

# Restricted host use by the herbivorous amphipod *Peramphithoe tea* is motivated by food quality and abiotic refuge

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**Abstract** There is a growing list of marine invertebrate herbivores known to restrict their host choices to a subset of available species, yet the relative importance of the evolutionary forces that select for specialized feeding habits remain unclear. One such specialist is the gammaridean amphipod *Peramphithoe tea* (F. Ampithoidae) that restricts its distribution to the brown laminarian seaweed *Egregia menziesii* in Oregon. A field survey indicated that among available seaweeds in the low intertidal zone of Boiler Bay, Oregon, *Egregia* housed greater than 90% of *P. tea* individuals. A set of laboratory-based habitat and feeding choice assays revealed that this specialized host distribution is likely the consequence of choices made by adult *P. tea*. The restricted host choice is apparently maintained by at least two evolutionary forces. First, a juvenile performance assay indicates that both *Egregia* and the co-occurring seaweed *Alaria marginata*, provide high food quality relative to other seaweeds available in the low-intertidal zone. Second, a field transplantation experiment revealed that *Egregia* protects adult amphipods from becoming dislodged with wave energy more readily than did *Alaria*. Thus, *Egregia*'s value as good quality food and refuge from abiotic stress together explain the restricted host use of *P. tea*. A comparison with previous studies suggests that use of *Egregia* is not con-

sistent across the geographic range of *P. tea*, suggesting the possibility that the host preferences of local populations may respond evolutionarily to geographic shifts in seaweed communities.

## Introduction

The forces that sculpt the evolution of specialization among small herbivores have been explored in terrestrial systems for decades and in marine systems only recently (Hay and Fenical 1988). As is the case with host vascular plants and herbivorous insects (Bernays and Chapman 1994), host seaweeds likely exert strong selection on the feeding choices, life-histories, morphology and physiology of smaller, 'insect-like' (c.f. Hay et al. 1987) invertebrates (Steneck and Watling 1982; Duffy and Hay 1991; Jensen 1997; Poore et al. 2000; Cruz-Rivera and Hay 2001; Sotka 2005; Taylor and Steinberg 2005). The mechanism of selection varies with the system in question, but generally, small herbivores specialize on particular host seaweeds because the seaweed minimizes loss to abiotic forces or predators, or maximizes growth or mate encounter rates, among other possibilities. Though a small, but growing list of animals specialize on a subset of available seaweeds (e.g., Trowbridge 1991; Hay et al. 1992; Sotka et al. 1999; Poore et al. 2000; Krug 2001; Trowbridge and Todd 2001; Cruz-Rivera and Paul 2006), the distribution and abundance of marine herbivorous specialists and the relative importance of the evolutionary forces that select for their specialized feeding habits remain unclear.

One potential example of a marine herbivore with a restricted host range is *Peramphithoe tea*, a

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gammaridean amphipod common to rocky intertidal shorelines of western North America from Alaska to Baja California (Conlan and Bousfield 1982). A series of papers by Gunnill (1982, 1983, 1984) described the population dynamics of *Ampithoe tea* (i.e., syn. *Peramphithoe tea* (Conlan and Bousfield)) on the fucoid *Pelvetia compressa* (syn. *fastigiata*), a canopy-forming seaweed that dominates mid-intertidal habitats in southern California. Seasonal fluctuations in the abundance of *P. tea* on *P. compressa* were related to shifts in temperature and wave energy (Gunnill 1984), and interestingly, *P. tea* appears to outcompete a number of other small commensal invertebrates. However, these studies did not address the evolutionary mechanisms that limit the amphipod *P. tea* to this particular seaweed (c.f. *Peramphithoe parmerong* Poore and Steinberg 1999, 2001; Poore 2004).

In this paper, I focus on the mechanisms that restrict a low-intertidal population of *P. tea* from central Oregon to the laminarian seaweed *Egregia menziesii*. *E. menziesii* ranges from Alaska to Baja California and is considered one of the most morphologically variable kelps known. Thallus fronds can reach several meters in length and consist of lateral blades and sporophylls whose profound variation in shape is partitioned within and among individuals and populations (Blanchette et al. 2002). The faunal community of *Egregia* species includes a specialist limpet (Black 1976), among other more generalist herbivores (Gunnill 1982).

