Marine Biology 116, 137–146 (1993)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Meiofauna on the seagrass *Thalassia testudinum*: population characteristics of harpacticoid copepods and associations with algal epiphytes

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Received: 14 August 1992 / Accepted: 18 January 1993

Abstract. The composition and abundance of blade-dwelling meiofauna was determined over a 15 mo period (1983–1984) from a *Thalassia testudinum* Banks ex König meadow near Egmont Key, Florida, USA. Harpacticoid copepods, copepod nauplii, and nematodes were the most abundant meiofaunal taxa on *T. testudinum* blades. Temporal patterns in species composition and population life-history stages were determined for harpacticoid copepods, the numerically predominant taxon. Sixteen species or species complexes of harpacticoid copepods were identified. *Harpacticus* sp., the most abundant harpacticoid, comprised 47.8% of the total copepods collected, and was present throughout the study. Copepodites dominated the population structures of the blade-dwelling harpacticoid species on most collection dates. Ovigerous females and/or copepodites were always present, indicating continuous reproductive activity. Results suggest that epiphytic algae influence meiofaunal abundance on seagrass blades, as densities of most meiofaunal taxa at Egmont Key were positively associated with percent cover of epiphytic algae throughout the study. The majority of significant correlations between meiofaunal density and cover of epiphytic algae involved filamentous algae, although encrusting algae dominated the epiphytic community. It appears that resources provided by epiphytic algae to seagrass meiofauna (additional food, habitat, and/or shelter from predation) may be associated with algal morphology.

Introduction

Meiofauna, especially harpacticoid copepods, are abundant in seagrass systems (Hicks 1986, Walters and Bell 1986, Hall and Bell 1988), and important as food for seagrass-associated fish (Sogard 1984, see also Tipton and Bell 1988 for review) and invertebrates (Leber 1983). While meiofauna in seagrass systems have received some attention, descriptive and experimental information is scarce compared to that for larger organisms from seagrass habitats (Bell et al. 1984, Hicks 1986). Temporal patterns of abundance and population characteristics are less well known for seagrass meiofauna than for meiofauna in other shallow marine habitats such as unvegetated sand or mudflats, salt marshes, or macroalgae on hard substrata (Hicks and Coull 1983, Bell et al. 1984, Hicks 1986). Population characteristics of sediment-dwelling meiofauna have been shown to vary with factors such as sediment properties (Coull 1970), hydrodynamic regime (Palmer and Gust 1985), and predation (Tito de Morais and Bodiou 1984, Gee 1987). In contrast, factors influencing meiofauna living on seagrass blades, which are often coated with a milieu of organic deposits and micro/macroflora (Humm 1964, Harlin 1980, Orth and Van Montfrans 1984, Meyer and Bell 1989), remain relatively unknown.

Population characteristics of meiofauna inhabiting macroalgae may be related to fluctuations in the amount of epiphytic algae (Colman 1940, Hagerman 1966, Kangas 1978, Johnson and Scheibling 1987a). Abundance of epiphytic algae on seagrass blades likewise may contribute to temporal and spatial variability of epifaunal assemblages on seagrass blades (Nagle 1968, Lewis and Hollingworth 1982, Novak 1982). The precise nature of the positive relationship between meiofaunal taxa and epiphytes has been proposed to include increased habitat area, food, and refuge from predation (Nagle 1968, Kito 1982, Lewis and Hollingworth 1982, Johnson and Schiebling 1987a, Hall and Bell 1988). Meyer and Bell (1989) suggested that epiphytes trap detritus on seagrass blades, thereby enhancing the abundance of the harpacticoid *Metis holothuriae*. If epiphyte cover changes seasonally (see Hall 1988), then meiofaunal populations on seagrass blades may track variation in epiphyte abundance.

The goals of this study were to: (1) determine temporal patterns of meiofaunal abundance on *Thalassia testudinum* Banks ex König, the dominant seagrass in the Caribbean and Gulf of Mexico; (2) examine temporal patterns in species composition and population life-histo-

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ry stages of harpacticoid copepods, the numerically dominant epifaunal taxon; (3) investigate the associations between different types of epiphytic algae and meiofaunal taxa. Such information provides insight into the possible role of epiphytic algae as a factor regulating meiofaunal abundance and copepod population characteristics. Additionally, comparisons between seagrass copepods and more widely studied sediment-dwelling copepods are presented.

Materials and methods

The study site was a *Thalassia testudinum* Banks ex König bed adjacent to the northeastern shore of Egmont Key, Florida (27° 35.5′ N; 82° 45.3′ W), a small island located at the mouth of Tampa Bay. This part of Egmont Key is exposed to limited wave action and supports an extensive seagrass meadow composed of pure and mixed stands of *T. testudinum* and *Syringodium filiforme* Kützing. The salinity range is narrow (30 to 35‰) and sediments are fine sand with a small proportion of silt-clay.

Epiphytic meiofauna were quantified from eight *Thalassia testudinum* blades gathered every 2 wk from September 1983 through January 1984, and approximately monthly thereafter through November 1984. Blades were chosen haphazardly by swimming over the seagrass bed, blindly reaching down, and selecting the closest undisturbed seagrass blade. All blades in the shoot were equally likely to be selected, with the exception of newly emerging blades. Thus, blades over a range of sizes and ages were collected. Blades were collected with a clear plastic tube covered at the end by 0.063 mm mesh. Prior to collection, the tube was filled with filtered seawater by inserting it into the water, mesh-side down, and corking. When opened, the tube was placed over a seagrass blade and stoppered, breaking the blade at the sediment surface. The contents of the tube were rinsed into a jar and preserved with 10% formalin-seawater and Rose Bengal. Water temperature was measured on each collection date with a mercury thermometer.

In the laboratory, seagrass blades were washed (>99% of fauna removed), and all animals retained on a 0.063 mm mesh were enumerated. Harpacticoid copepods were identified to the lowest possible taxon. Life-history stages (male, ovigerous female, non-ovigerous female, or copepodite) were determined for individuals from the five most numerous harpacticoid taxa. Samples with >1 000 harpacticoid copepods per blade were subsampled prior to species identification using a modification of the technique developed by Sherman et al. (1984).

