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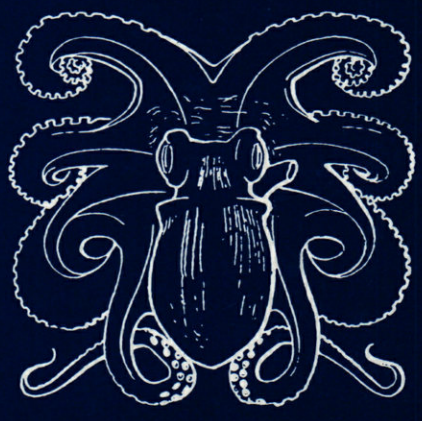

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Life and Environment

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DIVERSITY OF GROUNDWATER DWELLING CYCLOPOIDA (CRUSTACEA, COPEPODA) IN A DANUBE WETLAND IN AUSTRIA

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DIVERSITY
GROUNDWATER CYCLOPOIDA
LOBAU
DANUBE AQUIFER

ABSTRACT. – The taxonomic diversity of groundwater dwelling cyclopoid fauna (23 species, 10 hypogean and 13 epigean taxa) occurring within an area of about 0.8 km^2 of the Lobau, a Danube wetland at Vienna, is analysed using several metric scales. These data are compared with those of two other sites, Regelsbrunn and Deutsch-Wagram, located 16 km remote from the Lobau. Laboratory observations on selected cyclopoid species related to their search activity during the election of substrate and potential food items exemplifies aspects of the ecological diversity of groundwater cyclopoids occurring within the Danube wetlands. The origin and the "potential diversity" of the cyclopoids in the investigated area are discussed using statistical, ecological, biogeographic and evolutionary arguments.

DIVERSITÉ
CYCLOPOIDA DES EAUX SOUTERRAINES
LOBAU
AQUIFÈRE DU DANUBE

RÉSUMÉ. – La diversité taxinomique de la faune des Cyclopoïdes (23 espèces, 10 hypogées, 13 épigées) habitant la nappe phréatique du Lobau dans un périmètre d'environ 0.8 km^2 de la plaine alluviale du Danube à Vienne, est analysée au niveau de plusieurs échelles métriques. Ces informations sont comparées avec des données obtenues dans deux autres localités, Regelsbrunn et Deutsch-Wagram, situées à 16 km du Lobau. L'activité motrice différente de plusieurs Cyclopoïdes hypogés pendant la recherche du substrat et de la nourriture potentielle documente le problème de la diversité écologique chez les Cyclopoïdes souterrains de la plaine alluviale du Danube. L'origine et la "diversité potentielle" des Cyclopoïdes hypogés de la zone étudiée est discutée à partir d'arguments d'ordre statistique, écologique, biogéographique et de la biologie évolutive.

INTRODUCTION

In a stimulating review Marmonier *et al.* (1993) suggested that it will be important for the future research on the diversity of subterranean fauna to intensify the following activities:

(1) The continuation of faunistic exploration leading to a better understanding of the taxonomic or phylogenetic diversity – Until recently, many parts of the world remained practically unexplored. The unexpectedly rich stygobitic fauna which are continually being discovered in North America (Reid 1997/1998, Strayer & Reid 1999) or in the Western Australia (Humphreys 2000) are excellent examples. This exploration is a necessary activity even in Europe, where the studies on the fauna of subterranean waters (especially those dealing with animals in karstic systems) has a long tradition (Gibert 1992, Stoch 1995). The documentation of the taxonomic diversity should be encouraged because we observe that an ever increasing number of groundwater habitats is endangered by overexploitation or by anthropogenic pollution with fatal consequences for the subterranean fauna, which are becoming endangered or extinct (Sket 1999a, 1999b).

(2) The documentation of the ecological diversity of hypogean fauna – We know very little about the autecology of most of the hypogean aquatic fauna, especially how they exploit subterranean resources (Gibert *et al.* 1994, Stoch 1995).

(3) The study of the genetic diversity of hypogean organisms at infra– or inter-species level – Recent studies, especially those on crustaceans show for instance that the karstic populations display a high genetic diversity (Cobolli Sbordoni *et al.* 1990, Culver *et al.* 1995). Sbordoni *et al.* (1976) and Mathieu *et al.* (1997) documented dif-

Fig. 1. – Geographical location of the main sampling areas in the Danube Valley.

ferences between the genetic diversity of karstic and non-karstic populations of amphipods.

(4) The description of the functional role of groundwater organisms within subterranean ecosystems – Claret *et al.* (1999) showed how one can relate the adaptive traits of subterranean animals to functional aspects of ecosystems.

Moreover, Marmonier *et al.* (1993: p. 394) noted that one of the interesting aspects related to faunistic investigations should be the evaluation of the "potential biodiversity" in a groundwater system corresponding to the potential number of species that can be harboured by that system within its environmental and historical context.

In the present contribution we describe the faunistic and ecological diversity of groundwater dwelling Cyclopoida from a sector of the Danube wetlands in Lower Austria, the Lobau. We compare these data with those obtained from two other sites, the Regelsbrunn wetland and the Deutsch-Wagram area, both sites located at about 16 km remote from the former site (Fig. 1, 2). Long-term ecological investigation on the fauna of this area showed (Danielopol & Pospisil, submitted) that the Cyclopoida is a focal group for the evaluation of groundwater biodiversity at both local and regional scales. Until our investigations, the groundwater copepod fauna in Lower Austria was poorly known as demonstrated by the Austrian copepod checklist (Gaviria 1998). Additionally, we present laboratory observations on selected cyclopoid species related to their activity during the election of substrate and/or food items as well as information on their spatial distribution in the field; this will give us a better idea about the ecological diversity of these crustaceans. Finally, we will discuss the origin of the observed subterranean cyclopoid diversity and estimate the "potential diversity" of this group in the Lobau wetland.

MATERIAL AND METHODS

Study Area and Sampling Programmes: the ecological research was carried out on the Lobau wetland, which is situated on the left side of the Danube in the south-eastern part of the city of Vienna (Fig. 1, 2). The data were collected during various sampling campaigns between 1987 and 1998. Detailed descriptions of this area and the research programmes with their results are presented in Pospisil (1994a, 1994b, 1999), Danielopol *et al.* (1992, 1994, 1997, 1999a, 2000), Dreher *et al.* (1997), and Moesslacher (1994, 1998). Taxonomic descriptions of the fauna are presented in Pospisil (1989, 1994a), Pospisil & Stoch (1997, 1999), Stoch & Pospisil (2000a, b). The present publication deals with the diversity of cyclopoids from two areas called Lobau-B and Lobau-C by Pospisil (1994a). Both sites encompass a total area of about 0.8 km^2, located within the subregion Untere Lobau, which belongs to the former flood plain of the Danube. Since 1987 the Untere Lobau constitutes an UNESCO Biosphere Reserve and was incorporated in the Danube Flood Plain National Park in 1996. From the Lobau-B area (about 600x600 m large, Fig. 2) we present information on 12 widely dispersed groundwater observation wells used originally for hydrologic observations and 12 wells fixed in a regular 3x4 grid within a 27 m^2 area called BLM (details in Pospsil 1994a, b, 1999, Danielopol *et al.* 1999a, see also Fig. 2 and Table II). This small area

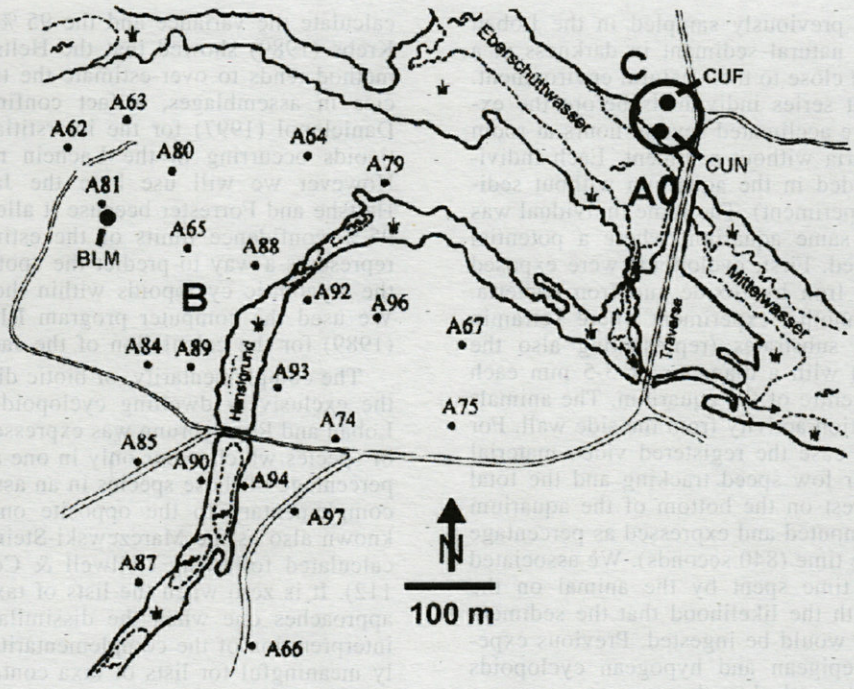

Fig. 2. – The sampling areas A, B, and C in the Lobau wetland (see text for further explanation).

was investigated twice monthly during June 1996 and August 1997, and monthly until January 1998. The groundwater domain of Lobau is part of the Marchfeld aquifer. The Lobau-B area is largely recharged by the Danube river (Danielopol *et al.* 1999a). Lobau-C represents an area of about 900 m^2 forming a mini-groundwater ecosystem that is hydrologically connected to backwaters of the Danube, the Eberschüttwasser and the Mittelwasser (Fig. 2). During 1991 and 1993 we investigated 26 wells seasonally (9 of them were multilevel piezometres sampled at various depths, e.g. 3, 6, 9, 12 m beneath the surface). In this paper we present data for 9 multilevel wells and 4 "simple" piezometres (Table II). In a comparative programme to the BLM we investigated two sites of 27 m^2 each, one located on the banks of the Eberschüttwasser (CUN, in Fig. 2, Table II), the other one some 35 – 40 m further inland (CUF, in Fig. 2, Table II). The CUN and CUF sites had the same 3 × 4 layout of 12 sampling wells as the BLM. At the CUN, CUF and BLM sites, a cluster of 3 wells was randomly chosen at each sampling date and 5 litres of groundwater and sediment from each well using the Bou-Rouch pumpage method were extracted (for more sampling details see Pospisil 1992, 1999, Danielopol *et al.* 1999a).

The cyclopoid fauna is here ecologically classified into two groups: (1) epigean species, which typically occur in surface water habitats but were sampled in various groundwater habitats within the Danube wetlands; (2) exclusively hypogean (or stygobitic) species, which we caught only in subsurface water habitats and never in surface water habitats at the sites investigated by us (for additional information see the Result-section).

Species diversity of the Cyclopoida in the Lobau will be presented at several metric scale levels: (a) metric scale, 1 m – 10 m length, (b) decametric scale, 10 m – 100 m L, (c) hectometric scale, 100 m – 1000 m L and (d) kilometric scale, more than 1 km L. We shall arbitrarily consider the "a" and "b" levels the local scale and "c" and "d" regional scales.

Regelsbrunn (Fig. 1) is a wetland area east of Vienna where old arms of the Danube are being reconnected to the main channel of the river since 1997 in order to revitalise the wetland ecosystems (Schiemer 1999). 10 sampling wells were fixed at 3 stations and different depths (Table II) along a transect of one km L from the Danube inland, crossing distinct types of old arms; they were sampled monthly during 1995 (Wenzl unpubl) and seasonally during 1997 (Steininger in prep). Cyclopoids were found in 7 wells (Table II).

Deutsch-Wagram is located north-east of Vienna (Fig. 1) and the investigated wells are located along the Marchfeld channel. The wells are commonly used for the observation of the local artificial groundwater recharge of the Marchfeld aquifer (Neudorfer 1999). Six wells along a 2 km sector of the Marchfeld channel were investigated by one of us (PP) during 1995 (Table II).

Laboratory observations: Using a SONY CCD video-camera, fixed on a WILD stereo-microscope (60x), we registered in infra-red light (wave length, 950 nm) the movement and the potential feeding behaviour of several species of stygobitic cyclopoids, 3 species of *Diacyclops* and 1 of *Acanthocyclops* (see Results for additional details). This method has been successfully tested during observations on the movement and feeding activity of isopods (Moesslacher 1994).

We used isolated individuals, placed in a cylindrical micro-aquarium with a diameter of 18 mm and a height of 2.5 mm; their activity were recorded for 14-15 minutes. For fully standardised and comparative observations we used only the series of 14 minutes (840

seconds). Copepods previously sampled in the Lobau were maintained on natural sediment in darkness at a constant temperature close to their natural environment. For each experiment series individuals before the experiment started were acclimated several hours at room temperature in aquaria without sediment. Each individual was first recorded in the aquarium without sediment (the control experiment). The same individual was then placed in the same aquarium where a potential food item was offered. First, cyclopoids were exposed to fine sediment of Iron hydroxide and Iron bacteria. It was followed by another experiment where Tetramin was offered. These substrates (representing also the potential food item) with a diameter of 3-5 mm each were placed in the centre of the aquarium. The animals started their exploration activity from the side wall. For each individual and case the registered video material was processed under low speed tracking and the total amount of time at rest on the bottom of the aquarium or substrate was computed and expressed as percentage of the total exposure time (840 seconds). We associated an increase in the time spent by the animal on the offered substrate with the likelihood that the sediment particles we offered would be ingested. Previous experiments with both epigean and hypogean cyclopoids (Pospisil unpubl) showed that these crustaceans generally spend more time on organic substrates than outside the substrate and/or in environments without substrate.

The two potential food items used here were chosen because of previous observations in the field and laboratory. We noted that in many cases samples from the Lobau contained large amounts of fine Iron hydroxide sediment and Iron bacteria. In many residues of sieved samples we found a high number of crustacean faeces (including cyclopoid faeces too) containing this type of sediment. Tetramin is a smelly product used as fish food. One of us (PP) observed large cyclopoids, like *Cyclops strenuus,* in aquarium conditions feeding on this solid medium.

For each of the 3 series of experiments (control without sediment, series with fine sediment and series with Tetramin) we calculated the arithmetic mean and the standard error of the mean.

On batch cyclopoid samples of *Diacyclops* species and *Acanthocyclops gmeineri* several series of observation were done in order to see the potential predatory activity of these cyclopoids.

Estimation of Species Richness: the amount of change in species richness of exclusively hypogean cyclopoids will be determined from the plot of the cumulative number of local species occurring at the main investigated sites, in the Lobau (CUN, Lobau-C, BLM, Lobau-B), Regelsbrunn, and Deutsch-Wagram, as discussed by Collwell & Coddington (1995).

The 1st order Jackknife model (Jack 1) of Heltshe and Forrester (Krebs 1989) was used to estimate the species richness which potentially exist in the Lobau. According to Baltanas (1992) the Jack 1 estimator, based on unique species occurring in various sample units, is the least biased one as compared to other estimators and is suited to assemblages with low number of species. Other specialists, e.g. Walther & Morand (1998), also found the Jack 1 as the least biased and the most precise estimator for the number of species in an assemblage. Using this metric, one is also able to calculate the variance and the 95 % confidence limits. Krebs (1989) showed that the Heltshe and Forrester's method tends to over-estimate the true number of species in assemblages, a fact confirmed by Rouch & Danielopol (1997) for the interstitial dwelling harpacticoids occurring in the Lachein riverbed sediments. However we will use here the Jacknife method of Heltshe and Forrester because it allows to calculate the 95 % confidence limits of the estimated value which represents a way to predict the "potential diversity" of the stygobitic cyclopoids within the investigated area. We used the computer program RICHNESS of Krebs (1989) for the calculation of the Jack1 estimator.

The complementarity, or biotic distinctness, between the exclusively dwelling cyclopoid taxa found in the Lobau and Regelsbrunn was expressed as the proportion of species which occur only in one assemblage, i.e. the percentage of those species in an assemblage which are complementary to the opposite one. The "C index", known also as the Marczewski-Steinhaus distance, was calculated following Collwell & Coddington (1995: p 112). It is zero when the lists of taxa are identical and approaches one when the dissimilarity increases. The interpretation of the complementarity index is especially meaningful for lists of taxa containing more or less equal numbers, as in our case with Lobau (10 stygobitic taxa in Lobau and 8 stygobites in Regelsbrunn). Note that one obtains a similar result using the Jaccard index for association in its special expression Jd = 1 – J, which represents the degree of dissimilarity.

RESULTS

Cyclopoida diversity and spatial distribution

During our long-term groundwater ecological research in the Lobau-B and Lobau-C areas we sampled 23 species: 10 exclusively hypogeans and 13 epigeans. Two additional stygobitic and one epigean species were discovered at the sampling sites Regelsbrunn and Deutsch-Wagram (Tables I and II).

From the total of 26 Cyclopidae species, 21 belong to the subfamily Cyclopinae and 5 to the Eucyclopinae (*Eucyclops graeteri* (Chappuis), *E. serrulatus* (Fischer), *E. speratus* (Lilljeborg), *Macrocyclops albidus* (Jurine), and *Austriocyclops vindobonae* Kiefer).

Considering the Cyclopoida of the Lobau area (Table I), one can recognise 2 types of species assemblages (Pospisil 1999): (1) an ecotonal assemblage, located at site Lobau-C, represented by both hypogean and epigean species and (2) a hypogean assemblage located within the Lobau-B area with exclusively dwelling hypogean taxa, (one exception is *D. disjunctus*).

D. disjunctus was repeatedly found at groundwater sites closely located to the Eberschüttwasser, hence we consider this species an hypogean

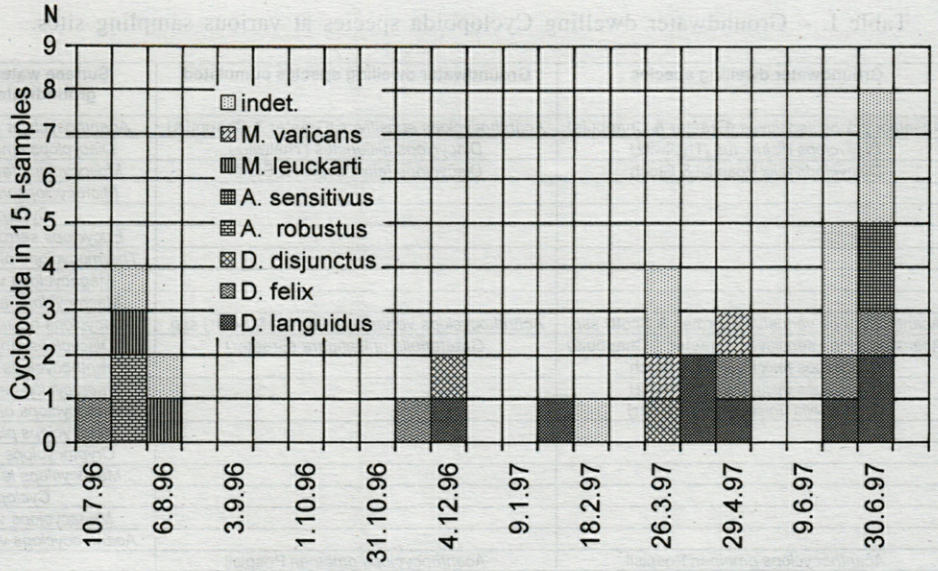

Fig. 3. – Quantitative distribution of cyclopoid species at the CUN site during 12 months; for each date, data cumulated from 3 sampling units.

ecotonal taxon (Pospisil 1999). *Acanthocyclops venustus venustus* (Norman & Scott) was recorded in surface water habitats (e.g. Fryer 1993) but several other subspecies are stygobitic taxa. *A. venustus* (Norman & Scott) *ssp.* from our sampling sites occurred exclusively in groundwater habitats, hence it is here considered a hypogean taxon. Following F. Stoch (pers comm), our populations represent a subspecies with affinities to *A. venustus italicus* Pesce & Maggi, a stygobitic taxon (Lescher Moutoué 1986).

Species diversity at the metric scale

The sites CUN and BLM (with a surface of 4.5 × 6 m each) differ from both the qualitative and quantitative point of view (Fig. 3, 5 and Tables I, II).

The CUN species assemblage (12 species) is represented by hypogeans (3) and epigeans (9) species (Tables I, II), occurring at low frequencies (Fig. 3).

The most frequent species is the epigean *D. languidus* (Sars) (Fig. 3). Besides this latter two other *Diacyclops* species occur (*D. felix* Pospisil & Stoch and *D. disjunctus*).

The BLM site displays 6 taxa (Tables I, II) which occur exclusively in groundwater. Figure 4 shows that their abundance is higher than those of the CUN sites, it appears however low as compared to the abundance of Cyclopoida at the site Lobau-A were several hundreds of individuals occurred in volumetrically equivalent samples (Danielopol 1983, Fig. 53, 55). One should note that from the 24 wells at the CUN and CUF sites, three of them (CUN-A2, CUF-B2, CUF-B4) remained completely barren during the whole investigation period.

Species diversity at decametric and hectometric scales

The sites Lobau-C (approx. 23 × 40 m L) and Lobau-B (approx. 600 × 600 m L) display generally the same pattern of qualitative diversity like the CUN and BLM sites, respectively, but with a slight difference in the species composition (Tables I, II). For instance, another epigean species, *Diacyclops bicuspidatus* (Claus), and the stygobitic species *Greateriella unisetigera* (Graeter) were caught in the Lobau-C area (Tables I, II). The stygobitic species *Eucyclops graeteri* and *Austriocyclops vindobonae* and the epigean *Diacyclops bicuspidatus* appeared rarely in the wells of Lobau-B and Lobau-C areas respectively (Table II).

No cyclopoids were found despite repeated investigations in several wells of Lobau-B (B-A67, B-A79, B-A80, B-A96).

The diversity of the Deutsch-Wagram and the Regelsbrunn cyclopoid assemblages follows the pattern of Lobau-B and Lobau-C (Tables I, II). One has to note the occurrence of additional taxa as compared to the Lobau fauna, i.e. the hypogean *Acanthocyclops kieferi* and the epigean *E. speratus* (Lilljeborg) in Regelsbrunn and the hypogean *Paragraeteriella* sp. in Deutsch-Wagram (Tables I, II). From the investigated 10 wells in Regelsbrunn wetland only in 7 we found cyclopoids. The piezometres RGB-SW 7m, RGB-M 3 m and RGB-D 2 m remained barren.

Table I. – Groundwater dwelling Cyclopoida species at various sampling sites.

Sampling Station	Groundwater dwelling species	Groundwater dwelling species cumulated	Surface water species in groundwater habitats
Lobau CUN	*Acanthocyclops sensitivus* (Graeter & Chappuis)	*Acanthocyclops sensitivus* (Graeter & Chappuis)	*Acanthocyclops robustus* (Sars)
	Diacyclops disjunctus (Thallwitz)	*Diacyclops disjunctus* (Thallwitz)	*Diacyclops languidus* (Sars)
	Diacyclops felix Pospisil & Stoch	*Diacyclops felix* Pospisil & Stoch	*Mesocyclops leuckarti* (Claus)
			Microcyclops varicans (Sars)
			Cyclops sp.
			Eucyclops serrulatus (Fischer)
			Thermocyclops oithonoides (Sars)
			Megacyclops viridis (Jurine)
			Macrocyclops albidus (Jurine)
Lobau-C	*Acanthocyclops venustus* (Norman & Scott) *ssp.*	*Acanthocyclops venustus* (Norman & Scott) *ssp.*	*Diacyclops bicuspidatus* (Claus)
	Acanthocyclops sensitivus (Graeter & Chappuis)	*Graeteriella unisetigera* (Graeter)	*Diacyclops languidus* (Sars)
	Diacyclops felix Pospisil & Stoch		*Acanthocyclops robustus* (Sars
	Diacyclops disjunctus (Thallwitz)		*Macrocyclops albidus* (Jurine)
	Graeteriella unisetigera (Graeter)		*Thermocyclops oithonoides* (Sars)
			Metacyclops planus (Gurney)
			Cryptocyclops bicolor (Sars)
			Mesocyclops leuckarti (Claus)
			Cyclops sp.
			Megacyclops viridis (Jurine)
			Acanthocyclops vernalis (Fischer)
Lobau BLM	*Acanthocyclops gmeineri* Pospisil	*Acanthocyclops gmeineri* Pospisil	
	Acanthocyclops sensitivus (Graeter & Chappuis)	*Diacyclops cohabitatus* Monchenko	
	Acanthocyclops venustus (Norman & Scott) *ssp.*	*Diacyclops danielopoli* Pospisil & Stoch	
	Diacyclops felix Pospisil & Stoch		
	Diacyclops cohabitatus Monchenko		
	Diacyclops danielopoli Pospisil & Stoch		
Lobau-B	*Austriocyclops vindobonae* Kiefer	*Austriocyclops vindobonae* Kiefer	*Diacyclops bicuspidatus* (Claus)
	Eucyclops graeteri (Chappuis)	*Eucyclops graeteri* (Chappuis)	
	Acanthocyclops gmeineri Pospisil		
	Acanthocyclops sensitivus (Graeter & Chappuis)		
	Acanthocyclops venustus (Norman & Scott) *ssp.*		
	Diacyclops felix Pospisil & Stoch		
	Diacyclops cohabitatus Monchenko		
	Diacyclops danielopoli Pospisil & Stoch		
Regelsbrunn	*Diacyclops felix* Pospisil & Stoch	*Acanthocyclops kieferi* (Chappuis)	*Eucyclops speratus* (Lilljeborg)
	Diacyclops cohabitatus Monchenko		*Acanthocyclops robustus* (Sars)
	Diacyclops danielopoli Pospisil & Stoch		*Thermocyclops oithonoides* (Sars)
	Acanthocyclops gmeineri Pospisil		
	Acanthocyclops venustus (Norman & Scott) *ssp.*		
	Acanthocyclops kieferi (Chappuis)		
	Acanthocyclops sensitivus (Graeter & Chappuis)		
	Eucyclops graeteri (Chappuis)		
Deutsch-	*Diacyclops danielopoli* Pospisil & Stoch	*Paragraeteriella sp.*	
Wagram	*Acanthocyclops gmeineri* Pospisil		
	Diacyclops felix Pospisil & Stoch		
	Paragraeteriella sp.		

Species Richness and Complementarity

The values of the species richness of Cyclopoida depend largely on the spatial scales we consider (Tables I, II). In the Lobau, the CUN area has 9 epigean and 3 hypogean species, while BLM displays 6 species at a metric scale. Several wells, like CUN-B2, CUN-B3 and CUN-C2, display a rich cyclopoid fauna, both epigeans and hypogeans (6-7 taxa). The highest number of species in the BLM wells is 4 (i.e. in the wells BLM-A1, BLM-A3, BLM-A4, BLM-C1 and BLM-C2).

Considering the decametric and hectometric scales, i. e. the cyclopoid fauna occurring within the Lobau-B and Lobau-C areas, one notices an increase in the species richness especially with regard to stygobites (Table I, Fig. 5). There are 5 hypogean taxa in Lobau-C and 8 in Lobau-B (Fig. 5). We recorded 13 epigean species in the whole Lobau-C area, including the CUN species too (Tables I, II). In several isolated wells of the Lobau-B area (B-A81, B-A84, B-A89), we caught between 5 and 7 stygobitic taxa while in Lobau-C the well D3 displayed 9 species (Table II).

The total number of the groundwater dwelling cyclopoids in Regelsbrunn (Tables I, II) is 11 (8 hypogeans, 3 epigeans), while in the Deutsch-Wagram wells only 4 hypogean dwelling species were sampled (Tables I, II).

The species richness of the exclusively hypogean taxa living in groundwater of the sites CUN, Lobau-C and Lobau-B approximately doubles (3 – 5 – 8) with the increase of the metric scales (Table I, Fig. 5).

The contribution to the total hypogean species richness by taxa found at the comparative areas, Regelsbrunn and Deutsch-Wagram, is reduced. It represents an increase of only 10 % per site as compared to the Lobau area (Table I, Fig. 5).

Table II. – Presence (1) absence (0) data of 26 Cyclopoida taxa found in 71 wells, within the Lobau, Regelsbrunn and the Deutsch-Wagram areas. The wells are named with the code we have in our original data-basis.

