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On primary production in the South Bight of the North Sea

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A B S T R A C T

The area of the North Sea next to the Belgian and the Dutch coast has been surveyed since January 1971. The photosynthetic capacity (potential production) of samples collected at 63 stations and 4 depths has been measured using the C-14 technique.

The homogeneity of the water column was demonstrated almost everywhere as figures were similar from the surface to the bottom. A general pattern of decrease of the potential production from the coast to the open sea was demonstrated in all seasons. Figures ranged from 3 to 30 mg C / m³ h. Primary production was also determined both by calculations, using the Steemann Nielsen (1952) formula, and by in situ measurements. The higher turbidity near the coast has proved to limit considerably the primary production. Figures usually ranged from 100 to 1500 mg C / m² day.

The following topics have also been discussed : relationship between photosynthetic capacity and pigments content, transparency of the water, solar radiation, comparison between production calculated from photosynthetic capacity and production measured in situ and nutrient uptake.

I N T R O D U C T I O N

Until 1971, the production of the North Sea had not been extensively studied. Cushing's review (1971) mentions the works of Steele (1956, 1957, 1958), Cushing (1957), Cushing & al. (1963), Steemann Nielsen & Jensen (1957) and Wimpenny (1958). All these contributions were limited geographically and of short duration. However, more recently, one can mention the work of Postma & Rommets (1970) on the Wadden Sea and especially the important work of Kroon (1971) and Gieskes (1972) off the mouth of the River Rhine. The primary production of the South Bight of the North Sea has been investigated since January 1971 as a part of a national programme for the study of pollution in the North Sea and for the design of a mathematical model of pollutant dispersion. Some results of the primary production studies have already been published (Mommerts, 1972 and 1973).

MATERIAL AND METHODS

The sampling network (fig.1) developed from the mathematical model network allows three types of cruise : sampling stations 1 to 25 (cruises 1, 2, 7), sampling stations 51 to 72 (cruise 3) and sampling stations 1097 to 2041 (cruises 6 and 8). A small network of seven sampling stations near to the coast was used for an introductory cruise (cruise 0).

Sampling and experimental scheme

Netplankton and nanoplankton production was estimated from water samples collected at about local apparent noon. At the beginning samples were taken from a range of depths corresponding to 100 %, 10 % and 1 % of surface irradiance. These depths were calculated with an immersible photometer equipped with a green filter. The samples were incubated in an artificial light incubator (see technique below).

On and after cruise 6, a deck incubator was also used. Samples were exposed to daylight directly and under neutral filters giving relative light levels of 35 %, 13 % and 4.5 %. The incubator was kept at sea surface temperature. The sampling depths were accordingly at 100 %, 35 %, 13 % and 4.5 % of surface irradiance. A few real in situ incubations were also performed.

Four light and two dark bottles were drawn from each sample, each was inoculated with 4 microcuries of $\text{NaHC}^{14}\text{O}_3$ and incubated under fluorescent light (about 0.055 ly/min) for 3-4 hours at sea surface temperature.

In 2 of the light bottles and one dark bottle, all planktonic organisms greater than $40\ \mu\text{m}$ (i.e. netplankton and zooplankton) were eliminated by filtering the water through fine-mesh net. The fractionation method has been discussed in a previous paper (Mommaerts, 1973).

Three more light bottles were inoculated and put in the deck incubator till sunset. Following incubation, the contents of the bottles were filtered through Sartorius $0.2\mu\text{m}$ and later $0.6\mu\text{m}$ membrane filters. The filters were washed with about 20 ml filtered seawater and dried. Their activity was measured at the International Agency for C-14 determination, Charlottenlund, Denmark. The results are expressed as $\text{mg C/m}^3\text{h}$. Netplankton production was computed by subtracting nanoplankton production from that of total phytoplankton.

Precision of the measurements

At the $30\text{ mg C/m}^3\text{h}$ level, the standard deviation represents 8 % of the average. This was determined experimentally by incubating 10 subsamples under the usual working conditions.

Measurements of light energy available to the phytoplankton

1. Irradiance

The global incident irradiance in the area is known from the measurements made at the meteorological station of Den Haan and computed at the Royal Meteorological Institute. The irradiance in Joules/cm^2 is known for periods of half an hour. It is likely that the irradiance variations occurring far off the coast would not deviate more than 10 % from those recorded on the coast (Dogniaux, comm. pers.).

2. Water transparency

For cruises 1 to 3 the Secchi disc was used for the computation of the "absorption coefficient" of the water and Poole & Atkins (1929) formula was used for the calculation. On and after cruise 5, water transparency was measured with an immersible photometer fitted with a green filter Chance Pilkington Ogr1 (range 450-650 nm with a maximum at 540 nm), a neutral filter ON32A and an opal filter. Several tests showed that the Lambert-Beer law was obeyed throughout the water column except near to the bottom.

DESCRIPTION OF THE AREA SURVEYED

Throughout the area depths are moderate (about 30 m). The floor is mainly composed of quartz sand (+ slime and broken shells). Salinity determinations made on the light-ship "West-Hinder", 20 miles off Ostend, showed an average of 34.25 ‰ for the 1950-1955 period (maximum : 35.35 ‰; minimum : 32.82 ‰). The influence of fresh water from the rivers is marked along the coast : Daro (1969) mentions a minimum of 25.8 ‰ in Knokke. Temperature measurements made during our surveys gave winter figures of about 6°C and summer figures of about 18°C (Meisch & Bay, 1971). The temperature seldom varied more than 0.5°C in a diurnal cycle. The difference between surface and bottom seldom exceeded 0.5°C.

The tides observed in the South Bight follow a semi-diurnal pattern. They are generated in an amphidromic point (52°32'N, 2°55'E) and reinforced by a wave coming from the English Channel. Tidal oscillations generate important horizontal water motions in the area surveyed. The diagram of speed vectors (fig. 2) around a given point has the form of an elongated ellipse with the long axis directed towards the tidal wave motion.

The general motion of water is thus that of a piston but the residual stream is very small : therefore no important change in the phytoplankton community is expected to occur as a result of tidal streams during the course of a survey.

OBSERVATIONS

POTENTIAL PRODUCTION

Photosynthetic capacity figures recorded in vitro allowed a comparison of the potential production of samples collected at different stations, depths and times.

The illumination in the incubator (0.055 ly/min) was such that the onset of light saturation of photosynthesis was probably reached for most phytoplanktonic species.

Relations between photosynthetic capacity and standing stock

The standing stock of phytoplankton has been estimated from pigments analysis (Van Beveren, 1971, 1972). The correlation between potential production and pigment content is very good. The ratio production / biomass (productivity sensu stricto) is fairly consistent for a given cruise. Table 1 summarizes the averages and deviations for potential production and productivity. All these figures lie in the same range as those mentioned by Steemann Nielsen [&] Hansen (1959). The reasons for discrepancies (implying differences in the physiological state of the phytoplankton) occasionally found, cannot be easily explained in terms of their location. We have noticed however that stations 5 and 6 which are sometimes characterized by higher productivities are close to the mouth of the River Scheldt. Unusual figures might also be related to the vicinity of dumping stations.

On cruises 1 and 2 the productivity has been calculated separately for nanoplankton and netplankton (Kommaerts 1972). The ratio was 5.5 for nanoplankton and 2 for netplankton. Malone (1971) has demonstrated such differences and also the diurnal variations of this ratio for both categories.

