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Fluctuation of dominant mesozooplankton species in the Black Sea, North Sea and the Baltic Sea: Is a general trend recognisable?

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Abstract: The distribution and fluctation of dominant pelagic species>300µ(Copepoda, Chaetognatha, Scyhozoa, Ctenophora and ichthyoplankton) of the southern Black Sea were compared with that of dominant species of the North Sea and the Baltic Sea in relation to oceanographic and environmental features. In all three seas, similar changes in the zooplankton composition took place at the end of the 1980's, and the beginning of the 1990's.

- decreasing or increasing abundances of certain species,

- occurrence of new species (North Sea: *Muggiaea atlantica* Lusitanean fish species; Black Sea: *Mnemiopsis leidyi*),

- changes with respect to onset and duration of the bloom period for certain species.

- high interannual fluctuations of some species, which were obvious since the end of the 1980's.

The changes in the zooplankton of all three seas could be related to a rise in temperature during 1988-89 (North Sea, German Bight: sudden rise in the annual average temperature and salinity during 1988-89; Baltic Sea, Kiel Bight: rise in the temperature of the subthermocline water in the same period; Black Sea: extraordinary cold winter 1987/88 followed by an extraordinary warm winter during 1988/89. It was concluded, that the changes in the zooplankton community since the end of 1980's in the Black Sea, North Sea and the Baltic Sea were triggered in all probability by climatic variabilities.

Key Words: Black Sea, Baltic Sea, North Sea, climate, mesozooplankton, *Aurelia, Mnemiopsis, Pleurobrachia, Engraulis.*

Baskın mezozooplakton türlerinin Güney Karadeniz, Kuzey Denizi ve Baltık Denizi'ndeki artma ve azalmaları: Genel bir eğilim tanınabilir mi?

Özet: Güney Karadeniz'deki (Copepoda, Chaetognatha, Scyphozoa, Ctenophora ve balık yumurta ve larvaları gibi 300'dan büyük) baskın pelajik türlerin dağılımı ve artma ve azalmaları çevresel ve oseanografik özellikler çerçevesinde Kuzey Denizi ve Baltık Denizi'ndeki baskın türlerle karşılaştırılmıştır. 1980'li yılların sonu ve 1990'lı yılların başlarında her üç denizde de zooplankton kompozisyonlarında benzer değişiklikler görülmüştür.

- belli bazı türlerin bolluğunun azalması ya da artması,

- Kuzey Denizi'nde *Muggiaea atlantica* Lusitan balık türü ve Karadeniz'de de Taraklılardan *Mnemiopsis leidyi* gibi yeni türlerin ortaya çıkması,

- belli bazı türlerin patlama (bloom) dönemlerinin değişmesi ve patlamanın erken başlayıp daha uzun sürmesi,

Her üç denizde zooplanktonda görülen değişme 1988/89 dönemindeki sıcaklık artışına bağlanabilir (Kuzey Denizi-Almanya Körfezi'nde 1988/89 döneminde yıllık ortalama sıcaklık ve tuzluluktaki ani artış; Baltık Denizi-Kiel Körfezi'nde aynı dönemde sıcaklık tabakasının altındaki su sıcaklığının artışı; Karadeniz'de 1987/88'de olağandışı soğuk kış'ı 1988/89'da da olağandışı sıcak kış döneminin izlemesi), 1980'in sonundan itibaren zooplankton topluluğunda görülen değişmelerin tüm olasılıklar dahilinde iklimsel değişikliklerden kaynaklandığı sonucuna varılmıştır.

Anahtar Sözcükler: Karadeniz, Baltık Denizi, Kuzey Denizi, iklim, mezozooplankton,*Aurelia, Mnemiopsis, Pleurobrachia, Engraluis.*

Introduction

The Black Sea, North Sea and Baltic Sea faced similar environmental problems since 1960 (1), due to high fishery exploitation, eutrophication, oxygen deficiencies, which led to changes in marine communities (2,3,4). The outburst of the accidentally introduced species *Mnemiopsis leidyi* in 1988 (5,6) and the collapse of the anchovy fishery during 1989 (3) drew the attentions of many researches to the Black Sea. The Institute of Marine Sciences of the Middle East Technical University started the investigation and monitoring of zooplankton and ichthyoplankton in the southern Black Sea in June 1991.

This review describes the distribution of the dominant zooplankton species (>300µ) of the southern Black Sea and compares it with the distribution of the same or similar species in the North Sea and the Baltic Sea. This paper attempts to trace some common features in the distribution and fluctuation of zooplankton in these semi-enclosed marine systems. To compare the species abundance in the different seas is difficult, since the species number and biomass are strongly dependent on collection methods. In the southern Black Sea the zooplankton was collected by vertical Hensen Net (mesh size 300µ, opening diameter: 0.7 m) hauls from the anoxic layer to the surface. The spatial distrubution of the zooplankton is controlled to a large extent by the hydrographic features of the seas. Therefore a short overview of the hydrography of the seas under consideration is presented first.

Hydrography of the Seas

Black Sea

The Black Sea (420.000 km^2) is a deep basin with steep slopes in the order of 4-6°. A major shelf area exists only in the northwestern part of this sea, comprising 27 % of the total area of the Black Sea (Fig. 1). The shelf areas, especially in the south eastern region of the Black Sea are very narrow (7). A permanent halocline exists in depth of 80-160 m (8). Below the halocline hydrogen sulfide is apparent.

Above the halocline, the salinity varies between S=18-18.5 ppt in the central Black Sea. The areas between the rim current and coast have a lower salinity from S=18-17.5 ppt. In the western Black Sea the salinity drops below S=16 ppt in near shore areas due to the influence of the river Danube (9).

In the open sea the temperatures above the thermocline vary between 23-25°C, with a maximum of 27°C in summer. The winter temperatures vary between 5-7°C, while the north-western shelf area the temperature falls to 2°C in winter (10).

The cyclonically meandering rim current constitutes the unique basin-scale feature of the Black Sea (Fig. 1). Along the axis of the rim current geostrophic currents attain speeds of 0.2-0.3 ms^{-1} (9). The interior of the rim current is formed by two separate cyclonic cells occupying the western (Western Gyre) and eastern halves (Eastern Gyre) of the basin.

A series of mesoscale anticyclonic eddies is distributed between the rim current and the coast. The two most

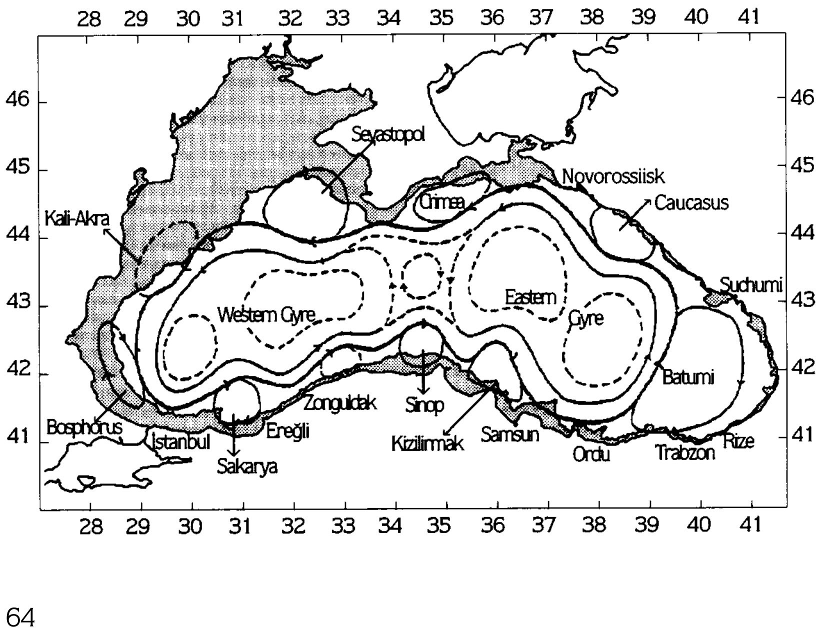

Figure 1. General circulation of surface currents in the Black Sea (redrawn from Oguz et al., 1993). The bold line shows the rim current.

persistent eddies are the Batumi and the Sevastopol Eddies. Eddy induced upwelling occurs along the central part of the Anatolian coast from early summer to early fall. The upwelling features do not translate along the coast (11). Most obvious is the periodically returning upwelling between Cape Kerempe and Cape Ince during summer (10).

