



HAL
open science

DO MACROFAUNA STRUCTURE MEIOFAUNA ASSEMBLAGES IN MARINE SOFT-BOTTOMS? A REVIEW OF EXPERIMENTAL STUDIES

Emil Ólafsson

► **To cite this version:**

Emil Ólafsson. DO MACROFAUNA STRUCTURE MEIOFAUNA ASSEMBLAGES IN MARINE SOFT-BOTTOMS? A REVIEW OF EXPERIMENTAL STUDIES. *Vie et Milieu / Life & Environment*, 2003, pp.249-265. hal-03205296

HAL Id: hal-03205296

<https://hal.sorbonne-universite.fr/hal-03205296v1>

Submitted on 22 Apr 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

DO MACROFAUNA STRUCTURE MEIOFAUNA ASSEMBLAGES IN MARINE SOFT-BOTTOMS?

A REVIEW OF EXPERIMENTAL STUDIES

Emil ÓLAFSSON

*Department of Zoology, University of Stockholm, 106 91 Stockholm, Sweden
emil.olafsson@zoologi.su.se*

MEIOFAUNA
MACROFAUNA
EXPERIMENTS
BIOTURBATION
DISTURBANCE
PREDATION

ABSTRACT. – During the past three decades a considerable number of studies have been conducted to reveal effects of macrofauna on meiofaunal assemblages in marine soft-bottoms. The aim of this review is to compile and summarize major findings of studies that have experimentally tested if a given macrofauna species affects some aspect of a meiobenthic assemblage. Altogether 77 studies on 44 macrofaunal species are reviewed. The bulk of the macrofaunal species are conspicuous members of the phyla Crustacea, Annelida and Mollusca, namely 20, 9 and 8 species respectively. Almost all the studies (86%) investigating biogenic structures of macrobenthos indicate some sort of effects on meiofaunal assemblages. Those studies in which diversity of a particular animal group has been considered, almost all agree on enhanced species diversity as a result of biogenic structures. The results of studies that have considered overall effects of macrofauna originating from processes such as predation, physical disturbance, competition for food and biogenic structures also indicate effects on meiobenthos. In only a few studies, researchers have used 3 or more density levels of disturbing macrofauna in their experimental manipulations, including natural levels, for the understanding of ecological rules behind biological disturbances. As biological disturbance created by macrofauna is incredibly variable among species and difficult to rate or categorise, it seems as yet difficult to apply theories to macrofaunal disturbance in general, predicting diversity or abundance patterns in meiofaunal assemblages.

MÉIOFAUNE
MACROFAUNE
EXPÉRIENCES
BIOTURBATION
PERTURBATIONS
PRÉDATION

RÉSUMÉ. – Durant les trois dernières décennies, un nombre considérable d'études ont été réalisées en vue de montrer les effets de la macrofaune sur les peuplements de la méiofaune des fonds meubles marins. Cette revue a pour objet de compiler et de résumer les résultats majeurs des travaux qui ont testé expérimentalement si une espèce donnée de la macrofaune a un impact sur un peuplement méiofaunique. 77 études portant sur 44 espèces de la macrofaune sont passées en revue. La plupart des espèces de la macrofaune appartiennent aux embranchements des Crustacés, des Annélides et des Mollusques, soit 20, 9 et 8 espèces respectivement. Presque toutes les études (68 %) à propos des structures biogènes du macrobenthos montrent un certain impact sur la méiofaune. Parmi les études où la diversité d'un groupe animal particulier a été considérée, presque toutes indiquent une augmentation de la diversité spécifique résultant des structures biogènes. Les résultats des travaux prenant en compte l'effet global de la macrofaune dû à des processus tels que la prédation, les perturbations physiques, la compétition pour la nourriture et les structures biogènes, montrent aussi des effets sur le méiobenthos. Seuls quelques auteurs ont considéré 3 niveaux de densité ou plus de la macrofaune responsable de perturbations dans leurs expérimentations, en incluant les niveaux de densité naturels, en vue de comprendre les règles écologiques des perturbations biologiques. La perturbation biologique générée par la macrofaune extrêmement variable selon les espèces, est difficile à évaluer ou à hiérarchiser. Il semble difficile d'appliquer des théories à la bioturbation due à la macrofaune en général, pour prévoir les patrons de diversité ou d'abondance des peuplements de la méiofaune.

INTRODUCTION

Large organisms are known to affect the assemblage structure of smaller ones in terrestrial and aquatic environments. Darwin (1859) found that mowing of a lawn could sustain higher plant species diversity than occurs in its absence, as competitively superior species are kept away from overshadowing the less vigorous plants. A similar kind of control was found to be exerted by grazers. Even though many of them avoid certain plants and prefer others, the net effect may be the same i.e. Tansley & Adamson (1925) found that species diversity became quickly reduced in plots where rabbits were excluded from grassland. Large predators often prey on a variety of smaller animals and may not only reduce their abundances but also change the dynamics of whole ecosystems. The classic work of Paine (1966) exemplifies this well. By removing a large top carnivore, the starfish *Pisaster ochraceus*, from an intertidal rocky shore, he found that the prey species returned successively, replacing each other and finally overcrowding the rocks until eventually, all but one algal species disappeared.

Large animals may also exert biological disturbance on smaller sympatric species through physical force, creation of microhabitats and by depleting food resources. This is often the case in marine soft-bottom habitats. Here, animals have traditionally been divided into macro-, meio- and microfauna. These animals are intimately associated with each other and are distinguished mainly by size, macrofauna being largest (typically few mm to several cm), meiofauna intermediate in size (typically 0.4 mm to 1 mm) and microfauna smallest, being unicellular animals (typically less than 0.4 mm). Even though this classification is artificial it has proven very practical, mainly because the groups tend to be taxon specific, i.e. almost all nematodes in soft-bottoms are of meiobenthic size. It has also been shown that meio- and macrofauna have often different life history characteristics e.g. meiofauna species have direct benthic development while most macrofauna species have pelagic larvae and meiofauna have normally much shorter generation times than macrofauna (Warwick 1984).

Macrobenthic invertebrates in soft-bottoms are highly diverse in taxonomy, morphology, functionality, mobility and life history characteristics. They are therefore a source of extremely variable disturbance to meiofauna. Additionally, one single macrofaunal species may also exert an array of effects on meiobenthos. On the other hand there are several species that display strong similarity in life styles and therefore may affect their small inmates in equivalent or similar ways. During the past three decades a considerable number of studies have been conducted to reveal effects of macrofauna on

meiofaunal assemblages in marine soft-bottoms. The aim of this review is to compile and summarize major findings of studies that have experimentally tested if a given macrofauna species affects some aspect of a meiobenthic assemblage. Several of these studies, especially the older ones, have flaws in their design, but they are included as they may be indicative of certain patterns. I have also included surveys that have explicitly tested if a certain macrofaunal animal affects the distribution of meiofauna, even though no manipulation has been performed. Conversely, I have chosen to exclude studies where combined effects of several and often unknown macrofaunal species have been investigated by using exclusion cages (see Ólafsson & Moore 1990, 1992, Schrijvers *et al.* 1995). I have also excluded studies on fish and bird species that may prey on or disturb meiobenthic soft-bottom assemblages, as these organisms are normally not tightly associated with meiofauna and normally show strong disparity from macrobenthic life history traits.

CASE STUDIES

This review is based on scrutinizing databases published by ASFA (Aquatic Sciences and Fisheries Abstracts) and ISI Web of Science (Science Citation Index Expanded™) from 1960 and 1985, respectively, to date, using the keywords meiofauna or meiobenthos. From about 3000 hits 77 studies of 43 macrofaunal species are summarized using the criteria listed above. Most of the studies consider species of the phyla Crustacea (20), Annelida (9) and Mollusca (8). Six other species belonging to the phyla Coelenterata (1), Brachiopoda (1), Echinodermata (2), Hemichordata (1) and Pripulida (1) have also been used in assessing effects of macrofaunal animals on meiobenthos. The studies have been summarized according to habitat, experimental procedure, mechanism studied i.e. *biogenic structure* where researchers have compared meiofauna associated with various structures such as faecal casts, burrows, etc with control sediments without these formations and *overall effects* when researchers have either been interested in certain factors such as predation but unable to distinguish from other modifying effects or they have been simply interested in overall effects of the macrofauna species in question, the taxonomic level studied, and the effects on density and diversity (Table I).

Crustacea

Approximately half of the macrofaunal species studied belong to the phylum Crustacea. In general these species are more mobile than species belong-

Table I. – Impact of macrofaunal species on meiofauna in soft sediments (int: intertidal, sub: subtidal, sa: sand, mu: mud, Exp: experiment, F: field, L: laboratory, ex: exclusion, en: enclosure, MT: major taxa, TM: total meiofauna, Nem: Nematoda, Harp: Harpacticoida, Turb: Turbellaria, Gnat: Gnathostomulida, (S): species level, (G) genus level, +: positive effect, – : negative effect, 0: no effect).

