Marine Biology (2005)
DOI 10.1007/s00227-005-0062-x

RESEARCH ARTICLE

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# A field colonization experiment with meiofauna and seagrass mimics: effect of time, distance and leaf surface area

Received: 3 December 2004 / Accepted: 10 June 2005


**Abstract** From a conservation point of view, it is essential to know how fast an ecosystem can recover after physical disturbance. Meiofauna and especially harpacticoid copepods are abundant in seagrass beds and are therefore useful to study ecosystem recovery after disturbance. In the western Caribbean coast, a fragmented *Thalassia testudinum* seagrass bed was selected to conduct a colonization field experiment by means of plastic seagrass mimics. Meiofauna colonization, with special emphasis on harpacticoid copepods, was followed in relation to: (1) colonization time (2, 4, 6, 10, 14 and 21 days); (2) distance to source of colonizers (*close* and *far* series) and (3) leaf surface area to colonize (small, medium, large). Colonization was recorded after 2 days with average meiofauna densities of 480 ind/100 $cm^2$ (*close*) and 1350 ind/100 $cm^2$ (*far*) of leaf surface area, while on average 400 ind/100 $cm^2$ were collected from the natural seagrass plants. In this early phase, the meiofauna diversity was high, with on average 8 taxa. A longer period of colonization (21 days) showed an increased meiofaunal density and diversity (average density: 3220 ind/100 $cm^2$, 13 taxa). Increasing meiofauna colonization with time is probably related to the development of a biofilm making the leaf more attractive for meiofauna. The effect of distance was not so pronounced as that of time. Total absolute densities were highest in the *far* series (5 m away from natural seagrass patch), mainly because of nematode densities. Meiofauna diversity was lower in the *far* series than in the *close* series (at the border of the natural seagrass patch). A larger individual leaf surface area did not affect the overall meiofauna densities but had a significant positive effect on copepod densities. Larger surface areas promoted the presence of epiphytic copepod families such as Tegastidae and Dactylopusiidae. Overall, we found a rapid recovery of meiofauna in fragmented seagrass beds with primary colonizers (both nematodes and benthic opportunistic copepods) originating from the sediment and later colonizers as epiphytic copepods and their nauplii from the local seagrass regeneration pool.

Communicated by O. Kinne, Oldendorf/Luhe

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## Introduction

Changes in land use have led to a steady loss of habitat and to an increasing isolation of habitat remnants throughout the world. Habitat destruction and fragmentation are major causes of the increase in the rate of species extinction in recent decades (Henle et al. 2004). The restoration of habitats in general gets more attention recently. As many coastal ecosystems are often directly influenced by natural and human-induced disturbance (e.g. recreation, harbours) (e.g. Short and WyllieEcheverria 1996), some restoration efforts have been undertaken through techniques such as ecological restoration and habitat creation (e.g. van Katwijk et al. 2000; Mechan and West 2002).

The resource value of natural seagrass beds has been well documented, however there have been few studies to evaluate the assumption that restoring or creating seagrass beds provides a concomitant recovery of commercially and recreationally valuable animal species and/or their food sources (e.g. McLaughlin et al 1983, Fonseca et al. 1990; 1996). Although seagrass beds are known as feeding and nursery grounds for many fish species (e.g. Marguillier et al. 1997; De Troch et al. 1998; Nagelkerken et al. 2000a, b, c, 2001), Connolly (1994) couldn't find any major impact of seagrass

canopy removal on small fishes. The same study suggested that prey availability was of major importance in the role seagrasses play as habitat for small fish. As such, the effective restoration of these habitats depends on whether the planting of seagrass beds provide living marine resource values similar to the natural beds they are intended to replace (Fonseca et al. 1996; Bell et al. 2001).

A major food source for juvenile fishes in seagrass beds is meiofauna (a.o. Sogard 1984; De Troch et al. 1998), i.e. Metazoa that pass through a 1 mm sieve but are retained on a 38 μm sieve. Despite the fact that meiofauna lack pelagic larvae (Giere 1993; Palmer et al. 1996), water-column processes exert an important influence on meiofaunal recruitment and colonization of new areas (Kern and Bell 1984; Palmer and Gust 1985). Two distinct patterns exist for recruitment via the water column: active entry of meiofauna into the water and passive erosion of meiofauna from the sediments or from surfaces (Palmer 1988). Harpacticoid copepods are often abundant in seagrass beds (Hicks 1977a, b, c, 1980; 1986; Bell et al. 1988; Bell and Hicks 1991; De Troch et al. 2001a, b) and are known for their active migration (e.g. Kern and Bell 1984; Arlt 1988; Bell et al. 1989) in contrast to the more passive dispersal of nematodes (Commito and Tita 2002 and references herein). In areas free of aboveground structures (e.g. bare sand), passive recruitment processes dominate (Palmer 1988). Aboveground structures probably act to enhance active emergence while disturbance events may lead to increased suspension (Palmer 1988).

In order to assess how habitat structure mediates dispersal, several studies have made use of artificial substrata to mimic seaweeds (Myers and Southgate 1980; Edgar 1991) or seagrasses (Thistle et al. 1984; Bell et al. 1985; Jenkins et al. 1998; Bologna and Heck 2000); or to create new habitats (Bombace et al. 1994; Bartol and Mann 1997; Atilla and Fleeger 2000; Atilla et al. 2003). The use of artificial units to test experimentally ecological hypotheses has many advantages (Chapman 2003).

In the present study, seagrass mimics were planted in a fragmented Caribbean seagrass bed in order to investigate short-term dynamics of meiofaunal colonization, with emphasis on harpacticoid copepods. As such, we were interested in the main factors related to seagrass restoration that we expect to have an effect on the recovery of associated meiofauna: i.e. colonization time, distance to natural seagrass bed and leaf surface area of the seagrass.

Time was analysed as a primary factor affecting colonization. We questioned whether successional stages of colonization would be reflected in the degree of community saturation, i.e. when and to what extent does a newly established community resemble the natural one. Therefore, meiofauna and more specifically copepod communities from natural seagrass beds were collected in order to evaluate how meiofaunal communities on mimics resemble those of natural substrates. In addition, organisms inhabiting the borders of a seagrass patch were compared to those from the more central area of the seagrass bed as they may be influenced by the varying arrangements of the natural plants.

Secondly, we hypothesized that the natural seagrass bed, rather than the sediment, was of major importance as a potential source of meiofaunal colonizers. Therefore, the impact of proximity of natural plants and associated meiofauna on the mimic-associated fauna was investigated. Thirdly, the importance of structural characteristics of the mimic, i.e. the leaf surface area available for colonization, was evaluated by means of seagrass mimics with different leaf width.

## Materials and methods

### Study area

Punta Allen (19°47′06″N and 87°28′08″W) is located on the western Caribbean, central part of the eastern coast of the Yucatan Peninsula (Quintana Roo State, Mexico); this area is part of the UNESCO Biosphere Reserve of Sian Ka'an, situated 170 km north of the Mexican border with Belize (between 19°05′–20°06′N and 87°22′–88°00′W) (Camarena and Villanueva 1991).

Espinoza-Avalos (1996) reported *Thalassia testudinum* Banks ex König as the climax vegetation and *Halodule wrightii* Ascherson and *Syringodium filiforme* Kützing as the main seagrasses found in the Yucatan Peninsula. A similar community was reported from the west coast of Florida (Zieman and Zieman 1989) and the Caribbean Sea (Dawes et al. 1991).