The photosynthetic capacity of samples collected along a vertical profile

The photosynthetic capacity remained very constant for most sampling stations on all cruises. The photosynthetic capacity of a sample collected at any level was equivalent, on an average, to 89 % of the highest figure recorded in the water column (fig. 3). This apparent homogeneity of the water column was matched by chlorophyll a determinations and nutrients analyses (Elskens [&] Janssens, 1971 and 1972). This indicates that the waters of the North Sea are well mixed in the area investigated and that turbulence remains high throughout the year. Exceptions were observed near the mouths ^e of rivers. In this case, the stratification of the water column was very apparent and the maximum phytoplankton was recorded near the surface or near the bottom according to the season and the circumstances.

The horizontal distribution of photosynthetic capacity (weighted means)

A pattern of a quick decrease from the coast to the open sea has been observed on each cruise (fig.4). The shape and the height of the curves are characteristic for each survey (i.e. each season). We have unfortunately not enough data to describe an annual cycle. The spring bloom has escaped our surveys. Table 1 shows the average levels of potential production at different times of the year.

Cruises 6 and 7 immediately preceded and followed the spring bloom. This may explain the low figures of cruise 7. Some abnormalities are shown in Fig. 4; sampling station 18 (cruise 2) was characterized by a very high photosynthetic capacity yet it was away from the coast. This station was also unusual in having a high productivity index. Another small group of sampling stations (2689 and 2552 of cruise 6) showed the reverse characteristic (low photosynthetic capacity near to the coast).

These stations are located just off Rotterdam. Sampling stations facing the mouth of the River Scheldt or Dunkerk sometimes also showed unexpected photosynthetic capacities.

However, the results indicate that the distribution of phytoplankton production is continuous and gradual for most places in the South Bight. Differentiated areas (patches) of primary production were seldom observed. Moreover, from 50 km off the coast, photosynthetic capacities did not depart from a narrow range (1 to 7 mg C/m³h) whatever the season (with the possible exception of the spring bloom). The maximum variation of photosynthetic capacity, caused by a tidal change, has been calculated for all sampling stations of cruises 1, 2 and 3. The average variation coefficient is 1.4 with extreme figures of 1.02 and 2.94. This confirms the impression of continuity of the phytoplankton density.

INTEGRATED PRODUCTION (table 2)

As no vertical gradient (e.g. temperature or phytoplankton concentration) other than that of light intensity was measured in the water column, the problem of estimating the in situ production is rather simplified. Steemann Nielsen⁽¹⁹⁵²⁾ has shown that in situ production can be calculated from photosynthetic capacity estimates, determination of the depth of the euphotic region (water transparency factor) and local irradiance data (e.g. length of the day between sunrise and sunset). This calculation has been used as a routine procedure but simulated and real in situ incubations have been performed to test this model and others.

The water transparency factor

The intercalibration of the Secchi disc and the immersible photometer has shown that the coefficient F in the Poole and Atkins (1929) formula $\eta = F/D$ (η is the absorption coefficient of the water; D is the depth of disappearance of the Secchi disc) varies with the distance to the coast (fig. 5). A shift in the spectral transmittance characteristics of the water (e.g. more yellow dissolved substances near to the coast) may explain this variation. The different nature and properties of the suspended particles near and away from the coast may also influence the readings.

The biological implications of this variation appear when one tries to ascertain the photosynthetically active energy (350-700 nm range) at any depth. This is possible if the spectral response curve of the photometer used (i.e. combination of spectral selectivities of photocell and filters) and the spectral transmittance characteristics of the water are known.

No complete results about the latter are known from the literature for the South Bight of the North Sea, but our photometric measurements made in the 540 nm range indicate that open-sea waters (farther than 50 km off the coast) belong to Jerlov's type 3 of coastal waters with an irradiance transmittance (% / m) of about 80 (Jerlov, 1968, 1970). Waters, such as the Baltic Sea which are very abundant in yellow substances, display a maximum shift of the transmittance peak (to 550 nm), while the ultra-violet of 375 nm is extinguished even at 5 m.

The measured transmittance in the North Sea decreases strongly near to the coast (to about 20 %) indicating the shift from water type 3 to water type 9. The measured proportion of available energy increases with depth (from about 1 % at the surface to about 5 % at 20 m, in the 350-700 nm range, for water type 3) as the spectral range is narrowing towards the photometer sensitivity range. Therefore, the real irradiance levels corresponding to the measured 100 %, 35 %, 13 % and 4.5 % would lie around 100 %, 10 %, 3 % and 1 % in the area investigated. This correction is considered in the interpretation of in situ experiments.

The absorption coefficient decreases very quickly in the first 50 km, in the same way as photosynthetic capacity. For each cruise, a specific curve has been drawn (fig. 6), its shape being mainly related to climatic circumstances but also to the abundance of plankton.

As a result of the antagonistic patterns of photosynthetic capacity and water transparency no predictable and consistent pattern of in situ production, as a function of the distance to the coast in the area studied, can be evolved. Near to the coast, high potentialities are checked by a low transmittance (about 20 % / m) and off shore, lower potentialities are almost unrestricted (transmittance : 80 % / m).

In both cases, the order of magnitude for in situ production is the same (see fig. 9).

The irradiance factor

In his model, Steemann Nielsen ⁽¹⁹⁵²⁾ has introduced the length of the day (number of hours between sunrise and sunset) as a parameter for the energy provided to the area studied. In the same way, many authors consider the ratio "length of the light day / time of the incubation" for the extrapolation of their production measurements to the whole day. Alternatively, one can consider the ratio "light energy provided for the day / energy provided for the time of the experiment". As the local irradiance varies much more quickly in our area than in tropical areas, the latter procedure has been chosen for the calculations of daily production with in situ (simulated and real) figures. This is an improvement on the first procedure as shorter incubation times give daily production figures very similar to those computed with results of half-day incubations (see sampling stations 11 and 18, table 3). The improvement should however be less outstanding, once the light saturated state of photosynthesis is reached. Fig. 7 (b) shows the evolution of the light-saturated depths for a summer day ($7 \text{ J/cm}^2 30 \text{ min. line}$). These considerations on real energy distribution in water have been taken into account for the computation of this line. Fig. 7 (a) shows the annual variation of local irradiance and allows comparison with the variation of day length.

In situ production calculated versus in situ production measured

The correlation coefficient between the calculated daily production (Steemann Nielsen formula) and the in situ measured production is very good ($r = 0.92$; see table 3).

The average vertical profile (fig. 8) calculated with deck incubations or real in situ incubations (cruises 6 and 7) shows the typical surface inhibition of photosynthesis. This inhibition pattern seems to appear from local irradiance $1000 (\pm 500) \text{ J / cm}^2 \text{ day}$.

Most of the discrepancies observed between our experiments will probably be explained by quantitative and qualitative energetical differences :

- a) It seems that the conclusions of Berge (1958) on neutral filters (showing that the results from simulated in situ experiments were not significantly different from those of corresponding samples suspended simultaneously at the normal depth in the sea) are not always matched by our experiments (fig. 8). This is probably related to the differences between photometer readings of energy levels and real energy levels.
- b) The comparison of the net- / nanoplankton ratio in vitro and in situ (simulated) measured for the same sample shows that, on an average, this ratio is always higher in situ, thus implying a relatively higher contribution of the netplankton than supposed from in vitro experiments. One finds this mostly at the surface (ratio 5.1 times greater) but also "deeper" : 1.6 times at 35 % irradiance (real), 1.9 times at 13 % irradiance (real) and 2.3 times at 4.5 % irradiance (real). It is thought that spectral differences between laboratory and deck incubators account for the differences recorded from 4.5 % to 35 % (about 2 times). At the surface photoinhibition would add its selective effect (affecting mostly nanoplankton). The individual response of net- and nanoplankton in situ will be studied in the future.

