PHYLOGENETIC AND GEOGRAPHIC VARIATION IN HOST BREADTH AND COMPOSITION BY HERBIVOROUS AMPHIPODS IN THE FAMILY AMPITHOIDAE

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Predicting the host range for herbivores has been a major aim of research into plant–herbivore interactions and an important model system for understanding the evolution of feeding specialization. Among many terrestrial insects, host range is strongly affected by herbivore phylogeny and long historical associations between particular herbivore and plant taxa. For small herbivores in marine environments, it is known that the evolution of host use is sculpted by several ecological factors (e.g., food quality, value as a refuge from predators, and abiotic forces), but the potential for phylogenetic constraints on host use remains largely unexplored. Here, we analyze reports of host use of herbivorous amphipods from the family Ampithoidae (102 amphipod species from 12 genera) to test the hypotheses that host breadth and composition vary among herbivore lineages, and to quantify the extent to which nonpolar secondary metabolites mediate these patterns. The family as a whole, and most individual species, are found on a wide variety of macroalgae and seagrasses. Despite this polyphagous host use, amphipod genera consistently differed in host range and composition. As an example, the genus *Peramphithoe* rarely use available macrophytes in the order Dictyotales (e.g., *Dictyota*) and as a consequence, display a more restricted host range than do other genera (e.g., *Ampithoe*, *Cymadusa*, or *Exampithoe*). The strong phylogenetic effect on host use was independent of the uneven distribution of host taxa among geographic regions. Algae that produced nonpolar secondary metabolites were colonized by higher numbers of amphipod species relative to chemically poor genera, consistent with the notion that secondary metabolites do not provide algae an escape from amphipod herbivory. In contrast to patterns described for some groups of phytophagous insects, marine amphipods that use chemically rich algae tended to have broader, not narrower, host ranges. This result suggests that an evolutionary advantage to metabolite tolerance in marine amphipods may be that it increases the availability of appropriate algal hosts (i.e., enlarges the resource base).

KEY WORDS: **Amphipods, herbivory, macroalgae, plant–animal interactions, specialization.**

Small marine herbivores that feed on macroalgae and seagrasses can alter the population dynamics of their hosts (Brawley and Adey 1981; Tegner and Dayton 1987), the structure of benthic assemblages (Lubchenco 1978; Jernakoff et al. 1996; Duffy and Hay 2000), and the success of invasive species (Trowbridge and Todd 2001; Levin et al. 2002; Wikström et al. 2006). Because virtually all herbivores are found on a subset of the available pool of local host plants, our ability to predict the effects of herbivores

on benthic assemblages depends largely on understanding the factors that underlie feeding preference and host choice (Lubchenco 1978).

Despite its central importance to algal–herbivore interactions, the host range of most small marine herbivores remain undescribed. Previous reviews (Brawley 1992; Hay and Steinberg 1992) have argued that marine herbivores are largely generalists, feeding from more than 10 families from all divisions of seaweeds, even supplementing their diets with "animals, detritus, and when available, such exotic foods such as cork, aquarium air stones, cheese and plastic cages" (Hay and Steinberg 1992). These impressions have been mostly gleaned from studies that included large fish and urchin herbivores, animals that are as likely to display restricted host range as would large terrestrial mammals like bison or deer. In fact, the best described examples of restricted host use among marine herbivores occur among slugs, isopods, amphipods, and small crabs because these small herbivores tend to be less mobile than fish and urchins (Hay et al. 1987; Taylor and Steinberg 2005) and will be more sensitive to the selective environment imposed by any one host species (Poore and Steinberg 2001; Sotka and Hay 2002). Thus, a more appropriate examination of the patterns of host range should focus on the small herbivores that are more likely to specialize, a task that has been rarely pursued in marine systems (Duffy 1990; Jensen 1997; Poore et al. 2000) but routinely explored among herbivorous terrestrial insects (e.g., Novotny and Basset 2005).

Numerous ecological factors influence the evolutionary trajectory of associations between small herbivores and their host plants (Bernays and Chapman 1994; Paul et al. 2001), including intrinsic traits of the host plant (e.g., nutritional value, chemical and morphological defenses) and the herbivore (e.g., feeding behavior, digestive physiology), as well as extrinsic traits determined largely by the environmental context of the interaction (e.g., plant availability and the value of the plant as refuge from predators or stressful abiotic conditions). In addition to these ecological factors, historical events can potentially influence extant plant–herbivore interactions (Vermeij 1992; Futuyma et al. 1993). These include genetically determined traits that have been inherited from phylogenetic lineages (Brooks and McLennan 1991). Phylogenetic influences on herbivore behavior appear common in several terrestrial insect lineages (Mitter et al. 1991; Farrell 1998; Novotny et al. 2002) despite evidence for the rapid evolution of some herbivore species and populations in response to host plant traits (Via 1990). An explicit examination of the phylogenetic influence on herbivore host use has been used to predict host shifts (Radtkey and Singer 1995; Dobler et al. 1996), evolution of host specialization (Morse and Farrell 2005; Nosil and Mooers 2005), the timing of coadaptation and cospeciation (Brooks and McLennan 1991; Becerra 2003), and the estimation of global species richness (largely dependent on the host speci-

ficity of insect herbivores, Lewinsohn et al. 2005; Novotny and Basset 2005; Novotny et al. 2006).

The importance of evolutionary history on the associations between marine herbivores and their hosts is poorly known. To our knowledge, the only groups of small marine herbivores whose host-use patterns have been examined in this context are the few species of kelp-associated limpets (Vermeij 1992) and the ascoglossan molluscs. In the only studies that have explicitly contrasted herbivore and host phylogenies, Jensen (1993, 1997) compiled patterns of host-use records for genera and orders of ascoglossan sea slugs. Although there was no empirical support for cospeciation, several phylogenetic patterns in host use emerged. Virtually all ascoglossans species consume only green algae, and most genera consume one to several species within only one algal genus, although some genera consume two or more algal genera. Finally, the apparently monophyletic group of shelled ascoglossans feed exclusively on the algal genus *Caulerpa*, a pattern that likely dates back to the split of *Caulerpa* from the other Udoteaceae species.

Another group of marine herbivores well suited to test for phylogenetic constraints in host use are amphipods from the family Ampithoidae. These marine amphipods are "insect-like" herbivores (Hay et al. 1987) in that they are locally abundant, small relative to the hosts that they use for both habitat and food, and can have large impacts on host community structure (Sotka et al. 1999; Duffy and Hay 2000). Ampithoid amphipods are found in algal and seagrass habitats worldwide and represent the most species-rich family of herbivorous amphipods (159 described species from 12 genera). Their interaction with host plants has received more attention than for any other taxon of herbivorous amphipods with numerous studies on their distribution (e.g., Edgar 1983; Taylor 1998), feeding preferences, and performance on algal diets (e.g., Duffy and Hay 1991; Poore and Steinberg 1999; Cruz-Rivera and Hay 2001), responses to secondary metabolites (e.g., Hay et al. 1987), susceptibility to predation (e.g., Hay et al. 1990; Holmlund et al. 1990), impacts on host plants (Duffy 1990; Chess 1993), and intraspecific variation in host use (Sotka et al. 2003; Poore and Hill 2006).

Our previous work has revealed preliminary evidence that species and genera of ampithoid amphipods differ in host specificity and composition. For example, species of the genus *Peramphithoe* generally occur on large brown macroalgae that lack nonpolar secondary metabolites (i.e., the orders Laminariales and Fucales) and appear highly susceptible to these chemical defenses (Poore and Steinberg 1999, 2001). This suggests that evolutionary history may constrain the ability of this genus to colonies other algal taxa. In contrast, the genus *Ampithoe* displays profound variation in tolerance for nonpolar metabolites among species (e.g., *Ampithoe valida* vs. *A. longimana,* Duffy and Hay 1994) and within species (e.g., northern vs. southern *A. longimana,* Sotka

and Hay 2002), suggesting that evolutionary transitions are more labile within this genus.

Here, we analyze published and unpublished reports of host use within the herbivorous amphipod family Ampithoidae to test the hypothesis that host use is phylogenetically constrained. We address three main questions. First, does host range (i.e., number of taxa) and composition (i.e., identity of host taxa) vary among amphipod genera? Second, does host range or composition vary across latitudinal zones or geographic regions? If there are few phylogenetic constraints, herbivore diets should more closely reflect the local availability of host plants rather than amphipod taxonomy. Finally, given the fundamental role of secondary metabolites in herbivore host use, we ask whether the amphipod genera differ in the use of hosts possessing nonpolar metabolites, and whether the host range or composition of herbivores found on such hosts differ from those species not associated with chemically rich hosts.

