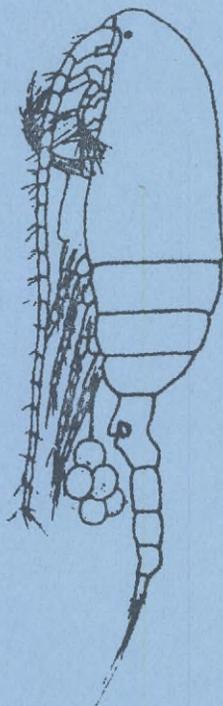
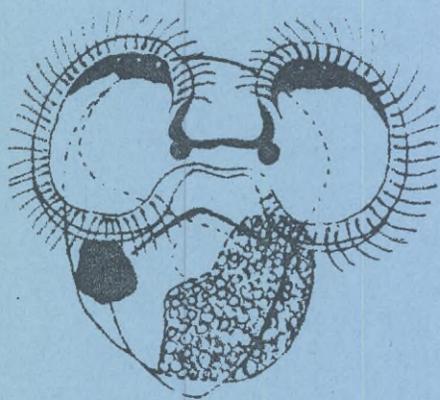
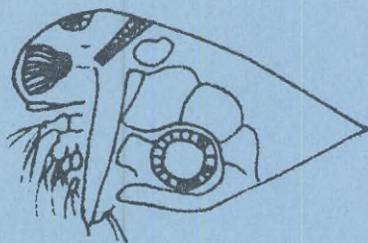
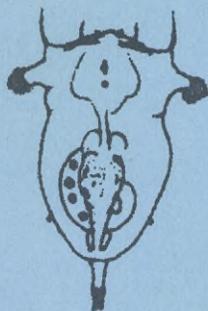




Det här verket har digitaliserats vid Göteborgs universitetsbibliotek och är fritt att använda. Alla tryckta texter är OCR-tolkade till maskinläsbar text. Det betyder att du kan söka och kopiera texten från dokumentet. Vissa äldre dokument med dåligt tryck kan vara svåra att OCR-tolka korrekt vilket medför att den OCR-tolkade texten kan innehålla fel och därför bör man visuellt jämföra med verkets bilder för att avgöra vad som är riktigt.

This work has been digitized at Gothenburg University Library and is free to use. All printed texts have been OCR-processed and converted to machine readable text. This means that you can search and copy text from the document. Some early printed books are hard to OCR-process correctly and the text may contain errors, so one should always visually compare it with the images to determine what is correct.





MEDDELANDE från  
HAVSFISKELABORATORIET • LYSEKIL

nr  
181

Production studies of zooplankton in relation  
to the total production in the Baltic proper

by

Hans Ackefors

March 1975

## Preface

The following paper was prepared in the beginning of 1973 for the Proceedings to the Third Baltic Symposium on Marine Biology. Due to certain regulations concerning the extent of the manuscript for the symposium papers the content of the paper had to be abridged. The abridged edition will now be published as "Production studies of zooplankton in relation to the primary production in the Baltic proper" in Merentutkimuslait. Julk./Havs forskningsinst. Skr. No. 239 (1974). This mimeographed edition is the full paper.

Lysekil, March 1975

Hans Ackefors

Production studies of zooplankton in relation to the total  
production in the Baltic proper.

by Hans Ackefors

ABSTRACT

The investigations took place in 1963-1965 in a coastal area and in 1963, 1968-1970 off the coast in the Baltic proper. The samples were taken with a Nansen net. The biomass of the different species was calculated and based on the volume for each species and its developmental stages. The wet weight was converted to dry weight and carbon content using standard values. The dry weight was considered to be 13 % and the carbon content 5 % of the wet weight.

The mean value of biomass in the investigated coastal area was  $2 \text{ g m}^{-2}$  or  $0.1 \text{ g C m}^{-2}$ . The corresponding values off the coast were  $9.3 \text{ g m}^{-2}$  or  $0.5 \text{ g C m}^{-2}$ .

The instantaneous mortality rate for the most important copepods was calculated in order to estimate the secondary production. The production in the coastal area was estimated to  $20 \text{ g m}^{-2} \text{ year}^{-1}$  wwt or  $1 \text{ g C m}^{-2} \text{ year}^{-1}$  and off the coast to  $100 \text{ g m}^{-2} \text{ year}^{-1}$  wwt or  $5 \text{ g C m}^{-2} \text{ year}^{-1}$ .

The production of zooplankton in the Baltic proper has been compared with the production of phytoplankton, benthic algae, bottom

invertebrates and fish. The potential yield in 5 trophic levels has been calculated on the assumption that the primary production is  $100 \text{ g C m}^{-2} \text{ year}^{-1}$ . The estimated potential yield has been compared with the calculated yield of the phytoplankton, macro algae, zooplankton, benthos and fish. It was concluded that a lower primary production than this would not suffice to sustain the actual secondary production in the Baltic.

## INTRODUCTION

The interest for the fish production and especially fish production in sea areas, has encouraged many authors during the last decade to study the secondary production of zooplankton as well as the primary production of phytoplankton. Even if the correlation between the plankton production and the fish catches seems to be inconsistent, it is important to study the pre-requisite conditions for production of fish. The gradually increasing pollution in many sea areas is another reason why such studies also are important.

Several models for studying the physical, chemical and biological processes in the Baltic have been published (Fonselius, 1969, 1971; Aitsam, 1971; Bolin, 1971; Svansson, 1972; Jansson, 1972 and Sjöberg et al., 1972). Some of the models are concerned with physical and chemical processes only. Others have tried to include both biological and physical-chemical conditions. Only one of the models has a complete biological model including the end of the food chain, i.e. the fish. In the present study, although the main subject is secondary production of zooplankton, the discussion is based on all collected knowledge of production including fish.

The author wants to thank Dr Bengt Sjöstrand, Lysekil and Dr Ragnar Elmgren, Askö, for valuable discussions when preparing this manuscript, and Miss Ann-Christin Rudolphi, who has drawn the illustrations.

## METHODS AND MATERIAL

Plankton samples were taken 1963-1965 at station 2 in the coastal area of Askö (pos.  $58^{\circ}48'N$   $17^{\circ}38'E$ ) in the northern Baltic proper and off the coast at seven plankton stations, each situated in seven

different subareas of the Baltic proper (see fig. 1) (cf. Ackefors, 1965, 1969 a, b; Ackefors & Hernroth, 1970 a, b and 1971).

The plankton samples were taken with Nansen net with a mesh size of 0.16 mm at different intervals from bottom to surface according to Ackefors 1969 a and 1972. The filtration coefficient is supposed to be in the order of 0,7 (cf, Tranter & Heron, 1967; Smith et al., 1968; Ackefors, 1972). The values have therefore been corrected by multiplying the numbers per  $m^2$  with 1.43. In order to express the volume of zooplankton the old technique to estimate the volume of the species and their developmental stages was used (Lohmann, 1908). If the density of zooplankton can be considered to be  $1 \text{ g cm}^{-3}$  the values can be converted to wet weight and the carbon content of zooplankton can roughly be estimated to 40 % of the dry weight. This means that about 5 % of the wet weight is carbon if we assume that the dry weight is about 13 % of the wet weight (Mullin, 1969).