Nutrients uptake

Among many authors, Fleming (1940), Ketchum & Redfield (1949), Vinogradov (1953) and Riley & al. (1956) have analysed marine phytoplankton in mixed populations or in pure cultures. The ratios they have observed between the major constituents of the cell (C, N, P and also Si) were statistically constant. As nutrients are withdrawn from the environment in the proportions required for the growth of primary producers, such ratios provide a stoichiometric basis for evaluating the uptake of nutrients resulting from phytoplankton activity. On an average, for a production of 1 mg C, 0.11 mg N, 0.01 mg P and 0.8 mg Si should be taken up.

Nutrients concentrations (e.g. NO_3^- determined by Elskens & Janssens, 1971 and 1972) plotted as a function of the distance to the coast, can be compared with primary production figures (averaged per m^3) (Fig. 9).

This only makes sense in a well mixed and shallow environment where the whole of the water column is concerned with upperlayer photosynthesis. One can see that the production is relatively independent of the distance from the coast, as discussed in the section on water transparency. On the contrary a definite pattern of decrease is demonstrated in any season. As pointed out by Joiris (1971), the same phenomenon is likely to occur in space in the North Sea as occurs with time in a closed environment. Here, a continuous input of nutrients at the coast is gradually metabolized by the phytoplankton community. At constant uptake rate along a given transect, a definite slope must characterize the disparition curve of the nutrients. The lower the uptake, the weaker the slope. This hypothesis will be discussed in a future paper.

CONCLUSIONS

Such topics as those reviewed in this paper have been emphasized at the Conference on North Sea Science, held in Aviemore (Scotland) in November 1971. It was then written in the Recommendations : "We lack detailed knowledge of such things as changes in, and the levels of, solar radiation, turbidity, mixed layer depth, wave action, C-14 uptake and supporting chlorophyll a levels. These are necessary to determine more exactly the levels of primary production in different parts of the North Sea and variations from year to year".

We feel a few answers have been given to these questions . One can attempt to review them in the same order :

1. Solar radiation

Coastal meteorological stations such as at Den Haan, Belgium, are thought to provide sufficient information on solar radiation in the area. We have seen that the annual variation of irradiance ranged from 55 to 2879 Joules/cm² day in 1971. The minimum range is 0-6 J/cm² 30 min. in the winter and 0-161 J/cm² 30 min. in the summer.

The penetration of light energy in water varies accordingly but also depends on turbidity and spectral transmittance characteristics.

2. Turbidity

Water transparency has been investigated with an immersible photometer sensitive in the 500-600 nm range. Our results indicate that the South Bight waters belong probably to Jerlov's coastal water 3, characterized by a shift of the transmittance peak to 550 nm. The transparency low near to the coast (transmittance at 540 nm : 20 % / m), is shown to increase very quickly in the open sea.

It is stabilized at 50 km off the coast (transmittance at 540 nm: 80 % / m). Accordingly, available energy can be computed for any depth. The $7 \text{ J/cm}^2 \text{ 30 min}$ limit (about 10.000 lux) above which light saturation or even inhibition of photosynthesis is likely to occur ranges from 0 m (5 h) to 11 m (13 h) deep on the sunniest summer day in open sea. On the other hand, the 1 % irradiance level (compensation depth) ranges from 2 m near to the coast to 25 m in the open sea.

3. Mixed layer depth

The first conclusion of our in vitro C-14 uptake experiments was that no stratification occurs in the water column as samples taken at different levels from the surface to the bottom give similar results. This observation was repeated for all cruises and sampling stations (the estuaries excepted). It thus appears that the mixed layer depth extends to the bottom in the South Bight of the North Sea.

4. Wave action

No conclusion was apparent from our study on the effects of direct wave action on primary production. It was however demonstrated that a change of tide modified the phytoplankton concentration by a factor 1.4 on an average.

5. C-14 uptake

Uptake experiments were performed at all sampling stations and cruises. In vitro measurements made under saturating light (potential production) indicate that inshore stations are potentially much more productive than off-shore stations. Such a pattern of decrease is exhibited for each cruise. Stabilization of the figures occurs at 50 km off the coast. The differences between summer and winter are much more important near to the coast (summer : $30 \text{ mg C/m}^3 \text{ h}$; winter : $5 \text{ mg C/m}^3 \text{ h}$) than in the open sea (summer : $8 \text{ mg C/m}^3 \text{ h}$; winter : $3 \text{ mg C/m}^3 \text{ h}$).

In the summer, the nanoplankton has been shown to be a major contributor to open sea production whereas netplankton contribution is greatest near to the coast. In the winter nanoplankton is dominant everywhere.

In situ production was calculated from in vitro figures using the Steemann Nielsen ⁽¹⁹⁵²⁾ Formula. Comparison with in situ experiments proved to be very good. The general picture is that of an in situ production pattern independent from the distance to the coast as a higher transparency in the open sea compensates the lower potentiality exhibited per unit volume. The figures of in situ production range from about 100 mg C/m² day in the winter to 1500 mg C/m² day in the summer. No information is available on spring bloom figures. The normal level for the South Bight of the North Sea seems to lie around 500 mg C/m² day.

6. Chlorophyll a level

Chlorophyll determinations made by colleagues led to similar conclusions. The computation of the productivity (i.e. production / biomass ratio) using potential production figures and chlorophyll a levels gave rather consistent ratios for each cruise. This indicates that the correlation between both parameters is good. The ratio level is significant for a given period. It is lower in the winter (average 3.8) than in the summer (average 5.4). Deviating figures characterize some sampling stations, implying a different physiological state of the phytoplankton.

As a last point, the relationship between primary production and nutrient uptake was discussed and production-uptake figures compared with nitrate levels in water.

It is thought that for a given cruise the rate of decrease of nutrients along a transect perpendicular to the coast is correlated with the general production level in the same way that it would be in time in a closed environment.

A C K N O W L E D G E M E N T S

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Table 1 . Average potential production and productivity for cruises 0 to 7 .

Cruise	Date	Stations	Average pot. prod. (mg C/m ³ h)	Average pro- ductivity	Std deviation productivity
0	230171 - 050271	within sta- tions 1-8-5 triangle	3.71	-	-
1	230671- 090771	1 - 15	8.68	3.6	2.0
2	170871- 260871	16- 25	18.00	5.4	2.0
3	070971- 230971	52 - 60 (+ 1,2)	15.51	5.4	1.7
5	030172- 140172	1 - 25	2.37	3.8	1.2
6	040472- 180472	radial network	6.17	-	-
7	260672- 140772	1 - 25	3.85	3.53	1.32

Table 2 . Integrated production (average and extreme figures) for cruises
0 to 7 .

