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The Importance of the Planktonic Ecosystem of the North Sea in the Context of Oil and Gas Development [and Discussion]

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The importance of the planktonic ecosystem of the North Sea in the context of oil and gas development

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Planktonic organisms are the primary source of food for the top level of the marine food chain, the fish. Yet only part of the plankton is ingested by fish, the remainder sediments to the bottom to provide food for benthic organisms (which may in turn be grazed by demersal fish) and to contribute to a detrital sink. Although the relative proportions of the plankton entering each of these compartments is still a matter of debate, some indication of its importance as a resource can be gauged from the North Sea fishery that has yielded 2–3 Mt per year since the mid-1960s. Calculations for the North Sea of the annual production of phytoplankton, zooplankton, fish and benthos as energy equivalents are contrasted with the annual energy yields of oil and gas.

Since 1948 the plankton of the North Sea has been monitored at a depth of 10 m by the Continuous Plankton Recorder (CPR) survey. Results for two large areas which encompass the Brent, Beryl and Forties oilfields are presented. Between 1948 and 1982 the plankton of these areas showed similar large changes in population structure in both phytoplankton and zooplankton with almost tenfold changes in levels of biomass during this 35 year period. The development of oil-related activities is discussed in relation to the plankton time-series with comment on possible causes of the changes which are believed to be the result of natural variability.

Introduction

Planktonic organisms are small, not readily visible to the naked eye, with patchy vertical and horizontal distributions in the water column and large seasonal variability. They are thus difficult to study in relation to pollution events and any potential pollution effect raises little public concern because of a lack of a visible impact. Their importance is underrated however, as the plankton includes the primary energy source and subsequent food for almost all other components of the ecosystem. Their size and rapid rates of production may make them particularly susceptible to small concentrations of pollutants and any impact is likely to be reflected higher up the food chain. To demonstrate the importance of the plankton the simplified energy budget for the North Sea compiled by Steele (1974) has been revised with the inclusion of an estimate of the input of solar energy. Using these results, and to place a value on the plankton, a comparison is made between yields of North Sea oil and gas with energy yields from components of the ecosystem.

Oil production activities off the British coast are concentrated in the central and northern North Sea. In these areas there is evidence of localized effects of oil pollution on the benthos and fish (Addy *et al.* 1984; Davies *et al.* 1984*a*, *b*). Time-series of plankton measurements are presented for these same areas, together with data on their physical environment as a backdrop against which the development of petroleum extraction can be compared and possible pollution impacts assessed.

Energy budget calculations

The North Sea as defined here is equivalent to the fishery statistical division IV of the International Council for the Exploration of the Seas (ICES). This area (figure 1), which covers 0.5872×10^{12} m^2, includes all currently producing oil and gas reserves in the North Sea. A

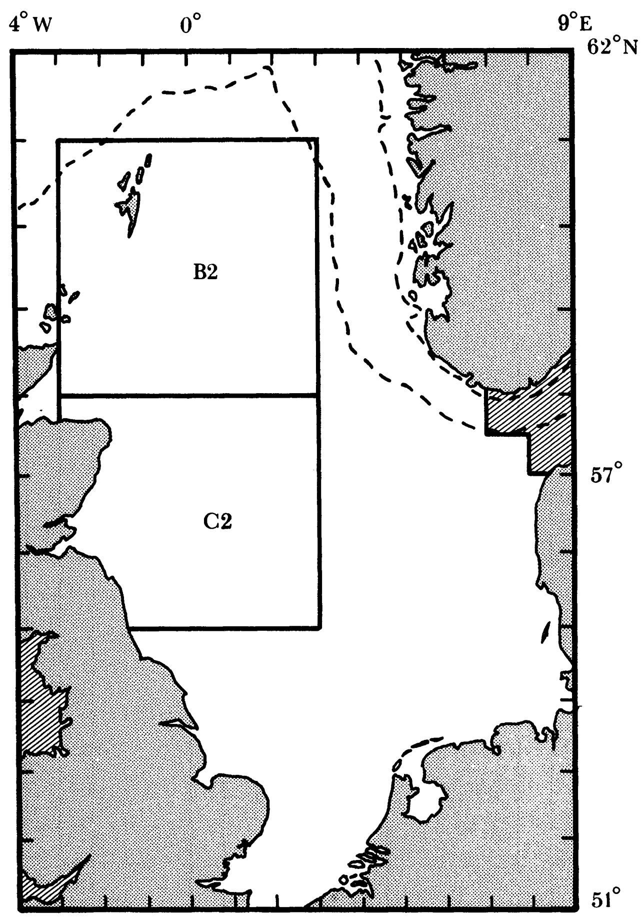

Figure 1. ICES fishery statistical division IV which extends from 51° N to 62° N and from 4° W to approximately 8° E. Sea areas outside the division boundary are hatched. The 200 m contour (broken line) and areas B2 and C2 for which data from the CPR survey have been processed are superimposed.

considerable variation in depth and hydrography is evident from north to south with a boundary between shallower mixed and deeper stratified waters at approximately 54°N in the summer months of the year (Pingree *et al.* 1978).

Solar energy input to the North Sea

The mean radiation penetrating the sea surface (R) was calculated by using tables and equations from Goldsmith & Bunker (1979). Cloud cover observations taken by merchant ships

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from 1961 to 1976 were provided by the Meteorological Office, Bracknell, U.K. The data used, in Watts per square metre, were $R = 96.6$, Q (the radiation received at the surface after penetrating cloud) = 104.3 and Q_0 (the radiation at the bottom of the atmosphere without cloud) = 195.7. Confirmation of these estimates was made by calculating an annual global irradiation on a horizontal surface of 95.7 W m^{-2} for Aberdeen from table 51 in Anon. (1980). Only 50% of R is available to plants (Monteith 1973) to use as 'Photosynthetically Active Radiation' (PAR) which I have taken as 48.3 W m^{-2}. Of this value an unknown proportion is utilized by plants and the remainder dissipates as heat.

