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II

Aspects of the zoogeography of the Mediterranean plankton

Introduction—Regional zoogeography—Western Basin—Adriatic Sea—Eastern Basin—Black Sea and its relations with the Mediterranean—Variation in the Mediterranean, source of diversity—Polymorphism and polytypism—Differentiation of physiological races—Regions favourable to variation—Place of the Mediterranean in the Atlanto-Mediterranean Province—Components of Mediterranean planktonic fauna—Mediterranean Region

Introduction

To speak of zoogeography in connection with plankton may seem odd. Is it possible that its components, notwithstanding their floating character and in spite of the fact that they belong to a moving world, have a characteristic distribution, especially in an almost isolated, relatively small area as is the Mediterranean? We shall see that the answer to this question can be positive. We shall show, in fact, the existence of real planktonic units, subordinate to hydrological barriers, and the effect of marine circulation which ensures faunistic exchanges between adjacent areas, sometimes resulting in variation of the species transported.

In spite of the quantitative poverty, known to exist at least in some zones, the variety of the Mediterranean plankton is great. This is due to the mixing of a limited number of autochthonous forms with Atlantic taxa, some from the north and others—more numerous—from the subtropics. The position of the Strait of Gibraltar at a latitude which grossly separates the subtropical and the temperate-cold ensembles, is the main cause of this mixing. The Mediterranean received the essential part of its population from the nearby ocean during the Post Glacial, but the passage of organisms via Gibraltar has continued ever since. Once introduced into the Mediterranean, these organisms, both from northern and southern origins, find themselves influenced by the local typical conditions. There they evolve in various ways, becoming adapted and developing, if they do not disappear more or less rapidly. But, though preponderant, the contribution of species from the Atlantic is not the only one the Mediterranean receives. There are others, distinctly tropical, coming from the Red Sea via Suez, and some from the Black Sea, a former Pontic cold sea, via the Bosporus and the Dardanelles.

The diversity of the Mediterranean plankton makes it impossible to consider all its aspects. Only some groups, characteristic and well studied: Chaetognatha, Copepoda, Euphausiacea, Pteropoda, pelagic Decapoda, Appendicularia, will be chosen for the analysis of the most prominent zoogeographic phenomena, for measuring their complexity and trying to deduce certain rules.

As the knowledge of this planktonic fauna grows, the inventory of its components gets more complete. Thus, the Copepoda, estimated at 209 species in 1948, at 260 in 1967, number more than 300 at present. In the same way, the list of Atlantic organisms considered up to now absent from the Mediterranean is diminishing: many of them have recently been recorded for the first time and also a large number of new species have been described. Are these latter endemic? It is too early to say. Nevertheless, we will take these various elements into account.

A new aspect of faunistics will have our attention: the distinction of Mediterranean subspecies in various animal groups, which is at present founded on highly precise methods. In this way, our study, though not complete, will render an account of both newly acquired data on this Mediterranean fauna, and also of the development of the concepts concerning its origin and dispersal. After a regional analysis of its distribution and the influences which control it, we will examine the repercussions of the species variation on the Mediterranean diversity and finally we will see how the planktonic fauna determines the position of the 'Mer Intérieure' within the great Atlanto-Mediterranean Province.

The term 'diversity' will be used in the sense of variety or species richness. For the ecological data we will use the 'index of diversity' which expresses the relative abundance of the species in an eco-system or an area. In order to lighten the text, many records of species have been brought together in tables I to IX on pages 194, 206, 212, 223, 241, and 249.

Regional zoogeography—determinant influences

The Mediterranean region is directly related to the Ibero-Moroccan one and forms part of the Atlanto-Mediterranean Province (cf. p. 251). The Mediterranean is situated between 30° and 44°N, except for the Adriatic Sea which reaches to 46°N. Traditionally it is divided into the Western and Eastern Basins, which in their turn are subdivided into several districts subject to their own climates, hydrological conditions and to various additional influences. In general, authors adopt the boundaries fixed for these areas by Schmidt (1912) making slight alterations (Fig. 1). Our purpose is to show the faunistic individuality of some of these geographic entities and to underline the cause of this individuality.

Western Basin—Atlantic and eastern influences

The characters typical of the areas which constitute this basin are for a great part the result of the more or less intense oceanic influence which determines in particular abundance and variety of the plankton (Tab. I, V-VII). Sometimes, though, there is also an influence of the waters coming from the E. Mediterranean. Therefore we will follow the Atlantic Current, first along its major branch (Alboran Sea, N. African coast) and afterwards along its ramifications in the Central Area, the Ligurian Sea, the Gulf of Lion and in the Catalunian Sea, to finish with the Tyrrhenian Sea, the transitional zone between the two basins. The hydrological conditions in each area will merely be evoked, according to the authors which have been consulted (Allain, 1966; Allain & Furnestin, 1969; J. Furnestin, 1960; Furnestin & Allain, 1962a, b; Gostan, 1967; Lacombe et al.,

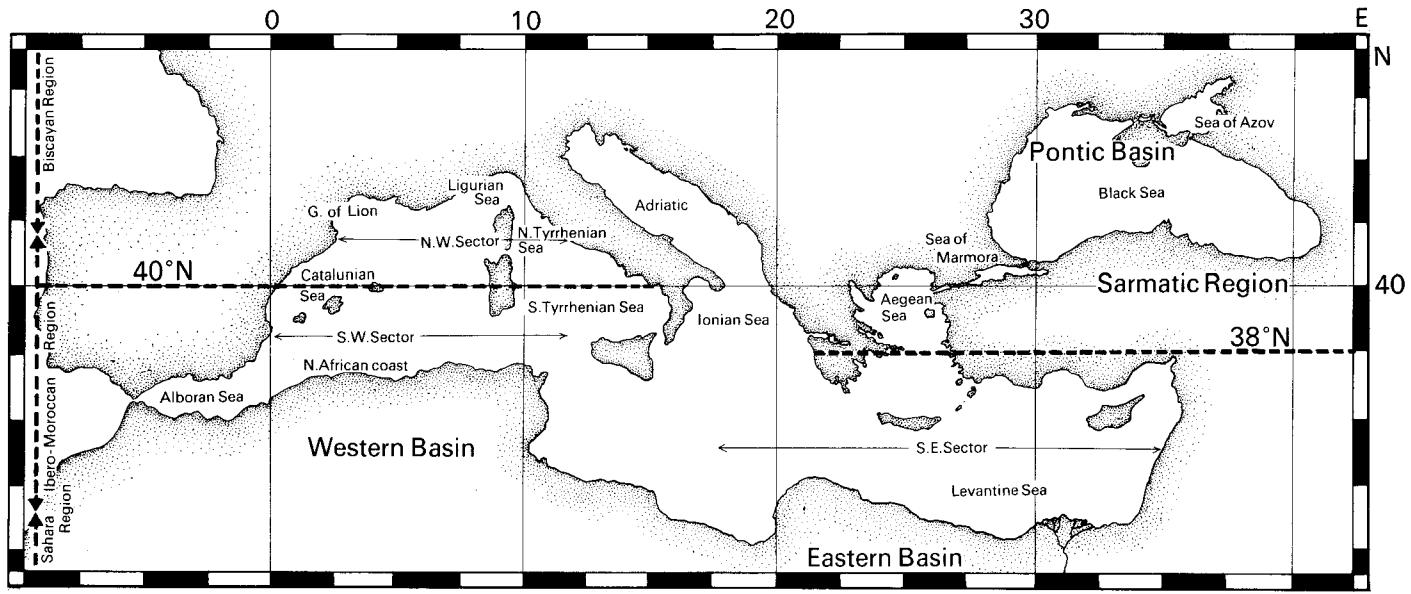


Fig. 1. The Mediterranean Region, its basins and relations with the Pontic Basin (Sarmatic Region).

Table I. West Mediterranean fauna elements not mentioned in the text

abbreviations used:

A = abundant	N = neritic
Ai = Atlantic indicator	Na = N.Adriatic
B = meso- bathypelagic/deep living	O = oceanic
Bl = also found in the Black Sea	Od = off Dubrovnik
C = common	P = present
Ct = constant	R = rare
D = dominant	S = surface/subsurface
DY = dominant throughout the year	Sa = S.Adriatic
Ei = indicator of Eastern Waters	Si = indicator of southern and central waters
En = endemic	T = seasonally/occasionally
Ep = epipelagic	V = Villefranche/Mer
Er = Eritrean influence	WB = W.Basin
Ex = exceptional	X = newly described
gC = Gulf of Gabès	X' = newly recorded
gT = Gulf of Trieste	X" = description completed
M = mesopelagic	? = with reserve
Ma = middle Adriatic	

Alboran Sea

COPEPODA

Pontellopsis regalis, Pontellina plumata, Macrosetella oculata, Lubbockia aculeata, Calanus (= Neocalanus) robustior: S,Ai; Calocalanus styliremis: Ai?; Eucalanus crassus, E.subcrassus, E.pileatus: M-B,Ai (Mazza, 1967); Rhincalanus cornutus, Scolecithricella abyssalis: WB,B,Ai; Gaetanus minor, Pleuromamma xiphias, P.borealis, P. robusta, Augaptitus longicaudatus, Vettoria granulosa, Oncaea conifera, O.dentipes: B,Ai (Vives et al., 1975); Oncaea furnestini: X (Shmeleva, 1978).

South West Area

COPEPODA

Temora longicornis, Corycaeus laetus, Candacia bipinnata (Rose, 1930; Bernard, 1955), Calanoides carinatus (Seguin, 1973): Ai; Vettoria longifurca, V.parva, Pontocilla abyssicola: T; Aegisthus dubius: T? (Rose et al., 1952; Soenen, 1969); Spinocalanus heterocaudatus, Scolecithricella subvittata, Drepanopsis lyra, Amallothrix farrani, A.sarsi (Rose, 1937, 1942), Calocalanus pseudocontractus, Ischnocalanus (Calanocalanus) equalicauda: X (Bernard, 1958a, 1963).

TINTINNIDAE

Favella azorica: Ai (Vitiello, 1964).

Central Area

COPEPODA

Clausocalanus arcuicornis, C.furcatus, Oithona helgolandica: O; Centropages typicus: N; C.bradyi: Ai,R; Temora stylifera, Acartia clausi: R,N; Neocalanus gracilis, Lucicutia flavigornis, Euchaeta acuta, Eucalanus monachus: A,0-500m; Monacilla typica: B,Ei; Gaetanus kruppi, L.longiserrata: B; Augaptitus megalurus: X',R,B,300-600m; Parapontella brevicornis, Pontella atlantica: Ai,R; Aetideopsis multiserrata: ?,X',R, 700-1000m (Soenen, 1969).

Liguro-Provençal Region (especially Villefranche)

COPEPODA

Pontellina plumata: Ai; Parapontella brevicornis, Paracalanus aculeatus: Ai,?; Clausocalanus lividus, C.jobei: X' (Carli & Crisafi, 1969); Mimocalanus distingocephalus, Spinocalanus spinosus: X' (Medit.) (Boucher et al., 1973); Euatideus giesbrechti, Chiridius poppei, Oithona setigera: X',R,WB (Falconetti et al., 1978).

AMPHIPODA

Bougisia ornata: B?,X,V (Laval, 1966)

table I continued

SCYPHOMEDEUSAE

Atolla wyvillei: X',? (Macquart-Moulin et al., 1968).

HYDROMEDUSAE

(68 spec.) *Paragotoea bathybia*, *Amphinema rubrum*, *A.turrida*, *Halitiara formosa*, *Octotriara violacea* (= *O.russelli*), *Calycopsis simplex*, *Krampella dubia*, *Amphogona pusilla*: X', V (Goy, 1972); *Haliscera bigelowi*: X' (Casanova, 1970); *Tregoubovia atentaculata*: X, V, B; *Merga tregoubovii*: X, V (Picard, 1958a, 1960).

SIPHONOPHORA

Cordagalma cordiformis, *Lilyopsis rosea*: V, X"; *Sphaeronectes gamulini*, *S.fragilis*, *S.bougisi*, *Prayola tottoni*, *Rosacea villafrancae*: X, En,? (Carré, 1968a, b, 1969a, b, c).

APPENDICULARIA

(32 spec.) *Appendicularia tregouboffi*, *Fritillaria fagei*: X, V (Fenau, 1960, 1961, 1963).

Gulf of Lion

COPEPODA

Temora stylifera, *Acartia clausi*, *Paracalanus parvus*, *P.pygmaeus*, *Ctenocalanus vanus*, *Labidocera wollastoni*, *Euterpinia acutifrons*, *Tharybis macrophtalma*, *Sapphirina nigromaculata*: N; *Clausocalanus furcatus*, *C.arcuicornis*, *Oithona nana*, *O.helgolandica*: O.

AMPHIPODA

Ampelisca serraticaudata, *A.spinimana*, *Cheirotrochus sundvalli*, *Megamphopus longicornis*, *Phtisica marina*.

MYSIDACEA

Hemimysis speluncola (Ledoyer, 1963; Macquart-Moulin & Patriti, 1966), *Leptomysis pereyi*, *L.burgii*, *L.banyulensis*: X, N (Bacescu, 1966a).

MEDUSAE

Hydromedusae: *Sarsia gemmifera*, *Podocoryna carnea*, *Rathkeia octopunctata*, *Phialidium* sp.: N; *Persa incolorata*, *Solmundella bitentaculata*, *Solmaris leucostyla*: O; *Solmissus albescens*: B; *Haliscera bigelowi*: B, X' (Razouls, 1971); Scyphomedusae: *Nausithoe punctata*, *Pelagia noctiluca*: O.

SIPHONOPHORA

Lensia meteori: N; *L.conoidea*, *Eudoxoides spiralis*, *Chelophyes appendiculata*, *Sulcularia quadrigivalvis*, *S.chuni*, *Abylopsis tetragona*: O; *Bassia bassensis*, *A.eschscholtzii*: B, O; *Clausophyes massiliiana*: B, X.

TUNICATA

Doliolum nationalis: N; *D.denticulatum*: R, O; *Thalia democratica*, *Salpa fusiformis*: O; *Pyrosoma atlanticum*: B.

POLYCHAETA

Pelagobius longicirrata, *Phalacrotophorus pictus*, *Callizona setosa*: N, X' (Braud, 1966).

Catalunian Sea

COPEPODA

(>100 spec. recorded) *Centropages typicus*, *Temora stylifera*, *Clausocalanus arcuicornis*, *Nannocalanus minor*, *Paracalanus parvus*, *Corycaeus ovalis*: D; *Calanus helgolandicus*, *Euchaeta acuta*, *Acartia negligens*, *Oithona nana*, *Microsetella norvegica*: P; *Heterorhabdus abyssalis*, *Sapphirina scarlata*, *Pleuromamma xiphias*: Ex; *P.piseki*: X' (Furnestin et al., 1963).

Castellon: *Heterorhabdus papilliger*, *H.spinifrons*, *Aetideus armatus*, *Scolecithricella dentata*, *Lucicutia flavidornis*, *Lubbockia squillimana*: B.

North Tyrrhenian Sea

COPEPODA

Temora stylifera, *Clausocalanus arcuicornis*, *C.furcatus*, *Nannocalanus minor*: D; *Neocalanus gracilis*, *Pleuromamma abdominalis*, *P.gracilis*, *Euchaeta acuta*: A, B; *E.media*, *Eucalanus monachus*: R, Ei (Mazza, 1963, 1967).

South Tyrrhenian Sea

COPEPODA

(115 spec. recorded) [dominating species in: *Clausocalanus*, *Paracalanus*, *Oithona*, *Oncaea*, *Microsetella*, *Corycaeus* (Della Croce, 1963)]; *Monacilla typica*, *Euchaeta hebes*,

table I continued

Euchaeta media, Mormonilla minor, Oncaea ornata, Spinocalanus abyssalis (Mazza, 1967), Haloptilus longicornis, H. mucronatus, Candacia tenuimana, Ratania flava (Vives, 1967), Spinocalanus abyssalis = S. paraoligospinosus: M, Ei; Eucalanus monachus: B, D (Huré et al., 1968a, 1969); [X': 20 spec. (Vives, 1967)]; Disco marinus: X (Gordejeva, 1974).
AMPHIPODA
Tetrathyrsus forcipatus: Ei (Stephensen, 1925; Vives, 1968).
MYSIDACEA
Europia grimaldii: X' (Medit.)? (Vives, 1968).
MEDUSAE
(14 spec.) Rhysomedusa pomponina: X (Vannucci & Moreira, 1966).
SIPHONOPHORA
(14 spec.) Rosacea plicata, Lensia fowleri, L. multicristata: X' (Kinzer, 1965).
TUNICATA
(21 Appendicularia-Naples and 27-Messina) Fritillaria drygalskii: X' (Medit.) (Bückmann, 1967).
ACANTHARIA
many newly recorded species (Schreiber, 1967; Botazzi-Massera et al., 1972).

1960, 1964; Le Floch, 1963; Miller et al., 1970; Nielsen, 1912; Tchernia, 1958; Trott, 1953), and will also be shown in some figures.

Alboran Sea

The Alboran Sea forms a transitional zone between the Atlantic and the Mediterranean; at the surface and in subsurface layers (to about 100 m) it shows hydrological characteristics analogous to those of the nearby Atlantic like a salinity below 36.5‰S. An important inflow from the ocean penetrates via the Strait of Gibraltar and spreads over the whole Alboran Basin, though preponderantly in the southern part; the northern part, an area of divergences, is occupied by more saline waters. The deeper strata are of Mediterranean origin with high temperature ($> 13^{\circ}\text{C}$) and high salinity ($> 38\text{‰S}$); here the northern waters prevail over the strongly altered eastern waters; these waterlayers flow out of the Mediterranean forming the Lusitanian Current (Fig. 2).

A striking characteristic of the Alboran plankton is its diversity, due to the hydrology and topography of the basin. On the one hand, owing to the presence of typically Atlantic water, there can subsist species which get more and more scarce towards the east and in the end disappear altogether. On the other hand, this deep and narrow channel permits the coexistence of neritic and oceanic species. This diversity has for example been demonstrated for Copepoda for which up to 46 species have been identified in some samples (Giron, 1963). The index of diversity (Vives et al., 1975) gives maxima of 2.14 at the surface and 3.24 for vertical hauls between 200-0 meter (against only 1.46 and 2.87 in the Ibero-Moroccan Basin under the same conditions). Nevertheless, oceanic forms are in the majority, even near the continent: more than 20 meso- or bathyplanktonic species have been counted and some 50 epiplanktonic species against less than 10 neritic ones. These latter are not very abundant with the exception of *Temora stylifera* and *Acartia clausi* which sometimes develop extensively.

All (13) Euphausiacea species known in the Mediterranean are mentioned; *Thysanoessa gregaria* is typical of this area. Although the Atlantic indicator-chaetognaths are all present among the 12 species enumerated, the aspect is already Mediterranean because of the prevailing of *Sagitta enflata*.

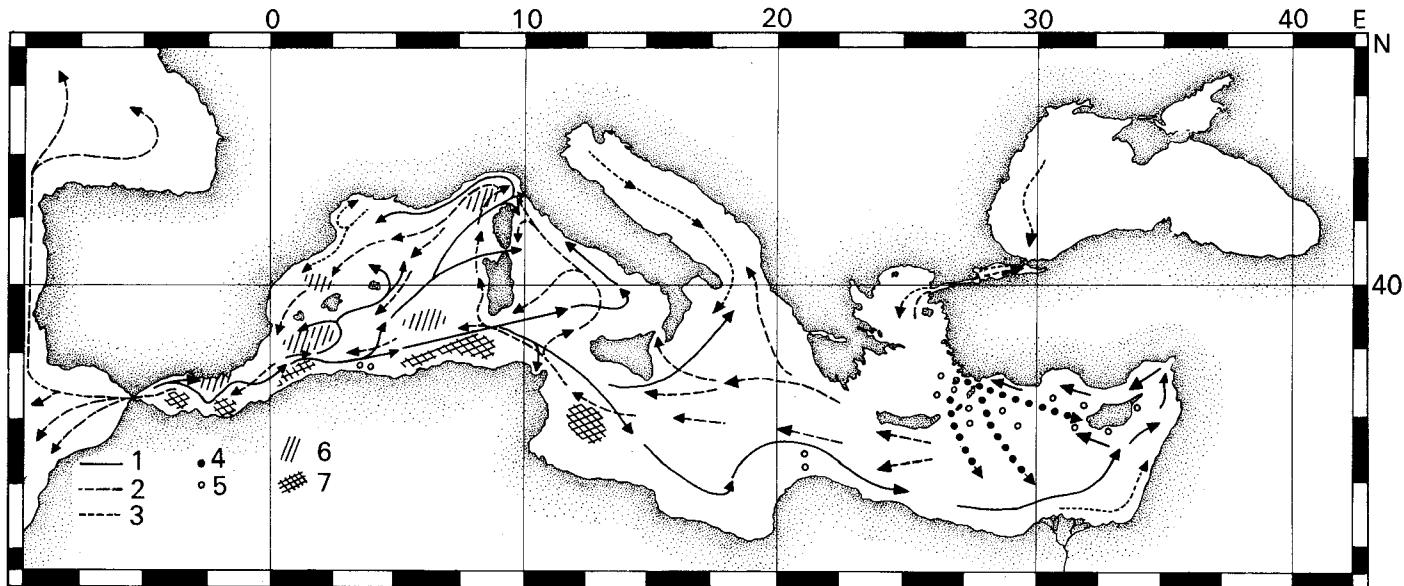


Fig. 2. General direction of major currents without taking into account the seasonal fluctuations. 1 = Surface currents of Atlantic origin, 2 = Intermediate Eastern Waters running to Black Sea and Western Basin, deep northern water flowing to the south of the Western Basin and Lusinian Current W. of Gibraltar, 3=diluted waters (Rhône Outflow, Countercurrent of Languedoc, Current of N. Adriatic Water, Nile Outflow, surface outflow of Black Sea), 4=eastern deepflow, 5=downwellings, 6=zone of divergences, 7=areas of accumulation of Atlantic Water.

Twenty-one species of pelagic Mollusca have been recorded; preponderant are the Thecosomata common in the S.W. Mediterranean, of which the Alboran Sea shows the principal climatic characteristics. The low abundance of *Hyalocylis striata*, decreasing from the E. Mediterranean westwards gives evidence of a very reduced deep oriental influence. The extreme abundance of *Limacina trochiformis* and the presence of *Cuvierina columnella* and *Diacria quadridentata* show the warm water character of the Alboran area (Rampal, 1975).

As a Mediterranean 'vestibule' the Alboran Sea strikes us because of the frequency of species of Atlantic origin. The transport of these species marks the actual flow in the water into the Mediterranean and they have the quality of hydrological indicators. When the migrants do not confine themselves to the Alboran Sea, they get more scarce as one crosses the boundaries of this sea eastward. By tracing these species it has not only been tried to estimate the importance of the Atlantic inflows and to determine seasonal maxima, but also to follow their courses and to note the most remote areas where Atlantic influence is manifest: an excellent example of the use of plankton as a hydrological indicator.

Thus there are 4 characteristic species for Chaetognatha (Fig. 3), 1 for Euphausiacea and 5 for Pteropoda (see Tables). The record of *Cymbulia parvidentata* in the Alboran Sea also gives evidence of transport from the nearby ocean (Vives

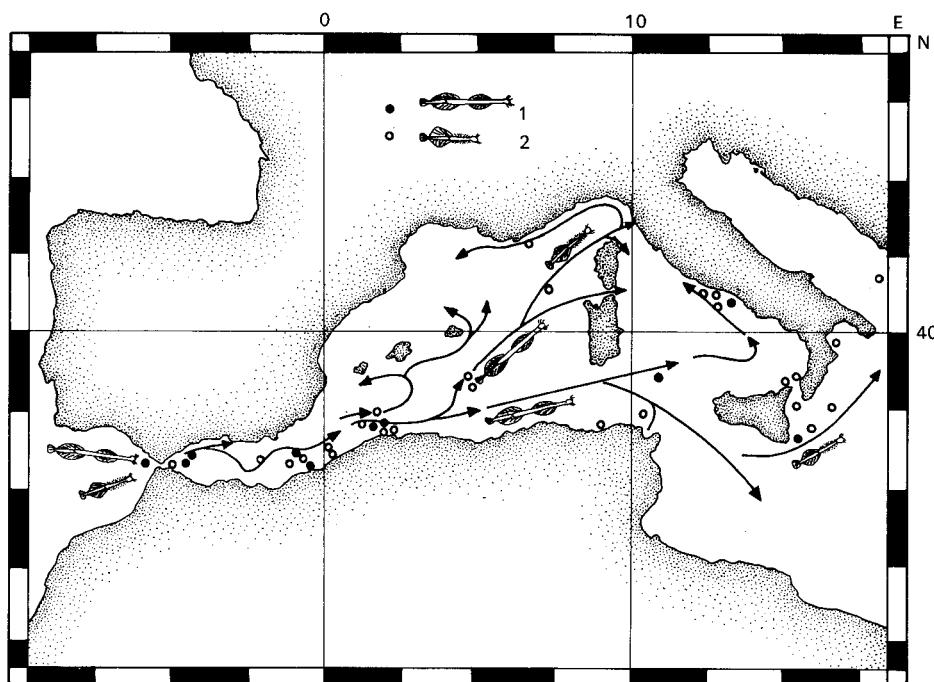


Fig. 3. Tracks of planktonic organisms marking the Atlantic influence and localities of two Chaetognatha marking the Atlantic Current. 1 = *Sagitta friderici*, 2 = *Pterosagitta draco*.

et al., 1975). Among Copepoda, besides the various surface and subsurface forms, one considers Atlantic indicators the deep living species with diurnal migration up to layers as shallow as 50 m: this enables them to cross the sill of Gibraltar (Group C of Vives et al., 1975), but also other meso-bathypelagic Copepoda are taken to be indicators (Tab. I).