Although many studies have been devoted to the biodiversity of Sian Ka'an (for overview see Navarro and Suárez-Morales 1992), information on benthic and epiphytic meiofauna from seagrass vegetation is rather scarce (De Troch 2001). De Troch (2001) reported a rich meiofauna community associated with different seagrass species in the area. At Punta Allen *T. testudinum* is affected by boat activities of local fishermen, resulting in small patches (personal observation). Seagrass beds at this site are of non-uniform morphology: patches of plants are separated by open sediment, and bed margins may be convoluted. In order to test the effect of this habitat fragmentation on the epiphytic meiofauna, colonization experiments were conducted between November 24th and December 12th, 2001.

### Seagrass mimics and experimental set-up

Plastic seagrass mimics (Fig. 1) were used in these field experiments. Mimic leaves were on average 33.4 ± 1.4 cm long and 3 different leaf widths were included but not mixed on a single plant (see experiment ***c***): 0.8–0.9 cm (small or narrow), 1.3 cm (medium) and 2.5 cm (large or wide) (Fig. 1, Bio Models Co., Sierra Madre, California, USA). Natural leaves of *T. testudinum* are on average

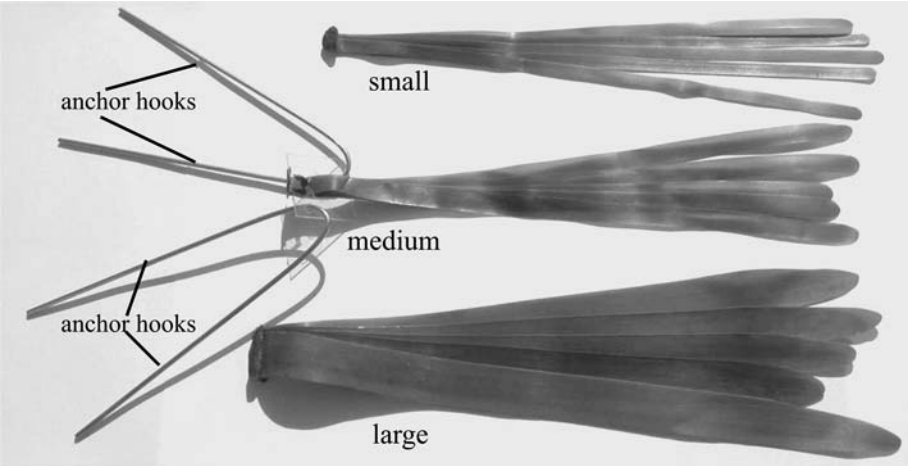


**Fig. 1** Illustration of the three leaf widths of seagrass mimics and anchor hooks used to fix them in the sediment

19.4 ± 4.3 cm long (max. length of the green part of the leaves = 26.8 cm) and 1.2 ± 0.2 cm wide (Van Tussenbroeck, personal communication). Each mimic plant consisted of 4 green and 1 brown leaf resembling natural plants with fresh (green) and dead (brown) leaves. Total leaf length per plant was on average 166.9 ± 4.8 cm corresponding to an average plant surface area of 133.5 ± 4.8 $cm^2$ (small), 217.0 ± 4.8 $cm^2$ (medium), and 417.3 ± 4.8 $cm^2$ (large). Each mimic sample consisted of 4 mimic plants (5 leaves each, see before) grouped together as a cluster in order to reduce variability.

Seagrass mimics were planted in the sediment by means of two U-shaped stainless anchor hooks (20 cm in length) (Fig. 1). All seagrass mimics were planted adjacent to a *T. testudinum* bed. Experiments ***a*** and ***b*** (see further) were conducted next to a *T. testudinum* patch (6 m long and 2.5 m wide, total surface area = 15 $m^2$), situated parallel to the beach at 19°47′51″N and 87°28′26″W. For experiment ***c***, seagrass mimics were anchored at the border of a *T. testudinum* patch of comparable size (6.5 m long and 3 m wide) about 50 m further south (19°47′50″N, 87°28′25″W). As tidal fluctuations are small (0–0.3 m) and water movement is predominantly wind driven at the sampling site, the seagrass mimics and natural seagrass patch were constantly submerged under a water cover of at least 1 m.

Before planting seagrass mimics, triplicate epiphytic meiofauna samples were collected inside (*in* series, Fig. 2) and at the border (*out* series, Fig. 2) of the natural *T. testudinum* patch as a control for the actual meiofauna community.

### *Experiment a: effect of time*

Colonization of seagrass mimics by meiofauna was investigated at 6 time intervals, i.e. after 2, 4, 6, 10, 14 and 21 days (Fig. 2). At the end of each interval, triplicate samples were collected at random from two locations (see experiment ***b***). Only medium-sized leaves (1.3 cm wide) were used for this experiment.

### *Experiment b: effect of distance*

The second experiment investigated whether the colonization of newly planted seagrass mimics was influenced by the distance between the new substrate and the potential source of colonizers; it was hypothesized that colonizers may originate from nearby seagrasses. Two series were included, i.e. one series at the border of the natural *Thalassia* patch (*close* series) and a second series in bare sediment about 5 m away from the natural patch (*far* series) (Fig. 2). Both series were sampled at 6 time

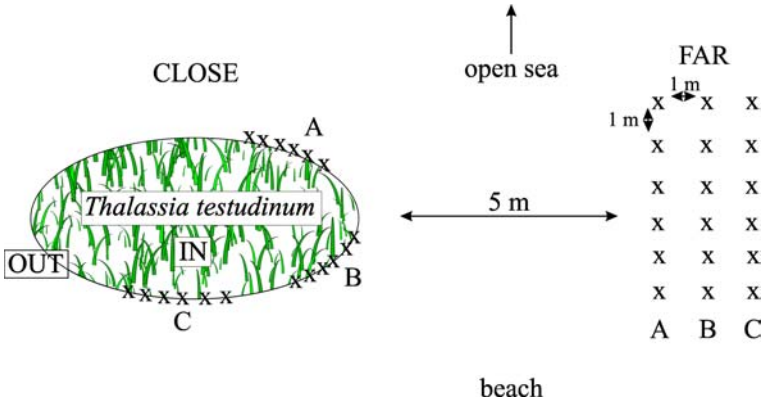


**Fig. 2** Field design of experiment a and b (effect of time and distance). Seagrass mimic clusters are indicated by an "x" for each sampling date i.e. after 2, 4, 6, 10, 14 and 21 days, respectively. Replicates are referred to as A, B and C

intervals as explained for experiment ***a***. As for experiment ***a***, only medium-sized seagrass mimics were used in this experiment.

*Experiment c: effect of leaf surface area*

Seagrass mimics with small, medium and large leaves were planted at the border of a *Thalassia* patch in order to test the effect of leaf surface area on colonization. Triplicate meiofauna samples were collected for each type at one time interval, i.e. after 14 days.

Sample processing

Seagrass mimics were collected by placing a plastic bag over the mimics; the cluster of mimics was collected by gently pulling up the anchor hooks from the sediment in order to minimise the amount of sediment enclosed. Upon return to the beach, an 8% $MgCl_2$-solution was added to all samples to stun the epiphytic fauna (Hulings and Gray 1971). The entire clusters of mimics (4 plants, 20 leaves in total) were washed in the field with freshwater over a 1 mm sieve and epiphytic meiofauna was retained on a 38 μm sieve.