Cruise	Production (mg C/m ² day) calculated		
	average	min. (stat.)	max. (stat.)
0	107	22 (2)	242 (6)
1	694	298 (1 & 11)	1488 (7)
2	1398	572 (24)	3226 (18)
3	971	224 (54)	1705 (60)
5	122	41 (5)	221 (23)
6	327	128(2689)	540 (1693)
7	646	214 (7)	1915 (5)

Table 3 . Calculated (Steemann Nielsen formula) and in situ measured primary production figures .Between brackets : incubation hours (otherwise : from noon to sunset)

Station	Production measured (mg C/m ² day)	Production calculated (mg C /m ² day)
<u>cruise 6</u>		
1344	262	230
1693	495	485
67	283	333
61	382	418
<u>cruise 7</u>		
1	251	395
2	955	667
3	268	341
6	358	305
9	272	390
11 (14-21)	1996	1425
11 (14-16)	1901	1425
15	713	712
18 (12-21)	512	572
18 (12-14)	548	572
18 (12-16)	502	572
20	800	345
21	621	590
22	875	690
25	217	440
<u>cruise 8</u>		
1930	167	277
1778	206	138
72	296	617
65	936	944
1	973	613

Legends of the figures

Fig.1 . Sampling network in the eastern half of the South Bight.

Fig.2 . Speed vectors of tidal streams measured at the surface in the Wielingen pass (after Codde and De Keyser ,1967).

Fig. 3 . Average depth profile of potential production.

Each potential production result has been expressed as a percentage of the maximum figure recorded in the water column. Then the figures were averaged for every cruise and relative irradiance level . The optical depth scale is such that each unit causes a halving of irradiance.

Fig. 4 . Potential production results of cruises 1 to 7 , plotted as a function of the distance to the coast .

Fig. 5 . Relationship between Secchi disc measurements and absorption coefficient as a function of the distance to the coast.

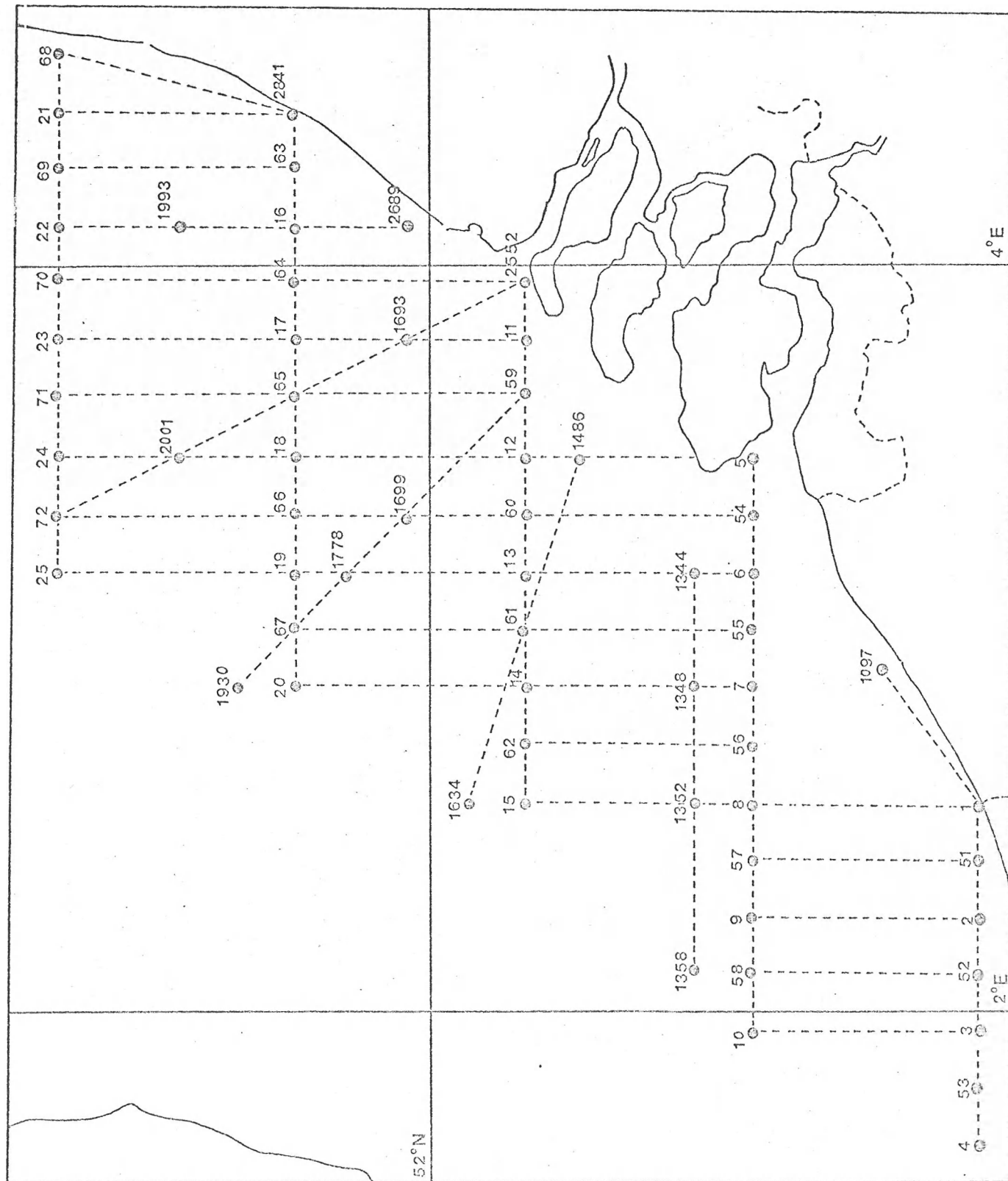
Fig. 6 . Absorption coefficients measured in the 500-600 nm range for cruises 1 to 8 and plotted as a function of the distance to the coast.

Fig. 7 A. Daily global irradiance from 21th december 1971 to 30th september 1972 (Den Haen meteorological station). The black dots show the evolution of day length (from sunrise to sunset). The hatched areas represent cruises (cruises 5 ,6,7 and 8).

B. Global surface irradiance (histograms) in the courses of a summer day (indicated by an arrow in (A)) and evolution of the light-saturated column ($7 \text{ J/cm}^2 \cdot 1/2\text{h}$ line).

Fig. 8 . Average depth profile of primary production . Black circles : real in situ incubations . White circles : simulated in situ incubations .

Fig. 9 . Nutrient concentrations (nitrate) at cruise 1 as a function of the distance to the coast (black circles with sampling station numbers) and primary production (white circles). The reason for stations 2 and 3 being exhausted is unknown at present time.