The whole part of the Alboran Sea covered by almost purely Atlantic water is of a richness comparable with that of the Ibero-Moroccan Bay, and, at least at some periods of the year, much richer than the waters which cover the rest of the W. Mediterranean. The surface-samples are particularly rich, especially in Copepoda, because of the swarming of some species like *Clausocalanus arcuicornis*, *Temora stylifera* and above all *Paracalanus parvus* which characterises the fauna of the area during summer.

There is a great faunistic similarity between the nearby Atlantic and the Alboran Sea, but this uniformity is not absolute. Several species present W. of Gibraltar have not been observed on the east side. Besides, there are differences in the relative abundance of the species, some being more important in the ocean and others in the Alboran Sea. The differences are accentuated in the depth where the latter is more typically Mediterranean. Finally, being a frontier zone with hydrological characteristics of both Atlantic and Mediterranean, the Alboran Sea constitutes a complex environment favouring high diversity but nevertheless forming a barrier to several elements from either Atlantic or Mediterranean origin.

South-West area, along N. African coast and S. of the Baleares

The N. African coast, with a topography and hydrology resembling those of the Alboran Sea, shows a certain faunistic affinity with the latter. Thus the Algerian coast has a markedly pelagic character, because of the relative narrowness of the continental shelf; it shows also a strong Atlantic influence. Here the Atlantic Current first spreads and afterwards passes along the Tunisian shores, while in the open sea the deep Eastern Current proceeds to the west (Fig. 2).

For a long time stress has been laid on the Atlantic affinities of plankton of the Bay of Algiers, characterized by the presence of numerous subtropical elements and Atlantic indicators (see Tables). In this bay, open to inflows from the open sea, 17 Appendicularia have been identified (Bernard, 1958b) and a rich meroplankton, among which the larvae of numerous Crustacea and Decapoda (Seridji, 1970). The warm period in this area is marked by the development of the Copepoda *Clausocalanus arcuicornis*, Corycaeidae, Centropagidae, Sapphirinidae, and the warming up of the water is also favourable to *Paracalanus parvus*; the cold period is characterised by the upward migration, favoured by the winter homothermy, of deep-living species among the Eucalanidae and Rhincalanidae (Seguin, 1973). Among Copepoda, species very scarcely found in the W. Mediterranean have been several times recorded offshore the Algerian coast and numerous new species have been described (Tab. I).

When we follow the Algero-Tunisian shores we come again across Chaetognatha of Atlantic origin. The richness of the taxon is extreme and its variety great with 13 species. With respect to the Alboran Sea, *Sagitta enflata* maintains its dominance and *S. lyra* is still abundant but *S. bipunctata*, in the minority so far, gets

more important. The percentages of *S. hexaptera* and *S. neodecipients* are decreasing whereas those of *S. minima* and *S. serratodentata* are on the increase. *S. megalophthalma* has been noticed off the Tunisian coast.

The diversity of Thecosomata, 23 species in the whole S.W. area, surpasses that of the Alboran Sea. The Atlantic indicators are not numerous but the oceanic nature of the area is favourable to more bathypelagic species. The prevalence of thermophilous species underlines the subtropical tendency of the area. A relative frequency of *Hyaloclysis striata*, on the other hand, reveals an eastern influence (Rampal, 1975).

Of the Euphausiacea (13 species) the temperate forms are still dominating. Nevertheless, species with warm affinities become more important, whereas cold species form a minority. Two species point out, respectively, the Atlantic and eastern influences.

The area S. of the Baleares is practically entirely covered with water from the Atlantic which crosses this region along a SW-NE axis. The deep layers are the domain of northern water entering through the Ibiza Channel and of eastern water which follows its general E-W direction but which is brought to the surface owing to an important divergence. Thus, in this area we come across species originating from the Atlantic on the one hand (*Chaetognatha*, *Pteropoda*) and on the other hand across meso- or bathyplanktonic species, such as the Thecosomata *Peraclis bispinosa* and *Diacia quadridentata*, brought to the surface at places where the upward flow is strong.

Central Area of the Western Basin

In the area between the Baleares and Sardinia the vertical distribution of the water masses is as follows: at the surface a decreased influence is found of the Atlantic Current, a branch of which flows towards Corsica and the Gulf of Genoa (sal. < 38‰S, 5.50 to 6.30 cc oxygen/l, in a 100 m sheet); below this, mixed northern water, overlying the eastern intermediate sheet of water (300-400 m), with a high salinity (> 38.5‰S) and with little oxygen (4.20 to 4.40 cc/l) is found, a ramification of which flows along the Sardinian slope, continuing along Corsica towards the Ligurian Sea. The bottom layer in the basin is formed by the deep northern water enriched with Atlantic water which, having submerged along the abrupt coast of Algeria, continues its deep course and tends to flow upwards at 40°N. The contact of these water masses creates contrary movements: upward (Algerian-Atlantic waters) or downward (eastern water). This affects the vertical distribution of the organisms: some normally epiplanktonic ones meet here in the depth whereas other, meso- or bathyplanktonic, organisms are found at the surface; this fact can be verified for numerous taxa. The area has a markedly pelagic character except in the vicinity of the Sardinian and Baleares' slopes; the Copepoda fauna is clearly oceanic while neritic species only occur in appreciable quantities close to the shores or are absent. The deep water species, on the contrary, are numerous and their species richness is great; the effects of the vertical currents are indicated by the upward movement of *Euchaeta acuta*, *Eucalanus elongatus* and *Rhincalanus nasutus* and the downward transport exceeding 1000 m of *Heterorhabdus papilliger* and *Neocalanus gracilis* (Mazza, 1967). Atlantic affinities are marked by several species (Tab. I). Eleven Chaetognatha have been counted. The abundance of *Sagitta bipunctata*

and its continuous presence favoured by the very pelagic character of this zone, one of the deepest areas of the Mediterranean, seems to be most typical. Atlantic indicators are also present. The Euphausiacea comprise 13 species, viz. three dominant ones of a temperate character accompanied in the north by species with a cold affinity and in the south by species with a warm affinity. Two species signalize the Atlantic and eastern influences (Tab. VI).

Among the 14 Pteropoda eight are abundant. They are found, roughly speaking, on both sides of 40°N, exclusive of seasonal variations: those very common in the south (*Limacina trochiformis*, *L. inflata*, *Styliola subula*, *Creseis virgula*) become scarce towards the north and the distribution of the others (e.g. *Cavolinia inflexa*) is the reverse. This distribution leads to a differentiation between two zones in the Central Area; S. of 40°N a fauna with a thermophilous tendency is found which undergoes a rather clear-cut eastern influence and shows certain affinities with the SW. area, differing from the latter in the relative scarcity of indicators of Atlantic origin. The more temperate fauna north of 40°N is connected with the northern part of the Western Basin. However, the boundaries between the two zones fluctuate because of seasonal conditions, especially temperature.

Liguro-Provençal region

In the area a vast elliptic eddy of Mediterranean Water is surrounded by a narrow Atlantic Current, strongly altered after its long journey. This narrow stream forms the Ligurian Coastal Current. In the centre of the eddy, deep water with high salinity and relatively low temperature comes to the surface in a divergence. At greater depth eastern water flows in the same direction as that of Atlantic type. In some places the greater density, caused by cooling in the winter, provokes a submergence of surface waters which subsequently spread in southern direction; the resulting turbulence joins the aforementioned phenomena in determining the plankton distribution.

The Copepoda fauna of this zone which, hydrologically, is more Mediterranean than the preceding ones, is less varied (c. 60 species, according to Della Croce, 1965; Carli et al., 1964; Carli, 1971). The Pseudocalanidae are in a dominating position (*Clausocalanus arcuicornis* and *C. furcatus*). Also well represented are the Oithonidae, Paracalanidae, Centropagidae (*Centropages typicus*), the Temoridae (*Temora stylifera*) and Acartiidae (*Acartia clausi*). The other families are only scarcely represented. The diversity of dominant forms fluctuates seasonally: a temperature rise is supposed to cause a decrease in the number of *Clausocalanus arcuicornis* (a winter species) and an increase of *Cl. typicus*, *Temora stylifera* and the Oithonidae (a summer group). On the other hand, the divergence promotes the presence of euryhaline species like *C. arcuicornis*. This factor, together with the reduced continental shelf, is responsible for the markedly oceanic character of the fauna (Pseudocalanidae); the neritic species are more or less strictly confined to the coastal zone (Mazza, 1967). The presence of Atlantic indicators is not regular. Several Copepoda have been recently mentioned in this area, some for the first time in the Mediterranean; some species, rare in the Western Basin but known in the Eastern Basin, also have been observed here (Tab. I).

Except in special places, the fauna of Chaetognatha is not very varied (eight species) and none of the taxa indicating an oceanic inflow is found in this region. The divergence enables the capture of deep living species like *S. lyra* and *S. hexap-*

tera which, already very numerous at the subsurface, are dominant. The spreading of highly saline water at the surface is favourable to *S. bipunctata*, but probably causes the relative scarcity of *S. enflata*.

In the Ligurian Sea the Euphausiacea are represented by all 13 species known for the Mediterranean, but their relative abundance is very unequal; the dominant forms are found together in the central divergence. Eighteen Thecosomata have been identified in the Liguro-Provençal Channel; more than half of them are (very) rare, some only occur at Villefranche (*Gleba cordata*, *G. chrysosticta* ?, *Peraclis apicifulva*). Only seven epi- or bathyplanktonic species, the latter favoured by the deep and narrow channel, form the major components of the fauna. *Cavolinia inflexa*, seasonally and bathymetrically uniformly distributed over the region, is the dominating species in the depth. At the surface *Creseis virgula* and *C. acicula* are dominant; other species show strong seasonal variations; warm water species are not very abundant past 40°N; Atlantic indicators, as well as deep Eastern Current indicators, are scarce.

In the area of Villefranche, reputed for the richness of its plankton several species have been found recently which had not been observed in the Mediterranean before, and a number of species have been newly described: Chaetognatha, Hydromedusae, Siphonophora, Appendicularia, Amphipoda (Tab. I). Finally, it may be stated that the fauna of the Liguro-Provençal region is of a temperate to temperate-cold character.

Gulf of Lion

The principal hydrological characteristic over the wide continental shelf ('planaise') is the permanent outflow of Rhône Water (35-36‰ S) which affects almost the entire gulf as the SW. flowing 'Rhône Current', with a variable seasonal expansion. After reaching Cape Creus in the west, this water partly returns, forming the 'Countercurrent of the Languedoc'. At the eastern border of the gulf highly saline water arrives from the Ligurian Divergence (>38.20‰ S) and from the Deep Eastern Current (38.10‰ S), as well as altered water from the Liguro-Provençal branch of the Atlantic Current (37.80‰ S). Depending on the season these various formations penetrate more or less far into the gulf. In winter the highly cooled surface water submerges and spreads out on the bottom, forming a cold sheet with a relatively low salinity. This is northern water which can be found over part of the Western Basin.

These topographical and hydrological conditions determine the very sharply contrasted planktonic fauna of this region (Furnestin, 1960).

A rich neritic fauna extends to the north and centre of the gulf over a fraction of the shelf; this facies corresponds with a diluted environment (35-36‰ S); besides some Medusae, Siphonophora and Tunicata it comprises a dense and very varied fauna of Crustacea: various Copepoda, many Gammaridea and benthoplanktonic Mysidacea [22 species at night in the plankton of the Gulf of Marseille, according to Champalbert & Macquart-Moulin (1970), Macquart-Moulin (1975)]. The exploration of particular littoral biotopes has resulted in the description of new Mysidacea species or subspecies (Tab. I). An investigation of Annelida larvae from the coastal plankton of Banyuls added some fifteen benthic and three holoplanktonic Polychaeta to the fauna. Moreover, the seasonal distribution of Chaetopteridae larvae leads to the separation of two bio-

geographical extremes, related to resp. the temperate-warm province (summer larvae of *Ranzanides sagittaria*) and to the temperate-cold province (winter larvae of *Chaetopterus variopedatus*) (Braud, 1966a, b).

A poorer fauna of the open sea, in much more saline water ($> 38\%$ S), is situated over the great depths of the southern border. Here the species of the surface layers are less numerous than in the neritic zone, but at night deep species appear (Tab. I).

As a result we find two contrasting groups, delimited at the same time by isohalines and isobaths. These groups are well characterised by the Chaetognatha *Sagitta setosa* in the diluted neritic zone and *S. bipunctata* in the open sea. Thus the variation of the distributions of the two planktonic communities, depending on the strength of the Rhône Current on the one hand and the penetration of the water masses from the open sea in the direction of the coast on the other hand, may be translated by the ratio of *S. bipunctata* and *S. setosa*: a very low ratio in diluted waters, average in mixed waters, at its maximum in the open sea (Falke, 1974).

The Copepoda fauna in the gulf is well-known (Gaudy, 1962, 1963, 1970; Mazza, 1967). Their variety is great with 186 species, but only 36 are considered common to all regions of the gulf; about 25 of these constitute the main part of the community and play an important role in the local secondary production. In spite of certain similarities, the regions of Banyuls and Marseille, for example, differ rather markedly; at Banyuls the fauna assumes a more constant neritic character, the number of deep living species is relatively low and no trace of Atlantic influence is to be detected, the region being outside the superficial circulation of the NW. Basin; the analogies with the Castellon region, on the contrary, are numerous. In the Banyuls region 119 species have been found with a generally high diversity (20-40 species per station) but the frequency of adults is very low; it is difficult to establish permanent representatives, let alone communities. A new species has been described in this region, *Oncaeae neo-obscura*, and a genus new to the Mediterranean has been noted, *Paroithona* (*P. parvula*) (Razouls, 1968, 1969, 1972).

Due to the heterogeneity of the environment the Copepoda fauna in the central part of the gulf shows locally different features. On the southern border the composition of this fauna is relatively stable, owing to the abundance of oceanic species with an uninterrupted succession of generations (Clausocalanidae, Oithonidae). Over the continental shelf, on the contrary, it undergoes important quantitative variations due to the predominance of seasonal neritic forms: in this way *Temora stylifera*, pre-eminent in autumn, is relieved in winter by *Paracalanus parvus*, *Acartia clausi* and *Centropages typicus* (Mazza, 1967). Finally, the presence of Copepoda like *Temora longicornis*, typical of the ocean and rare in the Mediterranean, is attributed to the much reduced Atlantic influence which manifests itself at the entrance of the gulf.

Because of the great extent of the continental shelf the gulf is little favourable to Euphausiacea, only their larvae are found, while the adults live near the limit of the gulf, close to deeper water.

The strong seasonal hydrological fluctuations cause much more important quantitative variation in the dominant Thecosomata than in the neighbouring areas situated N. of 42°N ; so, though there is a similar basic composition near the surface, the relative abundance of the species in the Gulf of Lion is very different

from that in these adjacent areas. Notwithstanding its very marked neritic character the gulf shelters young specimens of several deep living species of which the adults are rarely observed, with certain exceptions (e.g. *Cymbulia peroni*, known all along the coast where it reproduces almost during the whole year). The scarcity of thermophilous species (*Limacina trochiformis*, *Styliola subula* and especially *Hyalocylis striata* and *Cavolinia gibbosa*) lends to the region a temperate character; indeed, being subjected to the mistral, the gulf has a colder regime than the rest of the Western Basin.

Catalunian Sea

The Catalunian Current is of Mediterranean nature (38°-38.30° S) and, coming from the Gulf of Lion, it crosses the Catalunian Sea in a NE-SW direction and at 40°N it meets a central divergence. Except for this current the surface salinity is relatively low (36.90-37.60‰ S) under the influence of river water (Rhône Current and coastal rivers) in the western part and of an Atlantic stream in the eastern part. The deep water is mostly of northern origin; it constitutes two layers, one above, the other under the eastern sheet.

More than 100 Copepoda species are known for this region (Navarro & Massuti, 1940; Massuti, 1940, 1942; Duran, 1963). In addition to numerous permanent forms, well distinct seasonal groups are observed. Some species are particularly interesting like *Pareuchaeta norvegica*, considered to be a boreal relict, or like species which are exceptionally mentioned in the Mediterranean (Tab. I). In the west, in the waters off Castellon, *Paracalanus parvus*, typical of the surface, and *Clausocalanus arcuicornis*, a subsurface species, constitute the main part of the neritic plankton. *Ctenocalanus vanus*, *Nannocalanus minor* and *Calocalanus pavo* are relatively frequent. In winter, *Centropages typicus* swarms [the very big specimens living where temperatures are minimal (Deevey, 1960)], while *C. kröyeri* and *C. chierchiai* are sporadic; also the maximum for *Calanus helgolandicus* is registered and, at middle and deep levels, that of *Diaixis pygmaea* in concentrations exceptional for the Western Basin. Finally, in winter bathypelagic species (Tab. I) appear at the sub-surface because of the homothermy (Vives, 1963, 1966). It will be noticed that species indicating the arrival of Atlantic Water are lacking in this area (Duran, 1970).

In the eastern part the diversity is greater: quite a number of species new to the Catalunian Sea have been observed (Furnestin & Giron, 1963) and the Atlantic forms are present only here. In this area the continuation may be established of the faunistic diversity of the Alboran Sea, under oceanic influence. However, these two neighbouring faunas differ in the percentages of their fundamental species: *Paracalanus parvus* dominates (in summer) in the whole Alboran area, but is much less numerous in the Catalunian Sea, except in the neritic zone. *Centropages typicus* and *Temora stylifera*, on the contrary, are much less abundant in the Alboran Sea, especially in its western part.

The species variety of Chaetognatha is one of the lowest in the W. Mediterranean (8 species). Atlantic elements are lacking; the relative dilution promotes *Sagitta enflata* and a population of *S. setosa* at the mouth of the Ebro reminds one of a similar fauna near the mouth of the Rhône. The fauna of Euphausiacea of the Catalunian Sea reminds of that of neighbouring zones, though it is less varied (10 species). The Catalunian Current is too shallow to influence this fauna in

any way and lend to it some originality. With regard to the Alboran Sea, *Thysanoessa gregaria* is lacking and *Euphausia brevis* is more numerous.

The diversity of the Thecosomata population is relatively low (14 species). In the sediments *Peraclis triacantha* forms the only record of this species in the Mediterranean; the records of *Cavolinia longirostris* and *C. gibbosa* are also interesting. On the one hand the warm species, on the other hand Atlantic species are rare or absent; the abundant species are the same as in the northern part of the Western Basin to which the Catalunian Sea, a temperate area, is related.

Tyrrhenian Sea

The hydrology of this region is dominated by the inflow of deep, saline and warm eastern water and in a less degree by an Atlantic influence of relatively diluted water at the surface. The eastern water enters through the Sardinian Channel but also by way of the Strait of Messina (certain plankton species bear witness to that effect); it invades the southern region at a depth of 500-600 m to continue in northern direction and subsequently occupy the entire northern part from 200-300 m downwards. The shallows E. of Corsica force these waters back along the coast of this island. The Atlantic Water penetrates through the Sardinian Channel as far as the Italian shores; from a branch of the current which crosses the Western Basin in a SW-NE direction, also Atlantic Water enters through the Strait of Bonifacio, and along the north, rounding Cape Corse, flowing to about 42°N.

North-Tyrrhenian—The mentioned hydrological duality manifests itself in this area, as the Atlantic Water influences the area off E. Corsica while the open basin is for the most part the domain of eastern water. Thus the rare and localised indicators of diluted water acquire a special meaning in a fauna mostly typical of highly saline water. These indicators are: *Sagitta setosa* and *Penilia avirostris* near the E. coast of Corsica at the mouths of rivers and the Atlantic tracers *Pontellopsis regalis*, *Pontellina plumata* etc.

The Copepoda fauna off E. Corsica is relatively rich, comprising 58 species of which sometimes 30-40 are recorded in the same stations (Tab. II). Compared with this one, the fauna of the W. side is less dense and less varied (31 species to 58, during a simultaneous study). The dominant species are not in every respect the same; besides *Clausocalanus arcicornis*, very abundant in both areas, *Oithona helgolandica* replaces *Temora stylifera*. Finally, the forms of Atlantic origin are less numerous. The faunas of the Toscano Archipelago and of the Italian neritic zone are very similar to that of the Ligurian Sea (Della Croce, 1959; Cannicci, 1961; Carli, 1966).

The Euphausiacea comprise some ten species: together with the 'temperate' forms and rather great numbers of specimens of 'subtropical' species, small quantities of northern forms are found. In the southern Basin the lack of balance is accentuated to the advantage of the warm water forms.

Only ten Pteropoda species are recorded. Despite the Atlantic influence, Pteropoda originating from the ocean are practically unknown and, notwithstanding the eastern character of the deep waters, the scarcity of *Hyalocylis striata* and the absence of *Cavolinia gibbosa* are remarkable; these two phenomena are due to the geography of this area: it is situated too much to the north for these thermophilous

species. Like in all northern zones of the Western Basin, *Limacina trochiformis* is rare, but *Styliola subula* is much more frequent than in the other areas north of 42°N. Thus the character of the N. Tyrrhenian appears to be temperate-warm (Rampal, 1975). The bathypelagic Pteropoda fauna seems to be less rich than that of the S. Tyrrhenian.

South Tyrrhenian—The zooplankton richness is maximal near the Sicilian shores, owing to the extension of the continental shelf and the passage of the Atlantic Current. The Copepoda fauna is extremely varied and it changes much from one season to another: *Oncae*, very abundant in summer, is replaced by *Oithona* in autumn (Della Croce, 1963). One of the important differences with the N. Tyrrhenian is the marked regression of *Temora stylifera*, despite the extension of the neritic zone (Mazza, 1967). The fauna has a clearly bathypelagic character with many species among the Eucalanidae, Aetideidae, Metridiidae, Heterorhabdidae and especially Augaptilidae from which the genus *Haloptilus* is represented by seven species (Vives, 1967).

Also the variety of Chaetognatha is great, because of the mixture of Atlantic and eastern water, each with its own characteristic fauna (Tab. V). In deep water *Sagitta neodeciens* and, very abundant, *S. hexaptera* and *S. lyra* are found. At the surface the dominant species are *S. bipunctata*, in the open sea, and *S. enflata* near the shores; the preponderance of the first over the second is exceptional in the Mediterranean. In the Sardinian Channel, a zone of active mixing, they are found together. The situation is more complex in the Strait of Messina where the Ionian water submerges under the Tyrrhenian water forming turbulences accentuated by the adverse winds and where marginal countercurrents and gyres join the tidal currents. The results of this confused hydrological situation is to be seen in Chaetognatha: the presence of *S. serratodentata* and *Krohnitta subtilis* makes it possible to follow the penetration of Ionian waters, particularly in autumn and winter, in relation with an increased formation of eastern water; the presence of meso- and bathyplanktonic species at the surface indicates upward movements of deep water. In the S. Tyrrhenian *S. minima* is rarely found and *S. setosa* forms a permanent population in the neighbourhood of the Gulf of Naples.

The Euphausiacea fauna appreciably differs from that of the rest of the Western Basin, at least in ratio of species; here the thermophilous species become dominant. The Atlantic *Thysanoessa gregaria* is found together with 12 species generally of a warm character.

The Pteropoda show a diversity which corresponds with the hydrological situation described and which, together with the coexistence of species of various origins, lends to the S. Tyrrhenian a marked individuality. The abundance of thermophilous species, especially *Hyalocylis striata*, as numerous as in the eastern Mediterranean, leads to the conclusion that the S. Tyrrhenian is a zone with a warm water fauna related to the Eastern Basin.

