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Climatic fluctuations, current variability and marine species distribution: a case study in the Ligurian Sea (north-west Mediterranean)

Climate variability
Warm-water species
Dispersal
Epibenthos
Marine biogeography

Variabilité du climat
Espèces thermophiles
Dispersion
Epibenthos
Biogéographie marine

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ABSTRACT

The Ligurian Sea, situated in the north-east corner of the western Mediterranean, is colder than the Tyrrhenian Sea, situated just to the south. As a consequence, there are differences in the composition and physionomy of their respective marine biota. Episodical records of epibenthic warm-water species, of Tyrrhenian origin, in the colder Ligurian Sea were paradoxically linked to the occurrence of low mean air temperatures. This is explained by the peculiar pattern of water and heat exchanges between the Tyrrhenian and Ligurian basins mediated through the northward-flowing Tyrrhenian Current. In response to the greater cooling of the Ligurian Sea, induced by the more intense water and temperature losses, a seasonal flux of warmer water is drawn from the Tyrrhenian Sea in order to restore the altered budget: the more intense the Ligurian Sea winter cooling, the larger the volume of the warmer flow carried northward by the Tyrrhenian Current, increasing the probability of warm-water species transport into the Ligurian Sea. Survival of warm-water species in cold years is unlikely, and this explains the rarity of findings in the last one and a half centuries. In a few cases, warm-water species have succeeded in establishing adult pseudopopulations. However, this scenario is probably changing: the detection of warm-water species in the Ligurian Sea has become more frequent and nearly constant in recent years, even in the presence of high winter temperatures. It is hypothesized that present sea water warming is allowing former sterile pseudopopulations to reproduce in the Ligurian Sea, thus assuring independence from the larval supply by the Tyrrhenian Current. Future investigations should concentrate on monitoring the population biology of warm-water species established in the Ligurian Sea.

RÉSUMÉ

Fluctuations climatiques, variabilité des courants et répartition d'espèces marines: étude d'un cas en Mer Ligure (Méditerranée nord-occidentale).

La Mer Ligure, située dans la partie nord-est de la Méditerranée occidentale, est plus froide que la Mer Tyrrhénienne, située juste au sud. Par conséquent, la composition et la physionomie de leurs flores et faunes marines sont différentes. Les récoltes épisodiques d'espèces épibenthiques d'eau chaude, d'origine tyrrhénienne, dans la Mer Ligure plus froide sont paradoxalement liées à des faibles températures moyennes de l'air. Ceci est expliqué par la particularité des échanges d'eau et de chaleur entre les bassins tyrrhénien et ligure à travers le Courant Tyrrhénien, coulant vers le nord. En réponse au plus fort refroidissement de la Mer Ligure, dû aux pertes d'eau et aux baisses de température plus intenses, un flux saisonnier d'eau plus chaude provenant de la Mer Tyrrhénienne s'établit: plus le refroidissement hivernal de la Mer Ligure est intense, plus le volume d'eau chaude apporté par le Courant Tyrrhénien est grand, augmentant proportionnellement la probabilité de transport d'espèces d'eau chaude en Mer Ligure. La survie d'espèces d'eau chaude durant les années froides étant improbable, on s'explique bien la rareté des récoltes dans le dernier siècle et demi. Dans quelques cas, toutefois, les espèces d'eau chaude ont réussi à établir des pseudo-populations adultes. Ce cadre est probablement en train de changer: dans les toutes dernières années, l'observation d'espèces d'eau chaude en Mer Ligure est devenue plus fréquente et presque constante malgré les températures d'hiver élevées. On peut supposer que le réchauffement actuel de la mer permet à celles qui étaient des pseudo-populations stériles de se reproduire en Mer Ligure, devenant de cette façon indépendantes de l'apport larvaire par le Courant Tyrrhénien. Les recherches futures devraient porter sur la biologie de population des espèces d'eau chaude établies en Mer Ligure.

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INTRODUCTION

The consequences of climatic change on the marine biota have attracted the attention of marine biologists since the earliest evidence was collected (Southward *et al.*, 1975). The reviews of Cushing and Dickson (1976) and of Southward and Boalch (1994) are basic references on this subject.

Clearly, fisheries statistics provide most of the long-term data needed to make sound evaluations, and therefore our present knowledge mainly concerns fish (Laevastu, 1993): Southward *et al.* (1988), for instance, were able to relate climate fluctuations and fishery catches in south-west England as far back as the 16th century. Of course, information exists also on plankton and benthos (Southward, 1963; Glémarec, 1979; Evans and Edwards, 1993), but long-term data are scarce (Cabioch *et al.*, 1983; Warwick and Bayne, 1993).

Most benthic time series have been studied only for the last few decades (Heip *et al.*, 1987; Keegan, 1991). Blacker (1957) considered benthic animals as indicators of climatic change, but there is at present some debate on whether changes in benthic communities are due to climate variation or increasing eutrophication of coastal seas (Buchanan, 1993; Josefson *et al.*, 1993). Several authors observed changes in species distribution related to temperature fluctuations, and this especially in areas which are close to biogeographical boundaries (Wells and Gray, 1960; Glémarec, 1979; Southward and Boalch, 1992; Fowler and Laffoley, 1993); it has been said that climatic shifts induce biogeographical shifts (Southward, 1980; Dayton and Tegner, 1984). Grainger (1992) predicted that the foreseen global warming will probably make southern species extend their range northward.

This is apparently what is happening within the Mediterranean Sea, where warm-water pelagic fish and benthic organisms are presently seen in the northern sectors (Bussani, 1992; Bianchi and Morri, 1993; Francour *et al.*, 1994).

Bianchi and Morri (1994), on the basis of literature data and recent records, summarize existing information on warm-water algae, invertebrates, and reef fishes in the Ligurian Sea (located at the north-eastern corner of the western Mediterranean). They conclude that the increased occurrence of warm water species in the past few years merits attention as a possible biological indicator of climate change.

The present paper compares the above-mentioned records of warm-water species in the Ligurian Sea to climatic and hydrographical data, and discusses possible causes and mechanisms of such range extensions.

HYDROGRAPHIC AND BIOGEOGRAPHICAL SETTINGS

From a biogeographical standpoint, the Mediterranean Sea forms a well-defined unit (Briggs, 1974). However, the vastness of the basin, its tormented geological history, and the many climatic and hydrological aspects have caused an obvious differentiation within the marine biota of this sea (CIESM, 1981; Pérès, 1985). Thus, up to ten different "biogeographical sectors" are usually distinguished within the Mediterranean (Fredj, 1974).

As a whole, the major differences in species composition and community physiognomy occur along a North-South axis. The Tyrrhenian and Ligurian seas are a good example of this pattern.

The Tyrrhenian Sea can be considered the most isolated basin in the western Mediterranean (Astraldi and Gasparini, 1994). While the limits of the other basins are without a sill restriction at typical bottom depths of about 2700 m, the connections of the Tyrrhenian Sea with the rest of the western Mediterranean Sea occur through the Corsica Channel, having a sill depth at about 450 m to the north, and through the broad opening (strongly reducing with depth) between Sicily and Sardinia to the south. In addition, the Tyrrhenian Sea is contoured by mountains preventing the input of meteorological events which strongly influence the internal conditions of the other western Mediterranean basins. These features determine an increase of the mean surface temperature, which remains significantly higher all year round. This explains why the Tyrrhenian Sea is the sector of the western Mediterranean inhabited by the most thermophilic fauna and flora, with a fairly high percentage of species of subtropical affinity and endemic species adding to the Atlantic-Mediterranean background.