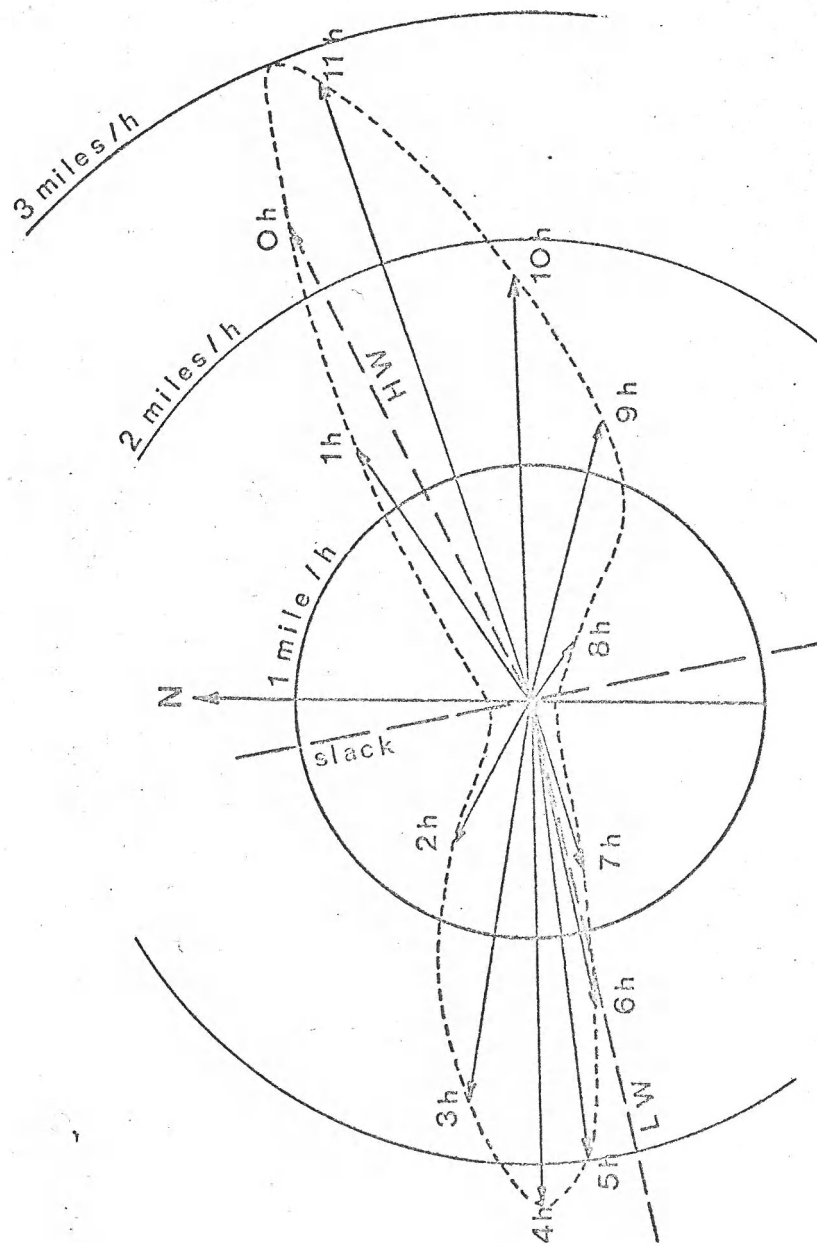


Fig. 2

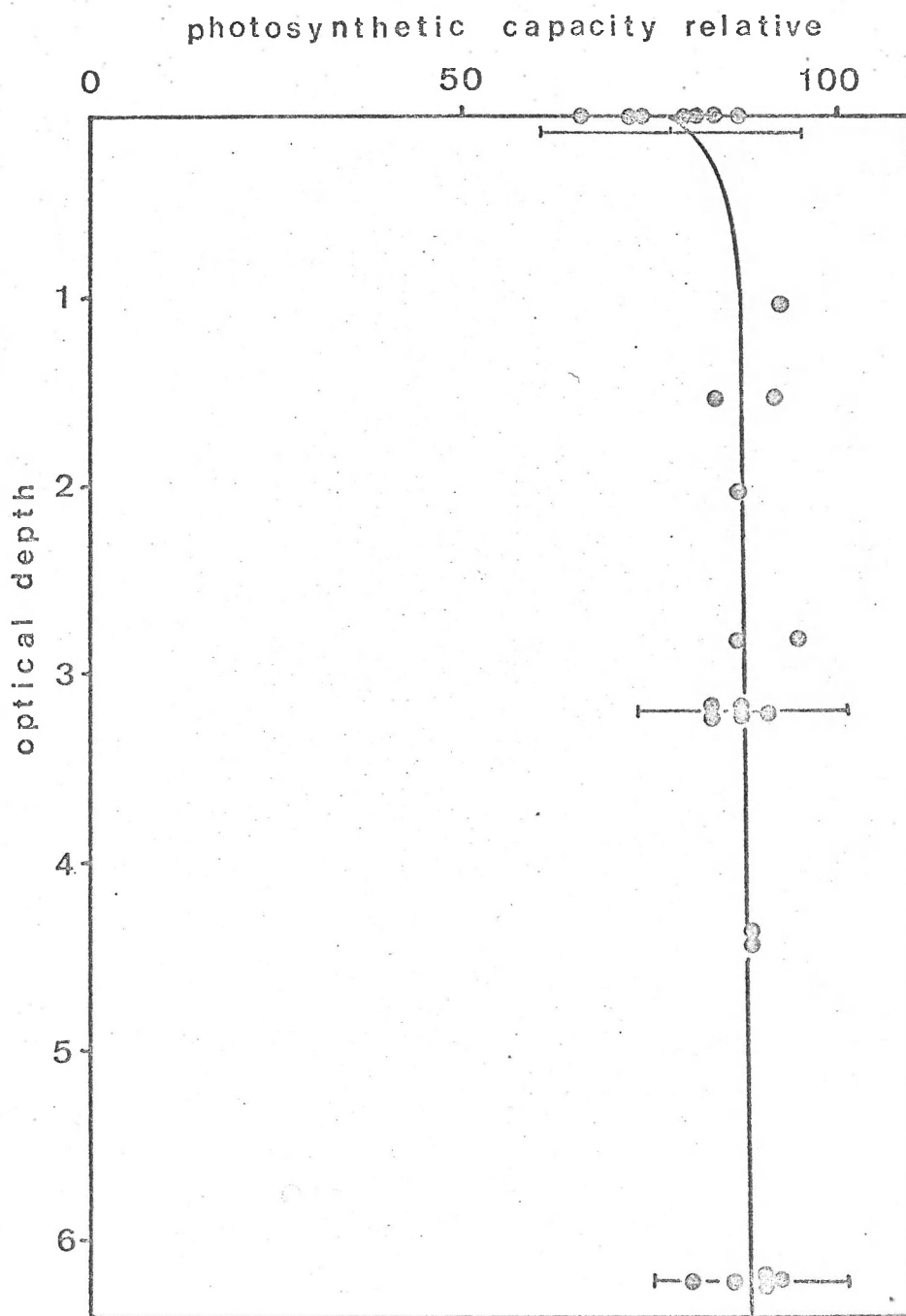
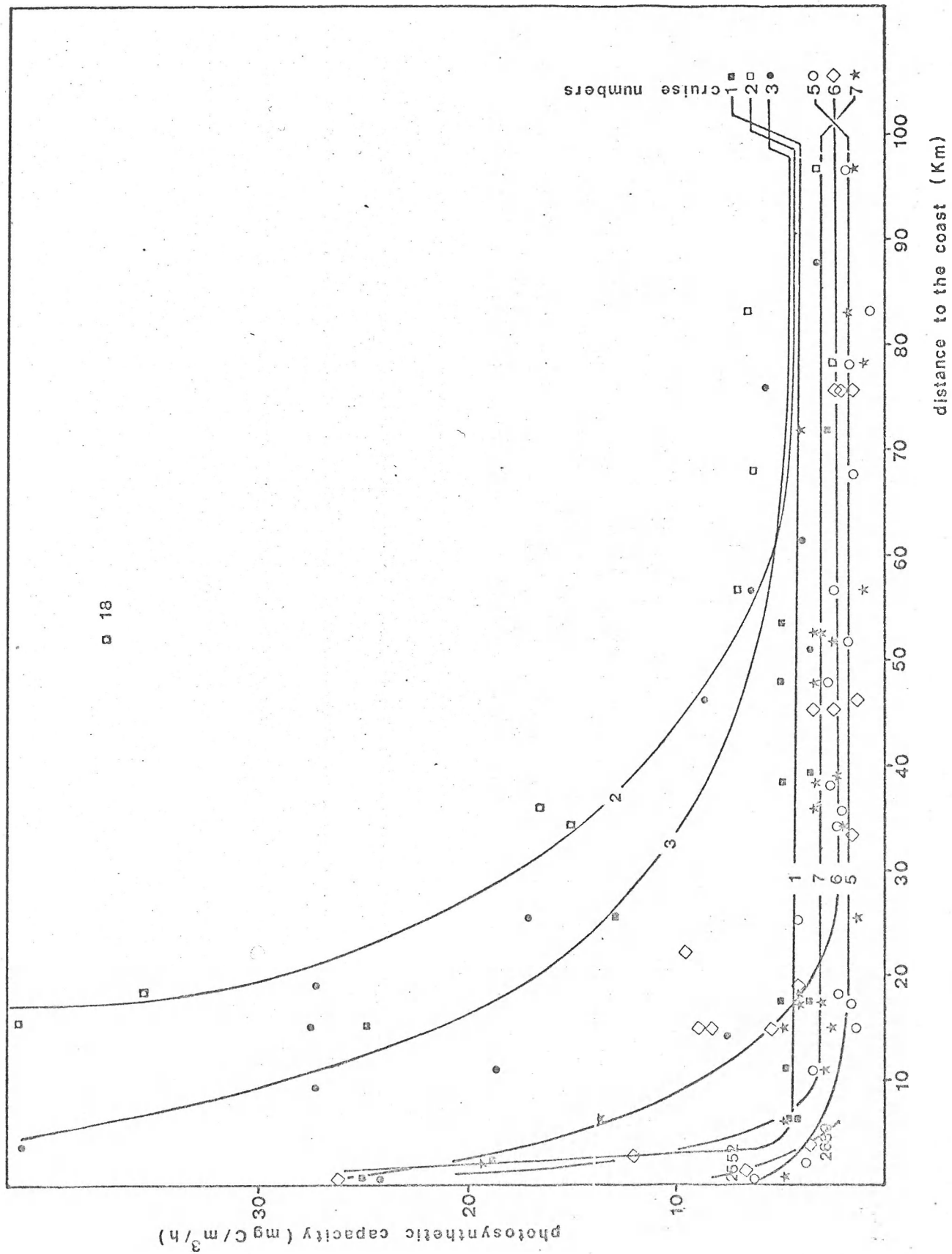