North Sea

Compared to the Black Sea the North Sea (575 000 km^2) is a shallow sea. The southern part, south of the Doggerbank is not usually deeper than 40 m, in general 25 m in coastal areas (Fig. 2). North of the Doggerbank the depth increases up to 60-100 m. The Norway trench with a depth of more than 300 m, with maximum depth of 450-750 m is the deepest part of the North Sea (12).

The salinity varies between S=34-35 ppt in the open areas, between 31-33 ppt in the German Bight. The temperature of the North Sea surface waters undergoes high seasonal variation, in the German Bight 24°C, in the English Channel 10°C. The winter temperatures vary around 7-9°C in the English channel, 5-7°C north of the Doggerbank and about 2°C in the German Bight. In the central North Sea, the summer temperature of the surface water is about 16°C. The salinity varies between S=34-35 ppt in the open areas, between S=31-32 ppt in the German Bight (13).

The general circulation pattern in the North Sea is a large basin-wide cyclonic gyre controlled predominantly by the in- and outflow and by the bottom topography (14). The predominant inflow into the North Sea is from the north, a minor inflow of Atlantic water comes through the English Channel and the characteristic low salinity inflow of Baltic Sea water enters via the Skagerrak (Fig. 3). The entire freshwater input from rivers into the North Sea of about 370 (km^{-3} Y^{-1}) is a little higher than that of the Black Sea (310 km^{-3} Y^{-1}) (15). The main outflow occurs northward along the Norwegian coast.

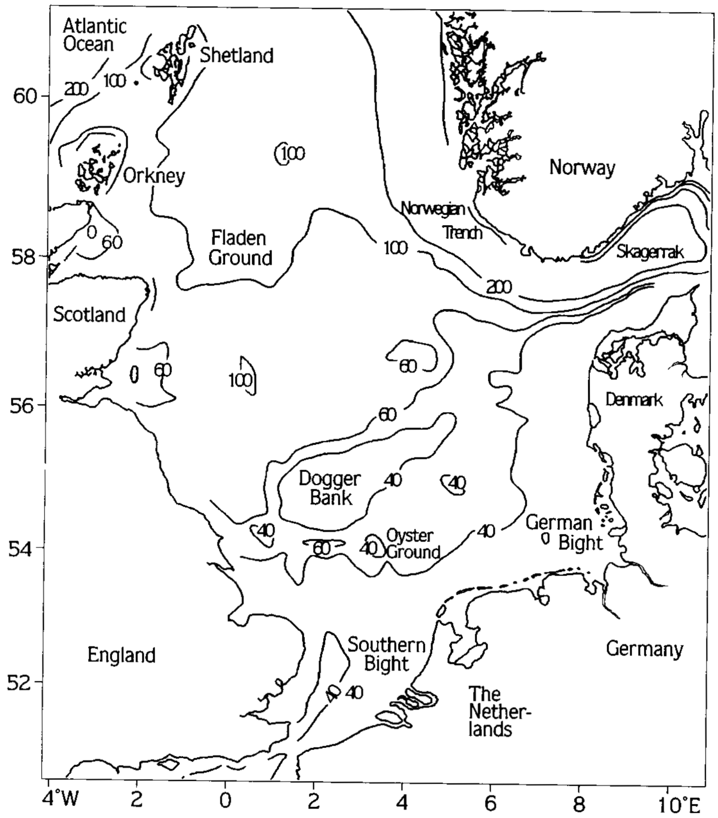

Figure 2. North Sea. Bathymetry (Sündermann, 1994).

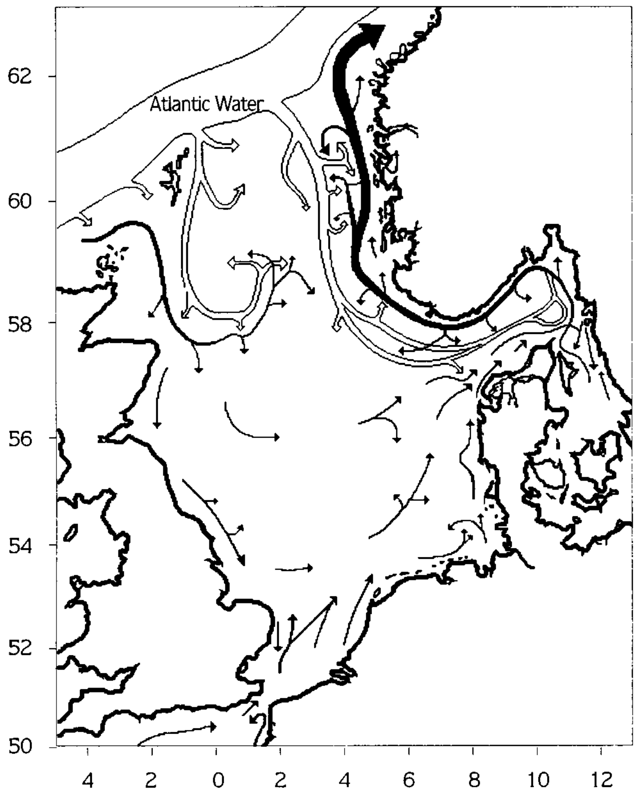

Figure 3. Currents in the North Sea (redrawn from Svendsen et al., 1994).

Baltic Sea

The Baltic Sea displays similar features with the Black Sea. Like the Black Sea, the Baltic Sea is connected to the North Sea by a small canal and the Baltic Sea has H_2S-formation in the bottom water in deep basins (4, 16, 17). Unlike the Black Sea however, anoxic conditions in the deep basins can be improved by irregular strong inflow of saline water from the North Sea driven by strong westerly winds (4, 18).

The Baltic Sea (382 000 km^2) is connected with the North Sea via Skagerrak and Kattegat by 3 shallow canals (Öre-Sund 7 m; Kleine Belt 10.5 m; Groeße Belt 30m). The open Baltic Sea basin is separated from these three canals by the Draßer ridge with a water depth of 18 m. The Baltic Sea towards the central part consists of a series of basins, each deeper than the previous and each separated by ridges from each other. The Baltic Sea is deeper than the North Sea. Wide areas are below 100 m. The Baltic proper is the deepest basin of the Baltic Sea with a maximum depth of 459 m (16).

The surface salinity decreases from S=29 ppt in the Kattegat, S=15 ppt in the southwestern area to S<2 ppt towards the northeast in the Gulf of Finland and Bothnian Bay (Fig. 4). The central Baltic Sea has a salinity of about S=6-7 ppt (16), Siedler & Hatje, 1974 in (17). Increases in surface salinity and especially in the bottom salinity occur due to irregular westerly wind driven inflows from the North Sea. These inflows are significant factors in bottom water mass formation and in the oxygenation of anoxic zones and have an essential effect on the biocenosis of the Baltic Sea (4).

The surface temperature of the central Baltic Sea is similar to the North Sea, in February 1-3°C, in August 15-16°C. But unlike the North Sea, due to its low salinity in winter, inc or drifting ice could be expected to cover all areas of the Baltic Sea expect the central area (16), Dietrich & Schoot, 1974 in (17).

In the Baltic Sea evaporation and precipitation are equal, thus the freshwater supply by rivers is dominant (Dietrich Schoot, 1974 in (17). Most of this water leaves the Baltic Sea by a surface stream via Öre-Sund and Großen Belt close to the Swedish coast. Easterly winds support the outflow, westerly winds between 2-3 on the Beaufort scale prevent the outflow. When wind forces reach 3 on Beaufort scale, the saline waters of the Kattegat enter the Baltic Sea (4).

