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THE MEIOFAUNA OF COASTAL LAGOON ECOSYSTEMS AND THEIR IMPORTANCE IN THE FOOD WEB

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LAGUNES
MEIOFAUNE
DISTRIBUTION
RÉSEAU TROPHIQUE

RÉSUMÉ – Les études de méiobenthologie en milieu lagunaire sont bien moins nombreuses que celles portant sur les autres environnements marins littoraux. En moyenne dans les sédiments marins, l'abondance du méiobenthos est de l'ordre de 10^6 ind. m^{-2} . En milieu lagunaire cette valeur représente plutôt la limite basse des densités de populations, malgré de fortes variations, à la fois dans le temps et dans l'espace. Contrairement au milieu marin, les Nématodes et les Copépodes Harpacticoïdes ne sont pas toujours les taxons dominants dans les lagunes à cause d'une grande diversité environnementale. La salinité est considérée comme un facteur clé dans les estuaires et les lagunes. Toutefois, pour le méiobenthos, les groupements établis en fonction de la salinité seule apparaissent artificiels, la nature du sédiment devant être prise en compte. De plus, à côté du régime de salinité, le degré d'isolement de la lagune (par rapport à la mer d'une part, par rapport aux eaux douces d'autre part) induit des évolutions différentielles d'abondance et de distribution des espèces. La méiofaune constitue une source de nourriture importante pour les juvéniles (30-60 mm) de Poissons, notamment ceux d'intérêt économique, particulièrement abondants dans les lagunes. Les Copépodes sont consommés sélectivement mais l'impact de la prédation sur leurs populations apparaît faible. Dans certaines lagunes isolées l'activité fouisseuse de Poissons plats ou d'espèces de la macrofaune invertébrée peut favoriser l'abondance de la méiofaune probablement en permettant une meilleure oxygénation du sédiment et en stimulant l'activité bactérienne. Ceci illustre la forte réactivité du sédiment lagunaire en comparaison avec la mer ouverte. Finalement, il apparaît souhaitable d'intensifier les études de méiobenthologie en milieu lagunaire pour répondre à des questions générales relatives à l'écologie ainsi qu'à des questions plus particulières concernant la biologie des organismes. En effet, l'accessibilité et la faible profondeur des lagunes les rendent particulièrement propices à des études expérimentales sur le terrain. D'autre part, les lagunes étant peuplées par un petit nombre d'espèces mais abondantes, les études de dynamique de populations et de production du méiobenthos, qui font grandement défaut, devraient être facilitées.

COASTAL LAGOONS
MEIOFAUNA
DISTRIBUTION
FOOD WEB

ABSTRACT – Meiobenthic studies in coastal lagoons are much less numerous than those concerning other littoral marine habitats. Meiofaunal numbers typically average 10^6 ind. m^{-2} in marine sediments. For coastal lagoons this value represents the low limit of meiofaunal abundance despite the high degree of variation, both in time and in space. Contrary to the marine environment, nematodes and Harpacticoid copepods are not always the most abundant taxa in lagoons because of the variety of the habitats. Salinity is considered as a key factor in estuaries and lagoons. However, groupings according to salinity alone appear to be artificial, the type of sediment must be taken into account. Furthermore, besides the salinity regime, the degree of isolation of the lagoon (from the sea on the one hand, from the river on the other) induces differential patterns of abundance and species distribution. Meiofauna are an important food for the small (30-60 mm) juveniles of some commercially important fish which are particularly abundant in coastal lagoons. Copepods are selectively consumed, but the impact of predation on Copepod populations is rather low. In some isolated lagoons the foraging activity of flatfish or other invertebrate macrofauna may promote meiofauna abundance by favouring oxygenation of the sediment and stimulating bacterial activities. This illustrates the strong reactivity of coastal lagoon sediments compared to the open sea. Finally, it is suggested to increase meiobenthic research in coastal lagoons in order to answer general question about ecology and to study in detail the life cycle of meiobenthic species. Due to their easy access and shallowness, coastal lagoons are particularly convenient for manipulative experiments. Since lagoons are populated by few species but in great numbers, life cycle and production studies, which are very few, should be easier.

INTRODUCTION

The term "meiobenthos" was introduced by Mare (1942) to describe fauna of intermediate size-animals, smaller than those traditionally classified as "macrobenthos", but larger than "microbenthos" including bacteria and most protozoa. Despite a certain vagueness in the definition, it is conventionally accepted that in operational terms, meiobenthos refers to those organisms which pass through a 0.5-1 mm sieve and are retained on a sieve with mesh width smaller than 0.1 mm (0.06 or 0.04 mm).

In shallow brackish waters, the ecological role of meiofauna has a twofold interest. Meiobenthic organisms have an important function in the remineralization processes in the sediment by reworking the detritus and enhancing the recycling of organic matter. On the other hand meiobenthic organisms constitute an important food source for young benthophageous fish such as flatfish and mugilid fish which are important resources for man in coastal lagoons.

Although the importance of meiofauna has been recognized since the 1970's, meiobenthic studies in coastal lagoons are much less numerous than those concerning sandy beaches, estuaries and marine subtidal areas. This lack of interest is surprising since lagoons cover 13 % of the world

coastal zone, most of them having an economic interest. Perhaps one explanation can be found considering geographical and socio-economical aspects. Most of the coastal lagoons are situated in developing countries which have not a sufficient scientific background or not enough money for meiobenthic studies.