Fig 3



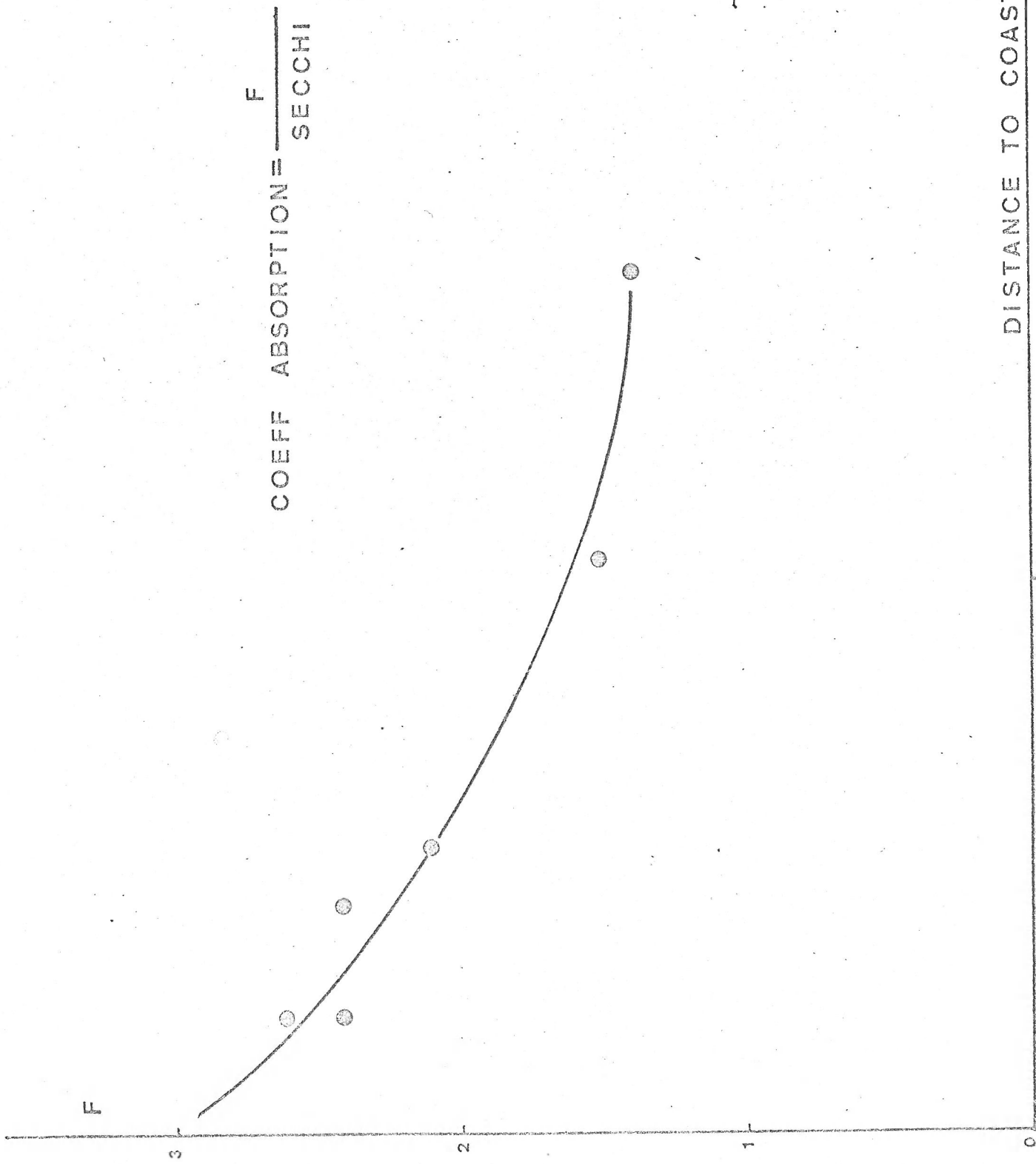


Fig 5