Material and Methods
HOST ASSOCIATIONS OF THE AMPITHOIDAE
We reviewed the literature for publications that described the presence or abundance of species in the family Ampithoidae on marine macroalgae or seagrasses. These publications included ecological studies of marine herbivores, descriptions of the epifauna inhabiting marine plants, and taxonomic studies that included the identity of the substrate on which material was collected. We included those studies in which the host plant was identified to at least the generic level, resulting in a presence–absence matrix of associations of amphipod species on all recorded host genera. Host genera were placed in orders according to the taxonomy of Guiry and Guiry (2007). Families were not used due to the similarity between the matrix of family associations and that of generic associations—64% of families were represented by only one genus.

The generic level taxonomy of the ampithoids used here is that of Poore and Lowry (1997), which includes a key to the genera and generic diagnoses. The list of known species of ampithoids was obtained from Barnard and Karaman (1991)'s review of marine gammaridean amphipods (which listed 106 species), the publications that have described new species since that review (Kim and Kim 1991; Mateus and Mateus 1991; Conlan and Chess 1992; Freewater and Lowry 1994; Poore and Lowry 1997; Just 2000; Appadoo and Myers 2004; Peart 2004, 2006, 2007a, b), and an extensive taxonomic review of Australian ampithoids (theses by Evans 1997; Peart 2002). The species included in the review are presented in online Supplementary Appendix S1.

The host specificity of ampithoids was contrasted with two existing datasets that detail the composition of diets for other marine herbivores. The algal host associations of ascoglossan slugs

were summarized within table 1 of Jensen (1993) from her own studies and a literature review. The algal diets of tropical herbivorous fish of the West Indies were compiled by Randall (1967) from a large survey of gut contents (i.e., those fish that had >50% of algal material in their guts).

VARIATION IN HOST RANGE WITH AMPHIPOD GENERA, LATITUDE, AND REGION
The hypothesis that host range may vary across amphipod clades was tested by contrasting the known number of hosts across amphipod genera. We quantified host range as the number of host genera or orders on which each amphipod species had been recorded. Amphipod genera were contrasted using analysis of covariance (ANCOVA) with amphipod genus as the categorical factor, and the number of published studies per species as a covariate. This covariate was used because the number of recorded hosts per amphipod species was strongly dependent on the degree to which that species had been studied, and the number of localities from which the studies derive (highly correlated with number of studies, $R^2 =$ 0.7, $P < 0.001$, log-transformed data). This is consistent with previous studies that have shown that the number of trophic links recorded is strongly dependent on sampling intensity (Goldwasser and Roughgarden 1997). This analysis was conducted for the four amphipod genera for which there were most available data and greater than 10 replicate species per genus (*Ampithoe*, *Cymadusa*, *Exampithoe*, and *Peramphithoe*). To test whether the patterns evident at the generic level were also present at the level of host order, a second analysis contrasted the number of host orders per amphipod species across these four amphipod genera.

Geographic variation in host use was examined by attributing each amphipod species to latitudinal zones (tropical and temperate) and to one of four biogeographic regions (North Atlantic, Eastern Pacific, Indo-west Pacific, and southern Temperate). The hypothesis that host range varies across these regions was tested by contrasting the number of host genera and orders among zones and regions in separate analyses of covariance, with zone or region as categorical factors, and the number of published studies per species as the covariate. The analyses were conducted with all amphipod genera and the few species that occurred in more than one region (*Ampithoe kava, A. lacertosa, A. ramondi, Cymadusa filosa, Peramphithoe lindbergi*) were assigned to the region for which the most comprehensive host-use data were available.

The uneven distribution of amphipod genera across geographic areas (Table 1) prevented a fully factorial design that would test for interactions between amphipod genera and regions. To test the degree to which among genus comparisons may be confounded by geographic variation, we conducted analyses of covariance of host range that contrasted the four genera used above within latitudinal zones and regions where possible (i.e.,

Table 1. Distribution of surveyed amphipod species across amphipod genera, latitudinal zones, and biogeographic regions.

Genus	Number of amphipod species	Zone		Region			
		Temperate	Tropical	Eastern Pacific	Indo-west Pacific	North Atlantic	Southern Temperate
Amphithoides	1		1		1		
Amphitholina	1	1				1	
Ampithoe	36	23	13	5	15	9	7
Cymadusa	23	7	16	1	16	2	4
Exampithoe	11	8	3		5		6
Macropisthopous	1	1					1
Paragrubia	2		2		2		
Peramphithoe	15	15		6	2	1	6
Plumithoe	1	1					1
Pseudoampithoides	1		1			1	
Pseudopleonexus	2	3			1		2
Sunampithoe	7	4	3		3	1	3
Total	102	63	39	12	45	15	30

when there were replicate species per factor combination). Conversely, contrasts of regions within amphipod genera were conducted where possible.

VARIATION IN HOST COMPOSITION WITH AMPHIPOD GENERA, LATITUDE AND REGION

A wide variety of statistical methods have been used to analyze and visualize structure in matrices of associations between two trophic levels (Leibold and Mikkelson 2002; Lewinsohn et al. 2006). We used a multivariate approach in which amphipod species were considered samples and the host taxa on which they occur variables to test the hypothesis that the host composition varies across amphipod genera and regions. We calculated the similarity in the host genera inhabited between each pair of amphipod species using Jaccard's coefficient for binary data. A similar approach to assess trophic similarity in a predator–prey food web was used by Raffaelli and Hall (1992). Permutational multivariate analyses of variance were then used to contrast host composition across amphipod genera and regions (Anderson 2001; McArdle and Anderson 2001). This procedure provides distance-based multivariate analyses for any linear model, with tests of the terms provided by permutation. We used the multivariate analogues of the analyses of covariance described above, with genus, zone, or region as categorical factors and the number of published studies per amphipod species as the covariate.

To test for variation in the ordinal composition of hosts, the analyses were repeated with the numbers of host genera per order as the dependent variables (i.e., weighted by frequency with which that order occurred in the dataset) using the Bray–Curtis dissimilarity index. The contrasts of amphipod genera used the genera *Ampithoe*, *Cymadusa*, *Exampithoe*, and *Peramphithoe* whereas the contrasts of regions used all available species (as above).

Differences in the composition of hosts among amphipod genera were visualized using canonical analysis of principal coordinates. This procedure produces a constrained ordination, presenting data on axes that are chosen to best distinguish groups in the data (Anderson and Willis 2003). A constrained ordination was chosen as much of the variation in an unconstrained ordination (e.g., multidimensional scaling) would have arisen from variation in the number of studies per amphipod species (a highly significant covariate in all multivariate analyses, see *Results*). Jaccard's coefficient was again used as the similarity measure for these analyses.

The host taxa that contributed most to similarities in composition within amphipod genera and regions were obtained from similarity percentages analysis (SIMPER, Clarke and Warwick 1994). The host taxa with the highest contribution to differences among amphipod genera and regions were those that had the highest absolute correlation with the canonical axis that best separated the genera and regions in the canonical analysis of principal coordinates (above).

ROLE OF NONPOLAR SECONDARY METABOLITES

For many herbivores, the evolution of host specificity is closely associated with tolerance to secondary metabolites that are specific to host taxa (Berenbaum et al. 1996). To examine patterns of host use with respect to host chemistry, we contrasted: (1) the number and composition of amphipod species associated with host genera that possess potentially deterrent nonpolar secondary metabolites with those that lack such metabolites, (2) the host specificity of amphipod species occurring on chemically rich genera with those that are not associated with such hosts, and (3) the frequency of chemically rich genera within the dataset among amphipod genera, latitudinal zones, and biogeographic regions.

Host genera were categorized as those with or without nonpolar secondary metabolites (online Supplementary Appendix S2) based on reference to MarinLit, a database of marine natural products (available from the University of Canterbury, New Zealand), and selected reviews of marine chemical ecology (Hay and Fenical 1988; Harper et al. 2001; Paul et al. 2001). The metabolites considered include terpenes, acetogenins, and bromophenols (online Supplementary Appendix S2). Our analyses assume that species within a host genus possess a similar suite of these broad categories of secondary compounds. Although the biological activity of metabolites present in many of the species of hosts recorded in our review is unknown, there are strong associations between the taxonomy of marine macroalgae and their secondary metabolites (Hay and Fenical 1988; Vallim et al. 2005), giving support to our assumption that species within a host genus share similar types of secondary chemistry. We do not consider potentially deterrent polar metabolites as there is little qualitative variation across large groups of host genera within our survey (e.g., almost half of our host genera are brown algae that all contain phlorotannins).