WELLS	*A. gmeineri* Pospisil	*A. venustus* (Norman & Scott) *ssp.*	*A. sensitivus* (Graeter & Chappuis)	*D. cohabitatus* Monchenko	*D. felix* Pospisil & Stoch	*D. danielopoli* Pospisil & Stoch	*D. disjunctus* (Thallwitz)	*E. graeteri* (Chappuis)	*A. vindobonae* Kiefer	*Paragraeteriella sp.*	*A. kieferi* (Chappuis)	*G. unisetigera* (Graeter)	*D. languidus* (Sars)	*M. varicans* (Sars)	*M. leuckarti* (Claus)	*A. robustus* (Sars)	*A. vernalis* (Fischer)	*Cyclops. sp.*	*D. bicuspidatus* (Claus)	*M. albidus* (Jurine)	*E. serrulatus* (Fischer)	*E. speratus* (Lilljeborg)	*T. oithonoides* (Sars)	*M. viridis* (Jurine)	*M. planus* (Gurney)	*C. bicolor* (Sars)
Lobau C																										
D3	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	1	1
D4	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
D5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
D9	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
D10	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
D11	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D15	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0
D17	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
T3	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0
R2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0
R3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
R4a-g	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
R6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
R8	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
R17	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
R18	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
R26	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUN-A1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUN-A3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
CUN-A4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
CUN-B1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
CUN-B2	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0
CUN-B3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0
CUN-B4	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
CUN-C1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
CUN-C2	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0
CUN-C3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
CUN-C4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-A1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-A2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-A3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
CUF-A4	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
CUF-B1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-B3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-C1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-C2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-C3	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
CUF-C4	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobau B																										
B-A63	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A66	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
B-A81	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A84	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A85	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A87	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A89	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B-A90	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM A1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM A2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM A3	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM A4	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM B1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM B2	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM B3	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM B4	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM C1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM C2	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM C3	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BLM C4	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Regelsbrunn																										
RGB-SW 3m	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
RGB-SW 6-7m	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RGB-SW 8m	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RGB-M 5m	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
RGB-M 6-7m	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
RGB-D 4m	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RGB-D 6m	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deutsch-Wagram																										
MF-EM4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-EM61	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-EM56	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-EM57	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-EM58	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MF-GW-Br.2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

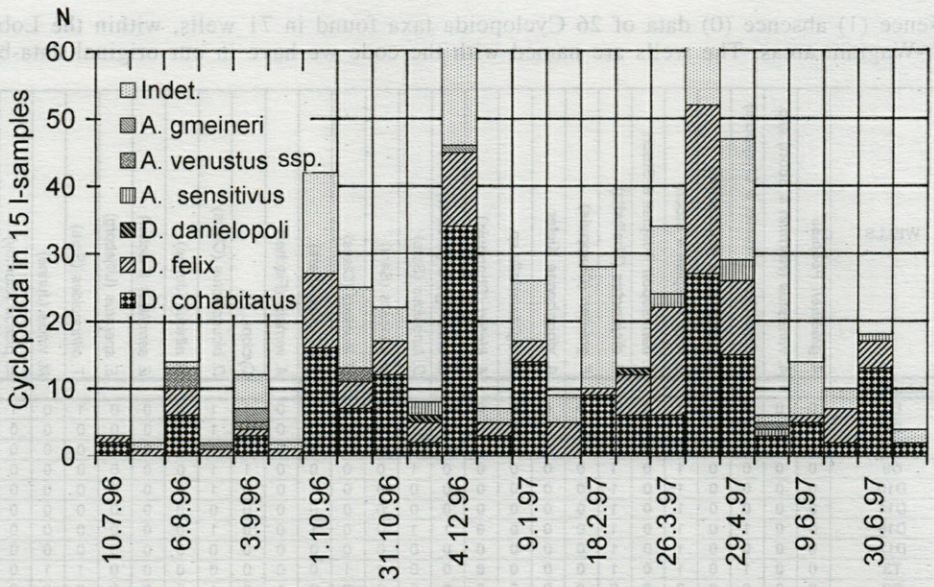

Fig. 4. – Quantitative distribution of cyclopoid species at the BLM site during 12 months; for each date, data cumulated from 3 sampling units.

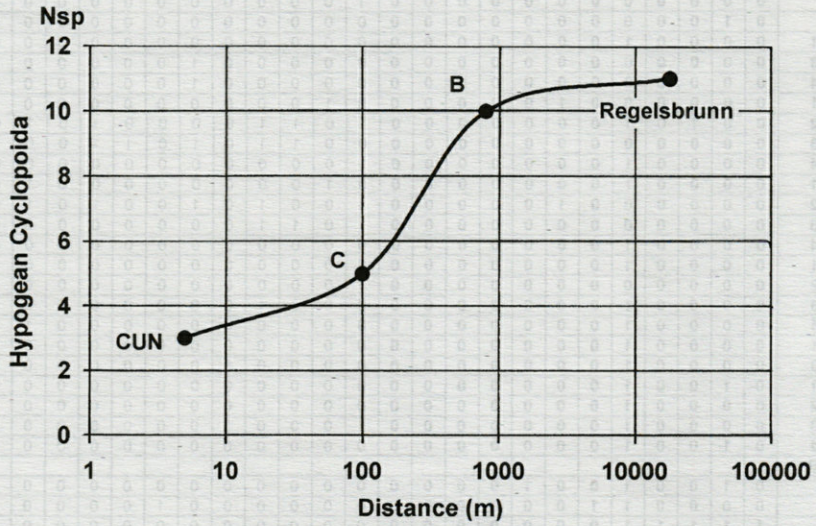

Fig. 5. – Cumulative number of stygobitic Cyclopoida species as a function of the linear distance between the sampling sites Lobau (Lobau-CUN, Lobau-C, Lobau-B) and Regelsbrunn.

Within the whole Lobau area we investigated, two cyclopoid genera display a high number of species (Table I), i.e. *Diacyclops* (6 species) and *Acanthocyclops* (5 taxa). Nine other genera (Table I) are represented by unique species and one genus (*Eucyclops*) by 2 species.

The frequency of the occurrence of various cyclopoid taxa for the whole Lobau area (Table II) is variable. One notes that the number of the exclusively hypogean taxa which were caught only once is 3 (*G. unisetigera, A. vindobonae, E. graeteri*), while there is only one species (*D. felix*) which occurs in 70 % of the wells containing cyclopoids (i.e. 43 cases from 58 wells). This latter species also appears as the most frequent species in all three areas, Lobau, Regelsbrunn and Deutsch-Wagram, i.e. it occurs in 52 wells from a total 71 containing cyclopoids (Table II). *Acanthocyclops kieferi* and *Paragreteriella* sp. are rare species, they occur only 2 and 5 times, respectively, in Regelsbrunn and Deutsch-Wagram. The other exclusively hypogean taxa display intermediary frequencies (they occur in 12-17 cases). Therefore, considering the exclusively hypogean dwelling cyclopids, there are more rare species than frequent ones.

When calculated with the non-parametric Jackknife method, the estimated diversity for the ob-

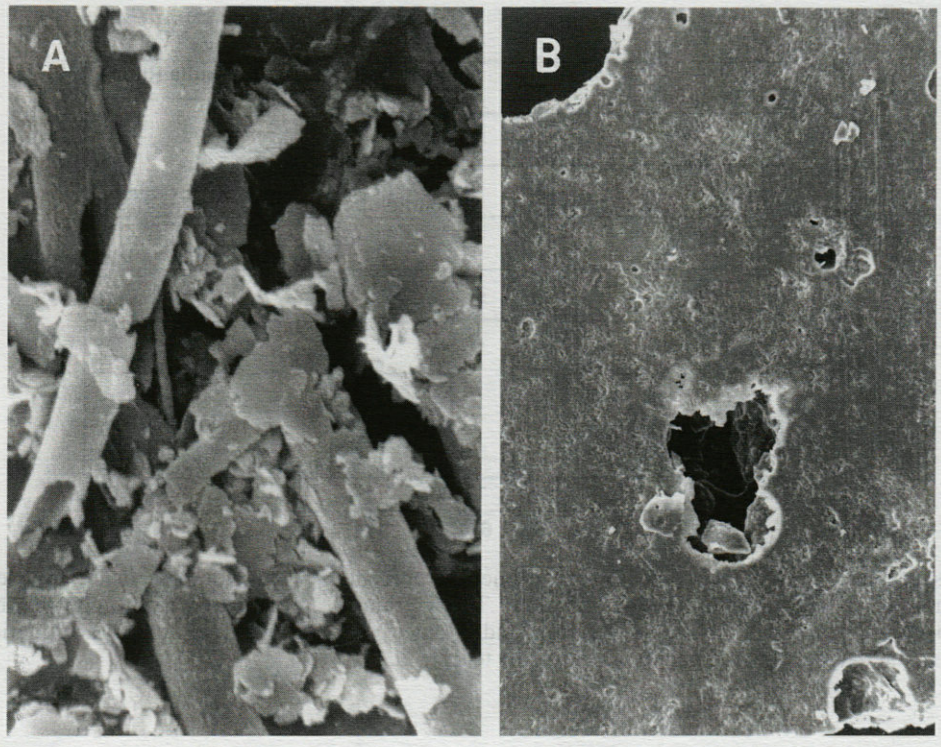

Fig. 6. – Sediment types used for movement and feeding experiments (Micrographs by T. Loser with a JEOL scanning electron microscope at the University of Vienna, Department of Marine Biology). A, fine Iron hydroxide sediment and filamentous rests of Iron bacteria (5000×); B, fragment of Tetramin (1000×).

served exclusively hypogean cyclopoid fauna of the Lobau gave a value of 12.9 (i.e. 13 species) with 95 % confidence limits between 9.6 (10 species) and 16.3 (16 species). The most frequent epigean species in our groundwater sites are *D. languidus* and *A. robustus,* they occurred in 13 wells (Table II). There are 9 epigean species which were rarely found, i.e. they occurred in 1-5 wells (Table II).

The complementarity, or species distinctness *sensu* Colwell & Coddington (1995), between the stygobitic fraction of the cyclopoid assemblages found in the groundwater of the Lobau and Regelsbrunn wetlands (Table I) has a C value of 0.36. The Jaccard Jd value is 0.38.

Movement and Feeding Behaviour of Selected Species

Figure 6 shows the type of substrate on which cyclopoids were successively exposed. One notices on Figure 6A that the fine sediment is composed by minute particles (approx. 1-3 µm length) of Iron hydroxide and filamentous Iron bacteria (3-4 µm diameter). The total content in organic Carbon and respectively Nitrogen of this sediment is low (TOC, 2.7 mg/g and TON 3.45 mg/g). Figure 6B shows the structure of a piece of Tetramin. This has a compact solid structure with slightly rugous surfaces. Tetramin is a standard fish food containing a high amount of proteins extracted from fish, mussels and/or crustaceans. Hence it has an important energetic value (TOC, 43.5 mg/g and TON 47.6 mg/g) and is able to act as a chemical attractor for the crustaceans used in these experiments.

Diacyclops disjunctus, D. felix and D. danielopoli

The individuals used for the experiments were all non-ovigerous female adults. Their body length varied between 0.5 mm and 0.7 mm.

Figure 7 shows that when placed in micro-aquaria without substrate (the control series), all individuals spend very little time at rest on the bottom, on the average only five percentage of the total exposure time (14 minutes).

In aquaria with Iron hydroxide substrate one sees that *D. disjunctus,* after discovering the substrate, spends long periods of time on it, on the average 26.2 % ± 11.34 of the exposure time. The number of visits of the substrate followed by longer stops is on the average 3.6 ± 1.4.

D. felix and *D. danielopoli* spend less time on the fine substrate, the former 11.1 % ± 4.21, the latter 3.54 % ± 1.2. On the average, *D. felix* visited the substrate 7.45 ± 1.1 times, which is more than the number of visits of *D. disjunctus* and *D. danielopoli* (4.0 ± 1.0 times).

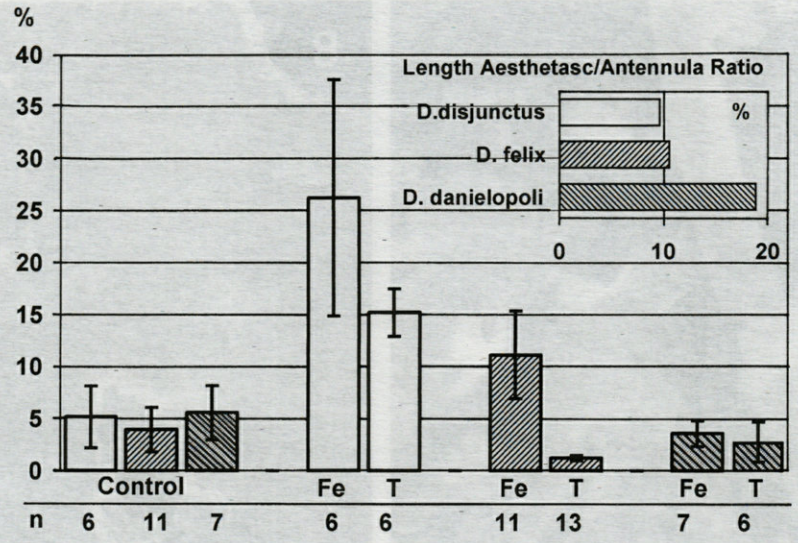

Fig. 7 – Results of the movement and feeding experiments; percentage (of a total exposure time of 840 seconds) spent on substrates (Fe – fine Iron hydroxide sediment, T – Tetramin) as compared to the control (no substrate); n – number of specimens recorded for each situation and species; bar and vertical line – arithmetic mean from n individual data ± standard error (further explanation in text).

When exposed to Tetramin again, *D. disjunctus* (Fig. 6) spends significantly more time on the substrate (15.2 % ± 2.3) as compared to *D. felix* (1.2 % ± 0.24) and *D. danielopoli* (2.76 ± 1.9). The number of stops on the Tetramin substrate is similar for *D. disjunctus* and *D. felix* (6.8 ± 1.2), while *D. danielopoli* visits this substrate only rarely, i. e. 2.8 ± 0.65 times on the average.

None of these species were observed to prey on living animals.

Acanthocyclops gmeineri

This species is much larger (1.2-1.3 mm body length) as compared to the previous *Diacyclops*. The observed specimen showed a highly significant (G-test for 2 × 2 contingency table, $p = 3.3 \times 10^{-9}$) preference for the Iron hydroxide substrate as compared to the Tetramin, i.e. 97.5 % from the total cumulated time spent on both substrates were used on Iron hydroxide substrate. Beside this, we observed one individual preying on a small *Diacyclops*. The large *A. gmeineri* reacted to the movement of the prey swimming by at a close range. The engulfing of the *Diacyclops* happened instantaneously.

DISCUSSION

Hotspots of Cyclopoida Diversity

The diversity of the exclusively dwelling hypogean species of different animal groups from the Danube wetlands is high (Danielopol & Pospisil submitted) as compared to other data sets at equivalent scales (Dole-Olivier *et al.* 1994, Rouch & Danielopol 1997, Culver & Sket 2000). This peculiarity applies also to the Cyclopoida as one can see from the following comparative data:

Within the Lobau area, the stygobitic cyclopoid taxa form the most diverse group of Crustacea; there are twice as many hypogean Cyclopoida species than stygobitic Harpacticoida (Danielopol & Pospisil submitted).

Considering the comparative species richness of hypogean Cyclopoida in Europe, we note that Rouch & Lescher-Moutoué (1992) found seven stygobitic cyclopoid species within an area of 70 m^2 in the Lachein, in the French Pyreneans, while we found six species within a 27 m^2 area (BLM) and seven species in one single well (B-A89). For the karstic system Postojna-Planina Caves (approximately 25 km passages explored) in Slovenia, Brancelj (1987) recorded six troglobitic species. Rouch & Danielopol (1987) documented that only 1–3 stygobitic cyclopoid species were registered at other groundwater sites.

The high number of *Diacyclops* taxa from Lobau (six species) can be compared with the data of Boxshall & Evstigneeva (1994) from Lake Baikal. They found 12 species in this lake which is about 600 km long. Stoch (in press) found between two and seven *Diacyclops* species in the subterranean water habitats of northern Italy and Slovenia, within areas of approximately 100 km^2. It is noteworthy that in several wells we found up to three stygobitic *Diacyclops* species (wells BLM-A3, BLM-C4, B-A84 and A89) or even four

species of both hypogean and epigean taxa (the well D3). A similar species richness (four stygobitic *Speocyclops* taxa) was mentioned for the Baget karstic system by Lescher-Moutoué (1973).

Origin of the Diversity of Hypogean Dwelling Cyclopoida

The surface dwelling cyclopoids encountered by us in the subsurface waters at both the Eberschüttwasser (the Lobau–C area) and the Regelsbrunn sites point out to the ability of these crustaceans to repeatedly colonise the alluvial sediments closely located to open water habitats. This supports the ecotonal model of Gibert *et al.* (1990).

The stygobitic genus *Austriocyclops* Kiefer, represented by a unique species, *A. vindobonae* in Vienna and Lower Austria, could represent an old phylogenetic lineage, relict of a once widely distributed group. Pospisil & Stoch (1997) noted that *A. vindobonae* displays closer morphological affinities with *Ochridacyclops brevicaudatus* Shen & Tai, from surface lotic habitats in Southern China.

Considering the present day geographical distribution of stygobitic species like *Acanthocyclops sensitivus, Eucyclops graeteri* or *Graeteriella unisetigera* in Europe, they could have migrated to the Lobau area along the subsurface alluvial sediments bordering the Danube Valley. These species are widely distributed in Western Europe within the Rhine and the Rhône drainage systems (Dole-Olivier *et al.* 1994, Pospisil 1994a). Due to repeated connections of the river systems of Rhine, Rhône and Danube during the Upper Pliocene and the Pleistocene, they may have migrated downstream along alluvial aquifers, reaching the Danube flood plain here investigated. Thienemann (1950) proposed a similar scenario when discussing the geographical distribution of the stygobitic amphipod *Niphargopsis casparyi* (Pratz).

Other species like *Acanthocyclops gmeineri, Diacyclops felix* and *D. danielopoli* could have originated locally in this area.

The high number of exclusively hypogean dwelling cyclopoid species reported here could also have its origin in the inter-specific ecological differences and in their diverse micro-geographical distribution.

In the field *D. disjunctus* occurs in habitats closely located to surface waters, whereas in the laboratory this cyclopoid spent the highest amount of time on the fine sediment representing an apparently palatable food item. It is interesting that *D. danielopoli,* which has very well developed antennary aesthetascs as compared to *D. disjunctus* and *D. felix* (Fig. 7), spent the least time on both substrates and it did not discover or elect the Tetramin substrate (supposed to be more attractive) faster than the fine Iron hydroxide sediment. The difference in the election of the substrate by *D. danielopoli* as compared to *D. disjunctus* is much similar with the differences observed for the search behaviour of the asellids (Isopoda) *Proasellus slavus,* a stygobitic species, and *Asellus aquaticus,* an epigean crustacean. *P. slavus* moved frequently and spent little time on the substrate (a dead leaf offered as food), while *A. aquaticus*, being very voracious, spent long periods of time on the leaf on which he fed (Moesslacher 1994, Danielopol *et al.* 1994).

D. felix, equipped with moderately developed aesthetascs (Fig. 7) and an intermediary behaviour between those of the two other *Diacyclops* species, displayed in our research area a very wide spatial distribution.

One should also observe the difference between the feeding preferences of *A. gmeineri* electing both fine sediment and living prey, and the *Diacyclops* species which were exclusively detritivores.

The subtle ecological differences displayed by the three *Diacyclops* species observed under laboratory conditions and their field distribution call to attention the data presented by de Bovée *et al.* (1995). These authors showed that three hypogean *Metacrangonyx* species from the High Atlas, in Morocco, display spatial ecological and micro-geographical distributions which could be related to different habitat preferences, i.e. different granulometric characteristics of the alluvial sediments.

One has to note that the data discussed here are partly in line with the "Collection storage model" of Culver *et al.* (1995), further refined by Danielopol *et al.* (1999b), and partly with the "Adaptive zone model" of Stoch (1995). This latter model postulates that the co-occurrence of closely related species at one groundwater site is due to their small non-overlapping niches. This is apparently the case with our *Diacyclops* species-group.

The «Potential Diversity» of Hypogean Dwelling Cyclopoida in the Lobau

The "potential diversity" of the exclusively hypogean cyclopoids to be found within our Danube wetland sector can be discussed using several types of arguments i.e. ecological and biogeographical ones, inferences from statistical data and evolutionary considerations of the potential speciation of selected cyclopoid groups.

Given the diversity of backwater systems in the wetlands of the Danube east of Vienna, it is to be foreseen that at a regional scale the epigean

species richness of Cyclopoida is high. Hence one has to expect the occurrence of other surface dwelling species in the peripheral alluvial groundwater systems connected hydrologicaly to the Danube backwaters.

Considering the exclusively hypogean cyclopoid species at a local and/or regional scale, within the Lobau sector of the alluvial Danube aquifer we expect to find additional species, especially taxa belonging to the genera *Acanthocyclops* and *Diacyclops*. These groups display minute morphological traits (i. e. useful for species identification) as shown by various publications (Pospisil 1994a, Reid 1997/1998, Stoch in press) or diverse behavioural reactions, as documented here. We already know that other *Diacyclops* and *Acanthocyclops* taxa exist around our Danube wetlands area, e.g. *Diacyclops languidoides goticus* (Kiefer), at Bad Vöslau, south of Vienna (Stoch & Pospisil 2000b) or *Acanthocyclops rhenanus* Kiefer, mentioned in Lobau-A (det. G. Pfaffenwimmer, in Danielopol 1983) and rediscovered by one of us in the province of Burgenland (Pospisil in prep) as well as the two species, *A. kieferi* and *Paragreteriella* sp., found in Regelsbrunn and Deutsch-Wagram. However, for the Lobau area investigated a dramatic increase in the diversity value for the exclusively groundwater dwelling cyclopoid species is not expected for the near future. The statistical estimation of the potential species richness lays not far away from the observed species richness, the degree of complementarity between the stygobitic assemblages of Lobau and Regelsbrunn is low (i.e. the two lists of taxa are rather similar) and the accumulation species curve presented for the stygobitic assemblages approaches an asymptotic trajectory.

CONCLUSION

The present contribution on the diversity on groundwater dwelling Cyclopoida in the Danube wetlands constitutes an excellent reference database for similar ecological studies in the future. We hope that this information will enable a better evaluation of the diversity state of other cyclopoid assemblages occurring in groundwater areas under environmental conditions which are different from those we studied, e.g. at sites variously impacted by anthropogenic activities.

Future studies on this topic have to consider that in addition to environmental constraints of a groundwater aquifer, which strongly influence the species richness of a given animal group, the organismic constraints displayed by the animals during the various colonisation events may also play a considerable role in the evolutionary process. Therefore in the future one needs thorough investigations of the ways animals perceive the subterranean environment and on their ability to develop adaptive responses to the various groundwater conditions. It appears now that from the multitude of colonists and colonisation events only few succeeded in the evolution of stable and durable stygobiontic solutions.

Finally, the high diversity of groundwater dwelling Cyclopoida we documented in the Danube wetlands, especially in the Lobau, supports Strayer's idea (1994: p. 289) that "groundwater invertebrates are not distributed randomly around the world, but are concentrated in regions that support very diverse communities. These areas are the underground equivalents of the tropical rain forests."

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MEIOFAUNA DISTRIBUTION IN A TROPICAL ESTUARY OF THE SOUTH-WESTERN ATLANTIC (BRAZIL)

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MEIOFAUNA
SUBTIDAL
ESTUARY
DISTRIBUTION
DRY SEASON
RAINY SEASON
BRAZIL
SOUTH-WESTERN ATLANTIC

ABSTRACT. – The horizontal distribution and abundance of metazoan meiofauna in relation to environmental variables were examined at 10 stations in the Jacuacanga Bay (Rio de Janeiro, Southeastern Brazil), at two seasons of the year (rainy and dry). Samples were obtained from 9 and 17 m depth. Environmental and biological variables were sampled by SCUBA diving and with a van Veen grab. Principal Component Analysis, Canonical Correspondence Analysis, SIMPER and Hierarchical Clustering were used to describe and evaluate associations of variables and samples. Meiofauna was composed by 22 faunistic groups, with mean densities varying from 1425 to 5226 ind. 10 cm^{-2}. The highest values were observed during the rainy saison. The communities were dominated by nematodes, followed by copepods. Statistical analysis showed that the main environmental variables influencing the meiofauna distribution were: coarse silt, dissolved oxygen, organic carbon, C/N ratio and depth. The dissimilarity between the stations can be explained by nematodes, copepods, rotifers, ostracodes and kinorhynchs. The comparison between rainy and dry seasons revealed the existence of temporal variability related to seasonal inputs of organic matter into the benthos.

MÉIOFAUNE
SUBTIDAL
ESTUAIRE
DISTRIBUTION
SAISON SÈCHE
SAISON HUMIDE
BRÉSIL
ATLANTIQUE SUD-OUEST

RÉSUMÉ. – La répartition horizontale et l'abondance du méiobenthos en relation avec les variables de l'environnement ont été examinées à 10 stations échantillonnées dans la Baie de Jacuacanga (Rio de Janeiro, Brésil), à deux périodes de l'année (saisons humide et sèche). Les échantillons ont été prélevés à 9 et 17 m de profondeur. Les relevés environnementaux et biologiques ont été obtenus en plongée et avec une benne van Veen. Les analyses en Composantes Principales, de Correspondance Canonique, hiérarchique et SIMPER ont été utilisées pour décrire et évaluer des associations des variables avec les échantillons. La méiofaune est composée de 22 groupes faunistiques, et sa densité moyenne varie de 1 425 à 5 226 ind. 10 cm^{-2}. Les plus fortes abondances ont été observées pendant la saison humide. Les communautés sont dominées par les Nématodes et les Copépodes. L'analyse statistique a montré que les principales variables de l'environnement influençant la distribution de la méiofaune sont le limon grossier, l'oxygène dissous, le carbone organique, la proportion C/N et la profondeur. La dissimilarité entre les stations peut être expliquée par l'abondance des Nématodes, des Copépodes, des Rotifères, des Ostracodes et des Kinorhynques. La comparaison entre saisons humide et sèche a révélé l'existence d'une variabilité temporelle en rapport avec la quantité de matière organique dans le sédiment.

INTRODUCTION

Meiofauna is represented by almost all the invertebrate groups and occurs in great abundance in estuarine sediment shet worldwide where they facilitate biomineralization of organic material and enhance nutrient regeneration, and serve as food for a variety of higher trophic levels (Coull 1999). According to Bodiou (1999), the predation on meiobenthos by young benthic fishes is a well-known phenomenon in which the harpacticoid copepods take an important part.

The meiobenthos exhibits a high sensitivity to anthropogenic inputs, making them excellent model organisms for the study of estuarine pollution (Coull 1999). They have been used more recently in many benthic studies because they have a number of advantages over the macrofauna in field and laboratory studies. These characteristics include their small size and high densities which permit collecting small samples and shorter gene-

ration times combined with a lack of a planktonic phase in their life cycles suggesting a potentially shorter response time and therefore higher sensitivity to anthropogenic disturbance (Heip *et al.* 1988, Warwick 1993). Furthermore the meiofauna is abundant and diverse even in habitats where it is subject to considerable natural, physical and chemical stress, where very few if any macrofauna species remain (Lampadariou *et al.* 1994).

There are several factors that control the composition and meiobenthos distribution. These factors usually act together, thus making difficult the evaluation of the role of each one in the community. Abiotic factors such as grain size, temperature, salinity, redox potential and oxygen concentration, are directly responsible for this variation (Findlay 1981, Coull 1988,1999, Giere 1993). The influence of microphytobenthos has also been pointed out by Gray (1981), Giere (1993) and Schewe & Soltwedel (1999). There is little information available on the scale of spatial distribution and usually it is very difficult to separate temporal from spatial variability (Fleeger & Decho 1987).

Organic content of the sediments seems to play a key role in the meiofauna density and it is a nutrient source that induces settlement and determines benthic organism distributions (Parsons *et al.* 1984).

In the south-western Atlantic, there are distinct variations in precipitation throughout the year, with either a high amount of rainfall or dry seasons. This phenomenon directly influences the amount of continental freshwater runoff and thus the biogeochemical processes in coastal and marine ecosystems of the south-western Atlantic (Ciotti *et al.* 1995).

The purpose of this work is to study the horizontal distribution of the benthic sublitoral major meiofauna taxa in Jacuacanga Bay, Rio de Janeiro, by comparing two seasons of the year (rainy and dry) and by trying to identify the environmental variables that most heavily influenced this distribution.