In contrast, the Ligurian Sea is tightly connected with the Gulf of Lions, which is subject to periodic intrusions of the northerly winds from the Rhône valley. These winds generate very energetic weather conditions, particularly severe in winter. The major large scale hydrodynamic feature (Astraldi *et al.*, 1994) is a well-defined cyclonic circulation active all year round, which helps to maintain the mean surface temperature lower than that of the adjacent basins, in particular the Tyrrhenian Sea. Accordingly, the flora and fauna of the Ligurian Sea are characterized by a very marked diminution of the subtropical elements and by the presence of some species of cold temperate waters which seem to be missing elsewhere. This gives the Ligurian Sea a boreal affinity (Rossi, 1969; Albertelli *et al.*, 1981). Both the hydrographic (Astraldi *et al.*, 1993) and the biogeographical (Castelli *et al.*, 1988; Lardicci *et al.*, 1990) boundaries between the Tyrrhenian and the Ligurian seas can be set at the Tuscan Archipelago (Fig. 1).

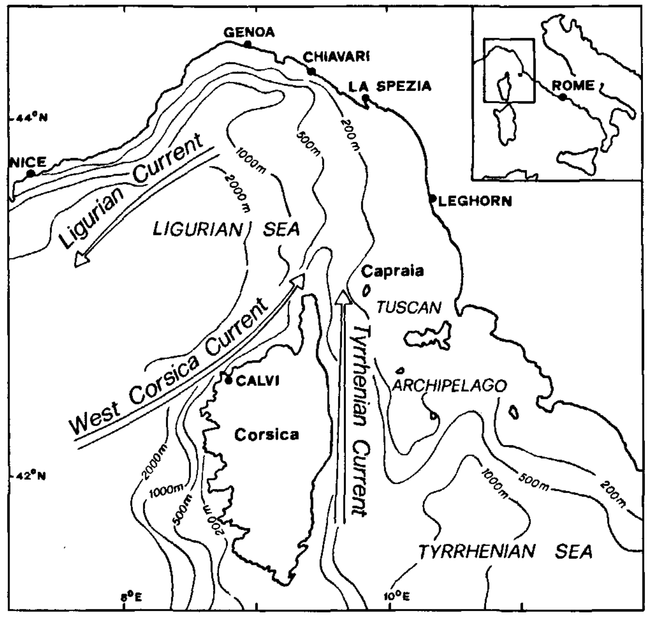

Figure 1

Geographical setting of the area in the north-western corner of the Mediterranean, showing the boundary between the Ligurian and Tyrrhenian seas (Tuscan Archipelago) and the other places mentioned in the text. Arrows illustrate the major current systems cited in the text.

Situation géographique de la région nord-occidentale de la Méditerranée, illustrant la limite entre Mer Ligure et Mer Tyrrhénienne (Archipel Toscan) et les autres localités citées dans le texte. Les flèches montrent les systèmes de courant majeurs cités dans le texte.

LIGURIAN SEA TEMPERATURES

Along with the other hydrographic data, the climatological aspect of the different basins can be deduced from the volume of the temperature data collected inside each basin in the course of years. These data are ordinarily stored in hydrographic data banks, such as the Mediterranean data bank set up at the **Centro Ricerche Ambiente Marino (CRAM)** in La Spezia, and containing the sea temperature records for this basin since 1909 (Bruschi and Sgorbini, 1986). Among the different basins of the western Mediterranean Sea, the Ligurian Sea has been the most investigated and the major climatological aspects are now fairly well known. Unfortunately, due to a temporal inhomogeneity in data sampling, the variability is not so well known, and if one wishes to derive some trends in the basin thermal conditions, one must refer to air temperature time series, more commonly found in the archives. Southward *et al.* (1988) have noted that surface water temperatures in coastal waters are reasonably correlated with air temperatures. We have tested this assumption for the Ligurian Sea in two cases: 1) by comparing annual means of the surface temperature existing in the CRAM data bank with the corresponding values of air temperature, for nine years between 1958 and 1979; 2) by taking into account the monthly means of sea surface temperature, measured fortnightly by Della Croce *et al.* (1980) from October 1978 to October 1979 off Chiavari, and the corresponding air temperature data collected by the local **Osservatorio Meteorico e Sismico** (Morri *et al.*, 1988). Since all correlations proved to be significant (Fig. 2), it was considered that air temperature data could serve as a guide for investigating trends in sea surface temperature.

The air temperature for the Ligurian Sea is based on the air temperature time series collected by the Meteorological Observatory of the University of Genoa since 1833 (Flocchini *et al.*, 1983). The annual means from 1833 to 1993 show large fluctuations, warmer periods alternating with colder ones in a rather irregular manner (Fig. 3). Smoothing the data by moving averages over eleven-year periods (Southward *et al.*, 1975), a trend becomes more apparent (Fig. 4). The Ligurian Sea appears to have been affected by two major warming episodes, while a third appear to be beginning at present. Between the warm periods, there are two cooling periods, the most recent being significantly warmer than the first one. A comparison with the average air temperature trend of the whole Northern Hemisphere (Jones *et al.*, 1984) shows that some discrepancies exist in the amplitude of the first warm period (before around 1880), considerably pronounced in the Genoa time series. This discrepancy is also found if we

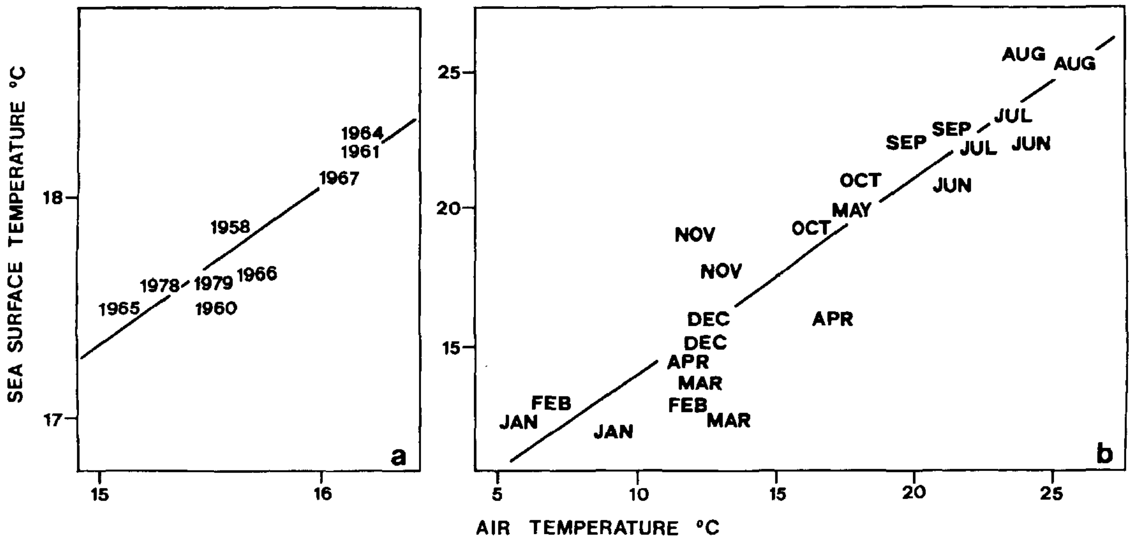

Figure 2

Linear regressions and correlations between sea surface and air mean temperatures: a) annual means, whole Ligurian Sea vs *Genoa,* $t_{sea} = (0.735 \pm 0.130)\ t_{air} + 6.275 \pm 0.144$, r = 0.906, n = 9; *b) monthly means, Chiavari,* $t_{sea} = (0.708 \pm 0.062)\ t_{air} + 6.911 \pm 1.715$, r = 0.927, n = 23.