Group	Species	Habitat	Research approach	Mechanism studied	Meiofaunal taxa studied	Effects on density	Effects on density	Reference
Crustacea								
Ocypodid crabs								
	<i>Uca pugnax</i>	int, sa	Sur	Effects of burrows	MT	+ Nem, - Cop		Bell et al. 1978
	<i>Uca spp.</i>	int,	Sur/Exp (F)	Effects of burrows	MT	+tot		DePatra & Levin 1989
	<i>Uca spp.</i>	int, sa	Sur	Effects of burrows	MT	+Nem, 0Cop		Dittmann 1996
	<i>Scopimera inflata</i>	int, sa	Sur	Effects of burrows	MT	0Nem, 0Cop		Dittmann 1996
	<i>Uca polita</i>	int, mu	Exp (F, ex)	Overall effects	TM	-TM		Dye & Lasiak 1986
	<i>Uca vocans</i>	int, mu	Exp (F, ex)	Overall effects	TM	-TM		Dye & Lasiak 1986
	<i>Uca pugnax</i>	int, sa/mu	Exp (F, ex)	Overall effects	MT	-Nem, -Cop		Hoffman et al. 1984
	<i>Uca annulipes</i>	int, sa	Exp (L, en)	Overall effects	MT, Nem (G)	0Nem, -Cop	0Nem	Ólafsson & Ndaró 1997
	<i>Dotilla fenestrata</i>	int, sa	Exp (L, en)	Overall effects	MT, Nem (G)	0Nem, 0Cop	0Nem	Ólafsson & Ndaró 1997
	<i>Mictyris longicarpus</i>	int, sa	Sur	Overall effects	MT, Nem (S)	0Nem	-Nem	Warwick et al. 1990
	<i>Mictyris longicarpus</i>	int, sa	Exp (F, ex)	Overall effects	MT, Turb (S)	-Nem,-Cop,-turb	0turb	Dittmann 1993
	<i>Chasmagnathus granulata</i>	int, mu	Sur	Effects of burrows	MT	+/-Nem		Botto & Iribane 1999
	<i>Chasmagnathus granulata</i>	int, mu	Exp (F, en)	Overall effects	MT	-Nem, 0Cop		Botto & Iribane 1999
	<i>Cyrtograpsus angulatus</i>	int, mu	Exp (F, en)	Overall effects	MT	0Nem, 0Cop		Botto & Iribane 1999
Portunidae								
	<i>Carcinus maenas</i>	int, mu	Exp (F, en)	Predation	MT	-MT		Scherer & Reise 1981
	<i>Carcinus maenas</i>	int, mu	Exp (F, en)	Predation	MT	0MT		Gee et al. 1985
	<i>Carcinus maenas</i>	int, sa	Su	Predation	MT, Harp(S)	0MT		Gee 1987
	<i>Carcinus maenas</i>	int, mu/sa	Exp (L, en)	Predation/disturbance	Nem (S)	-Nem	0	Schratzberger & Warwick 1999a
	<i>Carcinus maenas</i>	int, mu/sa	Exp(L, en)	Predation/disturbance	Nem (S)	see text	0	Schratzberger & Warwick 1999b
Shrimps								
	<i>Palaemonetes pugio</i>	int, mu/sa	Exp(L, en)	Predation/disturbance	MT, Nem (S)	-MT	0	Bell & Coull, 1978
	<i>Palaemonetes pugio</i>	int, mu/sa	Exp(L, en)	Predation	MT	0Mt		Smith & Coull 1987
	<i>Palaemonetes pugio</i>	int	Exp(L,en)	Predation	MT	0MT		Bell 1980
	<i>Palaemonetes varians</i>	int	Exp(F,en)	Overall	MT	+MT		Escarvage & Castell 1990
	<i>Crangon crangon</i>	int, sa	Su	Predation	MT, Harp(S)	0MT		Gee 1987
	<i>Crangon crangon</i>	sub	Exp(L,en)	Overall effects	MT	-Harp, 0Nem		Hedqvist-Johnson & André, 1991
	<i>Crangon crangon</i>	sub,sa	Exp(L,en)	Predation	MT	-Harp, 0Nem		Nilsson et al. 1993
	<i>Callianassa australiensis</i>	int,sa	Exp(F,ex)	Overall effects	MT, Tur(S)	-Harp, -Nem		Dittmann 1996
				Burrows	MT, Tur(S)	0Harp, +Nem		Dittmann 1996
	<i>Callianassa trilobata</i>	int, sa	Sur	Burrows	MT	-MT		Dobbs & Guckert, 1988
	<i>Callianassa kraussi</i>	int, sa	Exp(F,en)	Overall	MT	-MT		Branch & Pringle 1987
Amphipoda								
	<i>Monoporeia affinis</i>	sub, mu	Exp(L, en)	Overall effects	MT	-Nem, +Cop		Sundelin & Elmgren 1991
	<i>Monoporeia affinis</i>	sub, mu	Exp(L, en)	Overall effects	Nem(S),Harp(S),	-Nem,-ost, +Cop	0Nem	Ólafsson & Elmgren 1991
	<i>Monoporeia affinis</i>	sub, mu	Exp(L, en)	Distribution/migration	MT, Nem (S)	0Nem, 0 Cop	0Nem	Ullberg & Ólafsson 2003
Isopoda								
	<i>Saduria entomon</i>	sub,sa	Exp(L, en)	Colonization	MT	0MT		Aarnio et al. 1991

Table I. – (continued)

Group	Species	Habitat	Research approach	Mechanism studied	Meiofaunal taxa studied	Effects on density	Effects on density	Reference
Mollusca								
Bivalvia								
	<i>Atrina zelandica</i>	su, mu/sa	sur	Overall effects	Nem (S)	-nem	-nem	Warwick et al. 1997
	<i>Atrina zelandica</i>	su, mu/sa	Exp (F,en)	Overall effects	MT, Nem (g)	0MT, 0Nem	0Nem	Austen & Thrush 2001
	<i>Abra alba</i>	su, mu	Exp (L, en)	Overall effects	Nem (S)	0Nem	+ Nem	Austen et al. 1998
	<i>Nuculoma tenuis</i>	su, mu	Exp (L, en)	Overall effects	Nem (S)	- Nem	+ Nem	Austen et al. 1998
	<i>Cerastoderma edule</i>	int, sa	Exp (F,en)	Overall effects	Tur (S)	0Tur	0Tur	Reise 1983
	<i>Cerastoderma edule</i>	int, sa	Exp (F,en)	Overall effects	MT	~0		Kennedy 1993
	<i>Macoma balthica</i>	int, sa	Sur	Biogenic structure	MT	+Nem, + Tur		Reise 1981a
	<i>Macoma balthica</i>	int, sa	Exp (F,en)	Overall effects	Tur (S)	+ Tur	- Tur	Reise 1983
	<i>Macoma balthica</i>	su, mu	Exp (L,en)	Overall effects	MT, Nem (S)	0Nem, -Harp	0Nem	Ólafsson et al. 1993
	<i>Macoma balthica</i>	su, mu	Exp (L)	Dead tissue	MT, Nem (S)	0Nem, -Harp	+ Nem	Ólafsson 1992
	<i>Scrobicularia plana</i>	int, mu	Exp (F,en)	Overall effects	MT	~0		Kennedy 1993
Gastropoda								
	<i>Ilyanassa obsoleta</i>	int, mu	Exp (F, ex)	Overall effects	Nem (g)	-Nem	-Nem	Nichols & Robertson 1979
	<i>Terebralia palustris</i>	int, mu	Exp (F, en)	Overall effects	MT	-Nem, -Pol		Carlén & Ólafsson 2002
Polychaeta								
	<i>Arenicola marina</i>	int, sa	Sur	Biogenic structure	MT, Tur(S), Gna (S)	+Nem, +Harp, +Turb	+Turb	Reise & Ax 1979
	<i>Arenicola marina</i>	int, sa	Sur	Biogenic structure	MT	+Nem, +Harp, +Turb		Reise 1981a
	<i>Arenicola marina</i>	int, sa	Sur	Biogenic structure	Gnat (S)	+Gnat	+Gnat	Reise 1981 b
	<i>Arenicola marina</i>	int, sa	Sur	Biogenic structure	Tur (S)	+Tur	+Tur	Reise 1984
	<i>Arenicola marina</i>	int, sa	Sur	Biogenic structure	Tur (S)	+Tur		Reise 1987
	<i>Arenicola marina</i>	int, sa	Sur	Biogenic structure	Tur (S)	+ Tur		Noldt & Reise, 1987
	<i>Arenicola marina</i>	int, sa	Exp (F)	Overall	MT, Tur (S)	+Tur, +Nem	0Tur	Reise 1983 MarBiol
	<i>Streblosoma bairdi</i>	su, mu	Exp (L)	Biogenic structure	MT, Nem (S)	+Nem, +Harp	+/- Nem, Harp	Warwick et al. 1986
	<i>Tharyx luticastellus</i>	su, mu	Sur	Biogenic structure	Harp (S)	0Harp		Thistle & Eckman 1990
	<i>Tharyx luticastellus</i>	su, mu	Sur	Biogenic structure	Harp (S)	+Harp		Eckman & Thistle 1991
	<i>Melinna palmata</i>	su, mu	Sur	Biogenic structure	Nem (S), Harp (S)	0Nem, -Harp	0Nem	Ólafsson et al. 1990
	<i>Nereis diversicolor</i>	int, sa	Exp (F, en)	Overall	MT	-Nem, 0Harp		Reise 1979
	<i>Nereis diversicolor</i>	int, sa	Sur	Biogenic structure	MT	+Nem, +Harp, +Turb		Reise 1981a
	<i>Nereis diversicolor</i>	int, mu	Exp (F, en)	Overall	MT	~0		Kennedy 1993
	<i>Nereis virens</i>	int, sa	Exp (L, en)	Predation/disturbance	MT, Nem (S)	- Nem, -Harp	-Nem	Tita et al. 2000
	<i>Nereis virens</i>	int, sa	Sur	Biogenic structure	MT	+Nem, +Harp, +Turb		Reise 1981a
	<i>Nereis virens</i>	int, sa	Sur	Biogenic structure	Gnat (S)	+Gnat	+Gnat	Reise 1981 b
	<i>Ophelia bicornis</i>	int, mu	Exp (F, en)	Overall	MT	~0		Kennedy 1993
	<i>Pectinaria koreni</i>	int, sa	Sur	Biogenic structure	MT	+Nem		Reise 1981a
	<i>Pygospio elegans</i>	int, sa	Sur	Biogenic structure	MT	+Nem		Reise 1981a
Anthozoa								
	<i>Renilla reniformis</i>	int, sa	Sur/Exp(F)	BS, overall	MT	-Harp		Creed & Coull 1984
Brachiopoda								
	<i>Lingula anatina</i>	int, sa	Sur	Biogenic structure	MT, Tur (S)	+/- MT		Dittmann 1996
Echinodermata								
	<i>Brissopsis lyrifera</i>	sub, mu	Exp (L, en)	Overall	Nem (S)	0Nem	0Nem	Austen & Widdicombe 1998
	<i>Brissopsis lyrifera</i>	sub, mu	Exp (L, en)	Overall	Nem (S)	0Nem	0Nem	Austen et al. 1998
	<i>Mellita quinquesperforata</i>	sub, sa	Sur/Exp(F)	Overall	MT, Harp (S)	+Nem, 0Harp		Reidenauer 1989
	<i>Mellita quinquesperforata</i>	int, sa	Sur	Overall	MT	-Nem, -Harp		Creed & Coull 1984
	<i>Mellita quinquesperforata</i>	int, sa	Sur/Exp	Overall	MT	0MT		Findlay & White 1983

Table I. – (continued)

Group	Species	Habitat	Research approach	Mechanism studied	Meiofaunal taxa studied	Effects on density	Effects on density	Reference
Hemichordata								
	<i>Ptychodera bahamensis</i> sub, sa	Sur		Biogenic structure	Harp (S)	-Harp		Thistle 1980
	<i>Ptychodera bahamensis</i> sub, sa	Exp (F)		Biogenic structure	Harp (S)	-Harp		Varon & Thistle 1988
	<i>Ptychodera bahamensis</i> sub, sa	Sur		Biogenic structure	MT	0Mt		Dobbs & Guckert 1988
Priapulida								
	<i>Halicryptus spinulosus</i> sub, sa	Sur/Exp (F,L, en)		Overall	MT	-Nem		Aarnio et al. 1998

ing to the other phyla, are often epibenthic, browsing on the sediment surface and sometimes swimming in the water-column. They are also more conspicuous than inbenthic fauna and perhaps therefore studies on these species are over represented.