## Materials and methods

### Field distribution survey

Boiler Bay, Oregon (44.83°N, 124.06°W) is a protected embayment along the open shores of the northeastern Pacific Ocean (for details, see Nielsen 2001). In September 2001, I collected five individuals of the six most common seaweeds in the lower intertidal zone (0.6–0.0 m below MLLW): the green seaweed *Ulva*, the red seaweeds *Osmundea* sp. and *Cryptopleura* sp., and the brown seaweeds *Egregia menziesii*, *Alaria marginata*, and *Hedophyllum sessile*. Individual seaweeds (ranging from ~12 g of *Ulva* to 940 g of *Alaria*) were placed into Ziploc bags, returned to the Oregon State University's Hatfield Marine Station, and dipped into a weak solution of insecticide and freshwater. The macroinvertebrate epifauna was then sieved through a 500 µm mesh and preserved in 10% formalin solution and identified. Abundances of epifauna were divided by wet mass of individual seaweed in order to gauge relative density.

### Habitat choice assay

I assessed the host choices made by the amphipod using two sets of assays. The first assay, which I term a *Habitat choice assay*, provided individual amphipods with the opportunity to choose between relatively large pieces of tissue (10–15 cm) that maintained the seaweeds' morphological complexity. In September 2001, ten adult amphipods were placed into each of ten containers filled with ~12 L of seawater and the six seaweeds listed above. The amphipods used were collected from *Egregia* in the field within 24 h of collection. At the end of 44 h, the number of amphipods with tubes per seaweed was recorded. Dead or swimming individuals were discarded from the analysis (8 of 100 amphipods). All assays were performed within a running seawater system of Hatfield Marine Station using ambient seawater temperatures. In order to assess differences in the proportion of amphipods across seaweed species, I used a nonparametric Friedman's test for the whole dataset and also to evaluate pairwise posthoc differences among seaweeds (following Roa 1992).

### Feeding choice assay

I allowed the amphipods to feed on small pieces of tissue for nearly five days (i.e., *Feeding choice assay*). In September 2001, seaweeds and amphipods were collected from Boiler Bay and utilized within 12 h in this assay. Pieces were removed from each seaweed, blotted dry, weighed ( $\pm 1$  mg) and placed in each of twelve plastic bowls filled with ~1 L of seawater and three to five adult amphipods. To minimize bias in feeding preference due to encounter rates, tissues from each seaweed were added to the choice assay bowls at a blotted wet mass equivalent to 4 cm<sup>2</sup> ( $\pm 10\%$ ). For each bowl with amphipods, an identical bowl with pieces from the same plants was run without amphipods; this acted as a control for autogenic changes in plant mass unrelated to amphipod feeding. Replicates were stopped after the amphipods had eaten at least half of one plant piece, or when up to 114 h had elapsed. Plant pieces were blotted and re-weighed, and the change in wet mass of each piece was scaled to account for autogenic changes in plant mass using the formula  $T_i \times (C_f/C_i) - T_f$ , where  $T_i$  and  $T_f$  represent the tissue subject to grazing and  $C_i$  and  $C_f$  represent the control tissue, before (i) and after (f) the experimental run. I analyzed differences in consumption rates across seaweed species as described for the *Habitat Choice assay*.

## Juvenile performance assay

Juvenile *P. tea* amphipods were isolated on single seaweed species within a week after emergence from the brood pouch. They were held on only these foods for 25 days. To set-up this experiment, brooding females were left on *Enteromorpha* in small Petri dishes until juveniles had left the brood pouch. Juveniles from each mother were placed on one of seven treatments in individual 40 ml Petri dishes at ambient seawater temperatures. The seven treatments were: the six seaweeds that were offered adults in the multiple choice assays, or a starvation control that received no food. A single mother provided one offspring to each treatment. Every 2 days, the amphipods were checked for deaths and for reproductive maturity of the females. Water was changed weekly and food was added to dishes when depleted. The size of surviving amphipods at the termination of the experiment (as measured by the straight-line length of the dorsal edge of the first three segments) was also recorded. Survivorship data were analyzed via a *G*-test, while size of amphipods was analyzed via a nonparametric Mann-Whitney *U*.

## Field experiment of amphipod survival

In March 2002, I performed a field experiment to assess whether *Alaria marginata* and *Egregia menziesii* differed in habitat quality for *Peramphithoe tea*. I glued 10 live adult amphipods haphazardly onto 10 cm long pieces of tissue using KrazyGlue<sup>®</sup>. One individual of each seaweed species was attached in pairs to a single 5 cm piece of three-strand nylon rope. These ropes were then transported to Boiler Bay and cable tied to masonry bricks. Half of the blocks were placed within plastic Vexar cages (1 cm mesh). These cages eliminate the influence of fish and other large predators on the removal of glued amphipods. Three sets of caged and uncaged bricks were left for 24 h at MLLW, and subsequently examined for the number of glued amphipods remaining. After 24 h, no recorded amphipod was still alive. To assess the effect of seaweed species, cage and their interaction on number of amphipods remaining, I used a blocked two-way ANOVA design. However, there was no effect of cage ( $P = 1.000$ ) or the interaction of cage and seaweed ( $P = 0.668$ ) on the number of amphipods remaining. I subsequently removed cage as a factor and pursued a blocked one-way ANOVA. A visual examination revealed the data to appear normally distributed and homoscedastic.

