OCEANOLOGICA ACTA - VOL. 16 - N°3

Distribution of zooplankton populations in Marennes-Oléron Bay (France), structure and grazing impact of copepod communities

Marennes-Oléron
Zooplankton
Copepods
Biomass
Grazing

Marennes-Oléron
Zooplancton
Copépodes
Biomasse
Broutage

Benoît SAUTOUR and Jacques CASTEL

Centre d'Océanographie Biologique, Université de Bordeaux I, 2 rue Jolyet, 33120 Arcachon, France.

Received 30/10/92, in revised form 4/03/93, accepted 30/04/93.

ABSTRACT

Zooplankton distribution in Marennes-Oléron Bay (France) varies during the year and is essentially determined by seasonal rhythms. The whole set of zooplanktonic taxa can be divided into three groups: the first bearing oceanic affinities; the second with estuarine tendencies; and the third more intermediate. Important water flows inhibit the establishment in a specific zone of an autochthonous community (this community is reduced to such species as *Acartia discaudata*, *Acartia grani* and *Euterpina acutifrons*). Zooplanktonic populations reach their maximum abundances at the end of spring and during summer, particularly during spring tide in the inner neritic zone. The estimation of the grazing pressure of copepods (which are the dominant taxa) is variable according to water masses: an abruptly decreasing gradient of pressure of these organisms on algal stock can be seen from the oceanic to the estuarine zones.

Oceanologica Acta, 1993. **16**, 3, 279-290.

RÉSUMÉ

Distributions spatiale et temporelle du zooplancton dans le bassin de Marennes-Oléron (France), structure et pression de broutage des communautés copépodiennes

La répartition du zooplancton dans le bassin de Marennes-Oléron est très variable au cours de l'année et essentiellement régulée par les rythmes saisonniers. La totalité des taxons zooplanctoniques peut être divisée en trois sous-ensembles : le premier à tendance néritique, le second à tendance estuarienne, le troisième ayant des caractéristiques intermédiaires. Les importants mouvements d'eau empêchent l'implantation en un site précis d'une communauté zooplanctonique autochtone (réduite à quelques espèces, *Acartia discaudata*, *Acartia grani* et *Euterpina acutifrons*). Les populations zooplanctoniques présentent leurs abondances maximales en fin de printemps et en été, principalement en vives-eaux en limite de zone néritique. Les copépodes, taxons dominants, exercent une pression de broutage variable suivant les masses d'eau : un gradient abrupt de décroissance de l'impact de ces planctontes sur le stock algal est mis en évidence depuis les sites néritiques vers les sites estuariens.

Oceanologica Acta, 1993. **16**, 3, 279-290.

INTRODUCTION

Zooplankton is an important biological component of semi-enclosed littoral ecosystems. Its high biomass and production influences primary production, and it plays a role in secondary and tertiary predation represented by young instars of fishes (*see* for instance: Allan *et al.*, 1976; Baars and Fransz, 1984; Fransz *et al.*, 1984; Feurtet, 1989). In addition, the meroplankton component (especially oyster larvae) is important for economic interests during certain periods of the year.

For some years, the productivity of farmed species has been decreasing in ecosystems used for aquaculture. This diminution is probably due to overcrowding (Héral *et al.*, 1989). Changes are clearly related to all the variables of the ecosystem and have led to the development of analytical models of environments such as Marennes-Oléron Bay (Laboratoire des écosystèmes conchylicoles, IFREMER, La Tremblade, Héral *et al.*, 1989). Such models may allow industry to predict and anticipate the effects of changes in the environment.

Nutritional availability for farmed species (essentially bivalves) depends on the competition between them and other consumers in the system (Héral *et al.*, 1989). It has long been understood that consumed planktonic primary production is divided between zooplanktonic organisms and benthic filter feeders. This possible nutritional competition of zooplankton with bivalves (larvae and adults) must be accounted for in modelling exercises.

The study area (Marennes-Oléron Bay) is a semi-enclosed ecosystem receiving neritic and continental inputs. In such an environment, the zooplankton is a result of a mixing of several communities more or less adapted to the environmental variability. The interpenetration of neritic and estuarine communities closely depends on the hydrological conditions of the environment; there is frequent input of marine organisms to the estuarine zone and output of estuarine animals from the bay. Between these fluxes, the establishment of autochthonous communities depends on the balance between the neritic and estuarine water flows.

In order to determine zooplanktonic pressure on the algal standing stock, one can estimate the amount ingested by herbivorous copepods which are the most abundant taxa of zooplankton. Published results have varied according to the area studied. In the open sea, copepods may remove nearly 100 % of primary production (Menzel and Ryther, 1961). In contrast, in littoral zones it seems that this impact is much decreased (Deason, 1980; Joiris *et al.*, 1982; Nicolajsen *et al.*, 1983).

In the present work, this range of possible zooplankton impact was studied during the year 1986 in five areas of Marennes-Oléron Bay: two stations were located close to the neritic zone; two were near the estuarine areas and one was representative of the intermediate zone).

Two aspects were addressed: temporal variability by monthly sampling; and spatial variability with samples taken from the different characteristic water masses. In addition, the present work gives an estimation of copepod pressure on algal standing stock in the studied zones.

MATERIALS AND METHODS

Study area (Fig. 1)

Marennes-Oléron Bay is a shallow littoral area separated from the ocean by Oléron Island. It has two openings to the neritic zone: a large one in the northern part of the bay (Pertuis d'Antioche) and a smaller one in the southern part (Pertuis de Maumusson). In addition, the bay is subject to continental inflows through the Seudre estuary to the south and more strongly through the Charente estuary to the north.

Tidal flows have a great influence on the movement of water masses in the Bay. The two inlets have different roles: the Pertuis d'Antioche allows important water inflows whereas the Pertuis de Maumusson essentially permits outflows. Thus, the neritic influence differs between the northern part and the southern part of the bay. The mixing zone of these two tidal flows constitutes a "wantij" in the middle of the studied area and leads to definable streams in the whole bay (Tesson, 1973):

- during high tide, neritic water (T/S diagram of Boyard station, Fig. 1) enters through Pertuis d'Antioche and flows towards the south (T/S diagram of Le Chapus station) along Oléron island, while estuarine water masses (T/S diagram of La Mouclière station) of the Charente follow the same direction along the mainland shore;
- at low tide, these two streams are mixed and return to the north;
- during the following high tide, most of the mixed water masses return by the movements described above;
- gradually, these mixed water masses move to the south of the bay where they are mixed with water from the Seudre estuary (T/S diagram of Barat station) and the Pertuis de Maumusson;
- finally, they are ejected by the Pertuis de Maumusson (T/S diagram of Auger station).

This net water flow from the north to the south takes about ten days (Anonymous, 1975).

Marennes-Oléron Bay is a shallow sandy (in the zones of high currents) and muddy (in lateral zones) system. Average depths are around 10 m in the Pertuis de Maumusson and 5 m at the mouth of the Charente estuary, compared with an average depth smaller than 5 m in the middle and southern parts of the bay. The important water streams described above induce strong turbidity in the bay (data from the Laboratoire des Écosystèmes Conchylicoles, IFREMER, La Tremblade, pers. comm.). The highly important average values of suspended matter concentration obtained in the northern estuarine zone in 1986 (470 $mg.l^{-1}$) are due to great river discharges; on the other hand, the lowest values are found in the northern neritic zone (Boyard station, 40 $mg.l^{-1}$). The turbidity of the southern part of the bay is more homogeneous (60 $mg.l^{-1}$ near the neritic area and 54 $mg.l^{-1}$ at the mouth of the Seudre estuary) whereas the intermediate zone presents higher values due to the mixing of different water streams (66 $mg.l^{-1}$).