Distribution of The Zooplankton Species

Not all species, occurring in the Black Sea are represented in the North Sea and Baltic Sea as well. But

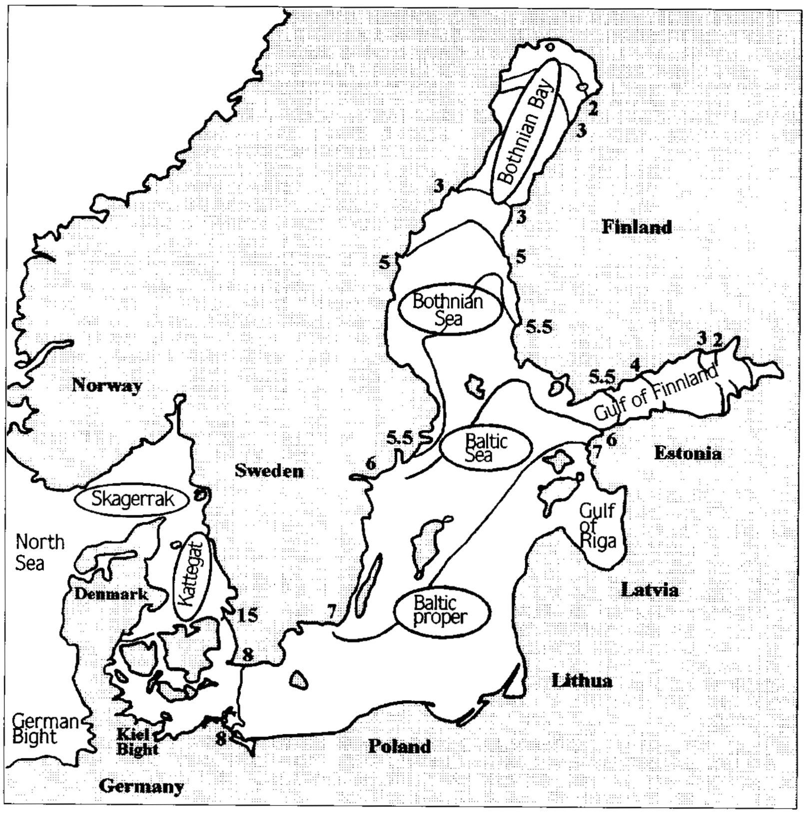

Figure 4. Baltic Sea regions (redrawn from Granli, 1990) and salinity of the surface water (Gessner, 1957).

they are represented by species of the same genus with similar behavior. For example *Calanus euxinus,* a copepod common in the Black Sea is represented by the very similar copepod species *Calanus finmarchicus* in the North Sea.

Due to the low salinity many zooplankton species occurring in the Black Sea and in the North Sea are not present or are very rare in the Baltic Sea. For example the copepods *Acartia clausi* and *Pseudocalanus elongates* are present only in the southwestern more saline part with a salinity S>7 ppt (19). C. *finmarchicus*, the chaetognath Sagitta setosa and the comb jelly *Pleurobrachia pileus,* species which are dependent on a higher salinity could serve as indicator species for an inflow of higher saline North Sea water and are distributed only in the southern part of the Baltic Sea (19, 20).

The dominant zooplankton species (>300µ) occurring in the southern part of the Black Sea are shown in Fig. 5. The species, which are for the most part living above the thermocline are placed in the upper section, those mostly species living below the thermocline are drawn in the lower section of Fig. 5.

Sagitta setosa, Pleurobrachia pileus and the copepods *Pseudocalanus elongates, Calanus euxinus* and in the North Sea C. *finmarchicus* display diel vertical migrations (21). During night these species are concentrated in the upper water, mostly just below the thermocline. In the early morning these species migrate down to the deep layer, stay there during the day and rise again to the surface in the late afternoon / early evening.

In the Black Sea during day time the species *Sagitta setosa*, *Pleurobrachia pileus, Pseudocalanus elongatus* and *Calanus euxinus* are concentrated in an narrow horizon just above the H_2S-layer in depths between 80 - 150 m. The oxygen values in this horizon vary between 0.4-0.5 ml O_2l^{-1}. In this oxygen poor zone the upper layer is inhabited by *P. pileus*, the middle portion by *C. euxinus* and the lowest part by *S. setosa* (21). Due to their deep dwelling, these species are more abundant in the southern Black Sea than in the shallow northwestern shelf of the Black Sea, because in the southern area the continental slope is very steep.

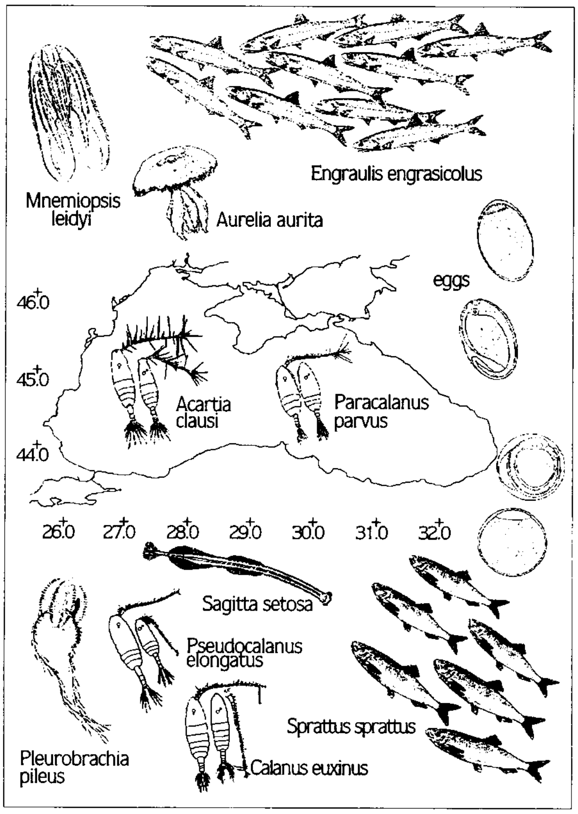

Figure 5. Dominant species (>300) of the southern Black Sea

The distribution of the deep dwelling *Sagitta setosa* reflects the topography and the overall hydrographic situation in the Black Sea. Since the species is distributed mainly in deep water, abundances are low in the shelf area. Individuals accumulate in the rim current and drift as relatively large clouds along the shelf edges around the basin. The abundances of *Sagitta setosa* follow the branches of the current into the open sea, but the numbers are low in the central gyres (Fig. 6).

The distribution of anchovy eggs in July 1992 also reflects the hydrographical features of the Black Sea (22). The bulk of eggs were distributed in the main spawning areas between shelf areas and the rim current (Fig. 7). After spawning the eggs were transported with the rim current in open waters. This is obvious in the area between the eastern gyre and Batumi eddy and in the western area. Regions with no or very small egg numbers were the cyclonic gyres in the central part and the Batumi eddy in the eastern part of the Black Sea. Anchovy eggs were also absent in the upwelling region west of Sinop with surface temperatures of 12°C. In contrast to the anchovy eggs, the cold water species *Pseudocalanus* elongates was very frequent in the upwelling area with about 30 000 individuals m^{-2} compared to the average value of 2210±720 individuals m^{-2} for the whole southern Black Sea area (23).

Jelly Zooplankton

Four species of gelatinous animals are common in the Black Sea: two scyphozoans, Aurelia aurita and Rhyzostoma pulmo and two ctenophores, Pleurobrachia *pileus* and *Mnemiopsis leidyi. While Rhyzostoma pulmo* is most common in coastal areas, the former three species are distributed in all parts of the Black Sea (24).