The hypothesis that the presence of nonpolar metabolites will alter amphipod host use was tested by contrasting the number and composition of ampithoid species between the two categories of hosts using a *t*-test and a permutational multivariate analysis of variance, respectively. The multivariate analysis used host genera as samples, the amphipod species they support as variables, and the presence or absence of nonpolar metabolites as the categorical factor. Jaccard's coefficient was used as the measure of similarity.

The hypothesis that tolerance of metabolites is associated with increased host specialization (Cornell and Hawkins 2003) was tested by contrasting the host range of three categories of amphipod species: (1), those found only on chemically poor hosts; (2) those found only on chemically rich hosts; and (3) those found on both host types. We analyzed number of host genera and orders per amphipod species for all species using ANOVA with these categories as a single factor. The number of amphipod species belonging to each of these categories was contrasted with the ascoglossan data of Jensen (1993) and tropical fish data of Randall (1967) using a contingency analysis.

The potential that amphipods with broad host range are associated with chemically rich host genera by chance alone was tested by comparing the observed regression slope of number of chemically rich genera versus number of all genera with that expected by chance (derived from the proportion of chemically rich genera in our dataset). The hypothesis that chemically rich host genera will on average support more specialized species of amphipods, was tested by comparing host breadth of amphipods associated with chemically rich hosts to those lacking nonpolar metabolites. This involved ANCOVAs with number of host genera and orders per amphipod species as the dependent variables, presence/absence of host metabolites as the categorical independent variable, and the

number of studies per amphipod species as the covariate (known to relate strongly to host range). We randomly selected records such that each amphipod species and each host genus appeared only once in the analysis (avoiding problems with nonindependence) and then repeated the analysis 10 times.

Finally, the proportion of host genera per amphipod species that are chemically rich was contrasted across amphipod genera (*Ampithoe*, *Cymadusa*, *Exampithoe*, and *Peramphithoe*), latitudinal zones, and geographic regions in three separate ANOVAs.

STATISTICAL ANALYSES

Univariate analyses (*t*-tests, ANOVA, ANCOVA) were performed using SYSTAT 10 (SPSS Inc. 2000). Data were assessed for normality and homogeneity of variance using frequency histograms of residuals, and plots of residuals versus means, respectively (Quinn and Keough 2002). When required, log transformations were applied. The number of studies per amphipod was contrasted across categorical factors with one-way ANOVA to ensure that this covariate did not differ among levels of any of the categorical factors used in the ANCOVA. For the analyses of host range and composition among regions, and of host specificity with respect to nonpolar metabolites, the eight species with five or more studies were excluded to equalize the range of the covariate across levels of the categorical factors.

Permutational multivariate analyses of variance (Anderson 2001; McArdle and Anderson 2001) were conducted with the program DISTLM (available at www.stat.auckland.ac.nz/∼mja) using 9999 permutations of raw data for the probability tests. Similarity percentages analyses (SIMPER) were conducted with the program PRIMER (Clarke and Warwick 1994). Canonical analyses of principal coordinates (Anderson and Willis 2003) were conducted with the program CAP (available at www.stat.auckland.ac.nz/∼mja).

Results
HOST ASSOCIATIONS OF THE AMPITHOIDAE

Our review of the literature provided a matrix of associations between 102 amphipod species from 12 genera in the family Ampithoidae (Table 1; online Supplementary Appendix S1) and 76 host genera. The family as a whole is not restricted to any host taxon, with the host genera coming from 20 orders and all three divisions of macroalgae (Phaeophyta, Chlorophyta, and Rhodophyta) and from 10 genera of seagrasses. Individual amphipod species are also found on a wide variety of hosts, with 30% of the species inhabiting hosts from two or more divisions of macroalgae. Thirty-six percent of the amphipod species were recorded from only one host genus (Fig. 1), however the majority of these species (83%) had data from only one study (dark shaded bars, Fig. 1). Thus, the apparent specialization likely reflects the limited amount of
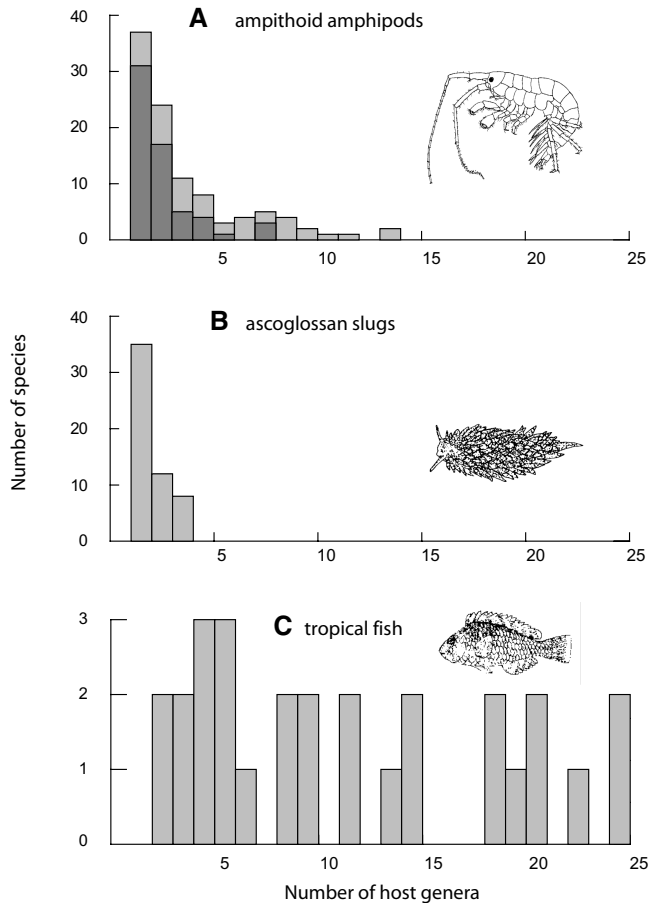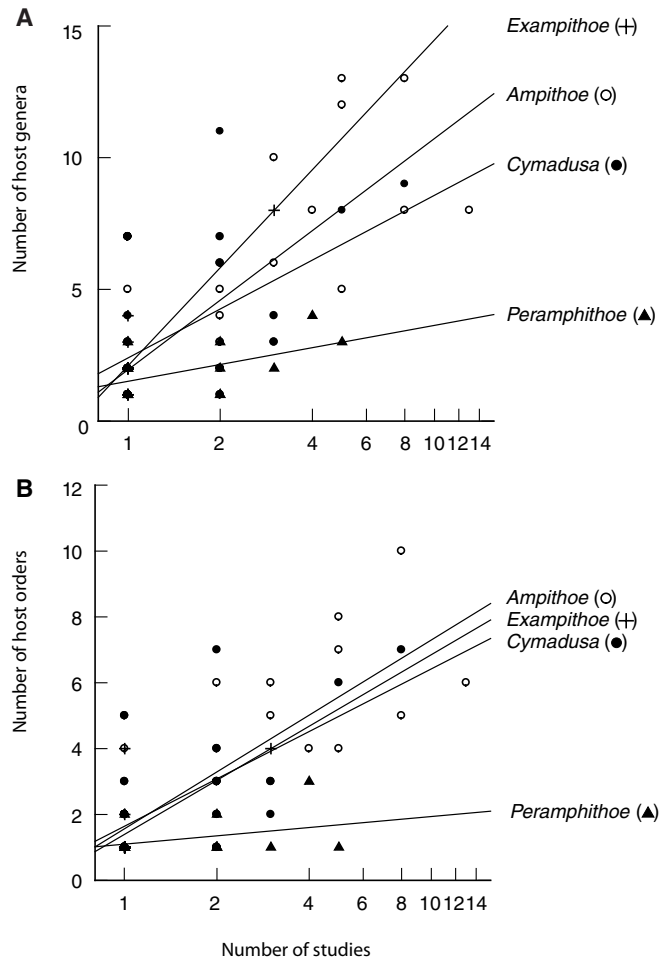
Figure 1. Recorded host breadth of amphipod species in the family Ampithoidae in comparison to other marine herbivores. Data are the number of host genera per herbivore species for (A) ampithoid amphipod species, (B) ascoglossan slugs from (Jensen 1993), and (C) the number of genera within the gut contents of tropical fish (from Randall 1967). The shaded bars in (A) are those species for which there is only one published study of host use.