Sampling and analysis of the data

From January to December 1986, horizontal zooplankton hauls were carried out at monthly intervals. Each month sample series were done at spring and neap tides; samples were taken both during high and low tide. Five areas were considered for this work (Fig. 1): two near the oceanic zone (Boyard and Auger); two close to estuaries (Barat and La Mouclière); and one with characteristics for the shellfish-farming area (Le Chapus).

Samples were taken with a standard WP2 net with 200 µm mesh size (Fraser, 1966). This mesh size was selected to avoid rapid clogging of the net during the periods of resuspension of benthic materials or during spring bloom. Thus, this study only concerns mesozooplankton. Hauls were carried out against the current and just below the surface for about two minutes. The volume filtered was about 4 to 20 m^3 (*Hydrodata digital* flowmeter, model 438110). Samples were rinsed and concentrated, then immediately stored in buffered 4 % seawater formalin.

In the laboratory, organisms were identified and counted; for each sample, one to three counts on subsamples were made. Copepods, which were generally the most abundant group, were identified to the species level. Total biomasses were calculated by multiplying mesozooplanktonic densities and individual dry weights.

The weight of copepods remains nearly constant after one month storage in formalin (after a slight decrease, Kulhman *et al.*, 1982). In order to determine dry weights, animals were rinsed and dried at 60°C for 24 hours. Three aliquots of thirty individuals of each species (pools of adults and copepodids) were weighed on a Mettler ME22 microbalance (sensitivity: 0.1 µg). Biomasses are given in weight of carbon (Tab. 1) by multiplying dry weight by a factor 0.4 (Parsons *et al.*, 1977; Gerlach, 1978; Baars and Fransz, 1984; Simard *et al.*, 1985).

Values obtained from the samples taken at high and low tide were averaged in order to represent the mean difference between spring and neap tide for each station and each month. A principal component analysis (PCA) was made (STAT-ITCF software) to obtain a global view of the annual variation of zooplanktonic communities in different areas of the bay.

Variables were considered well represented when the sum of the correlation square with regard to the PCA axes was greater than 0.65 (capital letters in tables) and moderately

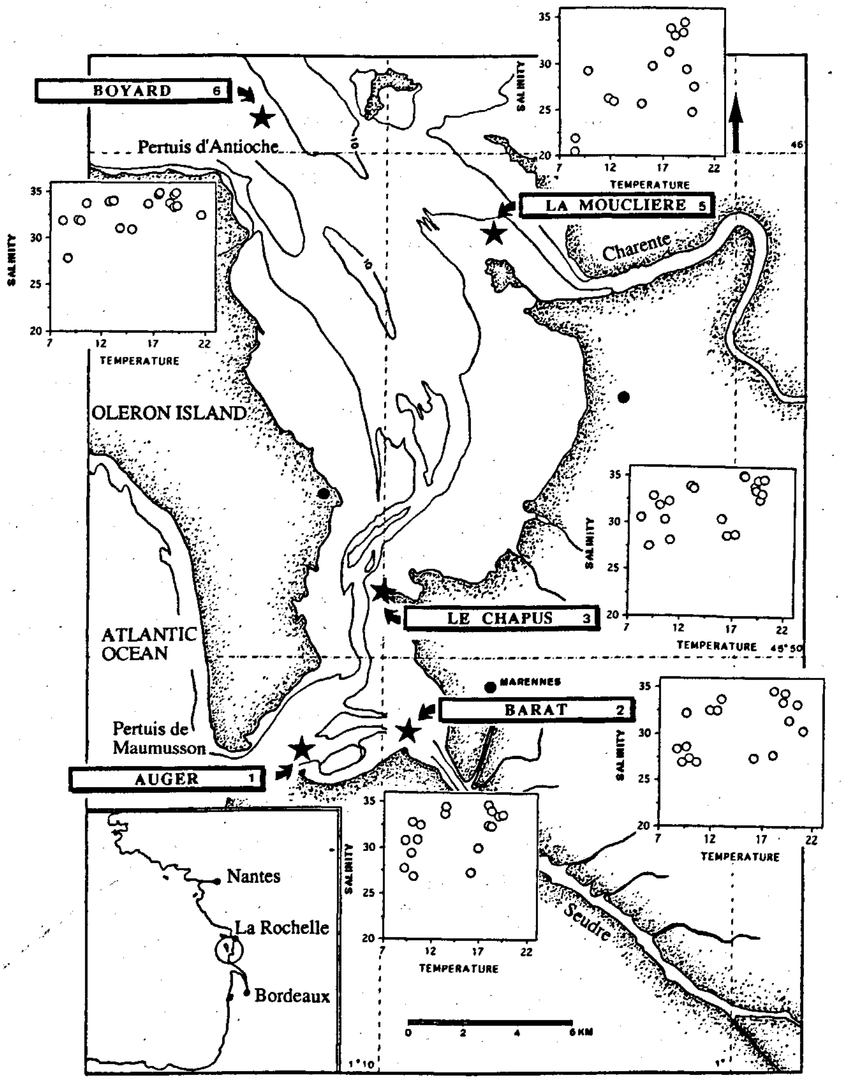

Figure 1

Marennes-Oléron Bay (1986), showing the sampling stations. Temperature and salinity values are given for each sampling (data from the Laboratoire des Écosystèmes Conchylicoles, IFREMER, La Tremblade, pers. comm.).

Bassin de Marennes-Oléron (1986). Stations de prélèvement. La température et la salinité sont données pour chaque échantillonnage (données du Laboratoire des Écosystèmes Conchylicoles, IFREMER, La Tremblade, comm. pers.).

Table 1

Marennes-Oléron Bay. 1986. Biomasses of the main zooplanktonic copepods. Determination on three replicates of thirty individuals (adults + copepodids) of each species (µg C ± standard error).

Marennes-Oléron Bay. 1986. Biomasses des principaux copépodes planctoniques. Détermination sur trois réplicats de trente individus (adultes + copépodites) de chaque espèce (µg C ± erreur standard).

SPECIES	BIOMASSES
Acartia bifilosa	1.920 ± 0.023
Acartia clausi	1.332 ± 0.005
Acartia discaudata	0.973 ± 0.081
Acartia tonsa	0.993 ± 0.013
Acartia grani	1.020 ± 0.042
Calanus helgolandicus	16.308 ± 1.646
Centropages hamatus	2.780 ± 0.208
Eurytemora hirundoides	1.650 ± 0.104
Isias clavipes	0.853 ± 0.093
Labidocera wollastoni	10.927 ± 0.441
Paracalanus parvus	1.400 ± 0.131
Pseudocalanus elongatus	1.513 ± 0.041
Temora longicornis	3.900 ± 0.169
Oithona helgolandica	0.417 ± 0.039
Oithona nana	0.556 ± 0.077
Cyclopina littoralis	0.667 ± 0.133
Oncaea subtilis	0.355 ± 0.022
Oncaea venusta	0.742 ± 0.035
Corycaeus anglicus	1.933 ± 0.107
Euterpina acutifrons	0.683 ± 0.015

represented when it was comprised between 0.60 and 0.65 (small letters in tables). Observations were considered well represented when the sum of cosine square with the axis was greater than 0.5.

