists, feeding from more than 10 families from all divisions of seaweeds. These impressions have been mostly gleaned from studies that included large fish and urchin herbivores, animals which are as likely to display restricted host range as would large terrestrial mammals like bison or deer. The more appropriate herbivores to contrast with the well described patterns of chemically mediated host specialization among terrestrial insects are among mesograzers such as slugs, isopods, amphipods and small crabs because these herbivores are small relative to their host plants, and adults tend to be less mobile than those of fishes and urchins (Hay et al. 1987; Taylor and Steinberg 2005). Thus, mesograzers will be more sensitive to the selective environment imposed by any one seaweed species [see Section 4a above].

The two groups of mesograzers for which host use has been well described are amphipods in the family Ampithoidae and the ascoglossan slugs. The two contrast profoundly. Ampithoid amphipods utilise a wide variety of taxonomically unrelated hosts from 20 orders across all three divisions of macroalgae and from 10 genera of seagrasses. This diversity is reflected within many individual species, with almost 60% of the amphipod species recorded on at least two or more host genera (Poore et al. 2008). While there are well studied examples of relatively specialized ampithoid species (e.g., *Pseudamphithoides* *incurvaria* Hay et al. 1990; *Peramphithoe tea* Sotka 2007), most of the species found on a single host genus were recorded from only one study, and thus the apparent specialization is likely to reflect insufficient data on these species. If amphipods are “insect-like” as has been previously proposed (Hay et al. 1987), then their rate of host specificity (~10% on one genus) is more in line with that of tropical root-feeders (Novotny and Basset 2005)

In contrast to the ampithoids, ascoglossans are far more restricted in their host range with virtually all ascoglossan slugs feeding on chlorophyte algae, and all shelled species feeding from the single genus *Caulerpa* (Jensen 1997; Marin and Ros 2004). The high specificity of ascoglossan slugs is analogous to that of lepidopteran caterpillars, or the combined grouping of leaf-chewing and sap-sucking insects. In each of these groups, the majority of species utilize only one plant family (Novotny and Basset 2005). Unfortunately, we lack similar analyses of host use from most other groups of herbivores (isopods, crabs).

It is counter-intuitive that amphipods are generalists while sea slugs have restricted host use. Ampithoid amphipods and isopods are brooders that produce crawl-away offspring that disperse very locally (except when able to occasionally raft on floating seaweeds; e.g., Sotka et al. 2003) while ascoglossans have planktonically-dispersed larvae that potentially disperse 10s of kilometres. Ampithoid mothers can essentially choose the host plant of their offspring in a manner analogous to butterflies (Poore and Steinberg 1999) while ascoglossan larvae must choose their host plants upon recruitment from the water column to the benthos. These traits predict that the amphipods, not the ascoglossans should have restricted host use, while the opposite pattern is found (Poore et al. 2008).

There has been some recent development of hypotheses surrounding generalism in marine herbivores. First, while there is evidence for fitness tradeoffs in using alternative hosts, these tradeoffs are not strong enough to drive the evolution of specialized feeding preferences (sensu Fry 1996). As mentioned in Section 4b, the isopod *Idotea balthica* and amphipod *Ampithoe longimana* both displayed tradeoffs that were likely mediated by chemical defenses. Similarly, molluscan herbivores (snails and slugs) produce radular types that differ in their effectiveness when grazing particular seaweeds (Steneck and Watling 1982), and tradeoffs arise when a mismatch between radular type and the available seaweed occurs (Padilla 1985; Trowbridge 1991).

At first glance, it is a paradox that tradeoffs exist within polyphagous herbivores given that tradeoffs should favor the evolution of specialization. One resolution of this conflict is that the benefit of using multiple hosts (i.e., broadening the resource base) outweighs its fitness cost (Poore et al. 2008). In *A. longimana*,polyphagy appears to be favored because it broadens resource use across seasons, and this benefit outweighs the fitness-based tradeoffs that favor the evolution of specialism on *Dictyota* (Sotka and Reynolds 2011). Similarly, the isopod *Idotea balthica* feeds on a variety of macrophytes but prefers the brown seaweed genus *Fucus* (Jormalainen et al. 2001) despite the fact that *Fucus* is a relatively poor quality food for *Idotea* relative to alternative hosts. However, *Fucus* can be found year-round while those alternative foods largely disappear during colder winter months. For these herbivores, the temporal variability of host plants and host breadth are positively related, a hypothesis that has broad theoretical and empirical support (see Sotka and Reynolds 2011 for discussion).