Biomass and percent cover of epiphytic algae, two measures of algal abundance, were determined by separate procedures. To quantify total algal biomass, epiphytes were scraped from the seagrass blades from which meiofauna were enumerated, dried for 24 h at 60 °C, and weighed (mg algae/cm^2 blade). Percent cover of total epiphytic algae and the dominant algal species were quantified from five additional blades on each sampling date using a point-sampling procedure (Hall 1988). Cover of epiphytes could exceed 100% if algae occurred in layers on the blades (see Hall 1988 for further description of methods). Spearman's rank-correlation coefficients (r_s) were calculated for mean densities of the most numerous epifaunal taxa and the five dominant harpacticoid copepod species, with mean abundance of epiphytic algae (total algae, dominant taxa, and major structural groups based on morphological characteristics).

Results

Major taxa

Harpacticoid copepods, copepod nauplii, and nematodes were the most abundant epifaunal organisms on *Thalassia testudinum* at Egmont Key (Fig. 1). Harpacticoid nauplii, the numerically predominant organisms, comprised 45.6% of the total epifauna throughout the study. The mean number of nauplii during the study was 139/10 cm^2, ranging from 5/10 cm^2 on 5 November 1983 to 376/10 cm^2 on 18 November 1983 (Fig. 2). Harpacticoid adults and copepodites ranked second in abundance and comprised 35.7% of the total epifauna. Mean number of

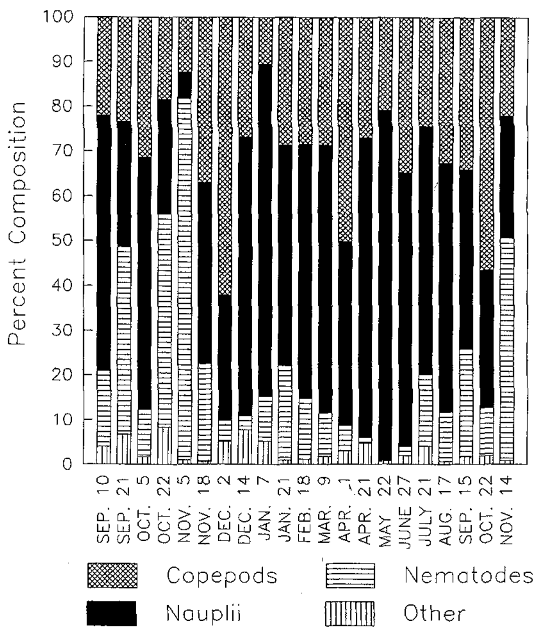

Fig. 1. Percentage composition of major epifaunal taxa on *Thalassia testudinum* at Egmont Key, 1983–1984

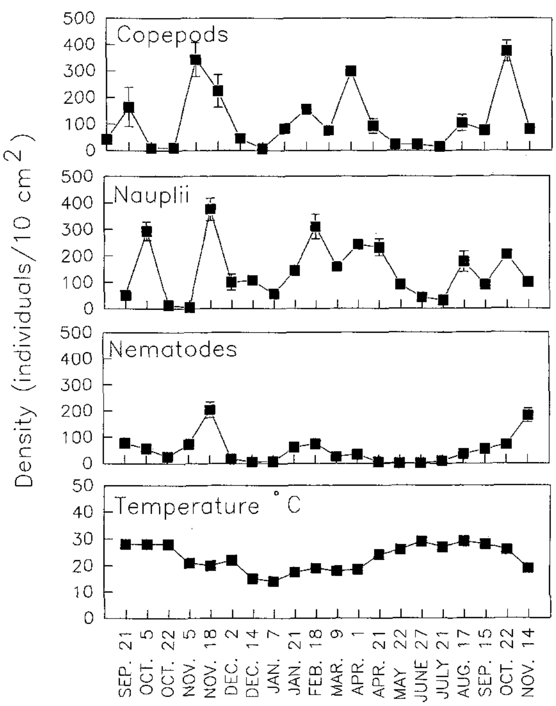

Fig. 2. Mean densities (±SE) of dominant meiofaunal taxa on *Thalassia testudinum* at Egmont Key, 1983–1984. Water temperature at each sampling data is also included

copepods during the study was 108/10 cm^2, with densities ranging from 8/10 cm^2 on 7 January 1984 to 374/10 cm^2 on 11 November 1983 (Fig. 2). Nematodes, the third most numerous taxonomic group, contributed 16.4% of the total epifauna, with a mean abundance of 49/10 cm^2 (Fig. 2).

Epifaunal abundance often fluctuated greatly between sampling dates, and no seasonal patterns were detected for copepods or nauplii. Densities of copepods, nauplii, and nematodes were not correlated with water temperature (Fig. 2) which varied seasonally over the study (Spearman's rank-correlation; $p > 0.05$). Abundance peaks of copepods and nauplii occurred irregularly during fall, winter, and spring, and generally paralleled each other (Fig. 2). Peak proportions of harpacticoid copepods were observed during fall and spring seasons, while nauplii were proportionally most abundant from winter through summer (Fig. 1). In contrast, nematodes constituted a greater proportion of the total meiofauna in the fall (up to 80%) than during the remainder of the year (Fig. 1), with highest numbers of nematodes being recorded in November 1983 and 1984 (Fig. 2).

Other taxa present on *Thalassia testudinum* at Egmont Key in low abundance included ostracods, amphipods, polychaetes, halacarid mites, turbellarians, juvenile bivalves, and juvenile gastropods.

Harpacticoid taxa

Sixteen harpacticoid taxa from ten families were identified from *Thalassia testudinum* blades at Egmont Key (Table 1). The copepod assemblage was composed principally of organisms considered to be phytal-dwelling species (Hicks and Coull 1983); however, a few itinerant forms (organisms inhabiting both sediments and seagrass blades) were also present.