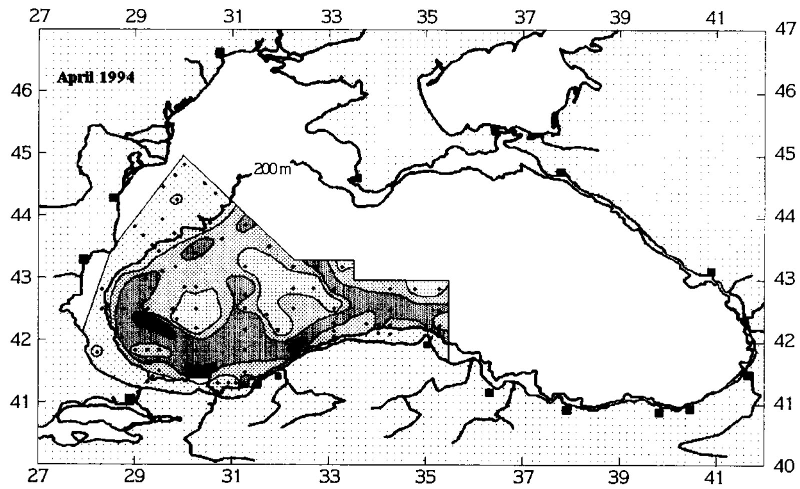

Figure 6. *Sattiga setosa.* Distribution in April 1994 in comparison to currents and gyres (IMS-METU data, unpublished).

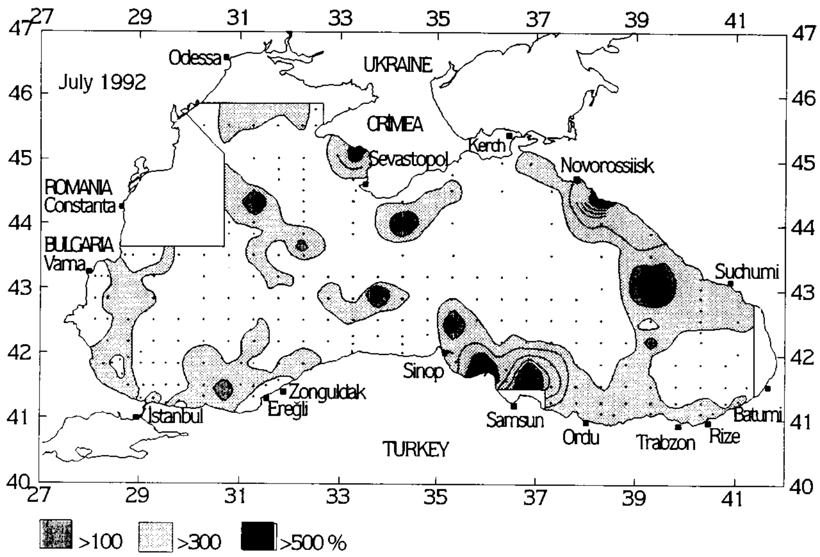

Figure 7. Distribution of anchovy eggs in July 1992 in relation to surface currents (see Figure 1) in July 1992 (Niermann et al., 1994). Indicated era the areas with egg numbers> 100% of the total number.

At the present time the combjelly *Mnemiopsis leidyi* is one of the most spectacular species of the Black Sea and is not present in the North Sea or Baltic Sea. This north-western Atlantic ctenophore species, which originated from eutrophic lagoons in North America, was accidentally introduced into the Black Sea in the mid 1980's and radically affected the entire pelagic fauna of the Black Sea (3, 5, 6, 25).

The outburst of *Mnemiopsis* started in the autumn of 1988, and reached a biomass of about 2 kg m^{-2} wet weight in the open Black Sea area in August 1989 (26) with a maximum of about 4.7 kg m^{-2}, consisting of approximately 3000 mostly small individuals m^{-2} in September 1989 in the northwestern shelf area (24). After spring 1990 the biomass of *Mnemiopsis* in the open sea started to decrease and varied between 0.2-0.3 kg m^{-2} Between summer 1991-1994 (Fig. 8). During 1995, a moderate increase about 0.5 kg m^{-2} was observed in the southern Black Sea (24,25,27).

Adult individuals of *Mnemiopsis leidyi* reach a total body length of about 12 cm. *M. leidyi* is present during the whole year with minimum abundances in March/April and a peak during July/August. Their biomass is minimal in May/June and reaches its maximum in October/November. During winter, the biomass remains high and small individuals are frequent during the winter months as well (24, 27).

Aurelia aurita is a very common jelly fish in the Black Sea and Baltic Sea, but is rare in the North Sea, where it

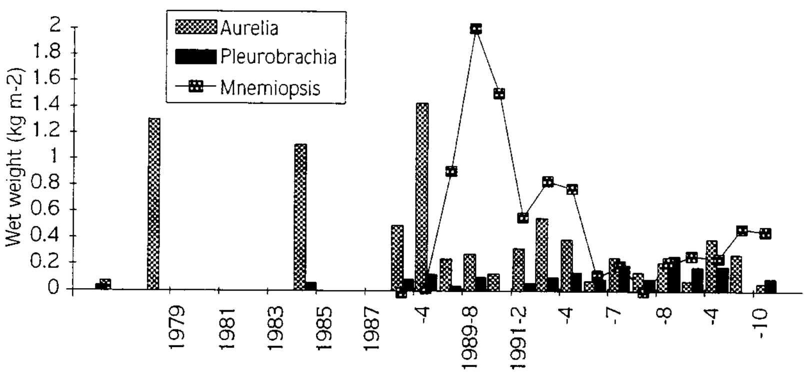

Figure 8. Fluctuation of the biomass (wet weight kg m^{-2} of Mnemiopsis sp., *Aurelia aurita* and *Pleurobrachia pileus* in offshore areas of the Black Sea from 1958-1995 (biomass of *A. arurita* of 1950's Shushkina and Musayeva, 1983; biomass from 1958-April 1993, Shushkina Musayeva, 1991, Table 2; biomass from 1993-95 Mutlu et al., 1994 and Mutlu 1996).

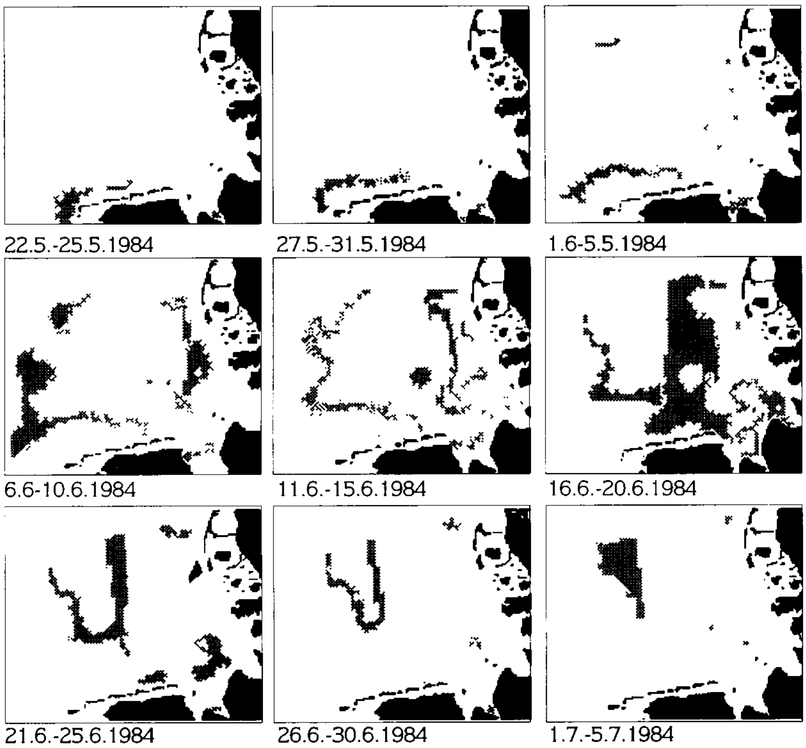

Figure 9. *Pleurobrachia pileus* in the German Bight (May 22-July 5, 1984). Each graph represents the areas of maximum abundance during 5 days (Grave & Reiners, 1988)

is controlled by the jelly fish *Chrysaora quinquecirrha*. In the southern Black Sea, *A. aurita* is very common in the mixed layer down to the subthermocline region. Small animals are mostly found above the thermocline, while larger individuals, up to 40 cm are found just below it. The biomass of *A. aurita* fluctuates seasonally (28), being high in spring (March, April) and autumn (September-November). The biomass of *A. aurita* of about 70 g m^{-2} (30) raised to a level of 0.9-1.3 kg m^{-2} wet weight averaged for the whole of the Black Sea in 1978/1979. From 1978-April 1988 the biomass kept a level of 1-1.3 kg m^{-2} (26, 32). In summer 1988 the biomass of *Aurelia* aurita dropped, possibly due to the effects of increase in *Mnemiopsis leidyi* (33) and varied till October 1995 between 0.2-0.4 kg m^{-2} in offshore waters (25, 26, 27).