The secondary production of zooplankton have been calculated using the formula  $P = Z \times B$ ; where  $P$  = production,  $Z$  = the total instantaneous mortality rate and  $B$  = biomass. The total instantaneous mortality rate can be calculated by the following formula:

$$N_t = N_o e^{-Zt} \quad N_o = \text{numbers at time } t = 0$$

$$Z = \ln \frac{N_o}{N_t} / t$$

The instantaneous mortality rate calculated on monthly basis for the most important copepods in the Askö area was in the range of 0.69 - 0.95 with an average of about 0.85. The annual secondary production can then be calculated by multiplying the monthly mean of production by 12 and using the above mentioned formula  $P = Z \times B$  (cf. Gulland, 1969).

As the instantaneous mortality rate varies slightly during the year for different populations of the species, the used technique seems to underestimate the production. During the summer with high temperature the B-values as well as the Z-values are higher. When using a monthly mean value both for biomass and total instantaneous mortality rate, the yearly production would then be slightly underestimated in the calculations.

## RESULTS

### a. The biomass and production of zooplankton in the coastal area of Askö

The total number of zooplankton at Askö varied very much during the 37 observations from 1963 to 1965 (fig. 2). The highest abundance was found in August both in 1963 and in 1964 when the water temperature was highest. The maximum value was 482 000 ind./m<sup>2</sup> in the middle of August, 1963. The minimum values were always found in January and February, 20 000 - 40 000 ind./m<sup>2</sup>, but even in May and June, 1963-1964, such low values were found. In 1965, however, the number of zooplankton per m<sup>2</sup> was much higher during that time, about 170 000 per m<sup>2</sup>. The dominating plankton group at Askö was the copepods and the most abundant species was Acartia bifilosa. During winter time this species made more than 95 % of the whole sample on many occasions. During summer the cladocerans especially Podon polyphemoides and/or the rotifers of the genus Synchaeta were sometimes the dominant plankton group.

The biomass was normally in the range of 2.5 - 8.0 g m<sup>-2</sup> wet weight from July to September, 1 - 2.5 g from October to December, 0.3 - 1 g from January to April, 0.4 - 2.5 g from May to June (fig. 2). The average

values for the first and second part of the year as well as individual values for different months shows that the productivity is higher in the second part of the year. The mean values of biomass for January-June, 1964, and January-June, 1965, are  $0.8 \text{ g m}^{-2}$  wwt. The corresponding values for July-December, 1963 and 1964, are 3.5 and  $2.7 \text{ g m}^{-2}$  respectively. The average for the whole year 1964 is  $1.8 \text{ g m}^{-2}$ . The figures indicate that the amount of zooplankton biomass (excluding microzooplankton) is 3 - 4 times higher during the second part of the year than during the first part of the year in the Askö area. In summary the maximum, mean and minimum values were as follows; the maximum value was  $8 \text{ g m}^{-2}$  wwt, the minimum value  $0.3 \text{ g m}^{-2}$  wwt and the monthly mean value for zooplankton biomass was  $2 \text{ g m}^{-2}$  wwt if the whole period 1963-1965 is taken into consideration. The annual production in the Askö area during the period 1963-1965 was estimated to  $20 \text{ g m}^{-2}$  wwt, which corresponds to  $1 \text{ g C m}^{-2}$ .

b. The biomass and production of zooplankton off the coast in the

Baltic proper

The highest productivity appeared in the Bornholm Sea (S 24) (cf. fig. 3). The greatest amount of zooplankton was found in September, 1968, when  $41 \text{ g m}^{-2}$  appeared at that station. Even in September 1970 the biomass was rather high,  $20 \text{ g m}^{-2}$ . If we study the values from most of the stations in the Baltic proper we found that the highest biomass appeared in September except for station S 12 in the Arkona Sea where no such tendency was found. The lowest biomass was found in the period March-April (May). In fig. 3 the mean values of zooplankton biomass have been arranged in two months interval and expressed as g wet weight  $\text{m}^{-2}$ . It is quite clear that the greatest biomass of zooplankton off the coast appeared in September-October. The biomass was in the range of

30.5 - 7.8 g m<sup>-2</sup> in the seven subareas of the Baltic proper, and the mean value for all stations during that time was 18.7 g m<sup>-2</sup>.

In general the plankton biomass was much lower in November-December. The mean value was less than half of the previous mentioned period or 7.8 g m<sup>-2</sup>. The lowest amount of plankton was found in the Bornholm area (S 24) which normally had greater amounts of zooplankton than the other areas. The greatest amount of zooplankton in November-December was instead found at station S 41 west of Gotland with a value of 12.4 g m<sup>-2</sup>.

In January-February the biomass of zooplankton was only slightly lower than in November-December. The mean value was 6.9 g m<sup>-2</sup> and the maximum biomass appeared at station S 24. The smallest biomass appeared during the next two months as compared to the other periods. The mean value for March-April was 4.9 g m<sup>-2</sup> and the lowest biomass ever found or 1.6 g m<sup>-2</sup> during the investigation appeared at station F 78 (the Landsort Deep) in the north-east Baltic proper.

In May-June the biomass was higher or about the same level as in November-December. The mean value was 7.6 g m<sup>-2</sup>, the minimum value appeared at station F 78 and the maximum at station S 24. July-August was next to September-October the most productive month. The mean value was 10.0 g m<sup>-2</sup>. The annual mean value for all areas during the period 1968-1970 was 9.3 g m<sup>-2</sup>. In summary the maximum, mean and minimum values were as follows; the maximum value off the coast was 41 g m<sup>-2</sup> wwt and the minimum value 0.87 g m<sup>-2</sup> wwt. The monthly mean for the period 1968-1970 was 9.3 g m<sup>-2</sup> wwt.

From the biomass values occurring off the coast the secondary production of zooplankton off the coast has been calculated. The annual production

for the period 1968-1970 was estimated to  $100 \text{ g m}^{-2}$  wwt, which corresponds to  $5 \text{ g C m}^{-2}$ . The total amount of zooplankton produced annually during the period studied would be  $10^{12} \text{ g C}$  or  $10^6 \text{ ton C}$  (cf. fig. 4). This corresponds to a wet weight of  $2 \times 10^7$  ton zooplankton. If we compare the annual production in the different subareas we find that the greatest difference to be between the Bornholm Sea ( $7 \text{ g C year}^{-1}$ ) and the northern area represented by station F 78 and F 72 (about  $4 \text{ g C year}^{-1}$ ). The same difference was also found when the Arkona Sea (S 12) is compared with the Bornholm Sea.

The dominant plankton group off the coast is the copepods just as in the coastal area of Askö, but other species dominate in the open sea. Temora longicornis is the most abundant (cf. Ackefors, 1969 a), and Pseudocalanus minutus elongatus is also very common. The latter species is the only plankton species abundant below 50 m depth.

## DISCUSSION

### a. The productivity in the Askö area

The zooplankton productivity near the coast in the outer archipelago of the northern Baltic proper seems to be very low in comparison with the conditions off the coast in the Baltic proper. During the most productive time in July-August the amount of zooplankton was only 3-8  $\text{g m}^{-2}$  wwt, with an average of  $5.9 \text{ g m}^{-2}$  in 1963 and  $4.5 \text{ g m}^{-2}$  in 1964, which is in the same magnitude as Andreasson (1972) found in the Askö area. This corresponds to an average of  $13.9 \text{ g m}^{-2}$  at station F 78 (the Landsort Deep) off the coast in the northern Baltic proper and an average for the whole Baltic proper of  $10.0 \text{ g m}^{-2}$  during the same time. (The corresponding carbon values are about 5 % as described

above.) While the Askö is most productive in the period July-August during the year the sea area off the coast is more productive in the period September-October. During this time the amount of zooplankton at station F 78 was  $18.8 \text{ g m}^{-2}$  and the average for the whole Baltic proper  $18.7 \text{ g m}^{-2}$ .