In the present paper I will review the original features of meiofauna living in coastal lagoons. Two main aspects will be taken into account: (i) the distribution of meiofauna and its relation to salinity gradients and (ii) the place of meiofauna in the food web. Readers interested in more general aspects can refer to McIntyre (1969), Fenchel (1978), Coull & Bell (1979). Excellent reviews exist for the dominant taxa: nematodes (Heip *et al.*, 1985), Harpacticoids (Hicks & Coull, 1983), oligochaetes (Giere, 1975), turbellarians (Martens & Schockaert, 1986).

DISTRIBUTION OF MEIOFAUNA IN LAGOON ENVIRONMENTS

Meiofaunal numbers typically average 10^6 ind. m^{-2} in marine sediments (Coull & Bell, 1979). Densities tend to increase in detritus-rich muddy sediments with the highest values in intertidal

Tabl. I. - Mean abundance of meiofauna in various lagoon ecosystems. Ranges of abundance are given for the dominant taxa.

Sites	Depth	Total meio (ind. m^{-2})	Nematoda (ind. 10 cm^{-2})	Copepoda (ind. 10 cm^{-2})	Others (ind. 10 cm^{-2})	Authors
Lagoonal environments						
Lagoon of Tunis, Tunisia	0.80 m	$5.70 \cdot 10^6$				Vitiello & Aissa (1979)
Mouth of the Pô, Italy	1.5-4 m	$5.43 \cdot 10^6$	460-11,507	6-775	34-6651	Ceccherelli & Cevdalli (1981)
Knysna Lagoon, South Africa	intertidal	$5.23 \cdot 10^6$				Dye (1977)
Bayou (Louisiana), USA	0-1 m	$2.31 \cdot 10^6$	875-4500	6-146		Fleeger (1985)
Arcachon (1984-1985), France	0.2-0.4 m	$2.11 \cdot 10^6$	185-2400	30-1080	54-1356	Escaravage & Castel (1989)
Lagoon of Tunis, Tunisia	0.4-0.8 m	$2.08 \cdot 10^6$	1400-2300	6-136	85-340	Aissa & Vitiello (1984)
Brackish pond (Louisiana), USA	0.5 m	$1.37 \cdot 10^6$	320-2790	53-307		Phillips & Fleeger (1985)
Niva Bay, Denmark	0.2-0.6 m	$1.26 \cdot 10^6$	310-1400	32-2060	56-452	Muus (1967)
Arcachon (1975-1976), France	0.3-0.5 m	$1.09 \cdot 10^6$	200-12,600	13-1660	1-3950	Lasserre <i>et al.</i> (1976), Castel (1984a)
Marisma de Chinquihue, Chile	intertidal	$1.08 \cdot 10^6$	270-2170			Clasing (1976)
Lake Grevelingen, The Netherlands	3 m	$1.05 \cdot 10^6$	300-2400	6-600	1-276	Willems <i>et al.</i> (1984)
Szczecin Lagoon, Poland	4 m	$0.26 \cdot 10^6$	0-?			Radziejewska & Drzycimski (1988)
Mangrove swamps						
Hunter river, Australia	intertidal	$3.40 \cdot 10^6$	55-11,763	0-71		Hodda & Nicholas (1986)
Mngazana, South Africa	intertidal	$2.46 \cdot 10^6$	620-4110	30-780	110-640	Dye (1983)
Kakinada Bay, India	intertidal	$2.13 \cdot 10^6$	483-4850	8-309		Kondalarao & Ramanamurty (1988)
Cape York, Australia	intertidal	$0.30 \cdot 10^6$	3-987	0-57	18-1446	Alongi (1987)
Exploited lagoon ecosystems						
Marennes (clams), France	0.5 m	$4.71 \cdot 10^6$	1354-5781	139-3088	11-7026	Castel (1984a)
Arcachon Bay (oysters), France	intertidal	$4.17 \cdot 10^6$	683-7252	18-207	8-366	Castel <i>et al.</i> (1989)
Bay of Morlaix (oysters), France	3.5 m	$3.15 \cdot 10^6$				Boucher & Boucher-Rodoni (1984)
Ile Tudy (clams), France	1 m	$2.24 \cdot 10^6$	890-4475	51-998	5-796	Castel (1984b)

mudflats of estuaries, lagoons or saltmarshes. For lagoons it is likely that 10^6 ind. m^{-2} represents the low limit of meiofaunal abundance (Table I). The very low values recorded in Baltic lagoons could be due to strong eutrophication and heavy pollution (Radziejwska & Drzycimski, 1988). In polluted part of the lagoon of Tunis, Aissa & Vitiello (1984) recorded a mean density of $0.72 \cdot 10^6$ ind. m^{-2} , to be compared with values of 2.08 and $5.43 \cdot 10^6$ ind. m^{-2} in the non polluted zone. Mangrove swamps are not exclusively found in lagoon environments, most of them are situated in sheltered estuarine areas. Mangroves are located in tropical and subtropical zones, however, when compared with many studies of estuarine muds elsewhere in the world, the densities reported in all the mangroves studies tend to be rather low. On the basis of density, mangroves appear to occupy a position intermediate between mud flat and salt marsh meiofauna (Dye, 1983). It seems that plant density is a determining factor in meiofauna distribution, and this could explain the variability existing between the different mangroves studies (Table I). Highest mean meiofaunal densities are found in lagoons which are exploited, especially where bivalves are cultivated. Several studies indicate that organic-rich bivalve biodeposits favour meiofauna by an increase of the trophic resources (Castel, 1984b; Castel *et al.*, 1989). All the studies mentioned in Table I show great variations in abundance, both in time and space, which is a common feature for lagoonar meiofauna.

