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PRIMARY RESEARCH PAPER

Intertidal meiofaunal biodiversity with respect to different algal habitats: a test using phytal ostracodes from Southern California

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Abstract Rocky intertidal algae harbor a diverse invertebrate meiofauna of arthropods, nematodes and other invertebrates. Despite its ecological importance, relatively little is known about the diversity and composition of this important component of intertidal biodiversity. In this study, we quantified species composition, abundance and distribution of ostracodes, an important group of phytal meiofauna, at two different intertidal areas in southern California. In total, we recovered 22 ostracode species from three different orders (16 podocopids, five myodocopids and one platycopid), nearly a quarter of which could not be assigned to existing taxa. The abundance of ostracodes differed significantly among algal types, with structurally complex algae bearing many more ostracodes per gram of algae than simple forms (blade-like algae and the surfgrass *Phyllospadix*). Although most ostracode species were recovered from multiple kinds of algae, different algae harbored distinct assemblages that could be discriminated statistically on the basis of relative abundances of ostracode species. This segregation of the ostracode fauna according to algal species is evident even over very short spatial scales (<1 m). Finally, ostracode samples from turf-forming algae were more species rich than samples from other kinds of macroalgae. Since turf-forming algae are easily damaged by human trampling, this component of ostracode biodiversity may be particularly vulnerable to anthropogenic impacts on the intertidal habitat.

Keywords Ostracoda · Intertidal algae · Abundance · Diversity

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Introduction

The algae living in shallow marine habitats harbor a rich meiofauna of arthropods, nematodes, mollusks, and other invertebrates. Although individually small, the total biomass of these organisms can be substantial (Gerlach, 1978), and many marine meiofaunal taxa are important as herbivores (Caramujo et al., 2005), predators (Watzin,

1983) and prey (Coull & Wells, 1983; Gee, 1989). Despite their ecological importance, little is known about the diversity, ecology, distribution and environmental tolerances of most meiofaunal taxa. This lack of baseline information complicates efforts to understand how these communities respond to natural and anthropogenic changes in the environment. This concern is particularly acute for intertidal meiofauna because this habitat is easily accessible and increasingly impacted by human activities and many meiofaunal taxa maybe particularly sensitive to such disturbances (Moore & Bett, 1989; Brown & Taylor, 1999; Ruiz et al., 2005).

Here, we present the results of an investigation into the abundance, diversity and distribution of one meiofaunal group (Ostracoda) at two rocky intertidal localities in San Diego, California (USA). Although there have been previous biogeographic surveys of California ostracodes (Swain, 1969; Valentine, 1976), these studies focused almost entirely on subtidal, soft-sediment environments. Quantitative ecological studies of phytal ostracodes from this region are currently lacking. Our goal in this study is to investigate the relationship between the nature of the algal habitat and distribution of ostracode species. In particular, we focus on testing whether there are significant differences in the abundance, diversity and species composition of phytal ostracodes across different kinds of algal habitats within the same locality.

Materials and methods

Sites and sampling

We sampled algae-associated ostracodes from the rocky intertidal areas of the Scripps Coastal Reserve (SIO; 32°52.30′ N, 117°15.20′ W) during low tide on April 1, 2004. Subsequently (November 12, 2004), we sampled a second site located about 6 km away, situated immediately south of the beach access point on Cortez Street (CS; 32°49.22′ N, 117°16.73′ W) in La Jolla. These two sites have a similar total tidal range (mean of about 1 m), but they differ in their physical configurations and degree of wave exposure. The SIO site is a low-exposure boulder field, with algae growing attached to large rocks distributed across a sandy substrate. In contrast, the CS site is more exposed with broad, horizontal and nearly continuous rocky substrate. As the focus of the present study is on comparisons among algal habitats within each locality, these two sites offer an opportunity to test if patterns hold across different types of localities and different seasons within a limited geographic area, bearing in mind that any differences between the localities may be attributable to site and/or seasonal effects.

We sampled algae using standard techniques employed in other phytal ostracode studies (e.g., Whatley & Wall, 1975; Hull, 1998, 1999b). For all algae except for turf-forming algal mats, all or part of an alga was placed into a open plastic bag while underwater, and scissors were used to cut the alga from its base, sealing it in the bag with the surrounding water. Using this method, we sampled the following species: *Sargassum muticum* (SIO and CS), *Zonaria farlowii* (SIO and CS), *Eisenia arborea* (SIO), *Egregia menziesii* (SIO), *Cystoseira osmundacea* (CS) and the angiosperm *Phyllospadix* sp. (CS), hereafter referred to by their generic names (algae taxonomy follows Abbott & Hollenberg, 1976). Epiphytes were present in many samples, but in all cases the vast majority of the biomass and habitable space were provided by the macroalgae.