Five taxa, *Harpacticus* sp., *Heterolaophonte manifera*, *Amphiascus* sp., *Schizopera* sp., and *Dactylopodia tisboides*, comprised 96% of the total copepod fauna. These species were present throughout the study, albeit occasionally in low densities. *Harpacticus* sp., the numerically predominant harpacticoid, comprised 47.8% of the total copepod individuals collected. *Harpacticus* sp. had density peaks in all seasons, and an extended period of high abundance during winter and spring (Fig. 3). Highest densities of *H. manifera*, *Amphiascus* sp., *Schizopera* sp., and *D. tisboides* were observed in the fall (Fig. 3). *Heterolaophonte manifera* was more than twice as numerous in fall 1983 than in fall 1984; however, *Amphiascus* sp. and *Schizopera* sp. abundances displayed an opposite pattern (Fig. 3). In addition to a fall peak, *D. tisboides* exhibited an abundance peak during the spring (Fig. 3). Generally, densities of *Amphiascus* sp. and *Schizopera* sp., abundant only during the fall, were more distinctly seasonal than *Harpacticus* sp., *H. manifera*, and *D. tisboides*. Densities of the dominant harpacticoid taxa were not significantly correlated with water temperature (Spearman's rank correlation; $p > 0.05$). Two additional taxa, *Porcellidium* sp. and ectinosomatid spp., were occasionally abundant in samples.

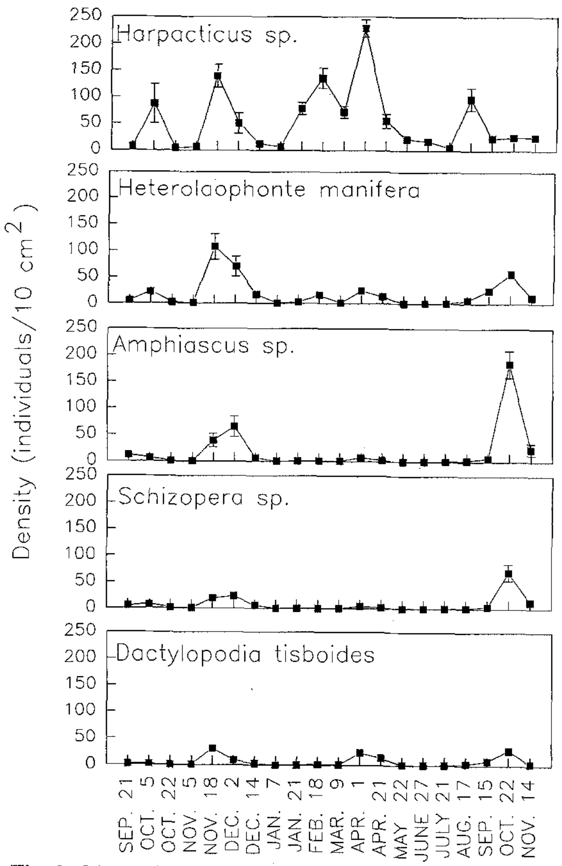

Fig. 3. Mean densities (±SE) of five most numerically abundant copepod taxa on *Thalassia testudinum* at Egmont Key, 1983–1984

Table 1. Harpacticoid copepods present on *Thalassia testudinum* at Egmont Key

Family	Species
Ectinosomatidae	Ectinosomatid spp.
Harpacticidae	*Harpacticus* sp.
Tisbidae	*Scutellidium* sp.
Porcellidiidae	*Porcellidium* sp.
Tegastidae	*Parategastes sphaericus sphaericus*
	Syngastes pietechmanni
Thalestridae	*Dactylopodia tisboides*
	Dactylopodia sp.
	Idomene purpurocincta
Diosaccidae	*Amphiascus* sp.
	Diosaccus sp.
	Schizopera sp.
	Paramphiascella robinsoni
Metidae	*Metis holothuriae*
Canthocamptidae	*Mesochra pygmaea*
Laophontidae	*Heterolaophonte manifera*

Harpacticoid population characteristics

Population characteristics (percent composition of females, males, and copepodites, proportions of ovigerous females, and sex ratios) of the five most numerous cope-

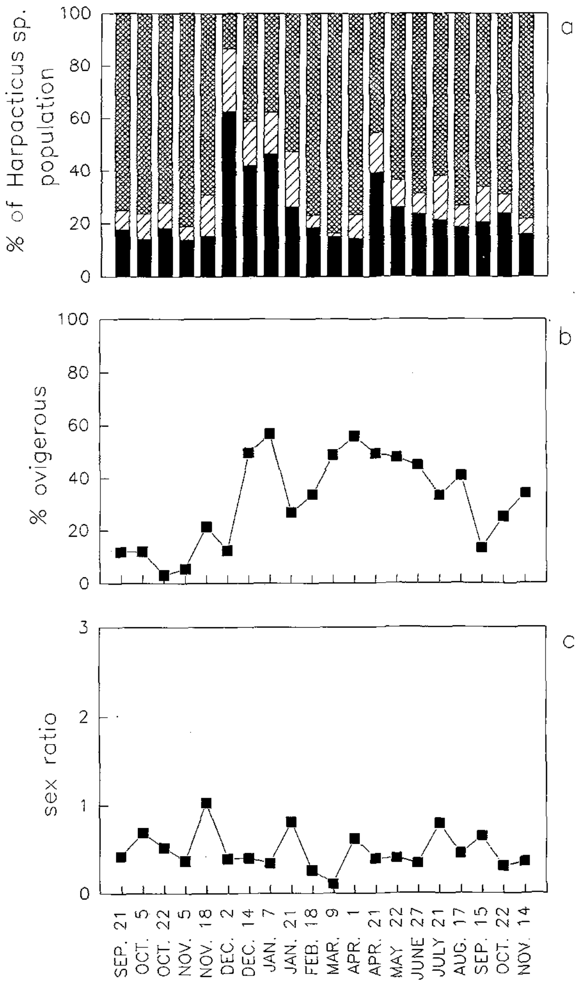

Fig. 4. *Harpacticus* sp. on *Thalassia testudinum* at Egmont Key, 1983–1984; population characteristics. (a) Percent composition of females (black), males (hatched) and copepodites (crosshatched); (b) percent of adult females bearing eggs; (c) sex ratio (male: female)