STUDY AREA

The Jacuacanga Bay (Fig. 1) is located south of Rio de Janeiro, between 22°59' and 23°03'S, and 044°13' and 044°17'W. It has a surface area of 24 km^2 and 5.2 km of width at its entrance. It is characterized by a hot and humid climate, presenting a high rainfall rate (1500 to 2000 mm annual) and a 22 °C annual mean temperature (FEEMA 1980). The water circulation near Ilha Grande Bay, in which Jacuacanga Bay is inserted, is gravitational, and influenced by an almost fixed flow induced by density gradients and being little influenced by tide and winds (Signorini 1980). The Jacuacanga Bay presents a strong anthropogenic influence due not only to the presence of shipyards, a petrol terminal but also to the Jacuacanga river, the main pluvial and continental runoff drainage. The sediment is predominantly composed by silt, clay and sandy silt. This sediment spreads up to the west portion of Ilha Grande Bay varying gradually in terms of sand grain sizes (Mahiques & Furtado 1989).

MATERIAL AND METHODS

Samples were taken during rainy (November 1997) and dry seasons (July 1998) in nine stations located along three transects of the coastline (Fig. 1). The station 10 was located outside of the Jacuacanga Bay (23°07'S and 044°16'W), close to Ilha Grande Island, named here Ilha Grande station. This station had been chosen because it is under low anthropogenic influence.

Sediment samples were taken with a modified seringe corer (3.5 cm inner diameter) by SCUBA diving. At each station, four core samples were taken for the meiofauna study, two for microphytobenthos, one for redox potential and temperature data and one for heavy metal data. Preliminary studies were carried out to determine the number of meiofauna subsamples sufficient to detect spatial and temporal differences within meiofauna populations. Sediment samples for granulometric analysis, organic carbon and organic nitrogen were collected with a van Veen grab covering 0.1 m^2.

Water samples for hydrological analysis of temperature, salinity, pH and dissolved oxygen were collected at 1 m above the sediment surface with a van Dorn bottle.

Sea water temperature and pH were measured with a pH-meter of Hanna Instruments, HI 8424 microcomputer. Salinity was determined by chemical titulation and dissolved oxygen was obtained by the Winkler method (Strickland & Parsons 1972).

Granulometric analyses were done according to Suguio (1973) and the separation of the different grain size followed the Wentworth scale. The redox potential was obtained in the uppermost cm layer using a platinum electrode. Organic carbon was obtained by wet oxidation with dichromate and the concentration of organic nitrogen through the Kjeldahl-method (Strickland & Parsons 1972). Heavy metals were analysed using I.C.P. – AEES (Inductively Coupled Plasma Atomic Emission Espectrometer-Optima 3000 – Perkin Elmer) by means of the total element analysis by wet digestion in aqua regia. For this study only the cadmium, zinc, lead and copper concentrations were considered. This analysis has been achieved by the Laboratory of Centro Nacional de Pesquisas do Solo (CNPS) of EMBRAPA (Empresa Brasileira de Pesquisa de Agricultura).

Microphytobenthic biomass of the sediment first cm was obtained by the chlorophyll *a* concentration and the pigment extraction being processed with 90 % acetone. Pigment analysis was done by spectrophotometry

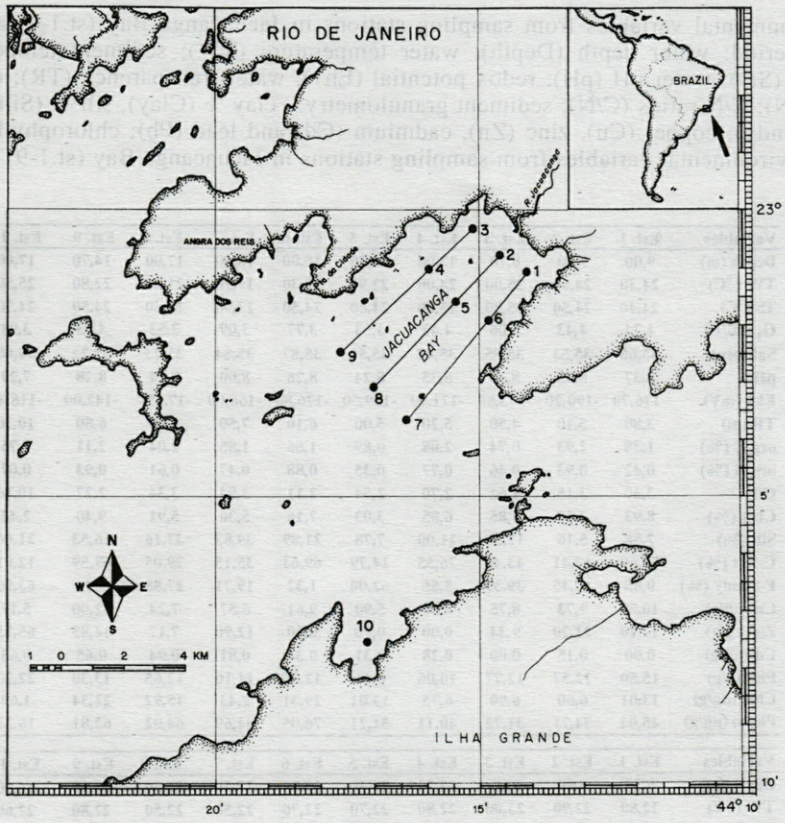

Fig. 1. – Map of the Jacuacanga Bay (Brazil, Rio de Janeiro State) showing the positions of sampling stations.

(Blanchard *et al.* 1988). Chlorophyll *a* concentrations as well as pheophytin *a* were calculated from modified Lorenzen's equations (1967) modified for Plante-Cuny (1978).

Meiofauna was studied in the first 5 cm of the sediment and the samples were preserved in 4 % formalin and stained with Rose Bengal. Meiofauna was extracted from the sediment by decantation and flotations in Ludox HS 40 % at a specific gravity of 1.15. To enable the meiofauna extraction, samples have been centrifuged and decanted into a 45 µm meshsieve. The preserved material was sorted under a binocular stereomicroscope and only major taxa of meiofauna were identified. The organism density of meiofauna taxa was calculated for 10 cm^{-2}.

Meiofaunal distribution patterns were determined by multivariate analyses, hierarchical classification and ordination, using logarithmic transformation log n (x + 1). The Bray-Curtis distance and Hierarchical Clustering were performed with the defined groups for UPGMA algorithm. The matrix used for statistical analyses contains 12 faunistic groups (nematodes, copepods, nauplii, polychaetes, oligochaetes, turbellarians, ostracodes, bivalves, kinorhynchs, cnidarians, gastropods and rotifers). A Principal Components Analysis (PCA) was used to determine if the stations were distributed in multidimensional space in function of environmental variables. 20 environmental variables and 20 samples were used for this purpose. The variables were centered and reduced (X mean/standart deviation). Canonical Correspondence Analysis (CCA) was used to correlate the environmental and biological variables. The variables utilized in multivariate analyses were selected by the BIOENV procedure. The SIMPER (Similarity Percentage Breakdown) was applied to determine the contribution of faunistic groups to dissimilarity between the stations (Clarke & Warwick 1994). Data manipulation, statistical and graphical summarization utilized STATISTIC, CANOCO (Ter Braak 1986) and FITOPAC (developed by Shepard, Universidade Estadual de Campinas– SP-Brazil) softwares.

RESULTS

Environmental variables

The predominant fraction of sediment in most of the sampling stations was coarse silt, especially in the stations near the coast and in station 9. Some stations however presented high fine sand percentages during the rainy season (station 5) and during the dry season (station 7). The Ilha Grande station also presented a high percentage of fine sand in both seasons (63.90 and 78.86 %). The redox potential values were already negative in the first cm of the sediment in both seasons (Table I).

Table I. – Top, environmental variables from sampling stations in Jacuacanga Bay (st.1-9) and Ilha Grande station (st.10) at the rainy period: water depth (Depth); water temperature (TW); sediment temperature (TS); dissolved oxygen (DO); salinity (Sal); water pH (pH); redox potential (Eh1); water transparency (TR); organic carbon (org C); organic nitrogen (org N); C/N ratios (C/N); sediment granulometry:– clay % (Clay), silt % (Silt), coarse silt % (C-Silt) and fine sand % (F-Sandy); copper (Cu), zinc (Zn), cadmium (Cd) and lead (Pb); chlorophyll *a* (Chl*a*), phaeophytin *a* (Phaeo*a*). Below, environmental variables from sampling stations in Jacuacanga Bay (st.1-9) and Ilha Grande station (st.10) at dry period.

Variables	Est. 1	Est. 2	Est. 3	Est. 4	Est. 5	Est. 6	Est. 7	Est. 8	Est. 9	Est. 10
Depth (m)	9,00	9,40	8,70	12,00	13,20	15,00	18,50	17,00	14,70	17,00
TW (°C)	24,30	24,60	25,00	24,00	22,90	22,30	19,90	21,30	22,80	25,50
TS (°C)	24,40	24,50	25,00	25,00	24,00	24,50	23,90	24,60	24,50	24,70
O_2 (ml/L)	4,74	4,43	5,06	4,42	3,53	3,77	3,09	2,53	4,53	3,98
Sal (psu)	35,65	35,53	35,55	35,47	35,51	35,87	35,84	35,73	35,22	34,68
pH	8,37	8,35	8,41	8,35	8,24	8,26	8,00	8,14	8,28	7,29
Eh1 (mV)	-176,70	-190,20	-173,80	-171,90	-169,50	-176,80	-166,00	-173,90	-142,00	-118,40
TR (m)	3,80	5,10	4,50	5,20	5,00	6,10	7,50	5,00	6,80	10,20
org C (%)	1,38	2,93	0,74	2,08	0,89	1,86	1,85	2,04	2,11	0,76
org N (%)	0,42	0,93	0,46	0,77	0,35	0,88	0,47	0,61	0,93	0,07
C/N	3,30	3,15	1,62	2,70	2,54	2,11	3,94	3,34	2,27	10,86
Clay (%)	8,93	7,99	4,85	6,85	3,03	7,16	5,30	5,91	9,40	2,42
Silt (%)	2,58	5,16	12,30	11,00	7,78	21,89	39,83	37,16	16,53	21,66
C-Silt (%)	87,69	67,41	43,46	76,55	14,79	69,63	35,15	29,05	67,59	12,01
F-Sandy (%)	0,85	19,45	39,39	5,55	62,00	1,32	19,71	27,88	6,48	63,90
Cu (µg/g)	10,78	9,73	8,75	7,60	5,90	9,61	6,57	7,24	12,00	5,17
Zn (µg/g)	14,20	21,20	9,34	0,00	0,00	0,00	12,90	7,17	14,85	65,73
Cd (µg/g)	0,00	0,15	0,00	0,28	0,31	0,34	0,81	0,94	0,65	0,63
Pb (µg/g)	15,50	12,57	12,77	10,06	6,41	12,25	11,10	12,65	13,30	22,20
Chl*a* (µg/g)	13,01	6,60	6,90	6,75	13,01	29,31	2,43	15,97	22,34	1,69
Pheo*a* (µg/g)	45,04	34,71	31,72	40,11	51,21	76,05	34,69	64,02	62,81	16,23

Variables	Est. 1	Est. 2	Est. 3	Est. 4	Est. 5	Est. 6	Est. 7	Est. 8	Est. 9	Est. 10
Depth (m)	9,50	8,90	9,00	12,70	14,40	15,20	17,70	16,50	14,20	16,90
TW (°C)	22,80	22,90	23,00	22,80	22,70	22,70	22,50	22,50	22,80	22,60
TS (°C)	22,70	22,70	22,80	22,10	22,80	22,30	22,10	22,40	23,10	22,00
O_2 (ml/L)	5,18	5,13	5,12	4,98	5,09	4,95	5,45	4,46	4,62	4,39
Sal (psu)	34,47	34,65	34,36	34,04	34,04	34,39	34,93	34,61	33,86	34,11
pH	8,16	8,10	8,15	8,20	8,19	8,18	8,20	8,18	8,20	8,18
Eh1 (mV)	-201,40	-97,80	-66,60	-99,90	-118,50	-207,20	-81,70	-76,50	-41,70	-31,10
TR (m)	7,60	8,30	8,10	10,70	10,90	11,50	10,90	8,00	10,40	9,70
org C (%)	1,07	1,66	1,07	0,92	0,94	0,89	0,48	0,65	0,98	0,85
org N (%)	1,70	1,80	1,10	1,90	2,60	1,60	0,60	1,80	1,90	0,40
C/N	0,63	0,92	0,97	0,48	0,36	0,55	0,80	0,36	0,52	2,13
Clay (%)	12,83	7,62	4,43	9,06	10,36	12,09	3,04	10,14	8,46	3,75
Silt (%)	17,27	7,60	10,06	24,34	15,41	15,40	4,28	32,20	15,64	7,81
C-Silt (%)	68,39	40,42	36,40	63,18	69,09	71,62	2,19	2,05	72,17	9,58
F-Sandy (%)	1,51	44,36	49,10	3,41	5,14	0,90	90,48	55,62	3,73	78,86
Cu (µg/g)	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Zn (µg/g)	56,00	66,80	48,80	57,60	54,20	50,20	0,00	42,20	43,50	0,00
Cd (µg/g)	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Pb (µg/g)	21,40	15,20	12,80	17,40	17,20	18,20	0,00	13,00	14,80	7,46
Chl*a* (µg/g)	34,86	114,25	3,43	17,69	21,43	60,11	0,89	2,29	5,36	0,46
Pheo*a* (µg/g)	38,63	129,67	14,60	96,86	40,86	113,82	37,67	35,41	107,22	17,01

Organic carbon and heavy metal concentrations were higher in the rainy season, especially in the stations near the coast and at the Ilha Grande station and only cadmium presented significant concentrations in the Jacuacanga Bay during the rainy season. On the other hand, the organic nitrogen concentrations were higher during the dry season mainly in stations 4, 5 and 9. The C/N ratio was very low in all stations, especially in the dry season, varying from 0.36 to 3.94 and the highest value was found in the Ilha Grande station (10.86). Station 2 presented the highest organic carbon concentrations. Dissolved oxygen concentrations were higher in the dry season when the temperatures were lower with higher values near the coast.

Chlorophyll *a* concentrations were clearly higher in stations 2 and 6 in the dry season (114.25 and 60.11 µg/g) while the station 7 and the Ilha Grande station presented low values in both seasons.

Meiofauna composition, abundance and distribution

A total of 22 faunistic groups was found including copepod nauplii. The mean density of the total meiofauna varied from 1425 to 5226.5 ind. 10 cm^{-2} (Fig. 2A) and reached its maximum at station 2 and at the Ilha Grande station in the rainy season. Nematodes, copepods and nauplii

Table II. – Mean density (n. ind. 10 cm^{-2}) of meiofauna groups at the sampling stations in Jacuacanga Bay (st.1-9) and Ilha Grande station (st.10) in the rainy period.

Stations	1			2			3			4			5		
Taxa	X	SD	%	X	SD	%	X	SD	%	X	SD	%	X	SD	%
Nematoda	1046	394.26	48.87	2448.00	639.36	69.56	1840.00	310.93	64.98	1886.25	380.73	59.38	2381.30	709.63	89.54
Copepoda	683.25	262.09	31.92	453.00	191.39	12.87	431.50	142.25	15.24	600.75	240.53	18.91	133.75	43.06	5.03
Nauplii	363	109.32	16.96	330.00	279.85	9.38	305.00	122.39	10.77	606.50	380.64	19.09	62.75	33.88	2.36
Polychaeta	10.25	7.89	0.48	43.75	13.45	1.24	9.25	3.50	0.33	36.75	14.06	1.16	16.50	12.79	0.62
Oligochaeta	2.5	1.73	0.12	6.75	3.50	0.19	1.25	0.,96	0.04	2.00	2.16	0.06	3.25	3.86	0.12
Turbellaria	7.25	4.99	0.34	8.25	7.09	0.23	6.75	7.89	0.24	6.00	2.83	0.19	2.75	2.75	0.10
Ostracoda	19.75	15.48	0.92	134.00	91.09	3.81	214.00	136.73	7.56	22.25	14.08	0.70	33.50	19.97	1.26
Bivalvia	4.5	1.00	0.21	6.75	6.29	0.19	7.25	5.12	0.26	12.00	10.74	0.38	12.00	9.83	0.45
Kinorhyncha	0.5	0.58	0.02	0.00	0.00	0.00	1.75	1.50	0.06	2.25	1.26	0.07	12.75	4.43	0.48
Cnidaria	0.5	0.58	0.02	9.25	6.65	0.26	4.25	4.19	0.15	0.00	0.00	0.00	0.50	0.58	0.02
Acarina	0.5	0.58	0.02	0.75	0.96	0.02	1.00	0.82	0.04	0.75	0.96	0.02	0.25	0.50	0.01
Cladocera	0.25	0.50	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.25	0.50	0.01	2.75	2.36	0.08	5.00	2.00	0.18	0.75	0.50	0.02	0.00	0.00	0.00
Rotifera	1.25	0.50	0.06	71.00	54.49	2.02	3.50	3.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00
Tardigrada	0.25	0.50	0.01	0.75	1.50	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gnathostomulida	0.5	1.00	0.02	3.25	3.77	0.09	1.00	1.41	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Archiannelida	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00
Gastrotricha	0.00	0.00	0.00	0.50	0.58	0.01	0.25	0.50	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Isopoda	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tanaidacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.01
Priapulida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total Meiofauna	2140.5	581.06	100.00	3519.25	1213.90	100.00	2831.75	660.86	100.00	3176.50	1000.06	100.00	2659.55	731.28	100.00

Stations	6			7			8			9			10		
Taxa	X	SD	%	X	SD	%	X	SD	%	X	SD	%	X	SD	%
Nematoda	2050.00	234.32	68.36	1711.25	1043.38	74.67	3122.50	1117.58	84.77	3639.75	967.74	86.84	4440.50	1069.72	84.96
Copepoda	368.50	86.93	12.29	270.75	159.39	11.81	213.00	118.85	5.78	190.50	104.21	4.55	417.75	174.01	7.99
Nauplii	295.50	79.72	9.85	225.50	230.86	9.84	206.50	196.16	5.61	226.75	188.37	5.41	217.00	217.46	4.15
Polychaeta	24.75	4.92	0.83	23.00	6.68	1.00	38.25	10.84	1.04	28.25	9.95	0.67	21.75	6.08	0.42
Oligochaeta	1.75	0.50	0.06	3.75	3.59	0.16	4.00	2.71	0.11	5.00	2.58	0.12	13.50	7.33	0.26
Turbellaria	4.75	2.50	0.16	3.00	0.82	0.13	7.25	7.85	0,20	5.50	3.87	0.13	2.00	2.45	0.04
Ostracoda	222.75	83.53	7.43	24.75	11.70	1.08	73.75	34.96	2.00	76.50	22.87	1.83	33.00	9.83	0.63
Bivalvia	17.00	7,30	0.57	9.00	8.25	0.39	14.00	10.61	0.38	10.50	5.74	0.25	12.50	12.71	0.24
Kinorhyncha	2.75	2.22	0.09	16.25	9.22	0.71	1.25	1.26	0.03	3.75	2.50	0.09	60.75	14.55	1.16
Cnidaria	8.25	4.92	0.28	0.50	0.58	0.02	0.75	0.5	0.02	1.00	0.82	0.02	0.25	0.50	0.00
Acarina	0.50	0.58	0.02	0.50	1.00	0.02	1.00	2.00	0.03	0.75	0.50	0.02	1.00	2.00	0.02
Cladocera	0.25	0.50	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00
Gastropoda	0.75	0.96	0.03	0.25	0.50	0.01	0.25	0.50	0.01	0.50	0.58	0.01	0.50	0.58	0.01
Rotifera	0.50	1.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00
Tardigrada	0.25	0.50	0.01	2.00	2.45	0.09	1.00	1.15	0.03	1.00	2.00	0.02	0.00	0.00	0.00
Gnathostomulida	0.25	0.50	0.01	0.75	1.50	0.03	0.00	0.00	0.00	0.25	0.50	0.01	1.50	1.91	0.03
Archiannelida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastrotricha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00
Isopoda	0.25	0.50	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00
Tanaidacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.50	6.45	0.09
Priapulida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermata	0.00	0.00	0.00	0.50	0.58	0.02	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00
Total Meiofauna	2998.75	163.52	100.00	2291.75	1451.51	100.00	3683.50	1456.33	100.00	4191.25	988.35	100.00	5226.50	1279.63	100.00

were the most abundant groups, representing more than 89 % of total meiofauna. However, some other taxonomic groups occurred in most of the stations showing significant densities, having therefore been included in the statistical analyses (ostracodes, polychaetes, oligochaetes, turbelarians, bivalves, kinorhyncs, cnidarians, gastropods and rotifers) (Tables II, III). Other groups with very low densities occurred only in some stations or in just one sampling season (acarins, cladocerans, tardigrades, gnathostomulids, archiannelids, gastrotrichs, isopods, tanaidaceans, priapulids and juveniles of echinoderms) and then they were excluded from the statistical analyses.

Nematodes were dominant in all stations. They were more abundant in the outer stations of the Bay as well as in the Ilha Grande station (Fig. 2B) while the copepods and nauplii were more abundant in the stations near the coast (Fig. 2C, D) which presented a high taxonomic diversity in relation to the outer stations. Kinorhynchs as well as nematodes were also more abundant in outer stations (Fig. 2L).

Most of the taxonomic groups show the highest densities in the rainy season with exception of nauplii, rotifers, cnidarians and gastropods, that were more abundant in the dry season. Some taxonomic groups did not show significant differences between the two sampling seasons (oligochaetes and turbellarians) (Fig. 2F, G). The density of all the major meiofauna taxa that were utilized in the statistical analyses is shown in Tables II and III.

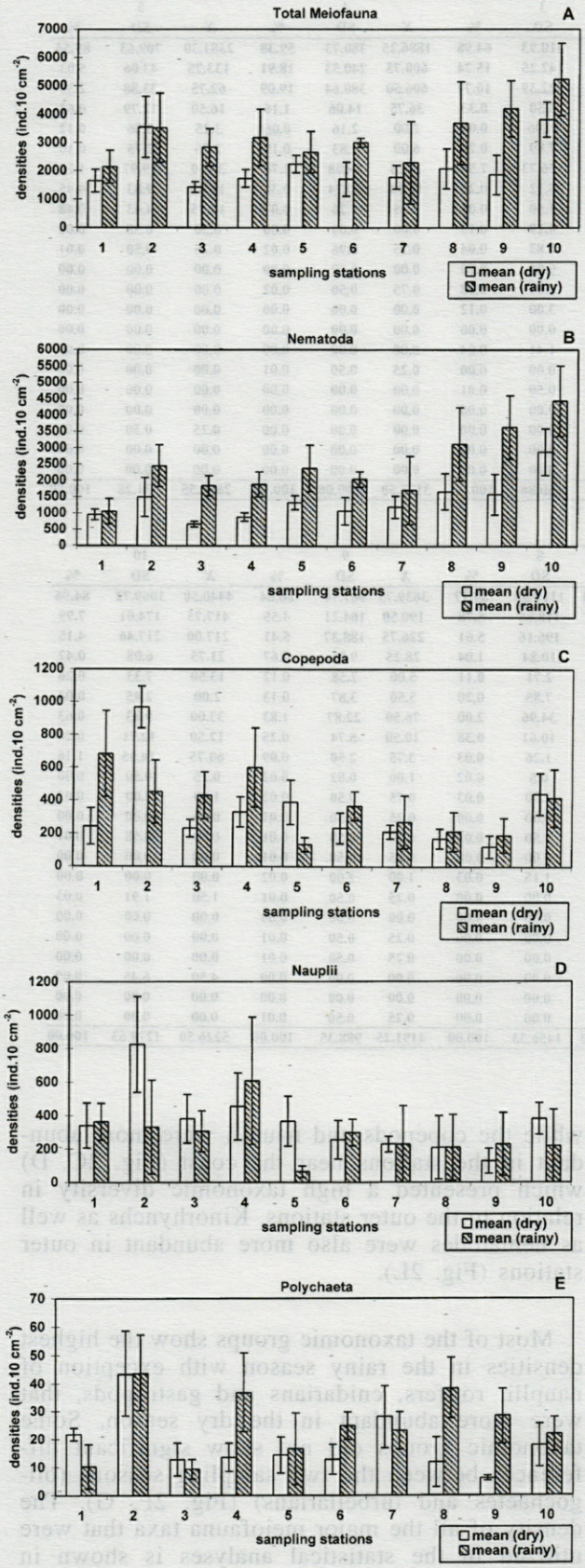

Fig. 2 (A-E). – Mean density (n. ind.10 cm^{-2}) and standart deviation of the main meiofauna groups in Jacuacanga Bay and Ilha Grande station (st.10).

SIMPER procedures (Tables IV and V) shows 16.62 % of dissimilarity between the stations of the dry season and 13.33 % in the rainy season. Nematodes, copepods, rotifers, ostracodes and kinorhynchs contributed with 50 % for this variability. The dendrogram of the rainy season (Fig. 3) indicates 3 station groups: group I formed by stations 1 and 4, group II formed by the outer stations (7, 8, 9 and 10) and st. 5, and group III formed by stations 2, 3 and 6. In the dendrogram of the dry season (Fig. 3) only two station groups are observed: group I formed by stations far from the coast (7, 8 and 9) and the Ilha Grande station and group II including stations near the coast (1, 2, 3, 4, 5 and 6). Canonical Correspondence Analysis represents the station distribution in relation to some environmental variables during the two seasons. During the rainy season (Fig. 4) 53.9 % of the variance was explained by the axis I, influenced by coarse silt and organic carbon. For this reason, it can be noticed that the st 2 location is due to its higher organic carbon concentration. St 5, 7, 8 and 10 are grouped together given their small percentage of coarse silt. The relationship between kinorhynchs and the stations 7 and 10 can be observed and it is probably due to the high fine sand percentage of these stations. In the dry season (Fig. 4), the variable that best explained the station distribution on the axis I (56.4 %) was the dissolved oxygen, while the axis II was represented by C/N ratio and organic carbon. They explained 9.5 % of the variability. The Ilha Grande station is isolated due to its C/N ratio high index as well as to its little amount of organic matter. On the other hand, the station 2 is isolated because of its high amount of organic carbon. The association of kinorhynchs with stations 7 and 10 can be observed once again.

Principal Components Analysis (Fig. 5) separates the two seasons, axis I being formed by granulometric variables and the axis II by physical-chemical variables. 5 station groups can be observed: group I was formed by the Ilha Grande station and st 7 (dry season); group II formed by st 1, 2, 3, 4, 6 and 9 (rainy season); group III formed by st 5, 7 and 8 (rainy season); group IV by st 1, 2, 4, 5, 6 and 9 (dry season) and group V formed by st 3 and 8 (dry season).