In order to characterize the copepod communities, Shannon index (Shannon and Weaver, 1948-1963) and equitability (Piélou, 1969) were used.

Estimation of the grazing pressure of copepods

The grazing pressure of copepods is described as the amount of algae ingested per unit of time (day) versus the algal concentration. The grazing pressure was estimated for each sample by calculating the ratio between the amount of pigments ingested by copepods ($h^{-1}.m^{-3}$) and the amount of pigments contained in a cubic metre of sea water (mg of chlorophyll *a* equivalent.m^{-3}). Total ingestion was calculated by multiplying copepod abundances and individual ingestion rates for the main species (*Acartia* spp., *Centropages hamatus*, *Temora longicornis* and *Euterpina acutifrons*). These species represent on average always more than 91 % of the herbivorous copepod community in each station. Thus, the results will be generalized to the copepod community. The ingestion rates were calculated from the relations given by Sautour (1991) between ingestion rates (I, ng chl *a* + eq.$Cop^{-1}.h^{-1}$) and algal concentration (C, ng chl *a* + eq.ml^{-1}):

Acartia spp.: $I = 1.1485C - 2.0966$;
Centropages hamatus: $I = 0.7751C - 0.0868$;
Euterpina acutifrons: $I = 0.5284C - 0.3264$;
Temora longicornis: $I = 0.6825C - 0.3729$.

These equations were established in the laboratory (temperature of 19°C) with small algae (*Skeletonema costatum*, 18 µm, one of the main species in the bay of Marennes-Oléron, Héral *et al.*, 1983). This does not allow seasonal comparisons of grazing pressure because the ingestion rates are strongly correlated to temperature, but it does permit relative comparisons between stations. These comparisons used the mean annual values for each site.

Table 2

Zooplankton of Marennes-Oléron Bay (1986). Pooling and coding of the variables used in the principal component analysis.

Zooplancton du bassin de Marennes-Oléron (1986). Regroupement et codage des variables utilisées dans l'analyse en composantes principales.

CODING	GROUPS	TAXA
ASB	Benthic taxa	Foraminifera, Trematoda, Nematoda, Kinorhyncha, Isopoda, Ostracoda
DIM	Marine taxa	Siphonophora, Ctenophora, Rotifera Phoronida, Echinodermata
HYD		Hydromedusae
POL	Larvae	Polychaeta
BRY	Cyphonautes	Bryozoa
CHE		Chaetognatha
BIV	Larvae	Bivalvia
GAS	Larvae	Gastropoda
CLA	Marine Cladocera	*Podon* sp., *Evadne* sp.
COE	Oceanic Copepoda	*Labidocera wollastoni*, *Calanus helgolandicus*, *Clausocalanus* sp.
PSE		*Pseudocalanus elongatus*
PAC		*Paracalanus parvus*
CEN		*Centropages hamatus*
TEM		*Temora longicornis*
DIN	Estuarine taxa	*Bosmina* sp., *Mysis* sp., *Neomysis* sp. *Mesopodopsis* sp., *Acartia bifilosa*, *A. tonsa*, *Eurytemora hirundoides*, *E. pacifica*
CON	Outer neritic Copepoda	*Acartia clausi*, *Isias clavipes*, *Cyclopina littoralis*
COI	Internal neritic Copepoda	*Acartia grani*, *Acartia discaudata*
OIT		*Oithona helgolandica*, *O. nana*, *O. Plumifera*
ONC		*Oncaea venusta*, *Oncaea subtilis*
COR		*Corycaeus anglicus*
EUT		*Euterpina acutifrons*
COB	Benthic Copepoda	
CIR	Larvae	Cirripeda
DEC	Larvae	Decapoda
APP		Appendicularians
MER	Total meroplankton	
TCL	Total Cladocera	
TCE	Total outer Copepoda	
TCP	Total planktonic Copepoda	
TOT	Total zooplankton	

Figure 2

Principal component analysis made on zooplankton of Marennes-Oléron Bay (1986). Projection of the whole set of observations on the plane 1-2.

Analyse en composantes principales faite sur le zooplancton du bassin de Marennes-Oléron (1986). Projection sur le plan 1-2 de l'ensemble des observations.

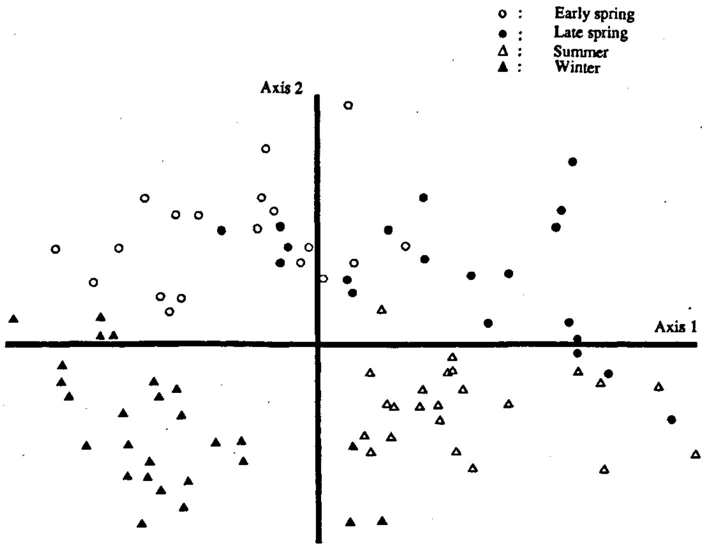

Figure 3

Principal component analysis made on zooplankton of Marennes-Oléron Bay (1986). Variables and observations considered well represented in the plane 1-2 (coding given in Tab. 2).

Analyse en composantes principales faite sur le zooplancton du bassin de Marennes-Oléron (1986). Variables et observations bien représentées sur le plan 1-2 (codage donné dans le tab. 2).

REPRESENTATIVE OBSERVATIONS		REPRESENTATIVE VARIABLES	
C6M C3M D2M D3M A5V C5M A3V C2M A6V D5M L2M 1	F5M F6V F6M E1V G3M 2 H5V	1	CON CLA Biv 2 CEN Tem
A2M A1V 4 A5M A3M L2V C3M L1M L3V K2V L6V K6V K1V K3V L1V	3 H3V F1V H6V H6M G1M L5V	4	3 CIR APP GAS Pac Coi CHE EUT

RESULTS

Analysis of the whole data set

Groups with a relative occurrence frequency > 50 % were used in the PCA. The data set was thus reduced to 30 variables for which coding is given in Table 2. Taxonomic groups with obvious identical ecological affinities were pooled. This is justified by the aim of this study, which was to characterize zooplanktonic populations in the different areas, but not to show faunistic groups already known. The last five variables in Table 2, as well as the water temperature (TMP), and the salinity (SAL), were used as additional variables. PCA made on annual and monthly data with other additional variables, such as chlorophyll, phaeopigments, suspended matter, *etc.*, did not give useful results and are not presented.

The coding of observations was realized by three sets of characters:

Sampling month	Station reference (Fig. 1)	
A = January	**(1, 2, 3, 5 and 6)**	M = neap tide
L = December	*See* Fig. 1	V = spring tide.

Thus, the principal component analysis was done on 90 observations corresponding to the two monthly samples (low tide and high tide) in the five sampling stations and 32 variables (30 biological groups + salinity + temperature).