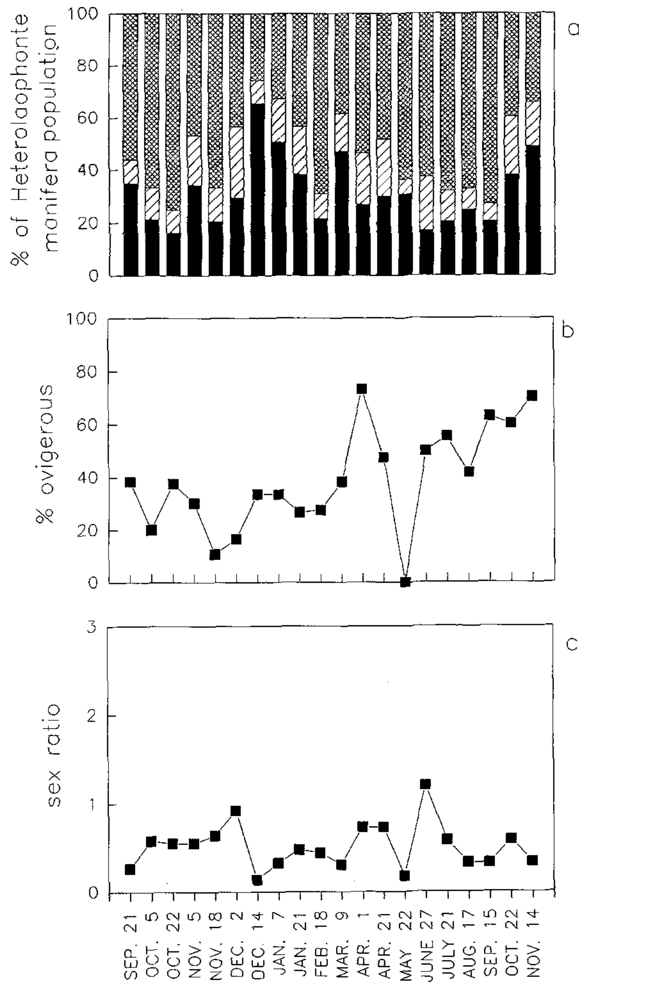

Fig. 5. *Heterolaophonte manifera* on *Thalassia testudinum* at Egmont Key, 1983–1984; population characteristics. Further details as in legend to Fig. 4

pod species are presented in Figs. 4–8. Abundances of females, males, and copepodites of the dominant taxa fluctuated widely over time, as did the total numbers of each taxonomic group; however, some general trends emerged.

For all species, females and copepodites were present during every month, and males during most months (Figs. 4–8). *Schizopera* sp. males were absent during January and summer (Fig. 7), when population densities were very low (Fig. 3). *Dactylopodia tisboides* males were occasionally absent (Fig. 8). Copepodites dominated the population structure of all species on most collection dates.

Ovigerous females of *Harpacticus* sp. were collected during every month (Fig. 4), and in 7 to 11 mo for all other species (Figs. 5, 6, 7, 8). Although ovigerous females of every species were not observed year round, copepodites were recorded for all species during every month, indicating continuous reproductive activity. Sex ratios of males to females sometimes exceeded one, but for the majority of species, generally twice as many females as males were present in the population (Figs. 4–8).

Abundance of epiphytic algae

Both the biomass and total percent cover of epiphytic algae on *Thalassia testudinum* displayed extended periods of high abundance during winter and spring, but temporal patterns of biomass and percent cover were not in complete concordance (Fig. 9). Encrusting algae, the dominant functional group, had peak abundance in late January (131.0% cover; Fig. 10). Percent cover of encrusting algae was lowest during fall months, but never fell below 30%. *Fosliella farinosa*, a coralline red alga, and *Myrionema orbiculare*, a brown alga, were the principal encrusting species (Fig. 10). Percent cover of filamentous algae peaked in fall and spring (Fig. 11), reflecting seasonal patterns of the brown algae *Giffordia rallsiae* and *Ectocarpus rhodochortonoides* (Fig. 11), the predominate filamentous species. Abundance of mat-forming algae, composed primarily of bluegreen algae, generally increased over the study period, reaching a maximum of 34% in November 1984 (Fig. 12). On 8 of the 20 collection dates, the mean cover of mat-forming algae was <10%. *Microcoleus lyngbyaceus*, a bluegreen alga

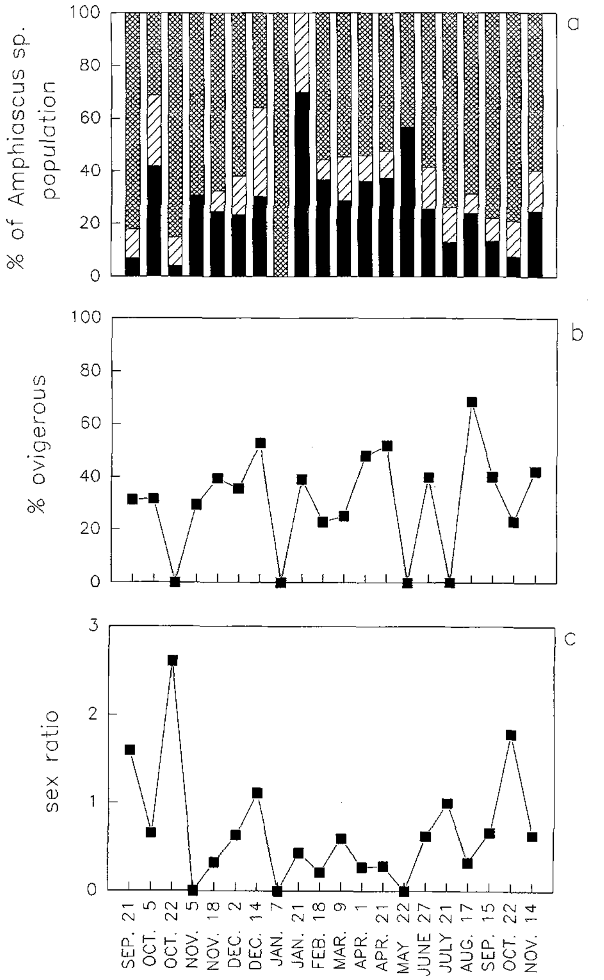

Fig. 6. *Amphiascus* sp. on *Thalassia testudinum* at Egmont Key, 1983–1984; population characteristics. Further details as in legend to Fig. 4

(Fig. 12), was the dominant mat-forming species. Abundance and seasonal patterns of additional algae epiphytic on *T. testudinum* at Egmont Key have been presented by Hall (1988).