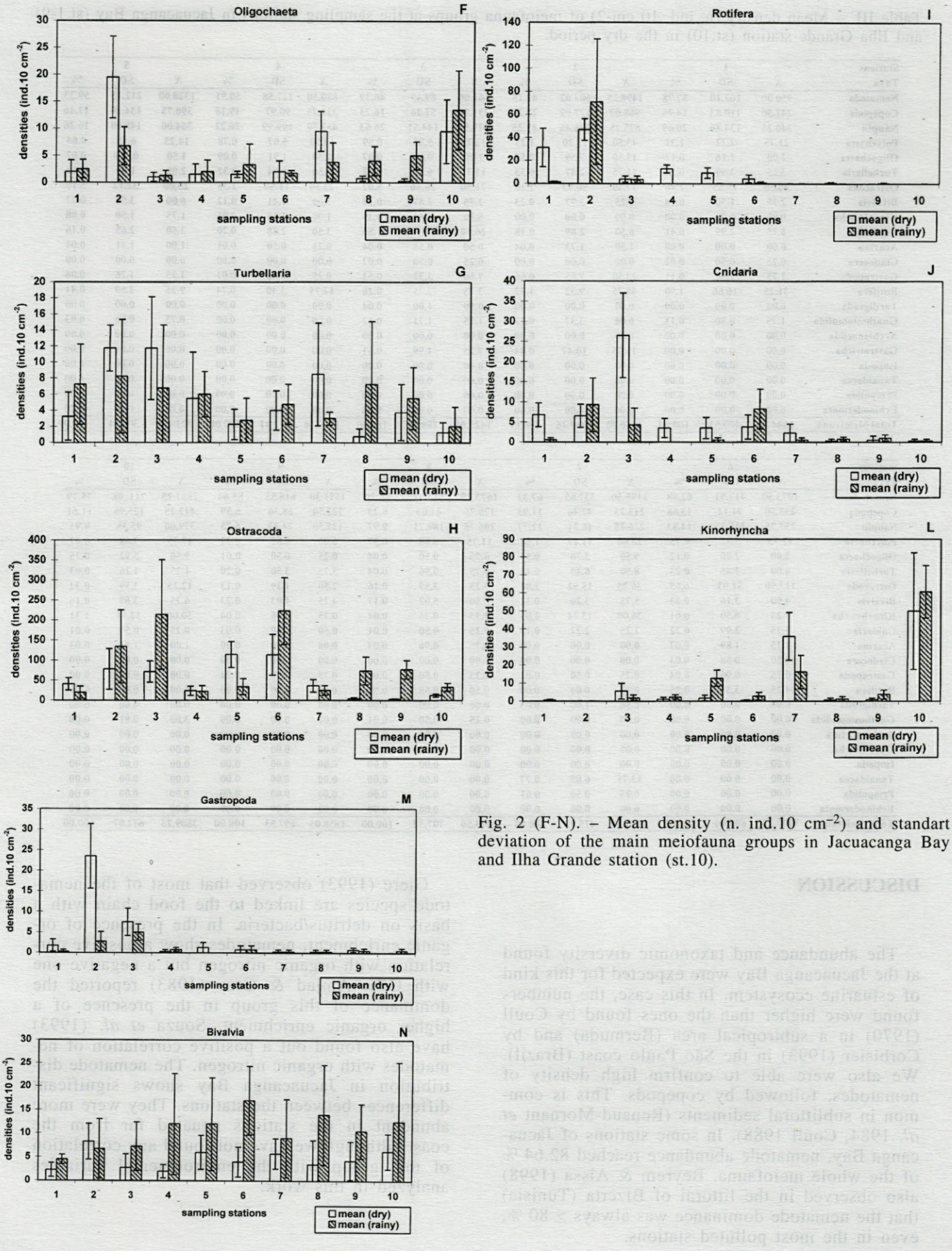

Fig. 2 (F-N). – Mean density (n. ind.10 cm^{-2}) and standart deviation of the main meiofauna groups in Jacuacanga Bay and Ilha Grande station (st.10).

Table III. – Mean density (n. ind. 10 cm-2) of meiofauna groups at the sampling stations in Jacuacanga Bay (st.1-9) and Ilha Grande station (st.10) in the dry period.

Stations	1			2			3			4			5		
Taxa	X	SD	%	X	SD	%	X	SD	%	X	SD	%	X	SD	%
Nematoda	950.00	162.10	57.78	1496.25	602.62	42.15	661.00	89.49	46.39	880.50	127.58	50.91	1328.00	212.13	59.33
Copepoda	242.50	110.83	14,75	968.00	127.09	27.27	231.25	52.26	16.23	331.75	90.97	19.18	390.75	134.19	17.46
Nauplii	340.25	134.86	20.69	825.25	286.46	23.25	379.50	144.51	26.63	453.50	199.99	26.22	364.00	148.90	16.26
Polychaeta	21.75	2.22	1.32	43.50	15.20	1.23	12.75	5.85	0.89	13.50	5.07	0.78	14.25	6.45	0.64
Oligochaeta	2.00	2.16	0.12	19.50	7.59	0.55	1.00	0.82	0.07	1.50	1.91	0.09	1.50	0.058	0.07
Turbellaria	3.25	2.99	0.20	11.75	2.87	0.33	11.75	6.40	0.82	5.50	5.74	0.32	2.00	1.89	0.10
Ostracoda	40.50	15.55	2.46	77.50	50.93	2.18	71.50	26.46	5.02	23.50	11.50	1.36	25,00	32.12	5.10
Bivalvia	2.25	1.50	0.14	8.25	3.77	0.23	2.75	2.87	0.19	2.00	1.41	0.12	6.00	3.56	0.27
Kinorhyncha	0.00	0.00	0.00	0.00	0.00	0.00	5.50	4.43	0.39	1.00	1.15	0.06	1.75	1.50	0.08
Cnidaria	6.75	2.99	0.41	6.50	2.89	0.18	26.50	10.54	1.86	3.50	2.38	0.20	3.50	2.65	0.16
Acarina	0.00	0.00	0.00	1.50	1.73	0.04	0.50	0.58	0.04	0.25	0.50	0.01	1.00	1.41	0.04
Cladocera	0.25	0.50	0.02	0.00	0.00	0.00	0.25	0.50	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	1.75	1.50	0.11	23.50	7.85	0.66	7.50	3.32	0.53	0.25	0.50	0.01	1.25	1.26	0.06
Rotifera	31.25	16.66	1.90	46.75	9.32	1.32	3.75	2.75	0.26	12.75	3.40	0.74	9.25	4.50	0.41
Tardigrada	0.00	0.00	0.00	0.00	0.00	0.00	0.50	1.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Gnathostomulida	1.75	0.50	0.11	6.00	3.37	0.17	1.75	1.71	0.12	0.00	0.00	0.00	0.75	0.96	0.03
Archiannelida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastrotricha	0.00	0.00	0.00	15.75	10.47	0.44	7.25	4.99	0.51	0.00	0.00	0.00	0.00	0.00	0.00
Isopoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tanaidacea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Priapulida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total Meiofauna	1644.25	400.53	100.00	3550.00	1080.46	100.00	1425.00	189.89	100.00	1729.50	312.31	100.00	2238.50	309.51	100.00

Stations	6			7			8			9			10		
Taxa	X	SD	%	X	SD	%	X	SD	%	X	SD	%	X	SD	%
Nematoda	1073.50	417.91	62.88	1195.50	337.85	67.33	1673.25	553.91	80.70	1591.30	618.55	85.64	2887.25	711.,08	75.79
Copepoda	233.50	94.12	13.68	212.25	42.46	11.95	170.75	61.05	8.23	122.50	68.36	6.59	442.25	125.96	11.61
Nauplii	253.25	116.15	14.83	226.75	46.21	12.77	206.75	189.71	9.97	125.50	74.43	6.75	379.00	95.35	9.95
Polychaeta	12.75	5.32	0.75	28.00	11.17	1.58	11.75	8.88	0.57	6.00	0.82	0.32	17.75	7.68	0.47
Oligochaeta	2.00	2.00	0.12	9.50	3.70	0.54	0.75	0.50	0.04	0.25	0.50	0.01	9.50	5.92	0.25
Turbellaria	4.00	2.45	0.23	8.50	6.40	0.48	0.75	0.96	0.04	3.75	3.50	0.20	1.25	1.26	0.03
Ostracoda	113.50	51.03	6.65	36.25	15.52	2.04	3.25	3.59	0.16	2.50	1.29	0.13	12.25	3.59	0.32
Bivalvia	4.00	3.16	0.23	5.75	3.20	0.32	3.50	5.07	0.17	4.25	4.03	0.23	6.25	3.69	0.16
Kinorhyncha	0.25	0.50	0.01	36.00	13.24	2.03	0.75	0.96	0.04	0.75	0.96	0.04	50.00	32.34	1.31
Cnidaria	3.75	2.99	0.22	2.25	2.22	0.13	0.25	0.50	0.01	0.50	1.00	0.03	0.25	0.50	0.01
Acarina	1.25	1.89	0.07	0.00	0.00	0.00	0.75	0.96	0.04	0.00	0.00	0.00	1.00	1.41	0.03
Cladocera	0.50	0.58	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	0.75	0.96	0.04	0.25	0.50	0.01	0.25	0.50	0.01	0.75	0.50	0.04	0.00	0.00	0.00
Rotifera	4.25	3.30	0.25	0.00	0.00	0.00	0.50	0.58	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Tardigrada	0.00	0.00	0.00	0.50	1.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gnathostomulida	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00	3.00	0.82	0.08
Archiannelida	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastrotricha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isopoda	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tanaidacea	0.00	0.00	0.00	13.75	6.85	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Priapulida	0.00	0.00	0.00	0.25	0.50	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total Meiofauna	1707.25	601.00	100.00	1775.50	415.93	100.00	2073.50	707.38	100.00	1858.05	697.53	100.00	3809.75	614.07	100.00

DISCUSSION

The abundance and taxonomic diversity found at the Jacuacanga Bay were expected for this kind of estuarine ecosystem. In this case, the numbers found were higher than the ones found by Coull (1970) in a subtropical area (Bermuda) and by Corbisier (1993) in the São Paulo coast (Brazil). We also were able to confirm high density of nematodes, followed by copepods. This is common in sublittoral sediments (Renaud-Mornant *et al.* 1984, Coull 1988). In some stations of Jacuacanga Bay, nematode abundance reached 82.64 % of the whole meiofauna. Beyrem & Aissa (1998) also observed in the littoral of Bizerta (Tunisia) that the nematode dominance was always > 80 %, even in the most polluted stations.

Giere (1993) observed that most of the nematode species are linked to the food chain with a basis on detritus/bacteria. In the presence of organic enrichment, nematodes show a positive correlation with organic nitrogen but a negative one with C/N. Amjad & Gray (1983) reported the dominance of this group in the presence of a higher organic enrichment. Souza *et al.* (1993) have also found out a positive correlation of nematodes with organic nitrogen. The nematode distribution in Jacuacanga Bay shows significant differences between the stations. They were more abundant in the stations situated far from the coast, although we have not found any correlation of this group with the environmental variables analyzed in this work.

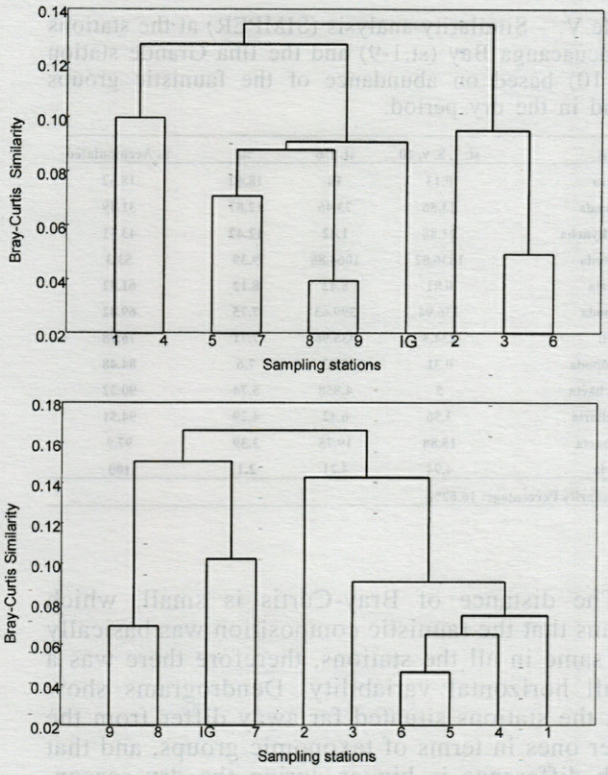

Fig. 3. – Dendrogram for hierarchical clustering of the Jacuacanga Bay stations and Ilha Grande station (IG) in the rainy period (top), and in the dry period (below).

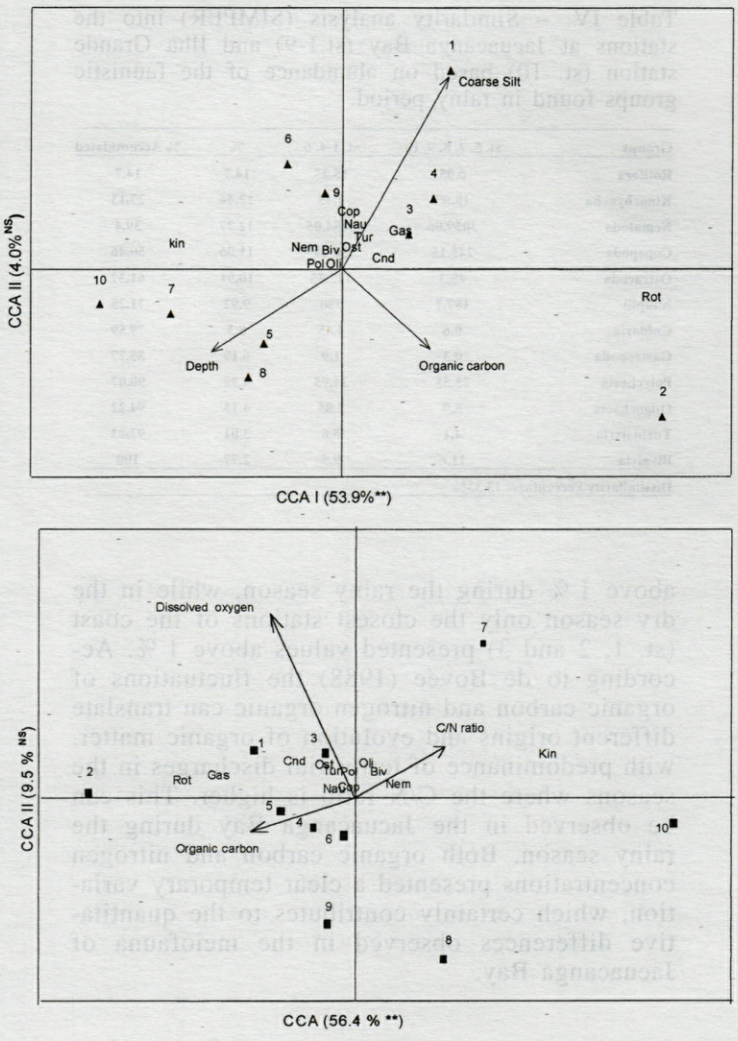

Fig. 4.– Canonical Correspondence Analysis (CCA) of the meiofauna group distribution and the sampling stations in the rainy period (top). Nem (Nematoda), Cop (Copepoda), Nau (Nauplii), Pol (Polychaeta), Oli (Oligochaeta), Tur (Turbellaria), Ost (Ostracoda), Biv (Bivalvia), Kin (Kinorhyncha), Cnd (Cnidaria), Gas (Gastropoda) and Rot (Rotifera). Canonical Correspondence Analysis (CCA) of the meiofauna group distribution and the sampling stations in the dry period (below).

Usually copepod distribution is influenced by the grain size, copepods being more abundant in coarser sediments (Tietjen 1969, Hicks & Coull 1983). However, this distribution patterns can also be explained by different types of feeding, some species being correlated with microphytobenthos (Dinet 1972, Giere 1993). The oxygen is another factor that has an influence on copepod distribution. Most of the species are sensitive to less oxygenated biotopes (Giere 1993). Copepods distribution in the Jacuacanga Bay was inverse to that of the nematodes. The highest densities were recorded in stations near the coast, where higher chlorophyll *a* values as well as higher dissolved oxygen concentrations are observed. In the Fal estuary system (Cornwall, UK), the heavy metal concentration was also an important factor that influenced the copepod community structures (Somerfield *et al.* 1994). However, the procedure of BIOENV indicated that other factors, for instance the percentage of silt and clay and the concentration of organic carbon, were also significant in the distribution of this group. This could also explain such a distribution of the copepods in the Jacuacanga Bay.

Organic carbon concentrations between 1 and 10 % indicate a level of sediment contamination that can be tolerated by the majority of benthic organisms (Mudroch & Azcuel 1995). In Jacuacanga Bay most of the stations presented values

Table IV. – Similarity analysis (SIMPER) into the stations at Jacuacanga Bay (st.1-9) and Ilha Grande station (st. 10) based on abundance of the faunistic groups found in rainy period.

Groups	st. 5. 7. 8. 9. 10	st. 1-4. 6	%	% Accumulated
Rotifera	0.05	15.25	14.7	14.7
Kinorhyncha	18.95	1.45	12.44	27.13
Nematoda	3059.06	1854.05	12.27	39.4
Copepoda	245.15	507.4	11.06	50.46
Ostracoda	48.3	122.55	10.91	61.37
Nauplii	187.7	380	9.92	71.28
Cnidaria	0.6	4.45	8.3	79.59
Gastropoda	0.3	1.9	6.19	85.77
Polychaeta	25.55	24.95	4.29	90.07
Oligochaeta	5.9	2.85	4.15	94.22
Turbellaria	4.1	6.6	3.01	97.23
Bivalvia	11.6	9.5	2.77	100
Dissimilarity Percentage: 13.33%				

Table V. – Similarity analysis (SIMPER) at the stations in Jacuacanga Bay (st.1-9) and the Ilha Grande station (st. 10) based on abundance of the faunistic groups found in the dry period.

Groups	st. 7. 8. 9. 10	st. 1-6	%	% Accumulated
Rotifera	0.13	18	18.62	18.62
Ostracoda	13.56	73.46	12.87	31.49
Kinorhyncha	21.88	1.42	12.42	43.91
Nematoda	1836.82	1064.88	9.39	53.3
Cnidaria	0.81	8.42	8.12	61.42
Copepoda	236.94	399.63	7.75	69.42
Nauplii	234.5	435.96	7.71	76.88
Gastropoda	0.31	5.83	7.6	84.48
Oligochaeta	5	4.858	5.74	90.22
Turbellaria	3.56	6.42	4.29	94.51
Polychaeta	15.88	19.75	3.39	97.9
Bivalvia	4.94	4.21	2.1	100
Dissimilarity Percentage: 16.62%				

above 1 % during the rainy season, while in the dry season only the closest stations of the coast (st. 1, 2 and 3) presented values above 1 %. According to de Bovée (1988) the fluctuations of organic carbon and nitrogen organic can translate different origins and evolution of organic matter, with predominance of terrestrial discharges in the seasons where the C/N ratio is higher. This can be observed in the Jacuacanga Bay during the rainy season. Both organic carbon and nitrogen concentrations presented a clear temporary variation, which certainly contributes to the quantitative differences observed in the meiofauna of Jacuacanga Bay.

The distance of Bray-Curtis is small, which means that the faunistic composition was basically the same in all the stations, therefore there was a small horizontal variability. Dendrograms show that the stations situated far away differ from the inner ones in terms of taxonomic groups, and that such difference is bigger during the dry season. In this season two other groups were formed including the outer stations, probably due to the presence of kinorhynchs in st 7 as well as in the Ilha Grande station. The st 2 is distinguished from the ones located near the coast by the abundance of almost all the faunistic groups except kinorhynchs and cnidarians. We should point out

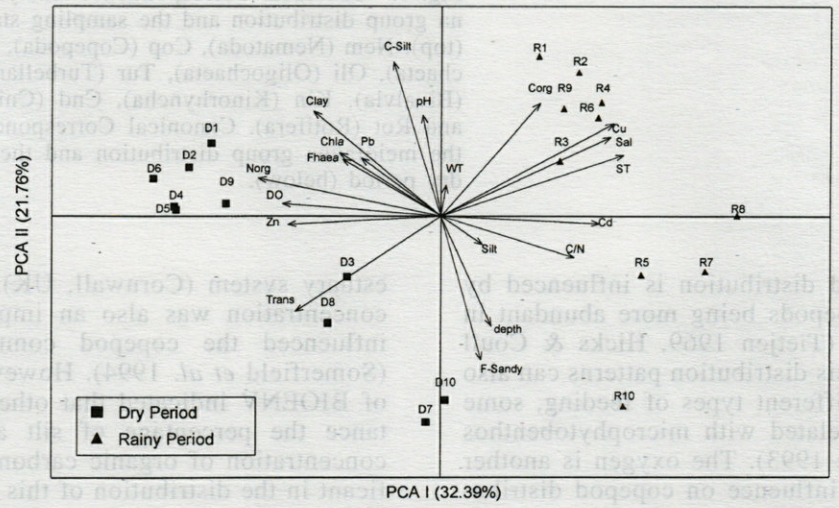

Fig. 5. – Principal Component Analysis (PCA). Projection of the 20 environmental variables and 20 sampling stations (R1-10: rainy period stations; D1-10: dry period stations) in the planes defined by the first two factorial axes (I and II). Environmental variables (vectors): water depth (depth); water temperature (WT); sediment temperature (ST); dissolved oxygen (DO); salinity (Sal); water pH (pH); water transparency (Trans); organic carbon (Corg); organic nitrogen (Norg); C/N ratios (C/N); sediment gramulometry: clay % (Clay), silt % (Silt), coarse silt % (C-Silt) and fine sand % (F-Sandy), copper (Cu), zinc (Zn), cadmium (Cd) and lead (Pb); chlorophyll *a* (Chl*a*), phaeophytin *a* (Phae*a*).

here that st 2 lies near the Jacuacanga river, receiving therefore a great amount of organic material.

During the rainy season, st 5 is near to the group of the most external stations, probably because of the low copepod number. The high values of ostracodes of st 2, 3 and 6 made these stations different from st 1 and 4.

Canonical Correspondence Analysis results show that grain size, organic carbon, depth, C/N ratio, and dissolved oxygen have a strong influence on the meiofauna distribution.

The SIMPER procedure provides evidence that the groups which contributed most to variability between the stations are nematodes, copepods, kinorhynchs, rotifers and ostracodes.

The organism abundance in the Jacuacanga Bay is higher in the rainy season, although presenting basically the same meiofauna composition observed in both seasons. In spite of this, the Principal Component Analysis (PCA) shows the evident influence of seasonal variation on the meiobenthic community mainly indicated by fluctuation of the studied physical-chemical variables, namely granulometry, dissolved oxygen, organic carbon, C/N ratio and cadmium that clearly distinguish the dry season from the rainy season.

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COMPOSITION AND TEMPORAL FLUCTUATIONS OF ICHTHYOPLANKTON COMMUNITY IN THE KORNATI ARCHIPELAGO AND MURTER SEA, EASTERN ADRIATIC

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ICHTHYOPLANKTON
COMPOSITION
TEMPORAL FLUCTUATIONS
KORNATI ARCHIPELAGO
ADRIATIC

ABSTRACT. – Temporal fluctuations of species composition and abundance of fish larvae in the Kornati archipelago and Murter Sea were studied over 12 months from January to December 1990 from seven stations. A total of 2145 larvae, representing 28 families and 52 species, were collected using two types of plankton nets on each station, "Helgoland" and "Bongo". The community was dominated numerically by a few species: *Sardina pilchardus* (29.2 %), *Engraulis encrasicolus* (28.7 %), *Serranus hepatus* (7.5 %), *Sarpa salpa* (5.2 %), and *Cepola rubescens* (4.7 %), constituting 75.3 % of the total catch. Similarity between patterns in the abundance of the 11 most common species were examined using correlation matrix-based principal component analysis. Results were compared to the abiotic factors leading conclusion that only a low amount of variation in the abundance field can be explained by temperature and salinity.

ICHTYOPLANCTON
COMPOSITION
VARIATIONS TEMPORELLES
ARCHIPEL KORNATI
ADRIATIQUE

RÉSUMÉ. – Les variations temporelles de la composition en espèces et de l'abondance des larves de Poissons de l'archipel de Kornati et de la Mer de Murter ont été étudiées pendant 12 mois (janvier-décembre 1990) sur 7 stations. Un total de 2145 larves représentant 28 familles et 52 espèces a été récolté à l'aide de 2 filets différents à chaque station « Helgoland » et « Bongo ». Les espèces dominantes sont *Sardina pilchardus* (29,2 %), *Engraulis encrasicolus* (28,7 %), *Serranus hepatus* (7,5 %), *Sarpa salpa* (5,2 %) and *Cepola rubescens* (4,7 %), soit 75 % du total. La similarité d'abondance des 11 espèces les plus communes a été étudiée à l'aide d'une matrice de corrélations (ACP). Les résultats analysés et l'étude des facteurs abiotiques permettent de conclure que la température et la salinité ne peuvent expliquer qu'une faible variation d'abondance.

INTRODUCTION

A number of studies and a variety of authors have studied the planktonic stages of individual fish species, particularly those of sardine (*Sardina pilchardus* Walb.) and anchovy (*Engraulis encrasicolus* L.) in the Adriatic. However, there is far less papers dealing with the composition and dynamics of individual groups or even of the ichthyoplankton community as a whole.

First joint data on the planktonic stages of the Adriatic fishes were given by Graeffe (1888), Steuer (1910), Stiasny (1910) and Vatova (1928) for the northern Adriatic. Karlovac (1953) provided the data on distribution, numerousness and the time of occurrence of planktonic stages of fish from the families Sternoptychidae, Stomiatidae and Scopelidae for the whole Adriatic. Varangolo (1964) studied the period of the occurrence and seasonal dynamics of the numerousness of larval stages of 21 fish species in the northern Adriatic in 1962-1963. In the course of investigations of the planktonic stages of sardine carried out in the central Adriatic in 1952-1953 period Karlovac (1967) recorded the larval stages of 68 fish species from the plankton. On that occasion this author studied their distribution and dynamics of abundance. Vucetic (1965, 1970, 1971) reported the seasonal and long-term distribution of the total numbers of the larval fish stages in the central Adriatic. The data on the qualitative and quantitative distribution of the larval fish stages in the central Adriatic in 1973 are also available (Regner 1976). Regner (1980, 1982) presented the results of the analysis of annual distribution and long-term fluctuations of the qualitative and quantitative composition of the larval fish stages in the plankton of the Kastela Bay and at the high sea of the central Adriatic for the period from 1970 to 1977, respectively.

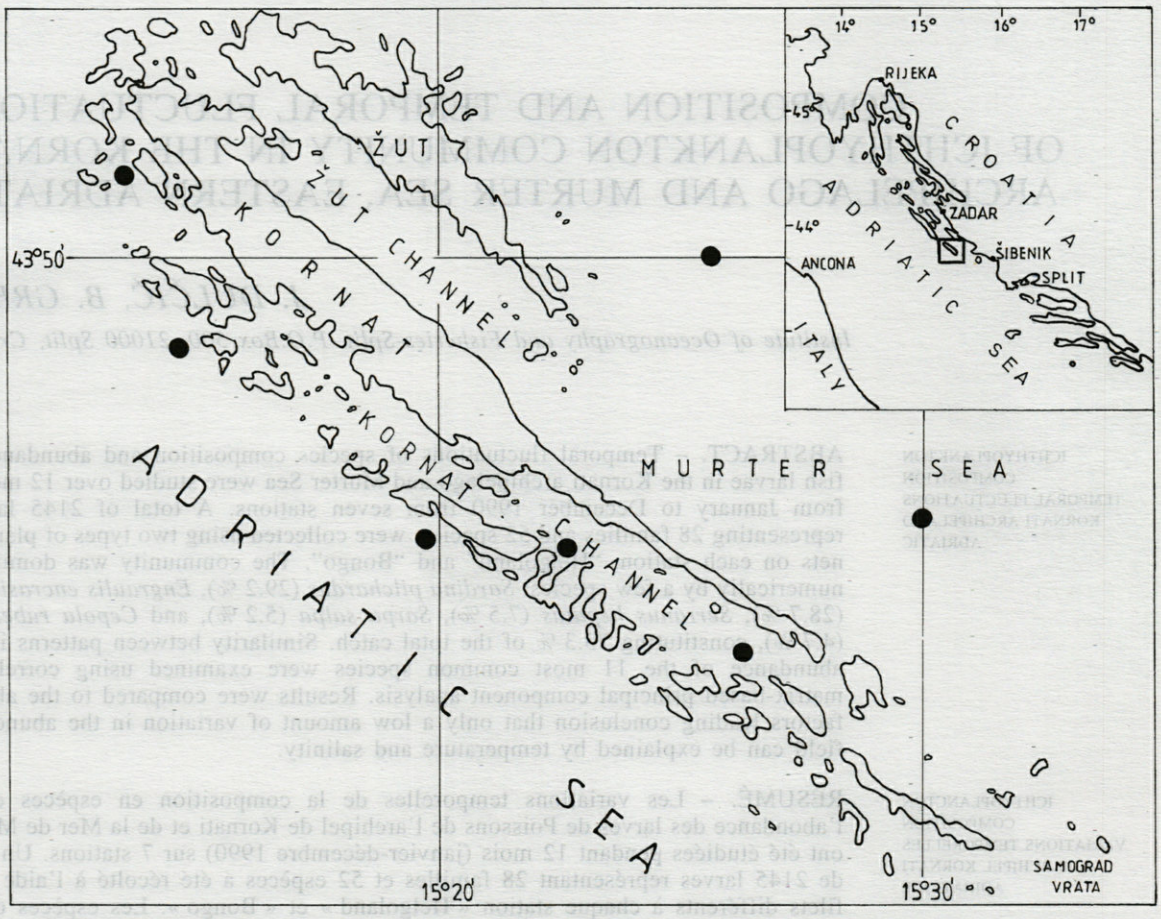

Fig. 1. – Locations of the sampling stations (•) in the Kornati Archipelago and Murter Sea, eastern middle Adriatic.