In the western Baltic Sea, *Aurelia aurita* occurred during the summers 1978-1993 with average numbers of 1-16 individuals 100 m^{-3}, corresponding to 0.2-4.4 g C. In bloom years a biomass up to about 5 kg wet weight 100 m^{-3} was observed. In these bloom years *A. aurita* consumes about 2/3 of the daily secondary production and is responsible for the decline in mesoplankton during these years (34). Especially reduced were the stocks of the copepods *Pseudocalanus elongates, Paracalanus* spp. and *Oithona similes*. However not all mesozooplankton species were affected by *A. aurita*. Bivalve-larvae and the copepods *Centrophages hamatus, Acartia* spp. Did not show significant changes during blooming years of the medusa. This differential response of the zooplankton due to the blooms of *A. aurita* led to differing trophic structures in the zooplankton community. Fine filter feeders and raptorial filter feeders were more abundant in years with a small *A. aurita* stock, whereas coarse-filter feeders dominated the opposite trend (35).

In the Black Sea *Pleurobrachia pileus* is found in the water column above the anoxic zone below the maximal pycnocline at depths between 60-170 m during the day at densities of 80-115 individuals m^{-3}. At night, this species migrates towards the surface. The adults reach a length of 2 cm in diameter, the biomass varying between 50-150 g m^{-2}. No major seasonal changes of annual fluctuations have been observed during the last few decades (26, 36). In the open southern Black Sea, the biomass of *Pleurobrachia* was in the range of about 200-260 g m^{-2} in July 1992 and August 1993. During 1995 (March and October) the biomass of *Pleurobrachia pileus* was smaller than in the previous years (50-100 g m^{-2}) (25).

In the North Sea in the German Bight, *Pleurobrachia pileus* exhibits a single dominant population maximum each year from mid May till the end of June. Beginning in the coastal area in May the population wave propagates outward into the central German Bight. After 45 days, in July, the population is nearly extinct (Fig. 9). The population decline is not related to starvation, but to the impact of *Beore gracilis*, which feeds on and terminates the *Pleurobrachia pileus* population (37).

In the Baltic Sea, occurrence of *Pleurobrachia pileus* is strongly dependent on the inflow of North Sea water. In the Kiel Bight variations in the ctenophore stock are primarily caused by advection and do not reflect the biological population cycle of this species (20).

Copepoda

Apart from *Oithona nana*, a species which is too small to be caught with a 300 µ gauze, *Acartia clausi* is one of the most abundant copepod species in the upper layers of the Black Sea.

The bloom period is during midsummer (24,35,38). In the southern Black Sea, the biomass and individual number of *Acartia clausi* varied between 0.08±0.02 and 0.63 ±0.07 g wet weight and 2620 ± 540 and 11640 ± 1945 individuals m^{-2} in January and July 1992 respectively (23).

This species is also common in the North Sea, where it occurs together with *Acartia longiremis.* In the Baltic Sea, *Acartia clausi* is present only in the western more saline part. In the northeastern areas of the Baltic Sea, it is replaced by three other brackish water species, *A. discaudata, A bifiliosa and A. tonsa* (19, 38).

Paracalanus parvus and *Centropages kröyeri (ponticus),* species typical of the upper layer, are not very common in the southern Black Sea. They occur only in low numbers during summer (23). *Paracalanus parvus* is a cosmopolitan species. In the North Sea, it is considered to be a neritic species inhabiting the warm surface layers. *Paracalanus parvus* is most abundant in the central (26000 individuals m^{-2}) and southern North Sea as well as in the coastal waters of the Netherlands and Germany (38). The distribution of *paracalanus parvus* in the Baltic Sea is restricted to the southwestern part dependent on salinity (19). Below S=7.8 ppt, this species does not occur.

Centropages kröyeri does not occur either in the North Sea or the Baltic Sea. In the North Sea, the genus is replaced by the species *C. typicus and C. hamatus. C. typicus* is an Atlantic species and enters the North Sea with the inflow of warmer Atlantic water (38). *C. hamatus* is a typical summer and coastal species and it is very common in the North Sea and English Channel. Hickel (1975, (39)) considered this copepod as one of the commonest species in the Dutch and German Wadden Seas. In the Baltic Sea *Centropages hamatus* occurs in low abundance between 200-1000 individuals m^{-3} in areas with a salinity S>7ppt (19,40).

The species *Calanus euxinus* and *Pseudocalanus elongatus* display diel vertical migrations (21). During day time, they inhabit the deep layers close to the H_2S-horizon and rise during the night to surface waters and remain just below the thermocline. Due to this vertical migration pattern, thes species are more abundant in the southern Black Sea with steep continental slopes, than in the shallow northwestern shelf of the Black Sea.

In the Black Sea, the vertical migration patterns of *Calanus euxinus* change seasonally as known from other calanoid species in other oceans (41). In August/ September the adults and copepodite V migrate to deeper waters where they overwinter close to the anoxic layer in about 80-170 m depth (42). During overwintering, the southern Black Sea spawning of C. *euxinus* takes place at the shelf edges, then the copepodites are carried by currents to offshore waters (23). Young nauplius and capopodite stages are present in surface waters throughout the summur, when they grow and reach adult stage, they start to display diel vertical migration.

In the Black Sea, *C. euxinus* exhibits the highest biomass of all copepod species. Before 1990 the biomass varied on average between 5-10 g wet weight m^{-2} (24). In the southern and western Black Sea the average biomass and individual number (n-m^{-2}) of *Calanus euxinus* varied between 1.6 and 5.7 g m^{-2} wet weight (Table 1). At some locations biomasses higher than 15 g m^{-2} were found during 1991-1995 (23 and unpublished measurements of the Institute of Marine Sciences-Erdemli).

Table 1. Calanus euxinus: average biomass (g wet weight m^{-2}) and individual number (n m^{-2}) in the southern and southwestern Black Sea.

Area of investigation and period		Average biomass	Maximum biomass	Average number
Southern Black Sea,	June 91	3.2±0.8	19.2	4320±1180
Southern Black Sea,	July 92	1.6±0.3	6.3	2430±370
Western Black Sea,	Apr. 93	4.9		
Southern Black Sea,	Aug 93	4.6		
Western Black Sea,	Apr. 94	5.7		
Western Black Sea,	Mar. 95			7987±7570

In the North Sea, *Calanus euxinus* replaced by *C. finmarchicus* and *C. helgolandicus. C. helgolandicus* is a summer/autumn species occuring mainly in the southern areas in relatively small numbers (38).

In the deeper northern North Sea, *C. finmarchicus* is very common. The seasonal migration pattern of *C. finmarchicus* in the North Sea is similar to that of *C. euxinus* in the Black Sea. Like *C. euxinus, C. finmarchicus* is a deep water species and therefore its main center of distribution is the more deep northern North Sea, especially the regions of the Norwegian trench and the Skagerrak (43). In the Norwegian trench this species is dominant in winter and summer. Numbers up to 43000 individuals m^{-2} were counted during spring 1987 (38). Overwintering takes place in the Norwegian trench between 450-750 m with high temperature and density gradients (44). Copepodites V and IV, enriched with lipids migrate into deep water during July/August. The ascent of the copepodites starts in February/March. They mature and mate in the surface layer coinciding with the early diatom spring bloom. In March the number of young copepodit stages increase off the Skagerrak (43) and in May the population is carried by currents all over the North Sea. Until the autumn *C. finmarchicus* undergoes 2-3 further reproduction periods

Only the deep waters of the Norwegian trench serve as a refuge for overwintering in the North Sea. Due to the shallow water depth especially in the southern North Sea, the individuals are not sheltered against turbulence or predators, thus virtually the whole stock does not survive the winter period in this area (38). The stock of *C. finmarchicus* in the southern North Sea is strongly dependent on the strength of the north western currents. Therefore the stock displays a highly variable fluctuation in the southern North Sea.