Régressions linéaires et corrélations entre températures moyennes de l'air et de la mer de surface: a) moyennes annuelles, Mer Ligure totale contre Gênes, $t_{mer} = (0.735 \pm 0.130)\ t_{air} + 6.275 \pm 0.144$, $r = 0.906$, $n = 9$; b) moyennes mensuelles, Chiavari, $t_{mer} = (0.708 \pm 0.062)\ t_{air} + 6.911 \pm 1.715$, $r = 0.927$, $n = 23$.

consider the air temperature data from Rome (Colacino and Rovelli, 1983), which has a trend more similar to that of the Northern Hemisphere. It could be argued that the actual site in Genoa at which the temperature were measured was changed some time in the 1870s or 1880s, but there are no records of such a site change in the archives (De Lucchi, 1927; Dagnino, 1978). Molinari (1987) distrusts temperature readings before 1883 but gives no explanation. Arseni-Papadimitriou and Maheras (1991) discovered different behaviour in the temperature trends of four Mediterranean stations. The air temperature time series of Leghorn (Meini *et al.*, 1979), at the boundary between Tyrrhenian and Ligurian Seas, also show a warm period in the 1860s, as Genoa's does. It must be concluded therefore that Genoa time series can be considered realistic and representative of the Ligurian Sea temperature variability.

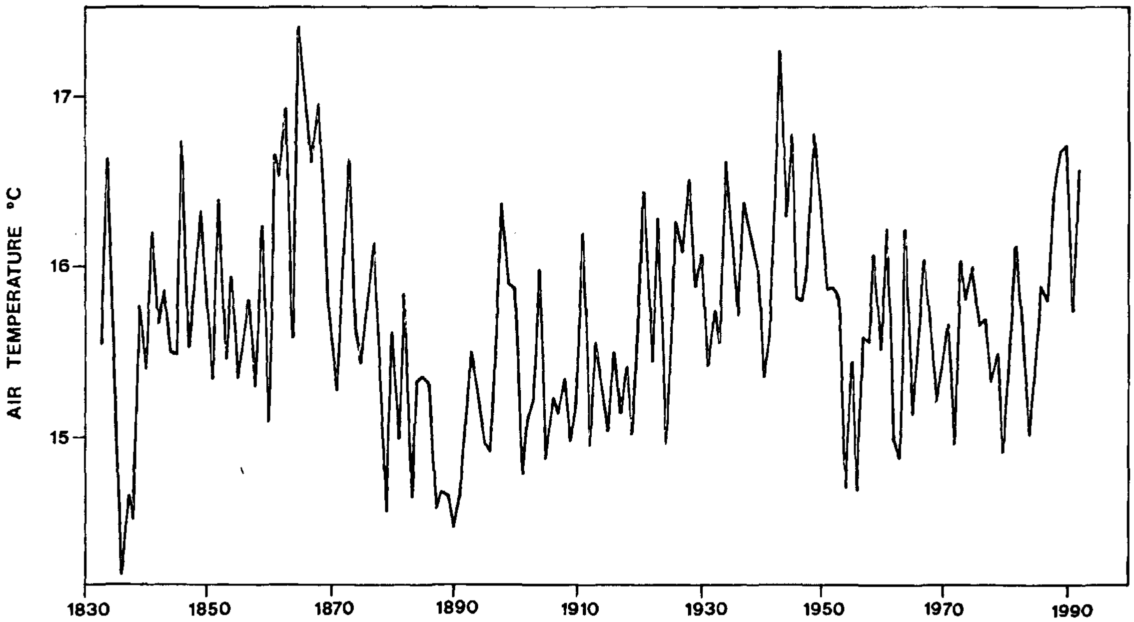

Figure 3

Trend of air temperature (annual means, °C) at Genoa (Meteorological Observatory), 1833 to 1993.

Fluctuations de la température de l'air (moyennes annuelles, °C) à Gênes (Observatoire Météorologique), 1833 à 1993.

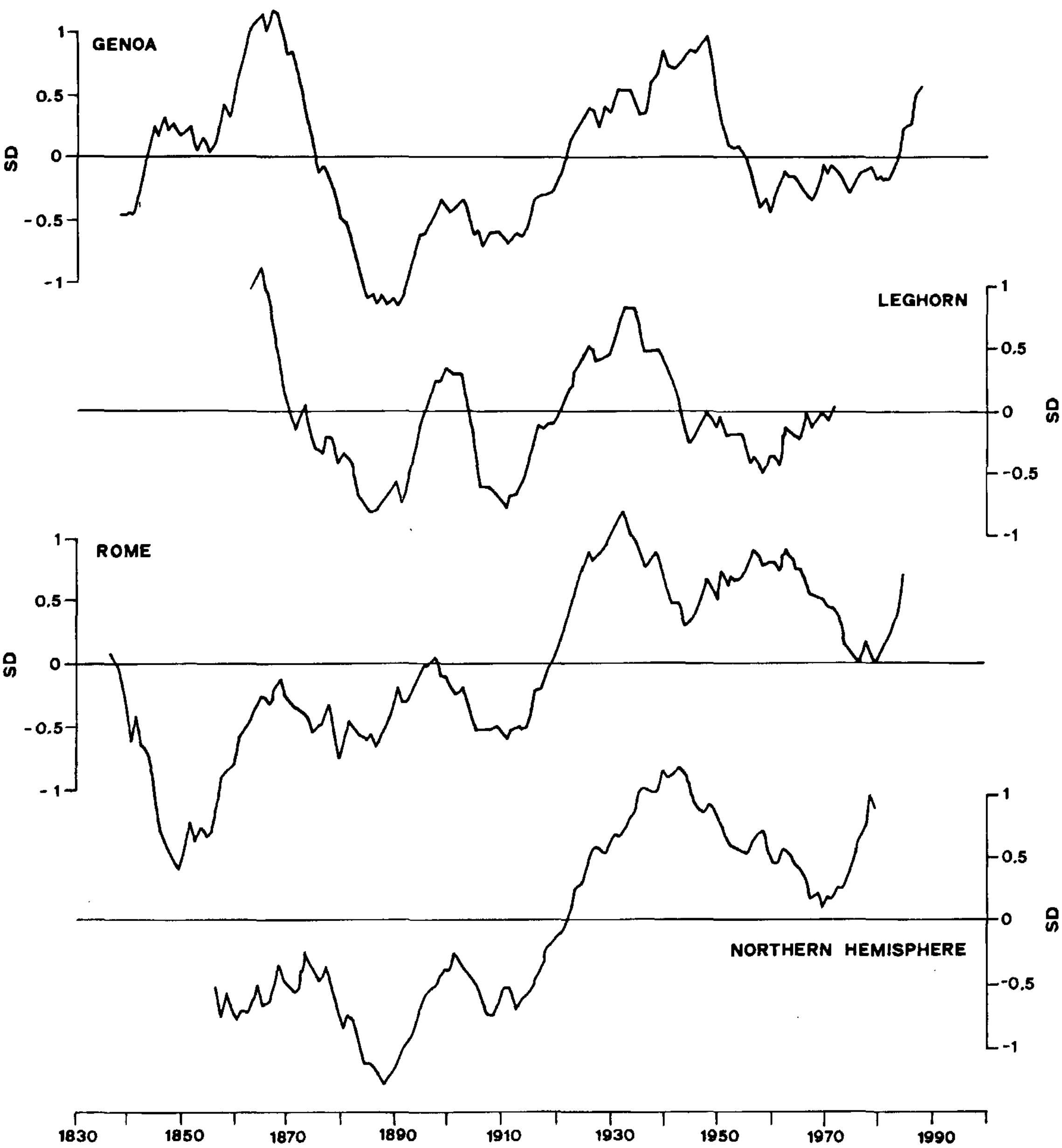

Figure 4

Trend of smoothed (moving averages over 11 year periods) standard deviations (SD) from annual mean air temperatures at Genoa, Leghorn, Rome, and Northern Hemisphere.

Évolution des écart-types (SD), avec lissage des moyennes mobiles sur des périodes de 11 ans, de la moyenne annuelle de la température de l'air à Gênes, Livourne, Rome, et dans l'hémisphère Nord.

WARM-WATER SPECIES OCCURENCE IN THE LIGURIAN SEA

Bianchi and Morri (1994) critically analysed existing information on twenty warm-water (or presumed so) epibenthic species recorded in the Ligurian Sea.