Figure 2. The variation in host range among amphipod genera. Data are the number of (A) host genera and (B) host orders per amphipod species in the genera *Ampithoe*, *Cymadusa*, *Exampithoe*, and *Peramphithoe* expressed as a function of the sampling intensity (number of studies per amphipod species).

information on those taxa rather than dietary specialization. As expected, the ampithoids occur on more host taxa than the highly specialized ascoglossans, with all species in that group occurring on three or fewer host genera (Fig. 1). Tropical fish in comparison have much broader diets, with individual fish species consuming as many as 25 host genera (Fig. 1).

VARIATION IN HOST RANGE WITH AMPHIPOD GENERA, LATITUDE AND REGION

The numbers of host genera and orders inhabited per amphipod species increased strongly with the number of studies included in the review for each amphipod species (Fig. 2), with a significant interaction between amphipod genus and the covariate (number of studies) (Table 2A). The interaction indicates that the accumulation of host taxa with increasing sampling intensity varied between the genera. *Peramphithoe*, in particular, was found on

few host taxa in contrast to *Ampithoe*, *Cymadusa*, and *Exampithoe* (Fig. 2).

Only *Ampithoe* and *Cymadusa* can be described as cosmopolitan, in that these species are found in all four regions and within temperate and tropical zones. In contrast, *Peramphithoe* is absent from tropical areas, whereas *Exampithoe* is absent from the Eastern Pacific and North Atlantic (Table 1; Barnard and Karaman 1991). However, this uneven distribution of amphipod genera cannot fully explain the apparent phylogenetic patterns in host breadth. When the four genera are compared within only the temperate latitudinal zone, there was again an interaction between amphipod genera and the number of studies ($F_{3,45} = 4.41, P = 0.01$). Further, comparisons of genera within the tropics (i.e., where *Peramphithoe* does not occur), found no differences in the numbers of host genera per amphipod species (ANCOVA, $F_{2,28} = 0.008$, $P = 0.94$).

Table 2. Analyses of covariance contrasting the host range of amphipod species across: (A) the amphipod genera *Ampithoe*, *Cymadusa*, *Exampithoe* and *Peramphithoe*, (B) tropical and temperate zones, and (C) biogeographic regions. The response variables are the number of host taxa (genus or order) per amphipod species. For each analysis, the number of published studies per amphipod was used as a covariate (log-transformed). The interaction between the categorical variable and the covariate was not significant in B) and C) and was not included in the final model. * denotes a significant result ($P < 0.05$).

Source	df	Number of host genera			Number of host orders		
		MS	F	P	MS	F	P
(A) Amphipod genus							
Amphipod genus	3	1.47	0.33	0.80	0.56	0.30	0.82
Number of studies	1	124.76	28.33	<0.001*	44.68	23.92	<0.001*
Amphipod genus × number of studies	3	12.63	2.87	0.04*	5.88	3.15	0.03*
Error	77	4.40			1.87		
(B) Tropical versus temperate zones							
Zone	3	9.92	2.14	0.15	3.14	1.41	0.24
Number of studies	1	331.22	71.40	<0.001*	180.02	80.88	<0.001*
Error	99	4.64			2.23		
(C) Region							
Region	3	12.34	3.26	0.025*	3.04	1.82	0.15
Number of studies	1	139.96	36.99	<0.001*	53.42	32.10	<0.001*
Error	89	3.78			1.67		

Within biogeographical regions, three contrasts of the number of host genera were possible: (1) between *Ampithoe* and *Peramphithoe* within the Eastern Pacific, where there was no difference between the two genera ($F_{1,8} = 0.12$, $P = 0.74$); (2) among all genera within the Indo–west Pacific, where there was no difference between genera ($F_{3,33} = 0.74$, $P = 0.54$); and (3) among all genera within the southern temperate region, in which there was again an interaction between amphipod genera and the number of studies ($F_{3,15} = 8.72$, $P = 0.001$), with *Peramphithoe* found on fewer host genera. All analyses for the numbers of host orders per amphipod species within regions provided results that were consistent with the generic results (statistical details not presented here).

Using all ampithoid species, there were no effects of latitudinal zone on the numbers of host genera or orders per amphipod species and no interactions between zone and the covariate (number of studies) (Fig. 3; Table 2B). The number of host genera, but not orders, differed among the biogeographic regions with no interactions between region and the covariate (number of studies) (Fig. 3; Table 2C). Amphipods from the Indo-west Pacific region were recorded from the highest number of host genera, whereas those from the Eastern Pacific region were found on relatively few host taxa (Fig. 3).

Within amphipod genera, four contrasts of the number of host genera across regions were possible: (1) all regions for *Ampithoe*, in which there was no difference among regions ($F_{3,26} = 1.02$, $P = 0.40$); (2) across each region except the Eastern Pacific for *Cymadusa*, in which there were no differences among regions ($F_{2,18} = 0.18$, $P = 0.84$); (3) between the

Indo-west Pacific and southern temperate regions for *Exampithoe*, in which there was no difference ($t = 0.053$, $P = 0.96$, ANCOVA not conducted due to no variance in covariate); and (4) across each region except the North Atlantic for *Peramphithoe*, in which there no differences among regions ($F_{2,10} = 0.34$, $P = 0.72$).

VARIATION IN HOST COMPOSITION WITH AMPHIPOD GENERA, LATITUDE AND REGION

The composition of host genera and orders differed significantly among the amphipod genera *Ampithoe*, *Cymadusa*, *Exampithoe*,
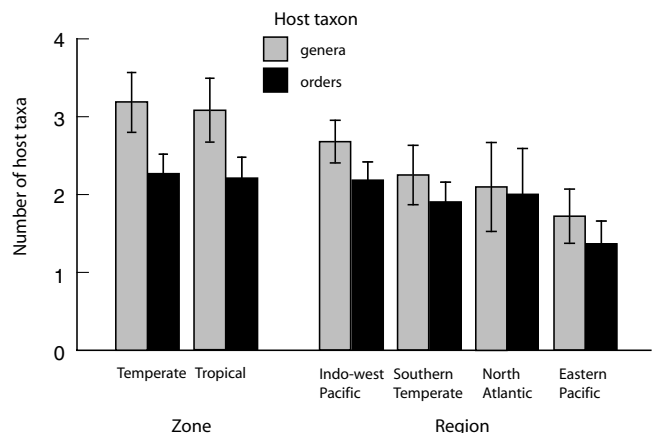
Figure 3. The variation in host range among geographic regions. Data are the number of host genera and orders ($\pm$ SE) per amphipod species contrasted between temperate and tropical zones, and among biogeographic regions.
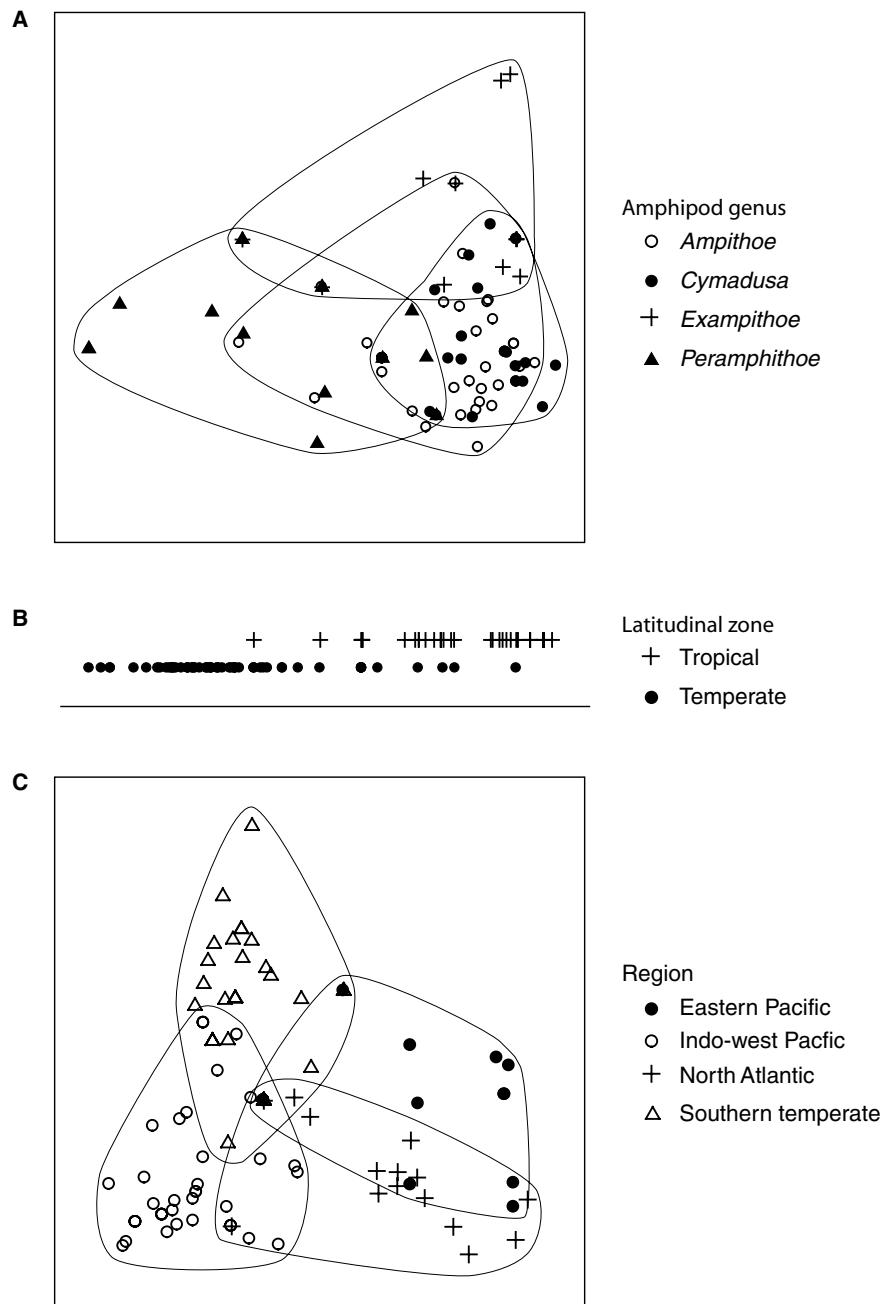
Figure 4. Ordinations of the composition of host genera recorded for each amphipod species, contrasting (A) amphipod genera, (B) latitudinal zones, and (C) biogeographic regions. Figures are constrained ordinations derived from the canonical analysis of principal coordinates where the axes are selected to best distinguish the groups. The ordination contrasting zones (B) has a single axis as the maximum number of axes required to separate groups is the number of groups minus one. The variables (host genera) with the strongest correlations with the first (x-axis) and second (y-axis) canonical axes are presented in Table 4. Jaccard's index was used as the dissimilarity metric for each ordination.