Moreover, in the various plankton groups one distinguishes quite a number of eastern indicators (Tables) (Fig. 4). Besides, several Aetideidae, Euchaetidae, Candaciidae and Pontellidae which become more rare from the Aegean and Ionian Seas towards the Tyrrhenian and W. of Sardinia, are supposed to give the same indication for eastern water (Cannicci, 1961; Mazza, 1967; Vives, 1967). The Atlantic influence manifests in Chaetognatha, Euphausiacea, Pteropoda

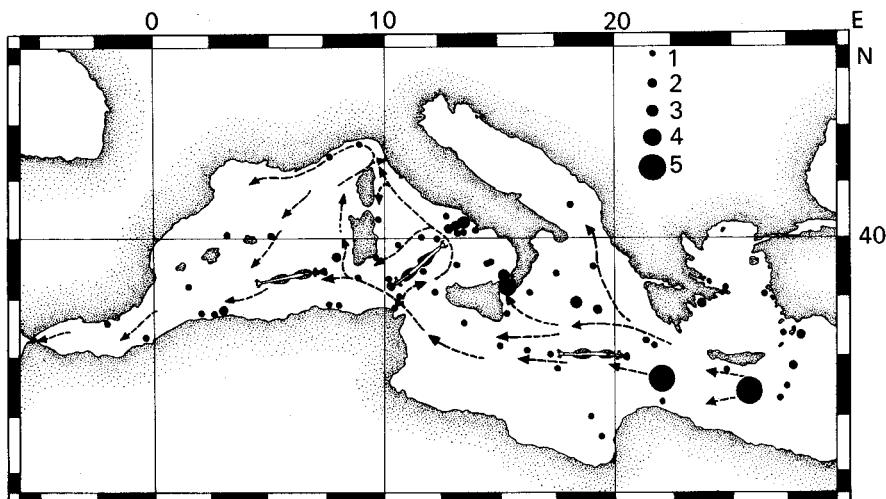


Fig. 4. Localities of planktonic organism marking the influence of Eastern Waters in the W. Mediterranean, 1-5=relative abundances of *Sagitta serratodentata* living at the level of 'intermediate waters'. Arrows indicate flow of Eastern Intermediate Water.

and various Copepoda, observed between the surface and 100-150 m (Della Croce, 1962 a, b, 1963; Vives, 1967).

This relation with Atlantic and eastern waters urges one to consider the S. Tyrrhenian a transition area between the two Mediterranean basins. The same role is played, in the east, by the Sicilian-Lybian region where also a mixture of faunas has been recognised (Rampal, 1975). Besides, the extensive S. Tyrrhenian Basin, where the neritic zones of Sardinia, Sicily and the Italian Peninsula surround a pelagic zone with important depths, offers a major interest from an ecological point of view. Recent research resulted in the discovery of species a) new to this region, b) new to the Mediterranean, c) new to science (Tab. I).

Adriatic Sea—Fluvial and Mediterranean influences

The northern position (c. 40 to 46°N) in the Eastern Basin, together with its typical topography and continentalish climate, lend to the Adriatic Sea a certain individuality (Tabs. II, V-VII); sometimes it is compared with the W. Mediterranean (Tortonese, 1964). The northern part is strongly diluted and has a rather rough winter climate; it consists of an extensive alluvial continental shelf with shallow depths, only S. of 42°N it exceeds 1000 m. Therefore the northern and southern regions should be discussed separately; they show water masses differing in temperature, salinity, density, origin and dynamics. These latter evolve during the year and from one year to another; indeed, a distinction is made between periods of active circulation and other more static ones; the hydrological phenomena concerned are the following (according to Zore-Armada, 1963, 1968; Buljan, 1968; Vučetić, 1970).

In the active period, in particular during winter, there is a large inflow of saline and warm Mediterranean water at surface- and intermediate levels, while the water of the northern section, less saline, but cold and therefore more dense, submerges and flows out into the trenches of the central and southern regions. In the period of reduced circulation Mediterranean water is only to be observed in the Otranto region, as a thin layer. The central and even southern waters then reach in greater quantities the surface of the N. Adriatic, while the northern water, covered by mixed waters, occupies the bottom of the trench of Jabuka. Therefore the northern and southern basins of the Adriatic are sufficiently different to constitute real biotopes. These biotopes are inhabited by two distinct communities, the composition of which, nevertheless, depends each year on the dynamics. Favoured by water mass movements, exchanges between these two communities occur, especially during the period of important Mediterranean penetration. The transitional zones (trench of Jabuka, ridge of Palagruza) and the zones where marine waters pass through (Otranto Channel) shelter faunas of a varying composition which is difficult to determine.

Upper Adriatic Sea

This area shows a markedly neritic character and is invaded, in spring and autumn, by strongly diluted cold water masses originating chiefly from the river Pô (e.g. 30.26‰ S and 6°C). In the Gulf of Trieste the salinity and temperature vary rapidly due to the combined effects of discharge of important quantities of fresh water, wind, especially the bora, and very shallow depths (25 m). The Upper Adriatic has been subdivided into five hydrographical areas, with the closely related Middle Adriatic included (Stirn, 1969): 1 Padane Area, stretching from the Gulf of Venice to Ancona, influenced by the river Pô (salinity at the surface: 35.04‰ S; in the deep: 38.04‰ S; average annual temperature: 13.8°C but < 7°C in winter in the vicinity of Venice, at the surface). 2 Northern Area (NW part) with average temperature and salinity of 14°C and 37‰ S; the thermo-haline fluctuations which are considerable at the surface of these two areas, are very weak in the depth, even near the river mouths; 3 Central Area with averages of 14.7°C and 36.68‰ S, influenced by the waters coming from 4 Quarnero-Istria Area (15.7°C and 37.60‰ S) and from 5 Middle Adriatic Area (15.7°C and 37.97‰ S).

Meroplankton is rich but holoplanktonic species are rather rare; the selection, severe due to the roughness of the ecological conditions, results in their scarcity compared with the middle and southern parts of the Adriatic; being eurytherm and euryhaline, they give several annual generations. Thus, particularly the Padane and Northern areas shelter a typically neritic plankton with a great biomass, but very little diversification. This situation is characterised by the Cladocera of which six species have been observed, at least in the Gulf of Kvarner. They find optimal conditions during the warm months and therefore the N. Adriatic is in summer a real 'Cladocera sea'; their distribution is related to the flow of the Pô water. In the neritic zone, which is diluted and rich in organic detritus, plankton is observed composed of *Penilia avirostris* (a species recently introduced into the N. Adriatic, according to Specchi, 1970), accompanied by the remarkably allotropic *Evdadne tergestina* and *E. spinifera*, *Podon polyphemoides* and *P. intermedius*. In spring *Evdadne nordmanni* is very abundant, especially in the

Table II. Adriatic fauna elements not mentioned in the text (for abbreviations see table I)

COPEPODA

(217 spec., Shmeleva, 1973), 3 communities (a,b,c): Sa (Huré et al., 1978):
 a) upper level (max. abundance 100-200m): Clausocalanus paululus, C. pergens, Lucicutia flavigornis, Oithona setigera, Pleuromamma gracilis etc.
 b) intermediate level (max. abundance 300-400m): Euchaeta acuta, P. abdominalis, Haloptilus longicornis etc.
 c) deep level (max. abundance >400m): Spinocalanus abyssalis var. pygmaeus (= S. parabyssalis), S. longicornis, S. oligospinosus, Mormonilla minor, Oncea ornata, Temropia mayumboensis, Monacilla typica: Od,C; Chiridius (*Pseudaeolidaeus*) armatus: Od, etc. Vettoria granulosa, V. parva (= Corissa p.), V. longifurca (= Corina l.): X", Od (& Naples), A (Huré et al., 1967); V. parva, V. longifurca: X,d.

AMPHIPODA

Westwoodilla rectirostris: X'-1955.

Oxycephalidae (5 + X' 4 spec.) Streetsia challengerii: X', Sa; Oxycephalus piscator, Cranocephalus scleroticus = Stebbingella typhoides -1955; Streetsia porcella -1963; Ma, Sa (in Hoenigman, 1963a).

MYSIDACEA

(12 + X' 20 spec. + 1 var.) X', Ma, Sa: 2 spec.-1953; 11 spec. + 1 var.-1955; 4 spec.-1960; 2 spec.-1961; Na, Ma: 1 spec.-1958 (in Hoenigman, 1963b, 1968).

OSTRACODA

Conchoecia procera, C. curta, C. magna, C. clausi, Archiconchoecia striata: Sa.

MEDUSAE

Persa incolorata, Podocoryne minima: Na, X'; Aglama hemistoma: Na, A (Benovic, 1973); Podocoryne hartlaubi: Na, gT, X (Neppi et al., 1913); Gonianemus murbachi: Na, gT, X' (Rottini, 1977); (18 spec. Od) Rhysomedusa pomponina, Octophialacium funerarium, P. incolorata: X', Od; A. hemistoma, Bythotira murrayi, Eirene viridula, Euphysa aurata, Laodicea undulata, Liriope tetraphylea, Obelia sp., Phialidium hemisphaericum, Rhopalonema velatum, Sminthea eurygaster, Solmaris leucostyla, Solmundella bitentaculata, Thamnostoma dibalia, Zanclea costata: Od (Benovic, 1976); Solmissus albescens: Od, B.

SIPHONOPHORA

Mugiae kochi: A, Ct, gT; Halistemma rubrum, Nanomia bijuga, Sphaeronectes gracilis: gT, Si; S. gamulinii, S. irregularis, Sulculeolaria quadrivalvis: gT, Si, R; S. chuni, Lensia subtilis, Eudoxoides spiralis, Abylopsis tetragona; all: Na, Ma, Sa. Lensia fowleri, L. meteori, L. campanella, Hippopodius hippopus, Diphyes dispar, Bassia bassensis, Chelophyses appendiculata: Ma, Sa (Rottini, 1966; Rottini & Gamulin, 1969); Sphaeronectes fragilis, Clausophyes ovata, Lensia conoidea, L. multicristata, Sulculeolaria turgida, Vogtia pentacantha, Velella velella, Porpita porpita, Rosacea cymbiformis: Sa (Rottini et al., 1969; Gamulin, 1977); Eudoxia dohrni: Sa, X, En? (Gamulin, 1966).

TUNICATA

Doliolum denticulatum, D. nationalis, Doliolina mülleri: Na, Ma, Sa; D. mülleri var. krohni, Doliolitta gegenbauri: Ma, Sa (Gamulin, 1948; Katavici, 1977); Salpa maxima: Na; S. fusiformis, Thalia democratica, Pyrosoma atlanticum: Sa (Gamulin, 1948); Oikopleura dioica: Na(D), Sa; O. longicauda: Na, Sa, D; O. fusiformis: Na(D), Sa; O. albicans, O. cophocerca: Sa, D; O. intermedia, O. mediterranea, Stegosoma magnum, Megalocercus abyssorum, Appendicularia sicula, Fritillaria borealis f. intermedia, F. formica, F. haplostoma, F. pellucida, Kowalevskia tenuis: Sa.

nocturnal hyponeuston (Varagnolo & Monte, 1969; Ghirardelli & Specchi, 1965; Specchi, 1968; Corni, 1971; Specchi et al., 1974). In the Middle Adriatic, *P. avirostris* lives more often in water warmer than 20°C, its thermophilous affinities distinguish it from other Cladocera (Corni, 1970). This species is the most frequently occurring Cladocera in the lagoon of Venice where it is abundant in the warm season, accompanied by numerous larvae of Lamellibranchia and Copepoda: *Acartia clausi* and several species of the genera *Oithona*, *Temora*, *Euterpina* and *Centropages* (Comaschi et al., 1969).

The Chaetognatha are well represented from June to October and in winter.

Sagitta setosa is an indicator of a group of factors characterising the littoral zones, the bays and coastal lagoons. This is the only species which reproduces in the Gulf of Trieste where also *Sagitta enflata* and *S. minima* are observed. In the S. Adriatic nine more species are found (Tab. V).

The number of most species of planktonic groups thus diminishes from the south to the north. The majority of the Copepoda are sporadic; on a total of 51 identified species, only six are abundant, which results in a monotonous fauna, especially in the warm season. In autumn the Copepoda (particularly *Oncaeae*) become more numerous and in winter and spring (*Oithona*) they dominate, especially in the coastal waters off Italy rich in nutritive material of terrigenous origin. Also species of the open sea and of deep water join them, brought there by currents and active migration (Huré & Scotto di Carlo, 1969). Indeed the Middle Adriatic is rich in Copepoda, with 63 species; the diversity index increases from the littoral waters (6.3) where its maximum, in autumn, corresponds with the salinity maximum, to the open sea (15.1) where it is at its maximum in summer; it is inversely related to the annual amplitude of the thermo-haline variation (Regner, 1973, 1976). The quantitative fluctuations of Copepoda in the Central Adriatic are directly related to the arrival of water from the E. Mediterranean and they are important enough to influence the concentration of pelagic fish (Vucetic, 1969b). The Pteropoda show very low variability. Only three species, ubiquitous in the Mediterranean, adapted to this very special environment: *Ceratostoma virgula*, *C. acicula* and *Limacina inflata* which penetrate as far as the Gulf of Trieste and the Gulf of Venice. Periodically, though, they leave the north of the Upper Adriatic, making seasonal recessions in the direction of its southern area. There (44°N) occur, besides, *Styliola subula*, *Limacina trochiformis* and juveniles of *Caecum*. In the Upper Adriatic Thecosomata are not in the best conditions either (Rampal, 1975).

The Gulf of Trieste comprises only five Siphonophora and the Upper Adriatic as a whole eleven. The fauna of the Middle Adriatic is more diversified and numbers 18 species (Tab. II). There exists a close correlation between the distribution of Calycophora and the ecological factors in the hydrographical areas as defined above (Rottini, 1970).

In the most northern part the Hydromedusae form a neritic fauna (30 species); S. of the line Rimini-Pula, however, oceanic Trachymedusae and Narcomedusae are abundant, especially during the cold months.

In this part of the Adriatic only three Thaliacea and 10 Appendicularia have been found. The density of the Appendicularia fauna, which is very high (an average of 67 specimens/m³), decreases from west to east because of the Pô water. The latter is favourable to *Oikopleura dioica* (which is also positively influenced by the shallow depth), and has a direct effect on its concentration; for the two other dominant species (cf. Tab. II) the gradient is the reverse (Fenaux, 1972). The oceanic or deep living species of Chaetognatha, Pteropoda, Siphonophora, Copepoda, Amphipoda, Mysidacea and Acantharia, which are observed scatteredly or accidentally as far as the Gulf of Trieste, mark the penetration of water from the middle and southern areas and have value as hydrological indicators (Rottini, 1966; Ghirardelli, 1968; Hoenigman, 1963a, 1968). The Acantharia are very characteristic for the group is practically not represented in the Upper Adriatic (Schreiber, 1967). The fresh water Rotifera *Kellicothia longispina*, on the contrary, is an indicator of river water (Voltolina, 1967).

Lower Adriatic

Being a deep and narrow basin with a less fluctuating seasonal hydrological and climatic regime, this area provides conditions which are more stable and more favourable to the development of certain meso- or bathypelagic species than the Upper Adriatic. The most conspicuous hydrological phenomenon is the penetration of eastern water. The plankton is varied and has a high ratio of holoplanktonic forms which are often stenotherm and stenohaline with a rather low number of annual generations. While no Euphausiacea are recorded in the north, 11 species live in the Lower Adriatic; the temperate and cold water species are dominant; one thermophilous species is abundant, *Stylocheiron suhmii* (Tab. VI). The Thaliacea (6 sp.) and Appendicularia (15 sp.) are more diversified than in the north. The Siphonophora comprise more than 20 species. The Scyphomedusa *Pelagia noctiluca*, observed here, does not appear in the north. The same holds for several Hydromedusae collected off Dubrovnik (Benovic, 1976). The planktonic Ostracoda, also practically unknown in the north, number five species. The Mysidacea and amphipod Oxycephalidae faunas are particularly rich (Tab. II). In spite of their low diversity (inferior to that of most Mediterranean sectors, nine species according to Steuer, 1911), the Pteropoda stress certain characteristics of the S. Adriatic. Several deep living species are well represented. Notwithstanding the vicinity of the Ionian Sea where they are abundant, *Hyalocylis striata* and *Cavolinia gibbosa gibbosa* are rare (the latter in the sediment); indeed, even if these species penetrate at the surface, together with the eastern waters, through the Otranto Channel, they quickly disappear because of the submerging as far as the bottom of these waters, mixed with the cold and diluted water masses from the north. Nevertheless, they are indicators of the entrance of Mediterranean Water (Rampal, 1975), together with, for instance, the Chaetognatha *Sagitta neodeciopiens* (Vucetic, 1969a) and the Acantharia, which are well represented and show, in their qualitative and quantitative composition, many analogies with the Acantharia fauna of the Gulf of Tarento (Massera Botazzi et al., 1972). The Copepoda comprise a very great number of species and their deep living fauna is very varied. Three communities are associated with three distribution levels (Tab. II). A comparison between the faunas of the Dubrovnik region and the Gulf of Naples reveals a marked similarity (Gamulin et al., 1968; Huré et al., 1968a, 1969). The diversity (about 150 species) and the composition of the faunas are rather similar; nevertheless, the coastal species are more abundant near Naples, whereas *Calanus helgolandicus* and *Euchaeta hebes* (one of the most characteristic among Copepoda in this sea, according to Hoenigman, 1958), are more abundant in the S. Adriatic. The deep living faunas differ little, but off Dubrovnik the density is superior and off Naples the diversity. The hyperid Amphipoda, mostly deep living, are likewise represented at the two localities (Huré et al., 1969). Among the Siphonophora, on the contrary, *Mugiaeae kochi*, *Eudoxoides spiralis*, *Lensia subtilis* and *L. meteori*, which frequently occur in the Adriatic, are more rare in the Gulf of Naples. As a conclusion we may state that, though geographically the Adriatic belongs to the Eastern Basin, and notwithstanding a certain number of analogies between its southern part and the neighbouring areas of the Western Basin, the Adriatic keeps a marked faunistic individuality owing to the special topographical, hydrological and climatic conditions.

Table III. East Mediterranean fauna elements not mentioned in the text (for abbreviations see table I)

Sicilian-Libyan Area

COPEPODA

Calanoides carinatus: X', Ai; *Calanus tenuicornis*, *Isochaeta ovalis*, *Lucicutia lucida*, *Lubbockia aculeata*, *Vettoria longifurca*, *V.parva*, *Corycaeus laetus*, *Amallothrix falciifer*, *Arietellus plumifera*: X'; *Pontocilla abyssicola*: ?X' (Medit.) (Bourcier et al., 1969; Soenen, 1974).

SIPHONOPHORA

(1^h spec.) *Rosacea* spec., *Hippopodius hippopus*, *Vogtia pentacantha*, *V.spinosa*, *Abylopsis tetragona*, *Bassia bassensis*, *Sulculeolaria turgida*, *S.chuni*, *S.quadrivalvis*, *Muggiaeae atlantica*, *M.kochi*, *Eudoxoides spiralis*, *Lensia subtilis*, *Nanomia bijuga*: P (Bigelow & Sears, 1939; Patriti, 1969a).

Ionian Sea

COPEPODA

Acartia negligens, *Clausocalanus arcuicornis*, *Corycaeus clausi*, *Euchaeta marina*, *Lucicutia flavigornis*, *Nannocalanus minor*, *Neocalanus gracilis*, *Oithona plumifera*, *Temora stylifera*: D.

HETEROPODA

Atlanta lesueuri: P, X'; *A.peroni*: A; *Proatlanta mediterranea* (= *P. sculpta mediterranea*).

Levantine Basin

COPEPODA

Acartia clausi, *Paracalanus parvus*, *Centropages kröyeri*, *Oithona nana*, *O.similis* (= *O.helgolandica*): Bl; *Undinopsis bradyi*, *Acartia danae* (East Medit.), *Scolecithrix fowleri* (Medit.): X' (Shmeleva, 1973b).

TUNICATA

Salpidae (6 spec.) *Thalia orientalis*: Ai; *T.democratica* f.*typica*, *Salpa fusiformis*, *S.cylindrica* ?, *Ihlea punctata*, *Pegea confoederata* bicaudata, *Cyclosalpa pinnata polae* (Godeaux, 1974).

Appendicularia (21 spec.) *Oikopleura longicauda*: D; *O.cophocerca*, *O.dioica*, *O.fusiformis*, *O.intermedia*, *O.parva*, *Megalocercus abyssorum*, *Appendicularia sicula*, *Fritillaria borealis* f.*sargassi*, *F.formica* f.*tuberculata*, *F.megachile*, *F.messanensis*, *F.tenella*, *F.pellucida*.

SIPHONOPHORA

(21 spec.) *Hippopodius hippopus*, *Muggiaeae kochi*, *Lensia multicristata*, *Chelophyes appendiculata*, *Bassia bassensis*, *Eudoxoides spiralis*, *Abylopsis tetragona*, *Agalma elegans*, *Physophora hydrostatica* (Bigelow & Sears, 1939; Lakkis, 1971a); *Chelophyes contorta*, *Diphyes bojani*, *D.dispar*, *Lensia subtilis*, *L.campanella*, *L.meteori*, *Sulculeolaria quadrivalvis*, *S.chuni*, *S.turgida*, *Rosacea plicata*, *Apolemia uvaria*: X'(region); *S.angusta*: X'(Medit.) (Alvariño, 1974).

Eritrean influences

COPEPODA

Calocalanus crassirostris, *Calocalanus pavonius* (Delalo, 1966; Shmeleva, 1973), *Calanopis elliptica*, *C.media* (Berdugo, 1968; Lakkis, 1976), *Arietellus pavoninus* (Moraitou-Apostolopoulou, 1969a), *Euchaeta concinna* (Casanova, 1973), *Acartia centrura* (Berdugo, 1974), *A.fossae* (A.hamata?), *Labidocera madurae*, *L.detrunata* (Lakkis, 1976), *Pontellina plumata* ? (El Maghraby, 1965); in the Suez Canal: *Canthocalanus pauper*, *Temora discaudata* (Gurney, 1927).

MEDUSAE

Laodicea fijiana, *Euphysora bigelowi* (Schmidt, 1972, 1973), *Turritopsis nutricula* (Kramp, 1959).

SIPHONOPHORA

Sulculeolaria chuni ? (Alvariño, 1974).

THALIACEA

Salpa cylindrica (Godeaux, 1960).

table III continued

CHAETOGNATHA

Sagitta neglecta (Guerguess et al., 1973).

DINOFLAGELLATA

Ceratium egyptiacum, Peridinium exiquipes, P. nipponicum, P. africanoides, Pyrodinum schilleri (Halim, 1970).

TINTINNIDAE

Tintinnopsis aperta, T. dadayi, T. gracilis, T. mortensenii, T. tocantinensis, Codonolopsis bulbulosus, Metacylis annulifera (Dowidar, 1974).

Aegean Sea

AMPHIPODA

Hyperia schizogeneios, H. latissima, H. galba: A; Hyperoche kröyeri. Parathemisto obliqua, Euthemisto bispinosa, Platyscelus serratulus, P. ovoides: C; Brachyscelus cruscum: B,C; Pseudolyceea pachypoda, Phronima sedentaria, Paraphronima crassipes, Euprino macropus, Vibiliia armata: P (Veini & Kiortsis, 1974).

MYSIDACEA

Anchialina oculata, A. agilis, Siriella thompsoni, S. norvegica: X', D; S. clausi, S. jaltensis, Gastrosaccus lobatus, G. normani, Leptomysis gracilis: X' (Hatzakis, 1974).

CIADOCERA, Evadne spinifera, COPEPODA, Temora stylifera, EUPHAUSTACEA, Euphausia krohnii, SIPHONOPHORA, Bassia bassensis, MEDUSAE, Liriope tetraphylla, Cotylorhiza tuberculata, TUNICATA, Thalia democratica, AMPHIPODA, Hyperia schizogeneios, MYSIDACEA, Anchialina oculata, A. agilis, CHAETOGNATHA, Sagitta enflata: DY.

Eastern Basin—Eritrean influence

The eastern and western part of the Mediterranean are separated by a rise, maximal depth less than 400 m, which bars the Sicilian Channel and isolates the waters of these two basins from 1500 downwards; at 2000 m T-s diagrams give resp. 38.7‰ S-13.35°C and 38.4‰ S-12.75°C for the eastern and western water. The Sicilian-Tunisian rise thus constitutes a geographical, hydrological and even climatic frontier between the Western and Eastern Basins. Two-thirds of the latter basin are situated S. of 36°N, therefore at relatively low latitudes compared with the former. Except for the north of the Aegean Sea it is characterised by a tropical climate (surface temperatures of about 27.6°C) favourable to thermophilous species (Tab. III, V-VII). The principal hydrological characteristics of these regions will be listed below (according to Allain, 1966; Burman & Oren, 1970; Engel, 1967; Gorgy, 1966; Lacombe & Tchernia, 1960; Miller et al., 1970; Oren & Engel, 1965; Oren & Komarowsky, 1961; Pollak, 1951; Tchernia et al., 1958).