Within 2 h after collection, all samples were fixed with warm (60°C) buffered formalin with a final concentration of 4%. In the laboratory, samples were rinsed with a jet of freshwater over a 1 mm sieve, then decanted ten times over a 38 μm sieve, centrifuged three times with Ludox HS40 (specific density 1.18) and stained with Rose Bengal. All meiofauna organisms were sorted, counted, and pre-identified to higher taxonomical levels using a Wild M5 binocular microscope. Copepods and nauplii were counted separately in view of their different ecology and dispersal abilities (Hicks and Coull 1983). Per sample, a maximum of 100 harpacticoid copepods (including copepodites) were picked out as they were encountered and stored in 75% ethanol for further species identification. Copepods were mounted in toto on glycerin slides and identified to species level.

Data analysis

One-way and factorial analysis of variance (ANOVA) with factors time and distance were performed with STATISTICA software. A posteriori comparisons were carried out with the Tukey HSD-test using 95% confidence intervals. Prior to analysis, Cochran's C-test was used to check homogeneity of the variances and Kolmogorov-Smirnov test was used to test for normality.

## Results

Effect of time and distance on meiofauna and copepod colonization *(experiments a–b)*

For both *close* and *far* series (Fig. 3a), meiofauna colonized the seagrass mimics very quickly as on average $480 \pm 239$ ind/100 $cm^2$ (*close*) and $1353 \pm 651$ ind/100 $cm^2$ (*far*) were collected 2 days after set-up. Total abundances remained relatively stable for the *close* series during the first 6 days. However, for the *far* series there was more variance as total meiofauna densities were halved from day 4 towards day 6.

After 10 and 14 days, however, total meiofauna densities doubled to $1155 \pm 225$ ind/100 $cm^2$ for the *close* series while the densities for the *far* series remained stable ($1077 \pm 47$ ind/100 $cm^2$) on day 10; and to $943 \pm 122$ ind/100 $cm^2$ (*close*) and $1830 \pm 407$ ind/100 $cm^2$ (*far*) on day 14, respectively. After an additional week (i.e. after 21 days), meiofauna densities doubled again to average values of $2050 \pm 230$ ind/100 $cm^2$ (*close*) and $3222 \pm 759$ ind/100 $cm^2$ (*far*). At this point, meiofauna densities reached up to 5 (*close*) to 7 (*far*) times the densities found on natural seagrass plants.

A significant effect of time on meiofauna abundances was found (factorial ANOVA, $p < 0.0001$). However, a post-hoc Tukey HSD test indicated that only day 21 was significantly different from the other sampling dates ($p < 0.001$, except for day 14 vs. day 21: $p < 0.05$). Overall, there was a significant difference in meiofauna densities between the *close* and the *far* series (factorial

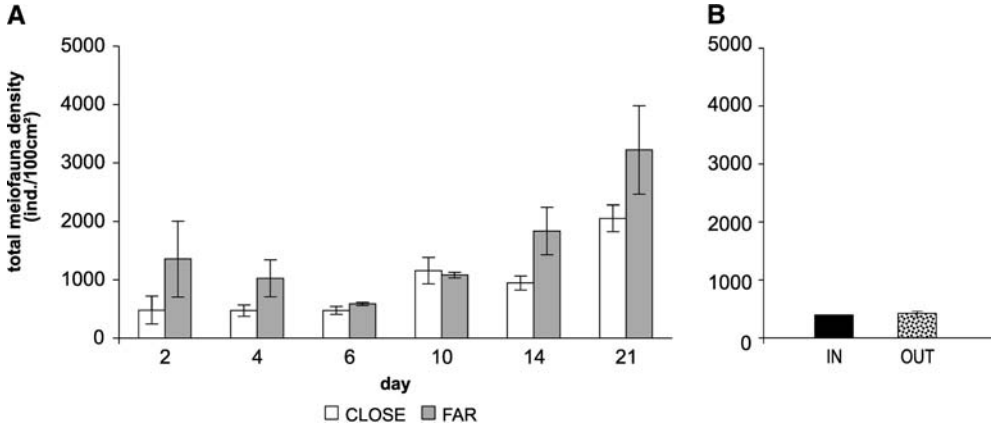


**Fig. 3** Total meiofauna densities (±standard error) on **a** seagrass mimics in the *close* and *far* series after 2, 4, 6, 10, 14 and 21 days and **b** natural seagrasses (inside-*in*—and at the border-*out*)

ANOVA, $p < 0.01$), while a post-hoc Tukey HSD test indicated a borderline non-significant effect of distance for the different dates. Overall (except on day 6 and 10), meiofauna densities were higher in the *far* series. No significant interaction between time and distance was found (factorial ANOVA, $p = 0.5$, Table 1). There was a high variability of meiofauna densities, mainly in the *far* series.

In comparison with the natural situation (Fig. 3b), meiofauna densities were on average higher on the mimics. The meiofauna densities recorded during the first sampling points in the *close* series were very much comparable to the natural densities. There was no significant difference (one-way ANOVA, $p > 0.05$) in meiofauna densities between the *in* series ($392 \pm 24$ ind/100 cm$^2$) and the *out* series ($423 \pm 60$ ind/100 cm$^2$).

In addition, the degree of variation of the meiofauna densities (as shown by standard errors, Fig. 3) was larger for meiofauna on the mimics.

Nematodes dominated the meiofauna community until day 6 (except day 2 *close* series) (Fig. 4). A major shift of dominance from nematodes to copepods occurred after 6 days. Copepods (mainly harpacticoids) increased their relative importance during colonization, ranging from 21% (at day 2) to 49% (at day 21) in the *close* series (Fig. 4a) and from 8% (at day 2) to 27% (at day 21) in the *far* series (Fig. 4b). The same pattern was found for the copepod nauplii, i.e. an important increase after 6 days of colonization and in some cases (day 14 and 21 in the *far* series, day 14 in the *close* series) copepod nauplii even became dominant.

The effect of distance of the mimics to the natural seagrass bed (*close* versus *far*) was reflected mainly in the relative abundance of nematodes, as initially, nematodes accounted for more than 70% of the meiofauna in the *far* series (Fig. 4b) while their share ranged between 28% (day 2) and 54% (day 4) in the *close* series (Fig. 4a). In addition, the *close* series was initially characterised by a slightly higher share of copepods and nauplii compared to the *far* series.

On the natural seagrass plants, however, the share of copepods was much higher as they accounted for almost half of the meiofauna, i.e. 44% in the *in* series and 46% in the *out* series (Fig. 4c). A comparable portion of copepods on the seagrass mimics was only found after 10 days of colonization and only in the *close* series. Again, there was no significant difference between the *in* and *out* series in terms of relative abundance of meiofauna taxa. Turbellaria were not plotted in Fig. 4c as they were of minor importance ($< 2\%$) in the epiphytic meiofauna of natural seagrass plants, whereas on mimics they accounted for a maximum of 23% of the meiofauna (*close* day 2).