Second, including chemically-rich seaweeds as part of a broad diet generates an even more consistent resource base. Poore et al. 2008 gathered diet information for ampithoid amphipods, ascoglossan slugs and herbivorous fishes (Sotka and Whalen 2009) and assigned genera as producing (or not producing) classes of lipophilic chemistry that are known to generally deter many marine herbivores (e.g., terpenes, acetogenins). Including chemically-rich macroalgae in the diet was associated with a dramatically increased diet breadth for herbivorous fishes and ampithoid amphipods. In the latter case, the advantage was proportionately greater than one would expect by chance (Poore et al. 2008). Interestingly, the host ranges of ascoglossan slugs, do not differ when chemically-rich and chemically-depauperate seaweeds are included. This suggests that their evolution may be driven by factors other than the presence of lipophilic chemistry.

A related point is that there arises an interesting contrast between terrestrial and marine systems in the relationship between specialization and chemically-rich plants. Among terrestrial insects and mammals, specialists seem to be associated with chemically-‘difficult’ plants (Berenbaum et al. 1996; Dearing et al. 2005), while in marine systems, generalists tend to consume chemically-rich plants (e.g., amphipods and fishes) (Sotka et al. 2009; Sotka and Whalen 2009).

The final hypothesis surrounding generalism centers on differences between large and small-sized herbivores. Nearly 30 years ago, Hay et al. 1987 predicted that small herbivores preferentially consume and inhabit seaweeds that are chemically-defended against larger, more mobile omnivores such as fishes and urchins. Support for this hypothesis can be found in several contexts (see Hay and Steinberg 1992; Paul et al. 2001 and Taylor and Steinberg 2005 for reviews). The opposite pattern has also been suggested (Hay et al. 1998): relative to larger grazers, small mesograzers may be deterred more strongly by secondary metabolites produced by tissues vulnerable to these small grazers (e.g., algal eggs or zygotes).

*5b. Phylogenetic influence on herbivore offense*

Most studies on phylogenetic constraint on herbivore preferences focus on terrestrial insects with relatively narrow host ranges or groups of insects with both specialist and generalist lineages (Winkler and Mitter 2008, Futuyma and Agrawal 2009). Phylogenetic constraints on the feeding preferences of marine herbivores have emerged from a relatively small number of studies. Species of ascoglossan slugs have a host specificity to seaweed genera (Jensen 1997). Genera of ampithoid amphipods show clear differences in tolerating seaweeds with lipophilic chemical defenses (Poore et al. 2008), with species in the genus *Peramphithoe* being the only genus that does not regularly utilize the chemically rich dictyotalean seaweeds (Poore et al. 2008). The feeding patterns of highly polyphagous urchins show surprisingly strong signals of phylogeny. Craft et al. (2012) offered lipophilic extracts from nine subtropical seaweeds at two concentrations to sea urchins and quantified urchin feeding resistance. Patterns of feeding resistance toward these lipophilic defenses were more similar within genera than across genera of urchins, indicating a substantial role for phylogenetic history. Species of fishes clearly differ in willingness to consume chemically-rich seaweeds (e.g., Burkepile and Hay 2011; Rasher et al. 2013), but these patterns have not been explored in a phylogenetic context. A strong phylogenetic signal emerges from fish responses to mineral defenses (i.e., calcium carbonate), as parrotfishes are more likely to ingest calcified seaweeds than are surgeonfishes (acanthurids), because calcium carbonate neutralizes the acidic gut of the latter and thus lowers their feeding efficiency (Horn and Messer 1992).

*5c. Diffuse coevolution - Australasia*

Because the fitness of both herbivores and seaweeds are affected by each other’s presence, it is possible, if not likely, that guilds of seaweeds and herbivores are reciprocally co-evolving. Here, we argue that such diffuse coevolution is common among marine seaweed-herbivore interactions. We should expect that because of the lack of intimate dependence between species, not all traits of either seaweeds nor herbivores are expected to be sculpted by their interaction. Rather the coevolution should be trait-specific (sensu Strauss et al. 2005) and largely centered on traits that mediate seaweed defenses and herbivore offenses.