The lowest amount of zooplankton biomass appeared in January-February but even in April-May the values may be as low as  $0.3 - 0.5 \text{ g m}^{-2}$  wwt. This is not in accordance with the conditions off the coast. In January-February the amount of zooplankton for the two northern plankton stations in the Baltic proper (F 78 and F 72) were 3.4 and 8.3, and the average for the whole Baltic proper was  $6.9 \text{ g m}^{-2}$  wwt. The lowest amount of zooplankton off the coast is found in March-April. It is therefore evident that both maximum and minimum values occur earlier in the season in the coastal area of Askö than off the coast.

The secondary production off the coast seems to be much higher than in coastal waters with unstable hydrographical conditions. The secondary production in the Askö area was only  $1 \text{ g C m}^{-2}$  per year, i.e. only 25 % of what is found off the coast at the same latitude, or 20 % of the mean value for the whole Baltic proper. The lower productivity in the Askö area in comparison to the area off the coast in the northern Baltic proper can be explained by different reasons. The area is rather shallow, about 20-40 m depth. Such species as Pseudocalanus m. elongatus, which prefer colder water, below the thermocline in summer has a great need for deep waters. This species as well as Temora longicornis - the most important species off the coast - are prevented to enter the area to a certain part because shallow areas form a barrier to the connection with deeper areas off the coast. The deeper water off the coast will also give a bigger volume for the plankton.

It is very likely that the microzooplankton is much more important in the coastal area of Askö than off the coast. Unfortunately this fraction of zooplankton is not sampled with the used net. This would probably explain to some extent the discrepancy between the low biomass at Askö and the high biomass off the coast.

The unstable hydrographical conditions in the coastal area of Askö probably affect adversely for the development of zooplankton populations. Changes in weather conditions influence the hydrography as well as the plankton populations (cf. Ackefors, 1965, 1969 a, 1969 b, 1971).

Very rapid changes of the water masses with temperature changes of 5-10°C from one day to the other may occur in the Askö area. The experiences of all our investigations are that such changes of water temperature occur very seldom off the coast where the amount of zooplankton do not change rapidly.

The slightly lower surface temperature in the area during the summer in comparison with both the inner archipelago and the areas off the coast in the southern Baltic proper strongly influence the abundance of certain species such as Bosmina coregoni maritima (cf. Ackefors & Hernroth, 1970, 1971).

Finally the salinity of 6-7 ‰ in the area is the critical limit for the distribution of many fresh water and marine species in the brackish water (cf. Remane, 1940). This is evident when studying the horizontal distribution of many copepods from the south to the north in the Baltic area (cf. Ackefors, 1969 a). In connection with the unfavourable conditions mentioned above the salinity factor may be more decisive than off the coast, where the salinity in deeper levels is just higher than the critical salinity of 6-7 ‰.

Thus the main reasons for the obtained lower values of productivity in the Askö area in comparison with off-shore areas of the Baltic proper seem to be; a. the shallower water, b. the microzooplankton is not sampled, c. the unstable hydrographical conditions, d. the lower surface temperature, e. the critical salinity of 6-7 ‰.

b. The productivity off the coast in the Baltic proper

The standing crop of zooplankton off the coast fluctuated during the year with maximum in September and minimum in March-April. The greatest amount of plankton ever found was  $41 \text{ g m}^{-2}$  wwt in the Bornholm Sea in the southern Baltic proper. The values are rather similar to those reported by Mankowski et al. (1959) from the southern Baltic proper. They found maximum values certain years in June and another maximum in August-September in the magnitude of  $40 \text{ g m}^{-2}$ . In January-February they reported values about  $5-6 \text{ g m}^{-2}$  as minimum values for the year.

The present investigation, however, found minimum values later or in March-April, off the coast in contrast to the conditions in coastal waters of Askö, in the northern Baltic proper, where the minimum values occurred in January-February.

The maximum values of standing crop were also found later in the year off the coast in September-October according to the author's investigations than in coastal waters where it occurred in July-August. The greatest food supply for plankton feeding fish off the coast as sprat and herring occurs evidently in the beginning of autumn. This can be correlated with the yearly fluctuation of fat content in sprat. In late autumn (October-November) the highest fat content in the adult sprats of the Bay of Gdansk was found (Elwertowski & Maciejczyk, 1964).

The Arkona Sea (S 12) has a lower productivity and the normal development of the plankton community seems to be disturbed by the unstable hydrographical conditions. This area is considered a transition area in the Baltic. It is greatly influenced by salt bottom waters which flow into the Baltic and outflowing brackish waters in the surface. This seems to be the reason why the average value of standing crop of zooplankton is lower or  $7.5 \text{ g m}^{-2}$  as compared to the Bornholm Sea.

The mean value for the whole Baltic proper was about  $9 \text{ g m}^{-2}$  with a range of  $7.5\text{-}13.4 \text{ g m}^{-2}$ . Laevastu (1961) has estimated the standing crop to be  $150\text{-}300 \text{ mg m}^{-3}$ . Assuming a mean depth of 60 m this value corresponds to  $9\text{-}18 \text{ g m}^{-2}$ .

The production of zooplankton was estimated to about  $100 \text{ g m}^{-2} \text{ year}^{-1}$  in wet weight; and the instantaneous mortality rate (estimated on monthly basis =  $Z \frac{1}{12}$ ) was 0.85. This corresponds to a value of about  $5 \text{ g C m}^{-2}$  for the annual secondary production of zooplankton in the Baltic proper (cf. Ackefors & Hernroth, 1972). Andrushaitis (1971) estimated the production to  $123.5 \text{ mg m}^{-3}$  corresponding to a value of  $4.4 \text{ g C m}^{-2}$ . It is therefore reasonable to suppose that the average level of zooplankton secondary production in the whole Baltic proper off the coast is in the magnitude of  $5 \text{ g C m}^{-2}$  or  $100 \text{ g wet weight m}^{-2}$  per year (not including microzooplankton).

#### c. Comparisons with the primary production

The annual secondary production of about  $5 \text{ g C m}^{-2}$  can be compared with the primary production in the Landsort area (not far from F 78, cf. fig. 1). Hobro & Nyqvist (1972) reported about an annual primary production of  $114 \text{ g C m}^{-2}$ .

This is nearly twice as high as Schulz & Kaiser (1972) found in the Gotland Sea, Bagge & Niemi (1971) and Bagge & Lehmusluoto (1971) in the Gulf of Finland. The annual primary production in the unpolluted areas of Gulf of Finland was in the range of  $15-60 \text{ g C m}^{-2}$ . However, they have used 24 hours <sup>as</sup> incubation time in the  $^{14}\text{C}$ -method and Hobro & Nyqvist only four hours. The latter method gives higher values. Experiments have shown that there is probably a leakage of radio-active substance from the cells when using incubation times longer than four hours. Therefore it seems reasonable to suppose, that the primary production must be higher than  $15-60 \text{ g C m}^{-2}$  in the Baltic proper. Fonselius (1971) reported an annual primary production of  $78 \text{ g C m}^{-2}$  from a lightship in the northern part of the Baltic proper. (Measurements with 24 hours incubation time.)