In the present study we present those data describing the composition and seasonal fluctuations of ichthyoplankton in the area of Kornati Archipelago and Murter Sea, eastern middle Adriatic. The relative importance of temperature and salinity on biotic factors was examined using multivariate techniques.

MATERIAL AND METHODS

The Kornati islands lie along the central part of the Croatian coast, between Zadar and Sibenik (Fig. 1). The Kornati Archipelgo covers an area of approximately 224 km^2 and has 141 islands, islets and reefs (Rubić 1952). The Kornati Islands have the most irregular coastlines of any islands in the Mediterranean. Murter Sea covers an area of 210 km^2 (Friganovic 1981) and lies between islands Pasman, Vrgada & Murter on the north, and island Kornat on the south-west (Fig. 1). Stations in study area were located at depths ranging from 35 to 96 m.

Sampling was conducted on a monthly basis from January to December 1990 from seven stations (Fig. 1). Fish larvae were collected using two types of plankton nets on each station "Helgoland" and "Bongo". The area of mouth aperture of "Helgoland" type is 1.6 m^2 and mesh size 0.516 mm. The net was towed from 35 m depth to surface at a speed of 0.5 m/sec. A plankton net type "Bongo" has mouth openings of 20 cm and 0.250 mm mesh size. Oblique hauls were performed, and net was towed up to the maximum depth of 5 m above the bottom, at the vessel speed between 1.5 and 2 knots. Wire angle and length of line were monitored during the tow. Note that oblique tows will underestimate the densities of organisms which are vertically stratified. Collected organisms were sorted and preserved in 5 % buffered formalin (pH from 8.5 to 9.0). Before being sorted, the material was sedimented for 24 hours in beakers. Fish larvae were afterwards extracted, identified and counted. Larvae and postlarvae were, as a rule, determined up to the species level. In cases when this was not possible they were determined up to the level of family. Temperature and salinity were measured by classical methods at every station before nets hauling. Measurements were taken of both surface and bottom waters.

Temporal fluctuations in community structure, abiotic factors and interactions between these variables were analysed using multivariate techniques: multiple linear regression and principal component analysis (Preisendorfer 1982). Community structure was specified by species richness (D), diversity (H), and evenness (J)

using formulae proposed by Margalef (1968), Shannon & Weaver (1949), and Pielou (1966), respectively. The degree of relationship existing between these variables and abiotic factors (temperature and salinity) was determined by R^2, e.g. the coefficient of multiple determination.

Abundance in the species composition was subject to the correlation matrix-based principal component analysis (PCA) (Preisendorfer 1982) to examine a minimal number of groups (clusters) the variability of which describes the maximum amount of the total variability in the larval fish community. The PCA was performed on the correlation matrix of standardised variables (zero mean and unit standard deviation). We used Bartlett's test (Fulgosi 1988) for testing the significance of the correlation matrix. The significance of extracted principal components (eigenvalues) were tested with Rule N (Overland & Preisendorfer 1982), using Monte Carlo simulation of the random matrix of the same size as the original data matrix. To enhance the interpretation of the components, Varimax orthogonal rotation was applied (Richman 1986).

The relationship of species composition between seven stations was compared using Spearman's rank correlation test on the basis of the yearly catch in terms of number of each individual species. For comparing abiotic factors between seven sampling locations, an ANOVA model was used.

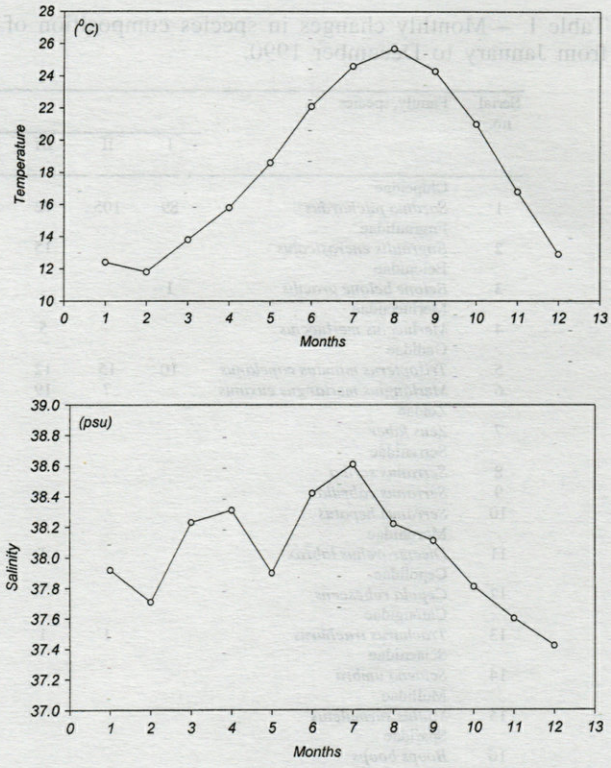

Fig. 2. – Monthly variations in the mean sea water temperature (°C) and salinity (psu) in the Kornati Archipelago and Murter Sea between January and December 1990.

RESULTS AND DISCUSSION

Analysis of variance revealed significant correlations between temperature and salinity ($p < 0.01$) among the seven sampling stations, respectively. Mean monthly temperature ranged from 11.8 °C (SD = 0.96) in February to 25.7 °C (SD = 1.53) in August, with no significant difference in temperature between the seven stations. Mean monthly salinity values, however, were more stable (ranging from 37.42 ± 0.89 to 38.61 ± 0.51 psu) (Fig. 2). While sea water temperature shows typically Adriatic seasonal cycles, seasonal cycles in salinity typically for the Adriatic are not evident, mainly because the sampling stations are situated in the coastal area which is strongly influenced by precipitation and evaporation and which is different along the Adriatic from North to South (Grbec *et al.* 1997).

Spearman's rank correlation coefficients of species composition among the seven stations were highly significant ($p = 0.01$), indicating that the rank of species composition was similar among sampling stations. So, data for all seven stations were combined. Fifty-two species, representing 28 families, were caught between January and December 1990 (Table I), the number of species was most abundant in June (20) and lowest in February (8). A total of 2145 larvae were collected: the number of individual was higher in August (318), and the lowest in January (109). This finding agrees well with the data of Karlovac (1967) and Regner (1980) for the Kastela Bay (eastern middle Adriatic) where the largest number of species of fish larvae may be found in the plankton during the warmer season of the year. *Sardina pilchardus* (29.2 %), *Engraulis encrasicolus* (28.7 %), *Serranus hepatus* (7.5 %), *Sarpa salpa* (5.2 %), and *Cepola rubescens* (4.7 %) comprised 75.3 % of the total catch abundance (Table I). *S. pilchardus* and *E. encrasicolus* were the two most dominant species. Therefore the seasonal succession of the occurrence of fish larvae may be divided into two seasons, i.e. sardine in the colder season (November-April), the anchovy in the warmer season (May-October). The similar seasonal succession was also found in the Kastela Bay – eastern central Adriatic (Regner 1980). *S. hepatus* has the highest abundance from April to August, while the *S. salpa* abundance was the highest from September to October. *C. rubescens* has the highest abundance from May to November. This could be correlated with the spawning periods (Jardas 1996) and duration of embryonic development of the mentioned species (Dulcic 1993). The remaining species comprised from 4.2 % to 0.05 % of the total catch. The occurrence time of fish larvae is also given in the Table I. To a certain extent this time is also an indicator of the approximate time of spawning of the adult fish (Regner 1980). Ecological separation of the dominant species by

Table I. – Monthly changes in species composition of fish larvae collected in Kornati Archipelago and Murter Sea from January to December 1990.

Serial no.	Family, species	No. Fish larvae												
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Total
	Clupeidae													
1	*Sardina pilchardus*	89	105	72	37	30					44	59	191	627
	Engraulidae													
2	*Engraulis encrasicolus*			15	8	10	15	100	215	188	65			616
	Belonidae													
3	*Belone belone gracilis*	1											1	2
	Merlucciidae													
4	*Merluccius merluccius*			5	12						10	19		46
	Gadidae													
5	*Trisopterus minutus capelanus*	10	15	12	12								7	56
6	*Merlangius merlangus euxinus*		7	19										26
	Zeidae													
7	*Zeus faber*											1	1	2
	Serranidae													
8	*Serranus scriba*					4	1	2	3					10
9	*Serranus cabrilla*						2	1						3
10	*Serranus hepatus*				27	15	29	48	29	10	2			160
	Moronidae													
11	*Dicentrarchus labrax*			1										1
	Cepolidae													
12	*Cepola rubescens*					12	20	10	15	10	18	11	5	101
	Carangidae													
13	*Trachurus trachurus*		1	1	2	1	2	3						10
	Sciaenidae													
14	*Sciaena umbra*								1					1
	Mullidae													
15	*Mullus surmuletus*							2	1					3
	Sparidae													
16	*Boops boops*				5	1								6
17	*Dentex (Dentex) dentex*					1								1
18	*Diplodus annularis*						15	20	31	6				72
19	*Diplodus vulgaris*											2	1	3
20	*Diplodus sargus sargus*				1	1	2							4
21	*Diplodus puntazzo*										5	1		6
22	*Sparus aurata*	2											1	3
23	*Sarpa salpa*					18	10				24	48	12	112
24	*Pagellus erythrinus*					1	1							2
25	*Oblada melanura*			5	3	4								12
	Centracanthidae													
26	*Spicara smaris*						7	2	5					14
27	*Spicara maena*										6	2	2	10
	Labridae													
28	*Labrus merula*				1									1
29	*Symphodus tinca*						1							1
30	*Symphodus ocellatus*							1						1
31	*Symphodus cinereus*						1							1
32	*Coris julis*					2	1	4	1	1				9
	Pomacentridae													
33	*Chromis chromis*					5	42	10	3					60
	Scombridae													
34	*Scomber scombrus*	1		2										3
35	*Scomber japonicus*										1			1
36	*Thunnus thynnus thynnus*							1		2				3
37	Gobiidae	2	4	1	5	8	22	15	10	6	6	2	9	90
	Callionymidae													
38	*Callyonimus maculatus*		1	4	7									12
39	Blenniidae					11	3	4	2					20
	Mugilidae													
40	*Chelon labrosus*												1	1
41	*Liza aurata*		1	2										3
	Atherinidae													
42	*Atherina hepsetus*	1											1	2
	Scorpaenidae													
43	*Scorpaena porcus*							1	1	1				3
44	*Scorpaena scrofa*						1							1
	Triglidae													
45	*Trigloporus lastoviza*			2										2
	Citharidae													
46	*Citharus linguatula*								1	1				2
	Bothidae													
47	*Arnoglossus laterna*	2	4	2	1		1	2						12
48	*Bothus podas podas*										1	1		2
	Soleidae													
49	*Solea vulgaris*	1											1	2
50	*Buglossidium luteum*				1									1
51	*Monochirus hispidus*										1	1		2
	Lophiidae													
52	*Lophius piscatorius*						1							1
	Total													2145

recruitment timing resulted in the fact that species did not compete one with the other for the same niche (Tzeng & Wang 1992). Temporal staggering of recruitment may be a mechanism for reducing possible interspecific competition, as has been observed in other fish communities (Doherty 1991). Segregation of some sparid species, for example, was seasonal in Kornati archipelago and Murter Sea since they recruit at different times of the year (*D. sargus sargus* in spring; *O. melanura* during summer; *S. salpa* during autumn; *D. puntazzo* at the beginning of autumn; *D. vulgaris* at the beginning of winter). Distribution of fish larvae is strongly affected by spawning seasonality, egg production variability, predation on eggs and larvae, larval starvation, duration of planktonic life, oceanographic features affecting plankton production, larval transport and competition (Richardson *et al.* 1980, Lasker 1985). The spawning strategies of fishes, the means of introducing the eggs or larvae to the plankton community, and the strategies for ensuring dispersal to new areas are quite numerous. The different combinations of spawning strategies in fish and the methods used to carry the eggs and larvae to the plankton give diverse but distinct patterns to plankton groups (Leiby 1986). These life-history strategies of fishes must be compatible with environmental features for species to persist, since the number of strategies meeting these requirements is finite, several species may converge on the same strategy; a consequence of these adaptive convergences is the formation of ichthyoplankton assemblages (McGowen 1993). Primary determinants of ichthyoplankton assemblage structure undoubtedly include mode, location, timing, duration and intensity of spawning by adults (Rakocinski *et al.* 1996). Aspects of larval biology, however, like planktonic stage duration (including stage duration, growth rates, and size at transformation) and transport mechanisms (including advection and mixing processes), also influence assemblage structure (Richardson *et al.* 1980). Recent studies that interpret ichthyoplankton community structure in terms of adult characteristics often find spatially heterogeneous distributions of larvae that are attributable to adult characteristics (Drake & Arias 1991a; Yoklavich *et al.* 1992). Some scientists even find interactions between adult reproductive models and larval biology may help explain spatial heterogeneity in ichthyoplankton community structure. For example, larval fish distribution in a small California estuary differed between inland and near-ocean stations in accordance with reproductive modes of constituent fishes and hydrographic conditions (Yoklavich *et al.* 1992). In another geographical region, Drake & Arias (1991) found that a shallow coastal inlet in southwestern Spain served primarily as a nursery for coastal pelagic spawners, and secondarily for benthic egg spawners and pouch brooder species. Knowing geographical locations of spawning adults can also help to explain spatial heterogeneity in ichthyoplankton community structure. Spatial and seasonal spawning behaviour of adults plays the key role in formation of ichthyoplankton communities. Mechanisms that may maintain ichthyoplankton community at islands include boundary layers, small scale frontal dynamics, tidal currents, topographically produced eddies, seasonally reduced on variable currents, and regions of no or returning flow. Behaviour of larvae particularly that affecting vertical distribution, can modify the influences of these mechanisms. The integrity of community can be disrupted by both biotic and abiotic factors (Boehlert & Mundy 1993). An abundant ichthyofauna was recorded from 141 localities of the areas of Kornati Islands and Murter Sea: 160 species and subspecies which make up 39.5 % of all known species and subspecies of the Adriatic Sea (Jardas *et al.* 1995). So, we collected larvae from 32.5 % of recorded adult species and subspecies in area of study. It is possible that sampling design (our choice in number of surveys, specific locations, type of net) could partially influence the results. The overall value of richness D was 6.65, ranging from 1.42 in February to 3.67 in June. H' values fluctuated from 0.74 in September to 2.31 in May and June, with an overall value of 2.25. J' ranged from 0.35 in December and January to 0.84 in May. Mean monthly variations in these biotic factors are presented in Fig. 3. These values could be comparable with values obtained in studies performed in similar areas bays and estuaries. Drake & Arias (1991) reported that mean H' value fluctuated from 0.77 to 1.08, and mean J' value from 0.29 to 0.46 for different sample fish groups in a shallow tidal channel of Cadiz Bay. The overall value of richness D fluctuated from 1.17 to 3.47, mean H' value from 1.19 to 2.36, while mean J' value from 0.57 to 0.80 for intertidal fish community in nortwestern Arabian Gulf (Ali & Hussain 1990). Therefore, we can suppose that the overall high richness values of ichthyoplankton community in Kornati archipelago underline the possible importance of the area as a nursery and spawning ground for several local species.

The relationship between abiotic factors such as temperature and salinity (included in model as independent variables) and the biotic factors (number of species, number of individuals, diversity and abundances: dependent variables) was analysed using multiple linear regression models. The significance level for the variables included in the model was set at $p < 0.05$. Results indicated that variations in abiotic factors could predict more than 80 % of monthly variations in number of species mainly because of the interaction affect of temperature and salinity. Variation in number of individuals showed significant correlations with temperature ($R = 0.6722$; $p = 0.017$), while va-

Table II. – Coefficient of multiple determination (R^2) identifying the association according to rank of the 11 most dominant species (abreviations in parentheses) with temperature and salinity.

Rank no.	Serial no.	Species	Temperature	Salinity	R^2	P
1	1	*Sardina pilchardus*	-0.78*	-0.64*	0.84	0.0001
2	2	*Engraulis encrasicolus*	0.78*	-0.17	0.66	0.01
3	4	*Merluccius merluccius*	-0.03	-0.17	0.05	0.789
4	5	*Trisopterus minutus capelanus*	-0.90*	0.66*	0.82	0.0001
5	6	*Merlangius merlangus euxinus*	-0.56	0.43	0.32	0.18
6	10	*Serranus hepatus*	0.46	0.71*	0.74	0.002
7	12	*Cepola rubescens*	0.84*	-0.53	0.71	0.004
8	18	*Diplodus annularis*	0.64*	0.31	0.62	0.01
9	23	*Sarpa salpa*	0.39	-0.63*	0.39	0.106
10	33	*Chromis chromis*	0.12	0.36	0.24	0.289
11	37	Gobiidae	0.42	0.25	0.38	0.114

*significant

riation in number of species with salinity (R = 0.5866; p = 0.045). The positive and statistically significant correlation coefficient between the number of individuals and temperature showed that the numbers of larval stages is objectively high at higher temperatures. Namely, since the development and growth of the larval stages of fish as well as those of all the poikilotherms, are higher at higher temperature, their probability of occurrence at higher temperatures is lower than when their development lasts longer. Therefore their increased numerousness at higher temperatures in the Kornati archipelago and Murter Sea may be held to be a real consequence of the higher production of eggs and probably lower mortality rates. This was to be expected since it is known that the number of species of fish of Mediterranean-Atlantic and circumtropical zoogeographical origin exceeds to a considerable extent the number of Mediterranean-borreal and Arctic-borreal species in the Adriatic (Regner 1980). Results also suggests that about 70 % of the variability associated with monthly fluctuations in diversity could be predicted by the temperature. These results indicated that even if there is a temperature "controlling" monthly fluctuations of number of species and diversity, derivation of a non-zero association between these biotic factors and sea water temperature does not necessarily imply a causal relationship. In temperate seas such as the Adriatic, most species have internalised their biological cycles according to seasonal patterns. They spawn or settle in a quite short and well defined period of the year. So, abundances of many species were positively or negatively correlated with sea water temperature (Table II), because they settle during the hot or cold season. This is the reason why multilinear correlation coefficients between the number of individuals and water temperature are nonsignificant. Based on the multiple linear regression model it was found that five of 11 common species were positively (*E. encrasicolus*, *C. rubescens*, and *D. annularis*) or negatively (*S. pilchardus* and *T. m. capelanus*) correlated with temperature, indicating that timing for settling of the individual species is different. Two species were correlated positively (*T. m. capelanus* and *S. hepatus*) and also two species (*S. pilchardus* and *S. salpa*) negatively with salinity.

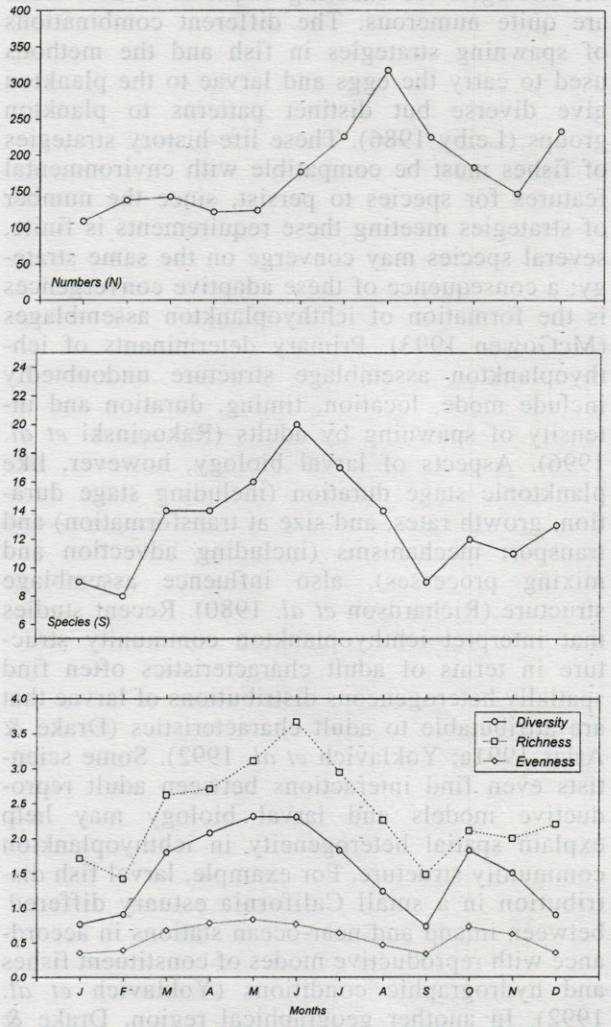

Fig. 3. – Monthly variations in the number of individuals (N), number of species (S), richness, diversity and evenness in the Kornati Archipelago and Murter Sea between January and December 1990.

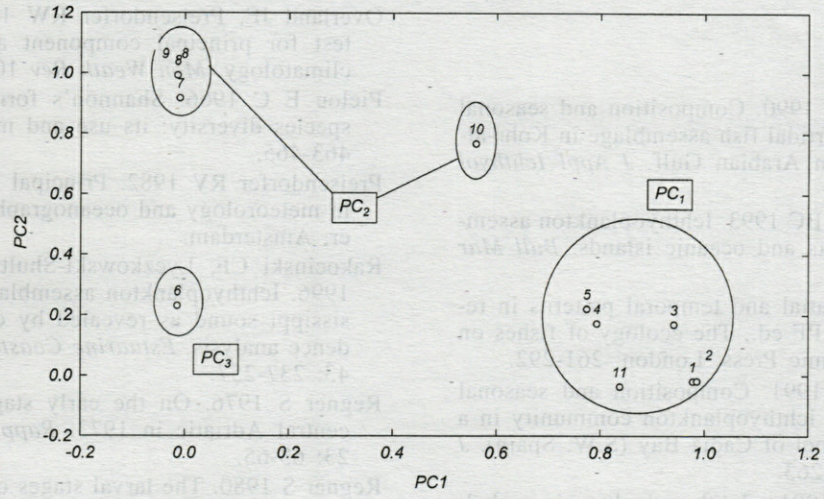

Fig. 4. – Scatter plot of the loadings along PC_1 versus PC_2 of 11 most common species. Letter coding, see Table II.

The number of species, abundances and indices of species richness and diversity of the community of fish larvae and juveniles in the Tanshui river estuary were positively correlated with temperature and salinity (Tzeng & Wang 1992).

To consider which species, or group of species, contributes significantly to the community structure, principal component analyses were performed. According to nonsignificance of the correlation matrix (Bartlett's test) for 11 common species, PC analysis was done. Correlation matrix was significant for $p = 0.05$. Three principal components together describe 91.12 % of the total abundance variance: PC_1 contributes with 52.56 %, PC_2 with 29.59 %, and PC_3 with 8.96 %. When using only percentages of total variances it is difficult to choose the number of PCs with significant meanings. Therefore, Rule N was applied. The first three PCs are significant because the eigenvalues of the real data matrix are smaller than those of the random data matrix. On the basis of the distribution of rotated loadings it was possible to distinguish three groups (Fig. 4). PC_1 has the highest loadings for *Sardina pilchardus*, *Engraulis encrasicolus*, *Merluccius merluccius*, *Trisopterus minutus capelanus*, *Merlangius merlangus euxinus* and family Gobiidae. In the case of PC_2 , four species were grouped: *Cepola rubescens*, *Diplodus annularis*, *Sarpa salpa* and *Chromis chromis*. PC_3 has the highest loading just for *Serranus hepatus*. It is difficult to explain species arrangement according to PC loadings. However, species in the case of PC_1 are species which were generally abundant and all of them (except Gobiidae) are offshore spawners and temporary residents. PC_2 has the highest loadings for species which are benthic species and permanent residents (mostly in coastal region, except *C. rubescens*) and characterised by a similar reproduction time (Jardas 1996). Most of the temporary resident species caught in this study, could be classified into two main groups: autumn-winter egg spawners and pouch-broader species. The main exception was a small group of early summer planktonic egg-spawners (for example, *E. encrasicolus*).

Scores of the first three principal components were compared with sea water temperature and salinity showing that significant linear correlation was found between temperature and PC_1 and salinity and PC_1 scores ($p < 0.0001$, $r = 0.91$; $p < 0.037$, $r = 0.61$).

Unfortunately, we don't have any data about the primary production and zooplankton volume for this area even though some correlation between both number of species and individuals with mentioned parameters could probably exists. This correlation was confirmed for the area of Kastela Bay and station Stoncica (high sea in the easterm middle Adriatic) (Regner 1980, 1982).

Preliminary results of the present study provide a basis for establishing the temporal and spatial patterns of recruitment in various fish species. Following this study, we recommended long-term research to establish wether the correlation between biotic factors and temperature really exists. This should be done after estimating seasonal patterns from both data sets. Further work is needed to elucidate which additional aspects (primary production, zooplankton volume, dissolved oxygen, currents) may influence the distribution and abundance of ichthyoplankton community in the Kornati archipelago and Murter Sea.

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NEARSHORE FISH ASSEMBLAGES ASSOCIATED WITH SHALLOW ROCKY HABITATS ALONG THE SOUTHERN CROATIAN COAST (EASTERN ADRIATIC SEA)

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FISH FAUNA
SEA URCHINS
ERECTED MACROALGAE
NEARSHORE ROCKY HABITAT
VISUAL CENSUS
ADRIATIC SEA

ABSTRACT. – Fish assemblages from shallow rocky habitats were studied in Cavtat Bay (Southern Croatia, Eastern Adriatic Sea) in May-June 1998 using the non-destructive visual census methodology. Censuses were carried out in two sites (A and B) characterised by different exposures to wave action and substrate characteristics. A significantly higher mean density of sea urchins and a lower algal cover were observed at the more sheltered station (site A), while at site B sea-urchins were less abundant and the macroalgal canopy was well developed. Comparable species richness (20 vs 18 fish species) and mean fish density (mean ± SE: 197.6 ± 30.6 vs 173.7 ± 5.8 individuals 125 m^{-2}) were recorded at sites A and B. Differences, instead, were observed in the demographic and trophic structures and in the relative density of some fish species. At site A, small-, medium-, and large-sized specimens were well represented, while large fish dominated at site B. Planktivorous species numerically dominated in both fish assemblages. Labrids were better represented at site B, while Sparids of the genus *Diplodus* and small-sized fish of several species were more abundant at site A. The distribution of different fish species and small-sized specimens in relation to the environmental characteristics, and the complex relationships among algae, sea urchins (grazers) and fishes (including sea urchin predators) are discussed.

ICHTHYOFAUNE
OURSINS
MACROALGUES DRESSÉES
ENVIRONNEMENT ROCHEUX CÔTIER
RECENSEMENTS VISUELS
MER ADRIATIQUE

RÉSUMÉ. – La faune ichtyologique du fond rocheux de la Baie de Cavtat (Croatie du Sud, Mer Adriatique Orientale) a été étudiée en mai-juin 1998 par la méthodologie non-destructive des recensements visuels. Les recensements ont été effectués à deux stations (A et B) caractérisées par une exposition différente à l'hydrodynamisme et différentes conditions du substrat. Une densité significativement plus élevée d'Oursins et une couverture algale plus faible ont été observées près de la station A. La richesse spécifique (20 contre 18 espèces de Poissons) et la densité des Poissons (moyenne ± ES: 197,6 ± 30,6 vs 173,7 ± 5,8 individus 125 m^{-2}) ne présentent pas de différence significative entre les deux stations. Par contre, la structure démographique et trophique et la densité relative de quelques espèces diffèrent significativement. Près de la station A, toutes les catégories de taille sont bien répresentées, tandis qu'en B les Poissons de grande taille sont les plus nombreux. Les Poissons planctonophages dominent aux deux stations. Les Labridae sont mieux representés en B, tandis que les Sparidae du genre *Diplodus* et les juvéniles de beaucoup d'espèces sont plus nombreux près de la station A. L'influence des caractéristiques environmentales sur la distribution des différentes espèces de Poissons et des individus de petite taille sont discutés, ainsi que les relations entre les algues, les Oursins (brouteurs) et les Poissons.

INTRODUCTION

In the last decade, an increasing attention has been paid to shallow rocky habitats in temperate regions. Hard bottoms covered by macroalgae, in fact, represent an important source of primary production often sustaining well diversified animal communities, including fishes (Choat & Ayling 1987, Sala & Boudouresque 1997). Moreover, vegetated rocky bottoms may also exert the crucial role of nursery grounds for many fish species (Carr 1989, Levin 1991, Garcia-Rubies & Macpherson 1995).