The Atlantic Water (salinity 37‰ S) invades the shelf along Tunisia and Tripoli, then reaches the Cyrenaica (min. 37.28‰ S) where it submerges in summer, while flowing as far as Palestine in winter, with strongly increasing salinity (Gulf of Sirte: 38.30‰ S; shores of Israel: 39.00‰ S). Chiefly from the Levantine Basin onwards this Atlantic Water changes as a result of evaporation and the salinity reaches 39.50‰ S at the surface; nevertheless this water retains its properties between 30-100 m where the salinity is still minimal (38.90‰ S between Cyprus and Ishendrum).

In winter the continental winds cool the surface layers (15-16°C in the area Rhodos-Cyprus) and make them submerge; thus intermediate water is formed which, starting from the Levantine Basin, flows to the west, its mean depth passing, through successive levels, from 100-150 m, 250-300 m to 300-500 m on

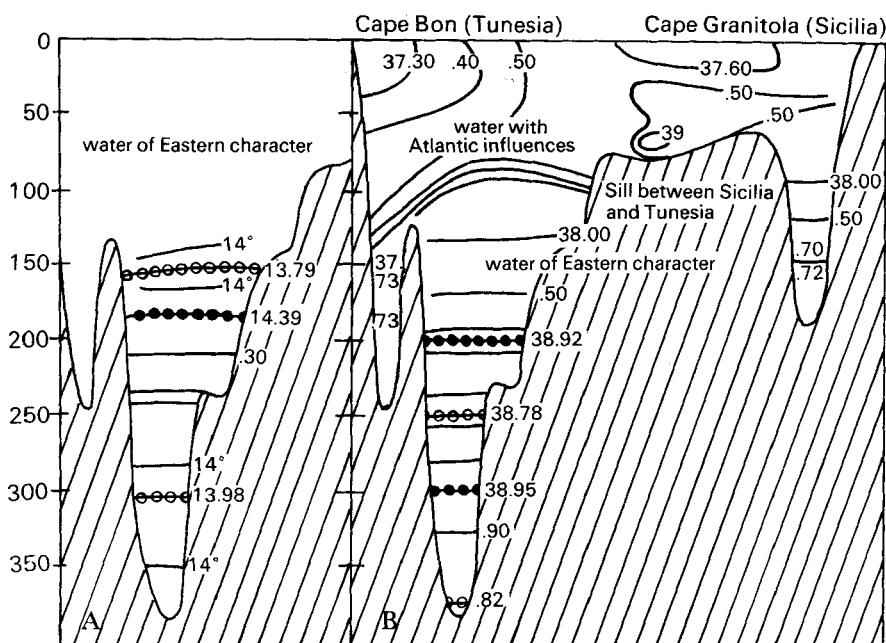


Fig. 5. Water exchanges between Eastern and Western Basin. Transversal section through the Sicilian Channel (isohalines and, partly, isotherms). A) temperature; B) salinity. Water of Atlantic origin occupies the whole width of the channel and a secondary channel off Tunisia. In the depths of both sides of the sill, the E. Mediterranean Water is heterogeneous, partly because of Adriatic influences. (modified after Furnestin & Allain, 1962).

reaching the Western Basin.

Some years ago the Nile still exercised a great influence on the Egyptian neritic area, in spite of the construction of dams in the most important branches of the delta. In a period of strong discharge its water covered the alluvial shelf with values between 28 and 38.60‰ S and its influence reached as far as the Israeli area. However, since the building of the high Assuan Dam the periodical discharge of such enormous quantities of fresh water does not occur any more. From that time, the exchanges with the Red Sea via the Suez Canal, which had long time remained insignificant, are intensifying, especially since the excavation of the canal.

Also the exchanges with the Black Sea have changed after the construction of important dams in the rivers flowing out into this sea. Even though the Aegean Sea continues to receive diluted surface waters from that direction, the deep current which drains Mediterranean water into the Black Sea has become stronger and we see a progressive 'mediterraneisation' of the Pontic Basin.

Sicilian-Libyan area

This region, which extends as far as the Gulf of Sirte, is of interest from three points of view: bathymetrical, topographical and hydrological. The continental

shelf which at places runs along the lagoon shores and is very different in breadth in the north and in the south, extends as far as hundred miles or so off the Gulf of Gabès; the depths do not exceed 1000 m, except in the vicinity of Malta. From the subsurface to about 100 m the shelf is covered by water of Atlantic origin which accumulates off Gabès (37.39-37.60‰ S). The attenuated Atlantic influence is also found off Tripoli, with great seasonal differences. The deep waters are typically eastern.

The circulation of intermediate water towards the Western Basin, especially in winter, is active. A main branch, at a depth of 300-400 m, passes through the Sicilian Channel in the direction of the N. African coast; two secondary branches detach from this main one: one joins the main branch again after a cyclonic circulation in the S. Tyrrhenian; the other continues towards the Ligurian Sea, along the Sardinian and Corsican shores. This water assumes a complex layered structure, disturbed by phenomena of turbulence. Therefore the notion of a homogenic water mass flowing from E. to W. does not correspond to reality (Furnestin & Allain, 1962b; Belliard, 1970) (Fig. 5).

The study of Chaetognatha has revealed the presence of 10 species: *Sagitta setosa* developed a large fauna in the Gulf of Gabès and is replaced by *S. friderici* where, in the eastern part, the continental shelf is narrow; *S. enflata* confirms its dominant position, in the east as well as in the west; *S. minima* is remarkably abundant along the continental slope; *S. bipunctata* is regularly recorded in the waters over the greatest depths; *S. serratodentata*, characteristic of the Eastern Basin, is common outside the continental shelf. The frequent occurrence of *S. hexaptera* indicates the existence of a deep living fauna of homogenic distribution in the E. Mediterranean and *Krohnitta subtilis* is present in the deep layers of this whole region of the Mediterranean.

Eleven Euphausiacea species are known for this region. Subtropical species are dominant (Tab. VI). Pteropoda number 18 species (and *Diacria trispinosa* in the sediment). Their distribution, like that of Euphausiacea, shows that this region is transitional, the fauna already being marked by the typically eastern taxa and still showing elements of the SW. Mediterranean: surface elements of the Algerian shores and subsurface elements of the S. Tyrrhenian. With its typically Mediterranean deep water the area is a kind of vestibule of the Eastern Basin where the thermophilous species (*Limacina trochiformis*, *Styliola subula*, *Hyalocylis striata*) begin to supplant the temperate forms of the western regions (Rampal, 1975). Fourteen Siphonophora species have been mentioned (Tab. III). Despite the fact that the continental shelf is covered by water of Atlantic origin the species indicating this presence are rare in most groups except Copepoda, at least in the Sicilian Channel where several indicator species have been recorded, in particular *Calanoides carinatus*, collected for the first time in this region, together with various other species which were not yet known here.

Ionian Sea

The plankton fauna of this region is in many respects similar to those of the neighbouring areas, due to hydrological analogies in the depth. The NW part, however, which is alternately diluted by water coming from the Upper Adriatic, in summer (Magazzu et al., 1972; Grancini et al., 1973) and, in winter, by a SW-NE Atlantic branch which reaches the Adriatic, locally shelters various elements of

less saline water or of Atlantic origin. Of 12 Euphausiacea species, the dominant ones are the same as in the Sicilian-Libyan and Levantine area. *Meganyctiphantes norvegica* and *Nyctiphanes couchii* are not typical of the Ionian fauna but they are transported from the Adriatic Sea (Tab. VI).

In the Ionian Sea the diversity of Chaetognatha attains the maximum of the E. Mediterranean (11 species). *Sagitta enflata* in the coastal zones and *S. bipunctata* in the centre of the basin, share the surface domain between them. In the depth, the most common are *S. hexaptera* and *S. neodecipiens*; *S. lyra* is very much less abundant, a general feature in the Eastern Basin. The eastern characteristic species *S. serratodentata* and *Krohnitta subtilis* are well represented. Three species have a special signification, despite their scarcity: *S. friderici* and *Pterosagitta draco*, both related to the waters of Atlantic origin, and *S. setosa*, related to the diluted neritic zones (for instance the Gulf of Tarento) mark the double current which affects the NW. shores of the basin (Furnestin, 1970a; Guglielmo, 1976).

The Pteropoda show an average diversity: 13 species; besides, three have been observed in the sediments. The Ionian Sea contains the six species ubiquitous in the Mediterranean. The eastern organisms are abundant and thermophilous ones are frequent; on the contrary, *Cavolinia inflexa* is very rare.

Fourteen Heteropoda have been collected during deep hauls (Di Geronimo, 1970), all known for the Mediterranean; yet, *Protatlanta souleyeti* had been only recorded in the Alboran Sea (Tab. III).

The inventory of Copepoda gave 123 species (Shmeleva, 1973a); east of Malta the fauna is very similar to the one established in the S. Adriatic (Evans, 1968; Tab. III); on the contrary, important differences are evident with regard to the Tyrrhenian Sea because of the Sicilian Strait topography. The indices of diversity are high: 3.27 (200-0 m) and 3.64 (400-200 m) at places where Adriatic, Levantine and Atlantic influences converge. *Gaidius tenuispinus* is considered one of the typically eastern species, which are scarce (Vaissière et al., 1978).

Levantine Basin, SE. area

Waters of Atlantic origin which show a rather high salinity after the long journey constitute a sheet of variable thickness (max. 50 m). Coming from the Cyrenaica, this current reaches the shores of Egypt and afterwards of Palestine, whereto, until recently, it drained the diluted water masses during the strong outflow of the Nile (a drop in salinity in September); after having reached Syria, this current continues westward along Asia Minor and arrives in the Aegean Sea. Between Crete and the eastern shores local currents transport Levantine surface waters into the Aegean Sea or into cyclonic movements. The intermediate water, with characteristic temperature and salinity maxima, occupies the Levantine Basin for the greater part and is the source of the E-W current. The cold and highly saline bottom water originally comes, in winter (cascading), from the Aegean Sea, by way of two outflowing currents which may be found at 500 m, one between Crete and Karpathos, the other between Rhodos and Turkey. These currents split off ramifications in the directions of Cyprus and the Egyptian shores (Gorgy, 1966; Burman & Oren, 1970).

The Euphausiacea are not very diversified, nor are the Chaetognatha (10-11 species). *Sagitta enflata* is dominant. *S. bipunctata* reaches a high percentage, especially S. of Crete; *S. friderici* remains localised along the shores (Israel, Leba-

non) and at the mouth of the Nile; this species has been considered an indicator of the Nile Current. Eastern organisms are abundant. In the depth *S. hexaptera* is dominant. *S. neglecta* and *S. megalophthalma* constitute two new records for Chaetognatha in the Levantine Basin or even in the Mediterranean (for the former). Also the Pteropoda show a low diversity (11 species). In the sediment *Diacria trispinosa* is found, perhaps brought there by the waters of Atlantic origin, but not capable of maintaining itself, and *Peraclis reticulata* which may also exist alive because it is common in the S. Mediterranean. The Levantine Basin is marked by the presence of the eastern and thermophilous species, but also shelters species with wide Mediterranean distribution as well at the surface as in the deep. In the Levantine Sea and the neighbouring Sirte 140 Copepoda species have been observed (among which *Oithona atlantica* (= *O. spinirostris*), *O. tenuis* and *Pleuromamma piseki* are peculiar to the latter region). Some neritic species are also found in the Black Sea (Delalo, 1966a) but they don't seem characteristic of the SE. Mediterranean. For details concerning the species of the Egyptian shores one is referred to Dowidar et al., 1970; Salah et al., 1970. In the northern part of the basin a differentiation has been made between neritic, epiplanktonic and meso-bathyp planktonic species and their respective abundances have been evaluated. *Centropages violaceus* is an important element in this eastern fauna (Berdugo & Kimor, 1968). In the Lebanese waters the dominant species have been identified for each season (Lakkis, 1971b, 1974). Finally, *Spinocalanus neospinosus*, the ninth Spinocalanidae for the Mediterranean, has been described in the vicinity of Rhodos (Grice, 1971) and several new elements for the sector have been recorded (Tab. III).

The Tunicata comprise Salpidae and 21 Appendicularia, the latter all known from the Western Basin (Tab. III). Their diversity shows important seasonal differences; the fact that it diminishes sharply from June to September could be an element of differentiation between the E. and W. Mediterranean (Fenau, 1970). The abundance of *Appendicularia sicula* is supposed to characterize the plankton of the SE. part of the Levantine Sea (Halim et al., 1974). The Siphonophora number 21 species, for the most part newly recorded (Tab. III).

Eritrean influence

This influence constitutes an interesting chapter of the Mediterranean zoogeography because of the evolution of the environmental conditions through the intervention of Man, realising a long term biological experiment of which the progress may be followed. The affinities and differences between the plankton of the Red Sea and that of the Mediterranean have already often been analysed as well as the role of the Suez Canal as a barrier or link between the two seas. Numerous recent data may be added.

Although the faunas of both the E. Mediterranean and the Red Sea are characterised by the presence of numerous tropical and subtropical forms, the differences between them are great; a good many species dominating in the Red Sea have not been recorded in the E. Mediterranean; the species common to both (among Chaetognatha, Euphausiacea, Thecosomata, Thaliacea and Appendicularia etc.) are usually cosmopolitan. Therefore the Eritrean influence in the Eastern Basin seems to be small. Nevertheless, several planktonic organisms have been considered (with proofs of unequal value) to have come from the Red Sea into

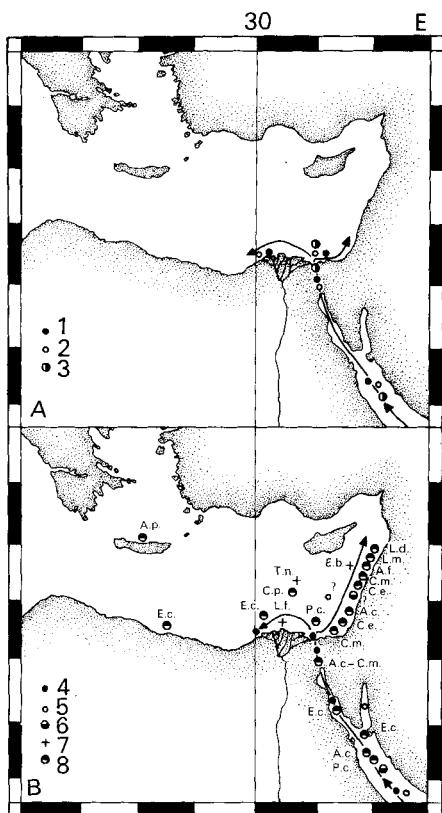


Fig. 6. Planktonic organisms demonstrating the Eritrean influence as migrants from the Red Sea into the Mediterranean. A) Phyto- and microplankton; B) Meso- and macroplankton. 1 = Diatomaceae, 2 = Dinoflagellata, 3 = Tintinnidae, 4 = Chaetognatha, 5 = Siphonophora, 6 = Thaliacea, 7 = Hydro-medusae, 8 = Copepoda. For names one is referred to the text, arrows = migratory tracks, ? = dubious migrant.

the Levantine area via the Suez Canal, participating in the 'Lessepsian migration' according to Por's expression (1969, 1971). Amongst phyto- and microplankton this is the case with the Diatomacea *Rhizosolenia alata f. indica*, with five Indo-Pacific Dinoflagellata, observed in abundance in the canal, at Port Saïd and some at Alexandria, while at least three of them are not recorded elsewhere in the Mediterranean. Seven Tintinnidae have the same meaning. Also witnesses of the Eritrean plankton extension into the E. Mediterranean are several Medusae, 1 Siphonophora, 1 Thaliacea, 1 Chaetognatha. (Tab. III, also for abbr. in Fig. 6). Among Copepoda, it is necessary to disregard old records of species (according to Pesta, in Sewell, 1948) of which the penetration into the Mediterranean via the Suez Canal has been accepted wrongly. One should only retain the more recent records of Indo-Pacific species which were observed, at the same time, in the Red Sea, the canal and in various places of the Levantine Basin (Egyptian, Israeli and Lebanese shores and sometimes as far as the south of the Aegean

Sea) which seem to bear witness of the present relations between the Red Sea and the Mediterranean.

Planktonic (especially holoplanktonic) species capable of passing through the canal, have long time remained very rare, because of a double obstacle: the first of topographic nature; the presence of shallows in the Gulf of Suez which constitute a barrier for all but the epipelagic forms, and the very shallow depth of the canal which limited the migration of pelagic organisms; the second of hydrological nature, consisting in the differences in salinity between the Gulf of Suez and the Bitter Lakes on the one hand and the outlet of the canal into the Mediterranean in the area of outflow of the Nile on the other hand. Yet, the situation is changing: the salinity of the Bitter Lakes is progressively decreasing (51.84‰ S in 1924-1925; 49.91‰ in 1966; 43-44‰ at the surface and 45-46‰ at the bottom in 1971) and the Assuan Dam which prevents the excess of the floods of the Nile from flowing out into the Mediterranean, maintains a relatively constant degree of salinity (39‰ S) off Port-Saïd. The reduction of the above-named barrier could result in an extension of the exchanges. The more so as the recent excavation and dredging of the canal have greatly enhanced the flow and the speed of the current traversing the canal. Under these conditions it will not be impossible to see epipelagic species which are abundant in the Red Sea (as for instance *Euphausia diomedae*) enter the Mediterranean, if they manifest a certain ecological tolerance. Nevertheless, the high degree of individuality attained by populations of the same species which have been observed at both ends of the canal (*Rhincalanus nasutus*, *Diphyes dispar*, among others) bears witness to a strong ecological pressure which, sooner or later, will affect the newly arrived migrants from the Red Sea.

Also the passage of planktonic larvae of benthic animals should be considered, although these larvae are, in general, more sensitive to high salinities than the adults; yet the chances of benthic organisms from the Red Sea to find themselves in the Mediterranean, have grown; one should expect a good many of these to establish themselves in the Mediterranean, and even, in a relatively near future, a radical change is to be expected of the entire fauna of the Eastern Basin (Thorson, 1971). In this case, the species richness of the latter region which is low compared with that of the Red Sea, would increase. Probably though, the immigrants would only be able to establish themselves within a limited zone, roughly restricted by the isohaline of 39‰ S and the winter isotherm of 16°C, that is to say, in the Levantine Basin as far as the Peloponnesus, their expansion to the SW. being prevented by the progression of the waters of Atlantic origin (Por, 1972).

The changes in ecological conditions will not only result in the arrival of allochthonous species, they will also affect the structure and succession of plankton and other communities of the E. Mediterranean. An example of this is the disturbance of the, till then particularly regular and typically periodical diatom bloom and also in the at present perceptible evolution of the pelagic fish fauna (Kimer, 1972).

The reverse passage, in the direction Mediterranean—Red Sea is of very restricted extent. The current in the canal going to the N. causes a much more important transport and exists during a much greater part of the year. We cite the case of three Hydromedusae: *Koellikerina fasciculata*, which had hitherto been restricted to the Mediterranean and the nearby Atlantic and was subsequently

observed on the Arabian shores (Vannucci & Navas, 1973a, b), *Podocoryne meteoris* and *Helgicirrha schulzei* (cf. Schmidt, 1972); with reserve is mentioned the Siphonophora *Chelophyses appendiculata* (cf. Alvariño, 1974); finally, the transport of *Thalia orientalis* into the Gulf of Suez, from the Eastern Basin, will have to be verified, because such a migration of a Thaliacea remains doubtful (cf. Godeaux, 1974).

Aegean Sea

The northern part of the Aegean Sea receives, from the Sea of Marmara, especially in summer, cold water with a low salinity (about 22‰ S) which flows to the south at the surface; with increasing salinity it penetrates into the Ionian Sea and the Levantine Basin. At middle depths, on the contrary, intermediate water characterised by temperature and salinity maxima (14-15°C; 38.94‰ S) enters the Aegean Sea and it also changes during the journey to the north.

Four Cladocera species are known to exist in this region: *Penilia avirostris* which occurs frequently, but only localised, in the northern area, due to the too markedly pelagic character and too high salinities of the southern part; two thermophilous forms, occurring only during the warm season, *Evdne spinifera*, the most abundant species, especially in the north, and *E. tergestina*; *Podon intermedius*, a cold water form (for the Mediterranean), is rare in the Aegean Sea and appears in winter (Moraitou-Apostolopoulou & Kiortsis, 1977).

Fourteen pelagic Amphipoda (Hyperiidae) have been recorded and two Isopoda species. There are first records of nine planktonic Mysidacea species in the south of the Aegean Sea (Tab. III).

The Appendicularia show a great diversity; 29 species have been identified in the Gulf of Saronikos (Fenau, 1974); with seven more species this inventory would contain all Mediterranean Appendicularia.

Euphausiaceae are of special interest when the accurate distribution of the various species is considered (B. Casanova, 1974). The progressive expansion of the temperate forms from the S. to the N. has been noted for *Euphausia krohnii*, *Stylocheiron longicornis*, *Nematoscelis megalops*, while *Meganyciphanes norvegica* and *Nyctiphanes couchii* appear in the northern area and, reversely, there is an increased abundance of the warm water forms in the southern part: *Euphausia brevis*, *E. hemigibba*, *Thysanopoda aequalis* and *Stylocheiron suhmi*; the latter is characteristic of the purely eastern waters and is observed at all stations, even at the entrance of the Sea of Marmara, but there it lives at a certain depth (deeper than 150 m the water still shows a salinity of 38.81‰ S). The record of *Nematoscelis atlantica*, *Stylocheiron abbreviatum* and *S. maximum* raises the number of Euphausiacea of the Aegean Basin to twelve.

The Chaetognatha are represented with 10 species. *Sagitta enflata* dominates in the epiplankton, owing to thick neritic swarms to the N. of the Peloponnesus and near the Sea of Marmara, and *S. hexaptera* dominates in the bathyplankton (Tab. V).

The Thecosomata number 13 species. In all localities (even in the Strait of the Dardanelles) and at all levels *Hyalocylis striata* and *Cavolinia gibbosa gibbosa* are found, characteristically eastern species, promoted by a strong penetration of Levantine water into the Aegean Sea where these species attain their highest Mediterranean percentages; this underlines the fact that the Aegean Basin be-

longs to the eastern domain. The species with a deep tendency are never very abundant but the frequent occurrence of *Peraclis reticulata* is remarkable and shows its thermophilous character in the Mediterranean. The cosmopolitans are in a majority in the surface fauna which is as a consequence less original.

The diversity of Copepoda is of the same order as in the W. Mediterranean: 120 species (Pavlova, 1966) but the dispersal of the species varies substantially within the Aegean Sea: its southern area shows a resemblance with the Eastern Basin but also characteristics which are transitional between the northern area and the rest of the Mediterranean. The north appears to be an ecologically isolated area, marked by the absolute dominance of *Temora stylifera* which swarms during the warm period, and by the abundance of *Corycaeus giesbrechti*, *Centropages violaceus* and *Candacia aethiopica*. In the south the number of specimens of these species diminishes, while that of Copepoda which are well represented in the Mediterranean increases (*Clausocalanus arcuicornis*, *C. furcatus*, *Oithona plumifera*, *Mecynocera clausi*). In the whole Aegean Basin a general rarefaction may be noticed, compared with the W. Mediterranean, of Calanidae and particularly of *Paracalanus parvus*. Let us recall the records of *Augaptilus spinifrons* (only known to exist in the Gulf of Naples) and of *Arietellus pavoninus*, observed for the first time in the Mediterranean near Crete (Moraitou-Apostolopoulou, 1969a, 1971, 1974). Thus a separation, approximately near 38°N, may be observed between the N. and S. Aegean Sea, as well in the pelagic as in the benthic domain. The north is of a boreal tendency and shows analogies with the northern regions of the W. Mediterranean or the Adriatic, it is diluted by abundant river water and seasonal inflows from the Black Sea; thus it forms a transitional zone with the Pontic Basin. In spite of the circulation present, it shows the character of a closed area where certain populations display signs of ecological isolation; this is the case with *Penilia avirostris*, *Candacia armata*, *Anomalocera patersoni*, *Labidocera wollastoni* and *Pontella lobiancoi*, which are absent from the southern region. The latter region, with a subtropical tendency and largely open, is more clearly related to the Eastern Basin. The Aegean Sea is also marked by a geomorphological diversity with a continental shelf which is relatively extended in the north and Kikladhes region, and reduced in the south with an extremely cut-up, and therefore extensive coast, a complicated system of currents and seasonal winds and a multiplicity of biotopes.