A recent published paper by Renk (1972) indicated an annual mean of primary production in the southern Baltic in the range of  $72.6-104.1 \text{ g C m}^{-2}$ . The highest production was found in the Bay of Gdansk and the lowest in the Arkona Deep. The time of incubation was from sunrise to noon (Renk, pers. comm.). To get a crude estimate of the primary production in the whole Baltic proper the author has used a mean value of  $100 \text{ g C m}^{-2} \text{ year}^{-1}$ . As the total area of the Baltic proper is about  $200\,000 \text{ km}^2$ , the total annual primary production will be 20 milj. tons C (cf. fig. 4). This is about the same amount of production as Fonselius (1971) estimated for the Baltic proper including the Gulf of Finland. The mean value of  $100 \text{ g C m}^{-2}$  is in the same magnitude as for most shallow coastal waters (Ryther, 1970). From the North Sea Cushing (in Gulland, 1970) has reported a range of  $44-200 \text{ g C m}^{-2} \text{ year}^{-1}$ .

#### d. Comparisons with the production of fish, benthos and macro algae

The fish catches in the Baltic proper was in 1969-1970 in the magnitude

of 0.5 milj. tons per year (fig. 5). The catch of pelagic fishes is twice as high as that of demersal fishes. The production of fish has been calculated to the range of 0.8-1.2 milj. tons per year (0.08-0.12 milj. tons C) and the total biomass to the range of 1.0-1.8 milj. tons (Ackefors & Hernroth, 1972) (cf. fig. 4). This is equal to a biomass of 5-9 g fish per  $m^2$  or about 0.5-0.9 g C  $m^{-2}$ , and the production of 0.8-1.2 milj. tons of fish corresponds to 0.4-0.6 g C  $m^{-2}$ . In order to get the relation to benthic food for demersal fish we can take into consideration the standing crop of benthos in the Baltic proper reported by Zenkevitch (1963). He found a density of 25 g  $m^{-2}$  in the Gotland Basin and 60 g  $m^{-2}$  in the southern Baltic. He estimated the total biomass to 8 100 000 tons. Assuming that the mean duration of life of benthos is one year these figures might be taken as equal to the annual production (Gulland, 1970).

The annual production of benthic algae in the whole Baltic has been reported to about  $1.7 \times 10^6$  tons (Jansson, 1972). This means that the production of benthic macroalgae in the Baltic proper is about  $1.0 \times 10^6$  tons if the production is proportional to the area.

Finally, if we sum the above mentioned figures we get a primary production of phytoplankton and benthic macroalgae of 21 milj. tons C per year, a secondary production of zooplankton and benthic evertbrates of 1.8 milj. tons C per year and a production of fish of 0.08-0.12 milj. tons C per year. The fish yield for human consumption is 0.05 milj. tons C.

e. Energy flow through the ecosystems and trophic levels  
of the Baltic proper

There are many gaps in our knowledge of energy flow in the ecosystems

of the Baltic proper. We have hitherto no knowledge about the production of meiofauna, bacteria, microzooplankton etc. and the estimate of benthic macrofauna production as well as the estimate for other parts of the Baltic ecosystems are rather crude. Inside the zooplankton community as well as other communities we need better knowledge about the flow of energy to be able to assess the production accurately.

In order to display the energy flow in the southern Baltic proper Wiktor (1969) published a model consisting of 6 trophic levels, indicating e.g. 2 trophic levels of zooplankton. She showed also that the energy from one trophic level to another could be transferred not only to the nearest upper trophic level but also directly to a higher trophic level. E.g. the herring could eat zooplankton either from trophic level nr 2 or 3. Petipa, Pavlova and Mironov (1970) proposed 6 trophic levels even within the plankton community of the Black Sea (cf. table 1). (As most of the plankton in the mentioned paper also occurs in the Baltic proper the idea can be applied for the model of the Baltic proper.) They showed that e.g. the copepod Oithona belongs to three different trophic levels during the development from nauplius stage to adult individual. Their knowledge about the relation food-predator which is evident in table 1 stress the importance of good information about the preference of food for various organisms. The authors have also given values for the consumption of food in relation to body weight.

As most organisms can get energy at more than one trophic level and the fact that most organisms during the development move from one trophic level to another complicates the calculation of energy flow. All careful production and energy studies must therefore be based on comprehensive feeding studies of the species concerned and their developmental stages.

The above-mentioned 6 trophic levels for the zooplankton community can be reduced to 3 trophic levels according to Steel (unpubl.) (fig. 6). Although the species in some cases eat organisms at the same level as they belong to themselves, it seems reasonable to reduce the number of trophic levels to 3 when studying the energy flow inside the plankton community. Fig. 6 gives us on the other hand a good idea that there are also an energy flow in horizontal direction inside each level as well as a vertical energy flow between the levels.

A simple comparison between estimated potential yield and calculated yield in table 2 will show us the difference between the theoretical calculated potential energy flow from one level to another with regard to the primary production and the calculated yield of phytoplankton, zooplankton etc. in the Baltic proper. The discrepancy between the potential yield of trophic level 2 and partly 3 (more than  $3.2 \times 10^6$  tons C) and the calculated yield of zooplankton and benthos ( $1.8 \times 10^6$  tons C) is natural since we probably measured only a minor part of the production (bacteria, meiofauna, microzooplankton etc. were left out because of lack of data). It is evident, that the loss of energy inside the plankton community and the benthos community between and inside the different trophic levels is conspicuous (cf. fig. 6). The calculated yield of fish ( $0.08-0.12 \times 10^6$  tons C) shows that the theoretical values for the estimated potential yield at level 4 and 5 ( $0.08 \times 10^6$  tons C) falls below the present production of fish. (cf. table 2). This indicates that the pelagic fish (herring and sprat) feed partly on trophic level nr 2. In such case a certain part of the pelagic stock belongs to trophic level nr 3.

The very rough model for the energy flow in the Baltic proper stress the importance of more sophisticated studies about food and predator and metabolic studies of each species within the various communities to

get a better estimate of the energy flow in the ecosystems of the Baltic proper. However, even today's rough model leads to an important conclusion. If we use our knowledge of trophic feeding levels in the Baltic ecosystem and assume an ecological efficiency as high as 15 %, we find that the primary production of the Baltic must be at least in the order of  $100 \text{ g C m}^{-2} \text{ year}^{-1}$  (cf. table 2). Otherwise it would suffice to sustain neither the total secondary production nor the fish production of the Baltic proper.

## REFERENCES

- Ackefors, H., 1965: On the zooplankton fauna at Askö. (The Baltic-Sweden.) *Ophelia* 2(2):269-280.
- Ackefors, H., 1969 a: Ecological zooplankton investigations in the Baltic proper 1963-1965. *Inst. Mar. Res., Lysekil, Ser. Biol. Rep. No 18:1-139.*
- Ackefors, H., 1969 b: Seasonal and vertical distribution of the zooplankton in the Askö area (Northern Baltic proper) in relation to hydrographical conditions. *Oikos*, 20:480-492.
- Ackefors, H., 1971: Studies on the ecology of the zooplankton fauna in the Baltic proper. Thesis, Stockholm, 15 pp.
- Ackefors, H., 1972: The amount of zooplankton expressed as numbers, volume, wet weight and carbon content in the Askö area (The Northern Baltic proper). *Medd. Havsfiskelab., Lysekil, nr 129, 10 pp., 2 figs., 5 tables (mimeo.)*.
- Ackefors, H. & Hernroth, L., 1970 a: Seasonal and vertical distribution of zooplankton off the coast in the Baltic proper in 1968. *Medd. Havsfiskelab., Lysekil, nr 76, 13 pp., 125 figs., 6 tables (mimeo.)*.
- Ackefors, H. & Hernroth, L., 1970 b: Ecological zooplankton studies in the Baltic proper in connection with oceanographic studies in 1969 during the Baltic Year. *Medd. Havsfiskelab., Lysekil, nr 89, 9 pp., 61 figs., 4 tables (mimeo.)*.
- Ackefors, H. & Hernroth, L., 1971: Seasonal and vertical distribution of zooplankton off the coast in the Baltic proper