In addition to these large species, at CS we also sampled the turf-forming algae, which forms dense, low-growing, multi-species mats at that locality. The turf samples were dominated by red algae, especially coralline algae (probably *Corallina* sp.), *Gigartina caniliculata*?, *Centroceras clavulatum*, and *Plocamium cartilagineum*. In addition, *Spyridia filamentosa*, *Ulva* sp., *Haliptylon gracile*, and *Polysiphonia* sp. were present in trace amounts. These turf algae were sampled by scraping the rock with a laboratory spatula directly into an open plastic bag.

All samples, both turf and macroalgae, were taken at approximately the same tidal height low in the intertidal (≈0.3 m below mean lower low water), minimizing the effect of tidal height on sample differences. All sampling locations were at least partially exposed; we did not sample enclosed tidal pools. Although algae were sampled while underwater, all of our sites were exposed subaerially on occasion during the lowest of the low tides. Where possible, we attempted to obtain at least three replicate samples per algae per locality. However, because several of the sampled algal species were uncommon, we were not always able to achieve this goal (Table 1).

In the laboratory, each algae sample was thoroughly washed with freshwater through 2 mm and 125 μm sieves. All ostracodes pass through the 2 mm sieve; those retained on the 125 μm sieve were placed in a gridded petri-dish for sorting. Ostracodes were separated from sediment and other meiofauna under a dissecting microscope, removed from the sample using a pipette, and transferred to 70% ethanol for later species identification. After removal of all meiofauna, algae samples were dried in an oven overnight at 70°C and then weighed. Ostracodes were later separated into species, largely on the basis of carapace morphology using a variety of primary sources describing East Pacific shallow water ostracodes (see Electronic supplementary material). Counts of individuals, excluding empty valves, were recorded for each species.

Data analysis

Following previous workers (e.g., Hull, 1997, 1999b), ostracode abundances were standardized by the dry weight of the sampled algae. We used analysis of variance to test for differences by algal type in the weight-standardized abundances. The abundance data were log-transformed prior to analysis, which stabilized the variance across groups. For this analysis, the three large, blade-like brown algae (*Egregia*, *Eisenia*, and *Cystoseira*) were grouped together, and Tukey's honestly significant differences method (Sokal & Rohlf, 1995, p. 244) was used to determine which pairwise abundance differences were individually significant.

We explored the effects of algal type on species richness in the three algal types that were best sampled: *Sargassum*, *Zonaria*, and the turf-forming algae. Since sample sizes differed greatly among samples, we constructed rarefaction curves (Sanders, 1968; Magurran, 2004) to compare richnesses at equivalent sample sizes. These curves, along with their confidence envelops, were generated using the software EcoSim (Gotelli & Entsminger, 2006), with all samples of each algal type lumped together.

In order to explore patterns of faunal similarity, we ordinated samples using non-metric multidimensional scaling (MDS), which is a robust, rank-based procedure for visualizing the relative faunal similarity of samples in a lower dimensional space (Legendre & Legendre, 1983). In order to eliminate some of the noise associated with low sample sizes, only samples with at least 20 specimens were included in the MDS. The exact value of this cutoff was not important; repeating the analyses using both higher and lower thresholds produced qualitatively similar results. This ordination was based on Bray-Curtis distances calculated from square-root transformed relative species abundances. Analysis of similarity (ANOSIM) based on the same Bray-Curtis distances was used to test the null hypothesis that the relative abundances of ostracode species did not differ with respect to algal habitat. ANOSIM is a randomization test, analogous to analysis of variance, commonly used to test for differences in assemblage composition among different groups of samples (Clarke & Green, 1988). Since we are interested in differences among algae but not differences between sampling localities, both the ordinations and ANOSIM tests were performed separately within each site. The species *Xestoleberis hopkinsi* and *Xestoleberis* species 1 could not be reliably distinguished (especially in juvenile instars, see Electronic supplementary material), so these two species were lumped for all analyses. All tests were performed using the statistical programming environment R (R Development Core Team, 2005), relying on functions from the Vegan community ecology package (Oksanen et al., 2005).