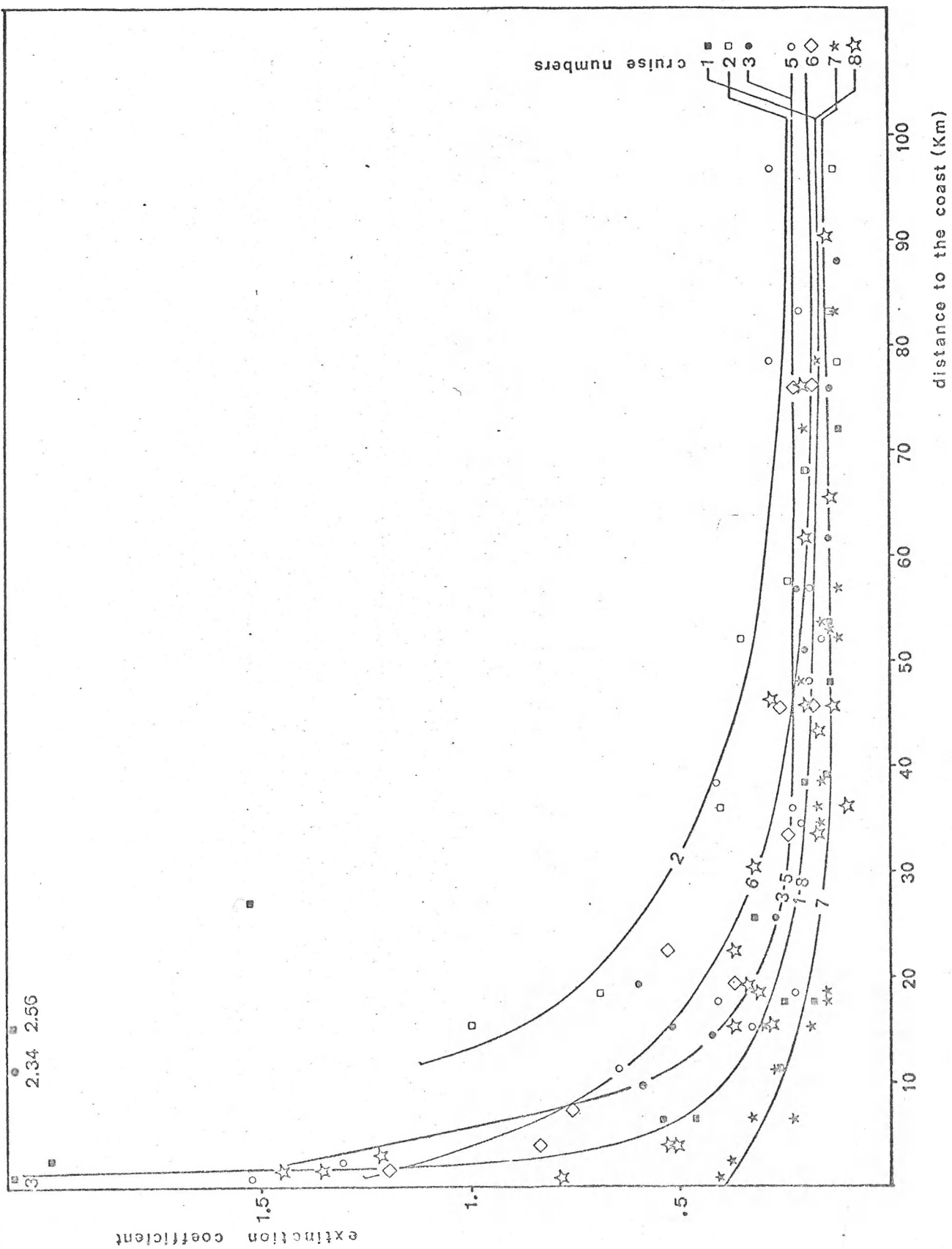
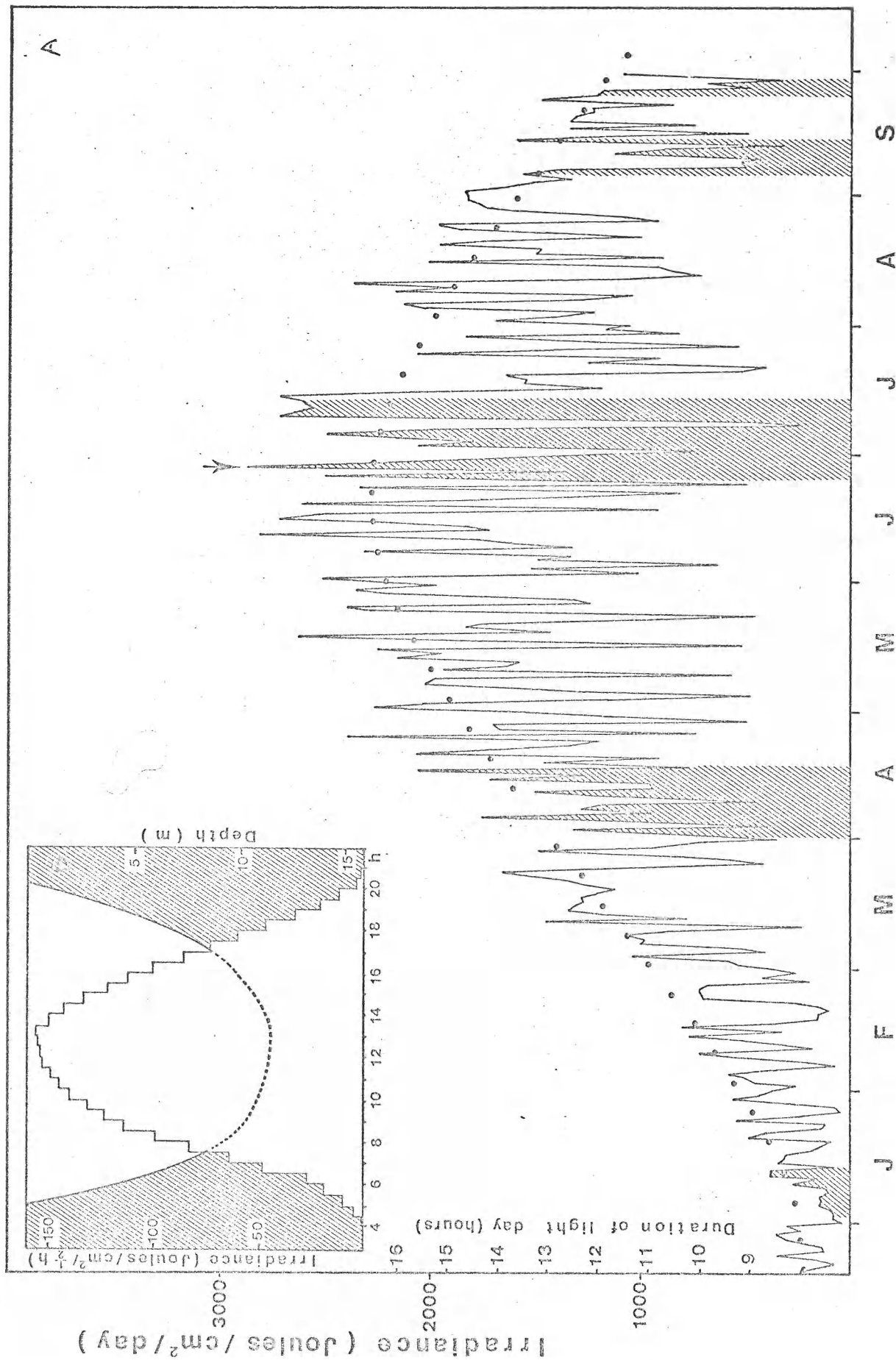