Calanus finmarchicus act in the low saline Baltic Sea only as indicator species for the inflow of saline North Sea water of the Kattegat (19, 20).

Pseudocalanus elongatus, a cold water species, with an upper temperature limit for occurrence of about 13°C (45) is very common throughout the Black Sea. High concentrations, of up to 22 000 individuals per m^3 of sexually mature and spawning females were found (46) and (36) above the pycnocline with oxygen values between 0.4-0.5 ml 0_2 l^{-1} during April-May.

In both the southern and western Black Sea, the biomass varied between 0.158-0.21 g wet weight m^{-2}, the individual numbers between 2200-6500 m^{-2} during 1991-1994 (23). In March/April 1995 an average of 20 000 individuals per m^2 were found, (Table 2, and unpublished measurements of the Institute of Marine Sciences-Erdemli).

Table 2. *Pseudocalanus elongatus*: average biomass (g wet weight m^{-2}) and individual number (n-m^{-2}) in the southern and south western Black Sea.

Black Sea region	and date	Average biomass	Maximum biomass	Average number
Southern Black Sea,	June 91	0.06±0.02	0.5	2210±720
Southern Black Sea,	Jan 92	0.16±0.06	1.0	4830±1750
Southern Black Sea,	July 92	0.17±0.03	1.2	6500±1200
Western Black Sea,	Apr. 93	0.21		
Southern Black Sea,	Aug 93	-		
Western Black Sea,	Apr. 94	0.158		
Western Black Sea,	Mar. 95			20 000

Pseudocalanus elongatus is also common throughout the North Sea. During winter this species is abundant in large quantities throughout the whole North Sea (38). In the Norwegian coastal waters it occurs in abundances similar to *Calanus finmarchicus* (47).

In the Baltic Sea, *Pseudocalanus elognatus* is one of the most important species in the southern and central regions (40). The distribution of this cold stenotherm species is limited by a salinity of S=5-7 ppt (19, 48). In accordance to the Black Sea, *P. elongatus* reproduces in the Baltic Sea during late spring, never during summer (49).

Chaetognatha

The species *Sagitta setosa* is the dominant chaetognath species in the Black Sea. In the southern and western Black Sea, abundances, of about 100-400 individuals m^{-2} on average were found between 1991-1995. High abundances were always found at the shelf edges and in the rim current (Fig. 6 see also Fig. 1)

Sagitta setosa performs diel vertical migration. During the night most individuals are concentrated below the upper thermocline but during the daytime the bulk of individuals are found just above the anoxic layer with oxygen values of about 0.4-0.5 ml $0_2 1^{-1}$ (21, 36,46).

In the Black Sea the peak of the *Sagitta setosa* bloom occurs in July/August (Fig. 10). Most of the juveniles do not perform vertical migration and stay in the upper layer (24). While small and large individuals occur in equal numbers during January and February. In May/June the juveniles have reached the adult stage. In July spawning starts and the number of adult individuals decreases rapidly. By August the adults are virtually diminshed and replaced by juveniles. This may indicate, that *Sagitta setosa* dies after breeding (50).

In the North Sea, the peak bloom of *Sagitta setosa* is later than in the Black Sea. It occurs between September and November, and displays high interannual variations (Fig. 11). In the English Channel with higher water temperatures the spawning time starts earlier, than in Kattegat (51). The single breeding period per year found in the Channel and in the Kattegat indicate a 1 year life cycle (50).

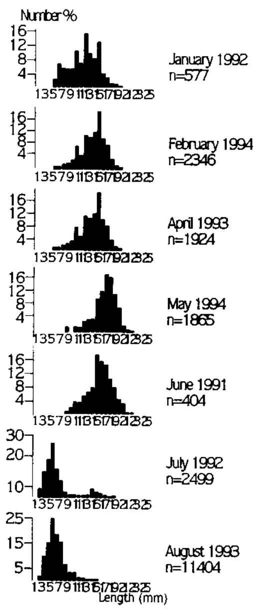

Figure 10. *Sagitta setosa*. Length distribution in different seasons in the Black Sea.

Temperature may be a dominant growth-regulating factor (direct and/or indirect) for this species (50). *S. setosa* is larger in the Black Sea (total length: 11-15 mm) and in the western Channel (9-12 mm) during winter and spring compared to *S. setosa* in the northern more cold Kattegat (4-7 mm).

In the North Sea, *S. setosa* is the indicator of pure North Sea water, whereas *S. elegans* indicates Atlantic inflow. The chaetognath *S. setosa* is more abundant in the deep areas of the North Sea than in the shallow coastal areas. The centers of high abundance are the English Channel, the central North Sea and the Skagerrak (38,50,51).

Like *C. finmarchicus,* individual numbers of *Sagitta setosa* in the North Sea are dependent on wind force and on the direction and duration of currents. In the Kattegat numbers at any one station may change drastically over a short period, because the inflow of different water masses from the North Sea is highly variable on time scales of a few days (51,52).

In the Baltic Sea *Sagitta setosa* is not common. Its presence in the southwestern Baltic Sea is always related to an inflow of high saline water from the Kattegat (19).

Ichthyoplankton

A total of 29 taxa of icthyoplankton were caught during all cruises from 1991-1994 in the southern Black Sea. The eggs of the two most economically important species *engraulis encrasicolus* and *Sprattus sprattus* dominated the ichthyoplankton in summer and winter respetcively. From other fish species only considerable amounts of eggs and larvae of *Merlangius merlangus, Platichthys flesus, Mullus barbatus* and *Mugil sp.* were present (Institute of Marine Sciences-Erdemli, unpublished data).

The sprat *Sprattus sprattus* occurs in all three seas. In the Black Sea, its main distribution is below the thermocline (53). The sprat spawns throughout the whole year. In the southern Black Sea the main spawning time is Nowember - March with a peak in January/February (54, 55, 56). During this period the spherical sprat eggs, characterized by segmented yolk and absence of an oil globule, are present in numbers between 50-150 eggs m^{-2}. In

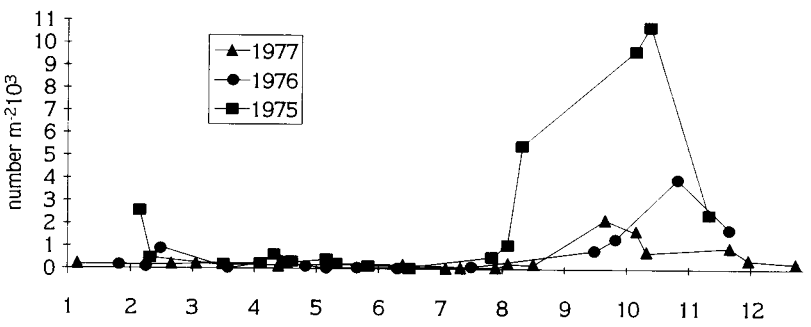

Figure 11. *Sagitta setosa*. Seasonal and interannual fluctuations in the Kattegat.

the southern North Sea, the spawning season starts in January/February. In the northern North Sea, the spawning season begins about one month later in February/ March (57).

The anchovy *Engraulis engrasicolus* is the most dominant fish in the Black Sea (29), but is not frequent in the North Sea and it does not occur in the Baltic Sea. In the Black Sea, the anchovy occurs mainly in the upper water layers and its eggs and larvae are very common in summer. The anchovy eggs are very easy to identify due to their ellipsoidal shape (54, 58).

The two subspecies of the Black Sea anchovy *Engraulis engrasicolus ponticus* and *Engraulis engrasicolus euxinus* undergo extensive migrations all over the Black Sea from the overwintering to the spawning areas (55, 59). According to earlier surveys the anchovy spawns throughout the whole of the Black Sea (60) but mainly in the northern half, especially in the shelf area (55).