Results

Overview

In total, 2,554 individual ostracodes from 22 species were recovered (Fig. 1). These taxa are

Table 1 Ostracode abundances for samples analyzed in the present study

Site	Sample	Algae	Wt (g)	*Xestoleberis scammonensis*	*Xestoleberis hopkinsi* & *Xestoleberis* species 1	*Xestoleberis* species 2	*Paradoxostoma striungulum*	*Paradoxostoma* species 1	*Hemicytherura santosensis*	*Cythere maia*	*Aurila lincolnensis*	*Caudites acosaguensis*	*Ambostracon glaucum*	*Sahnicythere* species 1	*Loxoconcha* species 1	*Loxoconcha lenticulata*	*Macrocyprina barbara*	*Bairdoppilata verdesensis*	*Cytherelloidea californica*	*Rutiderma judayi*	*Rutiderma rotundum*	Sarsiellidae indet.	Cylindroleberididae indet.	Philomedidae indet.	Total
CS	csA1	*Sargassum*	7.59	0	38	0	5	7	33	0	1	0	1	0	0	0	1	2	0	0	0	0	0	0	88
CS	csB1	*Sargassum*	2.95	0	4	0	0	1	2	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	10
CS	csC2	*Sargassum*	3.00	0	12	1	0	2	8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	25
CS	csC1	*Zonaria*	1.61	0	15	0	0	0	76	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	94
CS	csA2	*Phyllospadix*	14.33	0	1	2	0	0	6	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	10
CS	csB2	*Phyllospadix*	14.27	1	20	0	0	6	13	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	41
CS	csC3	*Phyllospadix*	6.68	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
CS	csA6	*Cystoseira*	8.21	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
CS	csA3	turf	1.68	0	51	3	2	12	97	5	5	0	3	0	1	0	0	4	14	1	11	1	1	1	212
CS	csA4	turf	0.42	0	0	0	0	2	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
CS	csB3	turf	6.06	3	36	0	27	7	415	3	6	0	6	0	0	0	0	0	8	0	19	0	0	0	530
CS	csB4	turf	1.49	1	9	0	2	15	27	1	0	1	2	0	0	1	0	0	3	1	2	0	0	0	65
CS	csC4	turf	5.82	1	17	0	0	6	78	1	3	0	2	0	0	0	0	2	14	0	10	0	0	0	134
SIO	sioA1	*Sargassum*	4.62	13	12	82	2	13	27	18	12	0	0	0	0	0	0	0	0	0	0	0	0	0	179
SIO	sioB1	*Sargassum*	4.01	31	60	161	3	95	56	18	8	0	0	0	0	0	0	0	0	0	0	0	0	0	432
SIO	sioC3	*Sargassum*	9.91	17	12	85	1	28	30	8	8	0	0	0	0	0	0	0	0	0	0	0	0	0	189
SIO	sioD2	*Sargassum*	6.15	4	6	88	0	22	25	4	7	0	0	0	0	0	0	0	0	0	0	0	0	0	156
SIO	sioA3	*Zonaria*	0.92	1	5	4	0	13	36	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	66
SIO	sioC1	*Zonaria*	1.17	3	7	14	0	10	48	4	4	0	1	0	0	0	0	0	0	0	0	0	0	0	91
SIO	sioD3	*Zonaria*	0.54	3	9	21	0	41	28	4	3	2	2	1	0	0	0	0	0	0	0	0	0	0	114
SIO	sioB3	*Egregia*	5.74	2	1	3	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
SIO	sioD1	*Egregia*	8.71	0	4	2	0	5	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
SIO	sioB2	*Eisenia*	5.89	2	1	1	0	2	1	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0	21
SIO	sioC2	*Eisenia*	51.32	6	3	7	0	1	8	23	1	0	1	0	0	0	0	0	0	0	0	0	0	0	51
		Total		88	325	474	42	290	1034	113	65	3	22	1	1	1	1	8	39	2	42	1	1	1	2554

For each sample at the two sites (CS, Cortez Street beach access, and SIO, Scripps Institute of Oceanography), the dry weight (wt) of the algae is presented, along with the abundance of all recovered species of ostracodes