Primary production

Until recently an annual net primary production of approximately 100 g C m^{-2} per year (the value accepted by Steele (1974)) was consistently quoted for the North Sea. This estimate was raised to 130 g C by Jones (1984) based upon data up to 1980. Since 1980 a growing number of studies (Fransz & Gieskes 1984; Gieskes & Kraay 1984; Joiris *et al.* 1982; Weichart 1985) have recorded primary production rates which are more than double the early estimates. (These estimates do not take into account production by benthic micro- and macroalgae and contributions from river inflow.) A thorough seasonal and spatial coverage of production measurements has not yet been made to evaluate true phytoplankton production, but it does not seem unrealistic to take an estimate of 200 g C m^{-2} for annual net primary production by all plants in the North Sea.

Zooplankton herbivore production

Traditionally, the copepods were considered to be the predominant herbivore grazers and they are the only group for which there are any accurate estimates of production. These values range between 2.5 g C m^{-2} per year (Evans (1977), but they are now considered to be an underestimate (F. Evans, personal communication)) and 12 g C m^{-2} per year (Fransz *et al.* 1984; Fransz & Gieskes 1984). As copepods are not the only component of the herbivores, and herbivorous planktonic larvae may at times dominate the plankton, an average total herbivorous production of 15 g C m^{-2} per year is taken as a fair estimate (see Baars & Fransz 1984).

There is at present no information on rates of production of the microzooplankton in the North Sea although they are known to occur in large numbers at certain times of the year (Fransz & Gieskes 1984). These small organisms may at times have an important grazing impact on nano- and picophytoplankton which appear to be the most productive size fractions of the phytoplankton (Joint *et al.* 1986). A microzooplankton production of approximately 12 g C m^{-2} per year calculated by Burkill (1982) for Southampton Water is used here as an estimate.

Benthic production

Rachor (1982) estimated a mean macrofauna biomass of 1.28 g C m^{-2} for the North Sea. Only 36% of the bottom of the North Sea has been sampled quantitatively for benthos, and most of these samples were taken with Van Veen or McIntyre grabs which only sample the top 10 cm or so of sediment. There are great contrasts between the macrofauna biomass of the deep northern North Sea and the more productive south. Recent benthic studies in the southern North Sea and especially those using box corers (De Wilde *et al.* 1984) give much higher biomass estimates than were previously determined. Almost 50% of the biomass was in sediment below 10 cm which would have been missed by grabs. In the northern North Sea in contrast, macrofauna levels may be very low (Hartwig & Thiel 1983) so Rachor's average estimate is accepted here. The productivity/biomass (P/B) ratio of the macrobenthos is dependent on the lifespan of individual organisms, a mean value for the North Sea of 1.5 is used to give a production of approximately 2 g C m^{-2} per year using Rachor's biomass estimate and De Wilde's conversion factor of 2.5 g ash free dry weight (AFDW) = 1 g C.

There are few production estimates for the meiofauna in the North Sea; they range from 1.5–2.0 g C m^{-2} per year in Belgian coastal waters (Heip *et al.* 1984) to 2.4 g C m^{-2} at the Oyster Ground (De Wilde *et al.* 1984) to 2.42 g C m^{-2} per year in the Fladen Ground (Faubel & Hartwig 1983). For the budget a mean value of 2.0 is used.

A proportion of the benthic epifauna is harvested for human consumption. Statistics on these catches have been kept by ICES since 1966. Adopting the conversion used by Steele (1974) for fish, of 1 g wet mass = 0.1 g C, the mean catches for 1966–69 and 1978–82 are 0.09 and 0.07 g C m^{-2} per year respectively. Total production is calculated by assuming the production of the commercial stock is ten times the fishing yield, multiplied by two for the epifauna which does not contribute to the commercial fishery, to give a total production of approximately 0.2 g C m^{-2} per year.

Fish production

In his energy budget, Steele (1974) took a mean of the years 1965 to 1969 for his estimates of fish production. This sequence of years was atypical as it represented a transition period which coincided with the introduction of Purse Seines, the development of a major industrial fishery on the mackerel and a rapid decline in the contribution of herring to catches. The high yields of the late 1960s represented an almost doubling of the catch over the immediate postwar years to 1964 which had an average yield of 1.75 Mt. Catches were again reduced to a lower level of 2.44 Mt from 1978 to 1982. Yang (1982) categorized the fish of the North Sea into three groups (planktophagic, benthophagic, and ichthyophagic) dependent on their dominant feeding habits. Production estimates for three periods 1948–52, 1965–69 and 1978–82 have been calculated with a subdivision according to Yang's (1982) feeding groups. A natural mortality estimate of 20% for the benthophagic and 50% for planktophagic species was used as by Steele (1974), an intermediate value of 35% was taken for the ichthyophagic species.

Detrital pool, bacteria and Protozoa

All organisms in the North Sea ecosystem contribute to a pool of soluble and particulate carbon through excretion. A further contribution to this pool comes from dead and decaying products. Soluble carbon becomes immediately available for bacterial production. The particulate fraction was divided into 'labile' and 'inert' by Postma & Rommets (1984). The former was estimated to turnover every five days and the latter remains at a background level of 40 mg m^{-3} over a longer period. If the average depth of the North Sea is taken as 87 m this gives a constant background detrital pool of 3.4 g C m^{-2}, which is approximately equal to the average biomass of the phytoplankton. The labile fraction provides an important substrate for bacteria and Protozoa and is an additional food source for higher trophic levels. Rates of carbon flow through the detrital pool are not known.

