

NOTES

OVERLAP IN DIET BETWEEN CO-OCCURRING ACTIVE
SUSPENSION FEEDERS ON TROPICAL AND TEMPERATE REEFS*Adele J. Pile*

Competition for resources between marine organisms is one of the suite of factors structuring benthic communities. Sessile marine organisms must compete primarily for substratum to attach to and then protect their territory. Research on this topic has resulted in a large body of literature that has examined the consequences of direct interactions between sessile benthic invertebrates across phyla resulting from either contact or direct interference of life functions (see review by Woodin and Jackson, 1979). However, benthic organisms may change the nearby environment such that it is unsuitable for habitation by other organisms. The role of indirect competition in structuring suspension feeding benthic communities remains to be examined.

Globally, sponges and ascidians are the predominant active suspension feeding invertebrates in communities growing on hard substrata (see review by Gili and Coma, 1998). Sponges and ascidians are active suspension feeders that graze primarily on the ultraplankton (Murphy and Hagen, 1985) of the plankton community (Reiswig, 1971; Fiala-Médioni, 1978; Randløv and Riisgård, 1979; Stuart and Klumpp, 1984; Pile et al., 1996, 1997; Pile, 1997, 1999; Ribes et al., 1998, 1999). Despite the large body of literature describing the feeding ecology of sponges and ascidians, only one study has simultaneously examined the feeding ecology of co-occurring species. Stuart and Klumpp (1984) conducted a laboratory study using artificial water column communities created from cultured bacteria and algae as a food source for sponges and an ascidian common to a kelp forest. They found that while the diets overlapped, the organisms were spatially separated and thus there was no competition for food resources. A study examining both the natural diets of co-occurring species and the role of indirect competition for food resources between phyla has yet to be conducted. Therefore, as a preliminary step in determining the role of interphyletic competition for food resource in structuring suspension-feeding communities, this study was designed to quantify the resource utilization in situ for co-occurring sponges and ascidians.

MATERIALS AND METHODS

The diet of co-occurring suspension feeders was quantified in situ at two locations, Pioneer Bay at Orpheus Island, Great Barrier Reef (18°50'S, 147°38'E) and Edithburg Jetty, South Australia (35°5'S, 137°45'E). Both locations are well described in previous studies (e.g., Kay and Keough, 1981; Klumpp and Griffiths, 1994). Water samples were collected from three ascidian species and three sponge species at each location. Species were selected because they were common and conspicuous members of the benthic communities and were frequently found next to each other (Table 1). One ml of ambient water (water that could be drawn into the organism) and water samples from the exhalent current of sponges and ascidians were collected by SCUBA divers using 5 cc syringes and preserved for flow cytometry using standard protocols (Pile et al., 1996). An additional 100 ml ambient water sample was collected within 5 cm of the benthos and chlorophyll *a* extracted using standard techniques to quantify the

Table 1. List of organisms used in this study. The identification of many south Australian invertebrates remains to be completed so the nomenclature of Kay and Keough (1981) has been employed.

Type of organism	Tropical	Temperate
Sponges	<i>Luffariella variabilis</i> (Poléjaeff, 1884)	<i>Dendrilla rosea</i> (Lendenfeld, 1883)
	<i>Auleta constricta</i> (Pulitzer-Finali, 1982)	<i>Aplysilla sulphurea</i> (Schulze, 1878)
	<i>Ircinia gigantea</i> (Poléjaeff, 1884)	Royal blue spiky sponge (SP46)
Ascidians	<i>Phallusia julinea</i> (Sluiter, 1919)	<i>Pyura</i> sp.
	<i>Polycarpa</i> sp.	<i>Halocynthia</i> sp.
	<i>Didemnum</i> sp. (yellow)	<i>Polycarpa pedunculata</i> (Heller, 1878)

fraction of cells larger than 10 μm (Strickland and Parsons, 1972). Samples were collected for the tropical organisms on 6 June 1997 and for temperate organisms on 6 January 1999.