In spite of a relatively high diversity, which is in any case higher than in the Black Sea or the Northern Adriatic, each group contains only one, or at most two basic species remaining dominant the whole year through, except for some seasonal variations (Tab. III). Considering the heterogeneity of the basin this monospecific dominance supposes a rise of the ecological potential in these basic species; indeed, their tolerance of several ecological factors is often greater than in the Western Basin. Nevertheless, the extension of certain species finds itself limited: *Liriope tetraphylla*, restricted by an isohaline of 36‰ S is not observed in the NE. part of the Aegean Sea. Others modify their seasonal dispersal: *Clausocalanus arcuicornis*, the whole year abundant in the south where the salinity remains high, does not acquire a certain density in the north until wintertime, when the salinity at the surface increases. Finally, phenomena of replacement (of one species by another with the same ecology) have been observed between the south and the north of the basin (a dominance of *Acartia clausi* in the north and of *A. negligens* in the south) or between the Aegean Sea and the W. Mediterranean (replacement

Abbreviations used in tables V, VI and VII

A	= abundant	Oc	= oceanic
Ad.i	= indicator of Adriatic influence	P	= present
B	= bathypelagic	R	= rare
C	= common	(S)	= south
Co	= cold water species	Sb	= subbenthic
D	= dominant	Sd	= sediment
E	= indicator of eastern waters	Sl	= seasonal
Ep	= epipelagic	Ss	= subsurface
Er	= Eritrean influence	T	= temperate
Eu	= eurybath	Th	= thermophilous
Ex	= exceptional	Tr	= tropical
F	= few	U	= ubiquitous Mediterranean
Fr	= frequent	(V)	= Villefranche/Mer
L	= larval	X	= newly described
M	= mesopelagic	X'	= newly recorded
(N)	= north	?	= with reserve
Nr	= neritic	?d	= doubtful presence

of *Abylopsis tetragona* by *Bassia bassensis*).

These conclusions, obtained by comparing the zooplankton of the Aegean Sea with that of the Adriatic and several eastern or western areas, tend to show the Aegean, at least its northern section, as an ecologically distinct entity (Pavlova, 1966; Kiortsis, 1974).

Black Sea – Its relations with the Mediterranean

The study of the above-named relations makes it necessary to evoke the system of currents which pass through the Dardanelles and the Bosphorus as well as the composition of the plankton in the vicinity of the places of communication between the two basins. (See also tables IV-VII.)

System of currents between the Black Sea and the Mediterranean

Very strong and generally very rapid currents traverse the Bosphorus: a surface current of light and low salinity water (18‰ S) which always flows towards the Sea of Marmara and a deep countercurrent transporting salt (35-38‰ S) and heavy waters. This results in large variations of salinity of the water column: in the Black Sea, 18‰ at the surface, 20‰ at 200 m and 22.5‰ S at the bottom; in the Sea of Marmara, 21‰ S at the surface, already 37.5‰ S at 30 m and more than 38‰ S from 50 m downward. The temperatures of the two seas are not very different at the surface but differ greatly in the deep: 9°C at 50 m in the Black Sea, 16°C in the Sea of Marmara. The surface current is permanently supplied by water from the outflow of the big rivers (Danube, Dnepr, Dnestr, etc.) into the Black Sea and by high precipitations, particularly in the eastern part. Before the active operation of important dams in these streams, the quantity of water flowing out into the Black Sea was twice as big as that of the water penetrating in the deep. Even now, the displacement of water goes in the direction of the Mediterranean,

Table IV. Black Sea fauna elements not mentioned in the text

abbreviations used:

A	= abundant	M(-P)	= Mediterranean (or Pontic) origin
Aa	= also in Atlantic		or first description
Ad	= Adriatic Sea	N	= not present
A-M	= Atlanto-Mediterranean endemic	Na	= Gulf of Naples
B	= meso- or bathypelagic/deep living	Ne	= neritic
Bo	= prebosporic	No	= not of M(-P)
Bl	= Bosphorus lower current	O	= oceanic
C	= cold, northern distribution in the ocean	P	= present
Ca	= Caspian type	Pt	= permanent
Co	= cold water species	R	= rare
Cp	= central part	S	= surface form
Cr	= near Crimea	Se	= sediment
D	= dominant	Sf	= surface at night
E	= epipelagic	Sl	= seasonal
Em	= East Mediterranean origin or first description	T	= Temperate Atlantic
En	= endemic	V	= Villefranche/Mer
Eu	= euhyponeuston	W	= warm, southern distribution in the ocean
Ex	= exceptional	Wm	= West Mediterranean origin or first description
I	= Indo-Pacific	X	= newly described
JE	= juveniles in euhyponeuston	X'	= newly recorded
Md	= with modified vertical distribution	?	= with reserve
Me	= Mediterranean influence		

Caspian type:

COPEPODA

Heterocope caspia, Eurytemora grimmi, Ectinosoma abrau

MEDUSAE

Moerisia (Odessa) maeotica

Western Area

COPEPODA

Acartia clausi: A,jE; Pseudocalanus elongatus: A,Co; Oithona similis (?= O.helgolandica), Centropages ponticus, Paracalanus parvus, O.nana: A; O.minuta, C.kröyeri: jE; Anomalocera patersoni: A,Eu,Pt; Labidocera brunescens, Pontella mediterranea: Eu,S1; Calanus helgolandicus: O (Margineanu, 1968; Petran, 1968; Porumb, 1972, 1974).

CLADOCERA

Penilia avirostris: D; Evadne tergestina, E.spinifera, Podon polyphemoides.

TINTINNIDAE

Stenosemella ventricosa, Tintinnopsis beroidea: A; T.rossolini: X,Eu (Morosovskaia, 1966).

Mediterranean influence

COPEPODA

Oncaea dentipes, Euterpinia acutifrons, Microsetella rosea: Bl,A; Corycaeus furcifer, Calocalanus pavonius, C.tenuis, Oncaea minuta, Corycella spec.: Bo,A; Clausocalanus arcuicornis, Calocalanus pavo, Oncaea mediterranea, Corycaeus typicus, C.flaccus, C. clausi, Calanus (= Neocalanus) gracilis: Cp,S; Calocalanus pavonius, Clausocalanus arcuicornis, C.paululus, Mecynocera clausi, Oncaea similis, Lucicutia flavidornis: Cr.

though river water which is strongly drained from the Danube Delta onwards, mostly in spring, and accumulates near the Bosphorus, cannot all enter that strait; partly this water is forced back to the shores of Anatolia forming a current to the east. The currents of the Dardanelles have characteristics which are more or less

Table V. Diversity and quantitative distribution of Chaetognatha in the Mediterranean and in the Black Sea

species	ecol. char.	Alboran Sea	S.W. Area	Central Area	Liguro- Provengal Region ¹	Gulf of Lion ²	Cata- lunian Sea ³
<i>Sagitta bierii</i>	?						
<i>S.bipunctata</i>	Oc,Ep	R	A	A	A	F	A
<i>S.decipliens</i>	M-B						
<i>S.enflata</i>	Nr	D	D	D	F	A	D
<i>S.euxina</i>							
<i>S.friderici</i>	Nr	Ai	Ai				?
<i>S.hexaptera</i>	M-B	C	F	C	D	R	F
<i>S.lyra</i>	M	C	A	A	D	R	D
<i>S.megalophtalma</i>			P		X(V)		
<i>S.minima</i>	M	R	R	F	R	F	A
<i>S.neodecipliens</i>	M-B	C	F	R	P		F
<i>S.neglecta</i>							
<i>S.planctonis</i>	0-100m	Ai	Ai	Ai			
<i>S.serratodentata</i>	0-500m	R	R	F	P	F	R
<i>S.setosa</i>	Nr				P(V)	A	A
<i>S.tasmanica</i>	subsurf.	Ai	Ai	Ai			
<i>Krohnitta subtilis</i>	M	R	R	R	R		
<i>Pterosagitta draco</i>	0-200m	Ai	Ai	Ai	Ai(V)		
<i>Spadella cephaloptera</i>	Sb				P(V)	P	
number of species	total: 18	12	13	11	8+4(V)	9	8

authors consulted:

for the Mediterranean and the Black Sea in general: Furnestin, 1970a

¹Ghirardelli, 1950; Dallot & Ducret, 1969; Dallot, 1978; ²Furnestin, 1960; ³Vives, 1966; Dallot, 1978; ⁴Furnestin, 1953b; Guglielmo, 1976; ⁵Vucetic, 1961, 1969a; Chirardelli, 1968, 1974; Ghirardelli & Rottini, 1973; Gamulin, 1977; ⁶Furnestin, 1974; ⁷Guglielmo, 1976;

Table VI. Diversity and quantitative distribution of Euphausiacea in the Mediterranean and in the Black Sea (for abbreviations see table V)

species	ecological characters	Alboran Sea	S.W. Area ¹	Central Area	Liguro- Provengal Region ²	Gulf of Lion ³
<i>Thysanopoda aequalis</i>	M,Th	P	A	P(N)A(S)	F	P
<i>Meganyctiphanes norvegica</i>	B,Co	P	F	A(N)P(S)	D	A
<i>Nyctiphantes couchii</i>	Ep-M,Nr,Co	P	F	P(N-S)	D	A
<i>Euphausia kronnii</i>	Eu,Te	D	D	D	D	D
<i>Euphausia brevis</i>	M,Th	P	A	P(N)A(S)	F	P
<i>Euphausia hemigibba</i>	M-B,Th	P	A	P(N)A(S)	F	L
<i>Thysanoessa gregaria</i>	Ep	D,Ai	Ai	R,Ai	Ex	L
<i>Nematoscelis megalops</i>	B,Te	D	D	D	D	A
<i>Nematoscelis microps</i>	?					
<i>Nematoscelis atlantica</i>	Eu-(M),Th	P	P	R(N)F(S)	Ex	P
<i>Stylocheiron abbreviatum</i>	Eu,U	P	P	P	F	L
<i>Stylocheiron maximum</i>	B,U	P	P	P	F	P
<i>Stylocheiron longicorne</i>	Eu,Te	D	P	D	D	P
<i>Stylocheiron suhmii</i>	Eu-(M)	R,E	E	R,E	Ex	Ex
number of species	total: 13	13	13	13	13	13

authors consulted:

in general: Ruud, 1939; Bacescu & Mayer, 1961; B.Casanova, 1968, 1974; Wiebe & d'Abromo, 1972

¹Soenen, 1969; ²Franqueville, 1971; ³Furnestin, 1960; Macquart-Moulin & Leveau, 1968;⁴Vives, 1966; ⁵Furnestin, 1960; Kinzer, 1963; Mayer, 1967; Vives, 1968; ⁶Evans, 1968;Soenen, 1970, 1972; ⁷Lebour, 1926a,b; Kimor & Berdugo, 1967; Casanova et al., 1973.

Tyrrhenian Sea ⁴	Adriatic Sea ⁵	Sicilian Libyan Area ⁶	Ionian Sea ⁷	Levantine Basin ⁸	Aegean Sea ⁹	Marmara Sea	Black Sea ¹⁰
X', Er							
D	C(S)	C	C	C	P	P	
?							
D	A(N)P(S)	A	D	D	D	P	R
Ai		F	Ai	P	?		
A	C(S)	P	A	D	D	P	
A	C(S)	P	F	F	P		
P	F(S)			X'	R		
R	C(N-S)	A	R	R	P		
P	C(S)E	P	C	R	P		
X'Er-Ex							
Ai							
E	P(S)	C	C	C	P		
P	A(N)P(S)	A	R	?	P	D	
E	R(S)	P	C	C	P		
Ai	R(S)		Ai		R		
13	3(N)12(S)	10	11	11	10	4	3

⁸Furnestin, 1953a; Oren & Komarovsky, 1961; Halim et al., 1967; Halim & Guergues, 1973; Dowidar & El Maghraby, 1971; Casanova et al., 1973; Guergues & Halim, 1973; Lakkis, 1977; ⁹Furnestin, 1958a; Vamvakas, 1973; ¹⁰Moltschanoff, 1909; Kursmorskaja, 1950; Russev & Dimov, 1957; Furnestin, 1958a, 1961; Elian, 1959; Mironov, 1970, 1973.

Cata-lunian Sea ⁴	Tyrrhenian Sea ⁵	Adriatic Sea	Sicilian Libyan Area ⁶	Ionian Sea	Levantine Basin ⁷	Aegean Sea	Marmara Sea
F	P(N)A(S)	P	A	A	A	P(N)A(S)	
F	F(N)R(S)	P	P	Ad.i	Ex	P(N)	P
L	F(N)R(S)	D	P	Ad.i		P(N)	
D	A	D	P	P	P	A(N)P(S)	P
A	P(N)A(S)		D	A	D	P(N)A(S)	
F	P(N)A(S)	P	A	D	A	P(N)A(S)	
	P(S)						
D	A(N)P(S)	A	P	P	P	A(N)P(S)	P
	?(S)				L?		
F	P(N-S)	P	P	P	P	P	
F	P(N-S)	P	P	P	P	P	
	P(S)	P		P		P	
A	P(N)A(S)	D	P	P	P	A(N)P(S)	
?	P(S)	A	A	A	A	P(N)A(S)	
10	10(N)	O(N)	11	12	10	12(N)	3
	13(S)	11(S)				10(S)	

Table VII. Diversity and quantitative distribution of Pteropoda in the Mediterranean and in the Black Sea (for abbreviations see table V)

species	ecol. char.	Albo- ran Sea ¹	South West Area ²	Central Area ³	Liguro- Provençal Region	Gulf of Lion ⁴	Cata- lunian Sea ⁵
<i>Limacina inflata</i>	M	P	D	D	D	D	D
<i>L.bulimoides</i>	Tr	Ai	Ai		Ai(R)	Ai(R)	
<i>L.trochiformis</i>	Th,Ep	D	D	D	P	P	R
<i>L.lesueuri</i>		Ai	Ai				
<i>L.helicoides</i>	B		Ai	Ai			
<i>Creseis virgula</i>	Sl,Ep	P	A	A	D	D	D
<i>C.acicula</i>	Sl,Ep	D	A	D	D	A	D
<i>C.chierchiae</i>	?d						
<i>Styliola subula</i>	Th,M	A	D	A	P	P	R
<i>Hyalocylis striata</i>	Tr,Ss	R	P	P	P	R	
<i>Cuvierina columnella</i>	Tr	Ai	Ai				
<i>Clio pyramidata</i>	B	D	D	A	P	A	D
<i>C.cuspidata</i>	B	A	P	P	A	Fr	P
<i>C.polita</i>	B,?			?			
<i>C.balanitum</i>	Tr,Sd						
<i>Diadria trispinosa</i>		Ai	Ai	Ai	Ai(R)	Ai(R)	Ai(R)
<i>D.quadridentata danae</i>	Tr,M-B	Ai	Ai				
<i>Cavolinia tridentata</i>	M	P	P	P	Fr	P	P
<i>C.inflexa</i>	Te,Eu	R	A	A	D	D	D
<i>C.gibbosa flava</i>		Ai	Ai				
<i>C.gibbosa gibbosa</i>	Th,Ss				E(R)	R	Ex
<i>C.longirostris</i>			Ai				R
<i>C.globulosa</i>	?d						
<i>C.uncinata</i>				Ex			
<i>Peracalis apicifulva</i>					R(V)		
<i>P.reticulata</i>	Th,M	P	P	?	R(V)		
<i>P.bispinosa</i>	M-B	P	P			R	
<i>P.triacantha</i>	?						Sd
<i>P.rissoides</i>	?d						
<i>Cymbulia peroni</i>	B	D	D	A	D	P	P
<i>C.parvidentata</i>		Ai					
<i>Gleba cordata</i>	?		P		R(V)	P	P
<i>G.chrysosticta</i> ?					R(V)		
<i>Desmopterus papilio</i>			Ex				
number of species	total:	27	21	23	13	18	16
						14	

authors consulted:

for the Mediterranean in general: Rampal, 1975

¹Vives et al., 1975; ²Bernard, 1955; ³Soenen, 1969; ⁴Furnestin, 1960; ⁵Hidalgo, 1917; Witz-Mangold & Wyss, 1958; Vives, 1966; ⁶Furnestin, 1960; Rampal, 1978; ⁷Steuer, 1911, 1913; ⁸Soenen, 1970, 1972; ⁹Di Geronimo, 1970; ¹⁰Casanova et al., 1973; ¹¹Grosau, 1956.

analogous to the preceding ones: a surface current from the Sea of Marmara towards the Aegean Sea and a countercurrent in the deep.

Plankton composition

Of the former Sarmatic Sea, a vast stretch of shallow brackish water with swampy banks, only a relict fauna of so-called Caspian type is left. This fauna has refuged in streams and lagoons of the Azovopontic Basin, but has, during various periods (that of the Tethys for example), also reached other, especially Mediterranean, fluvial systems. The components of this fauna are presently in an active process of speciation and they are capable of occupying new domains. Various planktonic and benthoplanktonic (Tab. IV) elements of this fauna are observed in several places of the coastal or brackish zone of the Black Sea (Bacescu, 1966b).

Tyrrhenian Sea ⁶	Adriatic Sea ⁷	Sicilian Libyan Area ⁸	Ionian Sea ⁹	Levantine Basin ¹⁰	Aegean Sea	Dardanelles	Black Sea ¹¹
D(N-S)	P(N-S)	D	Fr	A	A		
Ai(S)		Ai	Sd		Sd		
R(N)P(S)	P(S)	D	Fr	P	P		
?		Ai					
D(N)R(S)	A(N-S)	D	D	P	D		
A(N)D(S)	A(N-S)	D	D	A	D	P	
			?d				
A(N)D(S)	P(S)	A	D	D	P		
E,R(N)D(S)	R(S)	P	D	D	D	P	
Sd(S)							
R(N)A(S)	Sd	P	A	A	P		Sl
P(N)A(S)	R	P	F	P	P		
Ex(S)							
Ai(S)	Sd	Sd		Sd	Sd		
Ai(S)							
A(S)	P(S)	P	P	P	Fr		
P(N-S)	Sd	P	R	R	P(N)		
E(S)	Sd	P	A	A	D	P	
Ai(S)	R	Ai					
?	d						
Ex,Ai(S)			Sd				
P(S)		P	Sd	Sd	Fr		
R(S)					Sd		
?d(S)							
R(N)D(S)	A(S)	P	A		P		
A(S)		P					
R(S)							
R(S)							
10(N)22(S)	10	17	12	11	13	3	1

The communication of the Sarmatic Sea with the Mediterranean, after upheaval of the Alpine chains, has profoundly changed its waters and fauna. Most of the dominant planktonic species at present living in the Black Sea are of Mediterranean origin; however, these constitute a fauna which shows very little diversity compared with that of the Mediterranean, a good many groups are lacking altogether: among others Foraminifera, pelagic Decapoda, Euphausiacea, and, with rare exceptions, Siphonophora and Pteropoda.

The basic plankton components of the Western area which is affected by the current flowing to the Bosphorus, present themselves as follows, in particular in Rumanian waters where approximately 40 species have been numbered. The fauna of pelagic Copepoda is composed of a very impoverished Atlanto-Mediterranean stock with some species of fresh water or Caspian nature, in the strongly diluted areas or the littoral lagoons (Porumb, 1975). The marine forms (Tab. IV) generally are bound by a clearly cut seasonal cycle. Besides, the marine fauna

numbers four Cladocera: the most characteristic is *Penilia avirostris*, with a strong summer development; also in this season, *Noctiluca miliaris*, *Pleurobrachia pileus* and *P. rhododactyla* are observed in great abundance. In winter appear several Tintinnidae (Tab. IV) and, in spring, numerous Rotifera (Porumb et al., 1965; Margineanu, 1965, 1971).

The Appendicularia are only represented by *Oikopleura dioica* (Fenaux, 1966a). Also the Chaetognatha show a considerable diminution of their diversity compared with the situation in the Mediterranean; this diminution is a progressive one via the Sea of Marmara, which still has four species (against at least ten in the Aegean Sea). *Sagitta setosa* suddenly becomes very abundant in the Bosphorus and it swarms in the Black Sea between the surface and 100 m. *S. enflata* is still observed near the Bosphorus; the two other species disappear. In its turn *S. euxina*, the species (or form) typical of this area, appears (cf. p. 238). The Euphausiacea follow the same process, but in a more pronounced manner; the number of specimens and species diminishes very sharply between the Aegean Sea and the Sea of Marmara where no more than three species are found: *Euphausia krohnii*, *Nematoscelis megalops* and *Meganyctiphanes norvegica* (a fauna reminding of that of the W. Mediterranean); but not one penetrates into the Black Sea.

The fresh water species which are abundant in periods of flood or dominating wind from the north, in spring, are Cyclopoida (*Cyclops vicinus*, *Diaptomus gracilis*) together with Tintinnidae and Rotifera (these two latter groups represent an important biomass) and Cladocera (*Bosmina longirostris*, *Daphnia longispina*, *Chidorus sphaericus*) (Petrani, 1968). These fresh and brackish water forms are observed as far as 3-10 miles from the mouth of the big rivers, and sometimes as far as 200 miles in periods of strong floods (Dimov, 1965).

Research on marine neuston, which is highly developed in the Black Sea (Zaitsev, 1961, 1964, 1968; Politchuk, 1965a, b) has shown the richness of the Protista and Bacteria in the epineuston. At night, mass concentration of hyponeuston occurs: Amphipoda, Cumacea, Mysidacea, Macroura and benthohyponeustonic Polychaeta and certain Calanidae; the euhyponeuston comprises three Pontellidae, developmental stages of other Copepoda, big quantities of *Evadne tergestina* and *Oikopleura dioica*, 21 Tintinnidae species and numerous larvae of Cirripedea, Polychaeta and Mollusca. The highest concentrations of neuston (e.g. *Anomalocera patersoni*) are found in the zones of hydrological fronts.

Pontic influence in Mediterranean, mediterraneisation of the Black Sea

Pontic influence chiefly manifests itself in the lowering of the salinities at the mouth of the Dardanelles and in the NE. part of the Aegean Sea. It has been mentioned how the planktonic fauna of the northern and southern region of this latter are distinct, especially due to this dilution. Some analogies (the significance of which should not be exaggerated) can be observed between the fauna of the north of the Aegean Sea and that of the Black Sea: for instance, the presence of abundant populations of Cladocera (*Penilia avirostris*) and of Pontellidae of which a certain isolation in the Aegean Sea is manifest. *P. mediterranea* constitutes real swarms which play an important role in the nutrition of planktonophagous fishes (Demir, 1959).

Doubtless also the presence of *Sagitta setosa* in the Sea of Marmara and at some

places of the Aegean Sea should be seen as the result of Pontic influence, because this species is practically absent from the E. Mediterranean. Likewise we will consider the presence in the Mediterranean: 1) of *Centropages kröyeri* forma *pontica* co-existing in several areas (Adriatic, Tripoli, etc.) with the typical form (Kovalev, 1967); 2) of *Odessaia maeotica*, a Medusa which is abundantly and constantly found in the Black Sea and again in the Aegean Sea and at various places of the Western Basin (and even as far as the Moroccan Atlantic coast: *O.m. marinæ*, cf. Picard, 1951), according to Kramp (1959).

The reverse, the mediterraneisation of the Black Sea becomes more pronounced with the years and it has been possible to follow the stages of this process, as well for the plankton as for the nekton and benthos, and also with regard to the hydrological conditions of the penetration of Mediterranean species (Pavlova, 1964; Puzanov, 1967; Bogdanova & Shmeleva, 1967). Nevertheless, it seems that the rate of immigration has not yet been calculated for planktonic organisms, as it has been done for the benthic invertebrates (23%, according to Caspers, 1968; Gomoiu, 1975).

Several Mediterranean Copepoda, some of them spotted in the Bosphorus lower current (Bogdanova, 1973), are observed in appreciable numbers near the strait; some reach the central part of the Black Sea (layers from 20 to 50 m) and even the Crimean coasts (Tab. IV) (Fig. 7). These immigrants can only live in the Black Sea after a period of acclimatization in the waters of intermediate salinity of the Sea of Marmara. *Eudoxoides spiralis* (Siphonophora) has been also recorded in the central part, but *Clio pyramidata* (Pteropoda) which sometimes invades the Black Sea, does not seem to remain here (Grossu, 1956).

Variation in the Mediterranean, source of diversity

After having examined the diversity of the fauna, we shall consider the diversity within the species and we shall see how the conditions of the Mediterranean environment are capable of modifying these species. Analyses of this kind, for several planktonic groups, have significantly shown the role of this environment in the phenomena of variation, and even speciation. The following examples will give an idea of these phenomena and, depending on the case, they will show phenotypic or infraspecific variations, or such variations as attain the species level.

Polymorphism and polytypism

A comparison of the morphological analyses of Thecosomata in various seas has revealed the existence of particular forms in the Mediterranean (Rampal, 1975). The specimens of *Clio pyramidata lanceolata* of the eastern areas are distinguishable by their short protoconchæ with practically straight ribs, those of the Alboran Sea distinguish themselves by their very wide and very flat teloconch (the Alboran race).