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Ecosystem energy budget

An energy budget for the North Sea was calculated by Steele (1974) with fish yields from ICES statistics as the terminal product of a simplified food web (figure 2*a*). For comparison with Steele (1974) all units used in this section are in kilocalories† per square metre per year. A conversion factor of 10 $kcal_{th}$ = 1 g C as per Steele (1974) has been used. From an estimated primary production of 900 $kcal_{th}\ m^{-2}$ per year a yield of 8 pelagic and 2.6 $kcal_{th}\ m^{-2}$ per year for demersal species was obtained. Steele (1974) concluded that transfer efficiencies of at least 20% were necessary to obtain such high yields. If only a 10% transfer efficiency was used, all the planktonic production would have been needed to satisfy the food requirements of the fish. By determining a more accurate estimate of fish food-requirements, Jones (1984) showed that transfer efficiencies of 10% would be possible in the unreal situation of a lack of predation by fish on other small fish. In reality, small-bodied fish such as sprats, Norway Pout, sand eels and juvenile specimens provide the main source of food for ichthyophagic species. Jones (1984) overcame this dilemma by raising primary production to 1300 $kcal_{th}\ m^{-2}$ per year and confirming the necessity for transfer efficiencies of 15–20%.

Figure 2*b* plots a revised energy budget for the North Sea from 1965–69 by using the data given in the previous sections. Almost all of the estimates of production are lower than those given by Steele (1974). This is partly because of his underestimation of the size of the ICES

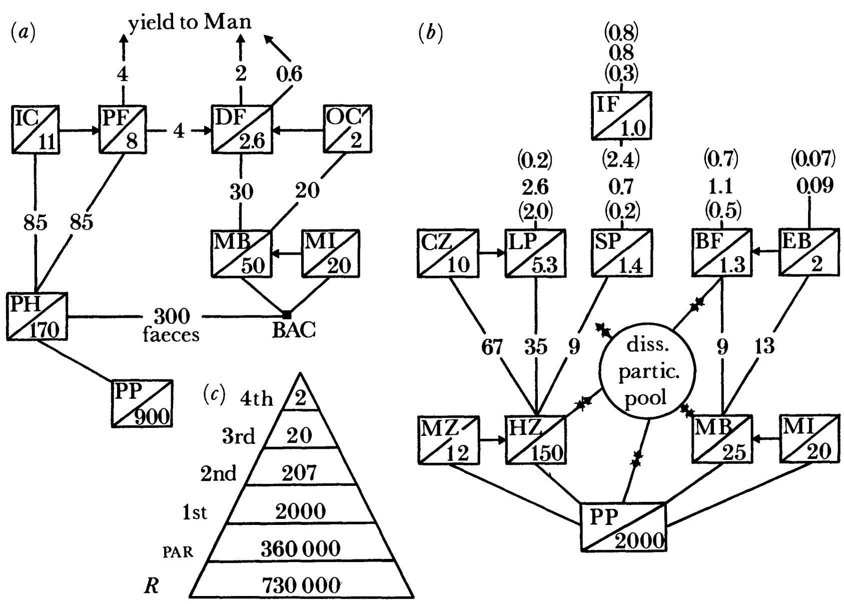

Figure 2. (*a*) A simplified energy budget for the North Sea redrawn after Steele (1974). IC, invertebrate carnivores; PF, pelagic fish; DF, demersal fish; OC, other carnivores; MB, macrobenthos; MI, meiobenthos; PH, pelagic herbivores; BAC, bacteria; PP, primary production. (*b*) A revised energy budget for the North Sea. IF, icthyophagic fish; CZ, carnivorous zooplankton; LP, large pelagophagic fish; SP, small pelagophagic fish; BF, benthophagic fish; EB, epibenthos; MZ, microzooplankton; HZ, large herbivorous zooplankton; MB, macrobenthos; MI, meiobenthos; PP, primary production. The circle represents a detrital pool of dissolved and particulate material. Superimposed above the fish and epibenthos production boxes are yields to Man, from top to bottom, for the years 1978 to 1982, 1965 to 1969 and 1948 to 1952. (*c*) A pyramid of energy production by each trophic level in the North Sea with, at the base, estimated PAR, photosynthetically active radiation and *R*, radiation penetrating the sea surface. 1st, 2nd, 3rd and 4th, trophic levels.

† 1 cal_{th} = 4.184 J.

fishery area (0.5×10^{12} m^2) compared with my calculation of 0.5872×10^{12} m^2. Mean fish and crustacean yields from the commercial fisheries are included above the production boxes for the periods 1948–52 (fish only), 1965–69 and 1978–82 with the oldest period at the bottom and the most recent at the top. A complete reversal in the contribution of the small and large pelagic fish between the first and last period is evident with a major contribution from benthophagic species (predominantly haddock) in the middle period. Yields of ichthyophagic species as a proportion of catches increased substantially in the two most recent periods. An unknown, but possibly significant, portion of the detrital pool may be lost to the system by sedimentation or export from the North Sea.