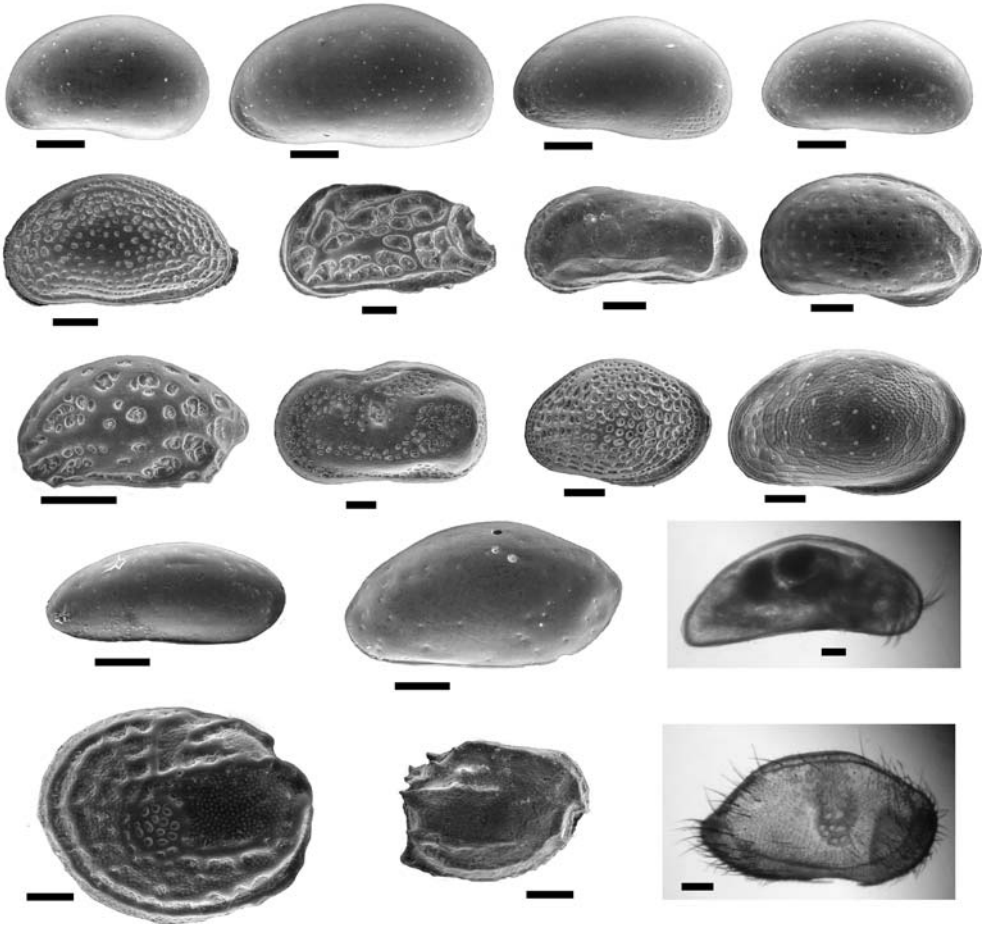

Fig. 1 Representative ostracodes from intertidal phytal samples in La Jolla, CA. Unless otherwise indicated, specimens shown are adult left valves. Scale bars are 100 μm in the first four rows, and 200 μm in the fifth row; congeners are shown at the same scale to facilitate comparison. First row: *Xestoleberis scammonensis* McKenzie and Swain, *Xestoleberis hopkinsi* Skogsberg, *Xestoleberis* species 1, *Xestoleberis* species 2. Second row: *Aurila lincolnensis* (Le Roy), *Ambostracon glacum* (Skogsberg), *Caudites acosaguensis* Swain and Gilby, *Cythere maia* Benson. Third row: *Hemicytherura santosensis* Swain and Gilby, *Cytherelloidea californica* Le Roy, *Loxoconcha* species 1, *Loxoconcha lenticulata* Le Roy. Fourth row: *Paradoxostoma* species 1, *Paradoxostoma striungulum* Smith, *Macrocyprina barbara* Maddocks whole animal, right lateral view. Fifth row: *Rutiderma rotundum* Poulsen, *Rutiderma judayi* McKenzie right valve, *Bairdoppilata verdesensis* (Le Roy) right valve

listed in Table 1 with their abundances in each sample. Many of the common species are from genera often found in phytal habitats (e.g., *Xestoleberis*, *Paradoxostoma*), while others are from clades common in littoral environments but not always associated with algae (*Hemicytherura*, *Cythere*, *Aurila*). A few species were found abundantly in many samples (several *Xestoleberis* species, *Hemicytherura santosensis*, *Paradoxostoma* species 1), but most species were rare, with nearly a third (7/22) of the species represented by just a single individual. Three species, all from the Order Myodocopida, were represented by single juvenile individuals and could only be identified to family (Table 1). Of the 19 that remain, 14 could be assigned to existing species known from shallow marine environments of the northeast Pacific Ocean and the rest were given informal species designations.