Records are rather rare and observations only concern 26 years in over one and a half centuries of temperature records. More than one-third of the records are posterior to the 1980s (Fig. 5). Findings (especially the older ones) are sometimes uncertain and greatly heterogeneous: the known occurrence of the species greatly reflects the availability of the relevant specialists. Algae, for instance, have been adequately investigated only during the present century (references in Barberis *et al.*, 1979). Cinelli (1979) and Meinesz (1980) reviewed and updated knowledge on the western Mediterranean distribution of some warm-water species of green algae. Studies on benthic invertebrates are very irregularly scattered: Francour (1991), Templado (1991), and Zibrowius (1978, 1980, 1991) are recent references on some important species. On the contrary, the Ligurian Sea fish fauna has been extensively studied since the beginning of the nineteenth century (see Tortonese, 1965, for a synthesis) up to now.

Despite such obvious limitations, Bianchi and Morri (1994) concluded that most information on warm-water

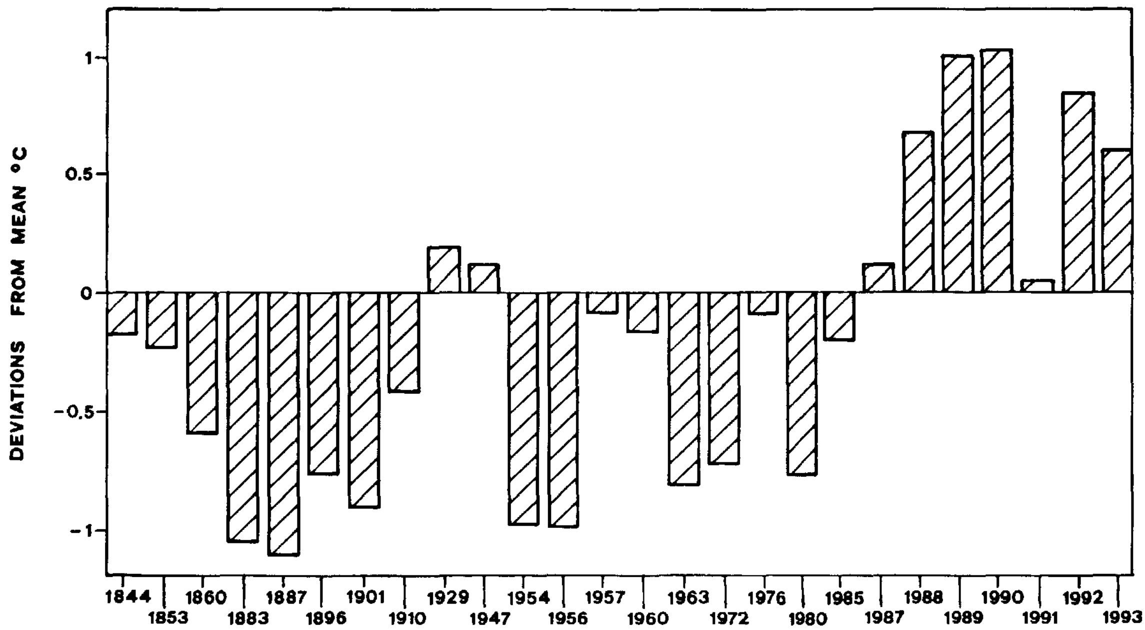

Figure 5

Temperature anomalies (deviations from the overall annual mean) at Genoa in the years when warm-water species of group 3 (see text) have been found in the Ligurian Sea (see Bianchi and Morri, 1994, for references).

Anomalies de température (écarts de la moyenne annuelle globale) à Gênes dans les années correspondant aux récoltes d'espèces thermophiles du 3e groupe (voir le texte) en Mer Ligure (voir Bianchi et Morri, 1994, pour les références bibliographiques).

species occurrence in Ligurian Sea could be accorded a certain reliability. Based on Bianchi and Morri's discussion, the species can be divided in three groups.

The first group contains the species which are rather rare and localized even in the Tyrrhenian Sea: therefore, new findings in the Ligurian Sea may not be clues to recent settlings, but simply records of previously overlooked populations. This could especially be true in the case of the brown alga *Cystoseira spinosa*, the sponge *Axinella polypoides*, the hermit crab *Calcinus tubularis*, and the seastars *Chaetaster longipes* and *Hacelia attenuata*. The red alga *Acrothamnion preissii*, a recent Indopacific invader (Cinelli *et al.*, 1984), could also be ascribed to this group.

The second group is formed by long-lived species, such as the corals *Astroides calycularis* and *Phyllangia mouchezi*, the gastropod *Charonia lampas lampas*, the sea urchin *Centrostephanus longispinus*, the sea star *Ophidiaster ophidianus*, and the parrot fish *Sparisoma (Euscarus) cretense*. Records concerning adults of these long-lived species do not identify the exact year of colonisation. *A. calycularis* and *S. cretense* were found only in the Tuscan Archipelago, not in the Ligurian Sea proper.

Finally, the third group is comprised of species with shorter life-cycles, such as most of the algae (*Caulerpa prolifera, Dasycladus vermicularis, Galaxaura oblongata, Penicillus capitatus, Pseudochlorodesmis furcellata*), the hydroid *Halocordyle disticha*, and the limpet *Patella ferruginea*. The ornate wrasse, *Thalassoma pavo*, can also be included in this group because of the occurrence of different liveries as specimens grow and mature, thus helping to "date" specimens.

In trying to relate warm-water species occurrence to climate variability we took into account only species of the third group, as they appear to be the most informative with this respect. In particular, we compared records of such species with air temperature anomalies of the corresponding years. Temperature anomalies were computed as deviations from the overall annual mean: negative deviations were considered as indicative of "cold" years, and conversely positive deviations were taken as indicative of "warm" years.

Records of warm-water species in Ligurian Sea (see Bianchi and Morri, 1994, for references) coincide with "warm" years in nine cases out of a total of 26, and with "cold" years in the remaining 17 cases; even disregarding records before 1883, the above figures become 9 and 14, respectively. Records of warm-water species coinciding with 'warm' years mostly correspond to very recent years, *i.e.* from 1987 up to 1993 uninterruptedly (Fig. 5). An outstanding example of this trend is the well-known fish *Thalassoma pavo*, which has been found sporadically in colder years before 1985, and more constantly in warmer years since 1991.

Thus, with the exception of more recent years, warm-water species used to be encountered in the Ligurian Sea most often in "cold" years, rather than in "warm" ones. This result is paradoxical, being exactly the opposite of what could be expected.

THE HYDRODYNAMIC CONDITIONS

A possible explanation of this paradox comes from an understanding of the circulation pattern and the connected heat transport between Tyrrhenian and Ligurian seas.

The two basins communicate *via* the Corsica Channel, a narrow strait regularly deepening to about 450 m off Capraia Island, in the Tuscan Archipelago. Astraldi and Gasparini (1992), starting from current time series collected around northern Corsica from 1985 to 1988, demonstrated that two independent currents flow into the Ligurian Sea from the south.

The one off the north-western side of the island, called the West Corsica Current (Fig. 1), is part of the southern branch of the cyclonic circuit present in the Ligurian Sea, and flows northward all year round, keeping in the inner part of the basin. Also the current crossing the Corsica Channel, called the Tyrrhenian Current, flows northward. Since its energy is considerably higher in winter and spring and becomes weaker in summer and autumn, the Tyrrhenian Current has a marked seasonal variability. When active, it flows close to the Ligurian coast following the shelf-break bottom bathymetry.

Astraldi and Gasparini (1992) showed that the seasonal variability of the Tyrrhenian Current mostly depends on the different thermohaline conditions existing in the two basins in winter. In response to the larger cooling of the Ligurian Sea induced by the more intense water and temperature losses, a seasonal flux of warmer water is drawn in from the Tyrrhenian Sea in order to restore the altered budget. Due to the annual variability of the processes involved, the seasonal intrusions of warmer water change significantly from one year to another. We can say that the more intense is the Northern Basin winter cooling, the higher is the heat content needed to restore it and the larger is the volume of the warmer Tyrrhenian flow towards the Ligurian Sea (Fig. 6). This means that during periods of strong winter cooling there is an increase in the probability of transport of warm-water species into the Ligurian Sea.