Ocypodid crabs

Macrofaunal assemblages in tropical or semi-tropical intertidal habitats differ considerably from those in temperate intertidal habitats (generally dominated by polychaetes and bivalves), by having a prominent, diverse and abundant crustacean fauna. Burrowing decapod crustaceans are often the dominant feature of the macrobenthic assemblage in these areas where conspicuous ocypodid crabs are efficient sediment bioturbators (e.g. Hartnoll 1973, Katz 1980, Robertson *et al.* 1980). The crabs, which are relatively small (1-2 cm carapace width), create burrows in the sediment and normally feed upon drained surface deposits by forming pseudofaecal pellets (Hartnoll 1975). Most of the data to date indicate that these crabs extract mainly bacteria and diatoms from the sediment (Dye & Lasiak 1986, Meziane & Tsuchiya 2002, Meziane *et al.* 2002) although some authors have observed direct predation on meiofauna (Teal 1962, Robertson & Newell 1982). Their faeces are richer in carbon and nitrogen than the surrounding sediments (Macintosh 1984) and hence may represent a potential food resource for themselves or other animals. Because of these life history characteristics the crabs may affect meiobenthic communities in at least five ways i.e. negatively by direct predation, competition for food resources, or by physical disturbance and positively by creation of favourable physical microhabitats in and around burrows and by providing food resources in the form of faeces.

Altogether 8 studies have been carried out to assess the impact of ocypodid crabs on meiofaunal communities in soft sediments. These are summarised in Table I. All field surveys indicate some sort of effect of burrows on meiofauna. Bell *et al.* (1978) found that numbers of nematodes increased close to *Uca* burrows while numbers of copepods decreased or remained unaltered. Similarly, Depatra & Levin (1989) found meiofauna more abundant in the burrows than on the surface of the sediment. The reasons for the higher numbers in or close to burrows are not entirely clear, but Bell *et al.* (1978) attributed this to increased food levels, while Depatra & Levin (1989) showed that meiofauna was passively deposited in natural and artificial burrows. Unfortunately, none of the authors identified the nematodes, the most abundant taxon, to lower level than major taxon, and therefore it is difficult to say if their findings are due to colonisers that did not survive predation/disturbance on the surface or due to enhanced resident nematode fauna as a result of increased food resources. Also, the contradictory results of Dittmann (1996) (i.e. nematodes significantly more abundant in burrows compared to adjacent sediment in May but not in November), might be explained by different responses of particular species, the identification at major taxon level having masked effects at lower taxonomic levels.

Of the 7 studies designed to estimate the overall effects of ocypodid crabs on meiofauna, all exclusion experiments carried out in the field indicated that crabs affected the meiofauna negatively (Table I). Hoffman (1984) found that both nematodes and copepods were about 10 times more abundant in the absence of *Uca pugnax*. Dye & Lasiak (1986) who looked only at total numbers of meiobenthic animals, found a two to five-fold increase in the absence of fiddler crabs, and explained this by downward migration and/or competition for food. Finally, Dittmann (1993) found 5 times higher meiofaunal densities in cages excluding sol-

dier crabs compared to control cages, and concluded after finding no effects of physical disturbance of the sediment surface that the soldier crabs were reducing meiofaunal populations by predation. Despite the apparent clear pattern emerging from these studies, their results should be interpreted with caution, as all three experiments suffered from flaws in their design i.e. exclusion and inclusion cages of different size (exclusion cages 8 times smaller inclusion cages) (Dye & Lasiak 1986) with different mesh size (exclusion cages: 1×2 mm, inclusion cages: 50×50 mm) (Dittman 1993) and application of pseudoreplication (Hoffman *et al.* 1984). Botto & Iribarne (1999) found also that nematode densities were lower in the presence of *Chasmagnathus granulata* but not in the presence of *Cyrtograpsus angulatus*. Somewhat different results were found by Ólafsson & Ndaro (1997) in a laboratory experiment in which crabs were enclosed in experimental units for 10 days. Here, no effects on densities or diversity of nematodes were found, while harpacticoids were negatively affected. These results were in accordance to the survey of Ólafsson (1995) who could not relate density of fiddler crabs to variations in nematode numbers while there was a significant negative correlation between crabs and harpacticoids. Ólafsson & Ndaro (1997) concluded that the crabs do not regulate resident nematode assemblages but may inhibit settlement of colonisers that have not adapted to the intense surface disturbance or predation. Finally the survey of Warwick *et al.* (1990) on soldier crabs *Mictyris longicarpus* of an intertidal beach indicated no significant difference in the numbers of nematodes between areas inhabited by the crabs and nearby areas without the crabs but a clear difference in overall assemblage structure. The authors pointed out the flaw in such a comparison, i.e. its validity rests on the assumption that the areas differ only in the intensity of crab abundance. Nevertheless, they believed that this patchiness was most likely a reflection of the gregarious behaviour of the crabs and therefore considered that the results were representing the effects of the crabs. A recent study by Rossi & Chapman (2003), however, makes this assumption doubtful, as small-scale horizontal distribution of *M. longicarpus* seems to be governed by topography and sediment type, rather than by their social patterns.

Swimming crabs

The common shore crab *Carcinus maenas* is the only member of the swimming crabs that has been studied in connection with meiofauna. They are found both in rocky and sedimentary habitats in the North Atlantic and in the Mediterranean Sea. As other portunids, *C. maenas* is a tidally migrating species that explores and forages in the intertidal zone (Hunter & Taylor 1993). Reise (1978) found

that meiofauna comprised a major part of the diet of juveniles, while Pihl (1985) found that detrital matter was their preferred food item.

Two cage studies have been conducted to assess the predation effects on meiobenthos. Scherer & Reise (1981) enclosed crabs in cages and found that juvenile crabs reduced heavily numbers of individuals of all major meiofaunal taxa while there was a shift in diet, towards macrofauna, with increasing size of the crabs. These authors used about 100 and 1000 times the natural densities of juvenile and adult crabs respectively in their enclosure cages. Because of this unnatural set-up it is difficult to relate their findings to the field. It is plausible that the reduction in meiobenthic abundance inside the cages with crabs occurred because of intensive physical disturbance by these crustaceans in the surface sediments, resulting in, for example, amplified migration from the cages with tidal currents. Gee *et al.* (1985) enclosed crabs at natural field densities and found no convincing evidence, in three independent experiments, of negative effects by juvenile and adult crabs on meiofaunal numbers. On the contrary, in some of the experiments significantly higher numbers of harpacticoids were found in enclosure cages compared to control cages and uncaged areas. The authors found epipsammic harpacticoid species to increase while endo- and mesopsammic decreased and concluded that the crabs affected the composition of the copepods through selective predation. This may have been in fact the case, but disturbance of the sediment surface by the crabs may also be a plausible explanation. For instance, Alongi (1985) found that an epibenthic harpacticoid copepod became more abundant in cultures where the sediment surfaces were regularly disturbed, than in those with no disturbance. In any case, even if Gee *et al.* (1985) used more natural predator densities than Scherer & Reise (1981), both studies suffered from a different degree of pseudoreplication, so their results should be taken cautiously. Further enclosure experiments by Schratzberger & Warwick (1999a,b) showed that biological disturbance by the crabs had relatively little effects on nematode assemblages compared to artificial physical disturbance despite unnaturally high numbers of crabs (50 times field densities) inside mesocosms. They found density reduction in nematodes in one experiment and concluded that the different nematode assemblage structure in control and crab treatments was due to confounded effects of predation and physical disturbance by the crabs.

Shrimps

The grass shrimp (*Palaemonetes pugio*) and the brown shrimp (*Crangon crangon*) are both mobile epibenthic predators known to feed on meiobenthos (e.g. Sikora 1978, Pihl 1985). They disturb

the sediment surface while feeding and could therefore also affect the meiobenthos indirectly by physical disturbance. Their effects on meiobenthos, mainly predation, have been investigated in 6 studies (Table I). Both Bell & Coull (1978) who found negative effects of the grass shrimp on total densities of the major meiofauna taxa and Bell (1980) who found no effects did not satisfactorily replicate their experimental units and used pseudoreplicates in their statistical analyses. Although the average numbers of animals were almost always higher in absence of the shrimps, Smith & Coull (1987) found that the grass shrimp did not significantly reduce meiofaunal numbers. However, these authors replicated each treatment only twice, making the power of their statistical tests little. However, other studies performed with different shrimp species seem to support the results found for grass shrimps, and their apparent negative effect on some meiofaunal taxa. Contrary to other studies, Escaravage & Castel (1990) found that in a cage where shrimps (*Palaemonetes varians*) were enclosed meiofaunal numbers became higher than in a cage without shrimps. However, it is difficult to assess treatment effects from only one replicate experimental unit, using pseudoreplicates for the analysis. All in all there are no convincing evidence that the grass shrimps affect meiobenthos as all studies to date suffer from flaws in the experimental design.