Fish communities of tropical coral reefs have been intensively studied (see Hay 1991, Sale 1991, and references therein). By contrast, those inhabiting Mediterranean infralittoral rocky shores have been the object of a reduced number of investigations despite the extension of this habitat. The bulk of available studies were carried out in marine protected areas with the aim to provide evidence of the reserve effects (Harmelin 1987, Garcia-Rubies & Zabala 1990, Francour 1994, Dufour *et al.* 1995, Vacchi *et al.* 1998). Other papers dealt with the resource partitioning and microhabitat requirements for adult (Macpherson 1994, Fasola *et al.* 1997, Garcia-Charton & Perez Ruzafa 1998, Guidetti in press) and juvenile fishes (Harmelin-Vivien *et al.* 1995, Garcia-Rubies & Macpherson 1995) inhabiting rocky habitats.

This paper reports the first observations on fish assemblages from southern Croatia collected by using visual counts and provides a comparison of fish assemblages censused in sites characterised by different macroalgal cover. The possible role of sea urchins in altering the habitat complexity by grazing on erected macroalgae and in affecting indirectly the structure of fish assemblages is discussed.

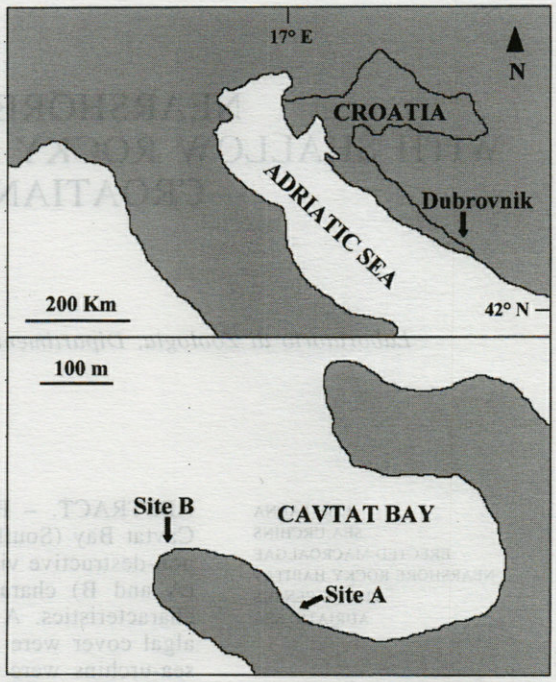

Fig. 1. – Sampling area.

MATERIALS AND METHODS

Sampling area: Censuses were carried out in May and June 1998 in the Cavtat Bay (Fig. 1), located at about 15 km to the south of Dubrovnik (Southern Croatia, Eastern Adriatic Sea; 42°30'N, 18°20'E). Two different sampling stations were selected: the first one (site A), characterised by sheltered conditions, was positioned in the bay; the second-one (site B) was located outside the bay and is more exposed to wave action (Fig. 1). Censuses were carried out along medium sloped rocky shores between the surface and 3 m depth. Erect macroalgal cover was quite completely absent at site A, whereas articulated Corallinaceae and *Cystoseira* spp. canopies were well developed at site B.

Sampling techniques and data analysis: Sea urchins abundance and the percent cover of erect macroalgae were estimated within a 1 m^2 frame randomly positioned at both sites (n=10 per site). On the basis of the assessment of normal distribution of data performed by Kolmogorov-Smirnov test, *t*-test or Mann-Whitney test were used to compare mean densities of sea urchins and the algal cover between the two sites. The relationship between the density of sea urchins and the abundance of erect macroalgae was tested by a correlation analysis.

Visual censuses were carried out by snorkeling along 25 m long and 5 m wide (125 m^2 of total surface) strip transects, according to standardised procedures (Harmelin-Vivien *et al.* 1985). On the whole, a total of 32 repeated visual counts were performed along 4 transects randomly placed at each site. Fishes were counted using an abundance scale on a basic geometrical progression of 2 (1, 2-5, 6-10, 11-30, 31-50, 51-100, 101-200, 201-500, 500) and calculation of fish density (number of individuals. 125 m^{-2}) was made by considering the mid-point of each class. The size of fish was evaluated by using three size categories, namely small, medium and large, on the basis of the maximum total length reached by each fish species (Fischer *et al.* 1987).

The whole mean fish density (number of individuals × 125 m^{-2}) with and without cryptic and planktivorous species, and the mean density of each fish species recorded, were calculated for both sites. The density of nectobenthic fish species only (without cryptic and planktivorous species) was calculated because of the different probability to detect cryptic species in vegetated and unvegetated sites by using a visual technique, and because of the so-called «masking effect» due to planktivorous species. These latter species, in fact, are well known to show patchy distribution patterns, which often mask variations in density of the remaining species (Ferrell & Bell 1991). Analysis of variance (two ways ANOVA) was used to test differences between sites and among transects in the data of fish density of whole assemblages (with and without cryptic and planktivorous species) and of each species recorded. «Site» has been considered as a fixed factor and «transect» as a nested-random factor. Before analysis, data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Cochran's test). Whenever necessary, they were opportunely transformed and newly tested (Underwood 1997).

With regard to the trophic composition, the assignment of feeding-guilds to each species was made according to the classification of Bell & Harmelin-Vivien (1983) based on the type of prey and its relative size to predator: 1) herbivores (*Sarpa salpa*); 2) microcarnivores (*Boops boops*, *Oblada melanura*, *Spicara* spp., *Chromis chromis*); 3) mesocarnivores type 1

Table I. – Density (mean SE of the number of individuals 125 m^{-2}) of fish species recorded at the two sampling sites and results of ANOVA for effect of sites (S) and transects (T): ns = non significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Family	Species	Site		ANOVA	
		A	B	Site	Transect
Atherinidae	Undetermined	91.2 ± 15.2	31.2 ± 3.3	ns	ns
Blenniidae	*Parablennius rouxi* (Cocco, 1883)	0.4 ± 0.2	-	-	-
	Lipophrys pavo (Risso, 1810)	0.5 ± 0.2	-	-	-
Gobiidae	*Gobius bucchichi* Steindachner, 1870	0.8 ± 0.3	-	-	-
Labridae	*Coris julis* (Linnaeus, 1758)	8.0 ± 2.0	17.2 ± 2.0	***	ns
	Symphodus cinereus (Bonnateree, 1788)	-	0.8 ± 0.2	-	-
	Symphodus mediterraneus (Linnaeus, 1758)	-	3.0 ± 0.4	-	-
	Symphodus melanocercus (Risso, 1810)	0.7 ± 0.2	-	-	-
	Symphodus ocellatus (Forsskal, 1775)	-	3.9 ± 0.7	-	-
	Symphodus rostratus (Bloch, 1797)	-	1.5 ± 0.3	-	-
	Symphodus tinca (Linnaeus, 1758)	1.2 ± 0.3	4.8 ± 0.6	***	ns
	Thalassoma pavo (Linnaeus, 1758)	0.7 ± 0.3	3.8 ± 0.9	**	ns
Moronidae	*Dicentrarchus labrax* (Linnaeus, 1758)	-	0.5 ± 0.3	-	-
Mugilidae	Undetermined	7.2 ± 1.3	1.1 ± 0.4	**	ns
Pomacentridae	*Chromis chromis* (Linnaeus, 1758)	8.6 ± 1.5	13.9 ± 2.4	ns	ns
Serranidae	*Serranus scriba* (Linnaeus, 1758)	-	1.0 ± 0.3	-	-
Sparidae	*Boops boops* (Linnaeus, 1758)	55.6 ± 16.9	77.5 ± 6.7	ns	ns
	Diplodus annularis (Linnaeus, 1758)	4.0 ± 0.8	1.8 ± 0.3	ns	ns
	Diplodus puntazzo (Cetti, 1777)	2.1 ± 0.3	0.5 ± 0.4	**	ns
	Diplodus sargus (Linnaeus, 1758)	0.6 ± 0.1	-	-	-
	Diplodus vulgaris (E.G. Saint-Hilaire, 1817)	4.2 ± 0.3	-	-	-
	Oblada melanura (Linnaeus, 1758)	5.5 ± 0.8	7.0 ± 1.3	ns	ns
	Sarpa salpa (Linnaeus, 1758)	4.8 ± 0.8	3.2 ± 0.5	ns	ns
	Spondyliosoma cantharus (Linnaeus, 1758)	0.6 ± 0.2	0.8 ± 0.4	ns	ns
Trypterigiidae	*Trypterigion delaisi* Cadenat & Blache, 1971	0.5 ± 0.2	-	-	-
	Trypterigion trypteronotus (Risso, 1810)	0.4 ± 0.2	-	-	-

(mainly Labridae), feeding on molluscs and small crustaceans; 4) mesocarnivores type 2 (Sparidae excluding *Boops boops* and *Oblada melanura*, and Gobiidae), preying on benthic invertebrates; 5) macrocarnivores (Serranidae, Scorpaenidae), feeding on fish, large crustaceans and cephalopods.

Data about proportions of the different size and trophic categories were compared by chi-square test.

RESULTS

Sea urchins density and algal cover

Sea urchins (mainly *Arbacia lixula* and, in turn, *Paracentrotus lividus* and *Sphaerechinus granularis*) were significantly more abundant at site A than at site B (7.0 ± 0.6 vs 2.7 ± 0.5 ind. m^{-2}, × ± SE; *t*-test, $p < 0.01$). By contrast, the mean percentage of the rocky substrate covered by erect macroalgae was significantly lower at site A than at site B (3.5 ± 1.3 vs 66.5 ± 4.1, × ± SE; Mann-Whitney test, $p < 0.001$). Sea urchins density and abundance of erected seaweeds were inversely related (Spearman correlation; $r = -0.73$, $p < 0.05$; Fig. 2).

Fish species richness and density

Sites A and B showed comparable values of species richness (20 vs 18 fish species), but different species composition. The complete list of fish species recorded at both sites and the relative mean densities are reported in Table I. Gregarious taxa, such as Atherinidae, *Boops boops* and *Chro-*

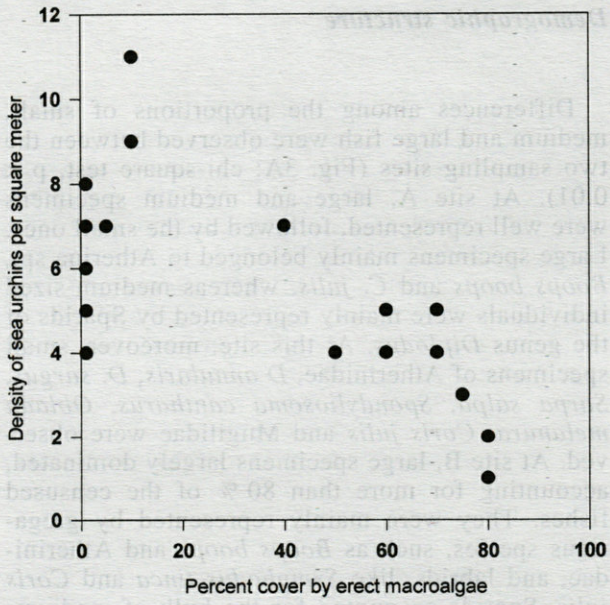

Fig. 2. – Correlation between density of sea urchins (number of sea urchins per square meter) and abundance of erect macroalgae (percent cover).

mis chromis, accounted for more than 70 % of the total fish density at both sites. Nectobenthic species, which include Labrids (mainly *Coris julis*), Sparids (except for *Boops boops* and *Oblada melanura*) and the serranid *Serranus scriba*, accounted for 11.2 % at site A and 24.3 % at site B. Cryptic species belonging to Blenniidae, Gobiidae and Trypterigiidae were recorded at site A only.

Mean fish density (± SE) of the whole assemblages were 197.6 ± 30.6 vs 173.7 ± 5.8 individuals. 125 m^{-2} at site A and B, while the values without the numerical contribution of schooling species were 40.9 ± 11.1 vs 50.4 ± 8.9 ind. 125 m^{-2}. Analysis of variance revealed that both the difference in the mean values of total fish density (no. ind. × 150 m^{-2}) and that evaluated by considering nectobenthic fish species only were non significant neither between sites ($p = 0.48$ and 0.08, respectively) nor among transects ($p = 0.35$ and 0.89, respectively).

The results of ANOVA on density of each single fish species are reported in Table I. *Lypophrys pavo*, *Parablennius rouxi*, *Gobius bucchichii*, *Symphodus melanocercus*, *D. sargus* and *D. vulgaris* were observed exclusively at site A, while Mugilidae and *Diplodus puntazzo* were significantly more abundant at site A than at site B. By contrast, some labrid fish (excluding *Symphodus melanocercus*) and *Serranus scriba* were exclusive or significantly denser at site B.

Density values of the remaining fish species did not show statistically significant differences between sites A and B.

Demographic structure

Differences among the proportions of small, medium and large fish were observed between the two sampling sites (Fig. 3A; chi-square test, $p < 0.01$). At site A, large and medium specimens were well represented, followed by the small ones. Large specimens mainly belonged to Atherina sp., *Boops boops* and *C. julis*, whereas medium-sized individuals were mainly represented by Sparids of the genus *Diplodus*. At this site, moreover, small specimens of Atherinidae, *D annularis*, *D. sargus*, *Sarpa salpa*, *Spondyliosoma cantharus*, *Oblada melanura*, *Coris julis* and Mugilidae were observed. At site B, large specimens largely dominated, accounting for more than 80 % of the censused fishes. They were mainly represented by gregarious species, such as *Boops boops* and Atherinidae, and labrids, like *Symphodus tinca* and *Coris julis*. Sparids accounted for the bulk of medium-sized individuals, while small specimens belonged to *Thalassoma pavo*, *Coris julis*, *Dicentrarchus labrax* and *Oblada melanura*.

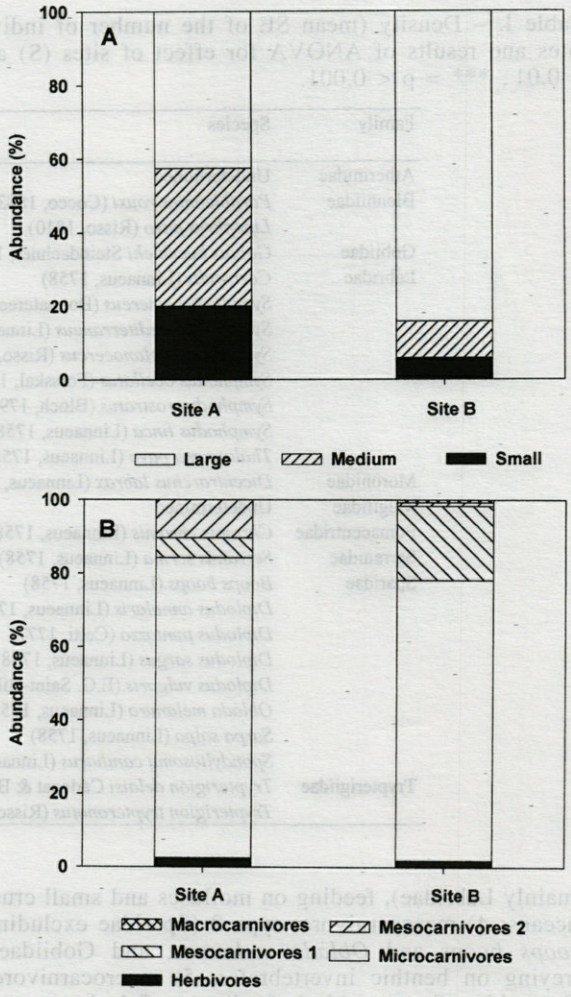

Fig. 3. – A, Relative percentage of size categories at the two sampling stations. B, Relative percentage of feeding-guilds at the two sampling stations.

Trophic structure

Chi-square test revealed a statistically significant difference ($p = 0.02$) between the two investigated sites. Very low proportions of Macrocarnivores (absent at site A) and Herbivores, and a dominance of Microcarnivores were observed at both sites, whereas Mesocarnivores type 1 and Mesocarnivores type 2 were more abundant at site B and A, respectively (Fig. 3B).

DISCUSSION

Relationships among fishes, sea urchins and macroalgal vegetation

The results of this study showed similarities and differences between fish assemblages from the two investigated sites. Some characteristics of

the fish assemblage, like species richness and whole density, were substantially comparable, while the relative density of some fish species and the demographic structure differed between sites providing evidence of differences in species composition.

From a general point of view, our results are consistent with the literature data. Several authors, in fact, emphasised the qualitative dominance of Sparids and Labrids and the quantitative dominance of schooling fish species in shallow rocky Mediterranean habitats (Harmelin 1987, Fasola *et al.* 1997, Guidetti 2000). The preference by Labrids for substrates colonised by macroalgae, as observed in this paper, was known not only for the Mediterranean (Garcia-Rubies & Macpherson 1995), but it is a common feature in temperate waters (Choat & Ayling 1987). The higher abundance of Sparids (mainly *Diplodus* spp.) at site A, instead, is difficult to be interpreted on the basis of our data and it is hardly attributable to the higher abundance of preys, represented by sea urchins (Sala 1997). Sala & Ballestreros (1997) demonstrated that, when sea urchins reach a threshold in size, *Diplodus* spp. prefer to eat smaller epifaunal invertebrates. In this sense, our data are not sufficient to support the above hypothesis, since we do not have data on size structure of the sea urchins populations.

Choat & Ayling (1987), Sala (1997) and Sala *et al.* (1998) stressed the importance of interactions among algal distribution, herbivorous invertebrates (mainly echinoids) and their predatory fishes, suggesting that these latter could exert an important role in structuring such assemblages. Alternatively, however, the biological structure of rocky habitats could be produced by demographic processes in echinoids and algae which occur independently from the activity of predators (Choat & Ayling 1987, Sala *et al.* 1998).

As pointed out by Hay (1984) and Sala *et al.* (1998), relative abundance patterns of fishes and sea urchins are also related to variations in the level of fishing activities. An increased fishing pressure, in fact, may indirectly mediate an increase in sea urchin populations by eliminating sea urchin predators. In this respect, Sparids of the genus *Diplodus* are of great economical interest, while Labrids, which are reported as important predators of juvenile sea urchins (Sala 1997), are not of great commercial importance. In our case, due to the relative vicinity of the two sites studied and the low local fishery effort, the impact of fishery activities can be considered similar and, in any case, low, which suggests that other factor than fishery determine the observed differences.

As far as the trophic composition is concerned, it has to be noted that, comparing the two fish assemblages, the only difference was represented by the abundance of Mesocarnivores types 1 and 2 at sites B and A, respectively. This ultimately reflects the differences in the relative abundance of Labrids and Sparids, and their relative different feeding behaviour, at the two investigated sites.

Although the data presented here are not supported by a sufficiently replicated sampling design, they could suggest a possible indirect effect of sea urchins grazing in affecting the fish community.

Distribution of small fishes

Small specimens of several Sparids appeared to prefer the less exposed station (site A), in agreement with previous studies (Harmelin-Vivien *et al.* 1995, Garcia-Rubies & Macpherson 1995), while small-sized *Coris julis* and *Thalassoma pavo* were recorded at the more exposed site. The time periods of occurrence of small fish of different species are consistent with the data reported by Dulcic *et al.* (1997), who studied juvenile fish populations in the eastern middle Adriatic. Some chronological discrepancy, probably due to differences at geographical scale, was instead observed in comparison to the results obtained in the north-western Mediterranean Sea (Harmelin-Vivien *et al.* 1995, Garcia-Rubies & Macpherson 1995). The fact that small Labrids (in our case *Coris julis* and *Thalassoma pavo*) were recorded over rocks with algae is consistent with Vacchi *et al.* (1998). From this point of view, moreover, Choat & Ayling (1987) and Garcia-Rubies & Macpherson (1995) affirmed that dense algal stands in shallow waters are often colonised by young labrids which use the algae for feeding and sheltering.

In conclusion, our results and the literature data suggest that the structure of fish assemblages associated with shallow rocky habitats is affected by a large number of interplaying and, in some cases, superimposed biological interactions (i.e. grazing, predation) and physical factors (i.e. habitat complexity, hydrodynamic forces). Therefore, on the basis of this preliminary study, an *ad hoc* sampling design including field manipulation experiments is necessary to investigate, on a wider temporal and spatial scale, the effects of biological interaction and environmental factors in structuring fish assemblages of shallow Mediterranean rocky habitats.

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ÉTUDE DES PEUPLEMENTS DE FORAMINIFÈRES DE TROIS SYSTÈMES PARALIQUES ALBANAIS

Foraminifera stocks from three paralic systems of Albania

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DOMAINE PARALIQUE
CONFINEMENT
FORAMINIFÈRES
ALBANIE
ACTUEL

RÉSUMÉ. – Les peuplements de Foraminifères de trois systèmes paraliques albanais sont étudiés. Les espèces sont celles que l'on rencontre habituellement dans les systèmes paraliques méditerranéens. Les bassins présentent tous une organisation quantitative semblable en fonction des gradients de confinement : une diminution de la richesse spécifique et de la densité depuis la communication avec la mer vers les confins marginaux. Cependant, les analyses multivariées montrent que chaque système possède une structure spécifique des peuplements qui lui est propre. Ces caractéristiques semblent être la règle chez les Foraminifères paraliques.

PARALIC REALM
CONFINEMENT
FORAMINIFERA
ALBANIA
PRESENT

ABSTRACT. – The populations of foraminifera of three paralic systems of Albania are studied. Species are the same as those usually encountered in Mediterranean paralic ecosystems. All basins display similar quantitative trends following the confinement gradient i.e., diminution of specific richness and density, from the communication with the sea toward the marginal areas. Meanwhile, multivariate analyses show that each ecosystem displays its own peculiar specific organisation of foraminiferal populations. Such features seem to be the rule for paralic foraminiferal populations.

INTRODUCTION

Diverses études récentes ont abordé l'étude des peuplements de Foraminifères de bassins paraliques méditerranéens comme la baie de Bou-Ismail (Lévy *et al.* 1980) et plusieurs ensembles étudiés par notre équipe : le golfe de Kalloni (Favry *et al.* 1997), l'étang du Prévost (Favry *et al.* 1998), les étangs de Diana et d'Urbino (Guelorget *et al.* 1999), la lagune de Nador (Guelorget *et al.* 2000). La présente étude concerne trois systèmes de la côte albanaise que l'un de nous a pu échantillonner en décembre 1994. Elle vient ainsi compléter, sur un littoral peu connu, le panorama qu'offre ce compartiment biologique en Méditerranée. Comme pour les autres bassins étudiés, la question de la représentativité de l'échantillonnage, effectué sur les deux premiers centimètres de sédiment, se pose. Il n'est pas nécessaire de reprendre ici cette discussion (Guelorget *et al.* 2000) ; nous estimons que les relations des peuplements de Foraminifères avec leur environnement ainsi que la structure biogéologique des systèmes étudiés sont suffisamment constantes dans le temps pour que l'échantillonnage permette de décrire une organisation globale.

La côte albanaise s'étend sur 400 km le long de la mer Adriatique au nord et de la mer Ionienne au sud (Fig. 1). Les systèmes lagunaires de Narta et de Karavasta se situent au nord de la ville de Vlorès, le long d'une plaine littorale sédimentaire bordant l'Adriatique. Le bassin de Butrinti s'ouvre une côte rocheuse et abrupte bordant la mer Ionienne.

Le climat est de type méditerranéen à nuance humide avec des précipitations moyennes annuelles comprises entre 1 250 à 1 800 mm.an^{-1}. Les vents qui soufflent sur cette région sont principalement de secteur nord et de secteur sud et sont généralement violents (Peja *et al.* 1992).

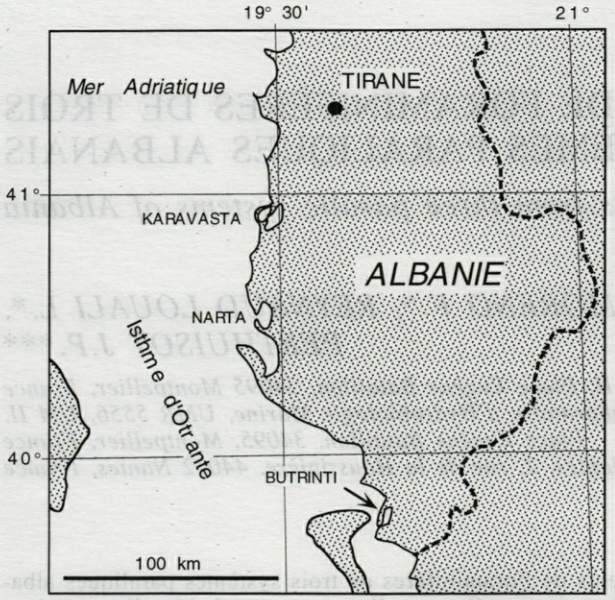


Fig. 1. – Localisation des sites étudiés.
Location of studied sites.

ÉCHANTILLONNAGE ET MÉTHODES D'ÉTUDE

Les stations de prélèvement couvrent l'ensemble des bassins. Les échantillons de sédiment ont été récoltés en juillet 1996 à l'aide d'une benne Eckman. Seule, la partie superficielle du sédiment, correspondant approximativement aux 2 premiers cm, est conservée et fixée à l'alcool sur le terrain. Au laboratoire, 50 cm^3 de ces échantillons sont lavés sur un tamis de 50 µm puis séchés à l'étuve.

Les Foraminifères sont isolés par flottation sur du tétrachlorure de carbone. Après l'évaluation du nombre total des tests, un comptage par espèce est réalisé sur 100 à 300 individus en fonction de la richesse spécifique de l'échantillon. Un comptage du nombre total d'espèces par échantillon vient compléter cette analyse. L'utilisation du même volume initial de sédiment (50 cm^3) permet une comparaison quantitative des échantillons (Debenay *et al.* 1987).

Les observations sont faites sur les peuplements totaux, biocénoses et thanatocénoses confondues, c'est-à-dire « l'association totale » au sens de Murray (1973). L'échantillonnage concernant la partie superficielle du sédiment, nous pouvons admettre que les individus morts et vivants présents *in situ* sont représentatifs, sur le long terme, d'une même communauté. Toutefois, les peuplements recensés peuvent comporter des individus allochtones résultant du transport *post mortem* des tests.

LE COMPLEXE DE KARAVASTA

Le site

Le bassin de Karavasta est un complexe lagunaire au sens strict (Perthuisot & Guelorget 1992). D'une superficie de 4 180 ha, il se compose de 2 lagunes disposées en série depuis la mer ouverte en direction du continent, qui communiquent par un chenal actif médian et par une passe de moindre importance intermittente au nord (Fig. 2A). Le bassin distal (par rapport à la mer ouverte) a une profondeur moyenne de l'ordre de 0,70 m. La profondeur du bassin proximal dépasse 1,50 m dans sa zone centrale. Il est séparé de la mer par un lido entaillé de 2 passes. La passe principale coupe le cordon lagunaire en son centre. Une passe secondaire est située au nord du lido au droit de la communication avec le bassin distal. Ces 2 communications, quoique entretenues, tendent à se colmater.

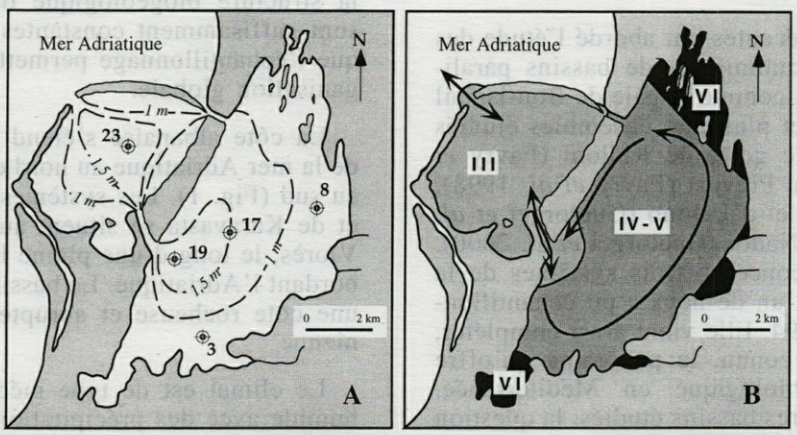


Fig. 2. – Karavasta. A, Bathymétrie et localisation des stations de prélèvement. B, Carte schématique des mouvements d'eau et des zones de confinement.
Karavasta. A, Bathymetry and sampling station location. B, Sketch map of water motions and confinement zonation.