## Results

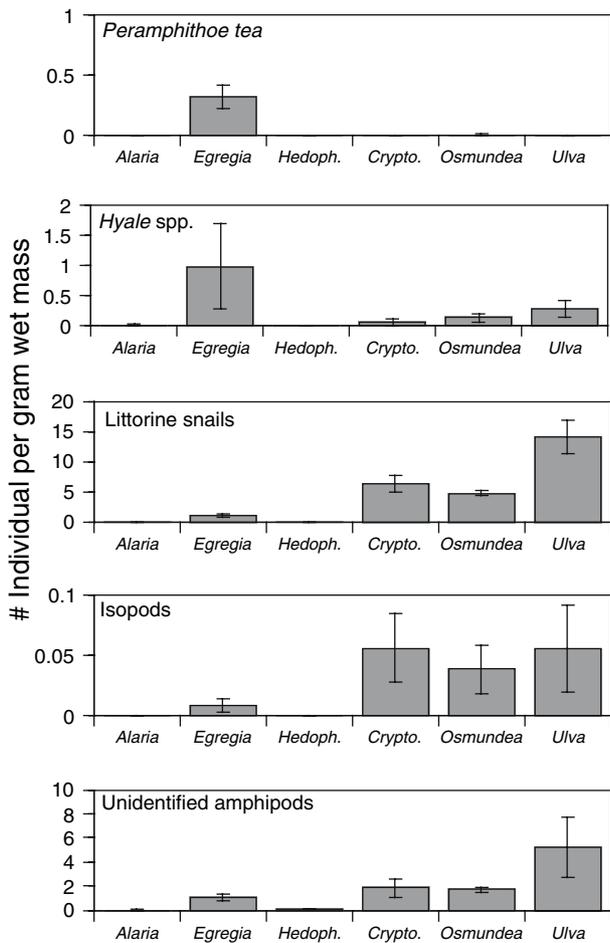
There were striking differences in host use among macroinvertebrates in the low-intertidal zone of Boiler Bay, OR (Fig. 1). Very few macroinvertebrates could be found on *Alaria* and only a few unidentified amphipods were found on *Hedophyllum*. In contrast, individuals of all macroinvertebrate groups were collected on *Egregia menziesii*. *Cryptosiphonia*, *Osmundea*, and *Ulva* was a host to virtually all individuals of macroinvertebrates with the exception of the herbivorous amphipod *Peramphithoe tea*. In total, 98% of *Peramphithoe tea* individuals and 96% of *Hyale* spp. individuals were found on *Egregia* (94% and 67%, respectively, when adjusted for wet mass of seaweeds sampled). Thus, these two mesograzers, and *P. tea* in particular, were largely restricted to a single host in Boiler Bay.

I explored whether habitat choice could help explain the restricted distribution of *Peramphithoe tea*. When given a choice between relatively large tissue (~10 cm length) from each of six seaweeds, adult *Peramphithoe tea* overwhelmingly preferred *Egregia* (Fig. 2) and almost never chose to settle on any other host ( $n = 10$ ; overall Friedman's test  $P < 0.001$ ). During the short duration of this *habitat choice assay* (<48 h), the animals did not appear to consume seaweed tissue.

To assess whether restricted host preference corresponds to the feeding preferences by *P. tea*, I allowed adults to feed for up to 112 h on small (~4 cm<sup>2</sup>), morphologically similar tissues from the same six seaweeds. There was a significant effect of seaweed species on feeding rate ( $n = 12$ ; Friedman's test  $P < 0.001$ ). Interestingly, a posthoc examination revealed that *P. tea* consumed both *Egregia* and *Alaria* at equivalently high rates, while *Hedophyllum*, *Osmundea*, *Cryptosiphonia* and *Ulva* were consumed at lower rates (Fig. 2).

In order to determine whether restricted host use is reflected in the fitness of their offspring, I isolated 11–13 juveniles on individual seaweeds for 25 days. All individuals without foods died within five days. Individuals could not survive past 12 days on *Hedophyllum*, *Cryptosiphonia*, *Osmundea* and *Ulva*. In contrast, 54 and 83% of juveniles survived 25 days on *Alaria* and *Egregia*, respectively (Fig. 2), though this difference in survivorship was not statistically significant (*G*-test;  $P > 0.10$ ). An examination of the size of these survivors at day 25 revealed that the juveniles on *Alaria* ( $n = 8$ ) and *Egregia* ( $n = 11$ ) grew at statistically indistinguishable rates (Fig. 2; Mann-Whitney  $W = 20.00$ ;  $P = 0.150$ ).