Cavolinia inflexa imitans which has a very great phenotypic plasticity, presents three distinct types: a 'northern' type (from the Ligurian-Provençal channel) which is the biggest and the most globulous one, a 'southern' type (from the Algerian shores, the S. Tyrrhenian Sea and the Central Area) which is less massive, and finally a smaller 'eastern' type with a relatively long posterior spine; between

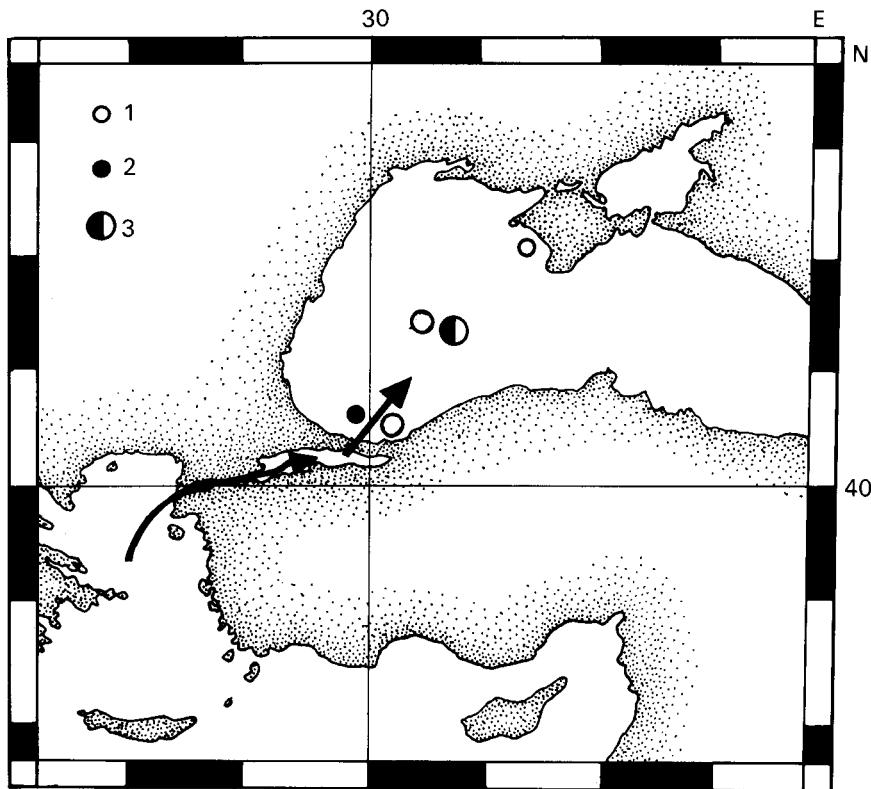


Fig. 7. Planktonic organisms demonstrating the 'Mediterraneanisation' of the Black Sea by penetrating the Black Sea by way of the deep current leaving the Aegean Sea via the Dardanelles and the Bosporus. 1 = Copepoda species mentioned in table IV, 2 = *Clio pyramidata*, 3 = *Eudoxoides spiralis*.

the northern and southern types exists a clinal variation as the populations adjust to local conditions; nevertheless, there is a distinct Algerian race with very long lateral spines which forms a homogenic population. Thus *Cavolinia inflexa imitans* constitutes a polymorphous aggregate of dense and widespread populations and races; its presence in the Mediterranean seems to date back to the Post Glacial (Blanc-Vernet et al., 1969; Froget, 1974) and it is probable that it represents the original type from which the subspecies *inflexa* and *labiata* have derived. The polymorphism of *C. inflexa imitans* is accompanied by ecological heterogeneity; though in the Atlantic and Pacific Oceans this species shows a preference for subtropical and tropical areas, in the Mediterranean it behaves as a temperate organism (distribution with a northern tendency and reproduction in winter). Though it is true that the present-day Mediterranean is favourable to an elaborate phenotypical differentiation, it has also been possible to follow a comparable evolution during the Post Glacial period and besides forms closely related to recent ones, remarkable specimens have been observed which most likely be-

longed to a purely Post Glacial subspecies (sediment levels from 10-14 cm); in deeper strata (20 cm and more) it is possible to distinguish forms which vary according to the climatic fluctuations of the corresponding periods. This proves that, at the same locality, the climate changes of the Mediterranean, even at relatively short intervals, have involved morphological variations discernible by way of biometrics.

Cavolinia gibbosa is represented in the Mediterranean by the two subspecies *flava* and *gibbosa*, distinguishable by their length and width. *C. gibbosa flava* which has a wide geographic distribution (particularly in the Eurafrican Atlantic) is only found in the Alboran Sea and in the SW. area, coming from the nearby ocean. Outside the Mediterranean vestibule, the species has not been collected from the Western Basin. *C. gibbosa gibbosa*, which on an average is much smaller and has established itself on the border of the area of the preceding one (in the S. African region, for instance), also exists in the E. Mediterranean and in the north of the Red Sea (Gulf of Elath). Nevertheless, the populations of these eastern regions differ from those S. of Africa by their inferior size and the regression of the dorsal ribs; they also deviate from those of the Indian Ocean (*C. gibbosa plana*) and they are geographically isolated. If their isolation continues it might lead to speciation.

The pelagic Decapoda provide examples of the same kind as the Mollusca but these are restricted to the present. Though a certain number of Natantia from the Subtropical and Temperate E. Atlantic, living in the Mediterranean, have kept their specific characters, with the exception of certain phenotypic variants (Forest, 1976), others present differences of a higher degree. The variations are related to both morphology and biology and have led to the description of a certain number of subspecies, justified by the fact that the observed divergences often affect very apparent characteristics which intervene in the diagnosis of species belonging to the genera concerned (for instance the form of the petasma, in *Sergestes*) (Casanova, 1977). Among the Carida, *Acanthephyra pelagica* is represented in the Mediterranean by the subspecies *pelagica* which is distinguishable from the other two Atlanto-Mediterranean subspecies (*A.p. borealis* and *A.p. mauritanica*) by several characteristics. It is not impossible that this very individualised form has already reached the stage of species. The important modification of the petasma of the male of the Pencida *Sergestes robustus* of the Mediterranean is also a reason to describe a Mediterranean subspecies, *S.r. mediterraneus*.

A similar case of geographic speciation is found in *S. corniculum*. It has been proposed to subdivide this species into two subspecies: *S.c. henseni*, covering especially the Mediterranean and *S.c. curvatus*, covering the Temperate Atlantic. It seems that here we witness speciation with neoteny in *S.c. henseni*. The specimens of this subspecies are believed to reproduce while retaining a juvenile habitus by way of blocking the growth. The Mediterranean specimens of *S. vigilax* distinguish themselves from their Atlantic relatives by the characteristics of the rostrum.

Differences also exist within the species *Pasiphaea multidentata*. The Mediterranean specimens of this species have been raised to the rank of subspecies: *P.m. sicula* (Zariquez-Alvarez, 1946), which distinguishes itself from the subspecies of the Boreal Atlantic, *P.m. multidentata*, by a longer rostrum and much smaller eyes. In the case of the Mysidacea *Eucopia hanseni* a Mediterranean race has been described (Nouvel, 1942, 1943) which differs from the Atlantic race in its perceptibly

smaller size, smaller eyes and important variations in the sex-ratio (the number of females doubles in the Mediterranean) and the fecundity rate (Casanova, 1977).

Also several Chaetognatha show phenotypic differences. *Sagitta setosa* is smaller in the Mediterranean than in the North Sea; its caudal segment is shorter, its ovaries less broad and relatively long, its anterior fins more clearly separated from the ventral ganglion. Besides, divergences concerning the same characteristics as well as the position of the seminal vesicles with respect to the caudal fin, manifest themselves in the Black Sea (Furnestin, 1958b). *S. serratodentata* reaches a bigger size in the Mediterranean (13 mm against 11 in the ocean); its caudal segment is longer, its ovaries shorter and maturity is reached at a bigger size (10 mm against 8 in the Ibero-Moroccan Area: Furnestin, 1957; Reyssac, 1963). In the Mediterranean *S. hexaptera* shows the biggest sizes known for this species [70 mm, against 52 mm in the tropical region (Ducret, 1968) and less than 40 in the vicinity of Madeira (Langerhans, 1880)]. Nanism, on the contrary, observed in a good many Mediterranean species and caused by the high temperature of the environment (Fage, 1952) has very frequently been noticed among Hydromedusae; the shortening of the biological cycle, of which one of the extreme manifestations is neoteny, has been noted in at least three species: *Zanclea costata*, *Laodicea undulata*, *Proboscidactyla ornata* (*Phialidium?*) (Goy, 1972). Later on we shall discuss size variation between Atlantic and Mediterranean populations in a general way. Specimens of the agalmid Siphonophora *Halistemma rubrum* have been compared in the Atlantic and the Mediterranean (Totton, 1954). Several differences came to light, apparent in the nectophores and bractes, which means a step in the direction of a separation between two subspecies or even two species (Pugh, 1974).

In three Salpidae with a wide distributional range, *Salpa fusiformis*, *Thalia democratica* and *T. orientalis* clinal variations have been the subject of a biometrical study (Van Soest, 1975). *Salpa fusiformis*, which is very stable all over its vast range, yet shows a certain variability in the musculature of the trunk; the number of fibres diminishes with the latitude; in the Mediterranean the specimens of the Levantine region possess less muscular fibres than the western specimens (Villefranche); this variation seems to be attributable rather to temperature than to salinity, because also the tropical populations have an inferior number of fibres. *Thalia democratica*, on the contrary, retains a rather extreme homogeneity in the area studied. Finally, *T. orientalis*, transported into the Eastern Basin by the Atlantic Current, shows the same number of muscular fibres in the ocean as in the whole Mediterranean.

Also among Copepoda, *Temora stylifera*, a neritic epiplanktonic species very common in the Mediterranean, is very sensitive to ecological conditions; it avoids the neritic zone rich in organic material and also regions disturbed by a horizontal or vertical turbulence. These hydrological barriers demarcate five principal regions with more or less independent populations for which the term race is used. Their tolerances of temperature and salinity differ; the five regions are the following: the Eastern Basin, the Aegean Sea, the Adriatic, the N.W. Mediterranean and the SW. Mediterranean. The most impervious barrier seems to correspond to the Sicilian-Tunisian sill which separates two groups of populations with clearly differing requirements. It is still necessary to bring to light possible morphological divergences which show whether the populations of the Adriatic

and the Aegean Seas have more affinities with the Levantine population or with those of the Western Basin (Bernard, 1970). The morphometric expression of the seasonal and local differentiations which affect the species forms one approach (Riera, 1972).

Can pollution cause variation, even speciation? The study of acartiid Copepoda, which are very common, particularly in the neritic zones, has shown that eight species (*Acartia clausi*, *A. latisetosa*, *A. discaudata* var. *mediterranea*, *A. italicica*, *A. adriatica*, *A. negligens*, *A. bifilosa* and *A. danae*) seem to be well adapted to the polluted waters. Some of them have a remarkable capacity of adaption to lagoon or harbour environments. Nevertheless, others show peculiar, even pathological reactions, maybe due to hydrocarbons, like a rectal prolapsus in *A. discaudata* var. *mediterranea* and *A. italicica*, or tumorous protruberances. In the polluted zones of the Tyrrhenian Sea two new species have been described, *A. josephinae* and *A. enzoi*. Their abundance is supposed to be the result of a process of selection with regard to species less tolerant of such environments (Crisafi & Crescenti, 1972, 1976; Crisafi, 1973).

A comparison of the optical organs of several Crustacea on both sides of the Strait of Gibraltar is interesting from ecological and biogeographical points of view (Casanova, 1977). In the mysid *Eucopia hansenii* the eyes of the Mediterranean specimens are smaller, whereas the size of the body is the same: the ocular pedoncles are less long and broad and the cornea occupies less space, due to a diminution of the ommatidia. The ocular diameter and the number of ommatidia has diminished in the carid *Acanthephyra pelagica* of the Mediterranean; the crystalline cones attain an inferior length. The Mediterranean specimens of the peneid *Sergestes robustus* have slightly smaller eyes, as the number and dimensions of ommatidia decrease, taking into account a certain sexual dimorphism; the size of crystalline cones is particularly discriminant.

In the euphausiid *Meganyctiphantes norvegica* the ocular diameters are superior in the Mediterranean compared with the N. Atlantic; the ommatidia are more numerous and the constituents (crystalline cones and rhabdom) are more elongated; the hexagonal facets are slightly bigger; the number of whorls of the rhabdom spires with helicoidal structure is higher. The species is represented in the Mediterranean by a distinct race (Casanova-Soulier, 1968; Mayzaud, 1971).

Relations have been established between the structure of the eyes and the ecology of Atlantic and Mediterranean populations of the various species, with regard to the quantity of light characteristic of their habitat (according to the depth or the latitudinal extension, or the transparency of the water in corresponding zones).

The species, like *A. pelagica*, *S. robustus* and *Pasiphaea multidentata*, which live at the same levels in the Mediterranean and the ocean (up to high latitudes) react to a stronger luminosity in the Mediterranean with a reduction of the eyes. The species living at the same levels and the same latitudes on both sides of Gibraltar do not show ocular variation: this is the case with *Sergestes corniculum*. Species living deeper in the Mediterranean, like *M. norvegica*, which occupies the surface or subsurface in the northern zones of the Atlantic and becomes meso- or bathypelagic in order to find the temperature conditions nearest to its optimum, undergo modifications reverse to the first, fitted to utilise the reduced light. The various populations of the same Malacostraca species are thus supposed to be susceptible to react to variations of illumination, not only by deposition or migration of pig-

ment, but also, in case of important differences as exist between the Mediterranean and certain Atlantic regions, with modifications of dimensions and structure of the eyes. These modifications on the subspecies level, to a large extent depending on the factor light, have been found to attain the same degree as those between different species.

The study of the size variation in species of several planktonic taxa, represented in the Mediterranean as well as in the E. Atlantic, throws new light on their determinant. The species concerned are divided into three groups with regard to the size they reach in the Mediterranean and in the Atlantic at equivalent latitudes (Casanova, 1968).

The first group comprises species with a smaller size in the Mediterranean; they are in the majority: examples are provided by the Mysidacea *Eucopia hansenii* [maximal L_c (length of the carapace) in females: 36 mm in the Bay of Biscay and 27 mm in the Mediterranean], Chaetognatha, Medusae, Siphonophora, Thecosomata, pelagic Decapoda and Euphausiacea. Besides, the juvenile phase in this latter taxon, e.g. in *Euphausia krohnii*, starts with a smaller size, compared with that observed in the N. Atlantic and also maturity is reached earlier (*E. brevis*, *Stylocheiron maximum*). Precocious maturity and limitation of the growth are, actually, phenomena known to occur in organisms living resp. at high or low latitudes (B. Casanova, 1974).

Species of the second group, with the same maximal sizes in the Mediterranean and the European Atlantic are rare; examples are provided by the Decapoda *Acanthephyra pelagica* ($L_c = 22$ mm) and *Gennadas elegans* (L_c males < 8 mm; L_c females < 10 mm).

Species of the third group, with bigger specimens in the Mediterranean than in the Atlantic, seem even more rare. The only examples are two Chaetognatha and one Thecosomata. *Sagitta serratodentata* reaches 13 mm in the Mediterranean and only 11 mm in the Ocean. In *S. hexaptera* the difference is more substantial: 70 mm in the Mediterranean against 52 mm in the Tropical Atlantic. For the Thecosomata no populations of the same species have been compared but the two constituents of a superspecies: *Cymbulia peroni*, which reaches 80 mm in the W. Mediterranean and *C. parvidentata*, which rarely becomes bigger than 45 mm in the Bay of Biscay.

The apparently contradictory fact that species in the Mediterranean are sometimes bigger and sometimes smaller than in the E. Atlantic depends on their boreal or tropical origin; it seems that populations of a species reach their maximal size in that part of their area situated at the highest or lowest latitude, depending if the species is of boreal or tropical nature (Casanova, 1977).

Thus the boreal *Sagitta setosa* is smaller in the Mediterranean than in the northern part of its area; the tropical *S. serratodentata* is bigger in the Mediterranean than in the Iberic region.

Differentiation of physiological races

In the Mediterranean we come across cases of ecophysiological variation leading to a differentiation into physiological races (or even species) among the Euphausiacea and pontellid Copepoda, and in the planktonic larval stages of a polychaeous Annelida. Besides differences in size and in morphology or structure of various organs (particularly the eyes), *Meganyctiphanes norvegica* shows differences

with regard to reproduction compared to the N. Atlantic population: the ripe ova are larger, the intensive period of reproduction has been shifted from the end of spring to the beginning, the larval phase is shorter, etc. (B. Casanova, 1974). Moreover, the comparison of respiration and excretion of the winter generations shows much higher averages in the Mediterranean than in the N. Atlantic; this marks a difference in metabolic systems related to differences in the environment, probably this indicates a different sensitivity to temperature variation (among other factors). As similar results have been obtained with *Phronima*, it seems that the Mediterranean induces the formation of thermal races by inurement of the specimens to a wider range of temperature than in the north oceanic region (Mayzaud, 1971).

The case of the hyponeustonic Pontellidae is more complicated. The two species in question, *Anomalocera patersoni* and *Pontella mediterranea*, stenotherm and stenohaline, have colonised very extensive areas marked by important divergences in temperature and salinity. The variety of regulatory systems present and the differences of biometric order which separate seasonal populations are such that one is induced to think that there exist physiological races peculiar to the various regions inhabited by these species and that each race shows strong adaptability (Champalbert, 1975).

The very wide dispersal and more particularly the presence of these two stenohaline species in the Black Sea actually implicate high possibilities of metabolic adaptation. The natural selection is supposed to have controlled the progressive appearance of populations physiologically capable of following the evolution of environmental factors while remaining morphologically identical and retaining the adaptive characteristics indispensable to life at the surface, particularly those with a protective function: the escape reaction and the pigmentation. It is assumed that in this way genetically different races have formed without the original adaptations being altered. Besides, the seasonal distribution of the two species concerned, which is restricted by their temperature requirements, as well as their disappearance for several months from the upper surface waters, lead to the supposition that they have resting eggs as known, for example, for certain Copepoda from the Temperate Waters—which only open at definite temperatures.

Probably it happened during extensive hydrological fluctuations which occurred at the end of the Tertiary and the beginning of the Quaternary that, in spite of the fairly strict temperature and salinity preferences of the Pontellidae, some species proved to possess a remarkable adaptive potential which, with the formation of local races, enabled them to occupy areas of a different nature. These phenomena have been shown particularly clearly in the Mediterranean and Sarmatic Basins. At present it would be desirable to know the elementary and pigmentary composition of the most typical species and to study simultaneously the fluctuations of their metabolism and of their behaviour in terms of the various ecological factors, at the same time in the Mediterranean, in the Black Sea and in the tropical or northern zones of the Atlantic where the Pontellidae occur. It would also be useful to define the modalities of reproduction, in particular of the species of which the biological cycle is interrupted by a discontinuity of appreciably long duration (Champalbert, 1975).

An ecophysiological and ethological comparison between the different ontogenetic phases in Mediterranean and Atlantic populations of the Polychaeta *Scolelepis fuliginosa* (Spionidae) has shown the existence of major differences while the adults

are morphologically identical. These differences concern the gametes and the larvae, consequently the planktonic stages, but also the reproductive behaviour of the adults. These differences are: in the Mediterranean, an inferior length of the spermatozoids, a practically smooth shell of the ovocytes, less accentuated pigmentary spots, gastrotrochs on all setigers from the third onwards, a shorter developmental period, dissimilar hatching and larval development.

These differences acquire their full importance when we consider all Spionidae. Actually this family consists of two groups according to the morphology of the gametes and the way of reproduction: the genus *Scolelepis* is intermediate between these two groups, with characteristics peculiar to the one and to the other group. In the first, the eggs have a thick shell and are laid freely; the fecundation is external; in the second group the ovocytes have a thin shell and are disposed in a cocoon and a kind of copulation takes place. In the Mediterranean *S. fuliginosa* a mass of mucus which embodies the egg serves as a cocoon; it limits the spilling of gametes assuring the fecundation of a majority of eggs; it keeps the embryos in surface water rich in dissolved oxygen and it serves as nourishment to the young larvae. These observations confirm the transitional position of *Scolelepis* between the two groups of Spionidae. But this species also breaks the unity of the genus as the Atlantic and Mediterranean populations of *S. fuliginosa* are different. The presence of the gastrotrochs on all the setigers in the Mediterranean larvae comes close to the first group, whereas, by the morphology of their gametes and their way of reproduction these same populations approach the second group (genera *Spio*, *Microspio*, etc.). The modifications arisen in these populations of *S. fuliginosa* which doubtlessly derive from the Atlantic populations, naturally fits in with the line of evolution of the Spionidae where exactly an economising of gametes is in progress. The acquisition of the capacity to secrete mucus which enabled the adults grown out of larvae which had come from the ocean, to reproduce and to initiate a Mediterranean population, came together with a morphological change of the gametes. This is a phenomenon of microevolution, perhaps triggered off under the influence of environmental conditions (the absence of tide?). This process which probably started as a local phenomenon, has led to speciation; afterwards other modifications occurred in the newly established population. The phenotype of the adults, however, has not yet changed, doubtlessly because it was adapted, in its present form, to its environment. The process of speciation is therefore relatively little advanced; in spite of the impossibility, at present, to distinguish between the adults (except by examining the gametes), it is certain that the Mediterranean and Atlantic populations of *S. fuliginosa* belong to distinct species: such is the conclusion of this interesting study (Guérin, 1975).

Regions favourable to variation

Certain regions of the Mediterranean Basin where environmental conditions, although natural, are very special, prove to be very propitious to variation. The Adriatic is one of these regions, where numerous planktonic organisms show this tendency.

A comparative biometric study of two populations of the Copepoda *Centropages typicus* and *Calanus helgolandicus*, the one from the Gulf of Trieste, the other from the most southern sector off Dubrovnik, reveals significant differences. The

population of Trieste is composed of specimens of different sizes: the average dimensions of the biggest ones approach those observed at Dubrovnik. One of these groups, characteristic of the gulf, is supposed to live there permanently and to reproduce there; the other is supposed to be composed of specimens transported from the S. Adriatic by currents flowing along the Dalmatian shores (Vianello, 1968; Catalfarno, 1968).

In the same way a comparative biometric study of populations of the Siphonophora *Muggiaeae kochi*, from the Gulf of Trieste and the Channel (Plymouth) or the Atlantic (Bay of Biscay) has revealed that the supporting float is smaller in the Upper Adriatic; besides, there is a significant difference between the specimens of Trieste and those of Biscay with regard to the ratio between the length of the stomatocyst and depth of the hydroecium (Rottini, 1974). Finally, there are the remarkable gonophora (known as *Ersaea elongata*) of which it is not known if they correspond with a polymorphism or with an anomaly; they represent 25% of the gonophora of the species (Gamulin & Rottini, 1966).

In the Lower Adriatic a small-sized form of *Cymbulia peroni* (35-40 mm against 50-80 mm in the Mediterranean) is supposed to form a local race (Steuer, 1911). Likewise, three of the Mysidacea of the Italian Adriatic shores are interesting because of their variability: *Siriella jaltensis gracilis*, *Gastrosaccus lobatus* and *G. sanctus* (Ariani, 1967). On the Yugoslavian coasts, variations (general habitus, size, reproductive ability) have also been noticed for *G. sanctus* and *Boreomysis megalops* with regard to populations outside the Adriatic (Hoenigman, 1963b).

We shall confine ourselves to these few examples for we already insisted on the notorious faunistic individuality of the Adriatic (p. 208). This individuality may be the source of the important number of new species which have been described in this region; nevertheless, many of these having been observed, since their description, in various regions within or outside the Mediterranean, their Adriatic origin has not been proved: 1 Medusa (also observed in the Atlantic Ocean), 1 Siphonophora, 2 Mysidacea, 23 Copepoda of the Middle and Lower Adriatic, some of which have also been found in the Tyrrhenian Sea or in the Eastern Basin or even in the Red Sea: 10 Calocalanidae, 11 Oncaeidae, 2 *Scaphocalanus* species (Tab. IX).

The Black Sea, in its turn, provides special ecological conditions and a sufficient isolation to make variations appear and remain. Though the adaptive particularities essentially concern the benthos (Gomoiu, 1975), the study of variability of planktonic Copepoda in the Black Sea (and the Sea of Azov), in comparison with the Adriatic and other Mediterranean sectors, is not less instructive (Koval'ev, 1968a, b; 1969).

Sizes have been compared in relation with the conditions of the habitat: of the eight species dominant in the Black Sea, four are smaller (*Pontella mediterranea*, *Centropages kröyeri*, *Paracalanus parvus* and *Oithona nana*), two are bigger (*Pseudocalanus elongatus* and *Calanus helgolandicus*); the sizes of *Acartia clausi* (eurytherm) and of *Oithona similis* (cryophile), on the other hand, do not vary from one sea to another. Also the variability of 11-16 indices regarding morphology and dimensions of various organs has been compared for six of these species (except *Oithona*). The populations of the Black Sea are distinguished by a marked individual variation. The variability of certain indices seems to have an adaptive character: especially in terms of the density and viscosity of the environment, in order to preserve good floating and motility. This analysis brings us to recall

the study in the neighbouring Aegean Sea, of the variability of several morpho-ecological factors in six Copepoda (*Temora stylifera*, *Centropages violaceus*, *C. typicus*, *Calanus* (= *Nannocalanus*) *minor*, *C. helgolandicus* and *Clausocalanus arcuicornis*). The results of this study showed how temperature affects the sex-ratio and directly or indirectly the size; how, for instance, the smallest size on reaching maturity corresponds with the highest temperatures of the water in which growth takes place (Moraitou-Apostolopoulou, 1969b).