The percentage weightings of the first 5 components are: 36.7, 12.6, 7.60, 5.50 and 5.10 % respectively. Only 70 % of the total variance was explained. This illustrates the complexity of the distribution of zooplanktonic populations.

Qualitatively, the observations seem to form seasonal groups (Fig. 2). Axis 1 separates the whole set of data into two parts: the negative part of this axis essentially shows samples made at the beginning and the end of the year, whereas samples taken from May to September are grouped in the positive part. This is probably a temperature axis. Axis 2 permits subdivision of these observations: the positive part of the axis exhibits observations from March to June, those from January, February and July to December are situated in the negative part of axis 2. This axis is probably a salinity axis. Thus, the principal plane is divided into four distinct areas (Fig. 2), illustrating seasonal grouping of observations : 1) beginning of spring (March and April); 2) end of spring (May and June); 3) summer (July to September); 4) winter (November to January). A total of 41 % of the observations and 32 % of the variables are well defined on this principal plane (Fig. 3).

Winter populations in the bay are quite poor (Fig. 4) and are distinguished by low densities in cladocerans, appendicularians, cirripede and bivalve larvae and in the copepods: *C. hamatus* and *T. longicornis* (Fig. 3). These assemblages increase at the beginning of spring, mainly caused by the copepod *A. clausi*. The end of springtime is characterized by the rise of zooplankton numbers essentially due to high abundances of cladocerans (*Podon* sp. and *Evadne* sp.), cirripede and bivalve larvae, appendicularians and the copepods *C. hamatus*, *T. longicornis* and mainly *A. clausi*. Large populations of cladocerans, cirripede and bivalve larvae, appendicularians and copepods (*C. hamatus* and *T. longicornis*) appear during summer in the outermost areas, and even in the centre of the bay during spring tide. The beginning of winter is characterized by a decrease of these populations. It is also characterized, especially in the outer

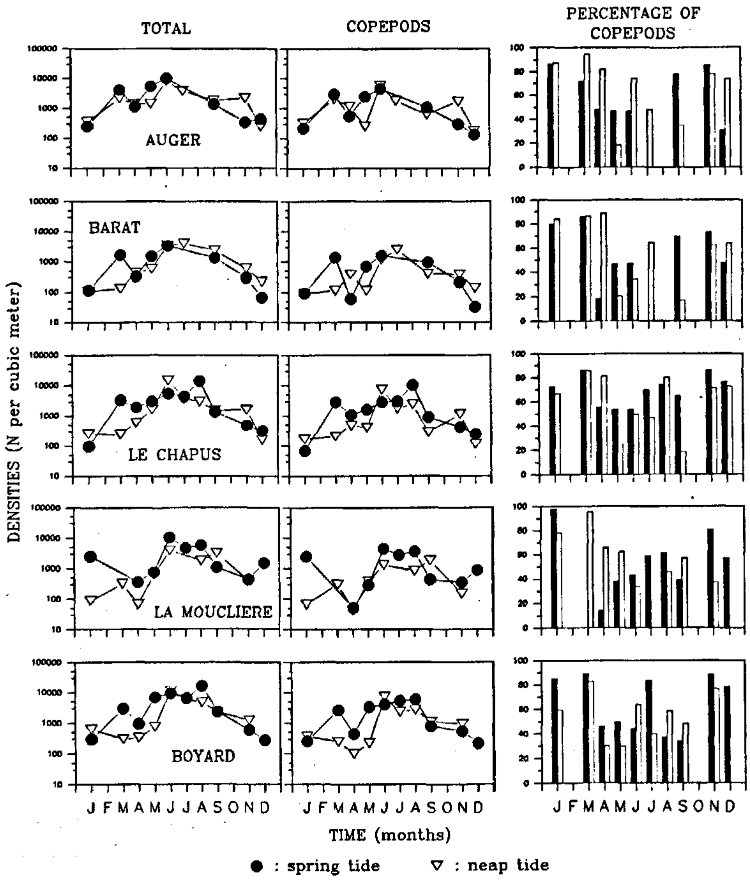

Figure 4

Marennes-Oléron Bay (1986). Densities of total zooplankton and Copepods (ind.m^{-3}). Relative abundances of copepods (white bars: neap tide; black bars: spring tide).

Bassin de Marennes-Oléron (1986). Effectifs copépodiens et zooplanctoniques totaux (ind.m^{-3}). Abondance relative de l'ensemble copépodien (barres blanches : mortes eaux; barres noires : vives eaux).

zones during spring tide, by the increase of chaetognatha, gastropod larvae, the copepod *E. acutifrons* and, at a lower level, by the increase of the representativeness of inner copepods (essentially *Acartia discaudata*) and *Paracalanus parvus*.

In summary, the winter is characterized by low abundances with copepods as the major component (Fig. 4). Summer is distinguished by an increase in number and diversity of the copepods. The transition between these two periods is characterized during springtime by an increase in the density of copepods, particularly the neritic species (*A. clausi*), and by a general decrease of abundances and greater importance of gastropod larvae, chaetognatha and copepods *E. acutifrons* in autumn. Copepods almost always represent more than 40 % of the total zooplanktonic community (Fig. 4) regardless of seasons.

In order to eliminate seasonal trends and to find accurate relationships between variables, each season was studied separately using PCA.

Seasonal studies

Only the variables with frequencies greater than 50 % during the considered periods are taken into account for each subgroup of observations. Others are grouped as described above. This new coding of variables is given in Table 3. In addition, only planes built from axes 1 and 2, having the greatest weighting, are considered. Although the weighting constituted by the plane 1-3 is greater than 30 %, the projection of values on this plane does not add any information.

Winter data set (Fig. 5)

· November

P. parvus, *E. acutifrons* and *A. discaudata* are the dominant species, particularly during neap tide and in the more outer stations (K1M, K6M and K3M). At a lower level, *T. longicornis*, oceanic copepods and neritic outer copepods (Tab. 2), trachyline medusae, gastropod larvae, chaetognatha and appendicularians are also representative. The close positions of GAS and the additional variable MER shows that gastropods constitute the most important group of meroplankton.

· December

The northern internal zone is characterized by gastropod larvae, chaetognatha, and appendicularians during spring

Table 3

Zooplankton of Marennes-Oléron Bay (1986). Additionnal coding and pooling used for principal component analysis made on seasonal values.

Zooplancton du bassin de Marennes-Oléron (1986). Regroupements et codages supplémentaires des variables utilisées dans les ACP saisonnières.

	VARIABLES	
Season	**Grouping**	**Coding**
Early spring (March, April)	PSE + CON	CNE
Late spring (May, June)	PSE + ONC + CON	POC
Summer (July, August, September)	PSE + CON	CNE

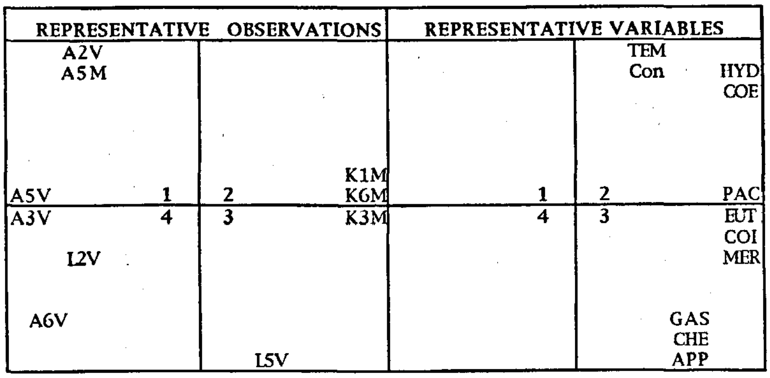

Figure 5

Principal component analysis made on zooplankton of Marennes-Oléron Bay (1986). Winter data set. Variables and observations considered well represented on the plane 1-2 (coding given in Tab. 2).