Thus, the performance and feeding choice assays indicates that both *Alaria* and *Egregia* both provide

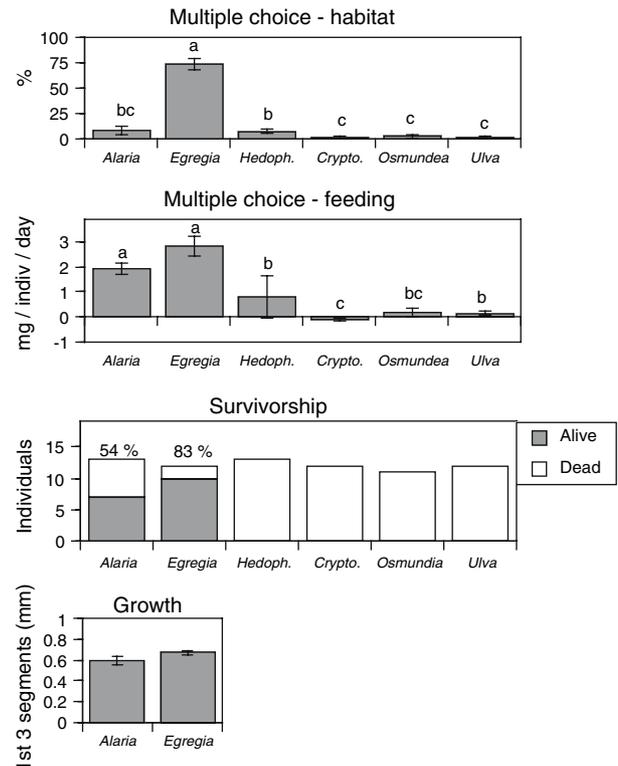


**Fig. 1** The number of animals per gram wet mass of seaweed (mean ± SE) collected from the six most common seaweeds at the low intertidal zone (−2.0 to 0.0 ft MLLW) in Boiler Bay, Oregon (September 2001;  $n = 5$ )

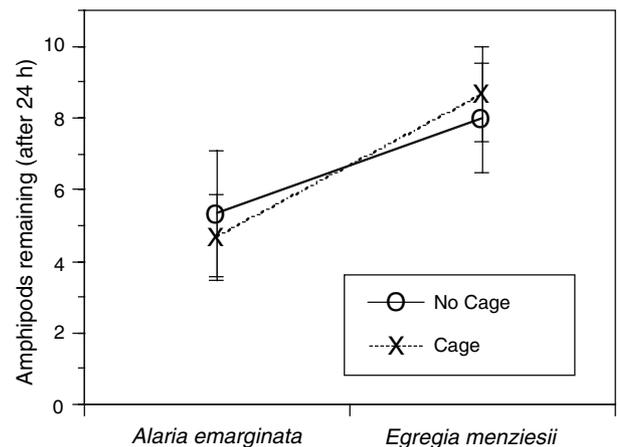
high food quality to *P. tea*. To assess whether these two seaweeds also protect amphipods from abiotic and biotic stresses in the field, I transplanted seaweeds with glued amphipods to Boiler Bay for 24 h either inside or outside predator-exclusion cages. There was no effect of caging on the number of amphipods remaining (Fig. 3; see “Materials and methods”). A blocked one-way ANOVA indicates that there were significantly more amphipods remaining on *Egregia* (mean = 8.3 individuals) than on *Alaria* (mean = 5.0 individuals) (Fig. 3;  $df = 1$ ;  $F = 6.25$ ;  $P = 0.031$ ).

**Discussion**

*Peramphithoe tea* is locally restricted in low-intertidal beds of Boiler Bay, Oregon to the laminarian *Egregia menziesii* (Fig. 1). My data are consistent with the notion that this specialized host distribution of *P. tea* is