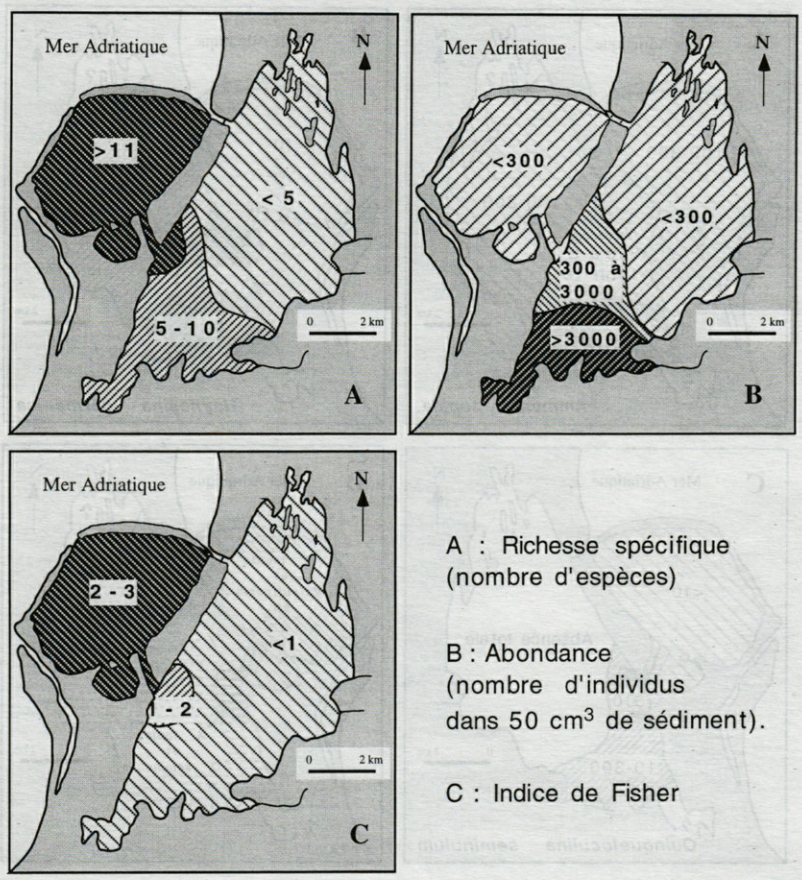


Fig. 3. – Karavasta. Distribution des principaux facteurs biologiques quantitatifs. A, Richesse spécifique. B, Densité (nombre d'individus dans 50 cm^3 de sédiment). C, Indice de Fisher.

Karavasta. Distribution of main biological quantitative parameters. A, Specific richness; B, Abundance (number of individuals in 50 cm^3 sediment); C, Fisher Index.

Les températures des eaux varient globalement de 5 à 35 °C au cours de l'année en fonction des variations de la température atmosphérique.

Durant l'hiver et pendant les périodes de forte pluviosité, principalement au printemps, les salinités sont inférieures à 25 ‰ dans les zones distales de la lagune (Peja *et al.* 1992). Ainsi, un gradient positif s'établit des marges vers la communication avec la Mer Adriatique dont la salinité moyenne est nettement plus faible que celle de la Méditerranée et se situe aux alentours de 34,7 ‰. Pendant l'été, en revanche, la salinité des eaux les plus confinées peut être importante sous l'effet d'un fort déficit hydrique et on observe une sursalure importante à l'extrémité orientale où la salinité peut atteindre 60 ‰ (Guelorget et Lefèbvre 1994).

Bien que le marnage soit faible (40 cm environ), les échanges d'eau avec la mer se réalisent principalement sous l'effet de la marée. La circulation interne est surtout liée au régime des vents. La figure 2B schématise l'idée que l'on peut se faire de cette circulation. La masse d'eau est relativement homogène et l'ensemble du complexe lagunaire ne présente ni stratification des eaux ni gradients verticaux significatifs.

Dans le bassin proximal, les fonds sont sableux en bordure du lido et sablo-vaseux dans la zone centrale. La rareté des herbiers est à mettre en relation avec un taux de sédimentation trop élevé pour permettre la colonisation par la macroflore (Guelorget & Lefèbvre 1994). La teneur en matière organique est de 7 % en moyenne (Deslou-Paoli 1996).

Dans le second bassin, les éléments fins dominent avec des teneurs en argile comprises entre 34 à 70 % (Deslou-Paoli 1996). Au débouché du chenal, les sédiments sablo-vaseux sont colonisés par un herbier à *Zostera noltii* qui montre une certaine influence marine jusque dans cette zone (Guelorget & Lefèbvre 1994). Les sédiments du centre et du nord du bassin sont des vases colonisées par un herbier à *Ruppia spiralis* et une association algale à *Cladophora* sp. et *Chaetomorpha linum*. Les taux de matière organique sont compris entre 7 et 18 %. Les teneurs les plus importantes se situent au centre et à l'est de la lagune (Deslou-Paoli 1996).

L'étude des peuplements macrobenthiques (Guelorget & Lefèbvre 1993) montre que l'ensemble du bassin proximal se situe en zone III de confinement (Guelorget & Perthuisot 1983, 1992) tandis que la majeure partie du bassin distal se situe en zone IV-V (Fig. 2B). Les régions périphériques les plus reculées, sous forte influence des apports continentaux, se placent en zone VI.

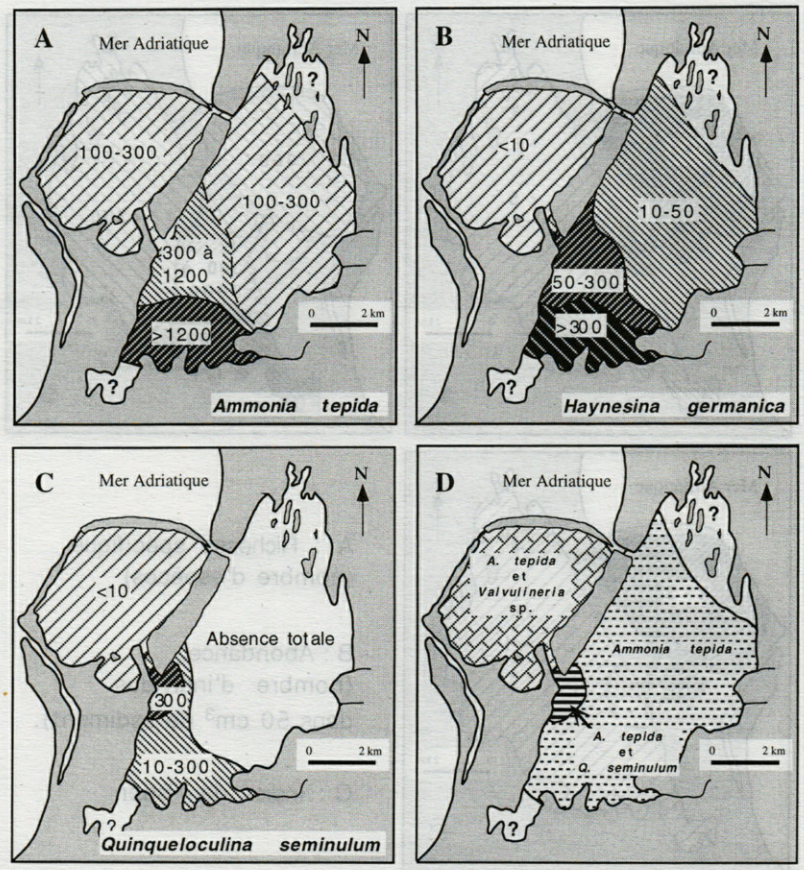


Fig. 4. – Karavasta. Distribution des principales espèces et des associations dominantes.
Distribution of main species and dominating associations.

Les foraminifères

Distribution quantitative des peuplements

22 espèces ont été dénombrées sur l'ensemble de la lagune de Karavasta. Les richesses spécifiques les plus élevées (Fig. 3A), avec une quinzaine d'espèces en moyenne, se situent dans le bassin proximal. Le nombre d'espèces diminue rapidement à l'intérieur du bassin distal, surtout vers les marges. Cette diminution est plus marquée vers le Nord où 3 espèces seulement composent les peuplements (stations 8 et 17).

La densité (Fig. 3B) est de l'ordre de 300 individus/50 cm^3 de sédiment dans la zone centrale du premier bassin. Elle augmente dans la partie proximale du second bassin (stations 19 et 3) où elle est comprise entre 2 000 et 4 000 individus puis diminue significativement dans la partie distale, située plus au nord, où les densités sont de l'ordre de 150 individus.

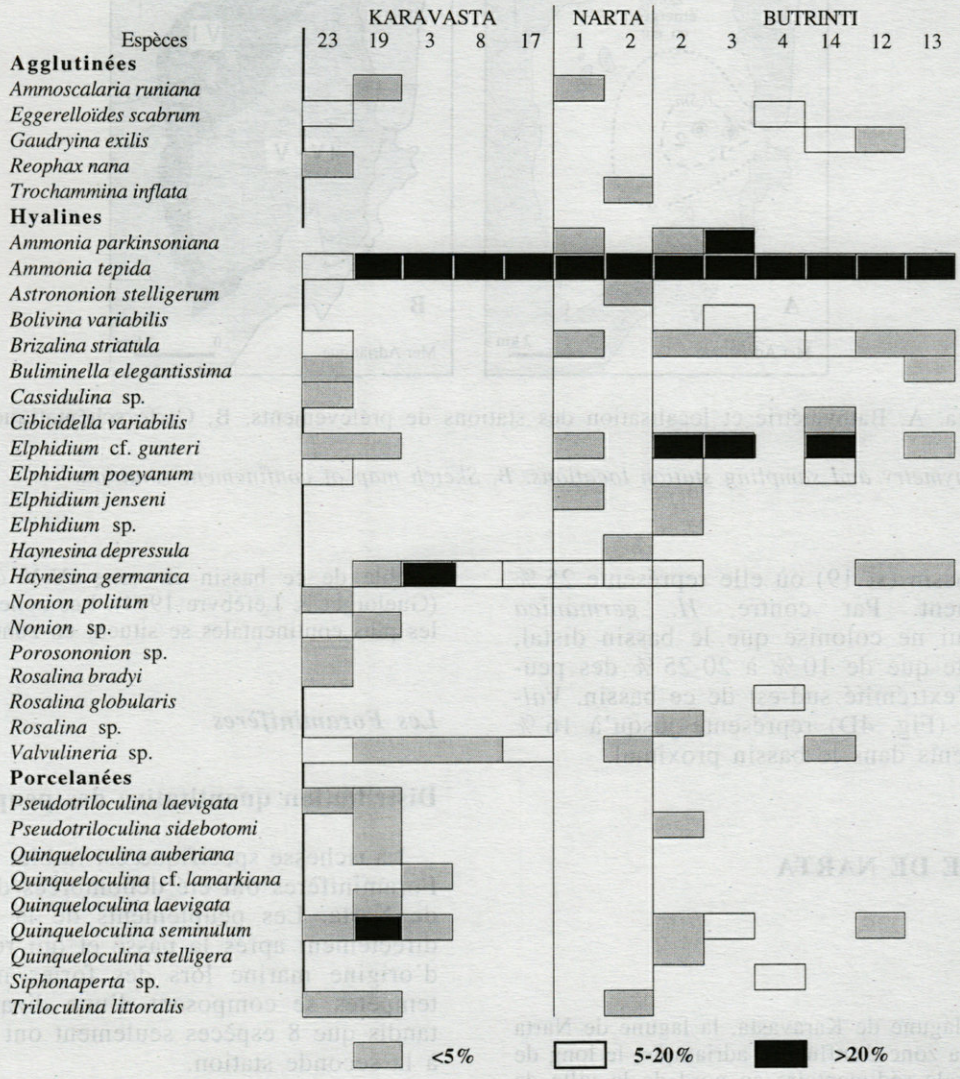
L'indice de diversité de Fisher (Fisher *et al.* 1943, Murray 1973) (Fig. 3C) varie de 3 à 0,5 sur l'ensemble de la lagune. Les valeurs maximales s'observent dans la zone sous influence des eaux d'origine marine (st 23 et 19), tandis que les valeurs minimales se situent dans les zones plus marginales du second bassin (st 3). Globalement, les indices de diversité observés sont faibles et correspondent à ceux qui caractérisent les lagunes où l'indice de diversité de Fisher varie de valeurs inférieures à 1 à 6,5 dans les lagunes hyper ou hypohalines et de 4,5 à 11 dans les lagunes à caractère marin (Murray 1968a).

Organisation des peuplements

La microfaune de cette lagune est dominée par les Foraminifères hyalins (*Rotaliina*) avec 54,5 % des espèces contre 32 % de porcelanés (*Milioliina*) et seulement 13,5 % d'agglutinés (*Textulariina*) (Tabl. I).

Les Foraminifères hyalins colonisent principalement le premier bassin. Leur nombre ne cesse de diminuer des zones sous influence marine vers les zones les plus confinées. Les espèces porcelanées sont mieux représentées dans la zone d'herbiers à *Zostera noltii* au droit de l'embouchure dans le second bassin. Aucune espèce de ce type n'a été recensée dans toute la partie nord de ce

Tabl. I. – Liste des espèces recensées et abondance relative à chaque station.
List of collected species and their relative abundance at each station.



bassin. Les espèces agglutinées ne sont présentes que dans le premier bassin et, dans le bassin distal, au voisinage de la communication où l'influence des eaux d'origine marine reste perceptible. Aucune espèce agglutinée n'a été recensée dans le reste du second bassin.

Les espèces les plus fréquemment rencontrées sur l'ensemble du complexe lagunaire sont *A. tepida, Haynesina germanica, Quinqueloculina seminula* et *Valvulineria* sp. (Tabl. I). *A. tepida* est présente à toutes les stations tandis que les autres espèces ont une distribution plus limitée. Les peuplements du bassin proximal (st 23) sont les plus diversifiés avec notamment *Brizalina striatula, Nonion* sp., *Eggereloides scabrus* et *Elphidium poeyanum* tandis que les peuplements des stations les plus confinées (st 8 et 17) sont essentiellement composés d'*A. tepida* (Fig. 4A), *H. germanica* (Fig. 4B) et *Valvulineria* sp.

Des cartes de répartition, exprimées d'une part en effectifs, d'autre part en pourcentages relatifs ont été établies pour chacune des espèces principales.

A. tepida, H. germanica et *Valvulineria* sp. (Fig. 4D) sont les plus abondantes à l'extrémité sud du bassin distal, tandis que *Q. seminulum* (Fig. 4C) se concentre presque exclusivement au voisinage de la passe dans la zone d'herbiers à *Zostera noltii.*

A. tepida représente 38 % du peuplement dans le bassin proximal et domine largement dans le bassin distal jusqu'à y représenter 85 % du peuplement dans les zones les plus confinées et domine les peuplements de Foraminifères de l'ensemble de l'écosystème. *Q. seminulum* (Fig. 4D) prend une part non négligeable des peuplements essentiellement dans la zone d'herbiers

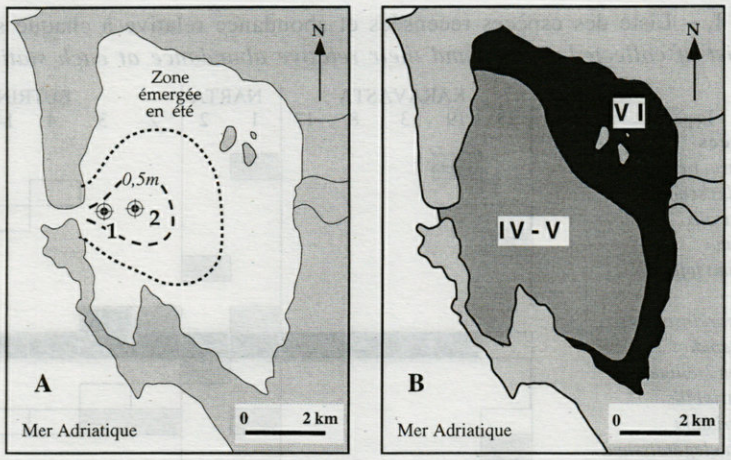


Fig. 5. – Narta. A, Bathymétrie et localisation des stations de prélèvements. B, Carte schématique des zones de confinement.
Narta. A, Bathymetry and sampling station locations. B, Sketch map of confinement zonation.

du second bassin (st 19) où elle représente 25 % du peuplement. Par contre, *H. germanica* (Fig. 4D), qui ne colonise que le bassin distal, n'y représente que de 10 % à 20-25 % des peuplements à l'extrémité sud-est de ce bassin. *Valvulineria* sp. (Fig. 4D) représente jusqu'à 16 % des peuplements dans le bassin proximal.

LA LAGUNE DE NARTA

Le site

Comme la lagune de Karavasta, la lagune de Narta se situe dans la zone d'influence adriatique, le long de la plaine littorale sédimentaire au nord de la ville de Vlorès (Fig. 1). Sa superficie est de 2800 ha environ. Sa profondeur moyenne est faible et n'excède pas 0,5 m. Pendant l'été, la tranche d'eau diminue de 15 à 35 cm, asséchant ainsi 30 % du bassin. En relation avec la mer par un étroit chenal soumis à un ensablement important, cette lagune en position très continentale, représente le stade quasi terminal, en termes d'évolution géomorphologique, de ce type de bassin.

Les 2 stations de prélèvement (Fig. 5A) se situent dans la partie proximale de la lagune qui constitue la seule zone toujours immergée de ce bassin.

Les variations de température des eaux suivent étroitement les variations de la température atmosphérique et varient globalement de 5 à 35°C au cours de l'année. Les échanges avec la mer ainsi que les apports d'eau douce sont intermittents. La salinité est généralement plus élevée que celle de l'eau de mer. De 36 ‰ en hiver elle peut atteindre des valeurs de 78 ‰ durant l'été.

Les sédiments de cette lagune sont constitués d'une boue riche en matière organique colonisée par un herbier à *Zostera noltii*. La zonation biologique (Fig. 5B) établie à partir de la macrofaune benthique situe l'ensemble de ce bassin en zone IV-V de confinement (Guelorget & Lefèbvre 1994). Les zones périphériques les plus continentales se situent en zone VI.

Les Foraminifères

Distribution quantitative des peuplements

La richesse spécifique est faible. 12 espèces de Foraminifères ont été dénombrées dans la lagune de Narta. Les peuplements de la station située directement après la passe et qui reçoit les eaux d'origine marine lors des fortes marées et des tempêtes se composent d'une dizaine d'espèces tandis que 8 espèces seulement ont été recensées à la seconde station.

La densité est de l'ordre de 3 000 individus/50 cm^3 de sédiment à l'embouchure du bassin et l'on observe une légère augmentation à l'intérieur de la lagune où 4500 individus ont été recensés.

L'indice de diversité de Fisher est de 1,2 dans la zone située immédiatement après l'embouchure (st 1) et diminue jusqu'à 0,9 vers l'intérieur du bassin (st 2). Ces indices de diversité très faibles caractérisent toujours des milieux très confinés hyper ou hypohalins.

Organisation des peuplements dans l'écosystème

La microfaune de la lagune de Narta est dominée par les Foraminifères hyalins (*Rotaliina*) qui représentent 75 % des espèces (soit 9 espèces) contre 16,5 % de type porcelané (*Milioliina*) (2 espèces) et 8,5 % de formes agglutinées (*Textulariina*) (soit 1 espèce) (Tabl. I).

Les espèces les plus fréquentes sont *Ammonia tepida* et *Haynesina germanica* (Tabl. I). Ces deux espèces représentent la quasi-totalité des peuplements. Toutefois, la zone de l'embouchure se caractérise notamment par la présence d'*Ammonia parkinsoniana*, d'*Ammoscalaria runiana* et des *Elphidium (E. cf. gunteri* et *E. jenseni)*. Par contre la seconde station, plus continentale, se caractérise par *Triloculina littoralis, Valvulineria cf. aubignyana, Astrononion stelligerum, Haynesina depressula* et *Trochammina inflata*.

Les effectifs d'*Ammoni tepida* sont de 2200 et 3800 individus pour 50 cm^3 de sédiment aux stations 1 et 2 respectivement. Les effectifs d'*H. germanica* varient peu, 400 à 450 individus ont été recensés. Ainsi, *A. tepida* représente entre 75 et 80 % des peuplements tandis qu'*H. germanica* en constitue moins de 10 %.

LE BASSIN DE BUTRINTI

Le site

Le bassin de Butrinti se situe au sud de Vlorès, le long d'une côte rocheuse et abrupte bordant la mer Ionienne (Fig. 1). Ce bassin paralique de type « bahira » (Guelorget & Perthuisot 1983, 1992, Perthuisot & Guelorget 1992) communique avec la mer par un chenal long d'environ 3,6 km sur 120 m de large et dont la profondeur moyenne est de 4 m (Fig. 6A). D'une superficie d'environ 1600 ha, le bassin a une profondeur moyenne de 11 m, et une profondeur maximale de 21 m au centre du bassin.

Pour des raisons techniques, seule une partie du bassin a pu être échantillonnée (Fig. 6A). Ainsi, la zone centrale et la côte ouest du bassin n'ont pas fait l'objet de prélèvement.

La température des eaux varie selon la saison et suit globalement les variations des températures atmosphériques. Elle est comprise entre 9°C, minimum atteint en janvier et février, et 26°C, maximum observé en juillet et août. Toutefois au-delà de 7 à 8 m de profondeur les températures sont pratiquement constantes (Guelorget & Lefèbvre 1994).

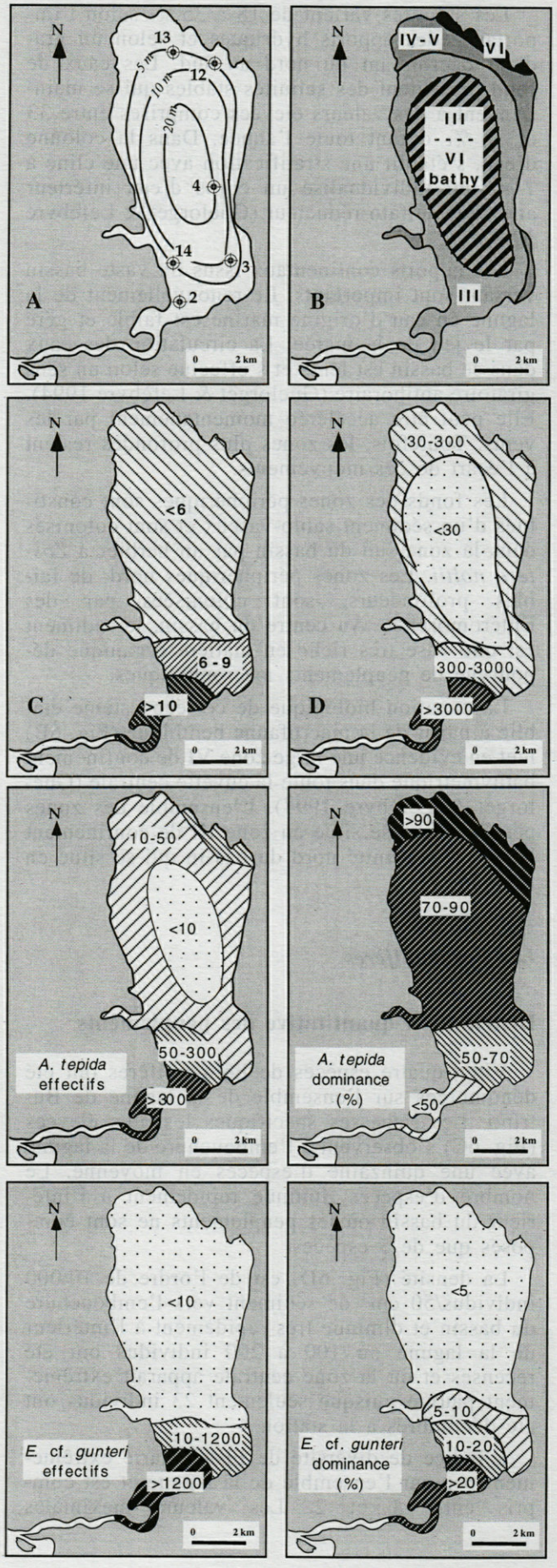


Fig. 6. – Butrinti. A, Bathymétrie et localisation des stations de prélèvements. B, Carte schématique des zones de confinement. C, Richesse spécifique. D, Densité (nombre d'individus/50 cm^3 de sédiment). En bas, Distribution des principales espèces (effectifs et dominance).

Butrinti. A, Bathymetry and sampling station locations. B, Sketch map of confinement zonation. C, Specific richness. D, abundance (number of individuals/50 cm^3 sediment). Below, distribution of the principal species (numbers and dominance).

Les salinités varient de 18 à 35 ‰ selon l'importance des apports hydriques et selon un gradient décroissant du nord au sud. Les eaux de fond présentent des salinités stables qui se maintiennent à des valeurs élevées comprises entre 33 et 36 ‰ durant toute l'année. Dans la colonne d'eau, s'établit une stratification avec une cline à 7 m qui individualise un corps d'eau inférieur anoxique sulfato-réducteur (Guelorget & Lefèbvre 1994).

Les apports continentaux issus du vaste bassin versant sont importants. Le renouvellement de la lagune en eau d'origine marine est faible et géré par le jeu de la marée. La circulation des eaux dans ce bassin est lente et s'effectue selon un sens giratoire antihoraire (Guelorget & Lefèbvre 1994). Elle peut être accélérée momentanément par les vents. Toutefois, les zones plus profondes restent à l'écart de ces mouvements.

Les fonds des zones périphériques sont constitués d'un sédiment sablo-vaseux et sont colonisés dans la zone sud du bassin par un herbier à *Zostera noltii*. Les zones périphériques nord, de faibles profondeurs, sont colonisées par des Entéromorphes. Au centre du bassin, le sédiment est une vase très riche en matière organique dépourvue de peuplements macrophytiques.

La zonation biologique de cet écosystème établie à partir de la macrofaune benthique (Fig. 6B) met en évidence une large zone VI de confinement bathymétrique dans toute la cuvette centrale (Guelorget & Lefèbvre 1994). L'ensemble des zones périphériques se situe en zone III de confinement hormis l'extrémité nord du bassin qui se situe en zone IV-V.

Les Foraminifères

Distribution quantitative des peuplements

Vingt-quatre espèces de Foraminifères ont été dénombrées sur l'ensemble de la lagune de Butrinti. Les richesses spécifiques les plus élevées (Fig. 6C) s'observent à l'embouchure de la lagune avec une quinzaine d'espèces en moyenne. Le nombre d'espèces diminue rapidement à l'intérieur du bassin où les peuplements ne sont composés que de 5 espèces.

La densité (Fig. 6D) est de l'ordre de 10 000 individus/50 cm^3 de sédiment vers l'embouchure du bassin et diminue très rapidement à l'intérieur de la lagune où 100 à 200 individus ont été recensés et où la zone centrale apparaît extrêmement pauvre puisque seulement 23 individus ont été dénombrés à la station 4.

L'indice de diversité de Fisher varie extrêmement peu sur l'ensemble de la lagune et est compris entre 1 et 2. Les valeurs maximales

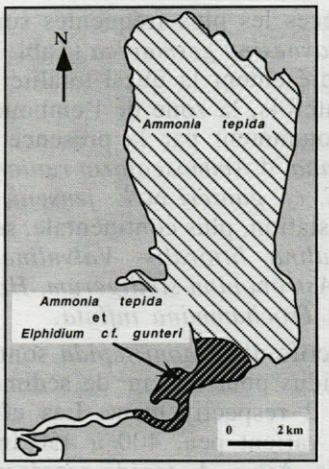


Fig. 7. – Butrinti. Associations dominantes.
Butrinti. Dominating associations.

caractérisent la zone sous influence des eaux d'origine marine (st 2), tandis que les valeurs minimales se situent au centre et dans la zone nord-ouest du bassin (st 13). Les indices de diversité observés sont faibles. Ils correspondent toutefois à ceux qui caractérisent les lagunes où l'indice de diversité de Fisher varie de valeurs inférieures à 1 jusqu'à 6,5 dans les lagunes hyper ou hypohalines et de 4,5 à 11 dans les lagunes à caractère marin (Murray 1968a).