Abundance patterns

Ostracode abundance per gram of algal dry weight varied over four orders of magnitude,

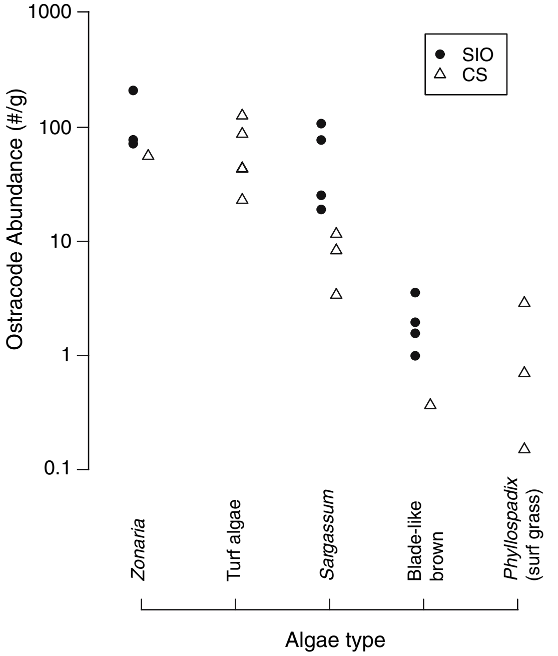

Fig. 2 Ostracode abundances per gram of algal dry weight for different algal types at two localities in La Jolla, CA. ''Blade-like brown'' algae includes species of *Egregia*, *Eisenia* and *Cystoseira*. SIO = Scripps Institute of Oceanography, CS = beach access near Cortez Street. Pairwise differences between the three high-abundance algal types and the two low-abundance algal types are all highly significant (see text)

from about 0.1 to over 100 ostracodes g^{-1} (Fig. 2). Algal types exhibited large and significant differences in ostracode abundance ($F_{4,19} = 19.27$, $P < 0.00001$). Pairwise comparisons of abundance revealed two different abundance groups: turf-forming algae, *Zonaria*, and *Sargassum* all have high ostracode abundances, while the blade-like brown algae species (*Egregia*, *Eisenia*, and *Cystoseira*) and the surfgrass *Phyllospadix* yielded many fewer ostracodes per gram of algae (Fig. 2). All pairwise differences between high abundance and low abundance algal groups were highly significant ($P < 0.002$), but no significant differences were found within either the high or low abundance groups. A substantial portion of the turf-forming algae is composed of calcified coralline algae. The high density of calcium carbonate increases the dry weight of these samples, and the standardized ostracode abundances may therefore be somewhat underestimated in the turf-forming algae. For those algal types that were collected from both sites (*Zonaria*, *Sargassum*, blade-like brown algae), abundances were higher at SIO, indicating some effect of site or season on ostracode biomass.

Diversity patterns

Rarefaction of samples from the three best sampled algal types show that the turf-forming algae yielded a much more species-rich assemblage of ostracodes than either *Zonaria* or *Sargassum* (Fig. 3). Although slightly more individuals were sampled from *Sargassum* (1079) than from the turf algae (959), almost twice as many species were recovered from the turf samples (19 species, versus 11 for *Sargassum*). The slope of the rarefaction curve near its termination is also considerably steeper for the turf algae than for *Zonaria* and *Sargassum*, suggesting that species sampling may be less complete for the turf than the other algae (Fig. 3). The greater richness of the turf samples is all the more striking because all five turf samples were from the same site (CS), whereas samples for both *Sargassum* and *Zonaria* were pooled across two sites. As a result, differ-

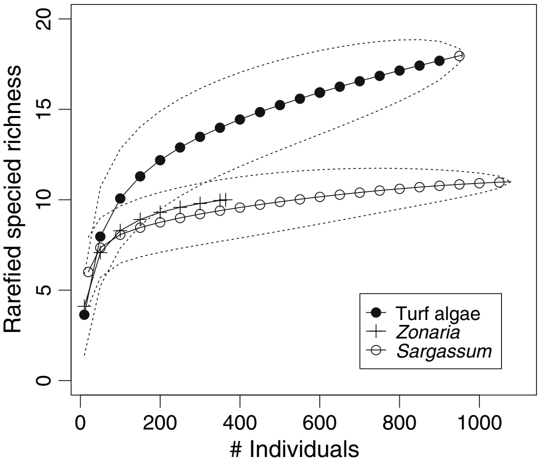

Fig. 3 Rarefaction curves for the algal types yielding abundant ostracode specimens. Dotted lines indicate 95% confidence regions. For clarity, the confidence region for *Zonaria* samples is not plotted, but is approximately the same size as shown for *Sargassum*. The rarefaction curve for the turf algae samples significantly exceeds those for *Zonaria* and *Sargassum*, indicating greater species richness for the turf algae at comparable sampling effort