Both enclosure experiments with the brown shrimp, *Crangon crangon*, show that the shrimp at natural juvenile densities significantly reduced harpacticoid copepods together with ostracods, while there were no effects on nematodes, the most abundant taxon in the sediment (Hedquist-Johnson & André 1991, Nilsson *et al.* 1993). This was expected as the brown shrimp has been shown to contain mainly microcrustaceans in their guts and nematodes to a much lesser degree (Pihl & Rosenberg 1984, Pihl 1985, Gee 1987, Matilla *et al.* 1990, Hedquist-Johnson & André 1991).

Thalassinidean shrimps often reside in deep burrows, creating mounds on the sediment surface. They have been studied in relation to sediment reworking, microgeochemistry, microbial and infaunal composition (e.g. Aller *et al.* 1983, Suchanek & Colin 1986, Posey *et al.* 1991). Dittmann (1996) found that nematodes and turbellarians were more abundant in burrows than adjacent sediment and that community composition of turbellarians differed. She also noted from her exclusion experiment that the overall effects of *Callianassa australiensis* were that the presence of the shrimp reduced the numbers of meiofauna by 55%. Contrary to Dittmann (1996) Dobbs & Guckert (1988) found, that nematodes and total meiofauna were in greater numbers in ambient sediment compared to burrows. Surveys indicate that *Callianassa* sp. reduces nematode diversity in subtidal sediments (Alongi 1986) and that *C.*

kraussi affects vertical penetration and seasonal fluctuation of meiofauna in intertidal beaches (Dye & Furstenberg 1978). In their cage experiment, Branch & Pringle (1987) found that meiofauna numbers were reduced in upper sediment layers in the presence of the sand prawn but not in lower sediment layers. Even though some microhabitats may have enhanced numbers of meiobenthic animals, all the studies indicate that overall effects of the sand prawns on meiofaunal numbers are negative.

Amphipods and isopods

Relatively little is known about the effects of amphipods and isopods on meiofaunal assemblages despite their importance in soft sediments. In the Baltic Sea, three studies have been performed on the effects of the amphipod *Monoporeia affinis* on meiobenthos. These crustaceans attain high densities in the Baltic, up to several thousands per m². They are deposit feeders and rework the sediment by daily migration into the water column during night and burrowing into the sediment at dawn. Sundlin & Elmgren (1991) showed that the amphipods affected major meiofaunal taxa differently i.e. nematodes and ostracods negatively, while turbellarians and harpacticoids positively. Ólafsson & Elmgren (1991) found that overall assemblage structure of nematodes was not affected by the presence of the amphipods even though they reduced total densities of the nematodes. They found also that the amphipods reduced the numbers of ostracods and the spat of *Macoma balthica*. Further the amphipods increased the total numbers of the two harpacticoid species present in the mesocosms as well as the numbers of Turbellaria. The similarities of these two studies are striking and indicate that effects of the amphipods on meiobenthos are reproducible. Similarly Ullberg & Ólafsson (2003) found that the amphipods had no detectable effects on nematode assemblage structure when assessing the effects of the amphipods on small-scale migration of nematodes. One of the most important invertebrate predators in the northern Baltic Sea is the isopod *Saduria entomon*. Their main prey items are amphipods although small individuals are likely to take meiofauna. Aarnio *et al.* (1991) found no difference in major meiofauna taxa when the isopod was added to an experimental unit. The reason for this may be that the authors used large isopods that most likely do not prey on meiofauna and used only one experimental replicate making the interpretation of the data difficult.

Annelida

Polychaetes are the only members of the phylum Annelida that have been studied in relation to biological disturbance on meiofauna in soft sediments. These worms are one of the most common and di-

verse groups in marine sediments and are likely to affect meiobenthos in many ways. The studies of Reise and co-workers (Table I) give an impressive account of how the lugworm *Arenicola marina* affects meiofauna. These worms live in U-shaped burrows with two openings i.e. funnel and faecal cast areas (Fig. 1). The burrows typically reach 15-20 cm into the sediment where the worms stay in a horizontal gallery. Sediment and detrital matter slide down the funnel through the head shaft into the pocket region where ingestion takes place. At the sediment surface above the tail shaft, coiled casts are stacked up in mounds. The worms pump water into the burrows through the tail shaft supplying the worms with oxygen rich water and consequently creating an oxic layer along side the burrow walls. The authors identified several micro-habitats generated by the worms and found higher densities of meiofauna in the vicinity of the burrows deep in the sediment compared to corresponding depths without burrows. They also found that some turbellarian species preferred or were confined to one or more of the microhabitats (Reise & Ax 1979, Reise 1984, 1987). This obviously increases the overall diversity of the sand flats as many of the species were not found or rarely so in control samples away from the microhabitats. Interestingly Reise (1987) found that species confined to some of the deep microhabitats had much more stable populations than those in the surface layers. Even if meiofauna is more abundant in the subsurface microhabitats associated with the worms than in normal subsurface sediments, the overall effects on density are small mainly because of two reasons. Firstly, these structures account for only a small portion of the subsurface sediment volume and secondly the faecal casts of the worms reduce

meiofauna abundance on the surface where it is otherwise richest. Reise (1981) calculated that the total fauna of the sand-flat increased by 5% due to the presence of the polychaetes. When the lugworm was removed from the sediments a considerable reduction (93%) in subsurface meiofaunal abundance occurred (Reise 1983). Despite the undoubted relevance/interest of these results, the experimental design calls for concern and may limit their scope of application. The fact that only two plots: control and treatment, were used is a classic example of pseudoreplication. Reise (1981) also studied the biogenic structures of the polychaetes *Nereis diversicolor*, *N. virens*, *Pectinaria koreni* and *Pygospio elegans*. He found that the burrows of these polychaetes also significantly increased densities of the major meiofaunal taxa in subsurface sediments.

Warwick *et al.* (1986) took a transect of cores across the feeding area, faecal mounds and background unaffected area of the terebellid polychaete *Streblosoma bairdi* in sublittoral mud mesocosms. Unlike the lugworm, *S. bairdi* feeds by gathering surface material with its extensible tentacles from the opening of its faecal mound. They do not feed from their mounds but rather bring food particles some distance around them. These mounds are relatively large (more than 10 cm in diameter) and can be active or inactive, old or young. The authors found that abundance of meiofauna was highest in the mounds but diversity lowest. Highest diversity was found in the feeding areas. Some species were also more or less confined to the mounds, while others were more ubiquitously distributed. Even if the results are clear, the drawback of the study is that the authors sampled only two mounds, one active and another inactive. Also, it is not unlikely

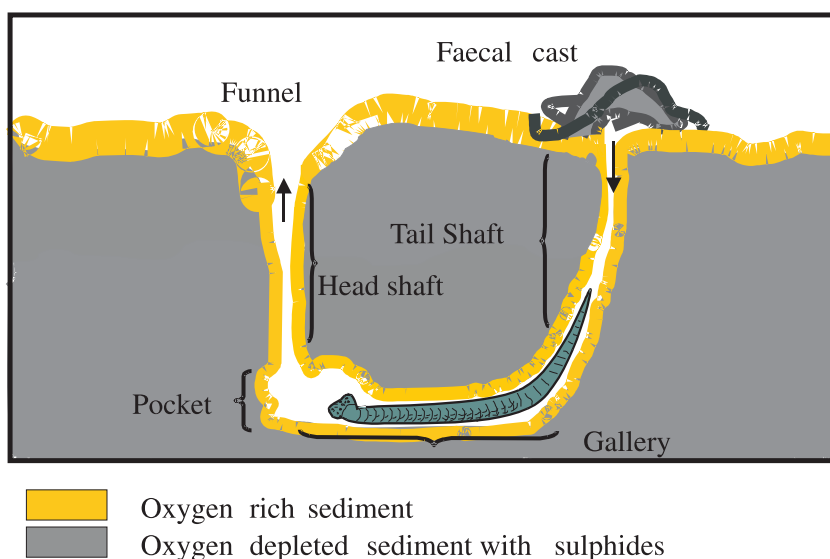


Fig.1. – Schematic representation of a lugworm, *Arenicola marina*, burrow.

that the age of the mounds is of fundamental importance, since the dispersal capability of the various colonising organisms is likely to be different depending on their mobility and life history characteristics.

The polychaete *Melinna palmata* is a small tube-dwelling ampharetid polychaete which is a surface deposit-feeder, making a mucus-lined U-shaped tube from which it can protrude to feed from the sediment surface. Faecal casts are produced ca 4 cm from the head opening. Ólafsson *et al.* (1990) sampled meiofauna from the feeding and cast areas of the polychaete together with background control areas. They found that nematodes were not significantly affected by the polychaetes, while copepods were in lower numbers in the cast and feeding areas compared to the background controls. However, they found that the dominant harpacticoid species, *Longipedia* spp., in the cast areas were about 4 times as abundant as in the other areas. Similarly one of the nematode species was found to be more abundant in the cast areas than in the other ones. However, the drawback in the design of this study was that the age of the casts were unknown and that the sampling did not discriminate between subsurface and cast fauna as cores were taken down to 4 cm depth, through the casts i.e. mixing both surface and subsurface assemblages.

In the San Diego Trough (1000m), the cirratulid polychaete *Tharyx luticastellus* builds and inhabits a robust mud concretion. Significant positive correlations between these worms and harpacticoid species have been demonstrated in surveys (Thistle 1979, 1982, Thistle & Eckman 1988). To shed light on the possible mechanisms behind the association between copepods and mudballs Thistle & Eckman (1990) measured responses to various types of mudball mimics to determine whether responses were to a habitat provided by the mudballs, to a refuge from predators or to hydrodynamically induced food resources around the mudballs. They found that some species used the mudballs as a refuge from infaunal predation, while others used the mudballs as habitat. The authors found no evidence for species responding to increased food resources due to hydrodynamic effects. However, when Eckman & Thistle (1991) compared patterns of abundance of harpacticoids about mudballs to patterns of shear stress produced by the deflection of flow around mudballs, they found that a large number of species was affected by flow about the mudballs. The sensitivity of harpacticoids to flow was associated with episodes of relatively strong currents. Some of the responding species were significantly more abundant within regions of increased shear stress about a mudball while others were significantly more abundant within regions of decreased shear stress.