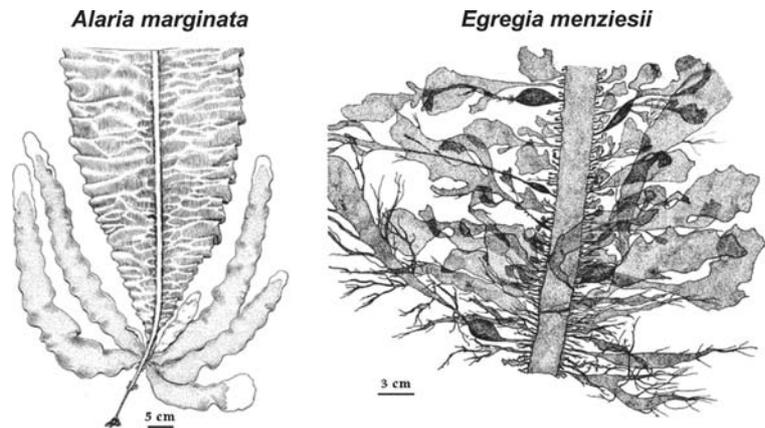
**Fig. 2** The host specialization of the herbivorous amphipod *Peramphithoe tea* on *Egregia menziesii*. Data are shown from the multiple choice assay for large tissue in 44 h (i.e., *Habitat choice assay*), multiple choice assay for small tissue across 112 h (i.e., *Feeding choice assay*), and the survivorship and size of juveniles *P. tea* after 25 days. Letters indicate groups of seaweed species that are statistically indistinguishable. Error bars represent the standard error of the sample



**Fig. 3** Persistence of glued *Peramphithoe tea* adults on the seaweeds *Alaria emarginata* and *Egregia menziesii* after 24 h within and outside cages (mean ± SE;  $n = 3$ )

the consequence of active host choices (Fig. 2) by the adult. Further, this restricted host-choice is favored by two evolutionary forces: *Egregia* represents high food quality to juveniles (Fig. 2) and protects adult

**Fig. 4** Illustrations of *Alaria marginata* and *Egregia menziesii*. The *Egregia menziesii* illustration was taken with permission from the DeCew's Guide to the Seaweeds of British Columbia, Washington, Oregon, and Northern California, University Herbarium, University of California, Berkeley. The *Alaria marginata* illustration was used with permission from University of California Publications in Botany. vol. 1: pl 21



amphipods from becoming dislodged with wave energy (Fig. 3).

The choice for *Egregia* as a host seaweed is cued in part by its complex morphology. When offered large pieces of tissue, adult amphipods overwhelmingly chose *Egregia* as habitat (Fig. 2). These ~10 cm pieces of tissue included the lateral blades and sporophylls that are highly pronounced in *Egregia* (Fig. 4) and between which the amphipod constructs its mucus tubes. Such morphological features add habitat complexity to the seaweed and are absent from the simpler architecture of the other seaweeds, most especially from *Alaria* (Fig. 4). When amphipods were offered small tissue (~4 cm<sup>2</sup>) that was devoid of complexity, *P. tea* consumed *Alaria* and *Egregia* at statistically similar rates (Fig. 2). Thus, habitat complexity appears to represent a strong preference cue for *P. tea*, as has been shown with other herbivorous amphipods (Nelson 1979; Hacker and Steneck 1990; but see Holmlund et al. 1990).

There appear to be two evolutionary forces that maintain the choice for *Egregia* in Boiler Bay, Oregon. First, selection to utilize *Egregia* as a host seaweed may be driven by the high food quality that the seaweed offers *P. tea* offspring (Fig. 2). The survivorship and growth of *P. tea* was highest on *Egregia* relative to all other seaweeds, though statistically indistinguishable from the growth and survivorship on *Alaria*. At the same time, *P. tea* juveniles cannot or do not utilize the other seaweeds to survive (Fig. 2). The close match between juvenile performance and adult preferences and host distribution in *P. tea* has also been noted in the congeneric amphipod *Peramphithoe parmerong* in Australasia (Poore and Steinberg 1999) and the confamilial amphipods *Ampithoe longimana* and *A. valida* from the northwestern Atlantic (Nicotri 1980; Cruz-Rivera and Hay 2001). Preference and performance are also linked within geographically separated popula-

tions of *Ampithoe longimana* that differ in local feeding preferences (Sotka and Hay 2002; Sotka et al. 2003). More broadly, a recent survey by Taylor and Brown (2006) concluded that, “food or habitat preference is positively correlated, to varying strengths, with juvenile performance in all the relevant studies that we could locate on herbivorous marine amphipods” (p. 460).

Second, a field experiment demonstrated that amphipods were more likely to persist on *Egregia* than on *Alaria* (Fig. 3), suggesting that selection to utilize *Egregia* may be driven in part by its value as a refuge from wave energy. Wave forces in intertidal zones can easily dislodge seaweed-associated amphipods from their hosts (Fincham 1970) and those seaweeds that minimize its loss are often favored habitats (Mackay and Doyle 1978; Moore 1978; Viejo 1999; Norderhaug 2004), especially when amphipod body size and the architecture of the seaweed habitat are closely matched (Edgar 1983b; Hacker and Steneck 1990; Sotka et al. 1999).