Analyse en composantes principales faite sur le zooplancton du bassin de Marennes-Oléron (1986). Données hivernales. Variables et observations bien représentées sur le plan 1-2 (codage donné dans le tab. 2).

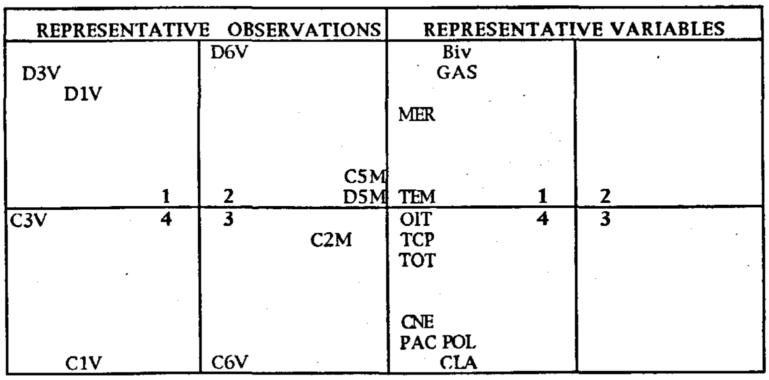

Figure 6

Principal component analysis made on zooplankton of Marennes-Oléron Bay (1986). Early spring data set. Variables and observations considered well represented on the plane 1-2 (coding given in Tab. 2 and 3).

Analyse en composantes principales faite sur le zooplancton du bassin de Marennes-Oléron (1986). Données de début de printemps. Variables et observations bien représentées sur le plan 1-2 (codage donné dans les tab. 2 et 3).

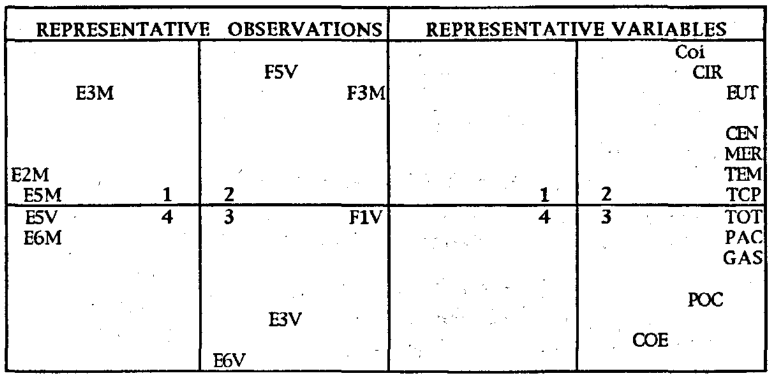

Figure 7

Principal component analysis made on zooplankton of Marennes-Oléron Bay (1986). Late spring data set. Variables and observations considered well represented on the plane 1-2 (coding given in Tab. 2 and 3).

Analyse en composantes principales faite sur le zooplancton du bassin de Marennes-Oléron (1986). Données de fin de printemps. Variables et observations bien représentées sur le plan 1-2 (codage donné dans les tab. 2 et 3).

tide (L5V). The importance of more neritic species (*T. longicornis*, outer neritic copepods, oceanic copepods and trachylines) decreases. The other internal station (Barat) is distinguished from the one above during spring tide (L2V) by decreases of the representation of all taxonomic groups. However, chaetognatha, appendicularians and gastropod larvae are still present.

· January

The outer station (Boyard) displays similar characteristics during spring tide (A6V) to those of the Barat station one month earlier (L2V). During spring tide, La Mouclière and Le Chapus (A5V, A3V) are distinguished by low representation of all the taxa. The internal zones (La Mouclière and Barat), are characterized by an increase of the importance of: *T. longicornis*, oceanic and outer neritic copepods and trachylines, respectively during neap tide and spring tide (A5M, A2V).

Early spring data set (Fig. 6)

· March

The intermediate zone (Le Chapus) is characterized by an entry of neritic species during spring tide (C3V): *T. longicornis*, *Oithona* spp. and, to a small extent, *P. parvus*, *A. clausi*, cladocerans and meroplanktonic organisms (polychaets, gastropods and bivalves). In the outer stations the same assemblages are found with exception of the two last groups. Internal areas during neap tide (C2M, C5M) feature a low representation of the neritic species cited above. Additional variables show high abundances of copepods, meroplankton and total zooplankton in the middle part of the bay during spring tide (C3V).

· April

The situation changes in Auger during spring tide (D1V) compared to the results of the previous month: meroplanktonic organisms (gastropods and bivalves) increase, and neritic taxa typical for March decrease. The representation of *T. longicornis* and *Oithona* spp. is similar. The contrast is clearer in the northern outer station during spring tide (D6V). It is characterized by gastropod and bivalve larvae and by a low representativeness of neritic groups cited above. The northern estuarine station during spring tide (D5M) presents the same characteristics as the internal zones during March at neap tide. Le Chapus station (D3V) is much characterized than in March by meroplanktonic taxa (bivalves and gastropods).

Late spring data set (Fig. 7)

- May

The intermediate zone during spring tide (E3V) is characterized by high abundances of copepods and total zooplankton. The most representative elements are oceanic copepods (*Labidocera wollastoni*, *Calanus helgolandicus*), *A. clausi* and to a lesser extent gastropod larvae, *P. parvus* and *T. longicornis*. The representation of some oceanic taxa (*L. wollastoni*, *C. helgolandicus*) increases, while the most internal species (cirripede larvae, *A. discaudata*, *C. hamatus* and *E. acutifrons*) decrease in the outer station Boyard during spring tide (E6V). Samples obtained from this station, from the two estuarine ones during neap tide (E6M, E2M, E5M) and from La Mouclière during spring tide (E5V) are characterized by lower densities of total zooplankton and lower representation of all the taxa mentioned above. The intermediate station during neap tide (E3M) is quite similar to the above ones. However, it is distinguished by an increase of *A. discaudata*, *C. hamatus*, *E. acutifrons* and cirripedes larvae.

- June

Zooplanktonic densities increase in all the characteristic stations. This is essentially due to higher densities of cirripede larvae, *A. grani*, *A. discaudata*, *C. hamatus* and *E. acutifrons* in the intermediate zone during neap tide (F3M) and in the northern estuarine area during spring tide (F5V). The outer zone of Auger during spring tide (F1V) is mostly characterized by *T. longicornis*, *P. parvus* and the decapod larvae.

Summer data set (Fig. 8)

- July

The outer station Boyard is distinguished by neritic zooplanktonic populations during spring tide (G6V): marine cladocerans (*Podon* sp.), *A. clausi* and *C. hamatus*.

- August

Neritic cladocerans, chaetognatha, *A. clausi*, *C. hamatus*, *E. acutifrons* and particularly *T. longicornis* are typical species for the station Le Chapus during spring tide (H3V). The northern neritic zone is characterized (H6M, H6V) by the decrease of neritic cladocerans, *A. clausi* and *C. hamatus*. *Temora longicornis* is represented in a relatively great quantity but chaetognatha and the copepod *E. acutifrons* constitute the most characteristic groups of these samples. In the estuarine zone of La Mouclière during neap tide (H5M), the importance of all taxa decreases with the exception of chaetognatha and *E. acutifrons*. This zone is therefore characterized during neap tide by several benthic species.