If net primary production is 2000 kcal$_{th}$ m^{-2} per year, transfer efficiencies must still be at least 15–20 % through secondary producers to allow for a contribution to herbivorous microzooplankton, the detrital pool and recycling by bacteria and Protozoa. Transfer efficiencies of at least 15 % are also necessary at the next feeding level for a flexible account of the energy flow. Food requirements based upon a 15 % transfer efficiency are plotted on the diagram, giving an excess for predators on the herbivores and benthic macrofauna of 39 and 3 respectively. The diet of ichthyophagic species depends upon their size and age, and although they predominantly feed on small pelagic species and juvenile fish of other groups they also feed on plankton and benthic organisms, especially when young. The total production of all fish and crustaceans at the third trophic level was estimated to be 10 kcal$_{th}$ m^{-2} per year from 1965–69 which would not balance the estimated food requirement (6.7, rising to 7.5 kcal$_{th}$ m^{-2} per year from 1978–82) of the ichthyophagic species at a 15 % transfer efficiency. Direct feeding of the ichthyophagic species on the plankton and benthos is necessary to balance the budget. Such a change in feeding habits is also implied in the marked reduction in the mean size of fish in this category now seen in catches.

The total production for planktophagic species in the three different periods is estimated as: 1948–52, 4.5 kcal$_{th}$ m^{-2} per year; 1965–69, 6.7 kcal$_{th}$ m^{-2} per year and 1978–82, 5.4 kcal$_{th}$ m^{-2} per year. High values in the last two periods, plus an additional demand from the fish eaters on the plankton, suggests that there may have been increased pressure on herbivorous plankton in more recent years. Such pressures would have been reinforced by the evidence given below of marked decreases in the biomass and, by analogy, production of zooplankton between the three periods.

By summing together the production estimates for each trophic level a 'pyramid of energy' (Odum 1953) is produced which suggests a total transfer efficiency between each trophic level of 10 % (figure 2*c*). The production of the highest trophic level was doubled to include the impact of birds, mammals and ichthyophagic species which do not contribute to the fishery. Input of light energy as PAR with 0.5 % transfer efficiency is included at the base of the pyramid. No account was taken of the detrital pool in these calculations; it is possible that fluxes through this compartment, which appears to remain at a relatively constant value, may have little effect on average trophic interactions.

Comparison of petrogas and ecosystem yields

The North Sea basin has existed since at least the Permian although source rocks for oil and gas are believed to be of Late Jurassic age. Fossil sedimented planktonic organisms are the most likely source of this petroleum energy. By assuming that the palaeo-sea in which the fossil

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hydrocarbons were formed was a similar size to the present North Sea, an attempt to place a value on the plankton is made by comparing it with oil and gas yields. Figure 3 presents a time series of annual gas and oil yields for the North Sea as million tonnes of oil equivalent (MTOE) from estimates compiled by the British Petroleum Company. As an energy rate, 1 MTOE per year = 1.37 10^9 W, mean gas production from 1968 to 1984 and oil from 1971 to 1984

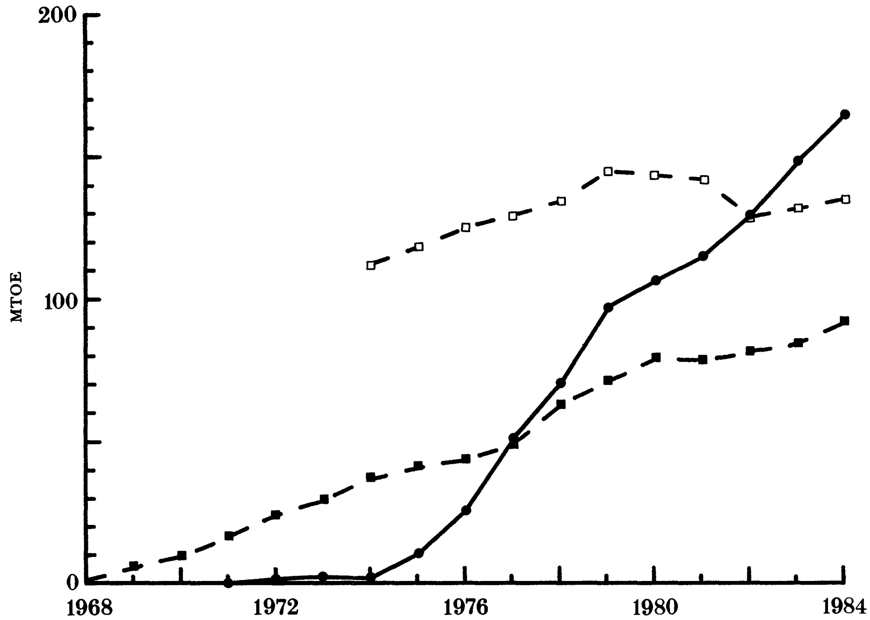

FIGURE 3. Total North Sea oil and gas production from first yields to 1984. (Sources Mr G. Pyne, British Petroleum Company, and Anon. 1985*a*). Oil is represented by the continuous line, gas is represented by the broken line; the top plot represents gas production from 1974 and includes output from onshore fields in the Netherlands. MTOE, Million Tonnes Oil Equivalent.

for the North Sea equals 0.11 and 0.15 W m^{-2} respectively to give a total for oil and gas of 0.26 W m^{-2}. A higher rate of extraction was calculated if the onshore gasfields of the Netherlands, which can be considered as within the same geological basin, were included. A conservative estimate of proved North Sea reserves for gas and oil (sources as for figure 3) is respectively 5.37×10^9 MTOE and 3.96×10^9 MTOE which gives a life of 39 years for gas extraction and 19 years for oil extraction at 1984 rates.

The average oil and gas energy yield per year from the North Sea over the past fifteen years and yields for gas and oil in 1984 are approximately equal to the annual primary production (figure 4). This figure also gives a comparison between yields and reserves of oil and gas as energy rates in the unreal situation of total extraction of the reserves in one year. As an energy equivalent, the annual mean fish yield to man for the three periods studied here is 0.2 % of mean oil and gas yields i.e. 500 years of fish harvest from the North Sea represents the mean oil and gas harvested in the last fifteen years. Extraction at 1984 rates is equivalent to almost 1600 years of fish harvest.