- in 1970. Medd. Havsfiskelab., Lysekil, nr 113, 11 pp., 113 figs., 6 tables (mimeo.).
- Ackefors, H. & Hernroth, L., 1972: Estimations of the amount of zooplankton and fish in the Baltic proper. Medd. Havsfiskelab., Lysekil, nr 139, 16 pp., 2 figs. (mimeo.).
- Aitsam, A.M., 1971: Mathematical models of the Baltic Sea for studying and prognosticating changes caused by pollution with regard to biological processes. In: Soviet-Swed. Symp. on the Pollution of the Baltic, Stockholm. Ambio Special Report No 1, 126 pp.
- Andreasson, A., 1972: Zooplanktonfaunans ekologi och biomassa i Landsortsområdet 1970-1971. Medd. Havsfiskelab., Lysekil, nr 130, 17 pp., 20 figs. (mimeo.).
- Andrushaitis, G., 1971: Hydrobiological investigations of the Baltic Sea in the USSR. In: Soviet-Swed. Symp. on the Pollution of the Baltic, Stockholm (mimeo.).
- Bagge, P. & Lehmusluoto, P.O., 1971: Phytoplankton primary production in some Finnish coastal areas in relation to pollution. Havsforskningsinst. Skr. No 235:3-18.
- Bagge, P. & Niemi, Å., 1971: Dynamics of phytoplankton primary production and biomass in Loviisa archipelago (Gulf of Finland). Havsforskningsinst. Skr. No 233:19-41.
- Bolin, B., 1971: Model studies of the Baltic Sea. Institute of Meteorology, University of Stockholm. Report GH - 4 (mimeo.).
- Elwertowski, J. & Maciejczyk, J., 1964: (Application of mathematical analysis to the study of the influence of physiological and ecological factors on the change of fat contents in the adult sprats of the Bay of

- Gdansk.) Prace MIR w Gdyni, 13 (B):7-18.
- Fonselius, S., 1971: On the biogenic elements and organic matter in the Baltic. In: Soviet-Swed. Symp. on the Pollution of the Baltic, Stockholm (mimeo.).
- Gulland, J.A., 1969: Manual of methods for fish stock assessment. Part 1. Fish Population Analysis. FAO Manuals in Fisheries Science No 4, 154 pp.
- Gulland, J.A., 1970: The fish resources of the ocean. FAO, Rome, 425 pp.
- Hobro, R. & Nyqvist, B., 1972: Pelagial studies in the Landsort area during 1970-1971. In: Askölab. Ekol. Unders. i Landsortsomr. 1970-1971, Rep. Swed. Envir. Prot. Board. Contr. I 10/35 and 7-85/70. Subrep. (mimeo.).
- Jansson, B-O., 1972: Ecosystem Approach to the Baltic Problem. Bull. Ecol. Res. Comm. Swedish Natural Science Research Council, No 16:1-82.
- Laevastu, T., 1961: Natural basis of fisheries in the Atlantic Ocean: Their past and present characteristics and possibilities for future expansion, pp. 18-39. In: Atlantic Ocean Fisheries, ed. Borgström, G. and Heighway, A.J., London.
- Mankowski, W., Rutkowicz, S. & Ciszewski, P., 1959: (Preliminary studies on the plankton production in the southern Baltic.) Prace MIR w Gdyni, 10 (A):131-161. (In Polish, English summary.)
- Petipa, T.S., Pavlova, E.V. & Mironov, G.N., 1970: The food web structure, utilization and transport of energy by trophic levels in the planktonic communities. Pp. 142-189. In: Marine Food Chains, ed. J.H. Steele, 552 pp.

- Remane, A., 1940: Einführung in die zoologische Ökologie der Nord- und Ostsee. Tierw. N.- und Ostsee, 1 a:1-238.
- Renk, H., 1972: Primary production and Chlorocphyll Content in the Baltic Sea. ICES, C.M. 1972/L:8, Plankton Committee (mimeo.).
- Ryther, J.H., 1970: Photosynthesis and Fish Production in the Sea. Science Vol. 166 (3901):72-76.
- Schulz, S. & Kaiser, W., Inpress: Biological effects of the influx of salt water into the Gotland Basin during the IBY 1969/70. In: Sec. Baltic Symp. on Mar. Biol., Stockholm, 1971. Oikos.
- Sjöberg, S., Wulff, F., & Wåhlström, P., 1972: Computer simulations of hydrochemical and biological processes in the Baltic. Contributions from the Askö Laboratory, University of Stockholm, Sweden, 91 pp.
- Smith, P.E., Counts, R.C. & Clutter, R.J., 1968: Changes in filtering efficiency of plankton nets due to clogging under tow. J. Cons. perm. int. Explor. Mer, 32(2):232-248.
- Steele, J.H., unpubl.: The structure of Marine Resources.
- Svansson, A., 1972: Canal models of sea level and salinity variations in the Baltic and adjacent waters. Fishery Board of Sweden. Series Hydrography, Rep. No 26.
- Tranter, D.J. & Heron, A.C., 1967: Experiments on filtration in plankton nets. Aust. J. mar. Freshwat. Res., 18:89-111.
- Zenkevitch, L.A., 1963: The biology of the seas of the USSR. Moskva. Izdat. vo. Akademiia Nauk SSSR 739 pp.
- Wattenberg, H., 1949: Entwurf einer naturlichen Einteilung der Ost-

see. Kieler Meeresf., 6:10-15.

- Wiktor, K., 1969: Tropische Stufen im südlichen Teil der Ostsee sowie im Oder- und Frischen Haff. Limnologia 7(1): 195-201.

Additional reference

- Mullin, M.M., 1969: Production of Zooplankton in the Ocean: The Present Status and Problems. - Oceanogr.Mar.Biol.Ann.Rev., 1969, 7:293-314.

Table 1. A model for various trophic levels of zooplankton and their relation to food and predator based on a report from the Black Sea by Petipa, Pavlova and Mironov (1970) and adapted for the conditions in the Baltic proper.

TROPHIC LEVEL	TYPE OF ORGANISMS	TYPE OF FOOD
1. Primary producers and saphrophagous organisms ( = Phytoplankton)	Dinoflagellata, Diatoms etc.	(Detritus)
2. Herbivorous organisms	a. <u>Oithona</u> , <u>Acartia</u> N.III-VI, C.I-III, <u>Pseudocalanus</u> b. <u>Oikopleura</u> , larvae of molluscs and polychaetes	Phytoplankton Phytoplankton and detritus
3. Omnivorous organisms	<u>Oithona</u> , <u>Acartia</u> , <u>Centropages</u> C.IV-V; <u>Acartia</u> and <u>Centro-</u> <u>pages</u> adult	Phytoplankton and zooplankton N. + C.I-II
4. Primary carnivores	<u>Oithona</u> adult	Small Copepoda and Cladocera
5. Secondary carnivores	<u>Sagitta</u>	Adult Copepoda
6. Tertiary carnivores	<u>Pleurobrachia</u>	Copepoda and <u>Sagitta</u>

Table 2. Estimates of annual potential yield based on primary production and calculated yield at various trophical levels. The ecological efficiency is supposed to be 15 % (cf. Ryther, 1969). Three trophic levels in the plankton community is applied for the estimate of energy transport (cf. fig. 6).