To study predation effect by polychaetes on meiofauna Kennedy (1993) placed two species,

Nereis diversicolor and *Ophelia bicornis* in experimental enclosure in an intertidal estuary. Despite 4 times higher abundances in the enclosure than in the field, neither species affected significantly the densities of the major taxa. However it is not unlikely that the polychaetes provided favourable habitat in deeper layers because of the tube building. Indeed the author found nematodes in enhanced numbers in deeper layers and reduced in upper layers though this was not statistically significant. Conversely, Tita *et al.* (2000) found in their laboratory experiment that the polychaete *Nereis virens* significantly affected assemblage structure of the meiofauna in the surface layers, with reduction in overall abundance of the major taxa and decrease in nematode diversity. They also showed that nematode assemblage structure was significantly affected in deeper sediment layers although diversity and abundance was similar among treatments. The authors categorized the nematodes into dead and alive by examining the decomposition status of their internal organs. By doing this they could distinguish between predation and disturbance effects and their data clearly indicate that disturbance caused by the sediment browsing of the polychaetes at high densities was mainly responsible for lower nematode abundances in the surface layers. This study shows the importance of enhancing resolution in data collection by working at low taxonomic levels (species/genera) and dividing the habitat sampled in a comprehensive way. For example, if the authors had not distinguished between surface and subsurface habitats and not identified the nematodes to lower taxonomic levels they would have found no or little effects on the meiofauna as Kennedy (1993) did.

Mollusca

Individuals of the phylum Mollusca are among the most conspicuous and familiar invertebrates in the marine environment, and the second species-richest (considering described species) invertebrate phylum after the arthropods. Gastropods and bivalves comprise the bulk of macrobenthic mollusc species inhabiting soft-bottoms. Large numbers of gastropod species live on the sediment surface while bivalves typically live buried in the sediment though often extending siphons to the sediment surface, where they may filter particles from the water column and/or feed from sediment deposits.

Despite the relative ease in collecting and keeping molluscs in the laboratory only a few experiments have been conducted in relation to meiofauna assemblages. Overall, effects of bivalves on meiofauna have been studied in 7 enclosure studies with conflicting results (Table I). Of the 5 experiments

conducted in the field only 1 indicated significant effects on meiofauna assemblage structure. Reise (1983) found, in sandy intertidal sediments, that density of Turbellaria significantly increased in treatments with enhanced numbers of the clam *Macoma balthica* but at the same time their diversity was lower. Earlier, he had shown in a field survey that both nematodes and Turbellaria increased in numbers in deeper sediment layers where the bivalves resided (Reise 1981). He attributed the increase in density to biotic enrichment by the clam due to termination of exhalant siphons below the surface which produced localized concentration of nutrients and oxic layers in subsurface sediments (Reise 1983). Ólafsson *et al.* (1993) found no such enrichment in their laboratory experiment using muddy subtidal sediment, on the contrary they found that harpacticoid copepods became fewer in the presence of *M. balthica* and suggested that competition for food resources best explained this pattern. This discrepancy may reflect the different habitats used in these experiments i.e. water percolation in the sediment is much more limited in muddy substrata than in sand, hence dispersion of nutrients may be negligible within muddy sediments. Finally, Ólafsson (1992) used *M. balthica* to assess the influence of decaying animals on the small-scale distribution of meiofauna. In a laboratory experiment, in which sediment was implanted with empty shells, shells with dead *M. balthica* or untouched, he found that even though densities of nematodes were not significantly different among areas the overall structure of the nematode community indicated shift to lower dominance and higher species diversity in the dead animal areas. All other taxa avoided these areas probably due to sulphide formation on the sediment surface. The only other study on the attraction of decomposing tissue of meiofauna is the one by Gerlach (1977). He planted fish tissue in an intertidal sediment and found, as Ólafsson (1992), that the dead tissue attracted some nematode species but not others. Both studies indicate that the models of Johnson (1970) and Grassle & Sanders (1973), which state that natural disturbances create a mosaic of patches that have different species compositions depending on their states of recovery, apply to rotting animal tissue as *in situ* decay of dead animals must be regarded as a very common phenomenon in nature.

The large (up to 30 cm) suspension feeding pinnid bivalve *Atrina zelandica* or horse mussel, may form extensive soft-sediment patchy reefs on intertidal flats and subtidal nearshore waters in New Zealand (Warwick *et al.* 1997, Norkko *et al.* 2001). The physical presence of the mussels changes the hydrodynamic conditions at the sediment water interface (Green *et al.* 1988) and biodeposits accumulate on the sediment surface within the mussel patches (Austen & Thrush 2001). Field surveys indicate that the horse mussels may have significant effects on macrofauna (Norkko

et al. 2001, Cummings *et al.* 1998) and meiofauna (Warwick *et al.* 1997) assemblages. In particular there were significant reductions in nematode species diversities, with different composition and more variable assemblage structure inside the horse mussel beds compared to control areas outside the beds (Warwick *et al.* 1997). Contrary to these results, enclosure experiments where the densities of the mussels were manipulated indicated no consistent effects of the mussels on the density or diversity of the meiofauna assemblages (Austen & Thrush 2001). The authors speculated that either *A. zelandica* do not affect the meiobenthos (i.e. some other environmental factor affects both meiobenthic communities and *Atrina* populations concurrently), or that the time-scale of the experiment was too short (47 days) to allow habitat modifications by the mussels to affect the meiobenthos. They also discussed that the choice of spatial scales in the experimental design may have been the cause for no treatment related differences i.e. modification of some factor, caused by *Atrina*, may have extended to the control plots.

The numbers of another bivalve, the suspension-feeding cockle *Cerastoderma edule* have been manipulated in two field enclosure experiments in European sandflats. Reise (1983) found no evidence for effects on turbellarians. Unfortunately, his experiment was unlikely to reveal effects convincingly as most of the cockles escaped the enclosures during the course of the experiment. Kennedy (1993) enhanced ambient densities of the cockles by a factor of 4 in his enclosures, but he also failed to find any significant difference in the densities of major taxa between enclosure and control experimental units. In his study Kennedy (1993) was examining predation and he concluded that cockles are unlikely to affect meiobenthos partly because they stay mainly in the sediment and also because the maximum particle size (7 µm diameter) taken from the water-column by the cockles is much smaller than that of meiobenthic animals. Obviously the cockles could have affected the meiobenthos indirectly for example by organic enrichment or by their biogenic structure. Kennedy (1993) also implanted the deposit feeding bivalve *Scrobicularia plana* in identical experimental design and found indication, albeit weak, that annelids moved down into the sediment when in presence of the bivalves although there was no significant difference in their overall abundance.

Austen *et al.* (1998) conducted an interesting experiment on two bivalves with different feeding and locomotion strategies in a large mesocosm. They compared nematode responses to variable densities of the bivalves *Abra alba* and *Nuculoma tenuis* in enclosure cages set within the mesocosm. *A. alba* feeds on the sediment surface using inhalant siphons while *N. tenuis* is a subsurface feeder using labial palps to gather food items and is much

more mobile whilst feeding than *A. alba*. Exposure of the nematode assemblages to the two bivalve species resulted in development of a different nematode assemblage structure in the enclosures of the respective bivalve species after 20 weeks. However, there was no clear difference in the nematode assemblage structure between density treatments of each bivalve species. The authors concluded that the results were consistent with the intermediate disturbance hypothesis of Connell (1978) that predicts that highest diversity will be attained at intermediate intensities of disturbance. The experiment of Austen *et al.* (1998) is one of the few where the intensity of biological disturbance has been graded into more than 2 categories i.e. disturbance or no disturbance, an improvement which may prove essential to understanding the mechanism behind the perturbation.

Only two studies have assessed the effects of sediment surface feeding gastropods on meiofauna. In the first one, Nichols & Robertson (1979) excluded the mud snail *Ilyanassa obsoleta* from a 1 m² sediment plot and compared micro- and meiofaunal abundances with those of an adjacent control plot of the same size. They found that diatoms increased in the exclusion plot together with diatom feeding nematode species. Although this study gives interesting results its validity rests on loose grounds because of limitations in the experimental design, i.e. pseudoreplication. The second one was performed on the gastropod *Terebralia palustris*, one of the largest prosobranchs found in tropical intertidal habitats. The adults of this species form feeding aggregations and frequently dominate the surface of muddy substrates, where they destabilize the sediment surface. Carlén & Ólafsson (2002) carried out a cage experiment where the gastropods were either enclosed or excluded. They found that after nine weeks of excluding the gastropods a cyanobacterial carpet developed while this was not evident in the enclosure cages. Several meiofauna groups were found in significantly reduced densities in the presence of the gastropods, presumably because of competition for food or sediment surface disturbance created by the molluscs. The authors also showed that the assemblages were more variable at high disturbance compared to low or no disturbance by the gastropods which indicates that they were under stress, i.e. Warwick & Clarke (1993) have shown that communities under stress are normally more variable than otherwise.

Miscellaneous groups

Only a handful of other macrofaunal invertebrate species (i.e. not belonging to the Crustacea, Polychaeta or Mollusca), have been studied in relation to biological effects on meiofauna (Table I).

Creed & Coull (1984) studied the effects of the sea pansy *Renilla reniformis* and the sand dollar *Mellita quinquesperforata* on an intertidal sandbar. They found that cores containing sea pansies had significantly fewer copepods than cores taken from bare sand. In a follow-up experiment where artificial and live sea pansies were planted in the sediment, no consistent effects were detected. Unlike sea-pansies, which remain more or less still on the sediment surface, the sand dollar moves slowly through the sediment (1-32 cm/hour), making distinct burrow trails (Findlay & White 1983, Reidenauer 1989) and is thought to be a ciliary mucoid feeder selecting particles <62 µm in size (Lane & Lawrence 1982). Three studies investigating the abundance of meiofauna occurring in front of the sand dollar and right behind in the burrow trails, give conflicting results. While Findlay & White (1983) found no effects on the major taxa (apart from foraminiferans), Creed & Coull (1984) found that nematodes were significantly reduced in burrow trails together with a single species of harpacticoids. Furthermore, Reidenauer (1989) found significantly higher abundances of nematodes in trails compared to control sediments, but reduced numbers of mites, foraminiferans and again, one harpacticoid species. The disparity in these results may be explained by several factors. Firstly, the studies were conducted in different habitats (intertidal vs. subtidal) and during different seasons. Moreover, Reidenauer (1989) argued that one of the possible reasons for enhanced nematode abundance was increased food availability in the form of mucus and/or excreted cells that line the sand-dollar gut. Such increased food availability may not have been possible in the intertidal areas where currents are likely to be stronger than in the subtidal area where Reidenauer did his experiments.