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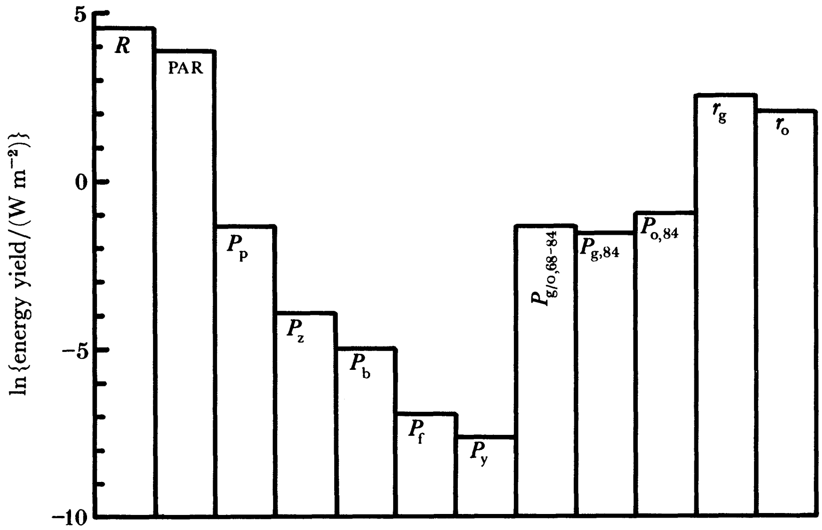

FIGURE 4. A comparative plot of the energy yields of components of the North Sea ecosystem, and oil and gas. R, radiation penetrating the sea surface; PAR, photosynthetically active radiation; P_p, primary production; P_z, zooplankton production; P_b, benthos production; P_f, fish production; P_y, fish yield; $P_{g/o,68-84}$, mean gas and oil production from 1968–1984; $P_{g,84}$, gas production in 1984; $P_{o,84}$, oil production in 1984. r_g, gas reserves, and r_o, oil reserves if exploited in one year.

TEMPORAL CHANGES IN THE PLANKTON

There can be few areas of the world with as comprehensive a baseline data set of plankton measurements before the development of an industrial resource as the North Sea. From 1948 Continuous Plankton Recorders (CPRs) have surveyed the North Sea on a number of standard routes at approximately monthly intervals. Details of the survey and methods are given in Edinburgh Oceanographic Laboratory (1973). Unfortunately, this survey only gives information on standing stocks; there are no comparable data sets of production for the plankton. However, gross changes in annual production can be inferred when marked reductions in biomass occur if P/B ratios are assumed to remain approximately equal. Figure 5 presents the mean monthly variability of phytoplankton and zooplankton sampled by the CPR in two areas (B2 and C2) of the North Sea (figure 1) between January and December from 1948 to 1982. Counts of the major zooplankton groups (copepods, thecosomes, euphausiids, large chaetognaths and hyperiids) were transformed to biomass by using mean wet mass values. The biomass estimates must only be considered as an index of biomass since the CPR only samples at 10 m depth and does not adequately sample young stages and soft-bodied plankton. Phytoplankton colour is a visual estimate of chlorophyll on the filtering silks; individual samples are allocated to one of four numerical categories according to their greenness. Counts of phytoplankton species are also made on CPR samples but can only be used for coarse estimates of abundance because of the size of the 270 μm mesh filtering silk which lets most phytoplankton pass through.

In areas B2 and C2, there was a marked shortening of the growing season and a progressive decline in levels of the zooplankton biomass index from 1948 to 1982; between the two sequences of years 1948–52 and 1978–82 this represents a reduction to 34% and 20% of the earlier period in areas B2 and C2 respectively. For area B2 phytoplankton colour showed the