The development of such considerations would lie outside the framework of this chapter, but they bear witness to the fact that the ecological and zoogeographical fields are related and that it is often difficult to define their limits. Thus, variation of certain species under the pressure of the environment is the source of forms peculiar to the Black Sea: among the Copepoda, *Centropages kröyeri pontica* differs from the typical form by its inferior size, as well as by characteristics of the abdomen (of the female) and of the 5th pair of appendages (of the male). This is the only form in the Black Sea (and Sea of Azov), but it coexists with the typical form in several sectors of the Mediterranean: Adriatic, shores of Tripoli etc. (Kovalev, 1967). In the same way, *Calanus helgolandicus*, which came from the Mediterranean to the Black Sea in the Post Tertiary, has formed there the subspecies *C.h. ponticus* (Jaschnov, 1955). Also other species react in this way to ecological conditions by a modification of biological characteristics: the greater number (7-9) of annual generations of *Acartia clausi* seems to be peculiar to the Black Sea, compared with the Mediterranean, the Adriatic and the Atlantic (Porumb, 1968).

Also Chaetognatha play a role in a study on variation. It is interesting to compare *Sagitta setosa* which swarms in the Black Sea, with specimens from the Mediterranean and from the N. Atlantic which represents one of the centres of distribution of the species. It is noted that in its various geographical areas, *S. setosa* is exposed to perceptible variations, particularly in size, length of the caudal segment and length of the ovaries, even if these variations do not go as far as disrupting the unity of the species (Furnestin, 1958a, b; Mironov, 1970, 1973). On the other hand, the Black Sea seems to have permitted the development of an endemic form, *S. euxina* of which several authors since Moltchanoff (1909) have specified the morphological and biological characteristics (Kursmorskaja, 1950; Russev, & Dimov, 1957; Elian, 1959).

Place of the Mediterranean within the Atlanto-Mediterranean province

A palaeogeographic outline

We shall only recall the broad outline of the Mediterranean palaeogeography (according to Furon, 1950; Tortonese, 1964; Klausewitz, 1969; Alvinerie et al., 1978) in so far as it reveals the origin of certain singularities of the present plankton fauna. The former Tethys, of a tropical nature, which extended from the Antilles to the Malayan islands and was confined between the N. Atlantic and the Equatorial continents provided, until the beginning of the Tertiary period, a direct communication between the three oceans. It is responsible for the Indo-Pacific affinities of a certain number of organisms still living in the Mediterranean. In the Miocene this sea undergoes great modifications due to the Alpine Foldings;

it becomes isolated from the Indo-Pacific but retains its relations with the Atlantic; it is now called Paratethys, still tropical, with a fauna which has affinities with that of the present-day Indo-Pacific and Tropical Atlantic.

In the Pliocene and at the beginning of the Quaternary a series of sinkings took place in the Mediterranean massifs, around which the Alpine Foldings formed: massifs of the W. Mediterranean, of the Adriatic, of the Aegean Sea, etc. The communication with the Atlantic which hitherto had passed through the Spanish (W. Iberic) and Moroccan (Rif region) straits, now go via Gibraltar. At about the same time the opening of the Dardanelles takes place and right after the sinking of the Red Sea area occurred, the isthmus of Suez establishes itself thus separating the Red Sea from the Mediterranean, where the temperature decreases and the fauna, therefore, becomes subtropical. With the end of the Pliocene a warm world dies out upon which a 'glacial catalysm' is going to sweep down. Only a small number of eurytherm species from the former Tethys and Paratethys are to survive. The Atlantic which is amply open to the north, provides, via the Strait of Gibraltar, an easy way in for boreal and even arctic species which progressively replace the local elements; their penetration is maximal in the Middle Pleistocene with an increased cooling down of the Atlantic. Nevertheless, cold and warm glacial and interglacial periods succeed each other; among the best marked periods are the Calabrian stage (First Glacial Period) which results in an invasion of boreal forms, whereas the Tyrrhenian I stage (Second Interglacial) is characterised by a warm water fauna replaced in its turn by another boreal fauna of the last glaciation, while a considerable marine regression (Grimaldien) temporarily isolated the Mediterranean of the open ocean. The settlement of these boreal forms, though, is of relatively short duration: the warming up in the Post Glacial period contemporaneous with the formation of the Gulf Stream and the Atlantic transgression of the Flandrien annihilate the greater part of this cold fauna and bring temperate, subtropical and even some tropical species back into the Mediterranean. At that moment the Mediterranean fauna assumes its present-day aspect.

Thus the Mediterranean received the bulk of its fauna from the Atlantic (the majority of the Copepoda from the Western Basin, for example, are known to exist in the Temperate Atlantic). However, because of the fact that the Mediterranean fauna has been renewed several times during its long history, while retaining witnesses of the successive contributions of cold and warm forms, this fauna presents numerous particularities.

Besides, though enough similarities exist between the faunas of the Mediterranean and the Atlantic to define an Atlanto-Mediterranean Province, the two sub-provinces (the Ibero-Moroccan subprovince and the Mediterranean one) present remarkable differences although situated at approximately the same latitude on both sides of the Strait of Gibraltar. These differences have various causes: the strait which provides the communication between the two regions is narrow and of shallow depth and is the seat of a deep current opposed to the superficial Atlantic Current; this situation causes a selection of the W. - E. exchanges; besides, the conditions met with by the introduced fauna are considerably different from those of their original environment; the temperatures and especially the salinities are much higher; there is yet another particularity which does not promote the settling of Atlantic forms: the homothermy of the deep (approx. 13°C in the Western and 13.5°C in the Eastern Basin). Some organisms

do not survive these new conditions, others adapt with apparent ease and a third group shows changes in the course of its adaptation. The shallow living fauna enters the Mediterranean most easily and the Transitional Waters it finds there promote its settlement; the deep living oceanic forms, on the contrary, as far as they have been able to get across the sill of Gibraltar, acclimatize with difficulty. They have been transported from the Atlantic where the deep layers are not warmer than 3°C and now they find an environment where the temperature is relatively high and uniform below 300 m.

Components of the Mediterranean planktonic fauna

The successive variation in temperature during the various geological periods have resulted in an overall reduction of the Mediterranean fauna. Although the organisms inhabiting the E. Atlantic underwent the same ecological influences, they have escaped destruction by migrating, either to the south (tropical and subtropical species) or to the north (Boreal and Arctic species), while the steno-therm species have practically disappeared from the Mediterranean and only the eurytherm species survived.

An impoverished Atlantic fauna

It is not possible to discuss point for point these gradual disappearances; it is easier to take one animal group at a time and note the Atlantic forms which do not appear in the Mediterranean (Tab. VIII); new records are gradually reducing their list which is therefore provisional. This is mostly the case with rare or accidental species in the Mediterranean, which were discovered owing to deep prospections or to adequate equipment.

Some forty years ago, 25 Siphonophora were considered absent from the Mediterranean (Bigelow & Sears, 1939). Since then at least two have joined the 48 species known in the Western Basin (plus 7 newly described species). From Kramp's fine study (1959) it follows that the Hydromedusae fauna of the Mediterranean may be considered an impoverished Atlantic fauna: thus, many neritic forms from the ocean have not been observed in the Mediterranean; at the same time this was also the case of 16 epiplanktonic warm water forms (on a total of 32 in the ocean) and of at least 18 bathyplanktonic ones (on a total of 25); the total inventory in the Mediterranean consisted of 92 Hydromedusae (65 neritic forms, 19 epaplanktonic and 8 bathyplanktonic forms). At present the number has risen to 116, owing to additions of species also known elsewhere, or of newly described species.

The deep living fauna has been greatly affected by the impoverishment recorded. More than a third of the Amphipoda, especially the exclusively deep living Hyperiidae as well as the Lanceolidae, are not observed in the Mediterranean, neither are Pelagonemertea, nor *Pyrosoma spinosum* and *P. agassizi* (a juvenile form of the first species?) (Godeaux, 1973a, b).

Of the Chaetognatha frequenting the deep waters of the Temperate Atlantic, two are not found in the Mediterranean. The total number in the Mediterranean is 18, including *Sagitta euxina* and the subbenthic *Spadella cephaloptera* (this number is 27 in the African Atlantic).

Table VIII. Composition of the Mediterranean fauna with regard to the Atlantic fauna
(for abbreviations see table IV)

COPEPODA

Pareuchaeta scotti, *P. barbata*, *Metridia princeps*, *M. longa*, *Lucicutia grandis*, *L. maxima*: N, B (Mazza, 1967); *Eucalanus elongatus*, *Chiridius poppei*, *Pleuromamma abdominalis*, *Lucicutia flavicornis*, *Oncaea conifera*: Md (Vives et al., 1975).

MYSIDACEA

Gnathophausia zoea: N; *Eucopia australis*, *E. sculpticauda*: N, B; *E. grimaldi*: N, P?.

EUPHAUSIACEA

Thysanopoda acutifrons: N, C; *T. obtusifrons*, *Euphausia gibbooides*, *Nematoscelis tenella*, *Nematobrachion flexipes*: N, B, W, Sf; *T. microphthalmus*, *T. pectinata*, *S. affine*: N, W; *Nematobrachion boopis*, *Stylocheiron elongatum*: N, B, T; *S. carinatum*: N, E, W; *Benteuphausia amblyops*: N, B; *Thysanoessa gregaria*: Md (Casanova, 1974).

DECAPODA

Funchalia woodwardi: P, R (Casanova, 1977); *Gennadas valens*, *Sergestes atlanticus*: P, Ex.

MEDUSAE

Colobonema sericeum, *Aegina citrea*: N, B; *Atolla wyvillei*: P?, B.

SIPHONOPHORA

Nectopyramis thetis, *Heteropyramis maculata*: N, B; *Abyla trigona*, *Abylopsis eschscholtzi*: X', Ex (Furnestin, 1958c; Casanova, 1977); *Chuniphyes multidentata*: Md? (Casanova, 1970).

APPENDICULARIA

Bathochorideus charon, *Althoffia tumida*, *Pelagopleura verticalis* species group, *Oikopleura labradoriensis*, *O. vanhoeffeni*, *O. fusiformis* f. *cornutogastra*, *Fritillaria helleae*, *F. abjornseni*, *F. aberrans*, *F. borealis* f. *typica*: N.

CHAETOGNATHA

Sagitta maxima: N, C; *S. macrocephala*, *Eukrohnia hamata*: N, B, T; *S. planctonis* f. *zetesi*: N, B (Pierrot-Bults, 1975); *S. tenuis*, *S. hispida*, *S. bierii*, *E. fowleri*, *E. proboscidea*, *Krohnitta pacifica*: N, W, M; *S. planctonis*: N, W, Md (Furnestin, 1963).

PTEROPODA

Peraclis moluccensis: N; N?, Se: cf. table VII; *Limacina bulimoides*, *L. lesueuri*, *Peraclis bispinosa*: Md (Casanova, 1977).

Although 32 Thecosomata have been recorded in the Mediterranean, it seems that only 27 species have been recorded with proof (Tab. VII). Besides, the participation of the species in the fauna is very different on both sides of Gibraltar: certain species which are very frequent or abundant in the ocean, are very rare in the Mediterranean. The bathypelagic forms which cross the strait rarely go beyond the Alboran Sea. This is the case with *Peraclis apicifulva* and *P. bispinosa*. In comparison with the temperate or warm regions of the Atlantic 12 Appendicularia species have not been collected in the Mediterranean (Fenaux, 1966).

Nevertheless, several of them are represented by a form of the same group; the relations of these forms with those living in the ocean has still to be studied.

Also numerous Crustacea species are lacking, Mysidacea for instance. *Eucopia hanseni* shows a Mediterranean race distinct from the Atlantic race. On the other hand, *Boreomysis semicaeca*, a Mysidacea with a distribution in the deep waters of the Atlantic between 45°5'N and 37°5'S, considered absent from the Mediterranean, has been noticed in the Western Basin (Casanova, 1970).

There are twelve Euphausiacea species, some of which are common in the nearby ocean, not observed in the Mediterranean. The absence of most of these is difficult to explain one of them is epiplanktonic and four others are meso- or bathyplanktonic but come to the surface at night. Besides, the generally superficial position of the larvae of all these species should be favourable to their transport through the strait. Finally, the number of Euphausiacea known beyond doubt to exist

in the Mediterranean is 13. The presence of *Thysanopoda subaequalis* and *Nematoscelis microps* remains doubtful (B. Casanova, 1974).

The pelagic Decapoda are rather badly represented in the Mediterranean: of the 38 met with west of Gibraltar only 14 have been recorded E. of the strait. *Sergestes japonicus* is the only bathypelagic Decapoda recorded in the Mediterranean (Sund, 1920; Franqueville, 1971). *Funchalia villosa*, thought to be absent, has been noticed in the Western and Eastern Basins (Casanova, 1977). The Mediterranean Copepoda fauna is also a very reduced Atlantic fauna. According to Sewell (1948), there are more than 350 species in the deep layers of the ocean between 20° and 60°N, and only some sixty have been recorded in the Mediterranean, most of them very rarely. The large species which are most obviously bathyplanktonic in the Temperate Atlantic, are not observed, especially those of which the diurnal migrations do not reach to 150 m depth (almost 30 species, according to Vives et al., 1975).

What has been said with regard to several elements of the benthos or necton, that is to say that there is no strictly abyssal fauna in the Mediterranean (in: Ekman, 1953), has thus been partly verified for the plankton.

Faunistic barrier of Gibraltar

The Strait of Gibraltar is 15-20 km wide, its average depth is 450 m and it includes a series of irregular shallows, the sill of Gibraltar, which comes to less than 200 m below sealevel; its maximum depth is 320 m. Three water masses, of Atlantic or Mediterranean nature, participate in the dynamics of the strait: the light Atlantic Waters with a salinity below 36.50‰ S occupy, roughly, the first 150 m; they have two origins: the most superficial layer essentially originates from the W. Iberic coasts (36.20-36.30‰ S; 15.50°-22°C) and flows through the north and the centre of the strait; underneath is a colder (< 15.50°C) and less saline (35.90-36.20‰ S) one, related to the waters from the open ocean at depths from 200-300 m. This layer has been brought to the surface in the region of Spartel and Tanger, by a flow which is a continuation of the Moroccan Upwelling (active in summer as far as Cape Spartel). This water mass with a low salinity, found right above the discontinuity layer, contributes to accentuate the contrast with the Mediterranean Waters; like the preceding one, this water mass is dragged in the direction of the Alboran Sea and chiefly flows in the southern part of the strait from where its branches flow northward; in the vicinity of the sill it may come to the surface as a result of the vertically pushing Mediterranean tongue (Fig. 8).

The Mediterranean Water found below the layer of discontinuity has a salinity of > 38.40‰ S and a temperature around 13°C (this mass originates from the association of the 'inferior northern water' formed in the Western Basin by the winter cooling, and the water with an eastern character, of a salinity > 38.50‰ S and a temperature > 13°C). Between 150-300 m this water mass forms an out-flowing current.

Local eddies in the N. and S. of the strait canalise the Atlantic Current into a very narrow bed giving it great power E. of the sill. Because of the Coriolis forces the Atlantic Waters tend to accumulate in the southern part of the strait, while the Mediterranean Waters are pressed to the surface in the Spanish region. The transversal interface between the two water masses is strongly inclined as the

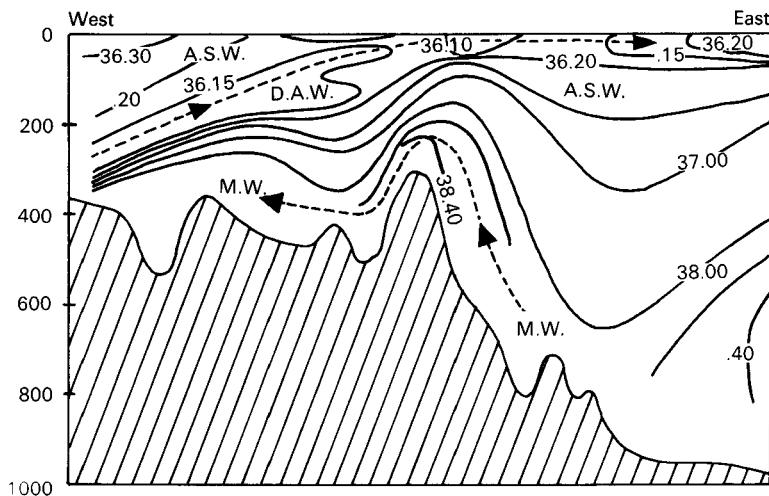


Fig. 8. Hydrological exchanges in and near the Strait of Gibraltar represented in a section along the axis of the strait. ASW = Atlantic Surface Water (36.20 - 36.30‰ S), DAW = rising Atlantic deeper water (< 36.20‰ S) coming from > 200 m depth to the surface, MW = Mediterranean Water (38.40 - 38.43‰ S) (modified after Allain, 1964).

depth of immersion of the discontinuity augments to the south (Allain, 1964; La-combe, 1971).

To what extent can the Strait of Gibraltar limit the passage of organisms from the ocean into the Mediterranean? In order to answer that question it is necessary to distinguish surface and subsurface organisms from the deep living ones. The absence in the Mediterranean of certain surface and subsurface forms which are common in the Ibero-Moroccan Bay is attributed to the hydrological characteristics of these former waters, especially to their salinity which is much higher than that of the ocean. For the deep living forms the existence of the sill of Gibraltar is supposed to be another obstacle in addition to the unfavourable conditions (high salinity and very high temperature: about 13°C from 300 m downward). Thus the absence in the Mediterranean of the bathypelagic species is explained (Tab. VIII). However, a hydrological section made along the axis of the strait and passing via the line of the greatest depths, suggests that the sill opposes rather the outflowing than the inflowing current; meso- or bathyplanktonic forms could probably take this latter current (promoted by the ascending movements in the region Spartel-Tanger). Besides, the nocturnal migrations, very frequent among deep living species, should be taken into consideration. Though organisms without these migrations can only accidentally cross the sill of Gibraltar, the latter does not form an obstacle for those species reaching the surface or subsurface during their nocturnal journeys; this is the case with the Euphausiacea, showing a diurnal rhythm (e.g. *Euphausia gibboidea*); besides, the generally superficial position of their larvae is a factor favourable to their introduction into the Mediterranean (B. Casanova, 1974). The same has been found for Copepoda, which are divided into three groups according to the levels they reach during their noctur-

nal migrations, namely 300, 150 and 50 m resp. The species of the first two groups are supposed to cross the sill only exceptionally, those of the third group, on the contrary, are able to penetrate into the Mediterranean where they form a contingent of Atlantic meso- or bathypelagic species. Also for pelagic Decapoda the amplitude of the diurnal rhythms is sufficient to bring these organisms to the surface or subsurface. However, yet other possibilities for crossing the shallows are open to the deep living species: the tendency of juveniles of numerous species to live less deeply than the adults, which brings them in the layer of Atlantic Water flowing into the Mediterranean (which is demonstrated by e.g. *Eucopia hanseni*, *Sagitta planctonis* and *Chuniphyes multidentata*). Another factor is the seasonally different bathymetric dispersal related to either the reproduction or to a relative homogenization of the temperatures in the water column during cold periods; these variations are liable to bring various deep living species into the Atlantic Current (Casanova, 1977). Thus it seems that chiefly the hydrological characteristics which are different on both sides of the strait limit faunistic exchanges, as the sill only obstructs strictly bathypelagic species.

Once introduced into the Mediterranean, however, not all organisms survive; the epipelagic species are best adapted. They stay in the current which remains superficial itself, and brings them at variable distances from the strait. The deep living species, on the contrary, are submitted to two ecological pressures of opposite nature: stay in the zone under Atlantic influence, with properties closest to those of their original habitat, where they have to adapt to surface conditions; or return to the original depth levels where they meet unfavourable ecological conditions. Modifications of vertical distributions are indeed frequently observed in organisms brought into the Mediterranean by the Atlantic Current (Tab. VIII); in the ocean these forms are meso- or bathypelagic for the most part, or eurybath and in the Mediterranean they are found in the layers between 0-200 m, which correspond to the water under Atlantic influence. This may be considered a biological necessity as well as a result of a hydrological nature. Besides the effects of the superficial cyclonic currents in the Alboran Sea, the contact zone between the Atlantic and the Mediterranean Waters seems to constitute a barrier which opposes the return of the deep living species to their depth preference. Those which nevertheless succeed in getting across the interphase are brought back into the ocean by the outflowing Mediterranean Current (Vives et al., 1975). The most dense water, however, moves cyclonically in the deep layers E. of the Strait and in the Alboran Sea, and therefore it avoids returning into the Atlantic (Allain, 1964).

Relative isolation of Atlantic and Mediterranean populations

Besides the exchanges at species level, it is interesting to study those between populations of the same species living both in the Mediterranean and in the ocean. Various examples indicate that the pelagic species of the Atlanto-Mediterranean Province show, on both sides of Gibraltar, sufficiently individualised populations to suppose the absence of interbreeding, judging from their respective incapacity to live in the domain of their homologues.

Among Thecosomata the morphological differences between Atlantic and Mediterranean specimens of the same species are so accentuated that one may speak

of Mediterranean races, apparently incapable of survival at the west side of the strait. For *Cavolinia inflexa imitans* an 'Algerian race' has been described which is very typical, with its long lateral spines. In the S.W. of the Mediterranean this race forms a homogeneous population which is different from that of the nearby Atlantic. In the same way there exists an 'Alboran race' of *Clio pyramidata lanceolata* which is broad and flat and very wide at the level of the lateral spines; this race is distinct from the neighbouring Atlantic forms (Rampal, 1975).

Among Decapoda none of the samples studied showed characteristics from both Mediterranean and Atlantic populations, which would be the case if their representatives could live as well E. as W. from the Strait. Thus the Atlantic form of *Sergestes robustus* (identifiable by the petasma of the male) which is abundant in the Ibero-Moroccan Bay and can clear the obstacle of Gibraltar during its nocturnal migrations to the surface, is never observed in the Mediterranean collections. Reversely, no male of the Mediterranean form appears in the pelagic trawlings executed in the Lusitanian zone. In the same way the specimens of *Acanthephyra pelagica* which have been identified either in the Mediterranean or in the Bay of Biscay belong, without exception, to the subspecies typical of these two regions.

The ecological adaptation of the various populations is such that the Atlantic specimens, when introduced into the Mediterranean, do not survive and that Mediterranean species cannot live in the ocean where they nevertheless initially came from. The boundary between two hydrological systems seems to realize an ecological barrier resulting in the genetic isolation of the populations. From this it would follow that the present-day Mediterranean could no longer be colonised by Atlantic populations of species which nevertheless adapted at a time when the hydrological conditions of the two basins were still more closely related (Casanova, 1977).

Under these circumstances the impact of Atlantic inflows into the Mediterranean could remain restricted to a more or less temporary enrichment of the regions concerned, mainly the Alboran Sea; however, they would not have any lasting effects as they do not result either in a real colonisation, or in interbreeding of populations of the same species W. and E. of Gibraltar (Casanova, 1977). This conclusion which is applicable to pelagic Decapoda can, as a matter of fact, not be generalised. The effects of the Atlantic contribution on the faunistic diversity of regions very distant from the strait make it possible to admit the survival of many organisms, some of which seem to constitute localised but permanent faunas at favourable places.

Relicts

The geological history of the Mediterranean leads to the consideration of two categories of relict faunas: a Tethyan warm water fauna and a boreal cold water fauna.

Tethyan relicts—At the end of the Pliocene the warm water forms in the Mediterranean Basin are dying out, because of the Ice Ages. Of the former Tethys and Paratethys only a small number of eurytherm species survived; these are witnesses of the link realised by the Mediterranean in the Oligo-Miocene between the Atlantic and the Pacific. In the north of the Red Sea, several Foraminifera

are known which have survived the glaciations from the Quaternary and are considere Tethyan relicts (Herman, 1965). It has been possible to follow the variation in the dispersal of those warm water forms during the fluctuations of the glacial periods: their regression to southern regions in cold phases and their return during interglacials and in the Post Glacial. In the Mediterranean the survival of such forms may be explained by the existence of certain less cold niches, chiefly in the Eastern Basin. Nevertheless there are a few examples among planktonic organisms: almost the only taxa for which examples have been noted are Copepoda, Pteropoda and Hydromedusae.