Nematodes and Harpacticoid copepods are usually the two most abundant taxa in all sediments. This may not be the case in lagoons. This lack of uniformity in the dominance pattern of the dominant meiofaunal groups is due to the variety of lagoon environments. In Cape York mangroves (Australia), Alongi (1987) found turbellarians to be the dominant taxon (58-67 %), followed by nematodes (27-31 %) and copepods (3-5 %). In the semi-enclosed lagoons of Arcachon Bay, Escaravage & Castel (1989) reported the following percentages: nematodes: 50-85 %, turbellarians: 8-33 % and copepods: 7-25 %. Turbellarians are resistant to desiccation and are able to reproduce intensively as soon as the hydrodynamical conditions become better (Armonies, 1986). Indeed, Alongi (1987) showed that turbellarians were significantly more abundant in summer when monsoonal rains occurred than during the winter dry season. In the man-made lagoons of Arcachon Bay, variations of the water level are frequent. The sediment may be air-dried for several days before filling the ponds. This may favour opportunistic turbellarians and may explain their relatively high numbers.

In some cases ostracods constitute the second most abundant taxon, after the nematodes. Clasing (1976) found a proportion of 8-27 % in the Chin-

Tabl. II. - Salinity tolerance of the dominant meiobenthic Nematodes and Copepods living in the lagoonar fish ponds of Arcachon Bay. Except when otherwise mentioned, the tolerance is from sea water (35 ‰) at the upper level to the noted salinity value on the lower level. For Nematodes, values are from field data. For Copepods, the limits were determined both from field data and in experimental conditions. (1) Lasserre *et al.*, 1976; (2) references in Heip *et al.*, 1985; (3) Garcia-Lanciego, 1990; (4) Raibaut, 1967; (5) Castel & Lasserre, 1977; (6) original data.

Species	Salinity (ppt)	References
Nematoda		
<i>Aegialoalaimus elegans</i>	27	(3)
<i>Anaplosoma viviparum</i>	0.5	(2)
<i>Axonolaimus demani</i>	32	(3)
<i>Calomicrolaimus honestus</i>	0.5	(2)
<i>Cervonema tenicaudata</i>	34	(3)
<i>Chromadora macrolaima</i>	27-37	(3)
<i>Chromadora nudicapitata</i>	25-84.5	(2, 3)
<i>Chromadorina germanica</i>	9-40	(1, 3)
<i>Cyatholaimus gracilis</i>	21-43	(3)
<i>Daptonema oxycerca</i>	0.9-43	(2, 3)
<i>Daptonema setosum</i>	0.5	(1)
<i>Diplolaimella stagnosa</i>	11-43	(3)
<i>Eurystomina ornata</i>	16	(3)
<i>Halalaimus amphidellus</i>	32	(3)
<i>Halalaimus gracilis</i>	7.5	(2)
<i>Mesotheristus setosus</i>	25-34	(3)
<i>Metachromadora remanei</i>	5.3-43	(2, 3)
<i>Metoncholaimus albidus</i>	16-43	(3)
<i>Molgolaimus lazonus</i>	39	(3)
<i>Monhystera anophtalma</i>	18-43	(3)
<i>Neochromadora paratectia</i>	21-43	(3)
<i>Neochromadora peocilosomoides</i>	18	(1)
<i>Oncholaimus paralangrunensis</i>	21	(3)
<i>Paracanthonchus caecus</i>	0.5	(2)
<i>Paracomesoma dubium</i>	16	(3)
<i>Prochromadorella ditlevseni</i>	32	(3)
<i>Ptycholaimellus ponticus</i>	0.5-43	(1, 3)
<i>Sabatieria ornata</i>	39	(3)
<i>Sabatieria punctata</i>	0.5-40	(2, 3)
<i>Sabatieria vasicola</i>	39	(3)
<i>Spirinia parasetifera</i>	21-43	(3)
<i>Symplocostoma tenuicolle</i>	27	(3)
<i>Terschellingia longicaudata</i>	0.9	(1)
<i>Thalassironus bipartitus</i>	40	(3)
<i>Thalassolaimus tardus</i>	22	(2)
<i>Theristus acer</i>	5.3	(2)
<i>Viscosia glabra</i>	0.9	(2)
Copepoda		
<i>Amonardia normani</i>	6-54	(5)
<i>Bulbamphiascus inermis</i>	15-53	(5)
<i>Canuella perplaxa</i>	0.5-70	(4)
<i>Cletocamptus confluens</i>	0.5-60	(5)
<i>Cyclopina gracilis</i>	7-64	(5, 6)
<i>Ectinosoma melaniceps</i>	13-37	(6)
<i>Enhydrosoma caeni</i>	11-39	(6)
<i>Enhydrosoma gariene</i>	3-39	(6)
<i>Halectinosoma curticorne</i>	5-32	(6)
<i>Halicyclops neglectus</i>	3-49	(5, 6)
<i>Harpacticus littoralis</i>	7-67	(4)
<i>Heterolaophonte strömi</i>	7-72	(5)
<i>Mesochra lilljeborgi</i>	4-85	(4)
<i>Microarthridion fallax</i>	8-35	(6)
<i>Nannopus palustris</i>	0.5-38	(6)
<i>Nitocra lacustris</i>	3-34	(4)
<i>Paracyclopina nana</i>	3-35	(5)
<i>Tachidius discipes</i>	0.5-32	(5)
<i>Tisbe holothuriae</i>	9-39	(6)