The exact mechanism that allows *P. tea* to be protected from abiotic forces is unclear. An analysis of the breaking strength of typical length *Egregia* from central California suggests that the seaweed is far stronger than it “needs” to be in order to survive wave forces of open Pacific shores (Friedland and Denny 1995), but the high abundance of *Alaria* and the other seaweeds in the low intertidal zone suggests that between-species differences in breakage cannot explain the abiotic refuge of *Egregia*. Rather, the refuge is likely the consequence of a morphologically complex *Egregia* that allows amphipods to avoid wave forces via the interfrond spaces. The relatively flat, slippery and morphologically simple *Alaria* (see Fig. 4) does not afford *P. tea* this advantage. One possible artifact of gluing amphipods haphazardly onto *Egregia* is that it may not mimic the behavioral tendency of *P. tea* to move to

inter-frond spaces of *Egregia* to minimize risk of dislodgement. However, this bias strengthens the argument that *Egregia* provides greater protection from abiotic forces than does *Alaria* because the inter-frond spaces were unavailable to the immobilized amphipods.

Other ecological factors appear to play little role in explaining *P. tea* host use. The field experiment indicates that caged and uncaged seaweeds did not differ in the number of amphipods remaining for either *Egregia* nor *Alaria* (Fig. 3). This result suggests predation risk does not play a substantial role in maintaining host use within *P. tea*. In this way, *P. tea* contrasts with several other mesograzers, which prefer seaweeds that minimize their risk to consumption by larger herbivorous or omnivorous fishes (Hacker and Steneck 1990; Hay 1992).

Two other explanations for restricted host choices lack empirical support. The field distribution data are consistent with a role for competition among habitat dwellers in determining host use (cf. Edgar 1983a, 1993); that is, there is an inverse correlation across seaweeds between the densities of group of littorine snails, isopods, and unidentified amphipods and the densities of *P. tea* (Fig. 1). However, it seems unlikely that *P. tea* would be competitively excluded from the three seaweeds (i.e., *Cryptosiphonia*, *Osmundea*, and *Ulva*) that allowed high densities of other species because these three seaweeds represent extremely poor foods for *P. tea* juveniles (Fig. 2). It is also theoretically possible that the host preference for *Egregia* is maintained in *P. tea* because the other seaweeds become locally unavailable on a seasonal basis (cf. Taylor and Steinberg 2005). However, these seaweeds are relatively abundant within Boiler Bay year-round (Sotka, personal observation). Thus, food quality and risk to abiotic forces alone readily explain host use of *P. tea* along this shoreline.

It remains unclear which nutritional or chemical traits of the seaweeds are responsible for the patterns of feeding and performance by *P. tea*. *Cryptosiphonia* occurs readily in high intertidal pools and can be readily consumed by *Littorina* spp. (Nielsen 2001). Kelps (e.g., *Alaria*, *Egregia*, and *Hedophyllum*) in these temperate zones tend to be relatively low in phlorotannin loads, a putative chemical defense against generalist herbivores (Steinberg et al. 1995; Van Alstyne et al. 1999) and are readily consumed by chitons and urchins (e.g., Burnaford 2004). *Ulva* spp. contains activated antiherbivory defenses via the DMSO pathway (Van Alstyne and Houser 2003). I could not find, however, any information in the literature on the nutritional and chemical traits that may deter *P. tea* from these seaweeds.

Alternatively, it is possible that the red and green seaweeds lack a feeding stimulant for *P. tea*, given that the genus *Peramphithoe* predominantly consumes brown seaweeds (Poore and Steinberg 2001; Taylor and Steinberg 2005).

One caveat to these results is that I field-surveyed the seaweed fauna only once (September 2001) and only during the daylight hours. Thus, there is a possibility that I may have missed host use patterns that vary on a seasonal (e.g., Kotta et al. 2004) or daily cycle (e.g., Buschmann 1990). However, it is unlikely that further sampling would profoundly alter the primary conclusion that *Egregia* is the predominant host seaweed for Oregon *P. tea* because the field survey and laboratory assays revealed consistent results and because *Egregia* persists year-round.