Association of epifauna with epiphytic algae

Densities of nauplii, harpacticoid copepods, and nematodes were positively associated with percent cover of filamentous algae, or a filamentous brown algal species during the 15 mo study period (Table 2). In addition, densities of the five numerically dominant harpacticoid species, with the exception of *Harpacticus* sp., were significantly correlated with percent cover of filamentous algae, and with one or more filamentous brown algal species (Table 2). In contrast, the abundance of *Harpacticus* sp. was associated only with total percent cover of epiphytic algae. Seventy percent of all significant correlations between meiofaunal density and abundance of epiphytic algae involved filamentous algae or individual filamentous algal species (Table 2).

Table 2. Relationship between density of major epifaunal and harpacticoid copepod taxa at Egmont Key with abundance of epiphytic algae. Data are Spearman's rank-correlation coefficients; *: $p < 0.05$

Taxon	Total biomass	Total % cover	*Fosliella farinosa*	*Myrionema orbiculare*	Total encrusting algae	*Ecotcarpus rhodochortonoides*	*Giffordia rallsiae*	Total filamentous algae	*Microcoleus lyngbyaceus*	Total mat-forming algae
Copepods	0.43	0.34	−0.05	0.95	0.13	0.28	0.41	0.57*	0.21	0.03
Nauplii	0.34	0.40	−0.22	0.27	0.32	−0.02	0.48*	0.33	−0.08	−0.16
Nematodes	0.48*	0.02	0.13	−0.24	−0.09	0.51*	0.03	0.19	−0.01	−0.16
Harpacticus sp.	0.31	0.48*	−0.21	0.31	0.37	−0.07	0.43	0.33	−0.06	−0.04
Heterolaophonte manifera	0.39	0.20	0.08	−0.19	−0.12	0.59*	0.22	0.65*	0.21	−0.10
Amphiascus sp.	0.37	−0.04	0.24	−0.42	−0.29	0.76*	0.22	0.63*	0.40	0.08
Schizopera sp.	0.49*	−0.13	0.18	−0.46*	−0.38	0.74*	0.21	0.75*	0.44	0.11
Dactylopodia tisboides	0.37	0.11	0.03	−0.16	−0.14	0.53*	0.45*	0.81*	0.50*	0.25

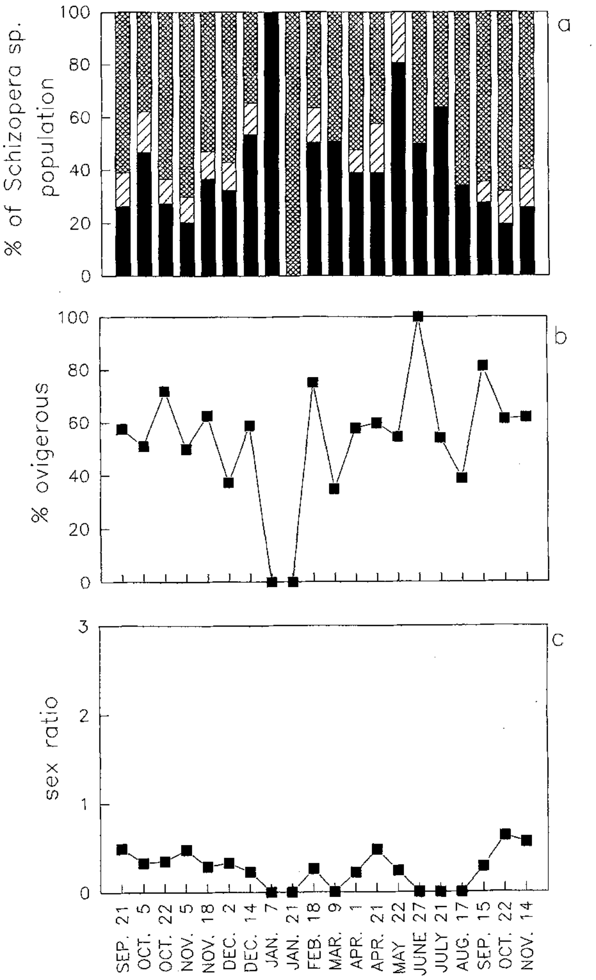

Fig. 7. *Schizopera* sp. on *Thalassia testudinum* at Egmont Key, 1983–1984; population characteristics. Further details as in legend to Fig. 4