quihue marsh and Radziejewska & Drzycimski (1988) indicated that ostracods constituted 17 to 43 % of the total meiofauna in Szczecin lagoon. The prominence of ostracods seems to be a typical feature in eutrophic and polluted Baltic coastal lagoons. Sometimes oligochaetes can constitute a non negligible component of meiofauna. For instance, Dye (1983) reported the following numbers from a South African mangrove : nematodes : 80.4 %, copepods : 6.4 %, oligochaetes : 4.7 %. Fleeger (1985) found oligochaetes in significant numbers in a bayou where the salinity ranged from 3-26 ‰. This latter observation corroborates the fact that marine oligochaetes prefer oligohaline and mesohaline conditions (Giere, 1975).

It has been known for many decades that benthic communities in brackish water have fewer species than either marine or freshwater communities (Remane, 1933). This is also true for meiofauna. For instance, Bilio (1966) listed 60, 59, 2 and 4 meiofauna species in eu-, poly-, meso- and oligohaline water, respectively. Heip *et al.* (1985) listed the dominant brackish water and marine nematodes invading brackish water. From the 155 species listed, only 18 are restricted to brackish water.

Brackish water nematodes have been divided into six groups according to salinity by Gerlach (1953) and this was later followed and adapted by several authors. However, such groupings appear to be artificial and differ from place to place; different environmental factors may interact, the most important being type of sediment. As an example, the structure of meiobenthic copepod assemblages was investigated from a range of sediment types collected in nine different biotopes along the French Atlantic coast (Castel, 1986). The sampling stations were representative of estuarine and lagoon environments with salinities ranging from 0.5 to 38 ‰. Using correspondence analysis it was shown that two stations with similar salinity regime had low faunistic affinity because the sediments differed greatly (% silt : 2-5 % and 80-90 % respectively). On the other hand, two stations with high faunistic affinity had different salinity regimes (0.5-23.5 ‰ and 22.4-34.8 ‰ respectively) but quite similar sediment characteristics (% silt : 80-99 % and 80-90 % respectively). Thus, sediment structure is probably a prominent factor in explaining the gradients of faunal assemblages.

Another factor that could influence the distribution of meiofauna is the degree of isolation. By definition lagoons are bodies of water connected to the sea by an inlet. Thus, lagoons are semi-isolated from the sea and a gradient of salinity (either positive or negative) is found from the inlet to the inner part of the lagoon. Salinity is regarded

by most authors as the abiotic master factor in brackish water habitats. However, brackish water species are strongly euryhaline (Table II). They are adapted, not only to low or high salinity, but also to fluctuations. So, one can wonder whether salinity or water regime characteristics, e.g. connection to freshwater and marine habitats, determine the species composition in lagoon environments.

The importance of isolation in structuring meiobenthic communities was suggested by Escaravage & Castel (1989). They studied more specifically meiobenthic copepods living in the dyked lagoons of Arcachon Bay by sampling different points located at an increasing distance from the sluice. The isolation from the sea resulted either in under- or over-salinity, depending on the presence or the absence of freshwater input. Dilution of seawater had two origins : direct input by a river in one case (station LT in Fig. 1) or rain and groundwater in the other (station C1 in Fig. 1). The abundance of meiofauna in the most oligohaline stations was very low (Fig. 1-A) which is a common observation for meiobenthos living near freshwater inputs (Hicks & Coull, 1983). Highest densities were found in the isolated and hypersaline stations. Nematodes were dominant near the marine input on the one hand, near the river input on the other. The species richness and diversity (Shannon index) of Copepods showed two peaks corresponding to fluvial influence on the one hand, to marine intrusion on the other (Fig. 1-B). The most isolated stations had lowest number of species and diversity. Four species constituted the bulk of the copepod community. *Canuella perplexa* dominated in the station situated near the sluice and decreased in abundance in the isolated stations (Fig. 1-C). *Halicyclops neglectus* and *Paracyclops nana* characterized the stations submitted to direct fluvial influence. In the stations characterized by the absence of external influence, *Cletocamptus confluens* was always dominant, whatever the salinity regime (2-15 ‰ in station C1 and 9-53 ‰ in station C5). Raibaut (1967) observed a similar pattern of distribution for meiobenthic Copepods living in the hypersaline lagoons of Camargue (12-102 ‰). *Canuella perplexa* associated to *Mesochra lilljeborgi* were the dominant species in the channel connecting the lagoon with the sea, whereas *Cletocamptus retrogressus* was dominating in the inner lagoon. From these examples it is clear that : (1) the species composition is different in two hypohaline areas of identical salinity if one area is submitted to direct fluvial input and the other is subject to dilution by rain and groundwater, and (2) the species composition may be the same in two areas with different salinity if their degree of isolation is identical.