The seasonal variability of the Tyrrhenian flow and its interannual changes also produce specific hydrographic conditions in the water masses flowing along the Ligurian margin (Astraldi *et al.*, 1994): in winter, the surface water off Nice has intermediate properties between those of the

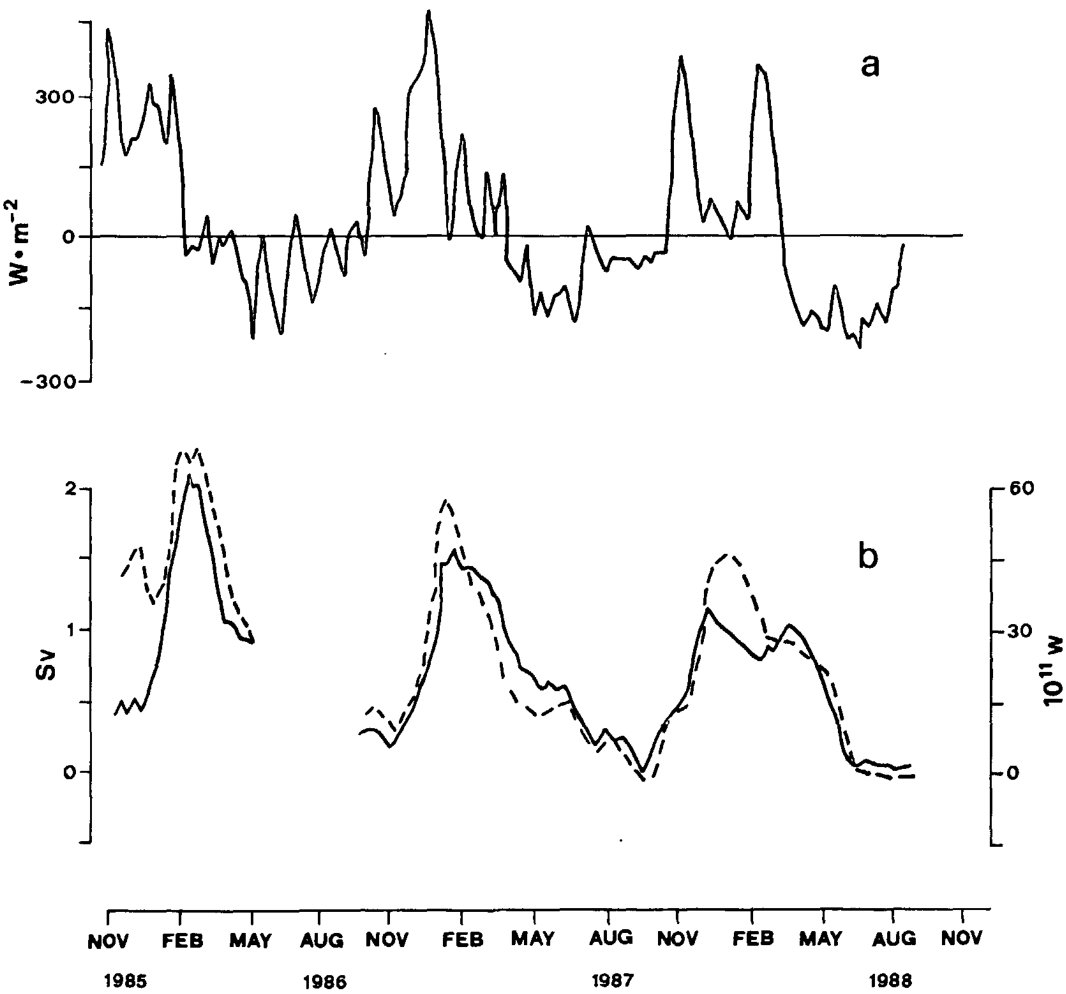

Figure 6

Time evolution of the weekly mean values of: a) the total heat flux (W m^{-2}) between sea and atmosphere and b) the total water transport (Sv, 10^6 m^3 s^{-1}, solid line) and the total heat advected (10^{11} W, dashed line) through the Corsica Channel (from Astraldi and Gasparini, 1992).

Évolution temporelle des valeurs moyennes hebdomadaires: a) du flux total de chaleur (W m^{-2}) entre la mer et l'atmosphère, et b) du transport total d'eau (Sv, 10^6 m^3 s^{-1}, ligne continue) et de la chaleur totale (10^{11} W, ligne hachurée) transportée à travers le Canal de Corse (d'après Astraldi et Gasparini, 1992).

two flows entering the Ligurian Sea, and then it results from a mixing of the two, whereas in summer this water is almost exclusively provided by the West Corsican Current.

This circulation has additional consequences in terms of heat content, as can be seen by the comparison of Genoa winter air temperature and the heat content in the Ligurian Current, before (Calvi) and after (Nice) its mixing with the Tyrrhenian Current. Nearly monthly hydrographic data along the Calvi-Nice transect for the winter periods 1970-1973 (Hydrokor Cruises, 1973; 1975) show that, while the heat content off Calvi follows the same trend of the air temperature in Genoa, this is no longer true off Nice, where the oscillations of heat content from one year to another are reduced (Fig. 7). Thus, notwithstanding the fact that sea surface and air temperatures are positively correlated, the heat advected by the Ligurian Current in this region is less influenced by air temperature; this may happen because the Tyrrhenian Current acts as a thermostat, allowing a major input of heat in correspondence to the coldest winter and vice versa.

DISCUSSION

The warm Tyrrhenian Current, flowing more strongly during colder periods, is likely to be the carrier of long-living pelagic larvae, eggs or propagules of the warm-water species coming from the Tyrrhenian Sea: almost all of these are known to have teleplanic dispersal stages (Tortonese, 1975; Russo *et al.*, 1990; Francour, 1991). Lewin (1986) called the arrival of allochthonous larvae to the benthos the "supply-side".

However, if we accept that cold winters could represent the mechanism which triggers the incoming of warm-water species, we must face an apparent inconsistency: how can these species survive the cold winters ?

Perhaps, larvae of warm-water species incoming into the Ligurian Sea benefit from the thermostatic effect of the Tyrrhenian Current and from the persistence of a lens of the warmer Tyrrhenian Current entrapped along the coast (see the surface temperature maps produced by Picco, 1990), perhaps forming the coastal 'thermophilic oases' hypothesised in the literature (Tortonese, 1958; Sarà, 1985).

Here, settled organisms could be able to withstand winter conditions. Adult specimens can then easily survive and grow in summer, but, in the case of species living more than one year, the arrival of the subsequent winter will most probably kill them: the adults usually have a narrower temperature tolerance than the larvae (Bhaud, 1993). However, the interannual trend of air temperatures is very irregular (Fig. 3), and a cold year is often followed by a warm year, thus increasing survival probability of warm-water species, which can succeed in establishing adult populations. According to most authors (Bini, 1968; Francour, 1991; Russo *et al.*, 1990), these should be sterile "pseudopopulations" (Mileikovski, 1971) and need to be restored by further invasions. Sarà (1985) affirmed that temperature maintains the differentiation of the biota of the northern and southern parts of the Mediterranean. Thus, according to Bhaud's (1983) terminology, the barrier between the Tyrrhenian and Ligurian seas is of a physiological nature: occasional crossing by jump dispersal (Rosen, 1991) should not allow the establishment of viable populations.