TROPHIC LEVEL	ESTIMATED POTENTIAL YIELD	CALCULATED YIELD
Nr	in tons of carbon	in tons of carbon
1. Primary production	$21 \times 10^6$	1. Phytoplankton + Macro algae $21 \times 10^6$
2. Herbivorous + Omnivorous plankton and benthos	$3.2 \times 10^6$	2. Zooplankton + Benthos $1.8 \times 10^6$
3. 1.-3. stage Carnivorous plankton, benthos and fish eating plankton	$0.47 \times 10^6$	
4. Fish eating plankton, benthos and fish	$0.07 \times 10^6$	
5. Fish eating fish from level nr 4	$0.01 \times 10^6$	3. Fish $0.08-0.12 \times 10^6$

## LEGENDS

- Fig. 1. Chart of the Baltic proper and the three subareas, the Arkona Sea, the Bornholm Sea and the Gotland Sea according to Wattenberg (1949). According to Ackefors (1969a) the Gotland Sea may be divided into five subareas. Hence we get seven subareas with one plankton station off the coast in each subarea and the coastal station at Askö. The depth for each station is recorded in the chart.
- Fig. 2. The amount of zooplankton in the Askö area, 1963-1965 expressed as number ind.  $m^{-2}$  and  $g m^{-2}$  (wet weight, about 5 % of which is carbon). All values are corrected for a filtration coefficient of 0.7. The temperature curves for 0 m, 15 m and 30 m are reproduced in the lower part of the figure.
- Fig. 3. The biomass of zooplankton expressed as  $g m^{-2}$  (wet weight, about 5 % of which is carbon) at Askö and at the seven plankton stations off the coast (cf. fig. 1). The values are arranged as two months intervals and corrected for a filtration coefficient of 0.7.
- Fig. 4. The yearly production of phytoplankton, benthic algae, zooplankton, benthic evertebrates, pelagic fishes and demersal fishes in the Baltic proper. For further explanation, see the text.
- Fig. 5. The total catch of fish 1961-1970 in the Baltic proper expressed as the total amount,  $g fish m^{-2}$  and  $g C m^{-2}$ .
- Fig. 6. The six trophic levels of zooplankton according to Petipa, Pavlova and Mironov (1970) (cf. table 1) have been modified and changed to three levels according to a proposal by Steele (unpubl.).