Another echinoid, the heart urchin *Brissopsis lyrifera* has been subjected to two experiments (Austen & Widdicombe 1998, Austen *et al.* 1998). It is a shallow burrower and a non-selective deposit feeder and therefore may affect meiofauna both through direct predation and lowered sediment stability. Both experiments indicate that density and diversity of nematodes were unaffected by the presence of the heart urchin but overall assemblage structure, as measured by ordination, was significantly affected by its presence. The authors also showed in both experiments that nematodes belonging to the genus *Odontophora* increased significantly in numbers in the presence of *Brissopsis*. Such a reproducibility of experimental results gives stronger weight to the reliability of the results.

Dittmann (1996) compared the sediment lining the burrows of the brachiopod *Lingula anatina* with adjacent control sediment. She found that meiofaunal abundances varied over time, being at one time higher in the burrows while at another in

the control sediment. Species distribution of turbellarians was also similar between burrows and adjacent sediment.

Thistle (1980) observed that in the faecal casts of the acorn worm *Ptychodera bahamensis* harpacticoid copepods were 7 times lower in abundance than in the background sediment. He then followed the re-colonization of these open patches and found that densities of harpacticoids no longer differed from the background densities after 23 hours. Early in the recolonization phase two of the 16 harpacticoid species were found in disproportional abundance in the mounds, indicating that they were exploiting the patches. Dobbs & Guckert (1988) collected sediment from freshly extruded fecal casts and adjacent feeding depressions of the acorn worm. There were no significant differences between casts and depressions in density of total meiofauna or that of nematodes. However, measures of total, viable microbial biomass were considerably lower in casts. If harpacticoids rely on microbial biomass, then one would expect most species not to become disproportionately abundant in the casts, as was the case in Thistle's observations. Varon & Thistle (1988) tested in field and laboratory experiments the theory that competitively inferior species are adapted to finding and exploiting newly disturbed patches, *sensu* Grassle & Sanders 1973, by using fecal mounds of the acorn worm as open disturbed patches. They identified a harpacticoid copepod species, *Zausodes arenicolus*, that responded positively to *Ptychodera* fecal mounds and then ran experiments to reveal the mechanism underlying the response. In a preference experiment they showed also that the harpacticoids chose mounds over background sediment and then ran another preference experiment to find out whether the attractive factor of the mounds was an absence of potential competitors. The authors found no evidence of competitive exclusion and concluded that the harpacticoids responded to food resources more abundant in the casts than elsewhere.

Finally, Aarnio *et al.* 1998 studied the effects of the priapulid *Halicryptus spinulosus* on meiofauna in the Baltic Sea. Their enclosure experiment in the field revealed that nematodes were significantly lower in abundance in the presence of the priapulids while other major meiofaunal taxa were not affected. Similarly they found in a settling experiment that numbers of *Macoma balthica* spat and nematodes were significantly lower in traps containing the priapulids compared to control traps without the priapulids. The authors concluded that the negative effects were a consequence of predation in combination with disturbance. Even though similar negative effects were found in two independent experiments, the authors used about 10 times the natural densities of priapulids in their experiments and therefore it is doubtful to conclude

that the priapulids significantly affect meiobenthos similarly in the field.

EMERGING PATTERNS

Almost all the studies (86%) investigating biogenic structures of macrobenthos indicate some sort of effects on meiofaunal assemblages (Table I). Those studies where diversity of a particular animal group has been considered, almost all agree on enhanced species diversity as a result of biogenic structures. In most of these studies the researchers have applied a survey approach by sampling particular microhabitats such as casts or burrow walls and then comparing with adjacent sediment without these features. While it is clear that on a small spatial scale these structures accommodate assemblages that differ from the ones living in the bulk sediment, researchers have not advanced from these observations to a deeper understanding of the processes in which they are involved (see though case studies by Eckman & Thistle above). Obviously, these biologically generated structures are often of a very different nature but one can see similarities between many of them. In a given area one might for example expect to see several macrofaunal organisms producing faecal casts on the sediment surface. It is likely that most of these are devoid of meiobenthic life when shed on the surface, though this has never been confirmed. These would then represent islands of different sizes and probably of different texture and microflora depending on the life history of the macrofauna producing them. If we know that they are at some stage colonized by meiofauna and smaller macrofauna, then one would like to know what kind of a role these islands have in the ecology of soft-bottom organisms. Can we apply some of the theories predicting species diversity (e.g. Connell's intermediate disturbance theory) under certain disturbance level to meiobenthos and biogenic structures? Or are these islands only increasing the habitat complexity and would we then expect highest diversity of meiofauna in areas where the diversity of faecal casts is highest? What role do these islands have in the population dynamics of species taking advantage of them? Does size or age of biologically produced islands set the limits for sustainable populations? Can we apply metapopulation theory/ies *sensu* Hanski (1997) to explain and predict population variation in these islands?

The results of studies that have considered overall effects of macrofauna originating from processes such as predation, physical disturbance, competition for food and biogenic structures also indicate effects on meiobenthos. Here the research approach has been predominantly experimental

manipulation with 20 and 25 studies performed in the laboratory and in the field respectively. Of these experimental studies 66% have shown positive or negative effects on meiobenthos. The underlying aim of most of these studies has been to see if the impact of biological disturbance effects meiobenthos or not by using only two treatments i.e. with or without the disturber. While the results may be of interest to local situations the generality of such an approach is limited. This is particularly important in those cases in which researchers have manipulated numbers of disturbing animals to 10-fold or more the natural densities and compared to experimental units without the disturber. In only a few studies, researchers have used 3 or more density levels of disturbing macrofauna in their experimental manipulations, including natural levels, for the understanding of ecological rules behind biological disturbances. For example, Austen *et al.* 1998 found that disturbance created by two macrofaunal species affected the diversity of nematodes according to the predictions of Connell (1978) i.e.: that at intermediate frequency and intensity disturbance levels, highest species diversity is to be expected. However, such relationship has not been found in other studies set out to test diversity theories on other macrofaunal disturbing species (Ólafsson & Elmgren 1991, Ólafsson *et al.* 1993, Austen & Widdicombe 1998, Austen & Thrush 2001). It is notable that in none of these studies an overall reduction in nematode densities was found, which is prerequisite for Connell's theory. Indeed, the majority of experiments (7 out of 8), on overall effects of macrofauna on nematode diversity showed no effects (Table I).

It seems clear that most information is available from intertidal areas, where 70% of all studies are derived from. The reason for this dominance is clearly the logistics of setting up and executing experiments. The majority of the intertidal studies are also from sandy sediments indicating that physical factors are relatively strong. One might expect, that in such habitats biological disturbance exerted on meiofauna by macrofauna is often overshadowed by physical forces, such as sediment instability, desiccation, temperature and salinity stress and so on. Subtidally these factors become more stable so biological factors might be expected to play a greater role in structuring meiofaunal communities. This summary, however, does not show such a great difference in meiofaunal response between subtidal and intertidal habitats. In fact, a higher percentage of intertidal studies showed response in density (69% vs. 65%) and diversity (53% vs. 42%) both when all studies were considered together, as well as when they were broken up into biogenic structure and overall effects. The reasons for this are probably many, but may also be explained in terms of feasibility of results to be published, since scientific papers are, unfortunately, more easily published when clear effects are shown

compared to when little or no effects are reported. Hence, the response ratio would be biased towards studies that show effects. There are also much fewer subtidal studies than intertidal ones, which might again influence editors in accepting them even if results show little or no effects.

Future studies

In their review on field experimentation in meiofaunal ecology, Coull & Palmer (1984) expressed concern over experimental design and the level of taxonomic identification in meiofaunal research. With only few exceptions, meiofaunal researchers during the last 15 years have designed their experiments in a much more satisfactory way than their predecessors. However, the level of taxonomic resolution has not improved to the same extent. The percentage of studies where some meiofaunal taxon was identified to species or genus level before and after 1990 is 41 and 59% respectively. Overall, every second study has been on major taxon level, which may mask many significant impacts by macrofauna on individual meiofaunal species or group of species. It is also notable that nematodes, by far the most abundant group in marine sediments, have only been identified to species or genus in less than 30% of all studies. The difficulty and the time consuming process involved in identifying meiofauna to species level, are probably the main factors contributing to the scarcity of studies at species level and to the fact that they are very seldom taken further than to an isolated impact study. Because of a rapid progress in the development of molecular methods and the decline in the cost of nucleotide sequencing, species identification by specific genetic markers is nowadays relatively easy. For example, the accurate determination of bacterial diversity has, until recently, been difficult as a very high proportion of the bacterial species cannot be cultivated (Amann *et al.* 1995). Today, however, new molecular techniques based on 16S rDNA PCR amplification, cloning and sequencing, make it possible to describe microbial assemblages with a much higher level of accuracy (Amann *et al.* 1995, Urakawa 2001). The tools applied on microbial communities seem to suit also eukaryotes like meiofaunal species. Researchers have for instance developed nematode-specific primers for use with the small subunit gene 18S rDNA. Within this gene there are deeply conserved stem regions and rapidly evolving loops which allow discrimination at order, family, genus and species level from one molecule (Fitch *et al.* 1995, Blaxter *et al.* 1998). It seems therefore very likely that within the near future, characterization of meiofaunal communities will be possible using molecular methods. With the painstaking identification process out of the way, many more samples may be processed to answer some of

the fundamental questions regarding the effects of macrofauna on meiobenthos in marine sediments. These may encompass population dynamics of certain taxa as well as diversity trends of whole communities.