Table 4

Marennes-Oléron Bay (1986). Mean annual values of algal concentrations (data from the Laboratoire des Écosystèmes Conchylicoles, IFREMER, La Tremblade, pers. comm., mg chl a *+ eq. .m^{-3}) and daily grazing pressure rates of copepods on algal stock.*

Bassin de Marennes-Oléron (1986). Moyennes annuelles des concentrations algales (données du Laboratoire des Écosystèmes Conchylicoles, IFREMER, La Tremblade, comm. pers., mg chl *a* + eq. .m^{-3}), taux de pression de broutage des copépodes sur le stock algal.

STATIONS	DAILY GRAZING PRESSURE RATE (%)	ALGAL CONCENTRATION
Auger	1.87	9.38
Barat	0.92	8.64
La Chapus	2.64	13.22
La Mouclière	1.68	21.68
Boyard	2.70	11.51

- September

The estuarine areas (I2V, I5V) have the same characteristics during spring tide: taxa described above are represented to a small extent. However, chaetognatha, *E. acutifrons* and benthic species are more characteristic in the south than in La Mouclière.

Grazing pressure of copepods

The most important average annual values of daily grazing pressure of copepods on the algal stock are found in the neritic waters (Boyard and Le Chapus stations, Tab. 4). The use of models of ingestion established for a temperature of 19°C induces an overestimation of the grazing impact of copepods during winter, spring and autumn (lower temperatures). However the values obtained during the summer are quite good estimations. During this season, high values are sporadically noticed: 12.43, 12.10, 10.42 % respectivelly in Boyard, Le Chapus and Auger stations during neap tide in June (average temperature: 19.6°C) and 14.63 % in Le Chapus station during spring tide in August (18.0°C).

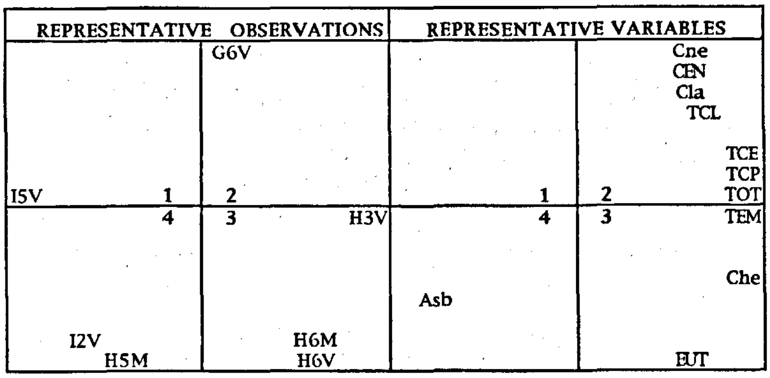

Figure 8

Principal component analysis made on zooplankton of Marennes-Oléron Bay (1986). Summer data set. Variables and observations considered well represented on the plane 1-2 (coding given in Tab. 2 and 3).

Analyse en composantes principales faite sur le zooplancton du bassin de Marennes-Oléron (1986). Données estivales. Variables et observations bien représentées sur le plan 1-2 (codage donné dans les tab. 2 et 3).

DISCUSSION

Characterisation of the zooplanktonic communities

The zooplankton of Marennes-Oléron Bay is, as in other similar ecosystems (d'Elbée, 1985; Lam Hoai *et al.*, 1985), quite diverse: 75 taxonomic groups were identified during this study. However, this diversity does not represent a functional or structural community, but is the result of a mixture of different water masses (Castel and Courties, 1982).

In some coastal environments water residence time allows the establishment of autochthonous communities. For example in Arcachon Bay, three zooplanktonic communities were clearly differentiated: an outer neritic one; an intermediate neritic one; and an inner neritic one (Castel and Courties, 1982). In Marennes-Oléron Bay the development of such groups is much less likely because of the complicated hydrology (Klingebiel *et al.*, 1971).

The results of the principal component analysis show the complex organization of zooplanktonic assemblages in the bay. Three areas are distinguished. An outer one which is characterized by stations of Boyard in the north and Auger in the south, a true estuarine one (La Mouclière) and an intermediate one which comprises the Le Chapus station and the internal southern part of the bay (Barat). The last station is located near the Seudre estuary but is under nearly continuous neritic influence due to the low continental inflow in this area (only 1/10 of total continental inflow to the bay: Héral *et al.*, 1983).

The taxa living in this ecosystem can be grouped in three distinct assemblages. An estuarine community with *Acartia bifilosa*, *Eurytemora hirundoides*, *Bosmina* sp., and *Mesopodopsis slabberi*, is particularly represented in winter. A neritic community with *P. parvus*, *T. longicornis*, *A. clausi*, *C. helgolandicus*, *Oithona* spp., *C. hamatus*, *Podon* sp., *Evadne* sp., appendicularians and chaetognatha, is found in the outer areas during spring and summer. An intermediate community characterized by: *A. discaudata*, *E. acutifrons*, and the whole meroplankton, is represented essentially during spring and summer.

Interpenetration of the zooplanktonic communities

The different zooplanktonic assemblages in the bay comprise of a mixing of these three ecological communities through stirring of water masses in the bay. Its overall character is essentially maintained by important oceanic inputs and interrupted by significant continental inflows. Oceanic inputs are made through the Pertuis de Maumusson in the south and the Pertuis d'Antioche in the north. Continental inflows are due to the Charente and the Seudre rivers. Their small estuaries respond rapidly to hydrological variations and do not produce important outflows of estuarine populations in the bay except during periods of high rainfall.

The juxtaposition of water masses of different origins is also revealed by biological indicators. In two lagoons of the Pô Delta, Ferrari *et al.* (1982 *a* and *b*) noted the importance of cirripede larvae in the lagoonal areas and a greater percentage of neritic copepods in the marine zones, when total zooplanktonic abundances reached highest values. This is also observed in Marennes-Oléron Bay in Auger and more clearly at Boyard station where neritic copepods dominate during spring tide. In the zone of La Mouclière, cirripedes are the dominant taxa during neap tide (40 and 42 % in June, 33 and 19 % in August). At Le Chapus and Barat their percentages are high during neap tide, whereas during spring tide the neritic copepods dominate.

Characterization of the copepod community

In areas of transition the development of copepod communities tends to a decrease of diversity and an increase of biomass from neritic to inner zones (Castel and Courties, 1979; 1982; Lam Hoai *et al.*, 1985; Madhupratap and Onbe, 1986). These characteristics were evident seasonally in Marennes-Oléron Bay (Fig. 9).