As a final note, a comparison of my data with Gunnill (1982) indicates that the Oregon population differs from southern California population in two intriguing manners. First, I found *Peramphithoe* at low-intertidal seaweeds in Oregon (−0.6 to 0.0 MLLW) and only rarely above this level (personal observation) (see also D'Antonio 1985; and Nielsen 2001), whereas Gunnill (1982) readily found California populations in the mid-intertidal zone (0.7–0.8 m above MLLW). This distinction raises the possibility that California populations are more tolerant of emersion than Oregon populations. Second, there appear to be geographic differences in the host use of *Peramphithoe tea*. *Egregia* is the most important host to Oregon *P. tea* and a less common host for southern California *P. tea* (Gunnill 1982). Further, the most important host to southern California *P. tea*, *Pelvetia compressa*, has not been reported from north of California (DeCew's Guide to the Seaweeds of British Columbia, Washington, Oregon, and Northern California; <http://www.ucjeps.berkeley.edu/guide/>). Thus, Oregon amphipods have not been exposed to *P. compressa* in their recent evolutionary history and consequently, may be unlikely to favor *P. compressa* as a host plant. An analogous situation occurs with the herbivorous amphipod *Ampithoe longimana*, in which geographic differences in seaweed communities has driven the local differentiation of host preferences (Sotka and Hay 2002; Sotka et al. 2003). These hypotheses could be readily tested using common-garden experiments.

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## References

- Bernays E, Chapman R (1994) Host-plant selection by phytophagous insects. Chapman and Hall, New York
- Black R (1976) The effects of grazing by the limpet, *Acmaea incessa*, on the kelp, *Egregia laevigata*, in the intertidal zone. *Ecology* 57:267–277
- Blanchette CA, Miner BG, Gaines SD (2002) Geographic variability in form, size, and survival of *Egregia menziesii* around point conception, California. *Mar Ecol Prog Ser* 239:69–82
- Burnaford JL (2004) Habitat modification and refuge from sublethal stress drive a marine plant-herbivore association. *Ecology* 85:2837–2849
- Buschmann AH (1990) Intertidal macroalgae as refuge and food for amphipoda in central Chile. *Aquat Bot* 36:237–245
- Conlan KE, Bousfield EL (1982) The amphipod superfamily Corophioidea in the northeastern Pacific region, family Ampithoidae: systematics and distributional ecology. *Publ Biol Oceanogr Natl Mus Can* 10:41–75
- Cruz-Rivera E, Hay ME (2001) Macroalgal traits and the feeding and fitness of an herbivorous amphipod: the roles of selectivity, mixing, and compensation. *Mar Ecol Prog Ser* 218:249–266
- Cruz-Rivera E, Paul VJ (2006) Feeding by coral reef mesograzers: algae or cyanobacteria? *Coral Reefs* 25:617–627
- D'Antonio C (1985) Epiphytes on the rocky intertidal red alga *Rhodomela larix* (Turner) C. Agardh: negative effects on the host and food for herbivores? *J Exp Mar Biol Ecol* 86:197–218
- Duffy JE, Hay ME (1991) Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* 72:1286–1298
- Edgar GJ (1983a) The ecology of south-east Tasmanian phytal animal communities. IV. Factors affecting the distribution of amphithoid amphipods among algae. *J Exp Mar Biol Ecol* 70:205–225
- Edgar GJ (1983b) The ecology of south-east Tasmanian phytal animal communities. I. Spatial organization on a local scale. *J Exp Mar Biol Ecol* 70:129–157
- Edgar GJ (1993) Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index. *Oecologia* 95:115–121
- Fincham AA (1970) Amphipods in the surf plankton. *J Mar Biol Ass UK* 50:177–198
- Friedland MT, Denny MW (1995) Surviving hydrodynamic forces in a wave-swept environment: consequences of morphology in the feather boa kelp, *Egregia menziesii* (Turner). *J Exp Mar Biol Ecol* 190:109–133
- Gunnill FC (1982) Macroalgae as habitat patch islands for *Scutellidium lamellipes* (Copepoda: Harpacticoida) and *Ampithoe tea* (Amphipoda: Gammaridae). *Mar Biol* 69:103–116
- Gunnill FC (1983) Seasonal variations in the invertebrate faunas of *Pelvetia fastigiata* (Fucaceae): effects of plant size and distribution. *Mar Biol* 73:115–130
- Gunnill FC (1984) Differing distributions of potentially competing amphipods, copepods and gastropods among specimens of the intertidal alga. *Mar Biol* 82:277–291
- Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71:2269–2285
- Hay ME (1992) The role of seaweed chemical defenses in the evolution of feeding specialization and in the mediation of complex interactions. In: Paul V (ed) *Ecological roles of marine natural products*. Comstock Publishing, Ithaca
- Hay ME, Duffy JE, Pfister CA, Fenical W (1987) Chemical defense against different marine herbivores: are amphipods insect equivalents? *Ecology* 68:1567–1580
- Hay ME, Fenical W (1988) Marine plant-herbivore interactions: the ecology of chemical defense. *Annu Rev Ecol Syst* 19:111–146
- Hay ME, Steinberg PD, Fenical W (1992) The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. Chemical mediation of seaweed-herbivore interactions. *Syst Assoc Spec* 46:319–337
- Holmlund MB, Peterson CH, Hay ME (1990) Does algal morphology affect amphipod susceptibility to fish predation? *J Exp Mar Biol Ecol* 139:65–84
- Jensen KR (1997) Evolution of the Sacoglossa (Mollusca, Opisthobranchia) and the ecological associations with their food plants. *Evol Ecol* 11:301–335
- Kotta J, Torn K, Martin G, Orav-Kotta H, Paalme T (2004) Seasonal variation in invertebrate grazing on *Chara connivens* and *C.tomentosa* in Koiguste Bay, NE Baltic Sea. *Helgoland Mar Res* 58:71–76
- Krug P (2001) Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*. *Mar Ecol Prog Ser* 213:177–192
- 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
- Moore PG (1978) Turbidity and kelp holdfast Amphipoda: I. Wales and S.W. England. *J Exp Mar Biol Ecol* 32:53–96
- Nelson WG (1979) Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J Exp Mar Biol Ecol* 38:225–245
- Nicotri ME (1980) Factors involved in herbivore food preference. *J Exp Mar Biol Ecol* 42:13–26
- Nielsen KJ (2001) Bottom-up and top-down forces in tide pools: test of a food chain model in an intertidal community. *Ecol Monogr* 71:187–217
- Norderhaug KM (2004) Use of red algae as hosts by kelp-associated amphipods. *Mar Biol* 144:225–230
- Poore AB (2004) Spatial associations among algae affect host use in a herbivorous marine amphipod. *Oecologia* 140:104–112
- Poore AGB, Steinberg PD (1999) Preference-performance relationships and effects of host plant choice in an herbivorous marine amphipod. *Ecol Monogr* 69:443–464
- Poore AGB, Steinberg PD (2001) Host-plant adaptation in an herbivorous marine amphipod: genetic potential not realized in field populations. *Evolution* 55:68–80
- Poore AGB, Watson MJ, de Nys R, Lowry JK, Steinberg PD (2000) Patterns of host use among alga- and sponge-associated amphipods. *Mar Ecol Prog Ser* 208:183–196
- Roa R (1992) Design and analysis of multiple-choice feeding-preference experiments. *Oecologia* 89:509–515
- Sotka EE (2005) Local adaptation in host use among marine invertebrates. *Ecol Lett* 8:448–459
- Sotka EE, Hay ME (2002) Geographic variation among herbivore populations in tolerance for a chemically-rich seaweed. *Ecology* 83:2721–2735
- Sotka EE, Hay ME, Thomas JD (1999) Host-plant specialization by a non-herbivorous amphipod: advantages for the amphipod and costs for the seaweed. *Oecologia* 118:471–482
- Sotka EE, Wares JP, Hay ME (2003) Geographic and genetic variation in feeding preference for chemically defended seaweeds. *Evolution* 57:2262–2276
- Steinberg PD, Estes JA, Winter FC (1995) Evolutionary consequences of food-chain length in Kelp Forest communities. *Proc Natl Acad Sci USA* 92:8145–8148