**Table 1** Results of factorial ANOVA testing effects of distance from the natural seagrass bed (*close* versus *far*) and colonization time on meiofauna densities (significant *p*-levels in bold)

| Factors | df | MS | *p*-level |
|---|---|---|---|
| Distance | 1 | 3100250 | **0.0075** |
| Time | 5 | 3405223 | **0.0001** |
| distance×time | 5 | 354582 | 0.4535 |
| Error | 24 | 364042 | |

Meiofauna diversity (expressed as number of meiofauna higher taxa) increased with time (Fig. 5) from 8 (day 2) to 13 taxa (day 21) and from 7 (day 2) to 12 taxa (day 21) for the *close* and the *far* series, respectively. From 6 days onwards, the number of meiofauna taxa on the mimics reached the minimum number of taxa (11 taxa) recorded from the natural seagrasses. At the end of the colonization experiment (after 21 days) the number of meiofauna taxa was not significantly different from that in the natural situation (both *in* and *out* series) (Fig. 5b).

As copepods (and their nauplii) were dominant in the natural situation and of major importance in the colonization process (see Fig. 4), they were further analysed at the species level. In total, 33 copepod species belonging to 18 harpacticoid families were identified. More than half of the copepods found on the mimics belonged to the harpacticoid copepod families Ectinosomatidae (2 species) and Tisbidae (mainly *Scutellidium longicauda* (Philippi 1940)) (Fig. 6). The same dominance was found in the natural situation (Fig. 6c) but in the *out* series the share of Ectinosomatidae ($39.6 \pm 3.4\%$) (same 2 species) was much higher than of the Tisbidae ($15.3 \pm 1.8\%$), while in the *in* series both families contributed equally (about 25% each). From day 10 onwards, the importance of the family Tisbidae increased and it became the dominant family in the *close* series, with two species only (*S. longicauda* and *Tisbe* sp. 1).

Species of the epiphytic family Dactylopusiidae (*Diarthrodes tetrastachyus* Yeatman 1976, *Paradactylopodia* cfr. *brevicornis* (Claus 1866), *Eudactylopus* sp. 1) were abundant at all time intervals of both *close* (on average 12%) and *far* series (on average 16%) and in the natural situation (on average 11%). Another epiphytic harpacticoid family, Tegastidae (represented by *Tegastes* sp. 1), was found in much lower relative abundance on the seagrass mimics (*close*: 3%, *far*: 0.8%) in contrast with the natural situation (9.5%).

The larger benthic species of the family Canuellidae (*Ellucane secunda* Coull 1971, *Scottolana antillensis* Fiers 1984) were initially relatively abundant in the *far* series (up to 20%) but decreased to low relative abundances from day 14 onwards (max. 3% on day 21). Canuellidae were of minor importance in the *close* series as they represented max. $3.7 \pm 2.8\%$ on day 4.

Aside from harpacticoids, some planktonic cyclopoids and calanoids were collected but were not further identified.

On average 10 to 14 copepod species were identified per sample. For both *close* and *far* series, a maximum diversity of 14 species was found on day 4 and 6. Copepod species richness on the natural seagrasses ranked within this range as on average 12 copepod species were found in both *in* and *out* series.

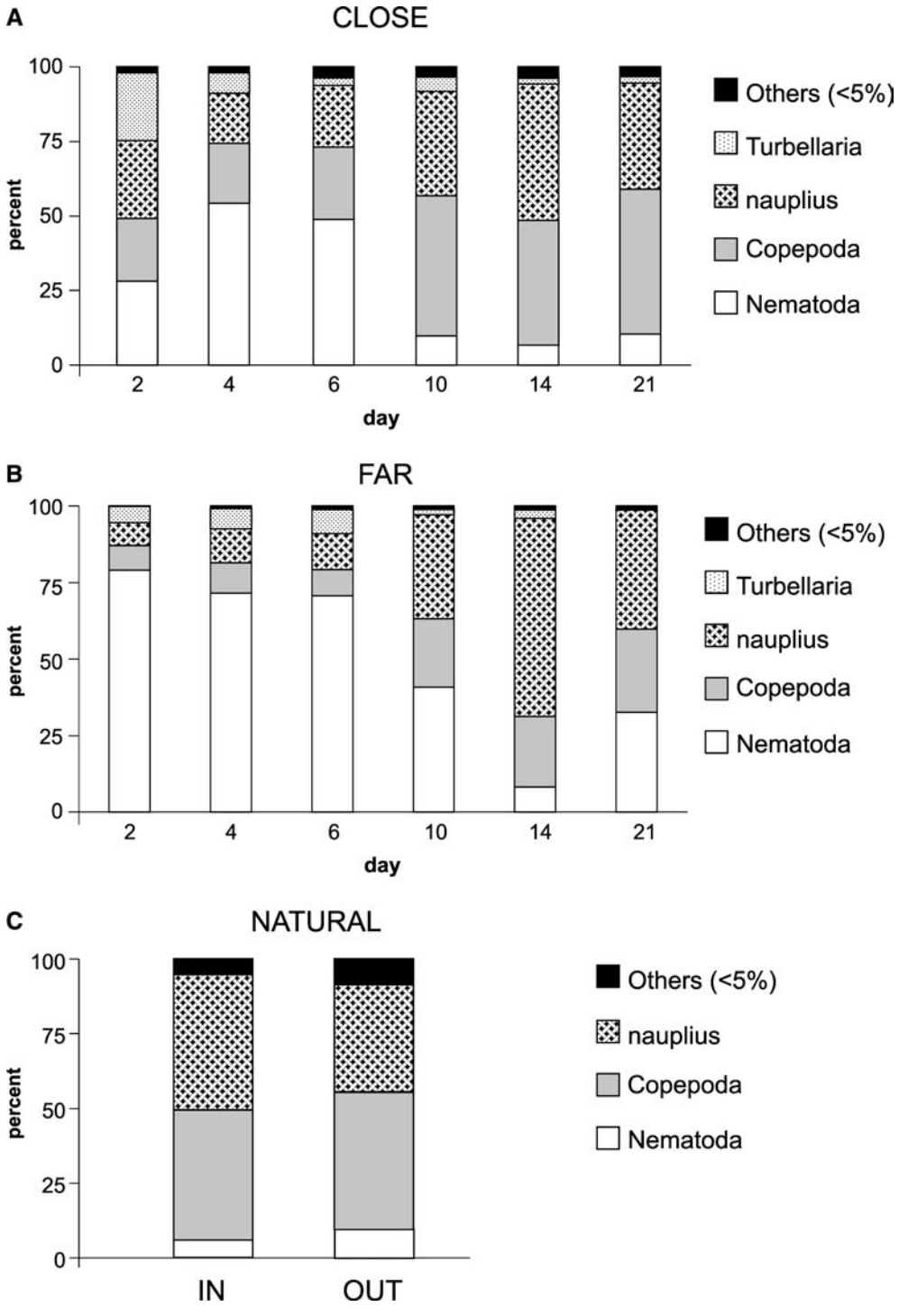


**Fig. 4** Relative abundance of dominant meiofauna groups at different days after planting of the **a** *close* and **b** *far* series; and **c** on the natural seagrass plants

Effect of leaf surface area on meiofauna and copepod colonization *(experiment c)*

Leaf surface area seemed to have a clear positive effect on meiofauna densities with higher densities on broader leaves (Fig. 7a). However, after standardisation to surface area unit (Fig. 7b) there was no significant difference between the three leaf surface areas used in the present study as meiofauna densities ranged between $464 \pm 125$ ind/100 cm$^2$ (large) and $551 \pm 34$ ind/100 cm$^2$ (small). These densities were very much comparable to the ones found on natural *Thalassia* plants (*in* series: $392 \pm 42$ ind/100 cm$^2$, *out* series: $423 \pm 103$ ind/100 cm$^2$).