and *Peramphithoe* (Fig. 4A; Table 3A). The composition was also dependent on the sampling intensity, with a significant effect of the number of studies on generic and ordinal composition (Table 3A). Table 4 lists the host taxa with the largest contributions to the observed similarities in composition within genera, and to the observed differences among genera.

The overall differences in the composition of hosts among amphipod genera were primarily due to the differential utilization of brown algae in the order Laminariales, seagrasses, and brown algae in the order Dictyotales (in declining order of correlation with the first canonical axis in Fig. 4A; Table 4). Algae in the Laminariales, in particular the kelp genus *Macrocystis*, had

Table 3. Permutational multivariate analyses of variance contrasting the composition of hosts inhabited by amphipod species across: (A) four amphipod genera (*Ampithoe, Cymadusa, Exampithoe* and *Peramphithoe*), (B) tropical and temperate zones, and (C) biogeographic regions. Data are the presence or absence of host genera or the number of genera per order. In each analysis the number of published studies per amphipod was used as a covariate. Jaccard's coefficient and the Bray–Curtis dissimilarity index were used as the distance metric in the generic and ordinal analyses respectively. A total of 9999 permutations were used to calculate probabilities. * denotes a significant result ($P < 0.05$).

Source	df	Composition of host genera			Composition of host orders		
		MS	F	P	MS	F	P
A) Amphipod genus							
Amphipod genus	3	0.60	1.41	0.02*	7952.95	2.63	0.001*
Number of studies	1	0.35	0.81	0.02*	3902.52	1.26	0.02*
Error	80	0.43			3020.99		
B) Tropical versus temperate zones							
Zone	1	1.76	4.25	<0.001*	16420.2	5.46	<0.001*
Number of studies	1	0.34	0.81	0.02*	4163.60	1.35	0.01*
Error	99	0.41			3004.03		
C) Region							
Region	3	0.99	2.45	<0.001*	7426.03	2.44	0.003*
Number of studies	1	0.20	0.48	0.01*	1065.35	0.34	0.16
Error	89	0.40			3041.23		

high contributions to within-genus similarities only for the amphipod genus *Peramphithoe*. Seagrasses were prominent in the host records of *Cymadusa* and *Exampithoe*, but not the other amphipod genera. Records of the Dictyotales (primarily *Padina* and *Dictyota*) were responsible for the observed similarities in host composition within each genus except *Peramphithoe*. The most frequently recorded host genus (*Sargassum* in the order Fucales) was primarily responsible for similarities among species within each of the amphipod genera except *Exampithoe*. Despite 30% of the host genera recorded being from the Rhodophyta, red algae had little influence on the differences among amphipod genera.

Host composition varied geographically, with significant differences in the composition of both host genera and orders between latitudinal zones (Fig. 4B, Table 5) and among biogeographic regions (Fig. 4C, Table 5). Brown algae in the Fucales (particularly *Sargassum*) had the highest contribution to within-zone similarities in both tropical and temperate regions, with the differences between the zones primarily due to a higher frequency of records of the Laminariales in temperate regions, and Dictyotales and seagrasses in tropical regions (Table 5). The relative occurrence of these two orders also contributed strongly to differences among regions, with the Laminariales most frequently recorded in the eastern Pacific and North Atlantic, and the Dictyotales from each region except the North Atlantic.

ROLE OF NONPOLAR SECONDARY METABOLITES

From the perspective of the host, genera that possessed nonpolar secondary metabolites were associated with more than twice as many amphipod species than those genera that lacked such

metabolites (mean $\pm$ SE of 6.3 ± 1.6 vs. 2.8 ± 0.4 species per genus, $t = 2.15$, df $= 74$, $P = 0.04$, log-transformed data). However, the amphipods associated with chemically rich and chemically poor algae did not differ in species composition (permutational multivariate analysis of variance (MANOVA), $F_{1,74} = 0.48$, $P = 0.67$) nor host breadth (ANCOVAs, number of host genera, all 10 permutations with $F < 3.9$, $P > 0.06$; number of host genera all 10 permutations with $F < 2.1$, $P > 0.16$).

From the perspective of the amphipod, the host range of amphipod species that were associated with both chemically rich and chemically poor hosts was greater than that of amphipods found either on chemically rich hosts or on chemically poor hosts (ANOVA, number of host genera, $F = 64.7$, df $= 2,99$, $P < 0.001$; number of host orders, $F_{2,99} = 52.1$, $P < 0.001$, log-transformed data). On average, the number of host genera utilized per amphipod herbivore increased by 161% when the herbivore included chemically rich macroalgae in their host range (3.61 ± 0.33. *vs.* 1.38 ± 0.15 for those species found only on chemically poor hosts). Amphipods that were found only on chemically rich hosts were no more specialized at the generic or ordinal level than those found only on hosts lacking nonpolar metabolites (Tukey's post hoc test following above ANOVAs). Amphipods with a broad host range were associated with a higher number of chemically rich hosts than expected by chance (Fig. 5, regression slope greater than slope expected if proportion of chemically rich hosts was equal to the proportion of these hosts in the dataset, $t = 3.5$, df $= 83$, $P < 0.001$).

The amphipod genera differed in the proportion of chemically rich hosts utilized (Fig. 6A, $F_{3,81} = 4.01$, $P = 0.01$,

Table 4. The host genera and orders that contribute most to similarities within each amphipod genus, and differences among genera. The percentage contributions to within-genus similarities were obtained from similarity percentages analysis (SIMPER, listing those with contributions > 10%). Differences among genera are the five highest absolute correlations between the original variables and the canonical axes that best separated the genera in a canonical analysis of principal coordinates (Fig. 4A).