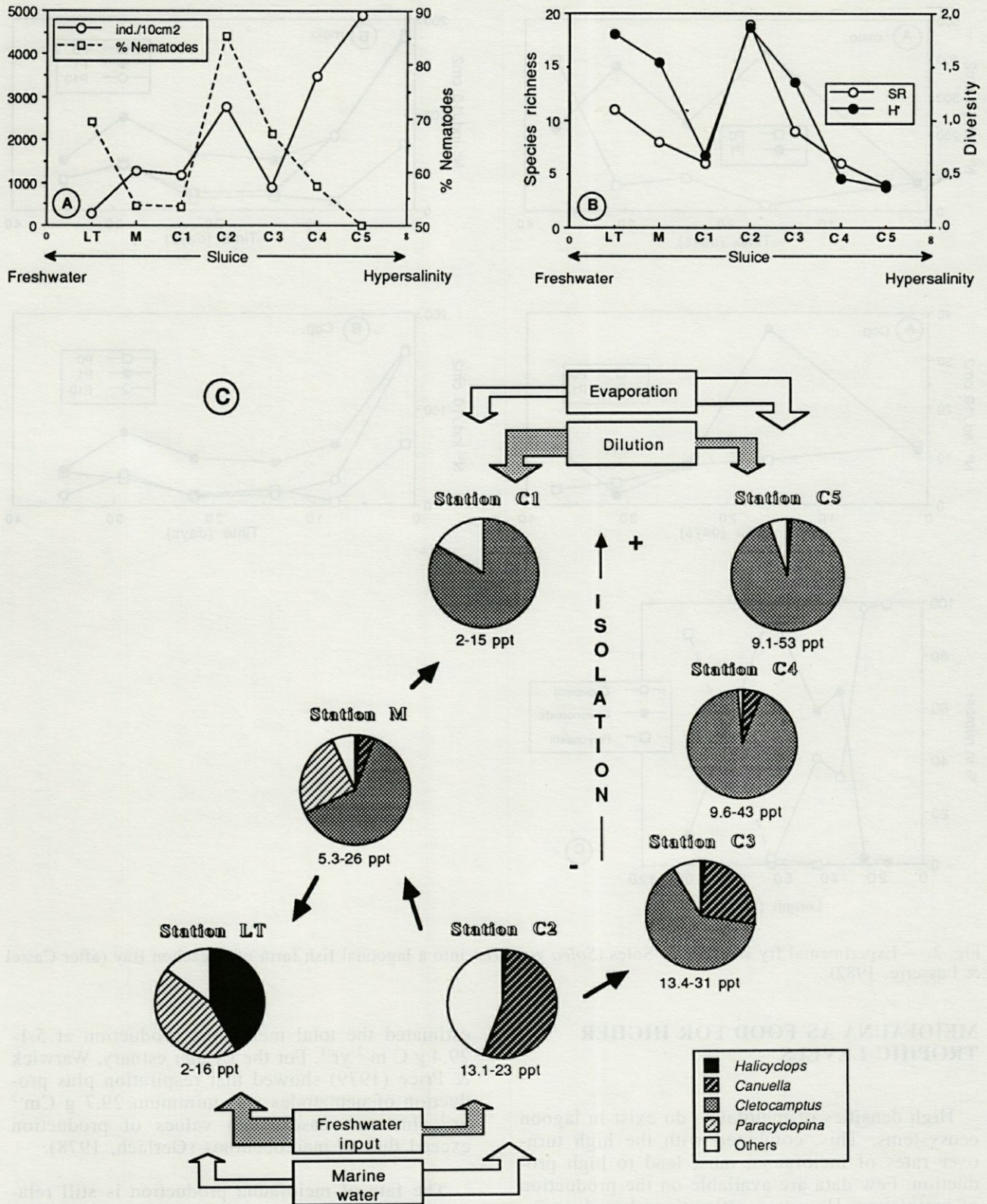


Fig. 1. - Meiobenthic copepods of the dyked lagoons of Arcachon Bay (modified from Escaravage & Castel, 1989). Station C2 : situated near the sluice connecting the lagoon to marine water. Station C5 : isolated, hypersaline station except during rainfall. Station C1 : isolated hypohaline station diluted by groundwater. Station LT : submitted to direct fluvial input.

A, Average abundance (ind. 10 cm⁻²) and % nematodes relative to the total meiofauna. B, Variation of the copepod species richness (SR) and diversity (Shannon index, H'). C, Relative abundance (in percent) of the dominant copepod species. The annual salinity range is indicated for each station.