Although no significant effect of leaf surface areas on meiofauna densities was detected (Fig. 7b), a change in meiofauna higher taxa composition was found (Fig. 8) on leaves of different width. Although the share of copepods ranged from 33% (small) to 49% (large), the

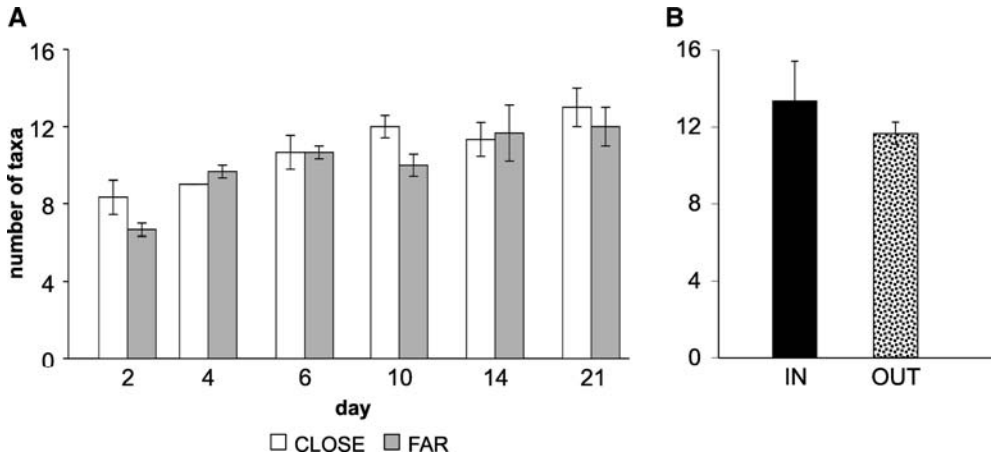


**Fig. 5** Number of meiofauna taxa (±standard error) on **a** seagrass mimics in the *close* and *far* series after 2, 4, 6, 10, 14 and 21 days and **b** natural seagrasses (inside-*in*—and at the border-*out*)

relative abundance of copepods was not significantly higher on broader leaves (one-way ANOVA, $p = 0.2$). There was no significant effect for their nauplii larvae either. Nematodes were affected inversely, as their relative importance on the broader leaves (15%) was only half of their share on the finer leaves (32%).

No significant effect of leaf surface area on copepod community composition was found (Fig. 9). However, typical epiphytic families such as Tegastidae and Dactylopusiidae were positively affected by a larger leaf surface areas as their share increased from 2.7% to 13.7% (Tegastidae) and from 14.7% to 22.7% (Dactylopusiidae) on small and larger leaves, respectively. On the other hand, interstitial families such as Ectinosomatidae accounted for half of the copepod community on finer leaves but decreased on broader leaves as epiphytic families took over. Other families such as Tisbidae, Canuellidae and Harpacticidae were not affected by leaf width. There were fewer cyclopoids on the broader leaves (2.3%) in comparison to the narrower leaves (7.3%), although not significantly different ($p = 0.2$).

## Discussion and conclusions

Mimics allowed us to follow colonization in a controlled way on a short-term basis and at the same time, we profit from the advantages of a field study such as natural environmental variability, 'openness' and realistic species combinations with shared evolutionary history (Srivastava et al. 2004). Moreover, the use of plant mimics eliminated many confounding effects of differences in leaf density, size, age or degree of epiphytism.

### Effect of time

Meiofauna colonization of seagrass mimics occurred very fast: at the first observation, i.e. day 2, meiofaunal densities of about 500 ind/100 $cm^2$ were counted. These initial meiofauna densities were even higher than in the natural situation (about 400 ind/100 $cm^2$). These artificial substrates seem to be suitable substrates for opportunistic meiofauna, mainly high numbers of nematodes (see also initial high densities in the *far* series). Ullberg and Ólafsson (2003) illustrated that marine nematodes can actively choose habitat. However, the level of variation in densities was much higher for meiofauna on seagrass mimics in comparison to the low-density variation on natural seagrasses.

As collection started at day 2, there is no information about the earliest stages after planting the mimics. However, the first colonization data (2 days) rank among the fastest ever reported for meiofauna. A fast colonization (after half a day) on seagrass mimics was also reported for macrofauna by Virnstein and Curran (1986). Recently, Mirto and Danovaro (2004) found comparable, but less dense total meiofauna densities (370 ± 41 ind/ brush) after 2 days. Given this rapid colonization time and meiofaunal sensitivity to changing environmental conditions, Mirto and Danovaro (2004) concluded that artificial substrates are a useful tool for monitoring studies. Especially in comparison with restoration of the seagrass plants itself (from $< 1$ year to centuries, see further), meiofaunal colonization occurs much faster. Meiofauna colonization experiments of azoic mangrove sediment by Zhou (2001) revealed hardly any meiofauna after one day; while after 10 days there was only 1/5 of the natural meiofauna densities and after 30 days the figure reached half of the natural controls. Fonseca et al. (1996) found that the development of cultivated *Halodule wrightii* patches and associated faunal communities (shrimp, fish and crab) took altogether 1.8 year to attain comparable densities, species composition and number of taxa equivalent to those found in natural seagrass beds. For macrofauna, Virnstein and Curran (1986) showed a rapid colonization on artificial seagrass clumps, with initial abundances of 67 ind/1000 $cm^2$ on the first day. Over the first 4 days, abundance and species richness increased linearly, both reaching a maximum value and levelled off in 4–8 days (Virnstein and Curran 1986).

Bell and Hicks (1991) reported recolonization levels of copepods on plant mimics after 3–5 days that were