Ultraplankton populations were quantified using either an Epic Elite flow cytometer (Coulter Electronics Corporation, Hialeah, Florida) at Harbor Branch Oceanographic Institution (tropical) or a FACscan (Becton Dickson, San Jose, California) at Flinders University of South Australia (temperate) following the techniques of Marie et al. (1997). Orange fluorescence (from phycoerythrin), red fluorescence (from chlorophyll), and green fluorescence (from DNA stained with SYBR Green) were collected through band pass interference filters at 650, 585, 530 nm, respectively. The five measured parameters, forward- and right-angle light scatter (FALS and RALS), orange, red, and green fluorescence were recorded on three decade logarithmic scales, sorted in list mode, and analyzed with custom-designed software (CYTOWIN, Vaulot, 1989). Ultraplankton populations were identified to general cell types of bacteria (Bac), *Prochlorococcus* sp. (Pro), *Synechococcus*-type cyanobacteria (Syn), autotrophic eukaryotes < 3 μm (Peuks), and autotrophic eukaryotes 3–10 μm (Neuks), visually confirmed, and mean cell diameter measured ($n = 50$) using epifluorescence microscopy. Differences between cell counts from ambient and exhalant current water of each type of ultraplankton were analyzed using two sample t-tests with a Bonferroni transformed experiment-wise experimental α of 0.01 to determine the effects of sponges and ascidians on ultraplankton (Zar, 1984). The mean retention efficiency of each species with regard to each type of ultraplankton was calculated as $\{[(\text{cell count ambient water} - \text{cell count exhalant current water}) / \text{cell count ambient water}] \times 100\}$ for the paired samples ($n = 10$) (Pile et al., 1996).

A conservative estimate of food availability was empirically calculated by converting the mean number of ultraplankton cells removed to an equivalent g C. Cell conversion factors of 20 fg C cell⁻¹ for heterotrophic bacteria and 150 fg C cell⁻¹ for *Synechococcus*-type cyanobacteria were selected, as they have been determined for cells with mean diameters \geq those found during this study (Ayukai, 1995 and references therein). Carbon in the form of the eukaryotic cells of Peuks and Neuks was determined from the formula fg C cell⁻¹ = 433 \times [biovolume (μm^3)]^{0.866} with Peuks and Neuks having biovolumes of 1.05 and 18.13 μm^3 in the tropics and 4.57 and 36.07 μm^3 in the temperate ecosystem, respectively, as determined from epifluorescence microscopy (Campbell et al., 1994 and references therein). Total carbon present in the photoautotrophic component of plankton was empirically obtained by subtracting the ultraplankton portion from the total C calculated from chlorophyll *a* measurements employing a conversion factor of 30 (Ayukai, 1995 and references therein). These types of calculations assume that on a global scale, all types of cells within these broad categories have the same amount of carbon regardless of species or location, which is most likely not true. Therefore, the data are presented so that if better cell-to-carbon conversions become available, fluxes may be recalculated.

Table 2. Food availability (\pm SD) at the tropical and temperate locations. Estimated carbon availability was calculated empirically using conservative cell to carbon factors. na = not available.

Type of plankton	Mean 10^4 cells ml^{-1}		Mean $\mu\text{g C L}^{-1}$	
	Tropical	Temperate	Tropical	Temperate
Procaryotes				
Heterotrophic bacteria	3.60 (2.18)	18.3 (4.11)	0.72	3.66
<i>Prochlorococcus</i> sp.	3.48 (2.53)	na	1.84	na
<i>Synechococcus</i> -type cyanobacteria	5.32 (3.30)	1.47 (0.81)	7.98	2.21
Eukaryotes				
Autotrophic eukaryotes $< 3 \mu\text{m}$	0.74 (1.00)	0.26 (0.10)	33.3	42.0
Autotrophic eukaryotes $3\text{--}10 \mu\text{m}$	0.01 (0.01)	0.09 (0.11)	3.03	18.1
Phototrophic sources $> 10 \mu\text{m}$			7.8	36.7
Total			54.7	103

RESULTS

Food availability differs between the tropical and temperate ecosystem (Table 2). The tropical community has less biomass but a majority (80%) of the biomass is present in the ultraplankton fraction. This is in contrast to the temperate community where the majority (54%) of the biomass consists of a larger size fraction. The temperate water column community, consisting of heterotrophic bacteria, *Synechococcus*-type cyanobacteria, and autotrophic eukaryotes $< 3 \mu\text{m}$ was also less diverse than the tropical community, which included *Prochlorococcus* sp.