Changes in the spawning areas of anchovy were noticeable off the Crimean coast by 1988, when the areas observed to be most abundant with anchovy eggs and larvae were towards the open sea rather than the typical distribution at the shelf areas found during 1950 to 1980. In 1992 and 1993, the bulk of anchovy eggs were obtained from the southern and particularly the south-eastern Black Sea and not from the northern Black Sea as usual. Comparison of the egg numbers found during an earlier survey about 40 years ago in July 1957 showed that the northern part of the Black Sea displayed nearly the same numbers of anchovy eggs as in 1957, whilst the egg numbers for the southern region were significantly higher in 1992 than in 1957 (22).

Niermann *et al.,* (1994 (22)) concluded, that the low egg and larvae numbers in 1957 and 1959 possibly reflect the mesotrophic state of the Black Sea in the late 1950's. With increasing eutrophication, the anchovy stock enlarged in the early 1960's, and consequently egg and larval numbers increased. The decrease in spawning of the anchovy in the northern Black Sea during the 1980's is consistent with the northern area of the Black Sea having become excessively eutrophic and more polluted than the southern area over the last two decades as a result of major rivers flowing into this region. They suggested, that the environmental deterioration of the shelf area due to dystrophication and the improved food conditions in the open sea due to eutrophication, has resulted in a shift of the spawning grounds to the open sea. Increasing eutrophication of the former mesotrophic coastal areas of the southern Black Sea could also be assumed as a reason for the expansion of the spawning grounds from the Bosphorous area to the eastern Black Sea coast of Turkey.

A sudden decline of anchovy eggs and larvae, reflecting the collapse of anchovy catches for the whole of the Black Sea, were recorded in 1989, coinciding with the outburst of *Mnemiopsis leidyi.* This species competes for zooplanktonic food with the anchovy and is an important potential predator of anchovy eggs, and, especially, of yolk-sac larvae (61, 62). *Mnemiopsis* could, therefore, be a threat to fishery years-class recruitment (63).

Longtern fluctation

The zooplankton shows high interannual variability in all three seas under consideration. The examples of *Sagitta setosa* and *Pleurobrachia pileus* showed, that zooplankton populations are extremely patchy and change in distribution and abudance at a scale which coincides with that of fluctuatioons in currents and predators.

The present state of the Black Sea, North Sea and Baltic Sea are determined by a continuing eutrophication process, which especially affects coastal communities (3, 64). The effects of eutrophication in the open waters are obvious as well, but as yet moderate. The eutrophication is related to the anthropogenic nutrient input and due to the remobilisation of nutrients from deep waters and the benthos (2, 3, 4, 40, 65). Comparing the zooplankton fluctuations in all enclosed seas under consideration, it is striking that major changes in the zooplankton community happened at the end of the 1980's.

Baltic Sea

Comparison of the data for the month of August from 1953 - 1988 (data of the Baltic Sea Fishery Research Institute in Riga) showed a steep increase in zooplankton biomass in the Baltic Proper during the 1970's (40). The increase of the zooplankton biomass was caused especially by the high increase of *Pseudocalanus elongatus* and *Acartia sp.* After maintaining a high level during the 1980's the populations of *P. elongatus* and *Acartia sp.* declined rapidly in 1988 (Fig. 12).

In contrast with the stock in the Baltic Proper, the stock of *Pseudocalanus elongatus* in the Kiel Bight has increased since 1988 after a period of extremely low abundance between 1986 and 1987. Individual numbers of the copepod *Othiona similis* and the appendicularia *Oikopleura dioica* have increased strongly since 1988/89 during the summer months and have since then displayed

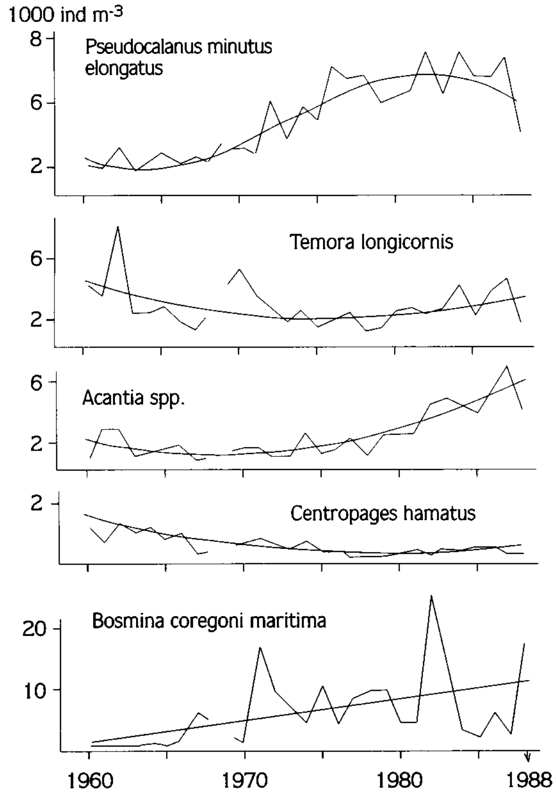

Figure 12. Fluctuation of main zooplankton species in the eastern and southeastern part of Baltic Proper during August 1960-1988 in 0-100 m depth (from Schulz et al., 1990)

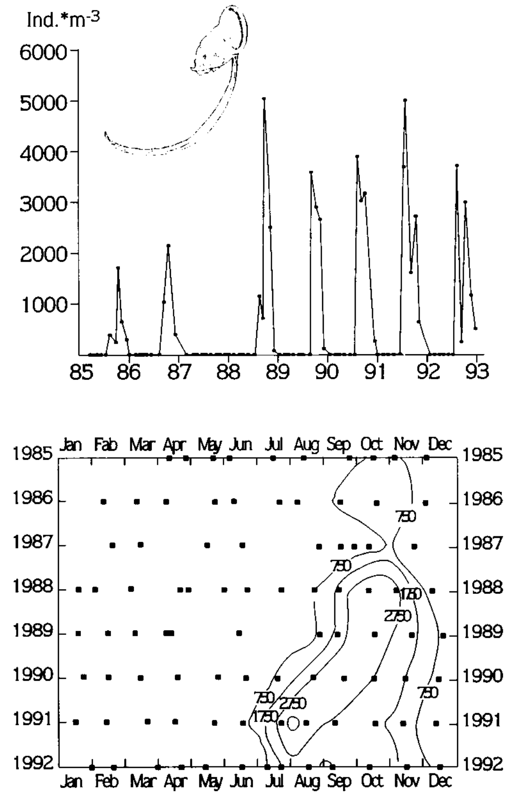

Figure 13. *Oikopleura dioica*. Fluctuation and seasonal distribution in the Kiel Bight, Baltic Sea during 1985-1993 (Behrends, in press).

high seasonal fluctuation. Since 1988, the blooming period of *Oikopleura dioica* has started in July, two months earlier than in previous years and continues as before till November (Fig. 13). In the Kiel Bight the rise in numbers of *Oikopleura* and *Oithona* corresponds to the rise in temperature at 20 m depth for the season July to December, while the years with low densities of *Pseudocalanus elongatus* correspond to years of low salinity at 5 m depth and partly at 20 m depth before and during the reproduction season (66).

Increasing abundances after 1988, as seen for the most of the mesozooplankton species in the Kiel Bight (67), were found as well in ichthyoplankton (68) and in zoobenthic species (69) after an abundance and diversity minumum in 1988 and 1985-1988 respectively. In contrast to the zooplankton, the phytoplankton did not show this tendency (70).

Besides the possible eutrophication effect of the Baltic Proper the changes in temperature and salinity have an overall influence on the composition of the zooplankton community. The years with cold water periods 1962-1970; 1979-1988 due to severe winters displayed lower levels of zooplankton development, than those years of warm water periods with mild winters 1954-1961 and 1971-1978. The decline of the zooplankton in the Baltic Proper could be related to the decreasing salinity as well (40).

North Sea

Sudden changes in the abundance of some species were detected as well in the German Bight, at Helgoland Roads during 1988/89 (71). For example, after 1988 the actinotrocha, the larval stage of *Phoronis müllleri* increased after a period of low abundance (Fig. 14a). After a blooming period 1983-1989, the stock of *Acartia sp.,* declined rapidly till 1993 (Fig. 14b). The abundance of *P. elongatus* and *Paracalanus sp.,* decreased after 1987-1992 after a blooming period from 1983-1986 (Fig. 14c). Starting in 1987, *Sagitta setosa* fluctuated with a high amplitude till 1991 (Fig. 14d). The abundance of *Sagitta setosa* decreased as well at the end of the 80's after a blooming period (1983 - 1988).