Organisation des peuplements

La microfaune du bassin de Butrinti est dominée par les Foraminifères hyalins (*Rotaliina*) qui représentent 62,5 % des espèces contre 29 % de type porcelané (*Milioliina*) et seulement 8,5 % de formes agglutinées (*Textulariina*) (Tabl. I). Le nombre d'espèces de type hyalin et porcelané (Fig. 7) diminue de la passe vers les zones marginales. Seules les espèces de type hyalin sont présentes sur l'ensemble du bassin. Les espèces de type agglutinées sont très rares et offrent une distribution plus erratique.

Les espèces les plus fréquemment rencontrées sur l'ensemble de cette lagune sont *Ammonia tepida, Brizalina striatula, Elphidium cf. gunteri, Haynesina germanica* et *Quinqueloculina seminula* (Tabl. I). Seuls les peuplements de l'embouchure (st 2) sont plus diversifiés avec notamment la présence d'*A. parkinsoniana, E. poeyanum, E. jenseni, Rosalina* sp., *Q. stelligera* et *Pseudotriloculina sidebotomi*.

Cependant, 2 espèces, *A. tepida* et *E. cf. gunteri,* dominent en fréquence et en abondance. Les effectifs de ces 2 espèces principales sont particulièrement élevés à proximité de l'embouchure (Fig. 7) puis diminuent rapidement vers l'intérieur du bassin notamment pour *E. cf. gunteri* qui est

Tabl. II. – Comparaison de la diversité spécifique globale de quelques bassins paraliques de Méditerranée. D'après les données de Favry (1997), Favry *et al.* (1997, 1998), Guelorget *et al.* (1999, 2000).

Comparison of global specific richness in some Mediterranean paralic basins. After data from Favry (1997), Favry et al. (1997, 1998), Guelorget et al. (1999, 2000).

	KALLONI (Lesbos)		NADOR (Maroc)		DIANA (Corse)		EL KANTARA (Golfe de Gabès)		URBINO (Corse)		PRÉVOST (Languedoc)		ALBANIE (Les 3 systèmes confondus)	
Zones de confinement dominantes	II		II-III		III		III-IV		III-IV		IV		III à VI	
Agglutinés	6	5,7	6	4,8	9	13,0	1	0,2	4	11,8	4	10,0	5	17,1
Hyalins	53	50,5	65	52,8	46	66,7	28	57.1	18	52,9	21	52,5	21	60,0
Porcelanés	36	34,3	52	42.3	14	20,3	20	40,8	12	35,3	15	37,5	9	25,7
Total	105		123		69		49		34		40		35	

pratiquement absente dans toute la zone centrale et le nord du bassin. Cependant, les images que donnent les cartes de dominance sont très différentes. *A. tepida* représente environ 45 % du peuplement à l'embouchure de la lagune et prend une part de plus en plus importante au sein des peuplements à l'intérieur du bassin, où elle domine largement jusqu'à représenter 95 % du peuplement dans toute la zone nord de la lagune. *E. cf. gunteri* constitue 38 % des peuplements à l'embouchure de la lagune mais la part prise par cette espèce au sein des peuplements diminue rapidement vers l'intérieur du bassin. Ainsi, les peuplements de Foraminifères sont dominés partout par *A. tepida* qui constitue plus de 50 % des peuplements. Seuls les peuplements de la zone située à l'embouchure du bassin (station 2) sont plus équilibrés, *E. cf. gunteri* y prenant une part non négligeable.

ANALYSES MULTIVARIÉES ET ORGANISATION DES PEUPLEMENTS

Une classification hiérarchique ascendante et une analyse factorielle des correspondances (Benzecri & Benzecri 1984) ont été réalisées simultanément pour l'ensemble des trois sites à partir d'un tableau de contingence (Dervin 1988) réunissant l'ensemble des stations et les 21 espèces ou genres les plus fréquents et/ou abondants dans les échantillonnages effectués. Cette approche permet une analyse plus globale de l'organisation des peuplements de Foraminifères dans ces écosystèmes (Lebart *et al.* 1982). Les deux premiers axes de l'analyse factorielle des correspondances constituent 42,2 % de l'inertie totale, dont 22,2 % pour l'axe 1. Seuls ces 2 premiers axes sont pris en considération.

Stations

L'ordination des stations effectuée par la classification hiérarchique (Legendre & Legendre 1979) (Fig. 9) permet d'opérer 3 groupements. Le premier (1) comporte la station située à l'embouchure de la bahira de Butrinti (B2) et la station K19 située au droit du chenal entre les 2 bassins de Karavasta. La station B2 est à l'évidence sous influence marine ; il n'en va pas de même de la station K19. Celle-ci pourrait illustrer l'« effet de chenal » qui provoque, à cause d'un flux accéléré localement, un déconfinement du milieu (Guelorget *et al.* 1984). Un 2e groupement (2) est constitué de la station K3 située au sud du bassin distal de Karavasta et 2 stations plus isolées : B14 de la bahira de Butrinti et K23 située dans le bassin proximal du complexe de Karavasta. Il correspond sensiblement à une zone située de part et d'autre de la limite entre la zone III et la zone IV-V. Les 2 stations échantillonnées dans la lagune de Narta (N1 et N2) appartiennent aussi à ce groupement malgré le très fort confinement du milieu : il est vraisemblable que le peuplement de Foraminifères est ici fossile. Enfin un 3e groupement (3) rassemble les autres stations et couvre les zones les plus confinées des systèmes.

Cependant on constate que l'axe 1 de l'AFC oppose l'ensemble des stations échantillonnées dans le bassin de Butrinti aux prélèvements effectués dans la lagune de Karavasta (Fig. 8). En effet, plusieurs espèces présentes dans le bassin de Butrinti telles que *Ammonia parkinsoniana, Elphidium jenseni* ou *Gaudryina exilis* n'ont pas été recensées dans la lagune de Karavasta.

Espèces

Le dendrogramme issu de la classification hiérarchique (Fig. 8) permet de définir 4 groupes d'espèces. Le 1er est celui d'*Ammonia tepida*, espèce omniprésente, dont le point figuratif est situé sur l'AFC au voisinage de l'origine. Le 2e est celui d'*Haynesina germanica*, 2e espèce par son abondance, surtout dans le bassin de Karavasta. Le 3e groupe comporte *A. parkinsoniana* et *E. cf. gunteri* qui ont une distibution voisine de celle d'*H. germanica*, principalement à Butrinti. Toutes

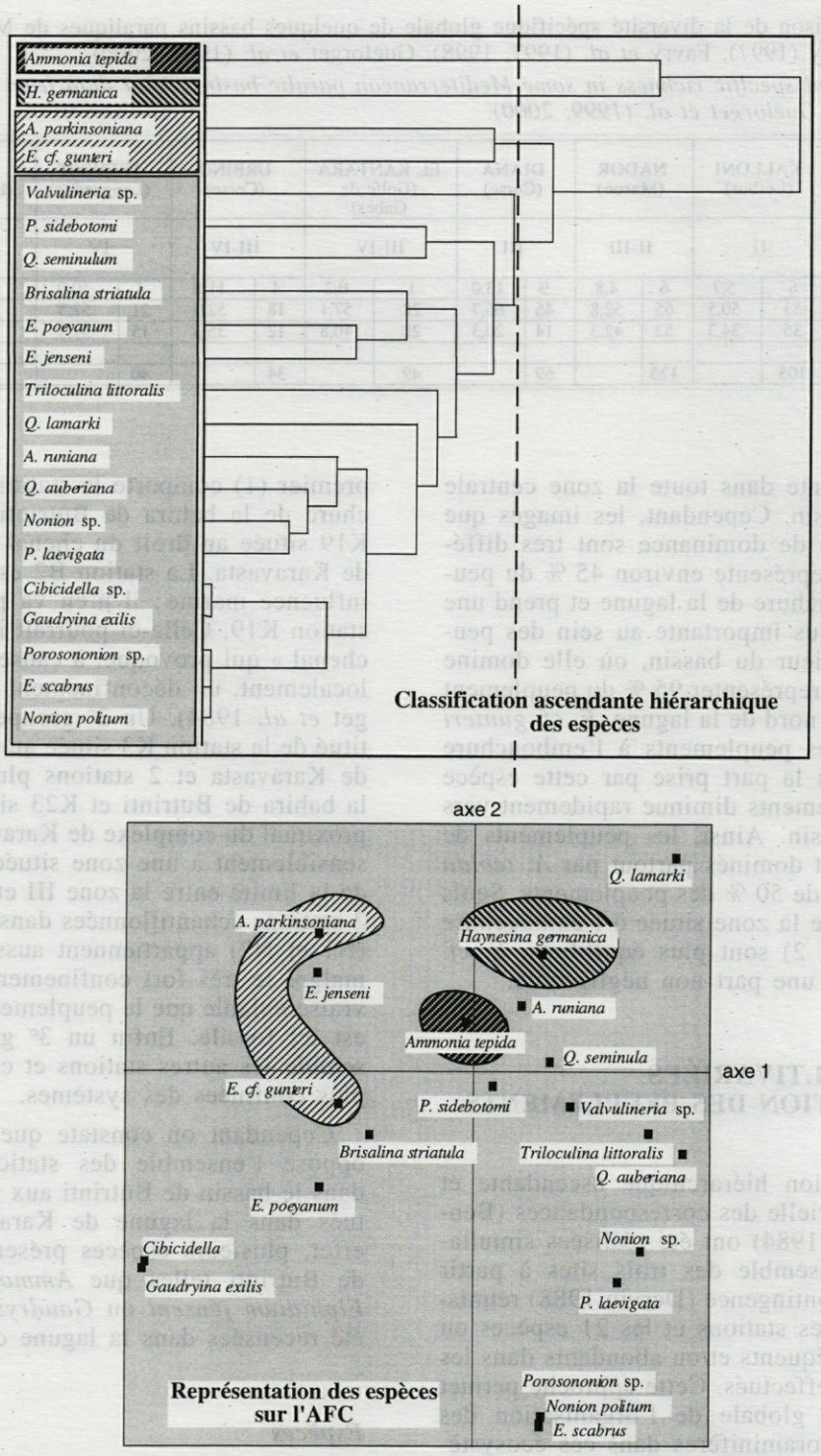


Fig. 8. – Analyses multivariées des espèces.
Multivaried analyses of species.

les autres espèces forment un 4e groupe. Il s'agit d'espèces à distribution erratique et en général faiblement représentées à chaque station. On peut remarquer que *Eggereloides scabrus* se situe dans ce groupe alors que dans d'autres bassins paraliques méditerranéens elle fait parfois partie des espèces dominantes (Guelorget *et al.* 1999, Favry *et al.* 1998).

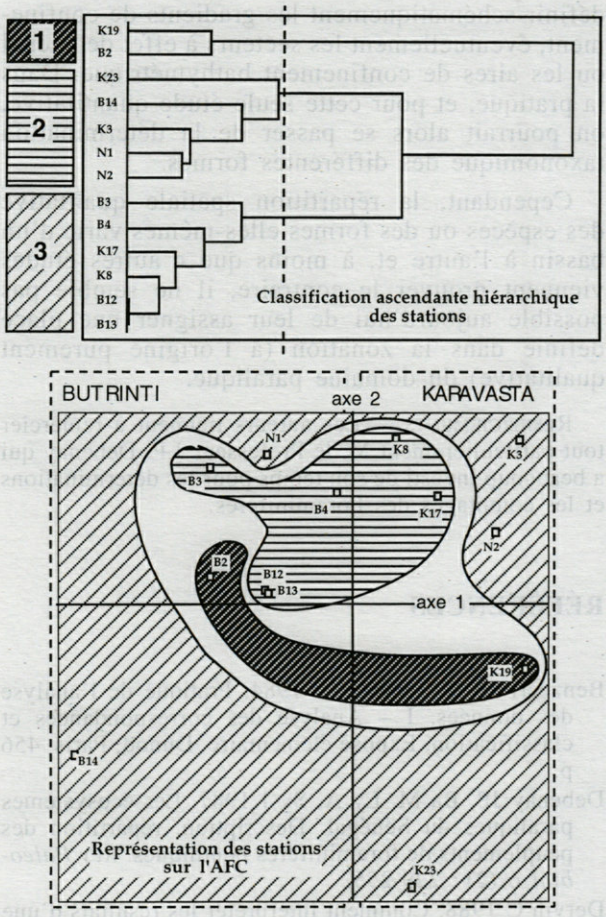


Fig. 9. – Analyses mutivariées des stations.
Multivaried analyses of stations.

DISCUSSION

Les espèces de Foraminifères recensées dans les trois systèmes albanais étudiés sont des espèces classiques du panorama qu'offrent les environnements paraliques méditerranéens. Toutes les espèces présentes se retrouvent dans l'une ou l'autre des lagunes de Nador, du Prévost, de Kalloni, de Diana ou d'Urbino, la plupart dans tous ces bassins. En revanche, ces microfaunes sont un peu différentes de celles que l'on rencontre dans les bassins paraliques du Golfe de Syrte, où figurent par ailleurs, à côté des espèces les plus classiques comme *Ammonia tepida*, des groupes à affinités indo-pacifiques comme les Soritidés (Médhioub *et al.* 1981).

La richesse spécifique globale des trois systèmes albanais étudiés est faible par comparaison avec d'autres bassins paraliques méditerranéens (Tabl. II) et c'est encore plus vrai pour chaque bassin pris séparément. Ceci est vraisemblablement lié à leur confinement élevé, peut-être aussi à la situation marginale de cette région vis à vis du bassin méditerranéen. En outre, on peut observer une représentation notable du groupe des agglutinés et une relativement faible représentation des Porcelanés, ceci semblant aussi aller de pair avec un confinement global élevé.

Comme dans la plupart des bassins paraliques méditerranéens, la richesse spécifique des peuplements de Foraminifères diminue dans chacun des systèmes étudiés depuis la communication avec la mer vers les marges les plus confinées.

Les variations de densité se conforment à un gradient de même sens, de façon très claire à Butrinti, moins évidente à Karavasta. Ici, c'est la partie sud du bassin distal qui présente les densités maximales sans qu'il soit possible d'en trouver la raison. La zone centrale de Butrinti, avec son corps d'eau profonde anoxique, se caractérise par une densité très faible : il est probable que les Foraminifères récoltés à la station 4 y ont été transportés et sont à l'état fossile.

En laissant de côté le bassin de Narta, en voie de comblement, où la microfaune est vraisemblablement fossile, l'organisation des peuplements dans les deux autres bassins est semblable, compte tenu du probable effet de chenal au voisinage de la communication entre les deux bassins de Karavasta (Fig. 10). Elle se calque dans chaque bassin, sur la distribution des zones de confinement et se traduit schématiquement par la disparition échelonnée de certaines espèces en fonction du confinement.

L'organisation quantitative décrite ci-dessus se retrouve dans tous les bassins ou ensembles paraliques que nous avons étudiés jusqu'ici. Il s'agit donc d'une tendance générale des peuplements de Foraminifères paraliques à s'appauvrir en espèces et en individus en fonction d'un confinement croissant. Les Foraminifères disparaissent d'ailleurs en zone VI, aux frontières de ce que nous appelons le Proche paralique (Guelorget & Perthuisot 1983, 1992), que l'on se dirige vers les environnements dulçaquicoles ou vers les environnements sursalés (Zaninetti 1982) ou encore dans les zones de confinement bathymétrique élevé comme à Butrinti.

Cependant, contrairement à ce qu'on observe avec la macrofaune benthique, la distribution qualitative et quantitative de chaque forme ou espèce n'est ni identique ni même toujours semblable d'un bassin à l'autre. Ceci a bien été montré par l'AFC en ce qui concerne les lagunes albanaises (Fig. 9, 10). Si l'on considère l'ensemble des sites étudiés par notre équipe, on retrouve cette disparité et cette originalité de chaque bassin. Chacun d'eux présente une répartition particulière et originale des espèces, notamment en ce qui concerne les espèces à effectifs restreints, et parfois même en ce qui concerne les espèces dominantes. Il n'y a pas de raison claire à ce phénomène. Tout se passe comme si les espèces benthiques des envi-

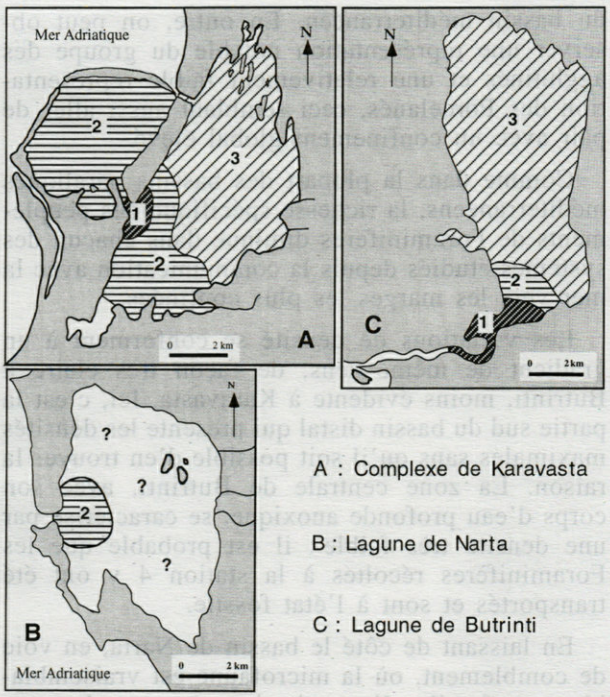


Fig. 10. – Répartition des associations de stations définies par les analyses multivariées dans les différents bassins. Les goupes 1, 2 et 3 correspondent à ceux définis par la classification hiérarchique des stations (Fig. 9).

Distribution of the station assemblages as defined by multivaried analyses in the basins. Groups 1, 2, 3, are defined by the hierarchic ascending classification of stations (Fig. 9).

ronnements paraliques n'avaient pas une place strictement définie dans l'écosystème et dans ses chaînes trophiques. Comme par ailleurs, il s'agit de bassins sub-fermés, l'organisation spatiale des formes de Foraminifères peut dépendre de nombreux facteurs intervenant lors de leur recrutement et au cours de l'évolution plus ou moins endémique de chaque bassin. Ainsi, il n'est pas possible de définir, dans le domaine paralique méditerranéen, une zonation qualitative des espèces de Foraminifères comme cela a été possible avec la macrofaune benthique (Guelorget & Perthuisot 1983, 1992).

CONCLUSION

Le présent travail confirme l'intérêt de l'étude de la distribution quantitative (richesse spécifique et densité) des microfaunes de Foraminifères pour la compréhension de l'organisation et du fonctionnement des écosystèmes paraliques. Elle permet en effet, en l'absence de tout autre indicateur, de définir schématiquement les gradients de confinement, éventuellement les secteurs à effet de chenal ou les aires de confinement bathymétrique. Dans la pratique, et pour cette seule étude quantitative, on pourrait alors se passer de la détermination taxonomique des différentes formes.

Cependant, la répartition spatiale qualitative des espèces ou des formes elles-mêmes varie d'un bassin à l'autre et, à moins que d'autres études viennent prouver le contraire, il ne semble pas possible aujourd'hui de leur assigner une place définie dans la zonation (à l'origine purement qualitative) du domaine paralique.

REMERCIEMENTS. – Les auteurs tiennent à remercier tout particulièrement M. le Professeur J.P. Debenay qui a beaucoup investi de son temps pour les déterminations et les comptages des Foraminifères.

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ARE LORICIFERANS PAEDOMORPHIC (PROGENETIC) PRIAPULIDS ?

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LORICIFERA
PRIAPULIDA
MORPHOLOGY
PAEDOMORPHOSIS
PROGENESIS
NEOTENY
LIFE-CYCLES

ABSTRACT. – Adult loriciferans are virtually identical in morphology to the lorica larvae of priapulids, except for the absence of gonads. It is argued that they are, in fact, progenetic priapulids. The normal adult/lorica larva life cycle of priapulids has evolved in two ways, omitting one or the other of these stages.

LORICIFERA
PRIAPULIENS
MORPHOLOGIE
PAEDOMORPHOSE
PROGENÈSE
NÉOTÉNIE
CYCLES

RÉSUMÉ. – Les Loricifères sont-ils des Priapuliens paedomorphes (progénétiques) ? Les Loricifères adultes sont pratiquement identiques morphologiquement aux larves lorica des Priapuliens, mise à part l'absence de gonades. Il est argumenté qu'ils sont en fait des Priapuliens progénétiques. Le cycle de vie normal de la larve adulte/lorica des Priapuliens a évolué de deux façons, omettant l'un ou l'autre stade.

INTRODUCTION

The sea is characterised by a much higher diversity of animal phyla than the land and new phyla are still being discovered, most recently by Funch & Kristensen (1995). The Loricifera were first described as a new Phylum by Kristensen (1983), and comprise small bilaterally symmetrical metazoans with a spherical eversible head or 'introvert', a neck and a thorax, all retractable into a cuticular loricate abdominal region. Adult loriciferans are similar in appearance to the loricate larvae of animals belonging to the Phylum Priapulida, the adults of which are large and soft bodied, but with a similar introvert. This similarity prompted me to speculate, in two editorials of the Newsletter of the International Association of Meiobenthologists ('Psammonalia') in 1990 and 1992 that loriciferans were simply paedomorphic priapulids. The objective of these articles was to stimulate debate, but to date no opposing views have been expressed and, since these views are now becoming cited in scientific journals (Morris 1995, Adrianov & Malakhov 1995) it seems timely to summarise the arguments formally. In the 'Psammonalia' editorials I used the term 'neotenous' priapulids, which is strictly incorrect. Gould (1977) distinguishes two types of paedomorphosis (the general term for the retention of juvenile ancestral features by adult descendants): 'neoteny' in cases involving retardation of somatic development and 'progenesis' in cases of genetically fixed precocious sexual maturation of animals still in a morphologically juvenile or larval stage. I was clearly arguing for the latter. Gould (1977) has pointed to progenesis as an important mechanism in the origin and evolution of higher taxa in general, and Westheide (1987) gives specific examples of its importance as a principle in meiofaunal evolution.

LARVAL PRIAPULIDS COMPARED WITH ADULT LORICIFERANS

Priapulids are remarkable in that they spend an extraordinarily long time in the larval stage (van der Land 1970), e.g. *Priapulus caudatus*, a common European species, spends at least two years as a lorica larva less than 2 mm long (Lang 1948), the adults eventually attaining a length of 20 cm. This suggests strong selective pressures to stay at this small size for a long period. The gonads are already beginning to develop in these larvae, and it would seem a very small evolutionary step for the gonads to attain functional maturity, avoiding the adult stage altogether.

Westheide (1987) has argued that 'the most convincing and clearest indication of speciation

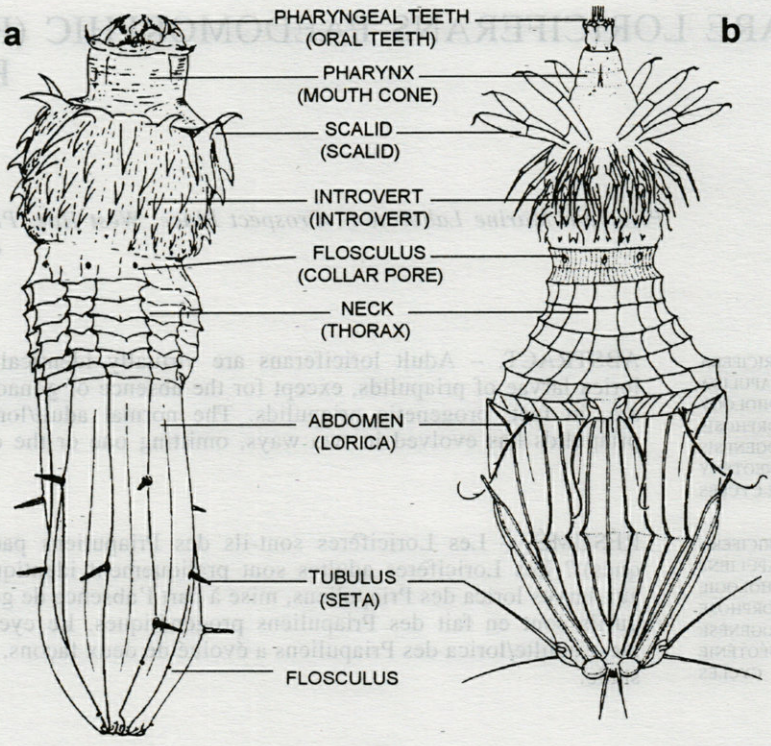

Fig. 1. – Can these two belong to different phyla ? a, larva of the priapulid *Tubiluchus corallicola*, length 730 µm (from van der Land 1970). b, the loriciferan *Pliciloricus gracilis*, length 227 µm (from Higgins & Kristensen 1986). Terminology used for homologous structures is given first for the priapulid and second for the loriciferan (in parenthesis).

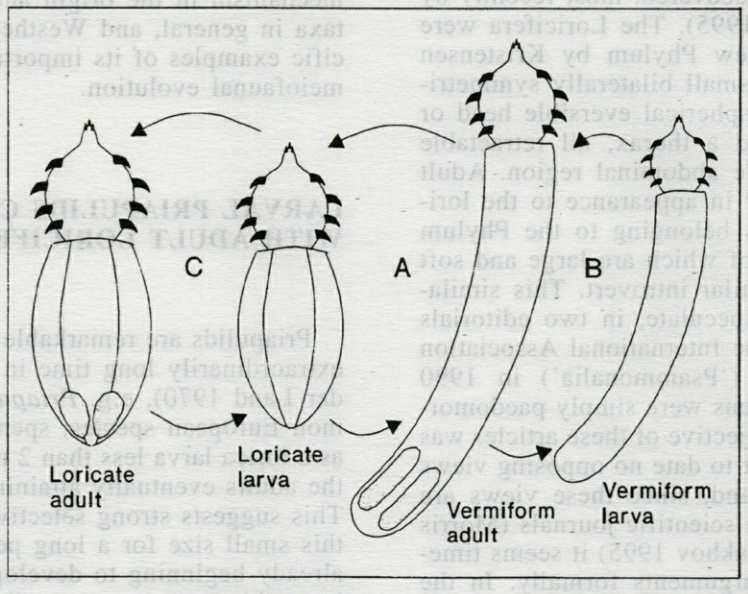

Fig. 2. – Diagrammatic representation of the life cycles of most priapulids (A), *Meiopriapulus* (B) and loriciferans (C).

by genetically fixed early maturation is present when an interstitial taxon shows great conformity with larval or juvenile stages of a macrofauna taxon'. Comparison of a priapulid larva with an adult loriciferan shows a very similar body plan, although the terminology traditionally used for some of the structures, presumed here to be homologous, differs (Fig. 1a, b). Finer details of the anatomy are also similar: the first crown of eight scalids on the introvert differ in structure from the numerous scalids in the more posterior crowns, the neck or thorax is covered in plates like a tiled roof, and the loricas have a similar structure and microstructure (Adrianov *et al.* 1989). However, there is a difference between larval priapulids and loriciferans in the way in which the cuticular plates of the lorica articulate, which Neuhaus *et al.* (1997) suggest casts some doubt on their homology. Many loriciferans, but not the one illustrated, have sensory organs termed flosculi located posteriorly on the lorica, similar to those of the *Tubiluchus* larva (Fig. 1a), and these are shared between these two taxa and the Kinorhyncha. In both taxa there is an internal septum that separates the proboscis from the trunk section, and the nervous and urino-genital systems are built on a similar plan. In short, there is nothing in the emended definition of the Phylum Loricifera (Higgins & Kristensen 1986), apart from the presence of mature gonads, that is contradicted by larval priapulids.

PRIAPULID LIFE-CYCLES

The finding of a priapulid species, *Meiopriapulus fijiensis,* that does not have the lorica larva stage (Higgins & Storch 1991), prompts the speculation that the ancestral priapulid life cycle (A in Fig. 2) has evolved along two lines in which either the lorica stage is eliminated by neotonic deceleration of somatic development (B), or the vermiform stage has been eliminated by progenetic acceleration of gonad development (C). Life cycle A is found in most species currently included in the Phylum Priapulida, life cycle C in the Loricifera, and B in *Meiopriapulus*. It is suggested that they all be encompassed within the Priapulida, and that forms with the three contrasting life cycles be established as distinct subgroups. The status of the Priapulida as a Phylum, however, remains equivocal: they have variously been regarded as a Class in the Phylum Cephalorhyncha (Adrianov & Malakhov 1995) along with the Loricifera, Kinorhyncha and Nematomorpha, or with the first two of these only as the Scalidophora (Schmidt-Rhaesa 1998).

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