The utilization of resources by sponges and ascidians differed between ecosystems. In the temperate community all three sponge species significantly reduced heterotrophic bacteria from the water they processed (*Dendrilla rosea*, $t_8 = 5.422$; *Aplysilla sulphurea*, $t_8 = 3.017$; Royal blue spiky sponge (SP46), $t_8 = 4.673$), whereas ascidians only significantly reduced Peuks from the water they processed (*Pyura* sp., $t_8 = 3.078$; *Halocynthia* sp., $t_8 = 3.614$; *Polycarpa pedunculata*, $t_8 = 5.823$) (Fig. 1). In contrast, among co-occurring tropical species, sponges significantly reduced the numbers of heterotrophic bacteria (*Luffariella variabilis*, $t_8 = 6.591$; *Auletta constricta*, $t_8 = 7.334$; *Ircinia gigantea*, $t_8 = 5.364$), *Prochlorococcus* sp. (*L. variabilis*, $t_8 = 4.631$; *A. constricta*, $t_8 = 3.952$; *I. gigantea*, $t_8 = 4.397$), *Synechococcus*-type cyanobacteria (*L. variabilis*, $t_8 = 5.611$; *A. constricta*, $t_8 = 6.727$; *I. gigantea*, $t_8 = 4.853$), and Peuks from the water they processed (*L. variabilis*, $t_8 = 6.379$; *A. constricta*, $t_8 = 6.648$; *I. gigantea*, $t_8 = 5.732$), and ascidians significantly reduced heterotrophic bacteria (*Phallusia julinea*, $t_8 = 3.856$; *Polycarpa* sp., $t_8 = 3.174$; *Didemnum* sp., $t_8 = 3.825$) and *Prochlorococcus* sp. from the water they processed (*P. julinea*, $t_8 = 3.697$; *Polycarpa* sp., $t_8 = 3.108$; *Didemnum* sp., $t_8 = 3.892$).

DISCUSSION

The first step in determining if competition for a resource exists is to demonstrate simultaneous utilization of the resource. Within each phylum of suspension feeders in this study and at each location there was an overlap in resource utilization. More interestingly, there was clear interphyla overlap of diets among tropical sponges and