One of the clearest examples comes from a comparison of Australasia with North American plant-herbivore interactions. Brown seaweeds of Australasia produce greater levels of water-soluble phlorotannins than do browns of the North-American Pacific coastline, and sea urchin and gastropod herbivores from Australia more readily consume phlorotannin-rich seaweeds than do North American herbivores (Estes and Steinberg 1988, Steinberg and van Altena 1992, Steinberg et al. 1995). The responses were largely consistent across seaweeds of phylogenetically-distant origin, suggesting (although not proving) that entire guilds of seaweeds evolved greater levels of chemical defenses. The most parsimonious explanation for weaker seaweed defenses and herbivore offenses in North America is the presence of urchin predators (sea otters), which reduce herbivory by keeping sea urchin populations low (Estes and Steinberg 1988; Estes et al. 2004). This suggests that the predator trophic level may have a cascading effect on chemical defenses of producers. Similarly, urchins and snails from Australia had greater tolerance for phlorotannin-rich seaweeds than did American herbivores.

*5d. Diffuse coevolution– tropical habitats*

There is emerging evidence that latitudinal gradients in seaweed chemical defenses occur that have arisen in part from coevolutionary dynamics. That is, temperate and tropical seaweeds can be defended against local herbivores but the type of defense (water-soluble vs. lipophilic) that is employed changes with latitude. Similarly, there is some evidence that herbivores are responding to these latitudinal changes in plant defenses in a coevolutionary manner. Here is the preliminary evidence to date:

***Tropical seaweeds have greater levels of lipophilic defenses than do temperate seaweeds***: Qualitative literature surveys, experimental evidence and field survey data consistently document that tropical herbivores more frequently encounter terpenes and other lipophilic metabolites than do temperate herbivores. For example, qualitative literature reviews (Hay and Fenical 1988, VanAlstyne et al. 2001, Paul et al. 2001) and limited experimental evidence (Bolser and Hay 1996) indicate that the concentration and diversity of lipophilic secondary metabolites, including terpenes, prenylated quinones and hydroquinones, polyketides and fatty acids, in tropical seaweeds are higher than those in temperate seaweeds. These studies are preliminary, however, in that no study has attempted to separate the co-varying effects of latitudinal origin and phylogenetic lineage on secondary metabolite production.

***Tropical herbivores have greater feeding tolerance for lipophilic defenses than do temperate herbivores:*** To our knowledge, only two studies have explored latitudinal decline in herbivore tolerance of lipophilic defenses, and both confirmed its existence. Cronin et al. 1997 found that three diterpenoid metabolites from the tropical Pacific seaweed *Dictyota acutiloba* deterred North Carolina fishes and urchins at a lower concentration than the concentrations required to deter a fish and urchin species from Guam. A more robust test was recently published by Craft et al.(2013), who quantified the feeding tolerances of four tropical (*Arbacia punctulata, Diadema antillarum, Echinometra lucunter,* and *E. viridis*) and three temperate sea urchin populations (*Arbacia punctulata, Strongylocentrotus droebachiensis, and S. purpuratus*) when offered foods laden with lipophilic seaweed metabolites. Craft et al. (2013) collected nine seaweed species that are common to Caribbean reefs and known to produce lipophilic compounds (including terpenes) that strongly deter feeding by herbivores. Tropical urchins tended to consume more foods coated with lipophilic extract than did temperate populations. The latitudinal decline was apparent for seven of nine seaweeds, and the two exceptions (*Spatoglossum schroederi* and *Palisada poiteaui*) were among the most readily consumed (and by inference, the least deterrent) of the nine seaweeds tested. Thus, the combination of increased levels of lipophilic chemical defenses of tropical seaweeds and elevated feeding tolerance of these defenses by tropical herbivores is consistent with a coevolutionary arms race in tropical habitats that is mediated by lipophilic metabolites.

**Latitudinal gradients mediated by water-soluble compounds?**

In contrast with the clear latitudinal decrease in lipophilic deterrence, there are conflicting lines of evidence on whether water-soluble chemistry, particularly polyphenolics, display a similar geographic pattern. Targett et al. (1992) found that tropical seaweeds in the Caribbean tended to have higher levels of water-soluble polyphenolics relative to more temperate seaweeds. However, Bolser and Hay (1996) found equivalent levels of deterrency among water-soluble compounds of temperate and tropical Atlantic seaweeds. Further, in the southwestern Pacific Ocean, temperate seaweeds have several fold greater levels of polyphenolics than tropical seaweeds (e.g., Steinberg 1986, 1989; Van Alstyne and Paul 1990), a strong contrast with the situation in the Atlantic Ocean. Interestingly, Antarctic seaweeds have phlorotannin levels that are relatively high (Amsler and Fairhead 2005), and some size classes of phlorotannins deterred some local consumers (Iken et al. 2009). Another widely-cited class of water-soluble metabolites is dimethylsulfoniopropionate (DMSP), but there is little information on how this may vary with latitude (Van Alstyne 2008).