Fig.1

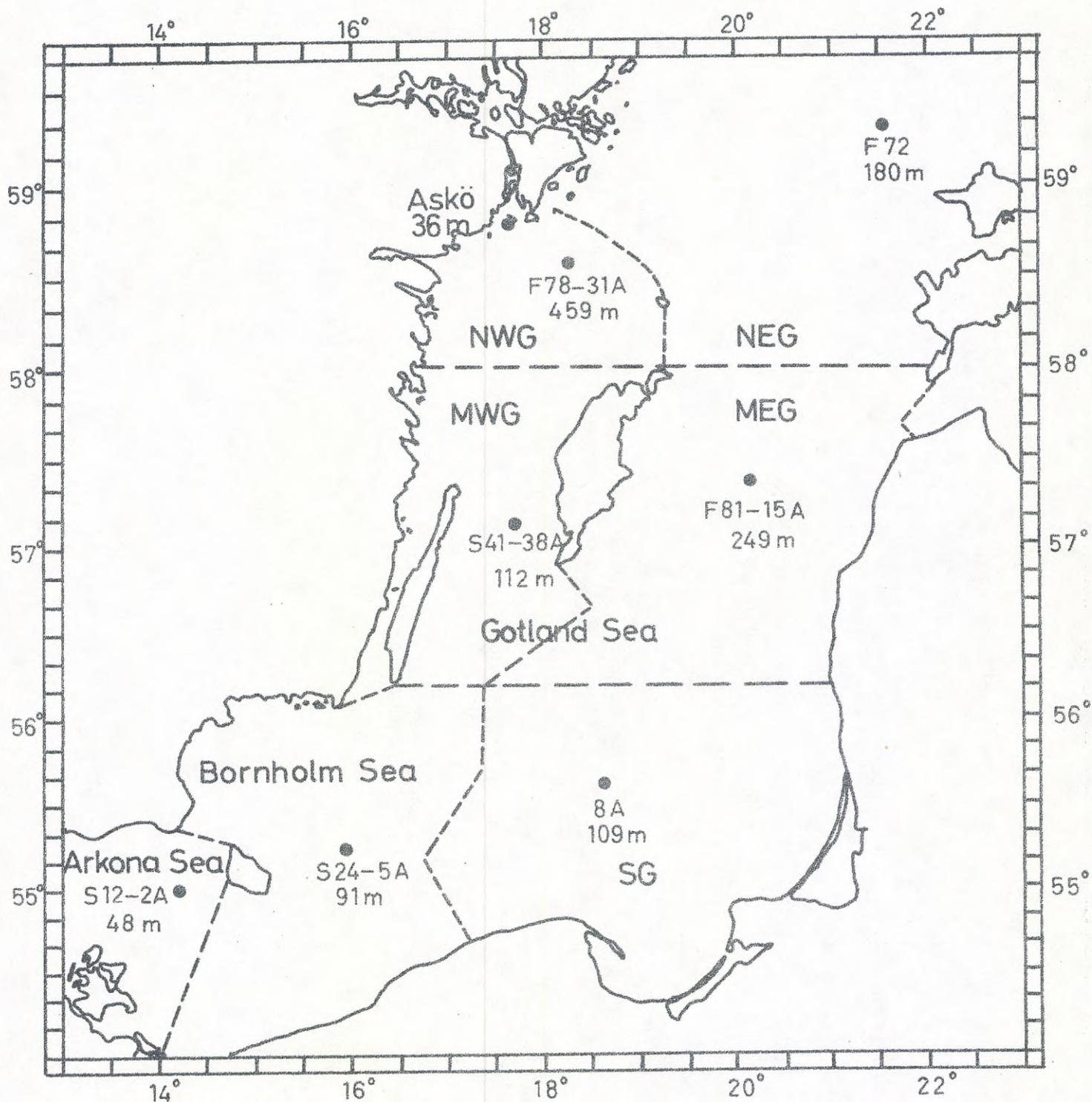


Fig. 2

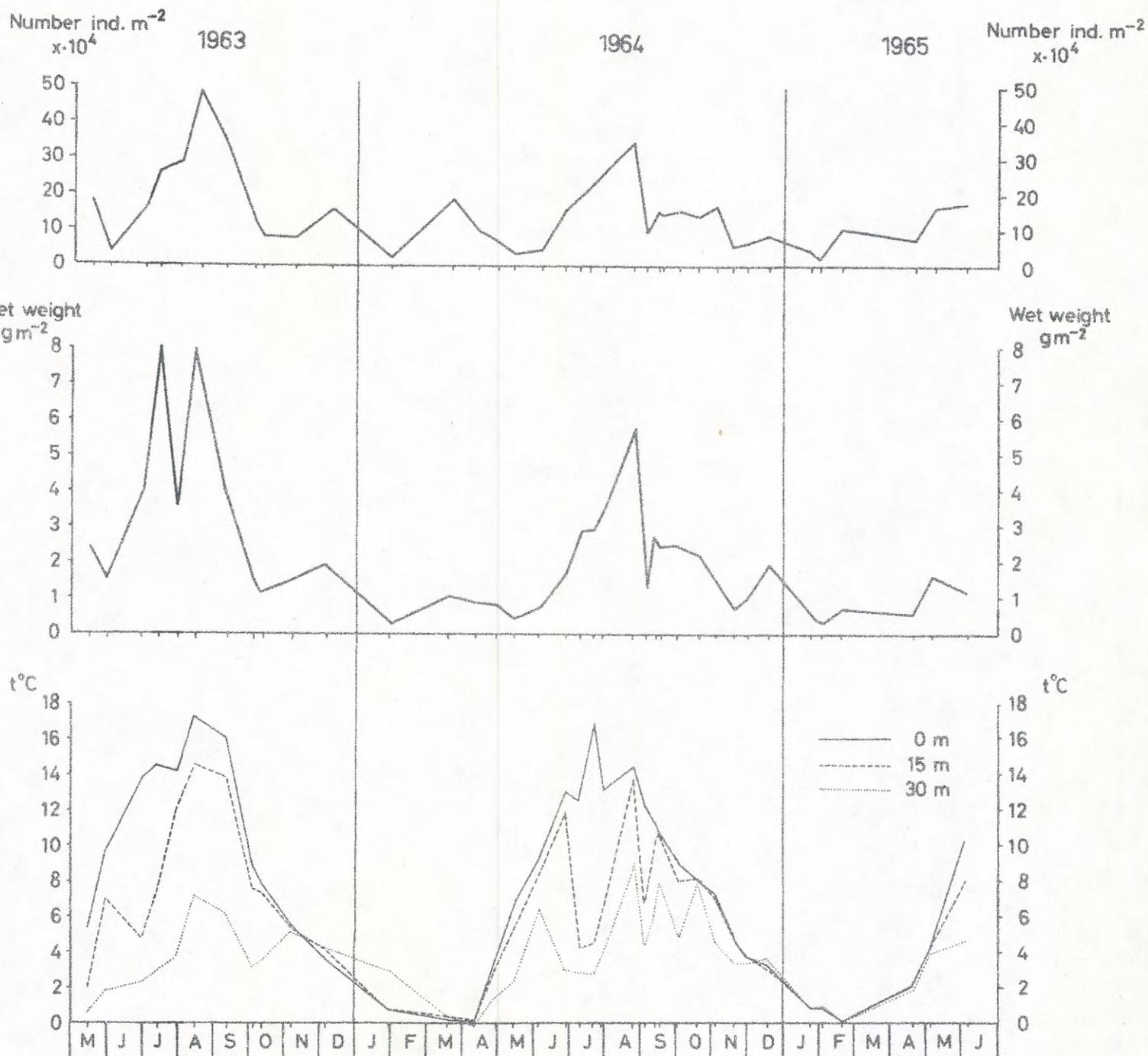


Fig. 3

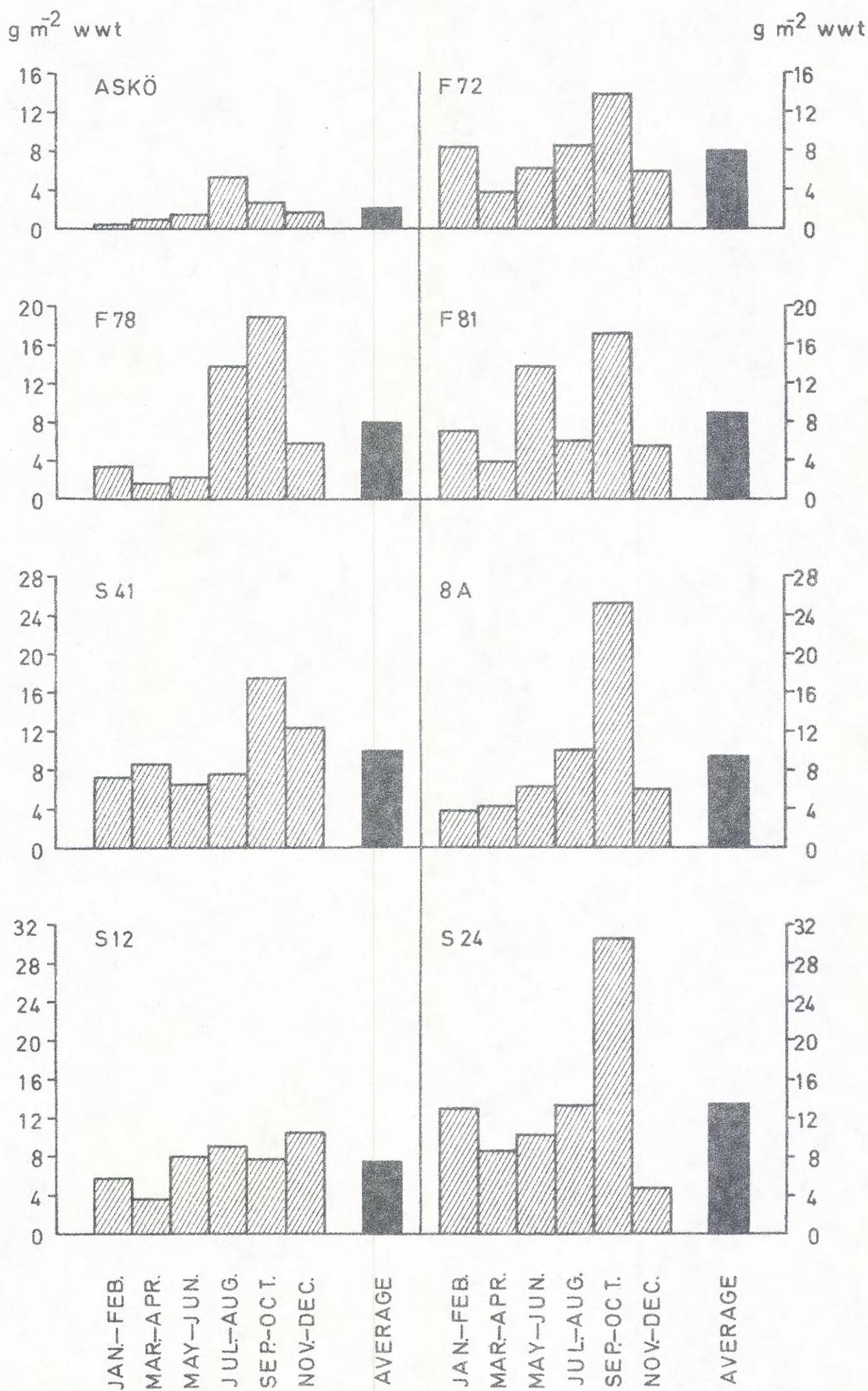
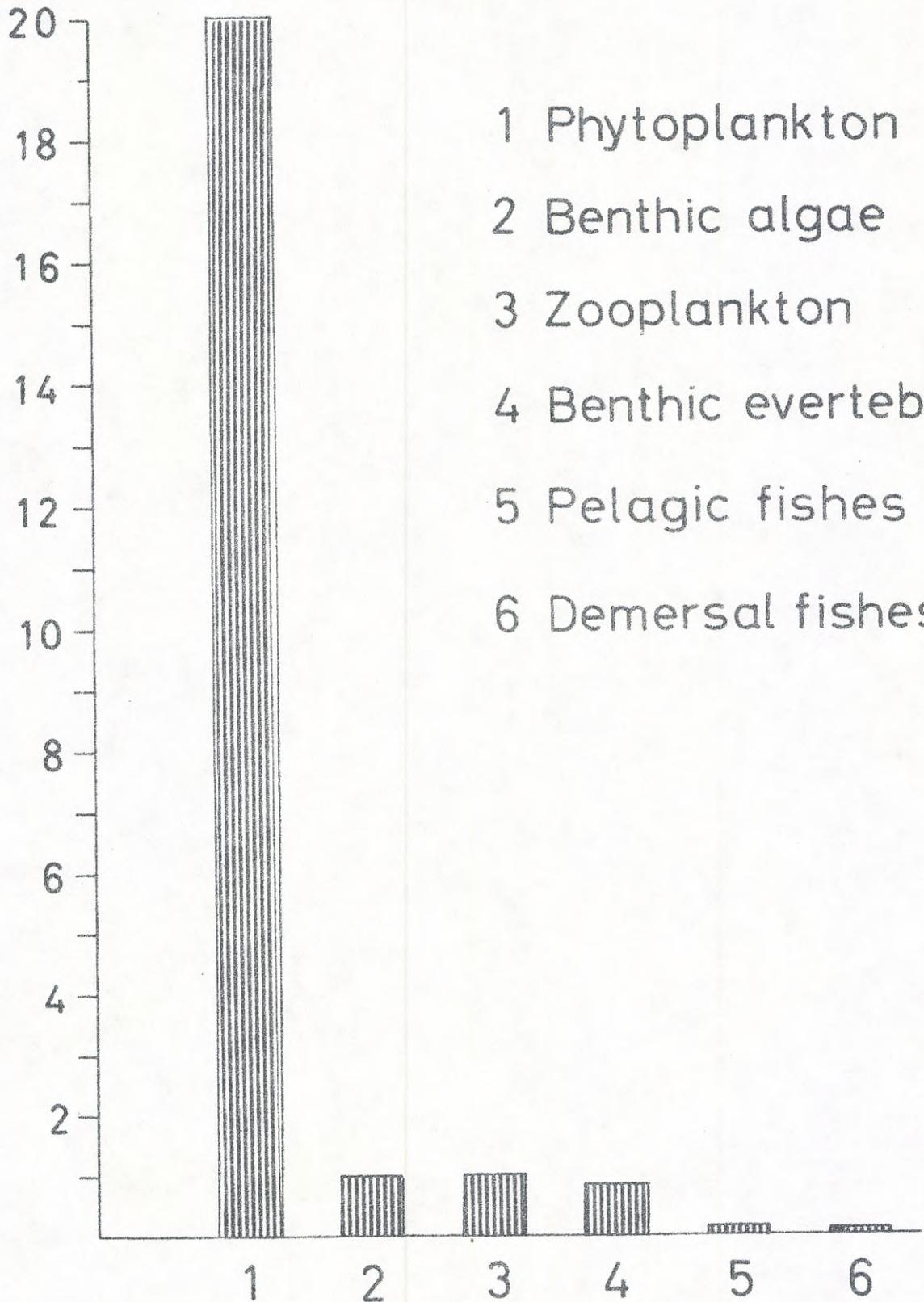