Among Copepoda it is a matter of tropical and subtropical species (*Eucalanus subcrassus*, *E. pileatus*, *Rhincalanus cornutus* f. *typica*); their present distribution is marked by a large discontinuity between their African habitat and the Mediterranean where they are supposed to have subsisted at favourable places. However, sometimes the hypothesis of a progressive adaptation to the conditions of the Atlanto-Mediterranean Province, or again that of an accidental and relatively recent penetration into the Mediterranean are opposed to their survival throughout the climatic and hydrological vicissitudes of the Quaternary (Mazza, 1967). Also is discussed in Sewell (1948) the case of various species known from Indo-Pacific, Tropical Atlantic and Mediterranean: *Centropages aucklandicus*, *Oithona hebes*, *Oncaeaa dentipes*, etc.

Among the Pteropoda we shall examine the case of *Cavolinia gibbosa*, a polytypic species composed of three subspecies: *C.g. plana* of the Indo-W. Pacific Ocean, *C.g. flava*, the original phenotype with a large distribution in the Atlantic and E. Pacific and *C.g. gibbosa*, smaller than the preceding one and situated along the border of the latter's area, showing a discontinued distribution: the populations of the E. Mediterranean and the north of the Red Sea constitute geographical isolats. The specimens forming these populations are morphologically identical and very different from the other representatives of the species; they are probably on the way to speciation. The disjunct distribution of *C.g. gibbosa*, isolated from the other centres of dispersal of the species may be explained if one considers this subspecies a Tethyan relict. The origin of these populations may lay at the end of the Tertiary, a period of great development of this group, its elements having resisted the glaciations in shelter-niches. In the Pliocene these two separate groups of specimens developed in a similar way, independently from the other populations of the species. The fact that the present-day specimens from the E. Mediterranean or the Red Sea are, morphologically, closer to the Atlantic and E. Pacific forms than to those of the Indian Ocean, supports the hypothesis of the survival of Tertiary descendants in the E. Mediterranean. A proof of this might be formed by the discovery of *C. gibbosa* in the Quaternary glacial sediments of the Eastern Basin and of the Red Sea (Rampal, 1975).

Relicts of the Tethys have also been found among the Hydromedusae. Numerous species of the Mediterranean also inhabit the Indo-Pacific (16 neritic, 10 epi-planktonic oceanic ones and 6 bathypelagic); their origin, however, is uncertain because they also live in the Atlantic with the exception of one, rare and dispersed neritic species, *Eutonina scintillans* which might be a Tethyan relict (Kramp, 1959). Also the Moerisiidae could be the subject of a discussion. According to Picard (1951) their dispersal is included within the range occupied by the Meso-gea until the Tertiary, from the Antilles to its oriental outlet into the Indian Ocean, passing through the Mediterranean and Pontic Basins. The *Halmomises*

enter perfectly into this geographic frame but they have no more marine representatives. One of the four forms of the species *Odessia maeotica*, though, does live in waters with a normal salinity: *O.m. marina* inhabits the Mediterranean and even extends beyond it as far as the Atlantic coast of Morocco. This species could derive, gradually transforming, from *Halmomises* which were widely distributed in Tertiary times, which resulted in the genus *Odessia*. The evolution of the Moerisiidae could thus be based upon 'Tertiary relicts' on the one hand and upon the relatively recent withdrawal from the marine environment of most descendants of this family which subsisted to our days in the Mediterranean, on the other hand. However, according to Kramp (1959) the presence of *O. maeotica* at various places of the Mediterranean (Aegean Sea, Gulfs of Trieste and Naples, Gulf of Lion) and in the Moroccan Atlantic Waters is probably the result of an immigration from the Black Sea where it is constantly and abundantly present.

For the sake of completeness we will finally mention the case of *Sagitta enflata* which sometimes has been taken as a Tethyan relict. This species is predominant among the Chaetognatha of the Western Basin (Alboran Sea and N. African shores), and well represented in the Eastern Basin; generally in the warmest months its populations in the Mediterranean are at their richest. This species is also well represented in the Indo-Pacific and in the Atlantic its density is particularly high in the equatorial zone (on both sides of this zone its abundance diminishes with the temperature); on the Moroccan continental shelf it is absent but it reappears in the Bay of Cadiz (Furnestin, 1970b); therefore its area contains an important gap in continuity which might be caused by the quasi-permanence of low temperature water from the N.W. African upwelling, unfavourable to the requirements of the species. This gap makes one think that settlement in the Mediterranean is of ancient origin. However, its present-day wide dispersal in the entire Mediterranean does not in any respect suggest the idea of a maintenance in refugium biotopes. One would rather suppose its population to have constituted itself promoted by the Post Glacial warming-up which brought back some elements of the Tropical Atlantic into the Mediterranean.

Boreal relicts—At the end of the Pliocene and more particularly in the Pleistocene, the Atlantic, cooled down by the glaciation and wide open to the north, offers the boreal species an easy way into the Mediterranean through an already formed strait. These boreal forms replace the local tropical elements, but their settling is temporary and the warming up which follows the glaciations is to destroy the greater part of this cold water fauna. This former cold water fauna can still be recorded by its fossils and its relicts which are actually not very numerous. The hypothesis of a relict boreal fauna is disputed; however, Ekman (1953) is of the opinion that certain boreal elements which established themselves during the Glacial Periods, subsist in such zones of the Mediterranean which have kept, even if attenuated, their hydrological and climatic characters of the Middle Pleistocene. Examples in connection with plankton are rare; it seems that three groups can provide some: Copepoda, Chaetognatha and Mysidacea. Sewell (1948) underlines the presence in the Mediterranean of Copepoda of a boreal origin, some of which could be relicts: *Ctenocalanus vanus*, *Pseudocalanus elongatus*, *Cyclopina elegans*, *C. longicornis*, *Ectinosoma neglectum*. It is necessary, however, to distinguish those species with a boreal origin which have been introduced

into the Mediterranean relatively recently and real boreal relicts which have been introduced long before. The former stock can be enriched by present-day contributions from the Atlantic (*Ctenocalanus vanus*, *Pseudocalanus elongatus*, *Pleuromamma robusta*, *Pseudaetideus armatus*, *Tharybis macrophtalma*). The distribution of the second group is marked by a discontinuity at the level of the Temperate Atlantic; they are widely distributed in the boreal zone and sporadically appear in the Mediterranean; like other relicts of the same type they are supposed to be more abundant in the deep but to come to the surface under the influence of climatic and hydrological factors. We shall mention three pelagic species. *Pareuchaeta norvegica*, a bathypelagic species of the Polar Seas and the North Sea, common in the vicinity of Norway and Scotland, observed in the Mediterranean in the Catalunian Sea and in the Bay of Villefranche (Furnestin & Giron, 1963; Djordjevic, 1963). *Diaixis hibernica*, known from the shores of Norway, Ireland and Scotland, also noticed several times in the NW. Mediterranean at Villefranche (Djordjevic, 1963), in the Catalunian Sea (Vives, 1966), in the Gulf of Marseille (Gaudy, 1970) and off Banyuls (Razouls, 1972), sometimes in abundance. *Paroithona parvula*, observed in the deep layers off Norway and N.W. of Ireland, also found in the Adriatic (Shmeleva, 1964) and once in the region of Banyuls (Razouls, 1968).

Among the Chaetognatha the case of *Sagitta setosa* is a typical one. Its principal habitat, characterised by a relatively low temperature and salinity, is formed by the seas on the border of the NE Atlantic; it also lives in the Black Sea, the Upper Adriatic and at various places in the Mediterranean: the mouth of the Ebro, the Gulfs of Naples and of Gabes, Gulf of Lion [at present the latter has a colder regime than the rest of the Western Basin (influence of the Mistral). Besides, the Quaternary layers of this area are richer in fossils of a boreal origin than those of the SW. region, and 'Senegalian' species, which are abundant at the Balearics during the warm sequences, are lacking.] Against the idea of a permanent transport into the Mediterranean by the Atlantic Current militates the discontinuity of its dispersal in the ocean where its southern limit is at about 45°N; at this latitude it confines itself within relatively closed biotopes (e.g. the Arcachon Basin). Its morphological variation in the Mediterranean Basin (p. 238) is considered an indication of isolation with regard to the Atlantic populations. Moreover, its abundance in the most diluted regions of the basin [the discharge area of the Rhône, for instance, is a real *S. setosa* zone (Furnestin, 1960)] prompts one to consider it a relict of the former Mediterranean faunas which were characteristic of water with rather low temperatures and salinity: 'elements with boreal affinity' or 'Celtic elements' which arrived by successive waves starting in the Calabrien (J. Furnestin, 1952; Mars et al., 1958; Pérès et al., 1960). And in the Black Sea, which still has kept particular characteristics of the Pontic Sea and faunistic affinities with the northern seas, in spite of its long-time communication with the Mediterranean, *S. setosa* is therefore very abundant.

Whatever the reality regarding their relict state, these psychrophile Copepoda and Chaetognatha forms with their disjunct dispersal constitute a quite interesting biogeographic problem in the Mediterranean.

The case of the Mysidacea *Gastrosaccus sanctus* can also be recorded; in Northern and Southern Adriatic it constitutes strictly littoral populations, rather different from those living upon British coasts and in the Black Sea; they could be remains of Glacial period populations which were more important and widely distributed

Table IX. Species, not mentioned in the text, of Mediterranean origin or first description from the Mediterranean (for abbreviations see table IV)

COPEPODA

Centropages ponticus, Stephos gyrans, Acartia adriatica, A.italica, Cyclopina esilis, Corycaeus brehmi: M-(P),E; Labidocera brunescens, A.latisetosa, Ratania flava: Aa, M(-P),E (Sewell, 1948); Calocalanus pseudocontractus: Aa,Wm,E; Ischnocalanus equalicauda, Oncaeа neoobscura, Acartia josephinae, A.enzoи, Disco (Paradisco) mediterraneus, D.marinus: Wm,E; Spinocalanus heterocaudatus, Drepanopsis lyra, Scolecithrincella subvittata, Amalothrix farrani, A.sarsii, Haloptilus fertilis, Xanthocalanus minor (Sewell, 1948), Oncaeа furnestini: Wm,B; Xanthocalanus mixtus, Scolecithrincella longipes, Spinocalanus neospinosus: Em,B; Calocalanus ovalis, C.elegans, C.neptunus, C.longisetosus, C.plumatus, C.adriaticus, C.elongatus, C.latus, C.kristalli, C.greesei (Shmeleva, 1965, 1968a, 1973a), Oncaeа vodjaninskii (Shmeleva et al., 1965), O.tregoubovii, O.bathyialis, O.longiseta, O.brodskii, O.longipes, O.minima, O.isleri, O.prendelii, O.zernovi, O.ovalis (Shmeleva, 1968b, 1969), Scaphocalanus similis, S.invalidus (Huré et al., 1968a): Ad,X; Euchaeta trunculosa (= E.marina), Onchocalanus steueri (= O.trigoniceps): No.

mysidacea

cf.table I, Gulf of Lion; Diamysis bahirensis (*Mysis relicta*): En (Genovese, 1956; Hoenigman, 1963b); Siriella adriatica, Anchialina oculata: Ad,X (Hoenigman, 1960).

HYDROMEDUSAE

Pachycordyle weissmanni, Stylactis pruvoti, Thamnostoma cidaritis, Eugymnanthes inequilina: En,Ne,Na; Bougainvillia maniculata: En,Ne,V; Ptychogastria asteroides: En, Ne,Ad,V; Mitrocoma aunaе: En,Ne; Podocoryne hartlaubi: Ad,A-M.

SIPHONOPHORA

Clausophyes massiliiana: A-M (Patriti, 1969b; Casanova, 1972; Pugh, 1975); cf.table I, Liguro-Provençal Region; Eudoxia dohrni: Ad,X (Gamulin, 1966).

APPENDICULARIA

Fritillaria urticans, Pegalopleura haranti, Appendicularia tregouboffi: En; Fritillaria aequatorialis, F.formica f.tuberculata, Kowalevskia oceanica: A-M; F.fagei: X,M, I; Megalocercus abyssorum: M,I,Aa (Tokioka, 1958; Fenaux, 1961, 1964, 1966).

PTEROPODA

Cavolinia tridentata tridentata (Mediterranean race); C.inflexa imitans, Clio pyramidata lanceolata (Alboran and Algerian races) (Rampal, 1975).

from the Atlantic areas into the Mediterranean (Hoenigman, 1964).

Species of Mediterranean origin

In various planktonic groups there exist Mediterranean species (Tab. IX); besides, more or less recently a certain number of new species have been described in the Mediterranean of which it is impossible to tell if they are endemic or if they have just not been observed yet in the Atlantic. We must also say that certain originally endemic species expand by degrees their area and thus reach the ocean. The following review of forms (endemic or not) of Mediterranean or Pontic origin indicates, as far as possible, their preferential bathymetric level.

Among the Copepoda there is a relatively high number of such species. To the nine epiplanktonic forms recorded by Sewell (1948) should be added the species since described: 23 from the Adriatic and 7 from the Western Mediterranean. In the deep are regarded as possible endemics 8 meso- or bathypelagic species described from the Western Basin and 3 from the Eastern Basin (Tab. IX). *Euchaeta hebes* (cf. Mazza, 1967) and *Calanus helgolandicus* (cf. Jaschnov, 1970; Fleminger et al., 1977) could be counted among Atlanto-Mediterranean endemics. About fifty Copepoda could thus be considered of Mediterranean origin; most of them seem to have come from the Adriatic but are not localised there as they have

also been found in the Eastern and Western Basins. *Centropages ponticus*, which originates from the Black Sea marks the Pontic influence in the Mediterranean, while *Calanus helgolandicus ponticus* seems to be confined to the Black Sea. The Hydromedusae are rich in endemic species: 17 neritic ones. If the endemism were extended to the Atlanto-Mediterranean Province, about 25 Hydromedusae would belong to this category. Among the Mediterranean species which colonised the ocean we mention *Podocoryne hartlaubi*, *Helgicirrha cari* which has reached the Aegean Sea and *Odessa maeotica f. marina* originally from the Black Sea, which is supposed to have progressively reached the Aegean Sea, the Western Basin and afterwards the Atlantic shores of Morocco (Kramp, 1959). The oceanic epipelagic species are thought to be only represented by three endemics (*Solmaris leucostyla*, *S. solmaris*, *Cunina proboscidea*) which shows the active exchange via Gibraltar for this category of Hydromedusae. Finally, the bathypelagic species which are very badly represented in the Mediterranean offer only one endemic [according to Casanova (1977) an Atlanto-Mediterranean one]: *Solmissus albuscens*, a species very common in the E. Mediterranean at the level of the intermediate waters which ensures its distribution in the Western Basin. Sometimes this species is brought to the surface as a result of upwelling water (indicator of upwelling). To the 20 endemic Hydromedusae should be added the newly described species which have not yet been observed outside the Mediterranean. (See tables)

Several Siphonophora have recently been described in the Mediterranean but the quality 'endemic' cannot yet be attributed to them. Some endemics and Atlanto-Mediterranean species are found among the Appendicularia. *Fritillaria fagei*, however, which has been described in the Mediterranean is also supposed to exist in the Indian Ocean. Likewise, *Megalocercus abyssorum* exists in the Indo-Pacific and Atlantic. The description of *Sagitta megalophthalma* (cf. Dallot & Ducret, 1969), a mesoplanktonic species observed at various places of the Mediterranean, but not elsewhere, gives an indication of a possible endemism. *S. euxina* is endemic to the Pontic Basin.

The Pteropoda are relatively rich in Mediterranean forms. *Cymbulia peroni*, which is extremely abundant in the Mediterranean and rare in the nearby ocean, might be an Atlanto-Mediterranean endemic, replaced in the ocean by *C. parvidentata* which latter enters the Mediterranean in small numbers owing to the Atlantic current. Mediterranean races are known for *Cavolinia tridentata tridentata*, *C. inflexa imitans* and *Clio pyramidata lanceolata*.

Several Mysidacea have been described in the Adriatic Sea and in particular littoral environments of the Gulf of Lion. Specially, eight of the ten species known of the genus *Leptomyysis* inhabit the Mediterranean and to this genus a Mediterranean-Lusitanian origin is attributed (Bacescu, 1966a). *Diamysis bahirensis* is confined to the Black Sea and the Mediterranean, near the coast and in brackish waters (Adriatic Sea, Sicily). A pelagic Mysidacea from the genus *Euchaetomeropsis* which has been observed in the Central Area (Casanova, 1968), perhaps is particular of the Mediterranean, as is suggested by comparisons with specimens of the Atlantic and Indian Oceans. The Amphipoda *Bouigisia ornata* has been described in the region of Villefranche, but its endemism is not proved. The Decapoda of the Mediterranean comprise a certain number of forms apparently without affinities with those from the E. Atlantic and which seem to be of a Mediterranean origin, even though some have migrated into the ocean, sometimes as far as the Canarian

Waters (Forest, 1976). Among these forms there are even endemic ones but they are not pelagic; the latter came, for the most part, from the temperate and subtropical zones of the E. Atlantic; while colonising the Mediterranean some have nevertheless acquired specific characteristics and have developed particular populations which seem to have lost the possibility of interbreeding with those from the ocean (this is the case with the subspecies *Acanthephyra pelagica pelagica*, *Sergestes robustus mediterraneus* and *S. corniculum hensenii* (p. 233).

Mediterranean Region

The above review of the components of the Mediterranean plankton makes one agree with the conclusions of Klausewitz (1969) related to the entire Mediterranean fauna, regarding it as being constituted of seven elements of different origin which are very inequally represented.

Like the temperate and subtropical zones of the E. Atlantic the Mediterranean possesses, in chronological order of their settlement: *a* some species characteristic of the Tethys; *b* Boreo-Atlantic migrants from the Glacial Period; *c* more numerous migrants from the Post Glacial which came from the temperate, subtropical and even tropical regions of the ocean. But besides these it also shelters: *d* Boreo-Arctic relicts of the Glacial Period which no longer live in the Temperate nor Subtropical Atlantic; *e-f* elements which came either from the Black Sea or from the Red Sea; *g* finally, a certain number of endemics which have differentiated from species of the various categories just mentioned.

As the connections of the Mediterranean with the Atlantic do not suffice to ensure a complete exchange, the similarity of their faunas mostly regards the organisms of the upper layers. The relative isolation is favourable to adaptations of ecological nature which tend to break the Atlanto-Mediterranean unity and to individualize a properly so called Mediterranean Region.

In 1953 Ekman, who, by the way, based himself very little on plankton, delimited three regions in the Atlanto-Mediterranean Province: a Lusitanian Region, from the Channel to Gibraltar, a Mauritanian Region, from Gibraltar to Cape Blanc of Mauritania, and a Mediterranean Region (the Black Sea being considered separately as the Sarmatic Region). Since then, the first two have been renamed the Ibero-Moroccan Region (Maurin, 1968) which separated the Biscayan Region in the north (Casanova, 1977) and the Saharian in the south. The Mediterranean Region has been maintained, from Gibraltar to the E. coast.

To be sure, the Strait of Gibraltar is no absolute zoogeographic barrier but the existence of a Mediterranean chorologic centre is due to the relative isolation of the basin. This basin, however, is not uniform. Even though the distinct Western, Eastern and Adriatic zones don't have value of distribution centres (Van der Spoel, 1976), we have seen that they show faunistic characters of their own, so that, at least for two of them, the Western and Eastern zones, the idea has been forwarded to consider them two sub-regions (Schmidt, 1912; Tortenese, 1964). For the plankton this idea has not been accepted for the following reasons: *1* the existence of resemblances between the northern areas of the E. and W. Mediterranean; *2* the existence of variations from N. to S. as well as from W. to E.; *3* the relative homogeneity of the faunas of several taxa in the whole Mediterranean (Euphausiacea and pelagic Decapoda, for example); *4* finally, the fact that the faunistic differences between the Western and Eastern

sectors are not more marked than those between the N. and the S. of the neighbouring Ibero-Moroccan Region, for which the unity has been maintained (Casanova, 1977).

However, from the Western to the Eastern Basin (and even, in certain cases, from the W. to the E. of this latter) a decreasing gradient of the species richness is to be observed, which may be accompanied by a decrease of the number of specimens in various taxa. Some examples:

Only about a quarter of western Hyperiidea exist in the Eastern Basin. The Pteropoda decrease from 25 species in the W. to 17 in the E. and the indices of diversity (for the summer, at the surface) show a greater variation in the W. ($0.3 \leq D \leq 2$) than in the E. ($0.7 \leq D \leq 1.5$). Also the Chaetognatha tumble, from 15 to 12 species, and their eastern fauna is quantitatively less rich.

Among the groups impoverished in the E. Mediterranean we also mention the Thaliacea (with only one Cyclosalpidae and no *Pyrosoma*, except in the Adriatic, *P. atlanticum*) and the Siphonophora; many species of this group which are observed in the W. Mediterranean are not recorded at all or only accidentally in the E. Mediterranean, only a few are really established there (Alvariño, 1974).

The reduction seems to be approximately: 26 species in the Eastern Basin against some fifty in the Western Basin, taking into account the recently described species. According to Kramp (1959), some 20 years ago only 12 of the 51 neritic Hydromedusae and 12 of the 19 epipelagic oceanic Hydromedusae existing in the Western Basin were also known in the E. Mediterranean. The difference has certainly grown because in the W. the inventory has been enlarged by new records of Atlantic species and by newly described species (p. 207) (tables). For the Appendicularia the margin is less wide: on a total of 36 species known to exist in the W. Mediterranean, 30 have been recorded in the E. This margin is also small for the Euphausiacea, only one of the 13 species identified in the W. Mediterranean does not appear in the Eastern Basin (*Thysanoessa gregaria*, a form related to the Atlantic Current).

An evolution of the eastern fauna under Eritrean influence is beyond doubt taking place at the moment; we have already pointed out (p. 219) that the number of migrants from the Red Sea augments progressively, and sooner or later a real modification of the structure and the periodicity of the planktonic community of the E. Mediterranean is to be expected. Such phenomena are already manifest for benthic or benthonectonic organisms and even for pelagic fish. It is also known that the addition of Indo-Pacific migrants to the Mediterranean fauna of Dinoflagellata adds to the tropical affinities which rather clearly distinguish this fauna from that of the Atlantic (Halim, 1965). It is likely that a similar divergence will progressively affect other groups as the tropical character will increase compared with the more temperate character of the Western Basin.

This penetration of Indo-Pacific elements and the correlative change of the fauna which alters the zoogeographic unity of the Atlanto-Mediterranean fauna, certainly constitute an additional argument to distinguish between two faunistic subregions in the Mediterranean. A recent diagram of the pelagic faunal provinces based on a study of sound-scattering levels using mesopelagic fishes (especially Myctophidae), clearly separates the W. Mediterranean from the Eastern Basin, each at one side of the Corsican-Sardinian axis (Backus et al., 1977). If, however, one does not want to accept such a radical division, because of an overall similarity of the faunas which the above cited facts do not entirely efface,

then it should be considered that, far from constituting a uniform unit, the Mediterranean is divided, by prominent discontinuities, into secondary basins. The geography of these basins largely determines their hydrology, which in its turn tends to individualize plankton and other faunas. The climate which is semi-desert-like along the S. coast and temperate in the north, also plays its part in demarcations, so that in this mosaic of secondary seas of which we described the principal aspects, faunistic assemblages emerge with evidently more or less precise outlines.

In this geographic framework the fauna of the Mediterranean *sensu stricto* comprises, with nevertheless variants between the different planktonic taxa: a a basis of ubiquitous species, mainly of a temperate character, common to the Western and Eastern Basins, but showing sometimes important quantitative variations which make it possible to distinguish elements with a cold or warm tendency among these cosmopolites; b a group of species with boreal affinities with a northern dispersal, i.e. they preferably live N. of 40°N in the Western Basin and in the northern parts of the Adriatic and Aegean Sea; c a group of subtropical species or species with tropical affinities, of Atlantic origin, with a southern and eastern dispersal, essentially located S. of 40°N in the Western Basin (for the subtropical ones) and in the S.E. region, for the others, where certain Indo-Pacific tropical species join them.

So, even if a wide dispersal of the ubiquitous species and the occasional record of ecologically definite forms outside their preferential areas may give the impression of a homogeneous composition and distribution of zooplankton in the Mediterranean, this homogeneity is merely apparent. We have to do with a real biogeographic diversification, marked by qualitative and quantitative differences which are swayed by the morphology of the secondary basins, their climates and their hydrologies. A systematic examination of the indices of diversity for the different seasons and the successive bathymetric levels in the various basins would help to specify this differentiated dispersal.

These aspects of the Mediterranean zoogeography show biogeography as a science which is alive, doubtless as a result of the constant augmentation of knowledge, but especially because of the evolution of the faunas themselves. The recent biogeographic transformations of the Eastern Mediterranean by 'tropicalisation' under Eritrean influence and of the Black Sea by its progressive mediterraneanisation, are at the same time an example of the modifications which the interventions of Man may provoke at the scale of a marine Province.