ences with respect to site or season of collection contributed to diversity for *Sargassum* and *Zonaria*, but not for the turf-forming algae. Therefore, the diversity advantage of the turf algae over the other algal types is likely to be even greater than the rarefaction curves indicate.

The elevated diversity of the turf samples persists at higher taxonomic levels. For example, *Sargassum* samples include ostracode species from seven families (Xestoleberididae, Paradoxostomatidae, Cytheridae, Hemicytheridae, Cytheruridae, Macrocyprididae and Bairdiidae). The turf samples include representatives from these families (except for the Macrocyprididae), but in addition include specimens from six other families (Loxoconchidae, Cytherellidae, Rutidermatidae, Sarsiellidae, Philomedidae and Cylindroleberididae).

Ostracode—algae specificity

Nearly all of the common ostracode species in this study were found on multiple types of algae, while the seven rare species were found only on a single type of algae (Table 1). Two possible exceptions to this are *Rutiderma rotundum* and *Cytherelloidea californica*, which were found in moderate abundance in the turf samples, but never with any other algae. It is also interesting that all but one (6/7) of the restricted rare species were found only in turf samples. Despite the large number of specimens collected from *Sargassum*, no ostracode species were found to be restricted to this alga. Thus our results suggest that the turf algae may contain several rare species of ostracodes that are specific to that habitat. However, given the difficulty of sampling very rare meiofaunal species, further sampling is needed to establish whether this apparent habitat specificity is a real phenomenon or whether it reflects incomplete sampling.

Although only a few ostracode species were restricted to a single type of algae, ostracode communities from different algal types were distinguishable based on the relative abundance of species. For both sites, the MDS ordination shows that samples from the same algal type had more similar ostracode assemblages than samples from different algal species (Fig. 4). ANOSIM results confirm this compositional difference with respect to algal type at both localities (SIO: $R = 0.92$, $P = 0.002$; CS: $R = 0.80$, $P = 0.008$). The segregation of ostracode species by algal type holds even over very small spatial scales. In Fig. 4, the samples marked by an arrow were collected within one meter of each other, and at least ten meters away from the remaining samples. Despite their proximity, the marked samples were not faunally similar to each other, and instead clustered with more distantly located samples of the same algal type.

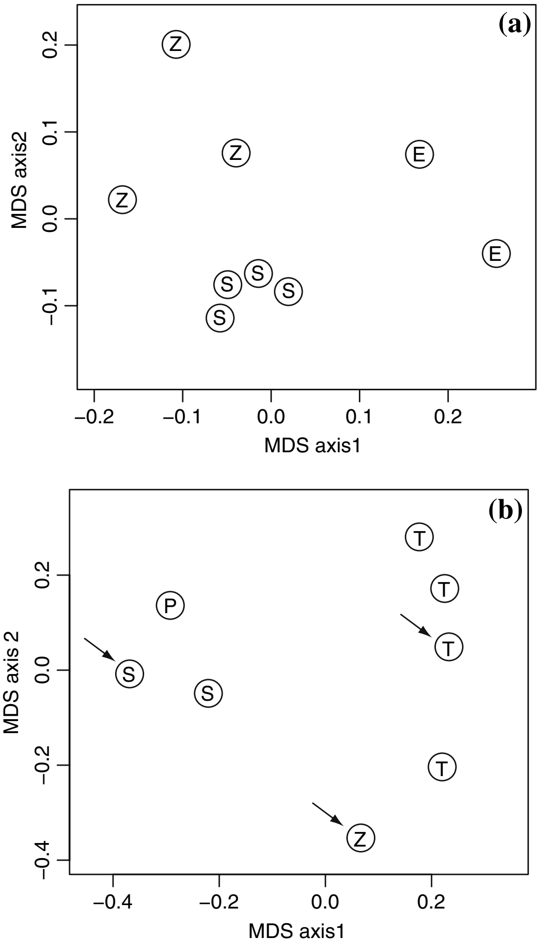

Fig. 4 Nonmetric multidimensional scaling ordinations of relative abundance data for SIO (**a**) and Cortez Street (**b**) sites. Letters indicate alga types: S = *Sargassum*, Z = *Zonaria*, E = *Eisenia*, T = turf algae, P = *Phyllospadix*. *Arrows* in (**b**) point to three samples collected within 1 m of each other. Note that samples from the same type of algae are generally more similar to each other than to samples from different kinds of algae