Fig.4

milj. tons C



1 Phytoplankton

2 Benthic algae

3 Zooplankton

4 Benthic evertibrates

5 Pelagic fishes

6 Demersal fishes

Fig. 5

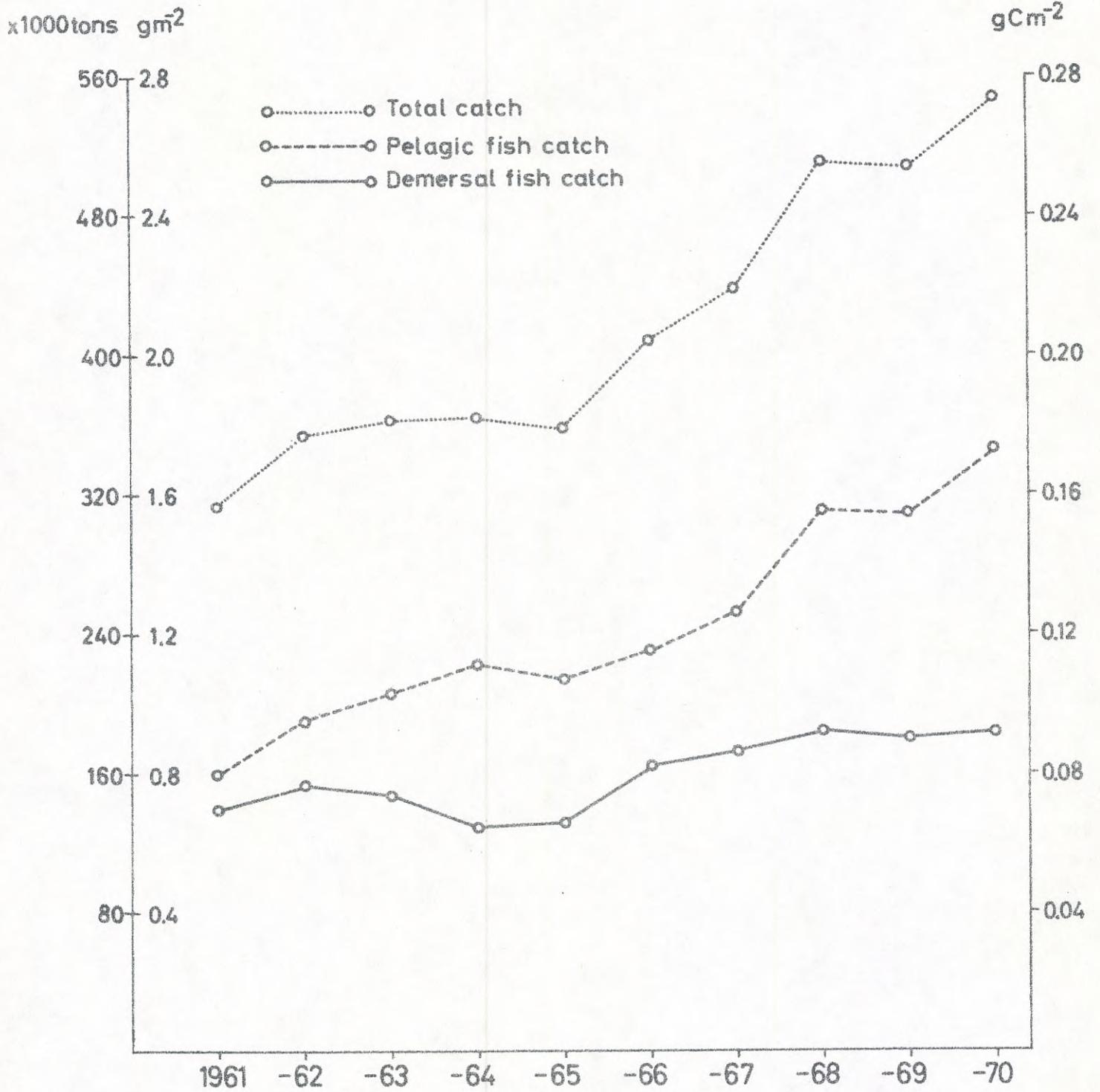


Fig.6

TROPHIC LEVEL

3rd

2nd

1st