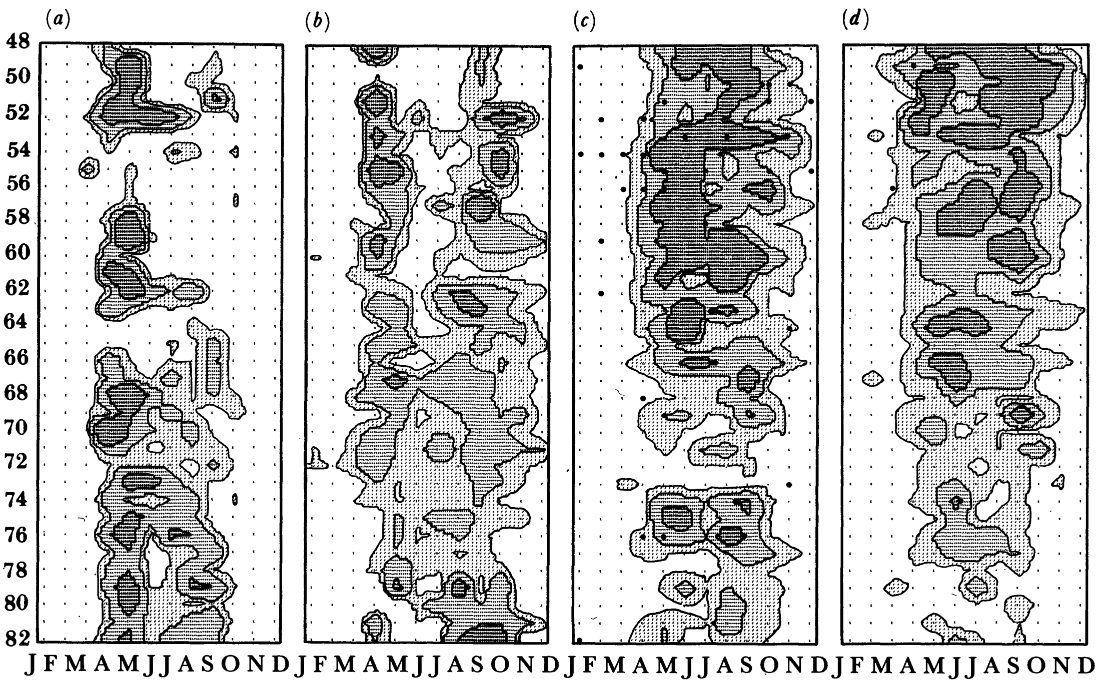

FIGURE 5. Monthly fluctuations in areas (*a*, *c*) B2 and (*b*, *d*) C2 of an index of (*a*, *b*) phytoplankton colour and (*c*, *d*) zooplankton biomass with values for every month (horizontally) in years (vertically) from January 1948 to December 1982. In (*c*) and (*d*) filled circles represent months that were not sampled but which have been interpolated in the contouring procedure. Contour levels for the phytoplankton are 0.07:0.12:0.23 units and for the zooplankton are 15:40:72 units.

reverse trend to the zooplankton (correlation −0.63*** (a correlation significant at the 0.1% level is indicated by ***)). Colour for area C2 also showed an increasing trend until approximately 1973 when a period of low levels occurred, but was not significantly related to the zooplankton trend. A marked seasonal and interannual variability is superimposed on these general trends. Large changes in the composition of the plankton have also occurred; for example, thecosomes which are small planktonic molluscs which once formed a major food source for the herring in the northern North Sea declined from 38% to 2% of the herbivorous zooplankton biomass averaged for B2 and C2 between 1948–52 and 1978–82.

A number of studies using data from the CPR survey have noted empirical relations between physical environmental variables and long-term changes in the plankton; Colebrook (1978, 1985) found relations with temperature and Lamb's westerly weather index, Dickson & Reid (1978) found correlations with wind strength, direction and turbidity, Reid & Budd (1979) with salinity and Robinson (1983) with wind and Lamb's westerly weather index. We do not know the mechanisms behind these apparent relations, changes in the plankton cannot be forecast and any impact from pollution is difficult to assess.

Annual means for zooplankton biomass, phytoplankton colour, diatoms and fish yield are plotted in figure 6 with similar graphs for temperature, salinity, scalar wind speed, cloud and Lamb's westerly weather index. Some of the relations mentioned above are confirmed with correlations between Lamb's westerly weather index and zooplankton for both area B2 and C2 of respectively 0.53*** and 0.62*** and between zooplankton and salinity in area C2 of

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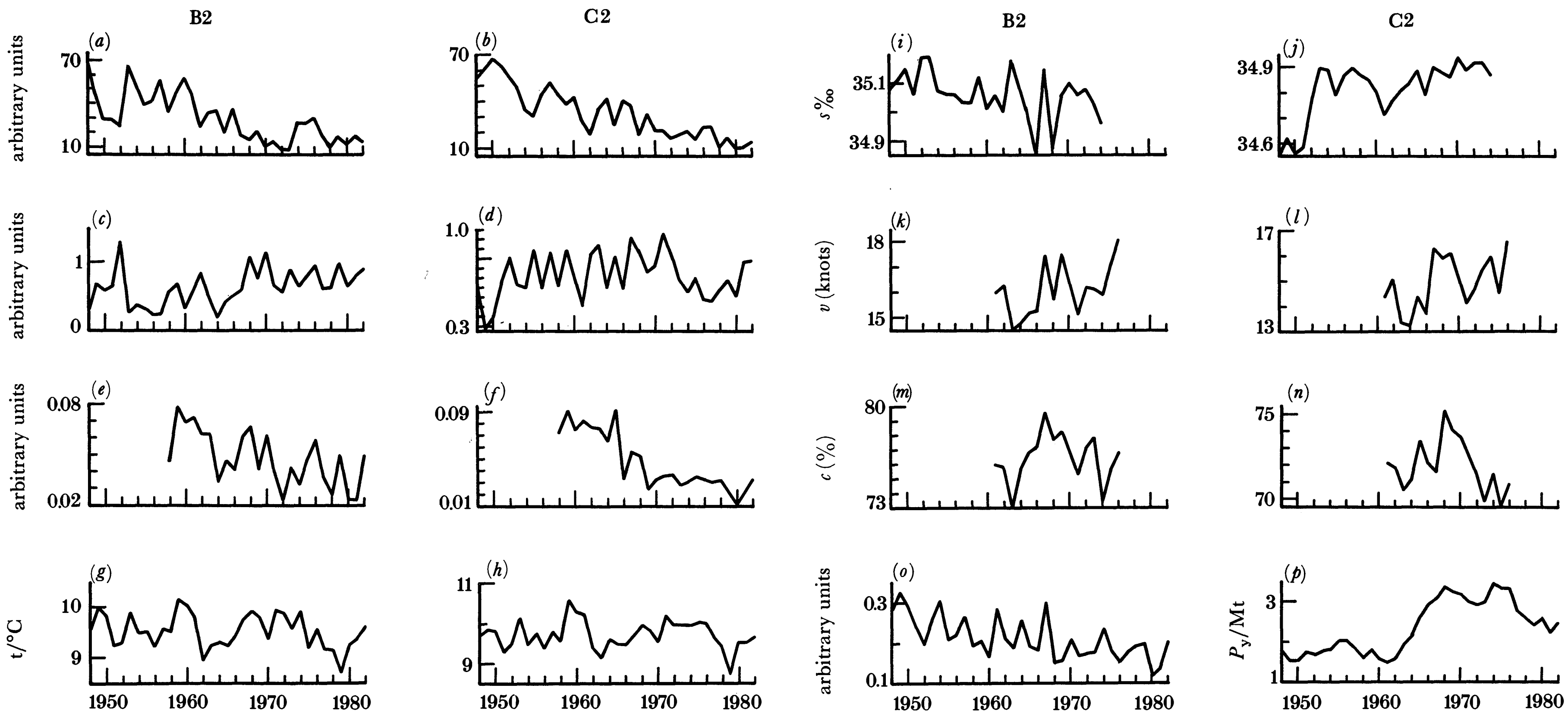