Another general problem emerging from the reviewed studies is that many of those dealing with predation are limited because of the confounding effects of predation and physical disturbance created by the macrofauna. Perhaps in this context the application of stable isotope techniques may help. Measurements of natural C^{13}/C^{12} and N^{15}/N^{14} isotopic ratios provide a powerful tool in determining sources of nutrition for consumers and trophic relationships among organisms as stable carbon and nitrogen isotopic ratios in animals are largely determined by those of their diet. For instance, if one is interested in predation on harpacticoid copepods by macrofauna, then one could label these crustaceans by applying enriched ^{13}C in their diet. If a signal is not found in the macrofauna species in question but there is a significant decline in the harpacticoid population then one might assume that the effects are not because of the predation *per se* but rather physical disturbance. Obviously, there is a whole scope of studies that could gain from using various tracer techniques, but unfortunately this still remains unapplied when it comes to studies on the effects of macrobenthos on meiobenthic communities.

As biological disturbance created by macrofauna is incredibly variable among species and difficult to rate or categorise, it seems as yet difficult to apply theories to macrofaunal disturbance in general, predicting diversity or abundance patterns in meiofaunal assemblages. Since most studies show that macrofauna influence assemblage structure of meiofauna then it would be interesting to see if diversity of macrofauna in a given habitat is related to the diversity of meiofauna. One might, for example, expect increasing diversity of meiofauna with increasing diversity of macrofauna. One might also expect increasing diversity of meiofauna with increasing functional diversity of macrofauna but not necessarily to overall diversity of the macrofauna. These relationships can be easily assessed in the laboratory. It would also be interesting to dig into surveys where assemblage structures of meio- and macrofauna have been assessed on local scales, and see if patterns emerge.

In terms of area, marine soft bottoms represent the most extensive habitat on earth. They are packed with meiobenthic animals, which normally lack pelagic larvae. Their dispersal capacity is therefore limited and often dictated by unpredictable forces. The most abundant taxon, the nematodes, is now thought to contain one of the highest numbers of species on a global scale (Lambshhead 1993). Reasons for such high diversity are likely to be a repeated isolation of populations through evo-

lutionary times. It seems that in the absence of strong physical forces, biological disturbance may be a driving force for such isolations and hence act upon species diversity. Still our knowledge is very limited when it comes to the role of biological disturbance in shaping meiofaunal assemblages. Certainly many current ecological theories concerning species diversity may explain some of the patterns we find in meiobenthic organisms, but most likely we need to tailor theories or invent new ones that may better apply to the particular conditions that reign in marine soft-bottoms. Exciting times are ahead.

ACKNOWLEDGEMENT. – I would like to thank L Arroyo for inspiring discussions and for reading an earlier draft of the manuscript. Special appreciation goes to J Perez, J S Bach & I Stravinsky for creating a special atmosphere while writing. I would also like to thank the editors for inviting me to participate in this volume and all the patience they have shown me during repeated delays. Finally, I would like to thank two anonymous referees for helpful comments.

REFERENCES

- Aarnio K, Sandberg E, Bonsdorff E 1991. Benthic predation on shallow-water macro- and meiofauna in the baltic sea: An experimental comparison between *Pomatoschistus minutus* (Pisces) and *Saduria entomom* (Crustacea). *Ann Zool Fenn* 28: 41-48.
- Aarnio K, Bonsdorff E, Norkko A 1998. Role of *Hali-cryptus spinulosus* (Priapulida) in structuring meiofauna and settling macrofauna. *Mar Ecol Prog Ser* 163: 145-153.
- Aller RC, Yingst JY, Ulman WJ 1983. Comparative biogeochemistry of water in intertidal *Onuphis* (Polychaeta) and *Upogebia* (Crustacea) burrows: Temporal patterns and causes. *J Mar Res* 41: 571-604.
- Alongi DM 1985. Effect of physical disturbance on population dynamics and trophic interactions among microbes and meiofauna. *J Mar Res* 43: 351-364.
- Alongi DM 1986. Population structure and trophic composition of the free-living nematodes inhabiting carbonate sands of Davies Reef, Great Barrier Reef, Australia. *Aust J Mar Freshw Res* 37: 609-619.
- Amann R, Ludwig W, Schleifer KH 1995. Phylogenetic identification and in situ detection of individual microbial cells without cultivation. *Microbiol Rev* 59:143-169.
- Austen MC, Widdicombe S 1998. Experimental evidence of effects of the heart urchin *Brissopsis lyrifera* on associated subtidal meiobenthic nematode communities. *J Exp Mar Biol Ecol* 222: 219-238.
- Austen MC, Widdicombe S, Villano-Pitacco N 1998. Effects of biological disturbance on diversity and structure of meiobenthic nematode communities. *Mar Ecol Prog Ser* 174: 233-246.
- Austen MC, Thrush SF 2001. Experimental evidence suggesting slow or weak response of nematode com-

- munity structure to a large suspension-feeder. *J Sea Res* 46: 69-84.
- Bell SS, Coull BC 1978. Field evidence that shrimp predation regulates meiofauna. *Oecologia* 35: 141-148.
- Bell SS, Watzin MC, Coull BC 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. *J Exp Mar Biol Ecol* 35: 99-107.
- Bell SS 1980. Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecol Monogr* 50: 487-505.
- Blaxter ML, De Ley P, Garey JR, Liu LX, Scheldeman P, Vierstraete A, Vanfleteren JR, Mackey LY, Dorris M, Frisse LM, Vida T & Thomas WK 1998. A molecular evolutionary framework for the phylum Nematoda. *Nature* 392: 71-75.
- Branch GM, Pringle A 1987. The impact of the sand prawn *Callinassa-kraussi* stepping on sediment turnover and on bacteria, meiofauna, and benthic microflora. *J Exp Mar Biol Ecol* 107: 219-235.
- Carlén A, Ólafsson E 2002. The effects of the gastropod *Terebrallia palustris* on infaunal communities in a tropical tidal mud-flat in east Africa. *Wet Ecol Man* 10: 303-311.
- Connell JH 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1309.
- Creed EL, Coull BC 1984. Sand dollar, *Mellita quinquesperforata* (Leske), and sea pansy, *Renilla reniformis* (Cuvier) effects on meiofaunal abundance. *J Exp Mar Biol Ecol* 84: 225-234.
- Cummings VJ, Thrush SF, Hewitt JE, J TS 1998. The influence of the pinnid bivalve *Atrina zelandica* (Gray) on benthic macroinvertebrate communities in soft-sediment habitats. *J Exp Mar Biol Ecol* 228: 227-240.
- Darwin C (1859) The origin of species by means of natural selection. John Murray, London
- Depatra KD, Levin LA 1989. Evidence of the passive deposition of meiofauna into fiddler crab burrows. *J Exp Mar Biol Ecol* 125: 173-192.
- Dittmann S 1993. Impact of foraging soldiercrabs (Decapoda, Mictyridae) on meiofauna in a tropical tidal flat. *Rev Biol Trop* 41: 627-637.
- Dittmann S 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. *Mar Ecol Prog Ser* 134: 119-130.
- Dobbs FC, Guckert JB 1988a. *Callinassa trilobata* (Crustacea, Thalassinidea) influences abundance of meiofauna and biomass, composition, and physiologic state of microbial communities within its burrow. *Mar Ecol Prog Ser* 45: 69-79.
- Dobbs FC, Guckert JB 1988b. Microbial food resources of the macrofaunal-deposit feeder *Ptychodera bahamensis* (Hemichordata: Enteropneusta). *Mar Ecol Prog Ser* 45: 127-136.
- Dye AH, Furstenberg JP 1978. An ecophysiological study of the meiofauna of the swartkops estuary. 2. The meiofauna: Composition, distribution, seasonal fluctuation and biomass. *Zool Afr* 13: 19-32.
- Dye AH, Lasiak TA 1986. Microbenthos, meiobenthos and fiddler-crabs – trophic interactions in a tropical mangrove sediment. *Mar Ecol Prog Ser* 32: 259-264.
- Eckman JE, Thistle D 1988. Small-scale spatial pattern in meiobenthos in the San Diego trough. *Deep-Sea Res* 35: 1565-1578.
- Eckman JE, Thistle D 1991. Effects of flow about a biologically produced structure on harpacticoid copepods in San Diego trough. *Deep Sea Res* 38: 1397-1416.
- Escaravage V, Castel J 1990. The impact of the lagoonal shrimp *Palaemonetes varians* (Leach) on meiofauna in a temperate coastal impoundment. *Acta Oecologica* 11: 409-418.
- Findlay RH, White DC 1983. The effects of feeding by the sand dollar *Mellita quinquesperforata* (Leske) on the benthic microbial community. *J Exp Mar Biol Mar* 72: 25-41.
- Fitch DHA, Bugajgaweda B, Emmons SW 1995. 18S Ribosomal-RNA gene phylogeny for some Rhabditidae related to Caenorhabditis. *Mol Biol Evol* 12 (2): 346-358.
- Gee JM, Warwick RM, Davey JT, George CL 1985. Field experiments on the role of epibenthic predators in determining prey densities in an estuarine mudflat. *Estuar Coast Shelf Sci* 21: 429-448.
- Gee JM 1987. Impact of epibenthic predation on estuarine intertidal harpacticoid copepod populations. *Mar Biol* 96: 497-510.
- Gerlach SA 1977. Attraction to decaying organisms as a possible cause for patchy distribution of nematodes in a bermuda beach. *Ophelia* 16: 151-165.
- Grassle JF, Sanders HL 1973. Life histories and the role of disturbance. *Deep Sea Res* 20: 643-659.
- Green MO, Hewitt JE, Thrush SF 1988. Seabed drag coefficient over natural beds of horse mussels (*Atrina zelandica*). *J Mar Res* 56: 613-637.
- Hanski I 1997. Predictive and practical metapopulation models: The incidence function approach. In D Tilman and P Kareiva eds, *Spatial Ecology*. Princeton University Press, Princeton, New Jersey: 21-45.
- Hartnoll RG 1973. Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. *Estuar Coast Shelf Sci* 1: 137-152.
- Hartnoll RG 1975. The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. *J Zool Lond* 177: 305-328.
- Hedqvist-Johnson K, Andre C 1991. The impact of the brown shrimp *Crangon crangon* L. On soft-bottom meiofauna: An experimental approach. *Ophelia* 34: 41-49.
- Hoffman JA, Katz J, Bertness MD 1984. Fiddler crab deposit-feeding and meiofaunal abundance in salt marsh habitats. *J Exp Mar Biol Ecol* 82: 161-174.
- Johnson RG 1970. Variations in diversity within benthic marine communities. *Am Nat* 104: 285-300.
- Katz J 1980. Effects of burrowing by the fiddler crab *Uca pugnax* (Smith). *Estuar Coast Shelf Sci* 11: 233-237.
- Kennedy AD 1993. Minimal predation upon meiofauna by endobenthic macrofauna in the Exe estuary, South West England. *Mar Biol* 117: 311-319.
- Lambshhead PJD 1993. Recent developments in benthology. *Oceanis* 19: 5-24.
- Lane JM, Lawrence JM 1982. Food, feeding and absorption efficiencies of the sand dollar, *Mellita quinquesperforata* (Leske). *Estuar Coast Shelf Sci* 14: 421-431.
- Macintosh DJ 1984. Ecology and productivity of Malaysian mangrove crab population (Decapoda: Brachyura) As. *Symp Mangr Env Res Manag UNESCO*, Paris: 354-377.