Discussion

At the generic and family levels, the ostracode assemblages recovered in the present study are similar to those reported elsewhere in the world. In particular, the genera *Paradoxostoma*, *Xestoleberis* and *Loxoconcha*, and to a lesser extent, *Cythere*, *Aurila* and *Hemicytherura* have been reported as common phytal taxa in the United Kingdom (e.g., Whatley & Wall, 1975; Horne, 1982; Hull, 1998), northern Europe (Hagerman, 1966, 1968), Cyprus (Athersuch, 1979) and Japan (Kamiya, 1988; Nohara & Tabuki, 1990). However, it is difficult to make more detailed regional comparisons at the species level due to the lack of previously published quantitative surveys of phytal ostracodes in California. This is surprising, given that the rocky intertidal habitats of California has been the subject of scientific investigations for over a century. Several studies have analyzed ostracode biogeography off the western coast of North America (Swain, 1969; Swain & Gilby, 1974; Valentine, 1976), but these were regional in scale and included few specifically algal samples. Nevertheless, these studies recovered many of the species observed in the present study. Some species have also been reported previously from fossil and modern samples from elsewhere in California (Le Roy, 1943; Crouch, 1949; Kornicker & Myers, 1981), Baja California (Benson, 1959; McKenzie, 1965; McKenzie & Swain, 1967), and Central America (Swain & Gilby, 1967). North of California, even fewer near shore ostracode studies have been completed. Although at least one species from the present study has been reported from British Columbia (Smith, 1952), there is apparently no species-level overlap between the present study and a thorough analysis of soft-sediment ostracodes from the Gulf of Alaska (Brouwers, 1990, 1993, 1994).

The relative scarcity of published research on intertidal ostracodes in western North America is also reflected in the fact that about a quarter of species recovered in this study could not be assigned to existing species. These undescribed forms include several rather common species of *Xestoleberis* and *Paradoxostoma* (Table 1), whose smooth and relatively featureless carapaces have been under-represented in many of the previous works that relied on carapace traits rather than soft part anatomy. In contrast, phytal ostracode faunas in Europe (especially Great Britain) are far better known. For example, in a series of studies on phytal ostracodes from several sites in Great Britain, Hull (1997, 1998, 1999a; b) recovered over 30 species of ostracodes, none of which were unknown to science. This difference between California and the United Kingdom is due in part to a series of taxonomic studies completed in the United Kingdom during the 1980s, culminating in the synopsis by Athersuch et al. (1989).

Although perhaps less well known than other phytal ostracode faunas, species richness in the present study is comparable to that observed in studies at similar spatial scales in Great Britain (Williams, 1969; Horne, 1982; Hull, 1997, 1999a), western Sweden (Elofson, 1941) and Okinawa, Japan (Nohara & Tabuki, 1990). Abundances per gram of algal dry weight were also within the range previously reported (Hull, 1997). Too few quantitative studies are now available to ascertain if similar richnesses are also characteristic of other regions, especially the tropics.

Phytal ostracodes are clearly not randomly distributed in the rocky intertidal environment, or among different algal habitats. Previous studies have implicated several factors as important for determining the distribution of ostracodes on intertidal macroalgae. Some of these, such as tidal height (Horne, 1982; Hull, 1999b) and wave exposure (Whatley & Wall, 1975), did not vary substantially within each of the two localities in the present study, and are not likely to account for much of the within-site variation seen here. One factor that does seem to be very important is algal type. Total ostracode abundances differed dramatically among samples, with higher abundances associated with algal types that offer more structurally complex environments (*Zonaria*, *Sargassum*, turf algae). This finding is consistent with Hull's (1997) quantitative study, which found perfect rank order agreement between algal complexity (measured as the number of branches per cm) and ostracode abundance on four different species of algae. There is also broader qualitative evidence that suggests a positive correlation between algal complexity and ostracode abundance (e.g., Whatley & Wall, 1975; Athersuch, 1979). Algal complexity is thought to increase meiofaunal abundance by increasing the number of surfaces on which to feed and live, and also by providing effective shelter against predation, desiccation, and wave action (Whatley & Wall, 1975; Coull & Wells, 1983; Hicks, 1986; Hull, 1997).