Within-genus similarities

Ampithoe		*Cymadusa*		*Exampithoe*		*Peramphithoe*	
Host genus	%	Host genus	%	Host genus	%	Host genus	%
Sargassum	54.7	*Sargassum*	41.9	*Posidonia*	17.9	*Sargassum*	75.2
Dictyota	12.4	*Padina*	26.2	*Ecklonia*	17.9	*Macrocystis*	15.4
Padina	11.8	*Turbinaria*	10.5	*Padina*	17.0		
				Cymodocea	13.4		
				Halodule	13.4		
Host order	%	Host order	%	Host order	%	Host order	%
Fucales	61.5	Fucales	50.0	Potamogetonales	55.6	Fucales	73.6
Dictyotales	21.3	Potamogetonales	23.5	Dictyotales	21.5	Laminariales	26.4
		Dictyotales	22.1	Fucales	15.6		

Differences among genera

First canonical axis		Second canonical axis	
Host genus	Corr.	Host genus	Corr.
Macrocystis	−0.55	*Sargassum*	−0.37
Padina	0.38	*Amphibolis*	0.37
Cystophora	−0.35	*Ecklonia*	0.34
Dictyota	0.33	*Posidonia*	0.32
Pelvetia	−0.30	*Turbinaria*	0.30
Host order	Corr.	Host order	Corr.
Laminariales	−0.57	Fucales	0.55
Potamogetonales	0.48	Ceramiales	0.53
Dictyotales	0.35	Corallinales	0.43
Ceramiales	0.24	Potamogetonales	−0.42
Gelidiales	0.23	Ulvales	0.38

log-transformed data) with *Peramphithoe* least likely to be found on host genera that possessed nonpolar metabolites. The proportion of chemically rich host genera per amphipod species was greatest in tropical regions (Fig. 6B, $t = 3.67$, df $= 100$, $P < 0.001$, log-transformed data) and lowest in the Eastern Pacific and Southern temperate regions (Fig. 6B, $F_{3,90} = 5.34$, $P = 0.002$, log-transformed data). The relative number of herbivore species that are found only on chemically rich hosts varied strongly among amphipods, slugs and fish ($\chi^2 = 43$, df $= 2$, $P < 0.001$). Amphipods were much less likely than the sacoglossan slugs to be found only on chemically rich hosts (37% of species compared to 63% of species from Jensen (1997)), whereas the tropical fish data of Randall (1967) feature no species consuming only chemically rich genera.

Discussion

Our compilation of records of host use among the herbivorous amphipods within the family Ampithoidae revealed at least two major conclusions. First, the specificity and composition of host use differs across amphipod genera. That is, phylogenetic influences on host specificity and composition remain after the variation in these traits due to latitudinal zone and geographic region are removed. Second, there is no evidence that the ability to use hosts producing nonpolar metabolites is associated with increasing specialization onto those hosts. This suggests that, for these amphipods, one evolutionary advantage to evolving a resistance to chemically rich algae may be that it increases the availability of appropriate algal hosts (i.e., enlarges the resource base).

Table 5. The host genera and orders that contribute most to similarities within the tropical and temperate zones, and differences between zones. The percentage contributions to within-zone similarities were obtained from SIMPER (listing those with contributions > 10%). Differences between zones are the five highest correlations (absolute value) between the original variables and the canonical axis that best separated the zones in a canonical analysis of principal coordinates (Fig. 4B).

Within-zone similarities				Difference between zones	
Temperate		**Tropical**			
Host genus	%	Host genus	%	Host genus	Correlation
Sargassum	63.6	*Sargassum*	48.5	*Egregia*	0.47
		Padina	19.0	*Caulocystis*	0.42
				Sargassum	0.39
				Chlorodesmis	0.37
				Thalassia	−0.37
Host order	%	Host order	%	Host order	Correlation
Fucales	64.6	Fucales	53.2	Laminariales	−0.68
Dictyotales	14.9	Dictyotales	20.0	Dictyotales	0.38
Laminariales	10.8	Potamogetonales	15.6	Tilopteridales	−0.23
				Potamogetonales	0.14
				Gelidiales	0.14

## HOST SPECIFICITY OF AMPITHOIDS VERSUS OTHER HERBIVORES

Ampithoid amphipods use 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
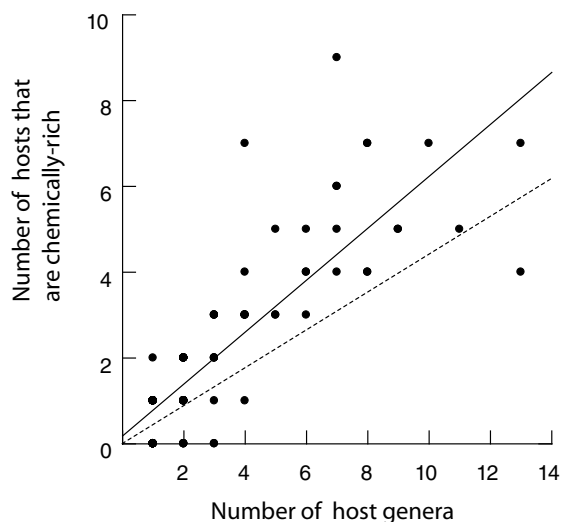
Figure 5. The number of host genera containing nonpolar metabolites versus the number of host genera associated with each amphipod species. The dashed line represents the proportion of chemically rich hosts per amphipod species that would be expected if the host composition of each species was a random subsample of host genera in the entire dataset (44% of host genera contained nonpolar metabolites).

species recorded on at least two or more host genera (Fig. 1). Although 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. Given the strong dependence of host range on sampling intensity, the true rate of ampithoid specialization to a single host taxon is likely to be much lower than observed in our dataset.

Our data support the earlier assertions that marine herbivores are relatively unspecialized (Hay and Steinberg 1992), but do demonstrate that there is considerable variation in specificity among marine herbivore taxa. In contrast to the ampithoids, ascoglossan slugs are far more restricted in their host range with virtually all species feeding on Chlorophyte algae, and all shelled species feeding from the single genus *Caulerpa* (Jensen 1997). Ampithoid amphipods do, however, appear to utilize fewer algal genera than do larger grazers, such as tropical fish. Differences in the dietary composition between mesograzers and macrograzers, as found by Taylor and Steinberg (2005) for temperate Australasian herbivores, may also be likely. Comparing the observed rates of host specificity in marine herbivores with those observed in terrestrial insects depends on insect lineage or feeding style. 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). In contrast, if amphipods are "insect-like" as has been previously
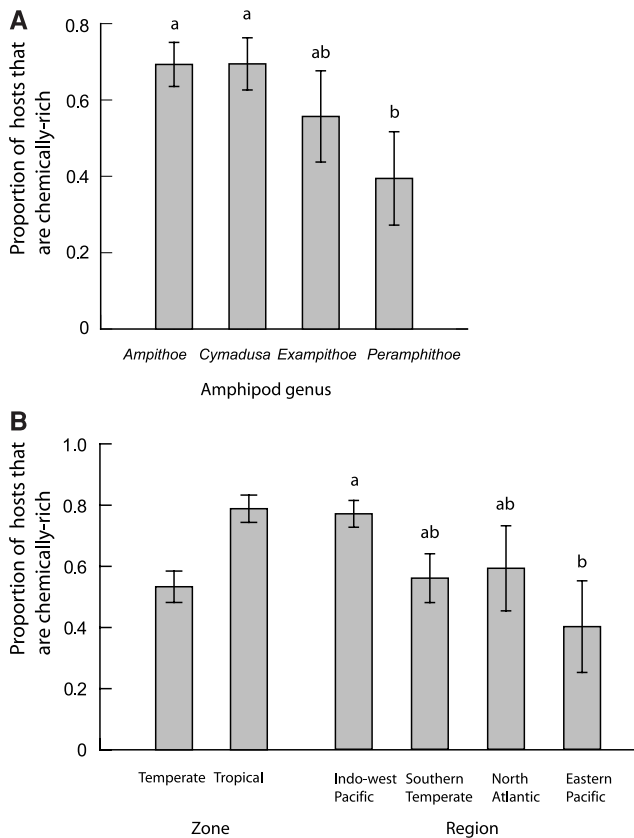
Figure 6. Variation in the association between amphipods and nonpolar secondary metabolites among their hosts. Data are the mean proportion ($\pm$ SE) of host genera per amphipod species that are known to contain non polar metabolites contrasted across: (A) the amphipod genera *Ampithoe*, *Cymadusa*, *Exampithoe*, and *Peramphithoe*, and (B) latitudinal zones and geographic regions for all amphipod species. Bars sharing a letter do not differ significantly in Tukey's post hoc analyses.

proposed (Hay et al. 1987), then their rate of host specificity is more in line with that of tropical root-feeders ($\sim$10%) (Novotny and Basset 2005).