During winter, Marennes-Oléron is divided in two parts. In the northern zone (Boyard and La Mouclière) the biomass gradient increases from outside to inside, whereas the number of species decreases and the dominance increases, and as a result the equitability decreases (Fig. 9). In the southern area (Auger and Barat) the development is inverted: the lowest biomasses (since the species have low individual weights and low abundances) and the highest equitabilities (since the number of species increases because of the mixing of estuarine and neritic communities) are found

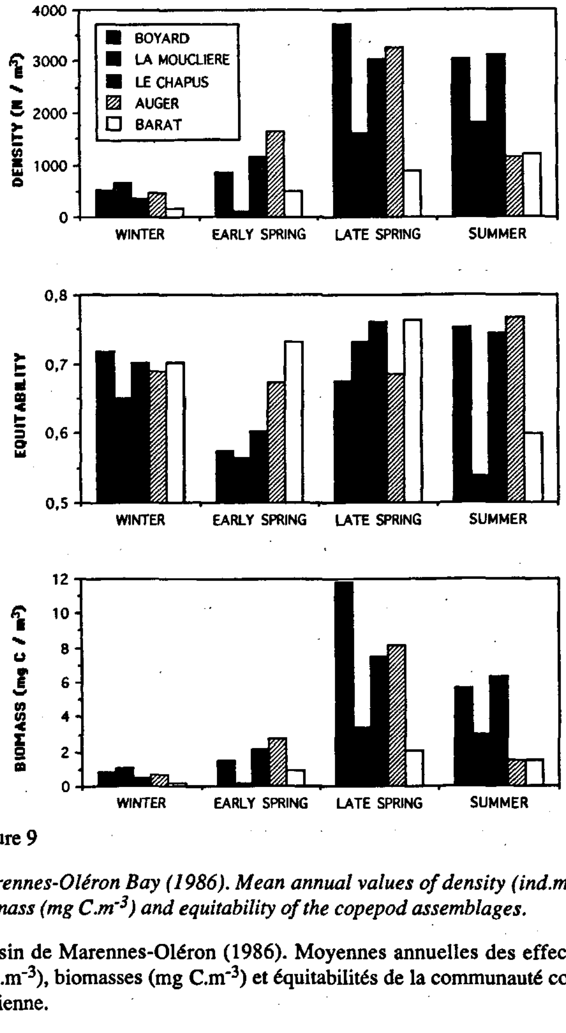

Figure 9

Marennes-Oléron Bay (1986). Mean annual values of density (ind.m^{-3}), biomass (mg C.m^{-3}) and equitability of the copepod assemblages.

Bassin de Marennes-Oléron (1986). Moyennes annuelles des effectifs (ind.m^{-3}), biomasses (mg C.m^{-3}) et équitabilités de la communauté copépodienne.

in the internal zone of Barat. This mixing of estuarine and neritic communities is also noticed during the following seasons, except in summer for Barat station.

At the beginning of spring (March and April) the high inflow of oceanic water leads to the appearance of neritic components in the bay. These are particularly diversified at the station Barat. However, *A. clausi* dominates in the other estuarine zone (92 % of the total copepod community) and provokes a high decrease of diversity. In addition, densities are very low in this area. Overall, water masses can be divided in two parts: in the north copepod assemblages are dominated by *T. longicornis* and *A. clausi*, and in the south communities are more diversified and the abundances of the species more equally distributed. During this period, the biomass gradient from oceanic to inner waters is not found either in the north or in the south. The diversity gradient is consistent in the northern part with observations mentioned in literature.

At the end of spring, the decrease in diversity and the increase of biomass from neritic to inner zones are not observed. The biomasses are more important in the outer stations where the densities are higher than in inner areas and where some larger copepods (*A. clausi*, *C. hamatus*, *T. longicornis* and *C. helgolandicus*) dominate which induces also a decrease of the equitability. In inner stations, the number of species increases because of the mixing of the estuarine and neritic communities and the larger copepods are less abundant than in outer zones : the biomass is lower and the equitability higher than in outer stations.

The summer tendencies are quite different from the above. Outer populations maintain a rather high equitability. Larger copepods (*T. longicornis*, *A. clausi*) are better represented in Boyard than in Auger, which explains the difference of biomass between both stations. In more internal areas, because of the clearer dominance of some species with smaller individual weights, diversity and biomass are lower : the diversity gradient is classical and the biomass gradient is inverted.

Comparisons with another ecosystem

The copepod community of Marennes-Oléron Bay can be compared with communities of similar ecosystems. This is done with data obtained from Arcachon Bay (Tab. 5).

In Arcachon Bay, copepod biomasses are almost always higher than Marennes-Oléron, particularly in internal water masses. Equitability values found in Arcachon Bay are similar to those calculated for Marennes-Oléron Bay in outer and intermediate zones; in the inner area the equitability of the copepod community is clearly lower in Arcachon. In the three similar situations studied, diversity is much higher in copepod communities of Marennes-Oléron. Thus the species richness is more important in Marennes-Oléron Bay than in Arcachon Bay but the distribution of organisms of the different species is quite similar in the two ecosystems. This can be explained by the geography of these two bays. Marennes-Oléron Bay is a really open system subjected to an important input of oceanic waters, which explains the high specific richness (due to the mixing of the different communities). Arcachon Bay is more closed and the inner stations are little influenced by oceanic water; the mixing of the different communities is less important and the characteristics of the inner stations are more pronounced than in Marennes-Oléron (lower equitability and higher biomass in Arcachon than in Marennes-Oléron).

Grazing pressure of the copepod community on algal standing stock (Tab. 4)

The important inflows of oceanic waters can be noted by calculating daily grazing pressure rates of copepods for the different stations of the bay. It is noticed that water masses streams in Marennes-Oléron Bay influence the grazing pressure of copepods on algal standing stocks. Classically, the daily grazing pressure rates are high (around 100 %) in neritic zones, whereas values obtained in more coastal areas are lower (Menzel and Ryther, 1961; Hargrave and Geen, 1970; Deason, 1980; Joiris *et al.*, 1982; Nicolajsen *et al.*, 1983; Baars and Fransz, 1984). These results are confirmed here. Furthermore, as this study was done on a limited geographical zone, a decreasing gradient of grazing pressure is shown from the oceanic to the estuarine zone. The pattern of grazing pressure is clearly related to the hydrology of the bay (Tesson, 1973):

- the entrance zone of marine waters in the bay is situated in the north, near Boyard where there is high grazing pressure;
- water masses head south along Oléron island, yielding important grazing pressure in the station Le Chapus (quite similar to the above);
- these water masses then move north and are mixed with estuarine ones, giving lower grazing impact of copepods at La Mouclière;
- the southern part of the bay is more characterized by the evacuation of water, so that the station Auger, near the oceanic zone, has little neritic influence and weaker grazing pressure than at Boyard although quite similar to those at La Mouclière;
- finally, the low grazing impact at Barat is due to its estuarine position, so that the lack of marine inputs leads

Table 5

Comparisons between similar areas of Arcachon Bay (Castel and Courties, 1982) and Marennes-Oléron Bay for biomass (mg C.m^{-3}), equitability, and diversity (Shannon index) of planktonic copepods. Average annual values. ARC: Arcachon Bay; MAR: Marennes-Oléron Bay (+ station).

Comparaisons entre des sites identiques des bassins d'Arcachon (Castel and Courties, 1982) et de Marennes-Oléron pour la biomasse (mg C.m^{-3}), l'équitabilité, et la diversité (indice de Shannon) des copépodes planctoniques. Moyennes annuelles. ARC : Arcachon; MAR : Marennes-Oléron (+ station).

	OUTER		INTERMEDIATE		INTERNAL	
STATIONS	**ARC**	**MAR6**	**ARC**	**MAR3**	**ARC**	**MAR5**
Biomass	3.90	4.73	7.11	4.55	36.36	2.15
Equitability	0.68	0.68	0.73	0.70	0.31	0.62
Diversity	1.51	2.13	1.57	2.25	0.58	1.84

to very low grazing pressure compared to those in the northern part.