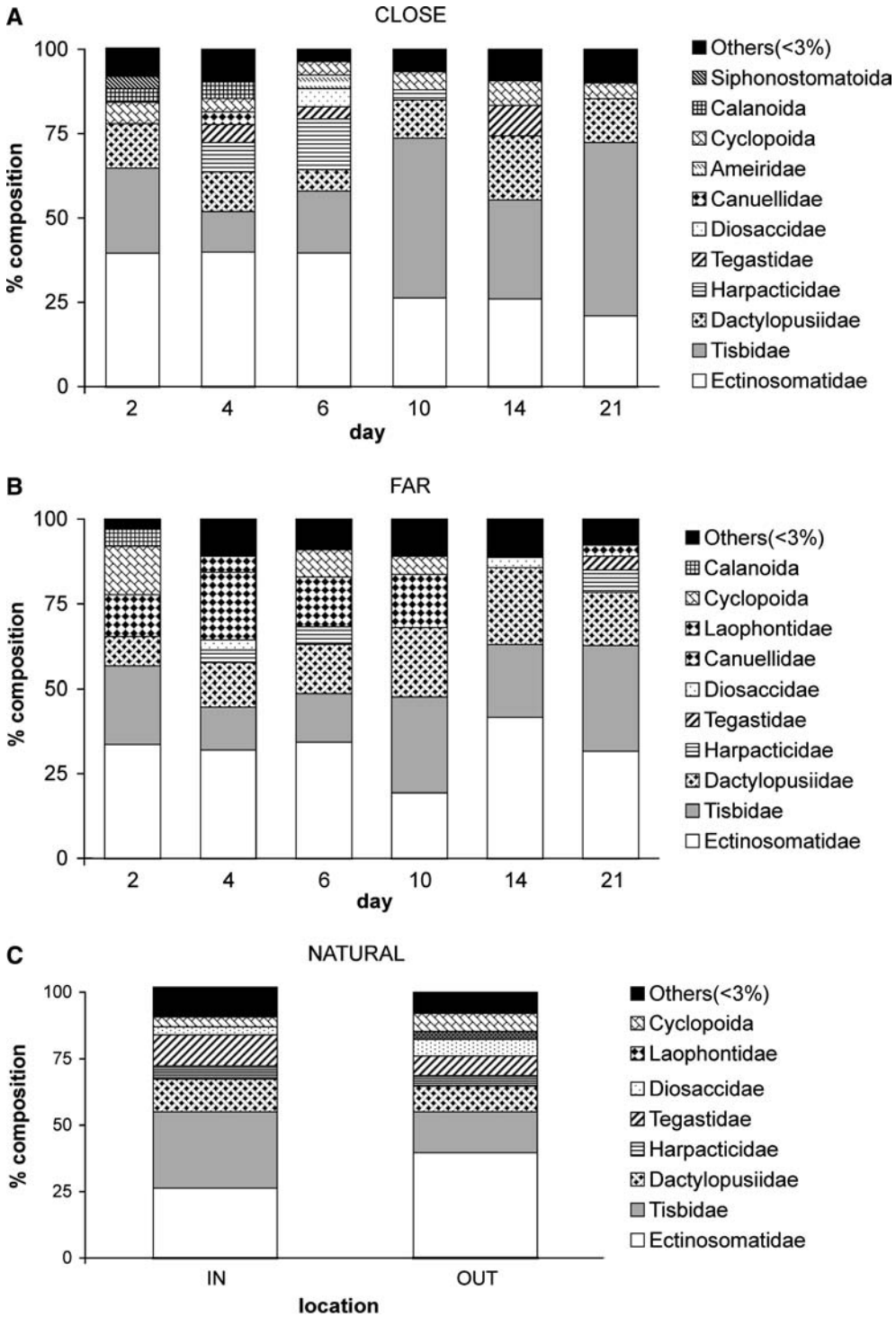


**Fig. 6** Relative abundance of dominant copepod families at different days after planting of the **a** *close* and **b** *far* series; and **c** on the natural seagrass plants

maintained for several weeks. Such a stable community was not found in the present study, the different sampling points in time were characterised by different meiofauna densities and composition. Our data support the proposition of Allison (2004) that although the recovery trajectory was similar in early successional stages, major differences emerged later.

A possible explanation for the increase in meiofauna densities (especially in the *close* series) may be that the leaf surface area (in this case the seagrass mimic) becomes progressively more attractive for meiofauna with time. Especially copepods and their nauplii showed a clear increase and even outcompeted nematodes, which were dominant initially. Hall and Bell (1988, 1993) found a significant positive association between the density of harpacticoid copepods and biomass of the dominant epiphyte. In general, abundance of epiphytes on mimics tends to continually increase during the col-

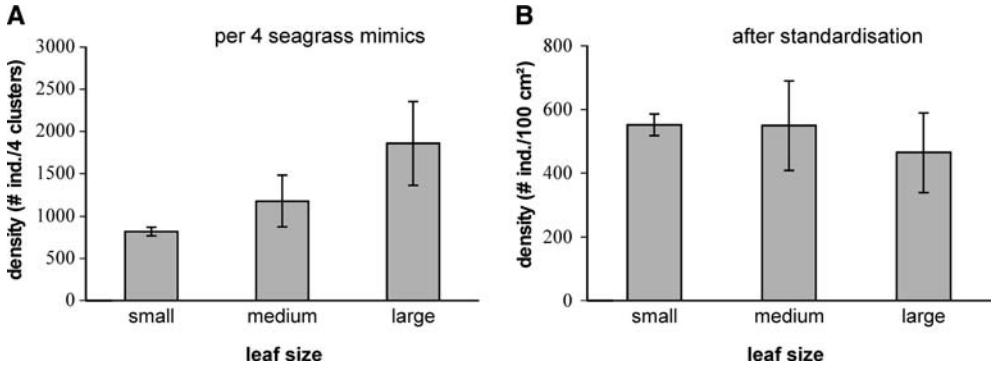


**Fig. 7** Average total meiofauna densities (±standard error) on small (0.8–0.9 cm wide), medium (1.3 cm wide) and large-sized (2.5 cm wide) mimic leaves: **a** actual densities per sample (i.e. 4 seagrass mimics) and **b** densities expressed per 100 $cm^2$ after standardisation