Although mesograzers frequently prefer to consume the algal species on which they are found (Taylor and Steinberg 2005), our measures of host use likely underestimate the true number of food sources for several reasons. Ampithoids are exclusively herbivorous, can have strong impacts on their host algae (e.g., Chess 1993), and live in close association with their hosts in silken tubes or burrows. The host occupied, however, may not always equate to food consumed. This is because epiphytes growing on marine hosts are readily consumed by some mesograzers (Duffy 1990; Jernakoff et al. 1996). The presence of epiphytes in particular makes contrasts with the measured host specificity of insect herbivores in terrestrial environments difficult. The presence of epiphytes on marine hosts, and thus the ability of amphipods to select among many diverse food types on small scales (Poore 1994), is not paralleled in terrestrial environments. We would expect the

identity of hosts to have a reduced effect on grazer composition for systems in which consumption of the host is rare. Further, there is often movement of adults among hosts within any habitat that can be missed by field surveys (e.g., day vs. night differences in distributions, Buschmann 1990). Given that factors other than food quality (especially refuge from predation) are an important determinant of host specialization in both marine (Duffy and Hay 1991; Sotka et al. 1999) and terrestrial (Bernays and Graham 1988) environments, data on host specificity are still required to understand the evolution of habitat preferences even if they do not closely reflect feeding preferences.

Second, our data likely underestimate the true host range due to variation in sampling intensity (i.e., more hosts were recorded from species that have been more thoroughly studied). This is a common problem of food web research, where the number of food species per consumer is a function of sampling intensity (Goldwasser and Roughgarden 1997). With incomplete data, we can argue for variation in host range by extensively sampling hosts from the field (e.g., Novotny 2002), or, by comparing the slopes of species accumulation with increased sampling of the literature, as was done here.

PHYLOGENETIC AND GEOGRAPHIC VARIATION IN HOST USE

A consistent pattern of genus-level differences in host range and composition indicates a substantial phylogenetic effect on host use. In particular, species in the genus *Peramphithoe* utilize a smaller number of host algal genera and orders than do species in *Ampithoe*, *Cymadusa*, or *Exampithoe* (Table 2, Fig. 2). An analysis of the composition of these host ranges (Tables 3 and 4, Fig. 4A) indicates two broad patterns. First, *Peramphithoe* is the only genus that does not regularly utilize dictyotalean algae (e.g., the genera *Dictyota* and *Padina*) despite coexisting with them in several regions including southern Australia, California, Japan, and the Mediterranean. Second, *Exampithoe* is unique because it does not use the widespread brown alga *Sargassum* (Table 4). The notion that *Peramphithoe* has a more limited diet relative to other genera is consistent with preliminary observations of Poore and Steinberg (2001) and Conlan and Chess (1992) that this genus is largely limited to algae from the Fucales and Laminariales. This is the only genus of herbivorous amphipods that readily damage large kelps (Tegner and Dayton 1987; Chess 1993). In areas in which *Peramphithoe* species co-occur with dictyotalean algae, their growth and survival has been poor (e.g., *Peramphithoe parmerong* on *Padina crassa* in temperate Australia, Poore and Steinberg 2001). In contrast, there is profound variation among species of *Ampithoe* in utilizing dictyotalean species. *Ampithoe longimana* is regularly found on *Dictyota menstrualis* and *D. ciliolata* in North Carolina estuaries, and their lipophilic extracts do not strongly alter the performance of *A. longimana*. The co-occurring *A. valida*, however, is

never found on *Dictyota* and is strongly deterred by their lipophilic extracts (Duffy and Hay 1994; Cruz-Rivera and Hay 2003). The ecological and evolutionary processes that have given rise to these interspecific and intergeneric differences (e.g., mating systems, tolerance to plant compounds, susceptibility to predation) remain largely untested for these herbivores due to the paucity of ecological data on most of the species. Several studies suggest a link between mobility and specialization (Hay et al. 1987; Duffy and Hay 1994) with the decreased host range of *Peramphithoe*, potentially a result of the increased intimacy of their association with their host alga (these species form substantial nests of burrows in their hosts (Poore and Lowry 1996). Unfortunately, there have been no efforts to contrast the mobilities of ampithoids across species or genera, and even species that build nests have been shown to be highly mobile among host algae (e.g., *P. parmerong*, Poore 2004).

The mostly generalized diets do not allow matching of species level phylogenies between amphipod herbivores and their hosts as is commonly done for terrestrial insect-plant systems (e.g., Becerra 2003; Morse and Farrell 2005). Unfortunately, there are no published cladistic analyses of the relationships among species and genera within the family Ampithoidae. The genera, however, are considered stable (Conlan and Chess 1992), and based on morphology, Conlan and Chess (1992) have argued that *Peramphithoe* and *Exampithoe* are derived taxa, with *Ampithoe* and *Cymadusa* ancestral within the family. This relationship among the genera indicates that the most specialized genus (*Peramphithoe*) is derived from more generalized genera, consistent with the hypothesis of increasing specialization over evolutionary time. With a published phylogeny of the ampithoids, further analyses could incorporate phylogenetic distance among herbivore species (Weiblen et al. 2006) as well as explicitly compare independent lineages within genera (Felsenstein 1985). Here we have assumed equivalence of taxa at the same rank (i.e., amphipod genus). Improved analyses could also make phylogenetic corrections for the relationships among host taxa (e.g., Novotny et al. 2006). Despite these limitations, our data indicate that we can add ampithoid utilization of host plants to the growing list of amphipod behaviors that are influenced by the amphipod's phylogenetic position. These include the tendency for amphipods to consume algae (found in only a few clades, Myers and Lowry 2003), tube-building behavior (Dixon and Moore 1997), and mating behavior (Conlan 1991).

The phylogenetic effects on ampithoid host range were similar when either host genus or order was examined (Figs. 2, 4A). Thus, the limits of host range seem to align with those of host genera, rather than those of orders or higher taxonomic ranks. We did not test whether the limits of host range could be revealed from an analysis of host species, but we doubt a similar pattern would emerge, given the virtual absence of monophagous species. In this manner, our results are analogous to that seen for terrestrial

herbivorous insects as a whole (Novotny and Basset 2005), which also revealed that patterns of host specificity were equivalent between plant genus and family. The finding suggests that ampithoid species that consume one species within a particular genus more readily consume congeneric hosts than do other ampithoids.

Our strongest argument for phylogenetic constraint on host use by *Peramphithoe* is generated by the interpretation of significant differences among genera within temperate latitudes (see Results). The flip side of this result is that there are differences among ampithoid species in host specificity and composition that can be partitioned by geographic position. For example, when all species were combined, there was a significant latitudinal effect (i.e., tropical vs. temperate) on host composition (Table 3B, Fig. 4B) but no effect on host specificity (Table 2B, Fig. 3). The difference in composition is largely explained by the greater frequency by which tropical amphipods were recorded from dictyotalean algae and seagrasses, whereas temperate amphipods were recorded more regularly from Laminarialean algae (Table 5). This pattern is probably not unexpected, in that Laminarian algae occur more commonly in temperate zones.

The finding that host specificity does not differ between tropical and temperate amphipods could result from temperate amphipods being associated with a smaller proportion of available hosts than those in the tropics, as temperate regions support a higher generic level diversity of algae (Kerswell 2006). Marine herbivore–algal interactions can vary between tropical and temperate regions (Bolser and Hay 1996; Cronin et al. 1997), however small-scale variation can outweigh latitudinal differences. Tropical insect herbivores appear not to divide the resource base any more finely than do temperate insects, suggesting that the higher diversity of tropical insects is largely a function of the higher diversity of tropical plants and not the consequence of higher host specificity (Novotny et al. 2006). Similar tests that partition possible differences in host specificity from spatial patterns in host diversity could only be made for amphipods with further data on the local availability of hosts at sites in which amphipods were studied. Given that the ampithoids were never found on more than 13 genera, from regions that could support as many as 450 genera (Kerswell 2006), information is needed on which of the local algae could act as hosts for these amphipods (e.g., they are unlikely to be found on very tiny filamentous forms).