Although daily grazing pressure rates vary within the Bay, it should be noted that these values match the lowest found in other ecosystems. Overall, it should be stressed that copepods have only a low influence on algal stock (note that grazing pressure is here calculated on algal stock, without taking into account primary production), which leaves a more-or-less important amount to their trophic competitors.

In conclusion, Marennes-Oléron Bay presents characteristics that are typical of littoral ecosystems. However, it differs due to its large opening towards the ocean, which induces important inputs of oceanic waters in the bay. As a result, the average rates of grazing pressure of planktonic copepods on the algal stock are similar in outer sites (Boyard) and in internal zones (Le Chapus). These pressure rates are calculated for the copepod community which represents on average more than 57 % of the zooplankton community in each station. According to these low rates, the grazing pressure of the whole mesozooplanktonic community will be also very low, and the most important part of the algal stock of Marennes-Oléron is either eaten by microzooplankton, benthic organisms or washed out of the bay.

Acknowledgements

Thanks are due to M. Héral for his help and to the whole staff of the Laboratoire des écosystèmes conchylicoles, IFREMER of La Tremblade (France) for their assistance. This investigation was financially supported by IFREMER. We are indebted to C. Jackel and to an anonymous reviewer for the revision of the English language.

REFERENCES

Allan J.D., T.G. Kinsey and J.C. James (1976). Abundances and production of copepods in the Rhode river subestuary of Chesapeake Bay. *Chesapeake Sci.*, **17**, 86-92.

Anonymous (1975). Études des phénomènes hydrauliques régissant le bassin ostréicole de Marennes-Oléron. Essai sur modèle réduit. Rapport général. Laboratoire Central d'Hydraulique de France. Direction Départementale de l'Équipement de la Charente Maritime.

Baars M.A. and H.G. Fransz (1984). Grazing pressure of copepods on the phytoplankton stock of the central North Sea. *Neth. J. Sea Res.*, **18**, 120-142.

Castel J. and C. Courties (1979). Structure et importance des peuplements zooplanctoniques dans la baie d'Arcachon: milieux ouverts et lagunes aménagées de Certes. Publications scientifiques et techniques, Centre National pour l'Exploitation des Océans, Actes de Colloques, 7, 559-574.

Castel J. and C. Courties (1982). Composition and differential distribution of zooplankton in Arcachon Bay. *J. Plankton Res.*, **4**, 417-433.

Deason E.E. (1980). Grazing of *Acartia hudsonica* on *Skeletonema costatum* in Narragansett Bay (USA): influence of food concentration and temperature. *Mar. Biol.*, **60**, 101-113.

d'Elbée J. (1985). Écologie et évolution structurelle des peuplements zooplanctoniques du bassin d'Arcachon; interactions avec l'Océan Atlantique. *Thèse 3ème cycle, Université Bordeaux I, France*, 124 pp.

Ferrari I., V.W. Ceccherelli and M.G. Mazzocchi (1982 *a*). Structure du zooplancton dans deux lagunes du delta du Pô. *Actes Symposium international sur les lagunes côtières, Bordeaux, 8-14 septembre 1981, Oceanologica Acta*, No. sp., 293-302.

Ferrari I., V.W Ceccherelli., M.G. Mazzocchi and M.T. Cantarelli (1982 *b*). Seasonal and diel variations of zooplankton populations in a lagoon of the Po river delta. *Neth. J. Sea Res.*, **16**, 333-344.

Feurtet A. (1989). Dynamique de population, caractérisation morphologique et production secondaire d'*Eurytemora affinis hirundoides* (copépode calanoïde) dans l'estuaire de la Gironde. *Thèse de Doctorat, Université Bordeaux I, France*, 169 pp.

Fransz H.G., J.C. Micquel and S.R. Gonzalez (1984). Mesozooplankton composition, biomass and vertical distribution, and copepod production in the stratified central North Sea. *Neth. J. Sea Res.*, **18**, 82-96.

Fraser J.H. (1966). Zooplankton sampling. *Nature*, **211**, 915-916.

Gerlach S.A. (1978). Food chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. *Oecologia (Berl.)*, **33**, 55-59.

Hargrave B.T. and G.H. Geen (1970). Effects of Copepod grazing on two natural phytoplankton populations. *J. Fish. Res. Bd Can.*, **27**, 8, 1395-1403.

Héral M., D Razet., J.-M. Deslous-Paoli, J.-P. Berthomé and J. Garnier (1983). Caractéristiques saisonnières de l'hydrobiologie du complexe estuarien de Marennes-Oléron (France). *Revue Trav. Inst. Pêches marit.*, **46**, 97-119.

Héral M., C. Bacher and J.-M. Deslous-Paoli (1989). La capacité biotique des bassins ostréicoles. in: *L'homme et les ressources halieutiques.* IFREMER Ed., 225-259.

Joiris C., G. Billen, C. Lancelot, M.H. Daro, J. P Mommaerts, A. Bertels, M. Bossicart, J. Nijs and J.H. Hecq (1982). A budget of carbon cycling in the belgian coastal zone: relative roles of zooplankton, bacterioplankton and benthos in the utilization of primary production. *Neth. J. Sea Res.*, **16**, 216-275.

Klingebiel A., A. de Rességuier and M. Tesson (1971). Contributions à l'étude de la circulation des masses d'eau dans le bassin de Marennes-Oléron. *C.r. Acad. Sci., Paris*, **273**, 1783-1786.

Kuhlmann D., O. Fukuhara and H. Rosenthal (1982). Shrinkage and weight loss of marine fish food organisms preserved in formalin. *Bull. Nansei Reg. Fish Res. Lab.*, **14**, 13-18.

Lam Hoai T., M. Amanieu and G. Lasserre (1985). Communautés du zooplancton superficiel de trois sites différemment éloignés de l'entrée des eaux marines de l'étang de Thau. *Cah. Biol. mar.*, **26**, 445-467.

Madhutratap M. and T. Onbe (1986). Structure and species diversity of the zooplankton community of the Inland Sea of Japan. *Estuar. coast. Shelf Sci.*, **23**, 725-737.

Menzel D.W. and J.H. Ryther (1961). Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production. *J. Cons. int. Explor. Mer*, **26**, 250-258.

Nicolajsen H., F. Mohlenberg and T. Kiorboe (1983). Algal grazing by the planktonic copepods *Centropages hamatus* and *Pseudocalanus* sp.: diurnal and seasonal variation during the spring phytoplankton bloom in the Oresund. *Ophelia*, **22**, 15-31.

Parsons T.R., M. Takahashi and B. Hargrave (1977). *Biological oceanographic processes. 2nd ed.* Pergamon Press, Oxford, UK, 332 pp.

Piélou E.C. (1969). *An introduction to mathematical ecology*. John Wiley & sons, New-York, USA, 286 pp.

Sautour B. (1991). Populations zooplanctoniques dans le bassin de Marennes-Oléron; dynamique de population, nutrition et production des copépodes dominants. *Thèse de Doctorat, Université Bordeaux I, France*, 283 pp.

Shannon C.E. and W. Weaver (1948-1963). *The mathematical theory of communication.* Urbana University Press, Illinois, USA, 117-127.

Simard Y., G. Lacroix and L. Legendre (1985). *In situ* twilight grazing rhythm during diel vertical migrations of a scattering layer of *Calanus finmarchicus*. *Limnol. Oceanogr.*, **30**, 598-606.

Tesson M. (1973). Aspects dynamiques de la sédimentation dans la baie de Marennes-Oléron. *Thèse de 3ème cycle, Université Bordeaux I, France*, 128 pp.