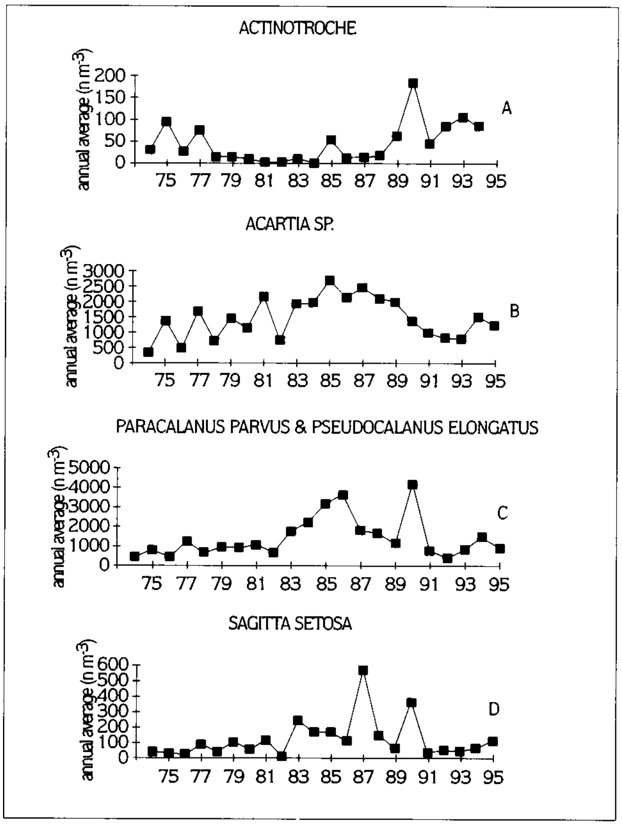

Figure 14. Fluctation of dominant zooplankton species at Helgoland Roads, German Bight, North Sea during 1974-1995 (Data from Marine Biological Information System of the Biologische Anstalt Helgoland; Greve and Reiners in press).

Since 1989, lusitanian fish species *Trachinus vipera, Zeus faber, Mullus surmuleuts* and other species were found in the North Sea (72). As evidence for an exceptional inflow of Atlantic water into the North Sea during 1989, an extraordinary population of *Doliolum nationalis* (Tunicata) was observed in the central and southeastern North Sea (73) As in the Black Sea a new species *Muggiaea atlantica* (Siphonophora, lusitanian plankton) invaded the North Sea in 1989 and caused changes in the biocenosis (74).

In the German Bight, the temperature and salinity of the surface water increased in similarity to the Baltic Sea suddenly in the end of 1980's (Fig. 15). The average surface temperature was below 10°C in the years 1984-1987, it increased in 1988 and was about 11°C in 1989/90, After 1990, the temperature varied between 10 and 10.5°C, remaining higher than in the mid 1980's. The salinity S>33 ppt as well was very high during 1988/89 and remained higher than in the period 1977-1987 when salinities were below S=32.5 ppt.

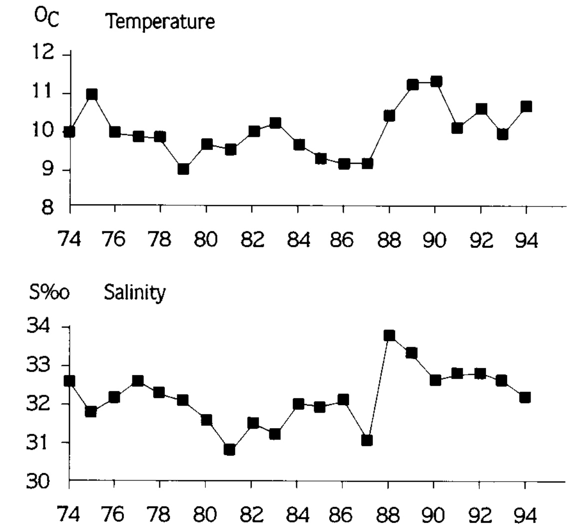

Figure 15. Changes in the mean annual temperature and salinity at Helgoland Roads during 1974-1994 (acc., to Greve and Reiners, in press).

Black Sea

In the open Black Sea the average air temperature decreased after 1986, was extremely low in 1987, increased in 1988 and thereafter decreased till 1994 (75 and Ovchinnikov, unpublished). It is obvious, that sudden changes in the zooplankton community of the Black Sea occurred as well during 1987-1989 as seen in the North Sea and Baltic Sea. The abundance and biomass of many zooplankton species in the Black Sea, such as *Aurelia aurita, Acartia, Oithona, Sagitta setosa* decreased during 1987/88 (5, 6, 26, 28, 76, 77). In the same period, the combjelly *Mnemiopsis leidyi* stock increased suddenly and the anchovy stock collapsed in 1989 (3, 22, 78).

To summarize, there are changes in the zooplankton community of the Black Sea which were obvious in the North Sea and Baltic Seas as well:

- Changes in the mesozooplankton community structure due to decrease or increase in the abundance of certain species.

- Occurrence of new species (North Sea: *Muggiaea atlantica* and lusitanian fish species; Black Sea: *Mnemiopsis leidyi).*

-Change in the blooming period of some species, namely earlier onset and longer duration.

-High interannual fluctuations of some species, which began at the end of the 1980's.

High fluctatiton in communities indicate a period of instability, which often is induced by a change in an environmental parameter (79). The changes ocurred in the Black Sea after an extraordinarily cold winter in 1987/88 and a very warm winter during 1988/89, in the German Bight after a sudden increase in temperature and salinity during 1988/89 and in the Kiel Bight after a rise in temperature of the subthermocline water during 1988/89. It could be concluded that, the changes in the zooplankton communities in the Black Sea, North Sea and Baltic Sea since the end of the 1980's are due to climatic variability.

Of course, the importance of eutrophication as a major forcing function for zooplankton, espescially in coastal waters, e.g. in the German Bight (65), and in most bays of the Baltic Sea (40) and the shelf area of the Black Sea (1, 15) should always be considered. In the Baltic Proper area of the Baltic Sea, for example, the fluctuation of the zooplankton population was in line with the increase and decrease of nutrients (40). But hydrographic changes as a long term decrease of the salinity may override or mask the effects of eutrophication (18, 80).

Examples of sudden changes in the community structure due to climatic variability, changes in the strength of currents or due to sudden extreme events, such as extremly cold winters or high wave action triggered by strong storms are well known in the North Sea and Atlantic (71, 81, 82, 83, 84, 85). Mann & Lazier, (1991 (86)) summarized the biological consequences of major perturbation of the North Atlantic during the 1960s'-1980's which affected the North Sea as well. Influehces of forcing conditions have been discussed and stated that sudden changes occurred in the biota of the North Sea in the seventies to eighties (87). Changes in the same period were obvious as well in the *Phoronis mülleri* population (85) and in the termination of the blooming period of small copepods in the German Bight (37).

Up to now, the events in the Black Sea after 1988, and especially the collapse of the anchovy fishery, were often related to pollution, overfishing and to the outburst of *Mnemiopsis leidyi* (5, 6, 26, 28, 88). Keeping in mind that changes in the zooplankton community in the late 80's were evident in all seas under consideration, a short term climatic event could have triggered the changes in the zooplankton community in the Black Sea at the end of 80's as well, which caused the conditions for the outburst of *M. leidyi* and the decline of the anchovy stock. In this context it is interesting, that the anchovy stock in the waters off South Africa collapsed as well during 1989 (89). The catch dropped in this area from about 600 000 tons to 150 000 tons.

Up till now the evaluation of existing long-term zooplankton data of the Black Sea in relation to climate has not been carried out. Therefore more effort should be made in the near future to evaluate the existing zoo and phytoplankton data of the Black Sea in relation to physical and meteorological changes.

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