The alternation of cold and warm years could serve as a "pulsating" mechanism for introducing new species into the Ligurian Sea benthic biota. So, climatic fluctuations act as a sort of "diversity pump", not only on an evolutionary scale (Sarà, 1985) but also on a present-day, ecological scale. According to Blandin (1987) climatic alternation favours the coexistence of species potentially redundant

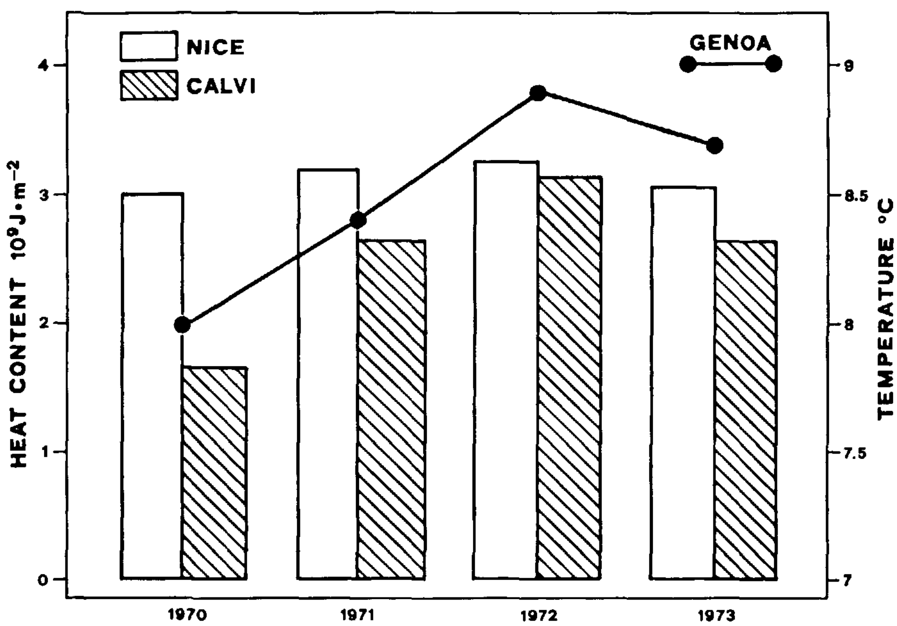

Figure 7

Comparison between the average winter air temperature at Genoa, and the water heat content between the sea surface and 300 m depth off Calvi and off Nice in 1970-73.

Comparaison entre les températures moyennes de l'air en hiver à Gênes, et le contenu thermique de l'eau entre la surface et 300 m de profondeur au large de Calvi et de Nice en 1970-73.

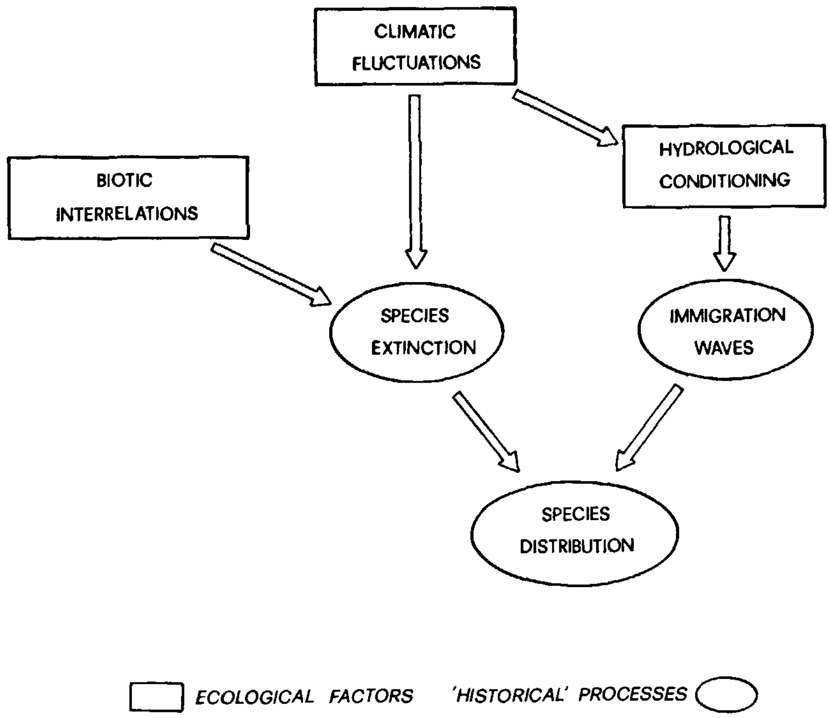

Figure 8

The hypothetical scenario of the interdependence of ecological factors and "historical" processes used to regulate warm-water species occurrence in the Ligurian Sea until very recent years (see text).

Cadre hypothétique de l'interdépendance des facteurs écologiques et des processus « historiques » qui réglaient la présence d'espèces thermophiles en Mer Ligure jusqu'aux années récentes (voir le texte).

from a functional standpoint and allows the formation of species-enriched assemblages.

However, even in the best conditions, survival of warm-water species in the Ligurian Sea must be, beyond any doubt, still more scarce than the "normal" figures (about 1 %) reckoned by Thorson (1966). As stressed by Holdgate (1986), migrants are marginal in the receiving habitats: they must combine ability to disperse (typical of r-strategist species) and ability to compete successfully with pre-existing biota (more of a K-character).

It comes clear that the establishment of warm-water species in the Ligurian Sea should be a rather unlikely event. Therefore, the scarcity of records in one and a half centuries seems quite realistic: even if the Tyrrhenian Current flows more or less strongly every winter, carrying huge amounts of larvae, biotic factors and climatic conditions act together against their survival.

Sarà (1985) stressed the interplay between ecological factors (which tend to be deterministic in nature) and historical processes (which are somewhat stochastic) in determining species ranges. Climatic fluctuations (an ecological factor) can affect species distribution (a "historical" process) in two independent ways: one, direct, on survival of settled populations; and one, indirect, on dispersal, through hydrological conditioning, since changes in climate are believed to alter the emphasis of water flow (Southward, 1980). In the Ligurian Sea these two ways are opposing to each other: the indirect one promotes immigration waves, while the direct one causes species extinction, thus attenuating the potential effects of the former (Fig. 8).

It must be admitted that this scenario is highly speculative, but it illustrates the complicated and subtle links between climatic fluctuations and species distributions, and to the manifold ways in which they affect biological communities. Moreover, and more important, it provides the background for a testable hypothesis.

It has already be noted that occurrence of warm-water species in the last seven years coincided with the establishment of warmer conditions in air temperature over the basin. It is indicative that during three years of measurements (1985 to 1988), Astraldi and Gasparini (1992) observed that the winter transport of current and heat through the Corsica Channel was progressively decreasing as a consequence of a corresponding reduction of the winter heat losses sustained by the Ligurian surface layer (Fig. 6).

Thus, the scenario is changing: it can be predicted that north-western Mediterranean water warming (Béthoux *et al.*, 1990; Sparnocchia *et al.*, 1994) will allow present-day Ligurian Sea pseudopopulations of warm-water species to become true populations, reproducing in the Ligurian Sea and thus gaining independence from larval supply by Tyrrhenian Current. The finding of two supermales (*i.e.*, sexually mature males) of *Thalassoma pavo* in summer 1992 in the Ligurian Sea (Bianchi and Morri, 1994) is consistent with this prediction. In this way, constant warmer conditions will allow many warm-water species, until recent times confined to Tyrrhenian Sea, to extent their area of occupancy (*sensu* Gaston, 1991), in agreement with the statements of Grainger (1992).

The future scenario will probably be very different from the one presented here and possibly characteristic of the Ligurian Sea past biogeography. Future investigations should therefore concentrate in monitoring population biology of warm-water species established in Ligurian Sea: these are probably efficient descriptors of climatic changes and offer the most obvious evidence of the effects of such changes on the marine biota.

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REFERENCES

Albertelli G., M. Cattaneo and N. Drago (1981). Macrobenthos du plateau continental ligure et de l'Archipel toscan: aperçus zoogéographiques. *Rapp. Comm. int. Mer Médit.* **27**, 2, 127-128.