FIGURE 6. Graphs of annual means averaged for areas B2 and C2 for zooplankton biomass index (*a*, *b*), phytoplankton colour (*c*, *d*), diatom counts (*e*, *f*), sea surface temperature, *t* (*g*, *h*) and salinity, *s*, (*i*, *j*), scalar wind speed, *v* (*k*, *l*), and cloud cover, *c* (*m*, *n*) with plots of Lamb's westerly weather index (*o*) for the British Isles and total fish yields, P_y (*p*) from the North Sea.

−0.66***. Annual yields of North Sea fish are significantly correlated with the biomass index in both areas B2 and C2 (B2, −0.63***; C2, −0.66***). These inverse correlations may be fortuitous, but further suggest that grazing by fish may have had an increasing impact on the plankton in recent years. Alternatively, feedback loops from the plankton to the fish as suggested by Steele & Frost (1977) may exist, or both mechanisms may operate (see Reid 1984).

Plankton and hydrocarbon pollution

Information on the impact of oil on planktonic ecosystems was assessed by Davenport (1982) and further aspects have been reviewed by Corner (1978), Gray (1982), Johnston (1984) and Anon. (1985*b*). While laboratory and experimental mesocosm research document marked effects from hydrocarbon pollution at relatively high doses, there is little evidence for any permanent damage to open-sea pelagic environments from either prolonged low-level inputs of oil or large accidental spills. These conclusions must be qualified however, as there have been few field studies on plankton in the open-sea in relation to hydrocarbon concentrations outside major spill events. Moreover, Davies *et al.* (1980) have shown that zooplankton community structure is susceptible to oil at concentrations as low as 5–15 mg m^{-3}. This level is not much higher than the average concentration (4 mg m^{-3}) determined by Massie *et al.* (1985) in fluorescence surveys around the Brent, Beryl and Forties oilfields.

Hydrocarbons entering the marine ecosystem from offshore platforms come from three main sources (Read & Blackman 1980; Davies *et al.* 1984*b*): production water, displacement water and oil-based drilling muds. There is considerable variability and error in estimates of inputs from other anthropogenic sources (Whittle *et al.* 1982; Johnston 1984; Anon. 1985*b*), but there is a general consensus that inputs from rivers, the atmosphere, coastal refineries, sewage and shipping spills are far more important than sources from production platforms. The northwestern North Sea is a special case because the human population on the adjacent land has a low density and there is relatively little industrialization and minor river runoff with prevailing offshore winds. Here drilling muds were estimated to account for more than 50% of a total input of 18.4 kt hydrocarbon by Davies *et al.* (1984*b*). From 1981 to 1984 discharges of oil-based drilling muds increased from 5780 to 19600 t (U.K. Department of Energy, personal communication) and paralleled increasing production levels of oil. Any impact on the plankton from drilling muds is likely to be extremely localized because the hydrocarbons are bound to rock fragments and drop rapidly to the bottom close to platforms.

Conclusions

The plankton of the North Sea is a major renewable resource of which only a small fraction is harvested via fish for Man's use. As a source of food for the fish plankton is approximately five times as important as the benthos. Revised calculations of the energy flow from plankton to fish imply that the North Sea ecosystem is not as efficient as deduced by Steele (1974), although transfer efficiencies of at least 15% are still necessary to balance an energy budget of the ecosystem. Both empirical correlations and energy budget calculations suggest that changes in the composition and production of fish stocks may have partly caused an observed decline in the zooplankton of the North Sea by an increase in grazing pressure.

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North Sea oil and gas are natural biological products, concentrated energy sources formed from the breakdown of plankton which was incorporated into sediments of a palaeo-North Sea basin. Like its antecedents, present-day plankton is capable of synthesizing a variety of hydrocarbons (Anon. 1985*b*). We know remarkably little about the rates and processes behind the formation of natural oils in the plankton, although natural oil-slicks associated with plankton blooms are a frequent phenomenon and certain planktonic organisms may have a large lipid content. Edyvean & Sneddon (1985) drew attention to the effects of lipids and natural oils from plankton on the blockage of pores in oil-bearing strata and filters used to clean the large volumes of seawater used on oil platforms. There is a need for further research on natural oils in plankton as cultured planktonic organisms may prove to be an alternative source of oil in the future.

The size and value of annual North Sea primary production is emphasized in a comparison with annual hydrocarbon yields which shows primary production to be approximately equivalent to both gas and oil production in 1984. Estimated reserves and oil and gas yields to date for the North Sea represent approximately 100 years of primary production at the rate determined for the present day. Yet only a minute fraction of the plankton is incorporated into sediment each year and is thus available for hydrocarbon formation, emphasizing the long temporal period required for diagenesis, maturation and concentration.