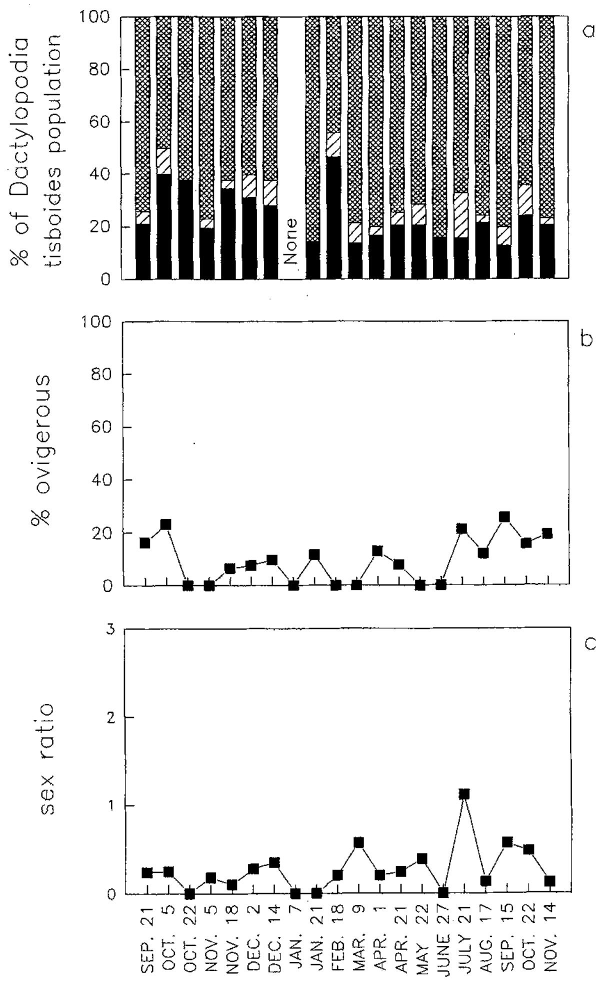

Fig. 8. *Dactylopodia tisboides* on *Thalassia testudinum* at Egmont Key, 1983–1984; population characteristics. Further details as in legend to Fig. 4

Discussion

Although nematodes generally dominate marine sediments (Hicks and Coull 1983, Hicks 1985), harpacticoid copepods and nauplii were the most abundant meiofaunal taxa on seagrass blades at Egmont Key. This community composition is typical of phytal assemblages where levels of accumulated sediment or detritus are low (Wieser 1952, 1959, Hicks 1977a, 1985, Coull et al. 1983, Hicks and Coull 1983). Previous investigations of meiofauna on seagrass blades (Hopper and Meyers 1967, Nagle 1968, Kikuchi 1980, Lewis and Hollingworth 1982, Novak 1982) report predominance of harpacticoid copepods, nauplii, and nematodes. Densities of harpacticoid taxa on *Thalassia testudinum* blades approached values reported for copepods from sediments and macrophytes in estuarine and coastal habitats worldwide, but nematode densities were < 10% of those usually found in sediments [Hicks 1977a (review), 1986, Hicks and Coull 1983 (review), Fleeger 1985].

The correspondence between the species composition of harpacticoid copepods on algae and seagrass blades was striking. True phytal-dwelling harpacticoids belong

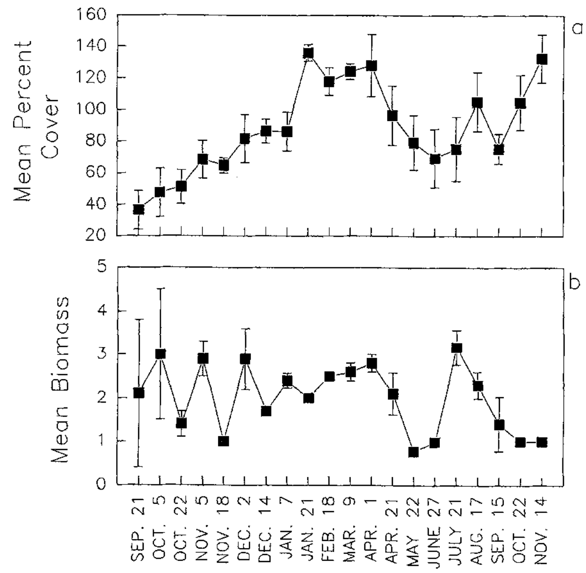

Fig. 9. Total epiphytic algae on *Thalassia testudinum* at Egmont Key, 1983–1984. (a) Mean percent cover (±SE); numbers can exceed 100% because of layering. (b) Mean biomass (±SE) (mg algae/cm^2 blade surface)

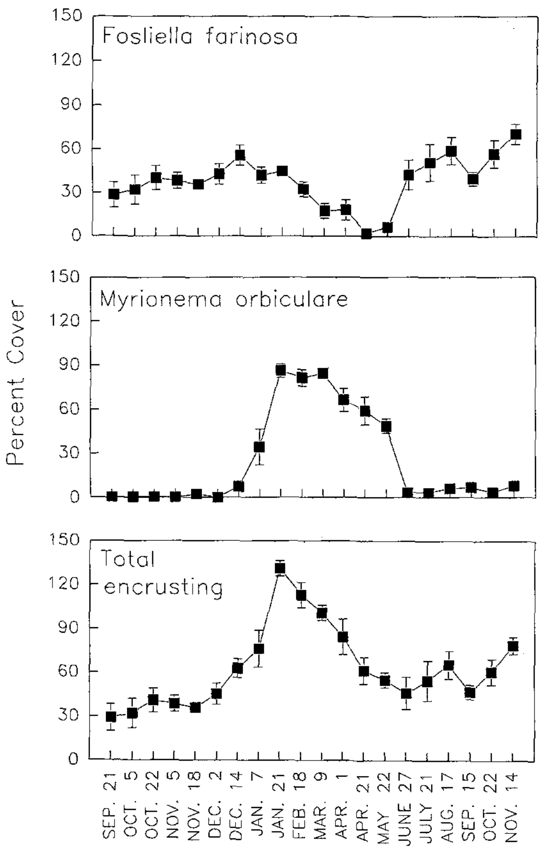

Fig. 10. Total encrusting algae and dominant encrusting taxa, *Fosliella farinosa* and *Myrionema orbiculare*, on *Thalassia testudinum* at Egmont Key, 1983–1984; mean percent cover (±SE)