Arseni-Papadimitriou A. and P. Maheras (1991). Some statistical characteristics of air temperature variations at four Mediterranean stations. *Theor. appl. Climatol.* **43**, 105-112.

Astraldi M., D. Bacciola, M. Borghini, F. Dell'Amico, C. Galli, G.P. Gasparini, E. Lazzoni, P.L. Neri and G. Raso (1993). Caratteristiche stagionali delle masse d'acqua nell'Arcipelago Toscano. In: *Arcipelago Toscano, studio oceanografico, sedimentologico e biologico.* O. Ferretti, F. Immordino, V. Damiani, eds. ENEA, Roma, 7-28.

Astraldi M. and G.P. Gasparini (1992). The seasonal characteristics of the circulation in the North Mediterranean basin and their relationship with the atmospheric-climatic conditions. *J. Geophys. Res.* **97** (C6), 9531-9540.

Astraldi M. and G.P. Gasparini (1994). The seasonal characteristics of the circulation in the Tyrrhenian Sea. In: *Seasonal and interannual variability of the Western Mediterranean Sea. Coastal and estuarine studies, 46.* P.E. La Violette, ed. American Geophysical Union, Washington, D.C.: 115-134.

Astraldi M., G.P. Gasparini and S. Sparnocchia (1994). The seasonal and interannual variability in the Ligurian-Provençal Basin. In: *Seasonal and interannual variability of the Western Mediterranean Sea. Coastal and estuarine studies, 46.* P.E. La Violette, ed. American Geophysical Union, Washington, D.C.: 93-113.

Barberis G., E. Martini and F. Orsino (1979). *Bibliografia geobotanica ligure.* C.N.R., Collana del Programma finalizzato "Promozione della qualità dell'ambiente", AQ/1/42, Pavia, 1-28.

Béthoux J.P., B. Gentili, J. Raunet and D. Taillez (1990). Warming trend in the western Mediterranean deep water. *Nature* **347**, 660-662.

Bhaud M. (1983). Cycles de vie et biogéographie: conclusions générales. *Oceanis* **9**, 4, 389-393.

Bhaud M. (1993). Relationship between larval type and geographic range in marine species: complementary observations on gastropods. *Oceanologica acta* **16**, 2, 191-198.

Bianchi C.N. and C. Morri (1993). Range extension of warm-water species in the northern Mediterranean: evidence for climatic fluctuations? *Porcupine Newsletter* **5**, 7, 156-159.

Bianchi C.N. and C. Morri (1994). Southern species in the Ligurian Sea (northern Mediterranean): new records and a review. *Boll. Ist. Mus. biol. Univ. Genova* **58/59** (1992-1993), 181-197.

Bini G. (1968). *Atlante dei pesci delle coste italiane.* Mondo Sommerso editrice, V, 1-175.

Blacker R.W. (1957). Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. *Fish. Invest.* Ser. II, **20**, 10, 1-49.

Blandin P. (1987). Évolution des écosystèmes et spéciation: le rôle des cycles climatiques. *Bull. Écol.* **18**, 1, 59-61.

Briggs J.C. (1974). *Marine zoogeography.* McGraw-Hill, New York, 1-475.

Bruschi A. and S. Sgorbini (1986). Banche dati ambientali: idrologia del mar Mediterraneo. *Acqua Aria* **6**, 565-578.

Buchanan J.B. (1993). Evidence of benthic pelagic coupling at a station off the Northumberland coast. *J. exp. mar. Biol. Ecol.* **172**, 1-10.

Bussani M. (1992). Ricomparsa nel Golfo di Trieste di alcune specie ittiche. *Hydrores information* **9**, 10, 5-7.

Cabioch L., M. Glémarec and J.F. Samain, eds. (1983). Fluctuation et succession dans les écosystèmes marins. *Oceanologica Acta*, n° sp. 1-225.

Castelli A., C.N. Bianchi, C. Lardicci, M. Abbiati, C. Morri and A. Giangrande (1988). Considérations biogéographiques sur le peuplement annélidien de l'île de Capraia (Archipel Toscan, Italie). *Rapp. Comm. int. Mer Médit.* **31**, 2, 317.

C.I.E.S.M. (1981). *Journées d'études sur la systématique évolutive et la biogéographie en Méditerranée.* Commission Internationale pour l'Exploration Scientifique de la mer Méditerranée, Monaco, 1-198.

Cinelli F. (1979). *Acetabularia acetabulum* (L.) Silva, *Acetabularia parvula* Solms-Laubach and *Dasycladus vermicularis* (Scopoli) Krasser (Chlorophyta, Dasycladaceae): ecology and distribution in the Mediterranean sea. In: *Developmental biology of Acetabularia.* S. Bonotto, V. Kefeli and S. Puiseux-Dao, eds. Elsevier/North-Holland Biomedical Press, 3-14.

Cinelli F., U. Salghetti and F. Serena (1984). Nota sull'areale di *Acrothamnion preissi* (Sonder) Wollaston nell'Alto Tirreno. *Quad. Mus. Stor. Nat. Livorno.* **5**, 57-60.

Colacino M. and A. Rovelli (1983). The yearly averaged air-temperature in Rome from 1782 to 1975. *Tellus* **35** A, 389-397.

Cushing D.H. and R.R. Dickson (1976). The biological response in the sea to climatic changes. *Adv. mar. Biol.* **14**, 1-122.

Dagnino I. (1978). L'osservatorio meteorologico della Università di Genova dal 1833 al 1900. Nota storica. *Atti Accad. Ligure Sci. Lett.* **34** (1977), 3-22.

Dayton P.K. and M.J. Tegner (1984). The importance of scale in community ecology: a kelp forest example with terrestrial analogs. In: *A new ecology: novel approaches to interactive systems.* P.W. Price, C.N. Slobodchikoff and W.S. Gaud, eds. J. Wiley and Sons, New York, **17**, 457-481.

Della Croce N., M. Fabiano and T. Zunini Sertorio (1980). Biomassa planctonica, sali nutritivi, parametri idrologici. Chiavari: Ottobre 1978). Ottobre 1979. Cattedra Idrobiologia e Pescicoltura, Università di Genova, Rapporto Tecnico n° 11, 1-14.

De Lucchi M.G. (1927). La temperatura di Genova dal 1833 al 1922. *Il Comune di Genova*, 31 Luglio 1927, 597-612.

Evans F. and A. Edwards (1993). Changes in zooplankton community off the coast of Northumberland between 1969 and 1988, with notes on changes in the phytoplankton and benthos. *J. exp. mar. Biol. Ecol.* **172**, 11-29.

Flocchini G., C. Palau, I. Repetto and M.P. Rogantin (1983). *I dati di temperatura dell'aria della serie storica (1833-1981) di Genova.* CNR, Progetto Finalizzato Informatica, 83-P2-TERRI-2.3-IGGGE-002, 1-307.

Fowler S. and D. Laffoley (1993). Stability in Mediterranean-Atlantic sessile epifaunal communities at the northern limits of their range. *J. exp. mar. Biol. Ecol.* **172**, 109-127.

Francour P. (1991). Statut de *Centrostephanus longispinus* en Méditerranée. In: *Les espèces marines à protéger en Méditerranée.*

C.F. Boudouresque, M. Avon and V. Gravez, eds. GIS Posidonie, Marseille, 187-202.

Francour P., C.F. Boudouresque, J.G. Harmelin, M.L. Harmelin-Vivien and J.P. Quignard (1994). Are the Mediterranean waters becoming warmer ? Information from biological indicators. *Mar. Poll. Bull.* **28**, 9, 523-526.

Fredj G. (1974). Stockage et exploitation des données en écologie marine. C - Considérations biogéographiques sur le peuplement benthique de la Méditerranée. *Mém. Inst. océanogr. Monaco* **7**, 1-88.

Gaston K.J. (1991). How large is a species' geographic range? *Oikos* **61**, 3, 434-438.