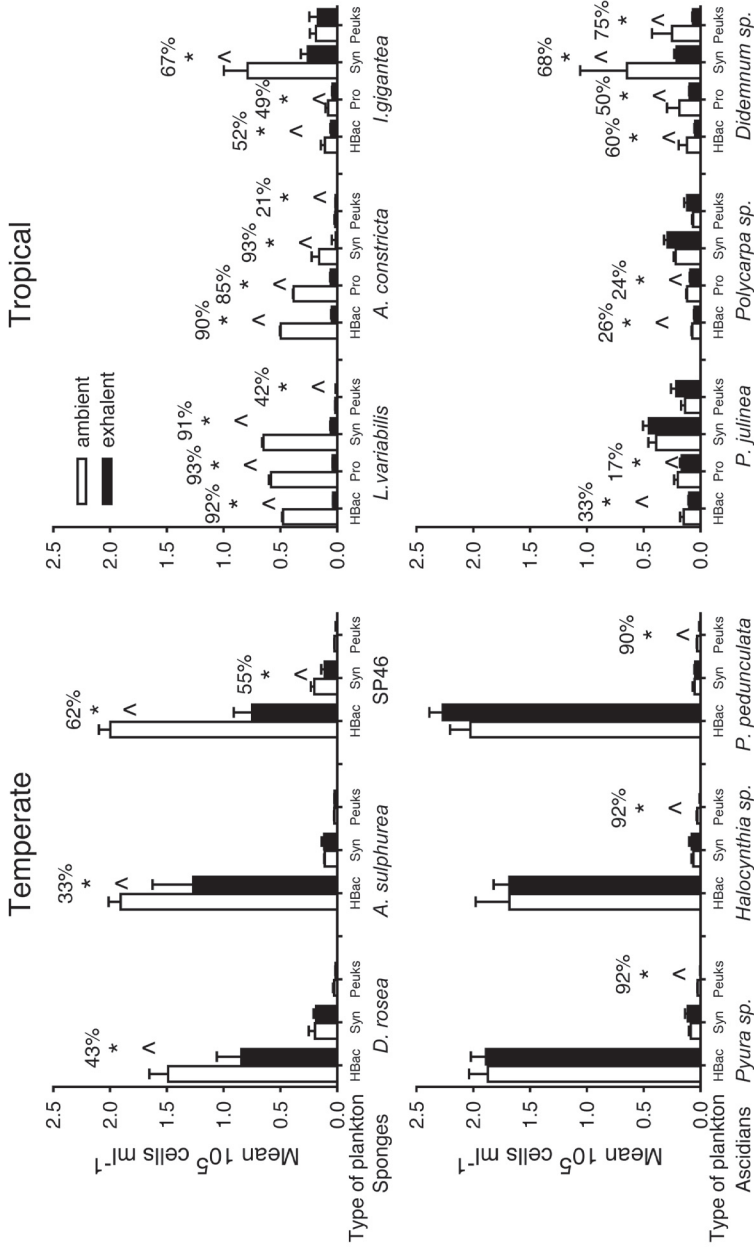


Figure 1. The effect of sponges and ascidians on ultraplankton in a tropical and a temperate ecosystem. White bars represent ambient water, black bars water from the exhalant current, error bars are \pm SD. Percent retained is indicated above means that are significantly different (* $\alpha = 0.001$). Plankton categories are abbreviated as heterotrophic bacteria (HBac), *Prochlorococcus* sp. (Pro), *Synechococcus*-type cyanobacteria (Syn), and autotrophic eukaryotes < 3 μ m (Peuks). Invertebrate species are abbreviated following Table 1.

ascidians that in the temperate ecosystem retained the same particles but utilized different portions of the ultraplankton community. Retention efficiencies for tropical sponges were generally high, 85%–93%, for all types of ultraplankton. In contrast, the retention efficiencies of heterotrophic bacteria and *Prochlorococcus* sp. by tropical ascidians were more variable and lower than that of sponges (26%, 60%, 30%, and 24%, 50%, 51% respectively). The natural diets and range of retention efficiencies of the sponges and ascidians in this study are typical of those reported in previous studies (Reiswig, 1971; Fiala-Médioni, 1978; Randløv and Riisgård, 1979; Stuart and Klumpp, 1984; Pile et al., 1996, 1997; Pile, 1997, 1999; Ribes et al., 1998, 1999).

These observations include only living carbon and do not consider the role of the detrital fraction as a food source. The detrital fraction of the ultraplankton community comprises up to 92% of the carbon fluxed by temperate ascidians (Ribes et al., 1998). Thus, detritus may supply an important dietary supplement for ascidians in temperate ecosystems and the utilization of this alternate resource may thereby limit competition with other suspension feeders.

During this limited sampling period, food availability varied between temperate and tropical reefs. Overall, the tropical environment is characterized as having fewer and smaller available food particles than those in the temperate ecosystem. There was nearly twice as much biomass available in the temperate plankton community as in the tropical community. The quality of the food also varied; in the tropical community, a majority of the carbon was incorporated in the ultraplankton fraction. These findings are typical of longer studies on ultraplankton community structure in both regions. It is not unusual to find that most of the carbon is present as the ultraplankton fraction on the outer portions of the Great Barrier Reef (Ayukai, 1995) and Pacific atolls (Charpy, 1996; Charpy and Blanchot, 1998). This is the first record of ultraplankton availability for South Australian waters and it is typical of other temperate ecosystems that have been quantified with similar techniques (Stuart and Klumpp, 1984; Pile et al., 1996).

Not surprisingly, the overlap in the diets of sponges and ascidians occurred in the tropics where fewer resources are available. Clearly, these observations made on a single date at a single location do not provide definitive proof that competition for food is structuring these communities. The limited sampling does not begin to examine spatial and temporal variation in food availability, yet it does provide some initial, fundamental information on resource utilization in both temperate and tropical systems within and across phyla, which can serve as a foundation for further studies.

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