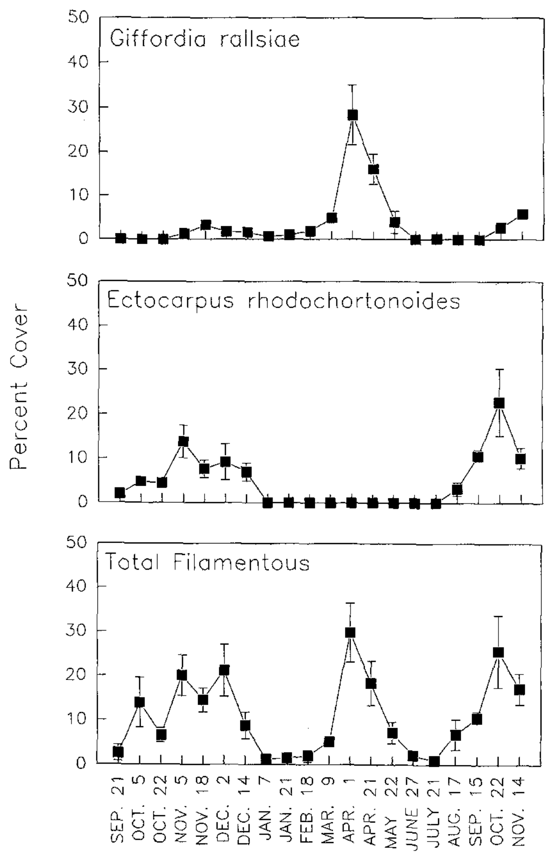

Fig. 11. Total filamentous brown algae and dominant filamentous taxa, *Giffordia rallsiae* and *Ectocarpus rhodochortonoides*, on *Thalassia testudinum* at Egmont Key, 1983–1984; mean percent cover (±SE)

to seven families: Harpacticidae, Tisbidae, Porcellidiidae, Tegastidae, Thalestridae, Diosaccidae and Peltidiidae (Hicks and Coull 1983). At Egmont Key, all phytal taxa except Peltidiidae were represented, and were frequent or even dominant members of the copepod assemblage. Harpacticoid taxa on *Thalassia testudinum* that were not members of one of the above families have been reported from macroalgae or seagrasses elsewhere [Hicks and Coull 1983 (review), Hicks 1985 (review), 1977a, b, 1986, Johnson and Scheibling 1987a, b). The copepod assemblage on *T. testudinum* at Egmont Key provides additional evidence for "parallelism" (similar substrata inhabited by the same dominant genera worldwide; *sensu* Thorson 1957) in phytal harpacticoid communities.

Harpacticus, the most abundant harpacticoid taxon present on seagrass blades at Egmont Key, has also been reported as a dominant genus on various macroalgae collected over a wide geographic range (United Kingdom: Fraser 1936, Hicks 1980; Azores: Chapman 1955; Germany: Noodt 1957, Ohm 1964; Argentina: Pallares and Hall 1974a, b; Japan: Kito 1975, 1977; United States of America: Gunnill 1982, Coull et al. 1983). Reasons for the success of *Harpacticus* spp. in phytal habitats are unknown. Community dominance by one or a few harpacticoid species seems to be a common phenomenon, having been reported from both sediments (Coull and Fleeger 1977, Fleeger 1980, 1985, Coull and Dudley 1985) and macroalgae (Hicks 1977a, Gunnill 1982, Johnson and Scheibling 1987a), and is clearly evident on seagrass blades as well.

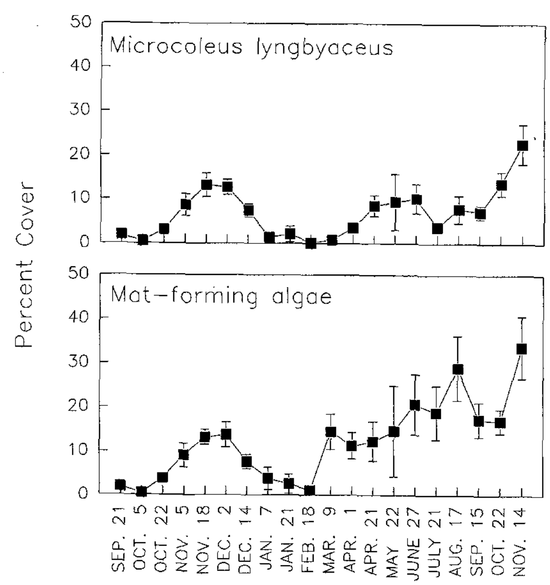

Fig. 12. Total mat-forming algae and dominant mat-forming taxon, *Microcoleus lyngbyaceus*, on *Thalassia testudinum* at Egmont Key, 1983–1984; mean percent cover (±SE)

Population structures of the dominant harpacticoid species on *Thalassia testudinum* blades varied little over the study, with copepodites constituting the most numerous life-history stage on the majority of collection dates. High proportions of copepodites have also been reported for populations of selected harpacticoid species on macroalgae (Hicks 1977c, Johnson and Scheibling 1987b), in sediments (Coull and Dudley 1985, Fleeger 1985), and on submerged wood (Knatz 1986); however, consistent dominance by copepodites over time as seen at Egmont Key appears to be unusual. Additionally, percentages of copepodites on seagrass blades at Egmont Key were approximately twice as high as those recorded for *Harpacticus* sp. and *Heterolaophonte manifera* collected from sediments within a nearby seagrass bed (Walters 1987). These latter results suggest that blade habitats may provide more favorable nursery sites than the underlying sediments.

The year-round presence of ovigerous females and/or copepodites indicated that all dominant species of harpacticoid copepods at Egmont Key were continuous breeders. Seaweed-dwelling harpacticoids in New Zealand and Nova Scotia also have prolonged or continuous reproduction (Hicks 1977c, Johnson and Scheibling 1987b). It seems that seagrass-dwelling copepods at Egmont Key differ from most of those inhabiting sediments not only in the persistent dominance by a single species within the community, but also in the continuous reproductive activity of most species. Whether such patterns of reproductive activity reflect a more available food source in the phytal compared with sediment habitats, as suggested by Hicks (1977c), awaits further investigation.

Although differences between population traits of seagrass- and sediment-dwelling copepods exist, some similarities were discovered. Harpacticoid females generally outnumber males in sediments and on macrophytes worldwide (Hicks and Coull 1983), and male-biased sex ratios were also observed for seagrass-associated copepods. Sex ratios for copepods collected from *Thalassia testudinum* at Egmont Key were similar to those of congeneric species collected from macroalgae in New Zealand (Hicks 1977c). Hicks (1977c) and Johnson and Scheibling (1987b) found that sex ratios favored females during periods of low population density for the majority of harpacticoid species on macroalgae in New Zealand and Nova Scotia. In contrast to other phytal assemblages, sex ratios of harpacticoid copepods at Egmont Key did not appear to be influenced by population density.