In addition to total abundance, the relative proportions of ostracode species differed enough by algal type to allow for clear separation when samples were ordinated. Moreover, this segregation of ostracode assemblages by algal type occurred over very short (<1 m) spatial scales. Although algal specificity of ostracodes has been reported previously (Whatley & Wall, 1975; Athersuch, 1979; Hull, 1997), differences in faunal composition are perhaps less easily explained than differences in abundance, especially over short distances. In addition to providing shelter from predators and environmental extremes, algae also provide food for ostracodes. With the possible exception of the paradoxostomatids, which have specialized piercing mouthparts (Horne & Whittaker, 1985), ostracodes are not thought to directly consume macroalgae. Instead, they are thought to graze on bacteria and microalgae, especially diatoms, that grow epiphytically on seaweeds (Elofson, 1941; Whatley & Wall, 1975; Athersuch, 1979). This generalization applies to the podocopids; platycopids such as *Cytherelloidea californica* are considered filter feeders, and myodocopids exhibit a range of feeding modes (Horne, 2003). Nevertheless, any palatability differences among macroalgae are unlikely to explain algae–ostracode associations seen here. It is conceivable that different seaweed species are characterized by different microflora, and that ostracodes are segregating along this resource axis. Alternatively, another possible hypothesis would be that algae of different growth forms and morphologies provide slightly differing physical environments in terms of desiccation, wave exposure, predation, etc., and ostracode species segregate according to their preferences for the these factors.

Another important finding of the present study is that turf algae provides habitat for an ostracode assemblage that appears to be more diverse than that found on other complex algae types (*Sargassum*, *Zonaria*). Several biological factors may explain this difference. First, turf algae is really a multi-species assemblage, comprised of up to six different algal species in the samples we analyzed. These species grow closely interspersed, creating a physical space that is structurally and biologically more heterogeneous than that offered by any single algal species. Another difference between the turf algae and the other algal types is that turf tend to be higher in sediment content, although previous studies have not found sediment content to correlate with abundance or diversity in a straightforward manner (Whatley & Wall, 1975; Hull, 1998).

In addition to these biological hypotheses, it is possible that the greater richness in the turf algae, at least partially, reflects the fact that some of the species recovered from the turf algae do not actually live there but were transported in by wave action from nearby sandy areas. The dense and low-growing turf may disproportionately trap ostracodes, at least temporarily, relative to more open and erect macroalgae. The fact that turf algae contains more sand than other algal types indicates that they would be more effective at retaining ostracodes, which in this context, are essentially sand-sized sedimentary particles. This mechanism is also consistent with the relatively large number of species represented by just a single individual, assuming that few individuals will be washed into the algae at any one time.

Although some of the individuals recovered from the turf samples may have been transported in from nearby benthic environments, there are several reasons why it is unlikely that this effect entirely explains the richness difference between the turf and the other algal types. First, two of the species that are restricted to the turf algae are not particularly rare (*Cytherelloidea californica* and *Rutiderma rotundum*), and so most likely live in situ in the turf algae. Second, two of the remaining restricted species are members of *Loxoconcha*, which is a common phytal genus that is less likely to be found in the surrounding sandy benthic environment (but see Kamiya, 1988 for an exception). Finally, even if we omit the turf species represented by a single individual, the rarefaction curve for the turf samples still significantly exceeds those of *Sargassum* and *Zonaria* (results not shown). Thus, even if all the rare and putatively transported species are removed, turf assemblage are still more diverse than those from other algae, albeit by a lesser amount.

Whatever the causes of the elevated ostracode abundance and diversity in the turf-forming algae, one practical consequence is that this habitat may be disproportionately important in terms of managing the meiofaunal biodiversity of rocky intertidal environments, especially if the same pattern of relative diversity exists in other phytal taxa. Algal turf and the fauna associated with it are particularly vulnerable to human trampling, (Addessi, 1994; Brosnan & Crumrine, 1994; Keough & Quinn, 1998; Brown & Taylor, 1999). So as human visitation to the rocky intertidal increases with increasing coastal populations in California (e.g., Roy et al., 2003), the high diversity of turf-associated ostracodes may be substantially affected. In order to properly assess the effects of such anthropogenic disturbances on the ostracode fauna, it will be necessary to conduct further inventories of other rocky intertidal sites in the region and perform targeted comparisons of matched sites that differ in their levels of trampling and other disturbance.

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