Fig 6



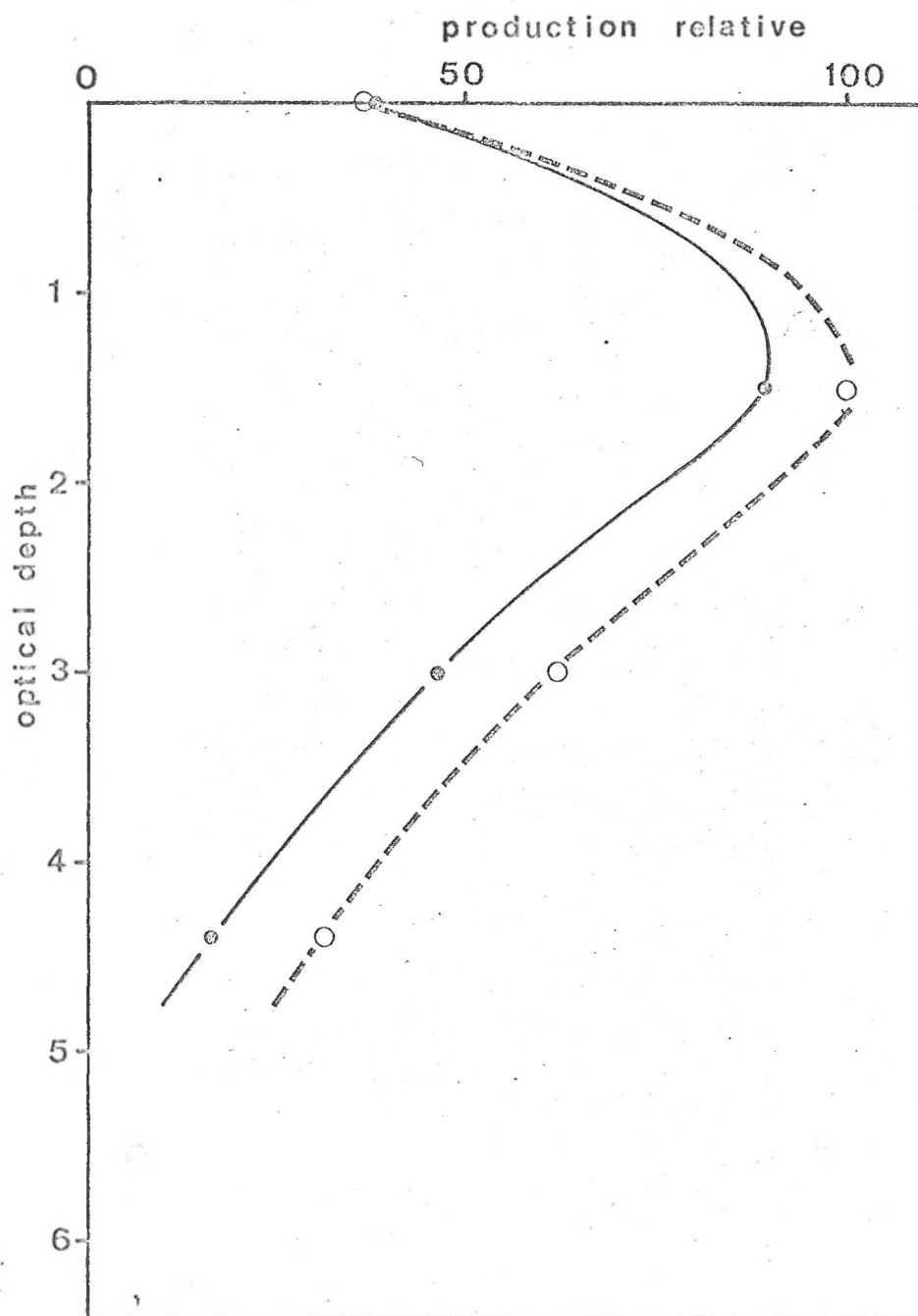


Fig 8

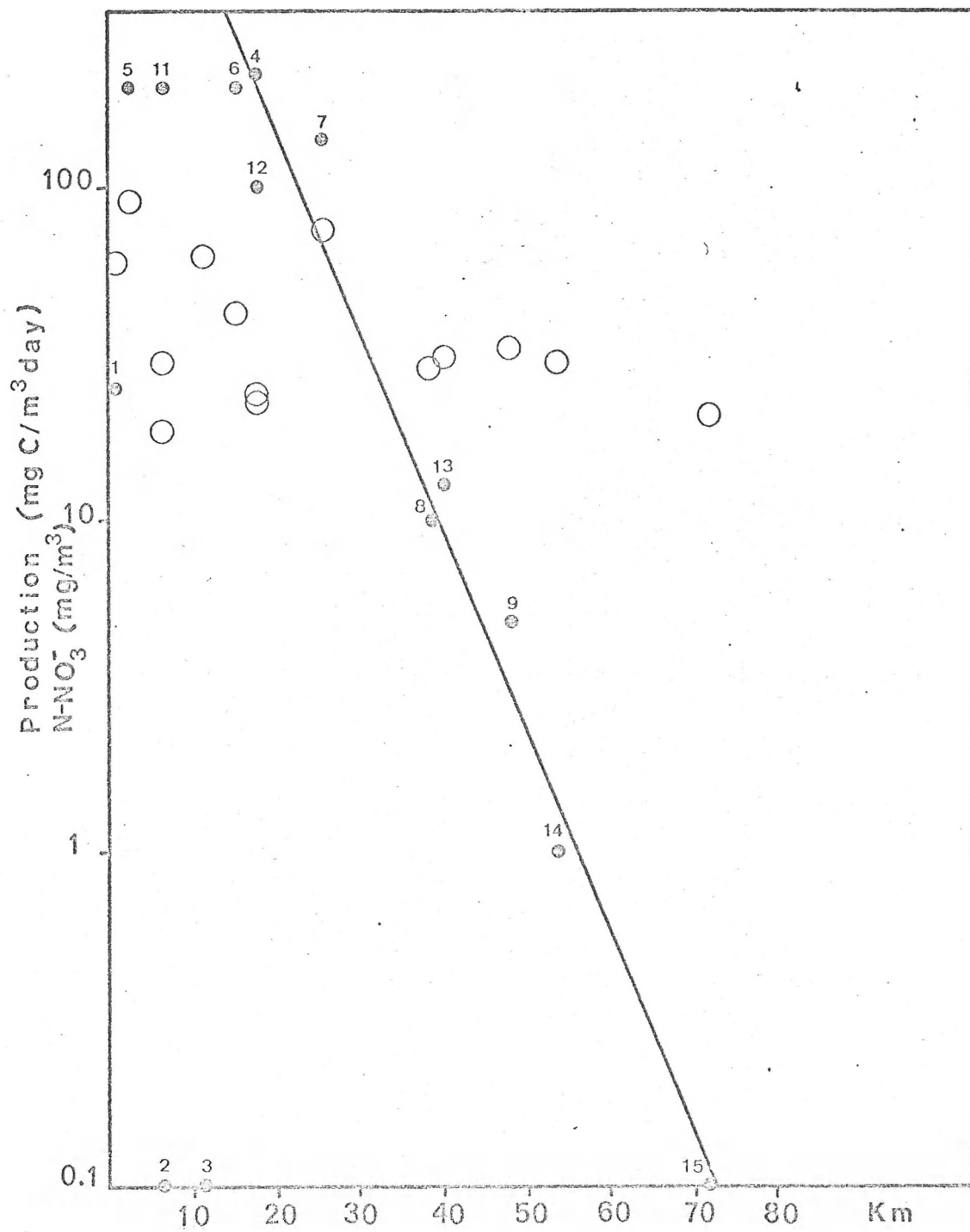


Fig 9