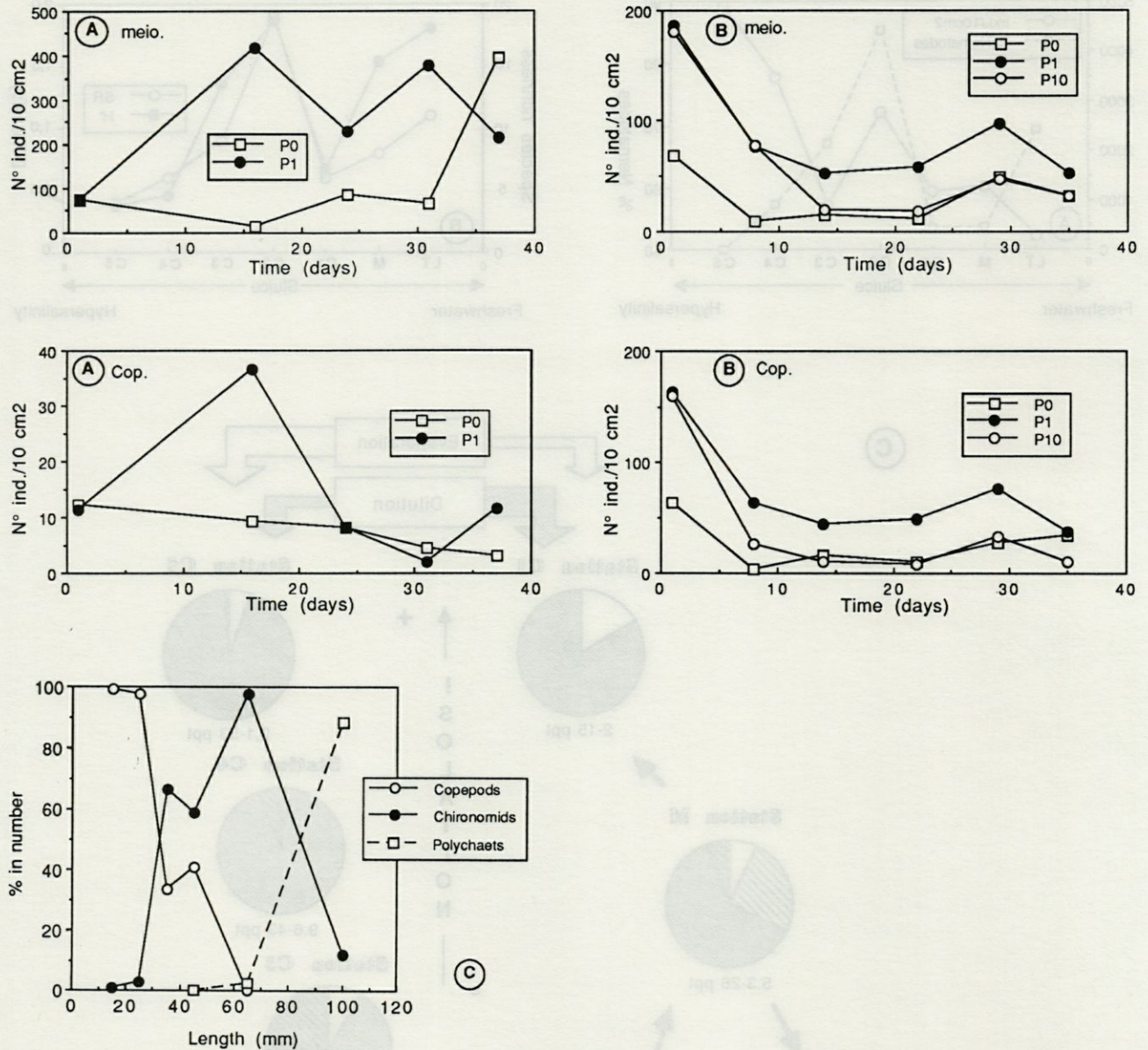


Fig. 2. - Experimental fry stocking of *Soles* (*Solea vulgaris*) into a lagoonal fish farm of Arcachon Bay (after Castel & Lasserre, 1982).

MEIOFAUNA AS FOOD FOR HIGHER TROPHIC LEVELS

High densities of meiofauna do exist in lagoon ecosystems. This, combined with the high turnover rates of meiofauna, must lead to high production. Few data are available on the production of meiofauna. However, estimations based on indirect methods and/or extrapolations indicate that meiofaunal production in estuarine and lagoonal areas is in the order of grams C m⁻² yr⁻¹. For instance, in the fish ponds of Arcachon Bay, Garcia-Lanciego (1990) computed values between 1 and 7 g C m⁻² yr⁻¹. In the oyster parks and seagrass beds of Arcachon Bay, Escaravage *et al.* (1989)

estimated the total meiofauna production at 5.1-29.4 g C m⁻² yr⁻¹. For the Lynher estuary, Warwick & Price (1979) showed that respiration plus production of nematodes was minimum 29.7 g C m⁻² yr⁻¹. In most cases such values of production exceed that of macrobenthos (Gerlach, 1978).

The fate of meiofauna production is still relatively unknown. Initially, meiofauna were thought to be an energetic dead-end and Mc Intyre (1971) suggested that meiofauna populations were controlled principally through internal predation. Examples of such predation are numerous (see Gee, 1989) but the real impact on the populations remains to be clarified. Heip & Smol (1976) calculated that, in a Belgian brackish water pond, much

Tabl. III. – Diet of six juvenile fish (Lt < 50 mm) living in the brackish ponds of Arcachon Bay (after Castel, 1985). Frequency of occurrence (in %) of the prey copepods. P = pelagic, E = epibenthic, B = burrowing.