In addition, there were significant effects of geographic region (i.e., from the Indo-west Pacific, east Pacific, north Atlantic, or southern Temperate) on host specificity (Table 2C, Fig. 3) and composition (Table 3C, Table 6, Fig. 4C). In particular, eastern Pacific ampithoids are found on the fewest host taxa, whereas Indo-west Pacific species were found on the most (Fig. 3). These differences are not simply explained by differences in the local availability of host genera. Ampithoids displayed the widest host breadth in the Indo-west Pacific, a region less diverse that the

Table 6. The host genera and orders that contribute most to similarities within each biogeographic region, and differences among regions. The percentage contributions to within-region similarities were obtained from SIMPER (listing those with contributions > 10%). Differences among regions are the five highest correlations (absolute value) between original variables and the canonical axes that best separated the regions in a canonical analysis of principal coordinates (Fig. 4C).

Within-region similarities

Eastern Pacific		Indo-west Pacific		North Atlantic		Southern temperate	
Host genus	%	Host genus	%	Host genus	%	Host genus	%
Sargassum	54.6	*Sargassum*	47.2	*Sargassum*	56.6	*Sargassum*	58.0
Pelvetia	27.7	*Padina*	19.1	*Cystoseira*	44.4	*Ecklonia*	13.7
Phyllospadix	17.7	*Turbinaria*	11.4			*Zonaria*	5.4
Host order	%	Host order	%	Host order	%	Host order	%
Fucales	50.0	Fucales	53.7	Fucales	59.0	Fucales	80.9
Laminariales	21.2	Dictyotales	18.9	Laminariales	12.8	Dictyotales	12.0
Dictyotales	15.9	Potamogetonales	15.4				
Potamogetonales	11.3						

Differences among regions

First canonical axis		Second canonical axis	
Host genus	Corr.	Host genus	Corr.
Padina	−0.47	*Zonaria*	0.45
Cystoseira	0.44	*Ecklonia*	0.37
Pelvetia	0.40	*Halodule*	0.34
Laminaria	0.37	*Turbinaria*	0.31
Turbinaria	−0.32	*Caulerpa*	0.30
Host order	Corr.	Host order	Corr.
Laminariales	−0.60	Ceramiales	0.54
Dictyotales	0.48	Potamogetonales	0.47
Tilopteridales	−0.21	Ulvales	0.44
Gelidiales	0.17	Corallinales	0.44
Bonnemaisoniales	0.13	Gigartinales	0.44

southern temperate and equally diverse to parts of the eastern Pacific region (Kerswell 2006) in which we detected our most narrow host breadth (Fig. 3). When analyzed within an amphipod genus, our findings of no differences in host breadth among regions known to vary in algal diversity (Kerswell 2006) again suggests that host breadth is not a simple function of algal availability. The geographic differences in host composition are driven by the higher frequency of Laminarialean hosts in the eastern Pacific and north Atlantic, and the lower frequency of Dictyotalean hosts in the north Atlantic.

NONPOLAR SECONDARY METABOLITES AND HOST SPECIFICITY

For many species of terrestrial insect herbivores, the evolution of host specificity is closely associated with the evolution of tolerance to deterrent secondary metabolites in their food sources (Ehrlich and Raven 1964; Berenbaum et al. 1996). In marine systems, secondary metabolites found in macroalgae are frequently deterrent to herbivores, however close associations between taxonomic groups of herbivores and classes of metabolites are rare (Hay and Steinberg 1992). From the perspective of the alga, we found that those genera producing nonpolar secondary metabolites were associated with more than twice as many amphipod species than those not known to produce such metabolites. Although we have no estimates of grazing intensity, this result does not support the notion that nonpolar metabolites provide plants with an "escape" from amphipod herbivory, and is consistent with previous reports of tolerance to algal metabolites among the ampithoid amphipods (Hay et al. 1987). The responses to individual metabolites among this group of marine herbivores (online Supplementary Appendix S2) have been highly idiosyncratic, where a given metabolite may or may not be deterrent to a range of

co-occurring herbivores, and similar types of metabolites may or may not deter a given herbivore. The higher number of species found on defended algae are consistent with the hypothesis that defended algae more frequently host mesograzers because these algae can lower predation risk to larger omnivores (Hay et al. 1987). Few studies have considered how algal metabolites affect the communities of associated herbivores, however Taylor and Steinberg (2005) recently demonstrated that algae deterrent to larger grazers did not support more individuals or species of mesograzers (including four species of ampithoids).

From the perspective of the herbivore, there was no evidence that the ability to use chemically rich hosts was associated with a reduced host range. In fact, those species occurring only on chemically rich hosts were equally specialized as those never found on these hosts. As expected if host chemistry does not limit the ability to use other hosts, it was the species occurring on both chemically rich and chemically poor hosts that had the broadest host range. If the ability to use at least some algae producing nonpolar chemistry represents tolerance to those metabolites, then tolerance expands, rather than restricts, the host range of these herbivores. This is consistent with the evidence from *A. longimana* showing that tolerance of metabolites is not associated with decreased ability to consume other species (Sotka and Hay 2002). This suggests for these amphipods, and similarly for the tropical fish diets of Randall (1967), that one evolutionary advantage to evolving a biochemical resistance (Sotka and Whalen, 2007) to chemically rich algae may be that it increases the availability of appropriate hosts (i.e., enlarges the resource base).

Comparisons of host use across amphipod genera again provide no support for increased specialization being associated with the use of chemically rich hosts. The genus *Peramphithoe*, the genus with the most restricted host range, was also the least likely to be found on chemically rich hosts, being largely restricted to genera within the Fucales and Laminariales that mostly lack nonpolar metabolites. When rarely present on chemically rich genera (*Cystophora* and *Cystoseira*), these were also genera from the Fucales. Given that *Peramphithoe* is likely a derived genus within the family, the specialization onto fewer host taxa is not associated with tolerance to secondary metabolites as expected by coevolutionary theory (Cornell and Hawkins 2003). These patterns contrast with the increased specialization seen among other groups of consumers that consume chemically rich prey (e.g., dorid nudibranchs on animal prey, Cimino and Ghiselin 1999). An alternative explanation is that chemically rich hosts support more "apparent generalists" that are truly local, cryptic populations of specialists (sensu Fox and Morrow 1981), a possibility that we currently cannot address. For species that may be consuming epiphytes rather than host tissue, the role of nonpolar metabolites is less clear, but there is evidence that host chemistry can affect amphipods that are not necessarily consuming the host, primarily by provid-

ing refuge from omnivores deterred by algal metabolites (Duffy and Hay 1994; Sotka et al. 1999). Furthermore, many macrophyte compounds that deter herbivores also deter settlement by epiphytic algae, potentially altering the availability of this alternative food source (Hay 1996).

These analyses assume that an algal genus is chemically rich if there is at least one published record of its genus possessing deterrent nonpolar metabolites across its geographic range. Despite the presence of intrageneric variation in secondary chemistry (e.g., among parts, Van Alstyne et al. 2001; individuals, Monro and Poore 2004; populations, Paul and Van Alstyne 1988, and species, Paul 1992), there are strong taxonomic associations between algal taxa and their secondary metabolites (e.g., within the Dictyotales, Vallim et al. 2005), and the geographic differences in secondary metabolites tend to be quantitative rather than qualitative. Furthermore, our contrasts of interest are across amphipod genera (Figs. 5, 6) using the same methodology and therefore robust to any potential errors in assigning host genera to our chemically rich and poor categories.

The possibility that host use of the ampithoids is mediated by polar metabolites was also not addressed in our review of host use. Work with larger fish and urchin herbivores suggests high levels of variation among herbivore taxa and geographic regions in the deterrent properties of polar metabolites (Amsler and Fairhead 2006). In contrast to nonpolar metabolites, few studies have tested whether polar metabolites, in particular the phlorotannins found in the brown algae, alter amphipod feeding and the evidence is rather mixed with reports of both deterrence (e.g., Poore 1994) and increased feeding (e.g., Jormalainen and Honkanen 2004; Kubanek et al. 2004). Although obviously simplified, our approach has revealed some striking patterns with respect to secondary metabolites that warrant further experimental tests.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1. The species from the family Ampithoidae included in the review of host use, with taxonomic authority, biogeographical region and literature used to determine host use.

Appendix S2. The host orders and genera included in our review of ampithoid host use with known nonpolar secondary metabolites and literature documenting their deterrence to marine herbivores and effects on ampithoid amphipods.

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