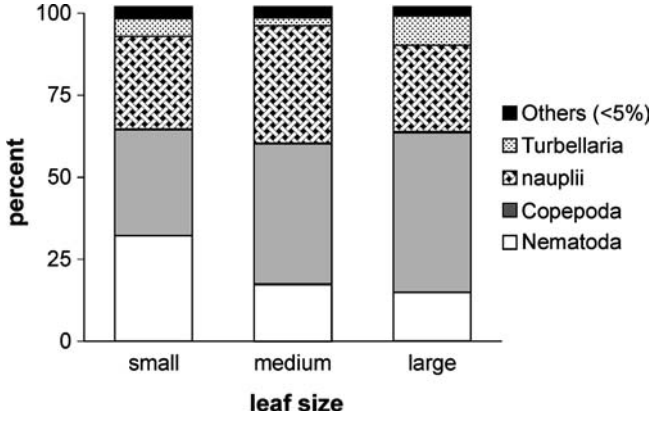


**Fig. 8** Relative meiofauna composition on small, medium and large-sized mimic leaves

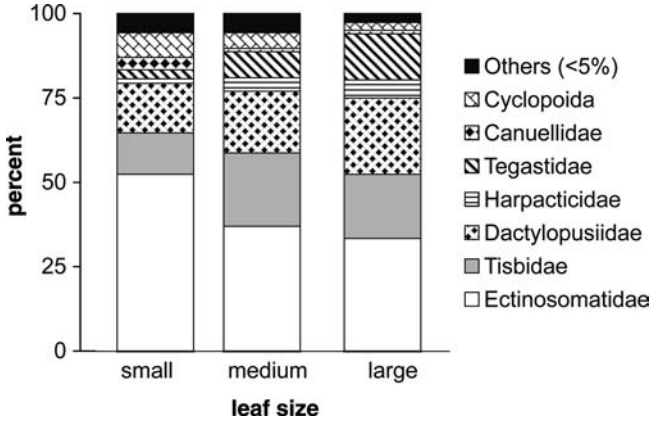


**Fig. 9** Relative abundance of dominant copepod families on small, medium and large-sized mimic leaves

onization process, resulting in an increase in habitat space and possible increase in refuge (e.g. Virnstein and Curran 1986, Hall and Bell 1993). Concurrent with the increasing complexity of epiphytic algae over time, we assume that the temporal increase in resource diversity in the form of a biofilm on the mimics is crucial in the colonization process. Novak (1984) studied the microbial colonization on leaves of a shoot of the Mediterranean seagrass *Posidonia oceanica* and found that diatom densities in general increased with time, while the highest bacterial density was observed at 7–10 weeks exposure. As main consumers of diatoms, an increase in copepod density, especially epiphytic families, was found as the seagrass mimics were longer in the field and could develop a more mature biofilm. Brown et al. (2003) found significant effects of the ages of leaf-surface biofilms on life-history parameters of freshwater copepods in streams. Longer conditioning of leaves led to greater hatching success but slower copepodid development (Brown et al. 2003). However, Gwyther and Fairweather (2005) followed meiofaunal recruitment on mimic mangrove pneumatophores and found that different aged biofilms had no consistent, different effect on the subsequent colonization of meiofauna. In addition, the epiphytic cover is not only determined by the length of time the substrate is available for colonization but also by changes in the structure of the substrate during this period. As the epiphyte cover increases throughout the colonization process, epiphytes may serve as substrates for further epiphytic settlement (Novak 1984). Gwyther and Fairweather (2005) came up with a comparable conclusion for mangrove pneumatophores as the divergence of phytal-based meiofauna assemblages depends upon the amount of coverage, as well as the type, of fouling macro-epibionts on the pneumatophores. Thistle et al. (1984) were the first to demonstrate, in the field, that an enhanced copepod abundance didn't result from the presence of the plant as a living entity. They found a two-fold increase of bacterial biomass in the sediment around both short shoots and mimics and especially harpacticoid copepods responded to this local increase of resources. Zhou (2001) found the same positive effect of decaying mangrove leaf litter on the nematode colonization of azoic sediments.

Concomitant with a larger share of copepods in the later colonization phases (i.e. from 10 days onwards), an increase in their nauplii was recorded. However, Kurdziel and Bell (1992) found that copepodites dominated after 2 days of colonization, while adults dominated on day 4. As meiobenthic copepods may use the watercolumn as an important habitat for their reproduction (Bell et al. 1988), the changing seagrass landscapes may affect these reproductive activities via modification of migration. As the proportion of nauplii reaches the same level

(about 40% of the total meiofauna) as in the natural situation, we assume that this sudden increase can be explained by local recruitment rather than by an enhanced reproduction.

As for densities and species composition, we found no major differences in terms of diversity between meiofauna on seagrass mimics and in the natural situation. In total 33 harpacticoid species were identified while a comparable study in Florida by Hall and Bell (1993) found only 16 species or species complexes. The latter found a dominance of *Harpacticus* sp. (family Harpacticidae) while in the present study representatives of the family Ectinosomatidae dominated. Munguia (2004) followed the successional patterns of marine organisms on pen shells and suggested that the degree of taxa/species saturation depends on the successional stage of a community. In the studied meiofauna community, this degree of species/taxa saturation was quite comparable in both cases (i.e. mimics and natural seagrasses), suggesting that no additional taxa/species will appear after more than 3 weeks of colonization. Moreover, the insurance hypothesis (Yachi and Loreau 1999) suggests that this saturated level of diversity may dampen perturbation dynamics within a community. Hence, this gives additional support for the use of seagrass mimics as a tool to study epiphytic meiofauna communities. In addition, this kind of short-term test will give information about the recovery capacities of the epiphytic meiofauna in a candidate restoration area.

## Effect of distance

Of course, the speed of recovery and strength of the newly established community strongly depends on which species were initially present in the area, so-called regeneration pool (Allison 2004). Both this initial community and the degree of disturbance will determine the resilience of a community (Allison 2004). Allison (2004) concluded that differences in the recovered community were attributable to the composition of the surrounding regeneration pool. Bell and Hicks (1991) found that while plant arrangement may influence recruitment of some copepod species, altering access to a source pool had a much greater effect on copepod densities on plant mimics. In the present study we hypothesized that potential sources of meiofaunal colonizers would be primarily the natural seagrass bed instead of the sediment, as typically epiphytic copepods avoid sediments (De Troch et al. 2003). For macrofauna, Virnstein and Curran (1986) prove that most of the colonizers originated from the surrounding seagrass bed and not from the adjacent sediment that was poor in macrofauna. Kurdziel and Bell (1992) reported for copepods that the adjacent *Thalassia testudinum* bed was the primary source of colonizers for experimental blades placed in bare substratum.

For meiofauna, seagrass mimics were initially colonized by nematodes, especially in the *far* series. These high numbers of nematodes partly explain the higher total meiofauna densities in the *far* series in comparison to the lower values in the *close* series. Concomitant with initial high nematode densities, there was more variability in meiofauna densities in the *far* series (except on day 6 and 10). We assume that the majority of these nematodes originate from the underlying sediment as they were the dominant taxon in additional sediment samples (unpublished data) and the nearest natural seagrass patch was about 5 m away. This idea of initial colonizers of mainly benthic origin was supported by the high numbers of representatives of the harpacticoid family Ectinosomatidae, typically known as epi- and endobenthic copepods. Hicks and Coull (1983) suggested already in their review that our traditional concept of benthic copepods as bound to the sediments must be re-assessed. In addition, members of the Ectinosomatidae occur in most marine habitats (sand, mud, phytal), they appear to be 'jacks-of-all-habitats' and may be strong colonizers, so-called r-strategists. Kurdziel and Bell (1992) found at least two *Ectinosoma* species in their emergence traps in a subtidal *Thalassia* bed. A classification of colonizers and persisters is available for nematodes (e.g. Bongers 1990) but doesn't exist for harpacticoids. However, we are rather sceptical towards such a radical classification as many other factors may interact and species-specific colonization speed may be expected. Bell et al. (1987) were the first to indicate that morphological characteristics of harpacticoid copepods may reflect their habitat utilization. Recently, Thistle and Sedlacek (2004) made an attempt to separate emergent from non-emergent harpacticoids based on the morphology and setation of swimming legs. They found that emergers and non-emergers didn't group taxonomically. Three representatives of Ectinosomatidae were classified as emergers since they had 3 instead of 2 endopodal segments of the second pereiopod and had more terminal setae on exopods as major characteristics of good swimmers.

In a later colonization phase (from day 10 onwards), the *far* series was mainly colonized by copepods and nauplii as a main contribution to the high total meiofauna densities in the *far* series. For meiofauna of areas which are hydrodynamically benign and dominated by active swimmers, which is the case in seagrass beds, water-column recruitment should involve substrate choice through active movement (Palmer 1988; Ullberg and Ólafsson 2003). In all habitats, structural aspects probably act to enhance active emergence to some extent while disturbance may also lead to increased suspension and possibly active emergence (Palmer 1988). In case of active mechanisms, copepods typically dominate (Palmer 1988), and Hicks (1986) found that a substantial proportion of the *Zostera* bed associated copepod fauna actively swim into the water column during high tide. Kurdziel and Bell (1992) concluded that active emergence of phytal-dwelling meiobenthic copepods from blade surfaces contributed to their dispersal towards newly created patches of vegetation. In the present field

experiment conducted in a site with negligible tidal range, copepods are actively attracted to the new leaf surface area and associated newly established biofilm. As both series (*close* and *far*) were situated at same short distance from the beach, one would expect only water movement because of tides, waves or wind-driven currents, but even those are minimal in the area, suggesting an active movement of copepods towards the new substrate.