The suggestion that there is no visible effect of hydrocarbon pollution on plankton should not lead to complacency. Sampling strategies for hydrocarbons in plankton and water have ignored their physical and biological dynamics; surveys at the surface may bear little relation to the 'real world' of the plankton. A trend for higher concentrations of hydrocarbons in the thermocline was noted for example by Johnston (1984). There are a number of processes, including biodegradation by microorganisms, which flush the plankton clear of contaminants to concentrate them in bottom sediments. Faecal pelletization (Prahl & Carpenter 1979) and absorption to particulates leads to a rapid sedimentation of hydrocarbons. In addition, there is accumulating evidence (Peinert *et al.* 1982; Davies & Payne 1984) that much of the spring bloom of diatoms settles rapidly to the bottom to provide direct food to the benthos. Reworking of hydrocarbons concentrated in bottom sediments by tidal action (Jenness & Duineveld 1985) or winter storms (Dickson & Reid 1978) may lead to repeated, temporary high doses of pollutants especially in the shallow, southern North Sea.

If oil pollution in the North Sea is taken as increasing in proportion with hydrocarbon production (see Read & Blackman (1980)) any impact might be reflected in long-term changes in the plankton. Zooplankton biomass and diatoms are inversely and significantly correlated with both oil and gas production curves for the North Sea at the 0.5% level in area C2. An absence of any correlation between zooplankton and oil in area B2 and the many relations that have been determined between hydrobiological variables and long-term changes in the plankton suggest that the correlation only reflects an inverse similarity in trends and no real relation. Moreover, recent results from the Continuous Plankton Recorder Survey provide evidence for a possible reversal of the downward trend in the zooplankton (Colebrook *et al.* 1984).

Many planktonic organisms form resting eggs and cysts as overwintering mechanisms; they contain high levels of natural oils and lipids as energy stores which may concentrate carcinogenic and mutagenic substances. Evidence from mesocosm experiments (Davies *et al.* 1980) suggests that copepod eggs are particularly susceptible to oil pollution. Colebrook (1984) has shown a link between overwintering in the North Sea and plankton abundance the following year. Plankton may therefore be more susceptible to pollution during winter months,

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Discussion

G. M. Dunnet (*Zoology Department, University of Aberdeen, U.K.*). In Dr Reid's energy budgets for the North Sea, he did not specifically refer to seabirds. Given that, in crude approximation, say 10 million seabirds may be feeding in the North Sea throughout the year (equal to *ca.* 10 kt live mass) with higher metabolic rate, and therefore food requirements, can they be considered to be negligible in terms of global budgets for the North Sea?

Because of recent winter mortalities of large numbers of emaciated (not oiled) guillemots in northern Scotland, and recent poor breeding success of kittiwakes in Shetland, and declines in kittiwake numbers, does Dr Reid consider it likely that these can be attributed to shortages of small pelagic fish?

Secondly, Dr Reid introduced his talk by showing how varied the hydrology of the North Sea is, and then he gave global values for the whole system. What is known about the patchiness in the planktonic communities dependent food chains? Could local shortages of food now be beginning to affect seabird populations?

P. C. Reid. In answer to the first part of Professor Dunnet's question, annual net production for seabirds in the North Sea is approximately 0.01 $kcal_{th}$ m^{-2} per year if it is taken as one third of Professor Dunnet's estimate of biomass and is thus an insignificant part of the total energy budget. Seabirds may, however, have an important impact on fish stocks as their food requirements are large. I have estimated this impact, using Professor Dunnet's estimate of biomass, in two ways, both of which give similar results.

First, I have applied the annual energy requirements for individual seabird species determined for Foula in the Shetlands by Furness (1978) to the total North Sea population, assuming the same porportions of biomass between species as in table 1 of Bourne (1983). Approximately 50% of North Sea seabirds as biomass (auks, gannets, terns, kittiwakes, shags, cormorants) feed almost totally on fish and most are selective for small fish. A small proportion of the diet of the remaining species, which are primarily scavengers, is also made up of fish. An estimated total of 60% (6 kt) of the seabird population feeding directly on fish is used here which equals a food requirement of 0.74 $kcal_{th}$ m^{-2} per year.

Second, by converting your biomass estimate to kilocalories (1.8 $kcal_{th}$ = 1 g live mass, a provisional conversion factor from Dunn & Brisbin (1980), and assuming the population eats fifty times its weight in a year (from Bourne (1983), considered an underestimate by Furness (1984)), and again considering 60% of the population as direct feeders on fish, a food requirement of 0.92 $kcal_{th}$ m^{-2} per year was determined.

The greater of these two estimates represents approximately 10% of the annual mean fish production in the period 1965 to 1969 and 13% in the period 1978 to 1982. Most of this predation would, however, have been on small pelagic species and would have represented 66% of the production of these species in 1965 to 1969 (a period when both stocks and fishing mortality were small) or a more realistic 19% in the period 1978 to 1982 when small 'industrial' fish species formed a larger and relatively more important component of total fish stocks. Seabirds may therefore have a major impact on North Sea fish stocks, an impact that is likely to increase if stocks of small pelagic species continue to decline.

To answer the second part of Professor Dunnet's question, guillemots and kittiwakes constitute approximately 40% of the total seabird biomass of the North Sea and have a diet that is primarily made up of small fish. Their population changes and breeding success are therefore likely to be closely linked to changes in fish stocks (Coulson & Thomas 1985; Birkhead 1986). Sprats, for example, which are a major winter food for kittiwakes (Coulson & Thomas 1985) have shown a major decline in the total North Sea stock due to poor recruitment (Anon. 1985); this decline has been especially evident off the east coast of Scotland since 1979 (McKay 1984).

Thirdly, little is known of the scales of variability and temporal change in patchiness of the plankton in the North Sea because of the logistics of sampling. Sampling by the Continuous Plankton Recorder smoothes out the effects of patchiness; trends determined from this data are consistent over the whole of the North Sea. Therefore any shortage of food linked to planktonic changes is likely to be experienced over a large area. Although there may be variability in sizes of local fish stocks between individual years, longer-term changes are also evident over the whole of the North Sea.

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