Glémarec M. (1979). Les fluctuations temporelles des peuplements benthiques liées aux fluctuations climatiques. *Oceanologica Acta* **2**, 3, 365-371.

Grainger J.N.R. (1992). The probable effects of climate change on invertebrate growth and reproduction with particular reference to Ireland. *Invert. Reprod. Develop.* **22**, 1-3, 239-244.

Heip C., B.F. Keegan and J.R. Lewis, eds. (1987). Long-term changes in coastal benthic communities. *Hydrobiologia* **142**, 1-340.

Holdgate M.W. (1986). Summary and conclusions: characteristics and consequences of biological invasions. *Phil. Trans. R. Soc. London* B **314**, 733-742.

Hydrokor Cruises (1973). Résultats des campagnes du *N.O. Korotneff*, 1969-71. *Rapp. Tech. Centre Rech. océanogr. Villefranche-sur-Mer*, **5**.

Hydrokor Cruises (1975). Résultats des campagnes du *N.O. Korotneff*, 1972-73. *Rapp. Tech. Centre Rech. océanogr. Villefranche-sur-Mer*, **16**.

Jones P.D., R.S. Bradley, H.F. Diaz, P.M. Kelly and T.M.L. Wigley (1984). Northern Hemisphere surface air temperature variations: 1851-1984. *J. Clim. appl. Meteor.* **25**, 161-179.

Josefson A.B., J.N. Jensen and G. Ærtebjerg (1993). The benthos community structure anomaly in the late 1970s and early 1980s – a result of a major food pulse ? *J. exp. mar. Biol. Ecol.* **172**, 31-45.

Keegan B.F., ed. (1991). *Space and time series data analysis in coastal benthic ecology.* Commission of the European Communities, Directorate-General for Science, Research and Development, Environment Research Programme, Brussels, 1-580.

Laevastu T. (1993). *Marine climate, weather and fisheries.* Fishing News Books, Blakwell Scientific Publications, Oxford, 1-204.

Lardicci C., C. Morri, C.N. Bianchi and A. Castelli (1990). Considerazioni biogeografiche sui policheti delle coste toscane: nota preliminare. *Oebalia*, sup. **16** (1), 123-131.

Lewin R. (1986). Supply-side ecology. *Science* **234**, 25-27.

Meinesz A. (1980). *Contribution à l'étude des Caulerpales (Chlorophytes), avec une mention particulière aux espèces de la Méditerranée occidentale.* Thèse Univ. Nice, 1-262.

Meini L., G. Mucci and S. Vittorini (1979). Ricerche meteomarine sul litorale toscano: centoventi anni di osservazioni meteorologiche a Livorno (1857-1976). *Boll. Soc. geogr. ital.* ser. 10, **8**, 449-474.

Mileikovski S.A. (1971). Types of larval development in marine invertebrates, their distribution and ecological signification: a re-evaluation. *Mar. Biol.* **10**, 3, 193-213.

Molinari M. (1987). Cent'anni di meteorologia. *La Casana*, Genova, **29**, 3, 18-25.

Morri C., C.N. Bianchi, V. Damiani, A. Peirano, G. Romeo and L. Tunesi (1988). L'ambiente marino tra Punta della Chiappa e Sestri Levante (Mar Ligure): profilo ecotipologico e proposta di carta bionomica. *Boll. Mus. Ist. biol. Univ. Genova* **52** sup. (1986), 213-231.

Pérès J.M. (1985). History of the Mediterranean biota and the colonization of the depths. In: *Key environments: Western Mediterranean.* R. Margaleff, ed. Pergamon Press, Oxford, 198-232.

Picco P. (1990). *Climatological atlas of the Western Mediterranean.* ENEA Centre S.Teresa, La Spezia, 1-224.

Rosen B.R. (1991). Biogeographic patterns: a perceptual overview. In: *Analytical biogeography.* A.A. Myers and P.S. Giller, eds. Chapman and Hall, London, 24-55.

Rossi L. (1969). Considerazioni zoogeografiche sul Bacino N.W. del Mediterraneo, con particolare riguardo al Mar Ligure. *Archo bot. biogeogr. ital.* XLV-4ª serie, **14**, 4, 139-152.

Russo G.F., G. Fasulo, A. Toscano and F. Toscano (1990). On the presence of triton species (*Charonia* spp.) (Mollusca Gastropoda) in the Mediterranean Sea: ecological considerations. *Boll. malac.* **26**, 5-9, 91-104.

Sarà M. (1985). Ecological factors and their biogeographic consequences in the Mediterranean ecosystems. In: *Mediterranean marine ecosystems.* M. Moraitou-Apostolopoulou and V. Kiortsis, eds. Plenum Press, New York, 1-17.

Southward A.J. (1963). The distribution of some plankton animals in the English Channel and approaches. III. Theories about long-term biological changes, including fish. *J. mar. biol. Ass. U.K.* **43**, 1-29.

Southward A.J. (1980). The Western English Channel: an inconstant ecosystem. *Nature* **285** (5764), 361-366.

Southward A.J. and G.T. Boalch (1992). The marine resources of Devon's coastal waters. In: *The new maritime history of Devon.* M. Duffy, S. Fisher, B. Greenhill, D.J. Starkey and J. Youngs, eds. Conway Maritime Press, London, 51-61.

Southward A.J. and G.T. Boalch (1994). The effect of changing climate on marine life: past events and future predictions. In: *Man and the maritime environment.* S. Fisher, ed. *Exeter Marit. Stud.* **9**, 101-143.

Southward A.J., G.T. Boalch and L. Maddock (1988). Fluctuations in the herring and pilchard fisheries of Devon and Cornwall linked to change in climate since the 16th century. *J. mar. biol. Ass. U.K.* **68**, 423-445.

Southward A.J., E.I. Butler and L. Pennycuick (1975). Recent cyclic changes in climate and in abundance of marine life. *Nature* **253** (5494), 714-717.

Sparnocchia S., G.M.R. Manzella and P.E. La Violette (1994). The interannual and seasonal variability of the MAW and LIW core properties in the Western Mediterranean Sea. *Coast. estuar. Stud.* **46**, 177-194.

Templado J. (1991). Las especias del genero *Charonia* (Mollusca: Gastropoda) en el Mediterraneo. In: *Les espèces marines à protéger en Méditerranée.* C.F. Boudouresque, M. Avon and V. Gravez, eds. GIS Posidonie publ., France, 133-140.

Thorson G. (1966). Some factors influencing the recruitment and establishment of marine benthic communities. *Neth. J. Sea Res.* **3**, 267-293.

Tortonese E. (1958). Bionomia marina della regione costiera fra Punta della Chiappa e Portofino (Riviera ligure di levante). *Archo Oceanogr. Limnol.* **11**, 2, 167-210.

Tortonese E. (1965). *Pesci e cetacei del mar Ligure.* Libreria editrice Mario Bozzi, Genova, 1-216.

Tortonese E. (1975). *Osteichthyes (pesci ossei). Parte Seconda.* Fauna d'Italia, XI. Calderini, Bologna, 1-636.

Warwick R.M. and B.L. Bayne, eds. (1993). Changes in marine communities. *J. exp. mar. Biol. Ecol.* **172**, 1-230.

Wells H.W. and I.E. Gray (1960). Seasonal occurrence of *Mytilus edulis* off the Carolina coast as a result of transport around Cape Hatteras. *Biol. Bull.* **119**, 3, 550-559.

Zibrowius H. (1978). Première observation du pagure *Calcinus ornatus* dans le parc national de Port-Cros (côte méditerranéenne de France), répartition et bibliographie. *Trav. sci. Parc nation. Port Cros* **4**, 149-155.

Zibrowius H. (1980). Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Mém. Inst. océanogr., Monaco* **11**, 1-284 (+ 107 pl.).

Zibrowius H. (1991). *Chaetaster longipes* (Echinodermata, Asteroidea): distribution in the Mediterranean and the Atlantic. *Mésogée* **51**, 75-81.