- Steneck RS, Watling L (1982) Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar Biol* 68:299–319
- Taylor RB, Brown PJ (2006) Herbivory in the gammarid amphipod *Aora typica*: relationships between consumption rates, performance and abundance across ten seaweed species. *Mar Biol* 149:455–463
- Taylor RB, Steinberg PD (2005) Host use by Australasian seaweed mesograzers in relation to feeding preferences of larger grazers. *Ecology* 86:2955–2967
- Trowbridge CD (1991) Diet specialization limits herbivorous sea slug's capacity to switch among food species. *Ecology* 72:1880–1888
- Trowbridge CD, Todd CD (2001) Host-plant change in marine specialist herbivores: Ascoglossan sea slugs on introduced macroalgae. *Ecol Monogr* 71:219–243
- Van Alstyne KL, Houser LT (2003) Dimethylsulfide release during macroinvertebrate grazing and its role as an activated chemical defense. *Mar Ecol Prog Ser* 250:175–181
- Van Alstyne KL, McCarthy JJ, Hustead CL, Kearns LJ (1999) Phlorotannin allocation among tissues of northeastern Pacific kelps and rockweeds. *J Phycol* 35:483–492
- Viejo RM (1999) Mobile epifauna inhabiting the invasive *Sargassum muticum* and two local seaweeds in northern Spain. *Aquat Bot* 64:131–149