		<i>Dicentrarchus</i> <i>labrax</i>	<i>Atherina</i> <i>boyeri</i>	<i>Gambusia</i> <i>affinis</i>	<i>Gasterosteus</i> <i>aculeatus</i>	<i>Mugil sp</i> <i>Liza ramada</i>	<i>Pomatoschistus</i> <i>microps</i>
<i>Temora longicornis</i>	P	1.9					
<i>Paracalanus parvus</i>	P	1.9				7.4	
<i>Euterpina acutifrons</i>	P	9.4	7.7				
<i>Acartia grani</i>	P	5.7	5.4				
<i>Acartia bifilosa</i>	P	74.1	16.9			40.7	
<i>Cyclopina gracilis</i>	E	1.9	16.2	41.2			9.1
<i>Mesochra lilljeborgi</i>	E	1.9	6.2		25.0	3.7	
<i>Ectinosoma melaniceps</i>	E	1.9	6.9	50.0		3.7	
<i>Tisbe sp</i>	E	17.0	3.8			7.4	9.1
<i>Amonardia normani</i>	E	3.8	43.1	66.7	62.5	7.4	27.3
<i>Heterolaophonte strömi</i>	E		7.7	33.3	25.0		27.3
<i>Harpacticus littoralis</i>	E	3.8	9.2	33.3	37.5		
<i>Paradactylopodia sp</i>	E	3.8	0.8			11.1	
<i>Halicyclops neglectus</i>	E	1.9				3.7	
<i>Halactinosoma curticorne</i>	B				25.0	3.7	
<i>Tachidius discipes</i>	B	7.5	13.8	16.7	37.5	22.2	63.6
<i>Bulbamphiascus inermis</i>	B					3.7	
<i>Nannopus palustris</i>	B	1.9					
<i>Paraleptastacus spinicauda</i>	B		3.8				18.2

of the production of Harpacticoid copepods could be consumed by the predatory Polyp *Protohydra leuckarti*, however in most studies dealing with intra-meiofaunal predation, quantitative data are lacking.

Over the past fifteen years, research on feeding of larger organisms has shown that meiofauna are much more integrated into the food webs. Evidence that selective deposit-feeding macrofauna, predatory macroinfauna and epibenthic crustacea utilize meiofauna becomes stronger and stronger (Coull & Bell, 1979; Gee, 1989). Similarly, it is now clear that there is a significant transfer of energy directly from meiofauna to fish. Flatfish and gobies, which are frequent in coastal lagoons, appear to be the main group of fish feeding on meiofauna. Other species of fish feeding on meiofauna include Mulletts (Lasserre *et al.*, 1976) which are prevalent in muddy habitats. Mangrove swamps (Odum & Heald, 1972) are inhabited by a wide variety of small, meiofauna-eating fish.

Meiofauna are small animals and are therefore most likely to be consumed by juvenile fish. Data from literature (see Gee, 1989) show that meiofauna form a significant food only for fish up to 30-60 mm (example in Fig.2). Furthermore, these data suggest that the switch from meiofauna to other sources of food is often very rapid.

Although nematodes are generally dominant in the sediments, their abundance in fish stomachs is negligible. In most instances, fish appear to consume copepods in preference to any other meiofaunal organisms. The selection for meiobenthic copepods is related to the behaviour of the fish. An example is given in Table III. The diet of six species of juvenile fish (Lt < 50 mm) was investigated in the fish ponds of Arcachon Bay (Castel,

1985). The preference was determined using the frequency of occurrence of copepod species in the stomachs. Copepods were classified according to Castel & Lasserre (1977) as planktonic, epibenthic and burrowing species. All fish fed primarily on copepods. Their overall frequency of occurrence in the fish foregut varied between 63 % and 100 %. Two other groups were also ingested, i.e. amphipods (F = 1-34 %) and chironomids (F = 21-53 %), but copepods were always the preferred preys. Amongst the copepods all ecological types were captured, from pelagic to burrowing species. However, some differences existed between the species of fish. The Sea Bass (*Dicentrarchus labrax*) mainly fed on pelagic copepods (F = 78 %) and secondarily on epibenthic species (F = 44.1 %). The Stickleback (*Gasterosteus aculeatus*), the Mosquitofish (*Gambusia affinis*) and the Smelt (*Atherina boyeri*) principally fed on epibenthic Copepods. However, the Stickleback and the Mosquitofish, which live in the shallowest part of the studied lagoon, are able to ingest significantly burrowing Copepod species (F = 37.5 and 16.7 % respectively), contrary to the Smelt which is more pelagic. Mulletts (*Mugil sp*, *Liza ramada*) and Gobies (*Pomatoschistus microps*) are the most benthophageous fish.

Furthermore, meiofauna-eating fish are able to select certain species of Copepods. Gee (1987) showed that, in a sandflat, Flatfish and Gobies were feeding almost exclusively on one species, *Asellopsis intermedia*, irrespective of its abundance in the sediment. During an acclimation experiment of Sole (*Solea vulgaris*) in the fish ponds of Arcachon Bay, Castel & Lasserre (1982) observed that the copepod *Cletocamptus confluens* was never eaten although it represented 26-47 % of the copepod fauna in the sediment. The Sole

preferred *Halicyclops neglectus* and *Paracyclopina nana* which live at the sediment surface. Gee (1989) discussed the selection of copepods in the fish diet. Generally fish locate their prey and pick individual items. The activity levels of copepods make them more vulnerable to predation. Furthermore, the superficial distribution of copepods makes them more available than nematodes. So far, only the Mullet, which feeds by indiscriminately sucking up the surface of the mud, has been reported to have a higher proportion of nematodes than copepods in the diet at size when they become detritivores (Lasserre *et al.*, 1976).