Similarly, the evidence for whether tropical herbivores have greater levels of feeding tolerance of water soluble metabolites is relatively weak, although to our knowledge, no study has compared the feeding tolerance of both temperate vs. tropical consumers toward these compounds. When temperate, phenolic-rich seaweeds are offered to tropical consumers (fishes), the results were equivocal. Fishes sometimes avoid consuming the seaweeds (Van Alstyne and Paul 1990) and in other cases the fishes consumed the phenolic-rich seaweeds readily (Steinberg et al. 1991). There are hints that the physiologies of some tropical herbivores better tolerate greater levels of polyphenolics, relative to temperate herbivores. Specifically, Targett et al. (1995) and Boettcher and Targett (1993) report that high concentrations of polyphenolics (~10% of tissue dry weight) lowered the assimilation efficiency of the temperate fish *Xiphaster mucosus*, but did not affect two tropical fishes (*Sparisoma radians* and *S. chrysopterum*) and a tropical crab (*Mithrax sculptus*). Thus, latitudinal patterns of water-soluble defenses and herbivore offenses toward those defenses are equivocal, and, it remains unclear whether a coevolutionary arms race occurs on all temperate reefs (although it clearly occurs on some: Steinberg et al. 1995).

**6. Conclusions and outlook**

Nearly 30 years of study on marine systems have provided several insights into herbivore responses to macrophyte secondary metabolites. First, it is now clear that macrophyte secondary metabolites alter the foraging behavior of consumers, their fitness, or both. The overwhelming pattern that emerges is one of variation: marine herbivores profoundly differ in feeding responses across individuals, populations and species. Second, we have gained some clarity on why most (but not all) marine herbivores have a generalist diet. Fishes and urchins have a broad diet, but tend to avoid chemically-rich macrophytes. Mesograzers have a narrower diet than do fishes and urchins, but their diets are more generalized than those of terrestrial insects, which are their ecological analogue. Mesograzers that can include chemically-rich macrophytes in their diet gain a broader and more consistent resource base, despite the fitness costs. Third, we now have strong evidence that some generalist herbivores (urchins and crustaceans) show among-population differentiation in their preference for and performance on chemically-rich diets. Some of these are likely to represent local adaptations. These microevolutionary shifts in the preference ranks minimizes fitness or ecological trade-offs that are incurred by a generalist diet. Finally, latitudinal and cross-basin comparisons of seaweed chemical defenses and herbivore offenses suggest diffuse coevolutionary arms races are common in the sea.

Our review has also pointed out some glaring gaps in the literature on marine herbivore responses to macrophyte chemical defenses. First, our understanding of how consumers may control the concentration of metabolites in the body and the mechanisms by which metabolites exert their effects (site of action and response) remains in its infancy. Second, with increasing recognition of the role of microbes in the tolerance of terrestrial herbivores to plant metabolites (Hammer and Bowers 2015) and the many new molecular tools to quantify their composition and function, we would expect that exciting new advances in this area will be made in the coming years. Third, preconditions and constraints for adaptive evolution of host ranges and feeding specializations, such as genetic variation and trade-offs in tolerance to specific macrophyte metabolites, still remain sparsely studied. Fourth, most studies of the macroevolution of marine herbivores lack an explicit phylogenetic component, either to test the effect of phylogenetic constraints, or to separate the effect of phylogeny and biogeography on the evolution of tolerance traits. The ease with which molecular phylogenies can be generated will facilitate such discoveries. Finally, the unprecedented rise in global ocean temperatures as a result of increased anthropogenic activity has facilitated the movement of tropical marine herbivores and seaweeds into temperate systems with dramatic consequences to ecosystem dynamics, function, and overall productivity (see Verges et al. 2015 for review). Because emerging evidence suggests the diffuse coevolution of seaweed-herbivore interactions is intensified within tropical habitats, we predict that ongoing movement of marine herbivores and seaweeds into temperate habitats may both increase the relative success of herbivores with higher tolerance for chemical defenses and seaweeds with lower palatability. Similarly, the strength of diffuse coevolution of herbivore offenses and macrophyte defenses can help to predict the impacts of invasions of both seaweeds and herbivores.

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