Similar to findings from both sediment (Coull and Dudley 1985) and other phytal habitats (Hicks 1977c, Johnson and Scheibling 1987b), peaks in ovigerous female abundance did not precede peaks in juvenile or total population density for harpacticoid taxa at Egmont Key. Coull and Dudley suggested that non-simultaneous hatching of eggs, differential development times, or overlapping cohorts would result in an inability to detect peaks in the abundance of ovigerous females prior to population peaks. Immigration of individuals from other areas could also lead to population increases without preceding peaks of ovigerous females. Data are not available to evaluate whether developmental or behavioral factors resulted in the discordant reproductive and abundance patterns observed in the present study, but Meyer (1990) noted the importance of immigration for initial population expansion of the harpacticoid *Metis holothuriae* in nearby seagrass beds.

Population densities of harpacticoid copepods on *Thalassia testudinum* at Egmont Key varied greatly over time. In previous studies, temporal variability in the population densities of harpacticoid copepods has been attributed principally to fluctuations in reproductive activity, as evidenced by the high numbers of juveniles present in population maxima (e.g. Hicks 1977c, Fleeger 1980, Hicks and Coull 1983). These juveniles are thought to be the result of in situ reproduction or immigration from nearby populations that are also reproducing. Temperature has been suggested to be the most important factor controlling the discrete reproductive periods of most sediment-dwelling species, which tend to breed during warmer seasons (Hicks 1977c, Hicks and Coull 1983, D'Amours 1988). In contrast, the population maxima of phytal-dwelling species, which usually have prolonged or continuous breeding cycles, often occur in both warm and cool seasons (Hicks 1977c, 1979, 1985). Given that no relationship between temperature and population density was observed for harpacticoid copepods on seagrasses or macroalgae, it follows that additional factors may regulate patterns of population growth in phytal systems.

The results of the present study suggest that epiphytic algae influence meiofaunal densities on seagrass blades, as most meiofaunal taxa at Egmont Key were associated positively with percent cover of algae over a 15 mo period. Moreover, meiofaunal–algal associations varied among the three structural groups of epiphytes. The majority of studies (including the present one) that reported positive relationships between epifauna and epiphytic algae revealed strongest associations with filamentous species. Johnson and Scheibling (1987a) found the densities of epifauna, including harpacticoid copepods, to be correlated positively with filamentous algal biomass on the intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus*. Limited data from other investigations indicated positive relationships between filamentous algae and epifauna on both seagrasses (Nagle 1968, Lewis and Hollingworth 1982, Novak 1982), and various species of macroalgae (Colman 1940, Wieser 1952, 1959, Hagerman 1966, Zavodnik 1967, Kito 1977, Kangas 1978, Hicks 1979, Gunnill 1982, Edgar 1983). Thus, the copepod–filamentous algal association detected in subtropical seagrass beds occurs on a variety of marine vegetation located over a broad geographic range.

Not all copepod taxa showed a strong relationship with filamentous algae, however. In the present study, densities of the predominant copepod, *Harpacticus* sp., were positively associated with total percent cover of epiphytic algae. Reasons for the positive associations with total cover of epiphytic algae are unclear, but may be a coincidence of the numerous population maxima of *Harpacticus* sp. during the study. Although *Harpacticus* sp. densities were strongly related to filamentous algal abundance on the time-scale of days in a recolonization experiment (Hall and Bell 1988), *Harpacticus* sp. must be responding to additional factors when viewed over the 15 mo of the present study.

The significant positive associations observed between filamentous algal abundance and densities of *Amphiascus* sp., *Schizopera* sp. and *Dactylopodia tisboides* appear to contrast with results of the earlier study by Hall and Bell (1988). These three copepod taxa showed little or no increase in abundance with increasing levels of filamentous epiphyte biomass in experiments conducted over a period of days (Hall and Bell 1988), but over the 15 mo examined in the present study, a positive association with percent cover of filamentous algae was detected. Results of the two studies can be reconciled if some copepod taxa respond to the presence of epiphyte cover, but do not proportionally use additional levels of epiphytic growth (e.g. a saturation effect). If this is true, patterns of algal and copepod abundance could be coordinated, as suggested by the long-term descriptive data, yet copepods might not demonstrate the strong linear responses to increased levels of epiphytes observed in short-term experimental trials. Interpreting the response by copepods to the amount or type of epiphytes requires observational data concerning copepod behavior on or near epiphytic algae, as well as determination of the nature of the resource (e.g. food accumulation, physical refuge, etc.) provided by the different algal taxa. Resources provided by epiphytic algae are probably related to algal morphology, and copepod use of epiphytes most probably reflects grazing and grasping capabilities. The responses of individual copepod taxa to algal epiphytes may vary with such characteristics as size, mouthpart arrangement and leg structure.

The findings presented here provide a more extensive documentation of the relationship between algal epiphytes and copepod abundance on seagrass blades than has been provided previously. Manipulative experiments will be required to determine exactly how copepods use algal epiphytes, and how morphological characteristics of copepods and algal epiphytes influence such use. Such studies may also help elucidate how selected copepod species in the seagrass habitat maintain high levels of abundance, dominance, and reproductive activity.

Acknowledgements. We thank J. C. Kern, R. Riechert, L. A. Smith and S. Watts for assistance in the field. C. J. Dawes, B. Cowell, D. Te Strake, R. Virnstein, W. Nelson, G. Hicks, K. Walters, and J. Quinn provided comments on the manuscript. Technical assistance was given by E. R. Ruark and S. A. Peck. Opinions, findings, conclusions, or recommendations expressed in this report are those of the authors and do not reflect the views of the State of Florida unless so designated by other authorized documents.

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Communicated by J. M. Lawrence, Tampa