A few authors have attempted to quantitatively estimate the uptake of meiofauna (principally Harpacticoid copepods) by fish to determine whether food limitation might be a factor in the survival of juvenile fish, whether predation might have a significant influence on Harpacticoid population dynamics. Feller & Kaczynski (1975), studying the predation of meiobenthos by juvenile Salmon observed that the density of Harpacticoid copepods decreased by a factor 3 between April and May. Conversely, Sibert *et al.* (1977), in another site, calculated that the total biomass of copepods represented 22 times the food requirements of the juvenile Salmon between March and May. However, Sibert (1979) indicated that the productivity of *Harpacticus uniremis*, the principal prey, was only slightly higher than these food requirements. In a Bermuda lagoon, only 0.1 % of a population of *Longipedia helgolandica* might disappear daily due to the predation by juvenile Pomasyidae (Alheit & Scheibel, 1982). In contrast, in a sublittoral fine sand site, Morais & Bodiou (1984) calculated that the Solonette (*Buglossidium luteum*) could consume between 56 % and 137 % of *Longipedia scotti* production.

From these studies, it appears that the impact of predation on copepods varies greatly from site to site and/or from one predator to the other. In his review of meiofauna as food for fish, Gee (1989) indicated that the impact of fish predation on meiofauna populations seems to be greater in sublittoral muddy sediments than in intertidal sediments. Thus it can be hypothesized that the impact of predation might be significant in lagoons which are in great part subtidal and where the sediment is often muddy. Unfortunately, quantitative data are very scarce. However, in one study by Castel & Lasserre (1982) fry stocking trials of Soles (*Solea vulgaris*) into lagoonal impoundments of Arcachon Bay have been made to estimate the influence of predatory activity on the food web. The interacting mechanism meiofauna-Sole was studied in experimental enclosures stocked with one Sole/m² and ten Sole/m², and compared to control enclosures (no Soles). Juvenile Soles, measuring 20-30 mm, feed selectively on copepods (Fig. 2-C); for 1 Sole/m²,

meiofaunal abundance, outside copepods which stayed at the same level, was increased significantly (Fig. 2-A). For 10 Sole/m², the abundance of all meiofauna populations decreased. Using Soles measuring > 80 mm (thus non feeding on meiofauna) at a density of 1 ind./m², all meiofauna groups, including copepods, were increased (Fig. 2-B). From these observations it can be concluded that: i) a high concentration of predators is necessary to significantly affect copepod populations and, ii) at reasonable densities Sole are able to promote meiofauna abundance. The high density of Sole used in this study (10 ind./m²) is much more than numbers found in natural conditions. Considering the high turnover rates of copepods in coastal lagoons it seems unlikely that fish predation could seriously affect their abundance. Furthermore, these observations support Gee's (1989) suggestion that copepods could be used in mariculture. One unexpected finding was the promotion of meiofauna by the presence of Soles. Such enhancement of meiofauna was obtained by Castel (1984 b) after introduction of Clams (*Ruditapes philippinarum*) in small ponds of the Atlantic coast and Escaravage & Castel (1990) with a Shrimp (*Palaemonetes varians*) introduced in the above mentioned fish ponds of Arcachon Bay. In all these shallow impoundments the water is rarely renewed and this creates eutrophic conditions, the organic-rich sediment being poorly oxygenated. The biological activity of the macrofaunal organisms may keep the surface sediment aerated. This, obviously, may favour meiofauna. Macrofaunal activities also stimulate microorganisms while excretion enhances bacterial and microphytobenthic production which results in an enhancement of the trophic resources available for meiofauna. These studies illustrate the peculiar nature of the lagoonal habitat and more specifically of the sediment and its associated productions which are probably much more reactive than in open marine systems.

CONCLUSION

Studies on (strictly) lagoonal meiofauna are rather few. It is somewhat surprising since coastal lagoons are generally of easy access and are populated by few species; this should render *in situ* studies easier. The accessibility and shallowness of the lagoon environment allow investigators to take undisturbed samples easily. This is undoubtedly an advantage for field experimentation. Coull & Palmer (1984) showed the usefulness of field manipulations with meiofauna as research tools. A number of difficulties encountered in intertidal areas or marine subtidal environments do not exist in lagoons. For instance, caging is not recom-

mended in sandy or hydrodynamically rigorous areas because of artifacts induced by the cages (e.g. altered sedimentation rates). Such artifacts do not occur to such a degree in lagoons due to the weak hydrodynamism.

Trophic interactions studies can be made without recourse to caging. Transplanting predators into naturally limited habitats is a fruitful approach for studying interactions. Coastal lagoons are suitable for such experiments insofar as part of their surface can be divided into compartments (see for instance Castel & Lasserre, 1982). The same design can be used for studying the impact of disturbance by macrofauna (see Castel, 1984b as an example).

Coastal lagoons appear to be more suitable than any other marine environment for meiobenthic population and production studies. Production estimates of meiobenthic populations in the sea do not exist, in great part because the logistics of sampling subtidal sediment prohibit the use of the classical methods in production studies (analysis of growth or mortality of cohorts in the field). To date, production in the field has been measured only for 5 species of Harpacticoid copepods: *Huntemannia jadensis*, *Microarthridion littorale*, *Tachidius discipes*, *Paronychocamptus nanus* and *Canuella perplexa*, and 1 species of ostracod: *Cyprideis torosa* (see references in Ceccherelli & Mistri, 1991 in which *P. nanus* is missing, see Herman & Heip, 1985 for this species). All these species, except *H. jadensis* live in estuaries and lagoonal environment. It is not surprising that the production of *T. discipes*, *P. nanus*, *C. perplexa* and *C. torosa* was effectively measured in lagoons.

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