- Mattila J, Ólafsson EB, Johansson A 1990. Predation effects of *Crangon crangon* on benthic infauna on shallow sandy bottoms. In Barnes M, Gibson RN eds, Trophic relationships in the marine environment. Proc 24th Europ Mar Biol Symp Aberdeen Univ Press, Aberdeen: 503-516.
- Meziane T, Tsuchiya M 2000. Fatty acids as tracers of organic matter in the sediment and web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. *Mar Ecol Prog Ser* 200: 49-57.
- Meziane T, Sanabe MC, Tsuchiya M 2002. Role of fiddler crabs of a subtropical intertidal flat on the fate of sedimentary fatty acids. *J Exp Mar Biol Ecol* 270: 191-201.
- Nichols JA, Robertson JR 1979. Field evidence that the eastern mud snail *Ilyanassa obsoleta*, influences nematode community structure. *The Nautilus* 93: 44-46.
- Nilsson P, Sundback K, Jonsson B 1993. Effect of the brown shrimp *Crangon crangon* on endobenthic macrofauna, meiofauna and meiofaunal grazing rates. *Neth J Sea Res* 31: 95-106.
- Norkko A, Hewitt JE, Thrush SF, Funnell GA 2001. Benthic-pelagic coupling and suspension-feeding bivalves: Linking site-specific sediment flux and biodeposition to benthic community structure. *Limnol Oceanogr* 46: 2067-2072.
- Ólafsson E 1992. Small-scale spatial distribution of marine meiobenthos: The effects of decaying macrofauna. *Oecologia* 90: 37-42.
- Ólafsson E 1995. Meiobenthos in mangrove areas in eastern Africa with emphasis on assemblage structure of free-living marine nematodes. *Hydrobiologia* 312: 47-57.
- Ólafsson E, Moore CG 1990. Control of meiobenthic abundance by macroepifauna in a subtidal muddy habitat. *Mar Ecol Prog Ser* 65: 241-249.
- Ólafsson E, Moore CG, Bett BJ 1990. The impact of *Melinna palmata* Grube, a tube-building polychaete, on meiofaunal community structure in a soft-bottom subtidal habitat. *Estuar Coast Shelf Sci* 31: 883-893.
- Ólafsson E, Elmgren R 1991. Effects of biological disturbance by benthic amphipods *Monoporeia affinis* on meiobenthic community structure: A laboratory approach. *Mar Ecol Prog Ser* 74: 99-107.
- Ólafsson E, Moore CG 1992. Effects of macroepifauna on developing nematode and harpacticoid assemblages in a subtidal muddy habitat. *Mar Ecol Prog Ser* 84: 161-171.
- Ólafsson E, Elmgren R, Papakosta O 1993. Effects of the deposit-feeding benthic bivalve *Macoma balthica* on meiobenthos. *Oecologia* 93: 457-462.
- Ólafsson E, Ndaro SGM 1997. Impact of the mangrove crabs *Uca annulipes* and *Dotilla fenestrata* on meiobenthos. *Mar Ecol Prog Ser* 158: 225-231.
- Paine RT 1966. Food web complexity and species diversity. *Am Nat* 100: 65-75.
- Pihl L, Rosenberg R 1984. Food selection and consumption of the shrimp *Crangon crangon* in some shallow marine areas in western Sweden. *Mar Ecol Prog Ser* 15: 159-168.
- Pihl L 1985. Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Mar Ecol Prog Ser* 22: 169-179.
- Posey MH, Dumbauld BR, Armstrong DA 1991. Effects of burrowing mud shrimp, *Upogebia pugettensis* (Dana), on abundances of macro-infauna. *J Exp Mar Biol Mar* 148: 283-294.
- Reidenauer JA 1989. Sand-dollar *Mellita quinquesperforata* (Leske) burrow trails: Sites of harpacticoid disturbance and nematode attraction. *J Exp Mar Biol Ecol* 130: 223-235.
- Reise K 1978. Experiments on epibenthic predation in the Wadden Sea. *Helgol Wiss Meeresunters* 31: 55-101.
- Reise K 1981. High abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea. *Helgol Meeresunters* 34: 413-425.
- Reise K 1983. Biotic enrichment of intertidal sediments by experimental aggregates of the deposit-feeding bivalve *Macoma balthica*. *Mar Ecol Prog Ser* 12: 229-236.
- Reise K 1984. Experimental sediment disturbances on a tidal flat: Responses of free-living platyhelminthes and small polychaeta. *Hydrobiologia* 118: 73-81
- Reise K 1987. Spatial niches and long-term performance in meiobenthic plathelminthes of an intertidal lugworm flat. *Mar Ecol Prog Ser* 38: 1-11.
- Reise K, Ax P 1979. A meiofaunal 'thiobios' limited to the anaerobic sulfide system of marine sand does not exist. *Mar Biol* 54: 225-237.
- Robertson JR, Bancroft K, Vermeer G 1980. Experimental studies on the foraging behaviour of the sand fiddler crab *Uca pugilator*. *J Exp Mar Biol Mar* 44: 67-83.
- Robertson JR, Newell SY 1982. A study of particle ingestion by three fiddler crab species foraging on sandy sediments. *J Exp Mar Biol Mar* 65: 19-28.
- Rossi F, Chapman MG 2003. Influence of sediment on burrowing by the soldier crab *Mictyris longicarpus* Latreille. *J Exp Mar Biol Mar* 289: 181-195.
- Scherer B, Reise K 1981. Significant predation on micro- and macrobenthos by the crab *Carcinus maenas* L. in the Wadden Sea. *Kieler Meeresforsch* 5: 490-500.
- Schratzberger M, Warwick RM 1999a. Differential effects of various types of disturbances on the structure of nematode assemblages: An experimental approach. *Mar Ecol Prog Ser* 181: 227-236.
- Schratzberger M, Warwick RM 1999b. Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. *J Exp Mar Biol Mar* 235: 255-271.
- Schrijvers J, Okondo J, Steyaert M, Vincx M 1995. Influence of epibenthos on meiobenthos of the *Cerriops tagal* mangrove sediment at Gazi Bay, Kenya. *Mar Ecol Prog Ser* 128: 247-259.
- Smith LD, Coull BC 1987. Juvenile spot (pisces) and grass shrimp predation on meiobenthos in muddy and sandy substrata. *J Exp Mar Biol Ecol* 105: 123-136.
- Suchanek TH, Colin PL 1986. Rates and effects of bioturbation by invertebrates and fishes at Enewetak and Bikini atolls. *Bull Mar Sci* 38: 25-34.
- Sundelin B, Elmgren E 1991. Meiofauna of an experimental soft bottom ecosystem- effects of macrofauna and cadmium exposure. *Mar Ecol Prog Ser* 70: 245-255.
- Tansley AG, Adamson RS 1925. Studies of the vegetation of the English chalk. Iii. The chalk grasslands of the Hampshire-Sussex border. *J Ecol* 5: 173-179.

- Teal JM 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43: 614-624.
- Thistle D 1979. Deep-sea harpacticoid copepod diversity maintenance: The role of polychaetes. *Mar Biol* 52: 371-376.
- Thistle D 1980. The response of a harpacticoid copepod community to a small-scale natural disturbance. *J Mar Res* 38: 381-395.
- Thistle D 1982. Aspects of the natural history of the harpacticoid copepods of San Diego trough. *Biol Oceanogr* 1: 225-238.
- Thistle D, Eckman JE 1990. The effect of biologically produced structure on the benthic copepods of a deep-sea site. *Deep-Sea Res* 37: 541-554.
- Tita G, Desrosiers G, Vincx M, Nozais C 2000. Predation and sediment disturbance effects of the intertidal polychaete *Nereis virens* (Sars) on associated meiofaunal assemblages. *J Exp Mar Biol Ecol* 243: 261-282.
- Ullberg J, Ólafsson E 2003. Effects of biological disturbance by *Monoporeia affinis* (Amphipoda) on small-scale migration of marine nematodes in low-energy soft sediments. *Mar Biol* 143: 867-874
- Urakawa H, Yoshida T, Nishimura Y, Ohwada K 2000. Characterization of depth-related population variation in microbial communities of a coastal marine sediment using 16S rDNA-based approaches and quinone profilig. *Environmental Microbiology* 2: 542-554.
- Varon R, Thistle D 1988. Response of a harpacticoid copepod to a small-scale natural disturbance. *J Exp Mar Biol Mar* 118: 245-256.
- Warwick RM 1984. Species size distributions in marine benthic communities. *Oecologia* 61: 32-41.
- Warwick RM, Gee JM, Berge JA, Ambrose W, Jr. 1986. Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. *Sarsia* 71: 11-16.
- Warwick RM, Clarke KR, Gee JM 1990. The effect of disturbance by soldier crabs *Mictyris platycheles* H Milne Edwards on meiobenthic community structure. *J Exp Mar Biol Ecol* 135: 19-33.
- Warwick RM, Clarke KR 1993. Increased variability as a symptom of stress in marine communities. *J Exp Mar Biol Ecol* 172: 215-226.
- Warwick RM, McEvoy AJ, Thrush SF 1997. The influence of *Atrina zelandica* Gray on meiobenthic nematode diversity and community structure. *J Exp Mar Biol Ecol* 214: 231-247.

Reçu le 14 novembre 2003; received November 24, 2003
Accepté le 27 novembre 2003; accepted November 27, 2003