## Effect of leaf surface area to colonize

Although standardised meiofauna densities were not significantly different on leaves with different width, a larger leaf surface area clearly favoured colonization by copepods. This outcome is in contrast to the results of Hicks (1986) who found no evidence of a direct relation linking copepod abundance and species richness to blade surface area. Hicks (1986) suggested that it is not the surface area per se that affects density and diversity of the copepod communities and that, subsequently, a better measure for plant abundance is needed. It is not surprising that copepods are affected by this surface area as several authors reported their dominance versus nematodes in epiphytic communities while they are of second importance in benthic assemblages (see Hicks and Coull 1983 for review).

Moreover, broader leaves were preferred by typically epiphytic copepods. e.g. representatives of the family Tegastidae which are laterally compressed like amphipods (Noodt 1971). Parker et al. (2001) also found a positive effect of total plant surface area on epifaunal abundance and biomass but not on diversity and evenness of epifauna. However, in their case, total plant surface area closely related to plant species and its structural diversity (i.e. branched versus unbranched). In the present study, the structural diversity of the plants remained constant except for the blade width. Therefore, it is most likely that the increase in copepod density and diversity is rather linked to the larger amount of detritus that was observed when collecting the broader leaves (personal observation) and not to surface area per se. Of course, the retention of detritus is directly linked to leaf surface area as broader leaves will capture more detritus and slow down water movements. Meyer and Bell (1989) showed that the amount of detritus had a highly significant effect on the abundance of the copepod *Metis holothuriae* as this species spent significantly more time feeding on detritus-laden leaves than on detritus-free leaves. Conversely, copepods spent more time swimming when present with detritus-free blades than when detritus was present. However, only detritus has a positive effect as Bell and Hicks (1991) showed that the covering of leaves with sediment (without detritus) significantly reduced recruitment. Novak (1984) reported significantly more macro-epiphytic growth on the outer leaf sides versus inner sides and microbial densities were significantly higher on the inner leaf sides, both on the leaf surface and the epiphyte surface. If this segregation of macro-epiphytes on the outer and microbes on the inner leaf sides is applied to broader leaves, one might expect both more macro-epiphytic and microbial growth.

In addition, the broader leaves move more slowly in the water column than narrow leaves and as such promote epiphytic growth on the inner leaves. The broader seagrass mimics (2.5 cm wide) used in the present study were even wider than average natural *Thalassia* leaves ($1.2 \pm 0.2$ cm wide; Van Tussenbroeck, personal communication). These findings suggest that the broader the natural seagrass leaves are, the more copepods they will harbour i.e. the carrying capacity of seagrass leaves in terms of epiphytic copepods largely depends on total leaf surface area and associated epigrowth.

## Implications for restoration

The full restoration of a seagrass communities, including epiphytic fauna and flora, always starts with the recovery of seagrass plants. Simulation techniques estimated recovery time of seagrasses to range from $< 1$ year to centuries depending on the species (Cunha et al. 2004). Moreover, *T. testudinum* is known as a slow-growing climax species with an average expansion rate of 0.5 m year$^{-1}$ (Kenworthy unpublished data in Calumpong and Fonseca 2001). Hence, many attempts have been made to meet these losses by artificially transplanting shoots and spreading seeds from intact meadows to non-vegetated sediment (e.g. Fonseca et al. 1996; Whitfield et al. 2004). As survival rates of transplants are rather low and collection of material from existing meadows may affect the donor meadows negatively, seagrass mimics were used as artificial units in the present study. However, we are aware that planting seagrass mimics in relatively low densities in comparison to the natural situation (approximately 1,000 leaf shoots per square meter; Van Tussenbroek, personal communication) is a weak point of our experimental set-up. In this sense, the starting point of our experiments correspond to the recovery of meiofauna after total disappearance of seagrasses and recovery of the plants in initially low densities. Bell and Hicks (1991) showed that plant arrangement may influence recruitment of some copepod species, but altering access to a source pool (i.e. natural seagrass bed or sediment) had a much greater effect on copepod densities on seagrass mimics. On the other hand, Bell et al. (2001) concluded that patch size alone does not appear to fundamentally influence variation in faunal abundance. Furthermore, the same authors suggested that restoration efforts should focus upon locating areas with similarity of landscape context or patch characteristics other than patch size.

Although the present study has some restrictions as the colonization experiment was limited to six points in time, over a single 3 week period, during one season, at only one distance from the natural seagrass patch, the results give some indications on the restoration of sea-

grass associated meiofauna. We found a quick colonization of meiofauna on the seagrass mimics, and so present a potentially useful biomonitoring tool. However, these mimics showed often higher meiofauna densities than on the natural seagrasses, especially in the far series and as such we may question the representativeness of the mimic community for the natural one. Rapid colonization by high numbers of nematodes could explain this phenomenon partially. On the other hand, lower numbers of meiofauna on living plants may suggest the possibility of anti-fouling substances produced by the plant as was also suggested to explain very sparse numbers of meiofauna on living mangrove pneumatophores (Gwyther and Fairweather, 2005).

In addition, we found a higher variance of meiofauna densities on the seagrass mimics in comparison to the natural situation. This is in conflict with the recent results of Gwyther and Fairweather (2005) who found less intrinsic patchiness in meiofaunal assemblages on artificial substrates than mature assemblages on natural pneumatophores. The duration of the experiment may explain this difference as the latter study run for 20 weeks while we allowed a maximum colonization period of only 3 weeks.

Several recent studies (e.g. Mirto and Danovaro 2004; Gwyther and Fairweather 2005) have put forward that artificial substrates are potential useful tools for monitoring studies. Our results suggest that seagrass mimics are suitable as an objective tool to follow restoration processes of meiofauna in the overall restoration of a seagrass ecosystem. However, one should take into consideration the mentioned limitations related to time and maximal growth of biofilm on mimics.

In conclusion, meiofaunal organisms seem to be very quick in colonizing new phytal habitats. In view of this fast colonization, we could not demonstrate any direct impact of disturbance on meiofauna as was suggested for macrofauna and fish (Bell et al. 2001). However, there are several aspects of disturbance and recovery involved that act at different time scales. The full restoration of a seagrass bed includes initially the growth of the plants (months–years) concurrent with a quick colonization of epiphytes and meiofauna (days). The colonization of meiofauna largely depends on the local regeneration pool, but in general we found that the primary source of colonizers originates from the sediment (both nematodes and benthic opportunistic copepods), followed by epiphytic copepods and their nauplii.

**Acknowledgements** The authors thank the director and the staff of El Colegio de la Frontera Sur (ECOSUR, Chetumal) for their logistic support. Special collecting permit was granted by the director of Sian Ka'an Biosphere Reserve, Dr. Alfredo Arellano. Dr. Brigitta Van Tussenbroek (Unidad Académica Puerto Morelos) kindly provided data on leaf sizes of *T. testudinum* from the sampling site. A special word of thanks for Guy De Smet for his efficient assistance in the field. The authors thank Dr. Tom Moens for his constructive criticism on the manuscript. The referee comments of Prof. Dr. S.S. Bell and Dr. R. Virnstein were very valuable and highly appreciated. The first author acknowledges a postdoctoral fellowship provided by the Fund for Scientific Research (FWO-Flanders, Belgium). The third author receives an aspirant grant from the same Fund. The FWO-Flanders provided additional support for a study stay in Mexico of the first author to conduct these field experiments. Further financial support was received from Ghent University (Belgium) (contract BOF 98-03, 12050398) and FWO research program 3 G.0199.03.

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