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Biological Oceanography Committee

FURTHER OBSERVATIONS ON ENERGY FLOW THROUGH THE MARINE FOOD CHAIN

by

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ENGLISH ABSTRACT (1)

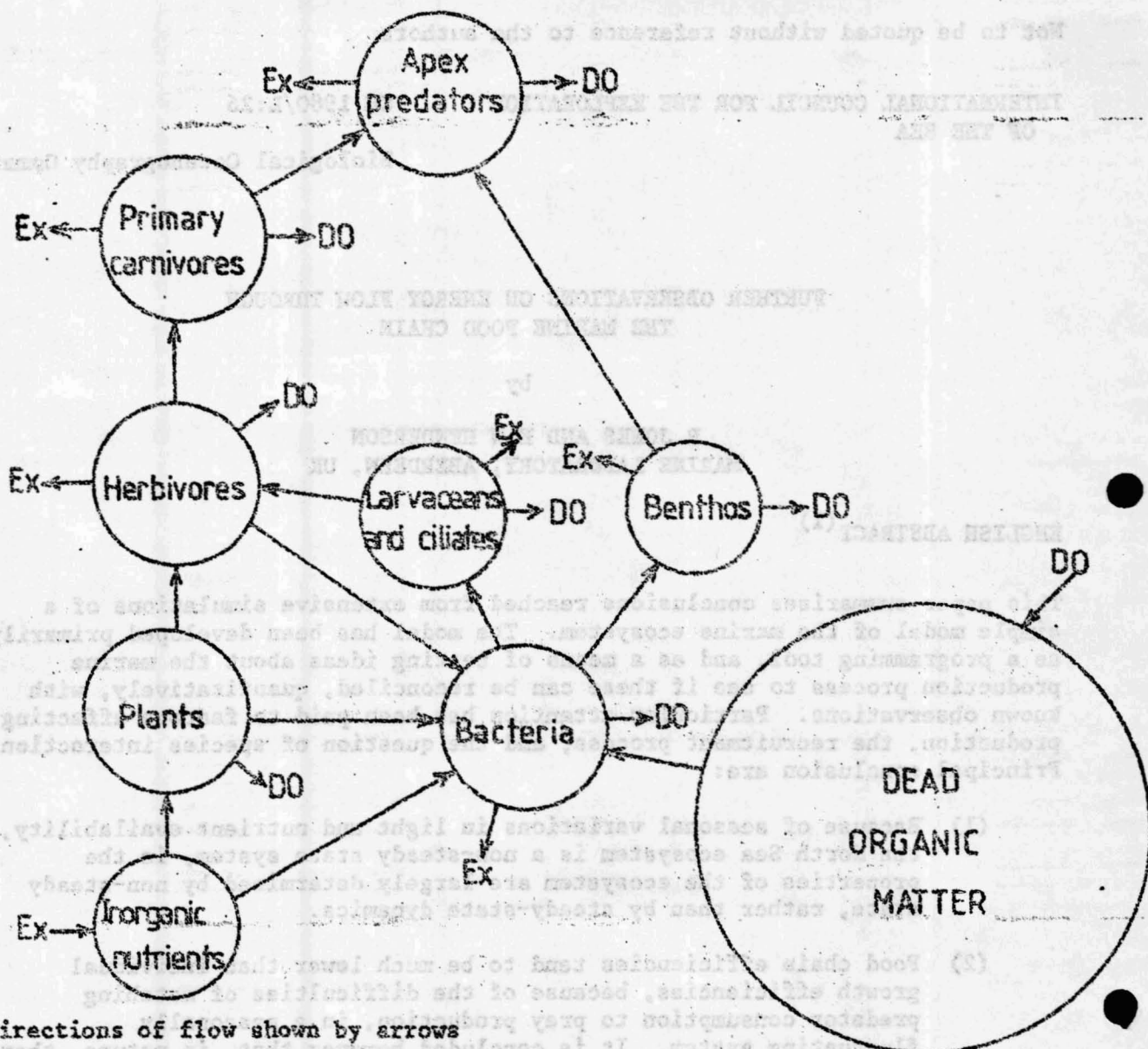
This paper summarises conclusions reached from extensive simulations of a simple model of the marine ecosystem. The model has been developed primarily as a programming tool, and as a means of testing ideas about the marine production process to see if these can be reconciled, quantitatively, with known observations. Particular attention has been paid to factors affecting fish production, the recruitment process, and the question of species interactions. Principal conclusion are:

- (1) Because of seasonal variations in light and nutrient availability, the North Sea ecosystem is a non-steady state system, i.e. the properties of the ecosystem are largely determined by non-steady state, rather than by steady-state dynamics.
- (2) Food chain efficiencies tend to be much lower than individual growth efficiencies, because of the difficulties of matching predator consumption to prey production, in a seasonally fluctuating system. It is concluded however that, in nature, there are many adaptations that have the effect of making transfer efficiencies higher than those generated in simple models.
- (3) Fish recruitment (for all species combined) tends to be almost independent of fish egg production (provided egg production is not zero).
- (4) Some suggestions are made about ways of reconciling co-existence of species with the observation that food sharing is commonplace.

(1) French abstract at end of paper

COMPONENTS OF THE ECOSYSTEM

1. A GENERALISED MARINE FOOD WEB (NITROGEN UNITS)



Directions of flow shown by arrows

Ex Flow of excretory products to inorganic nitrogen pool

DO Flow of dead material to dead organic matter pool

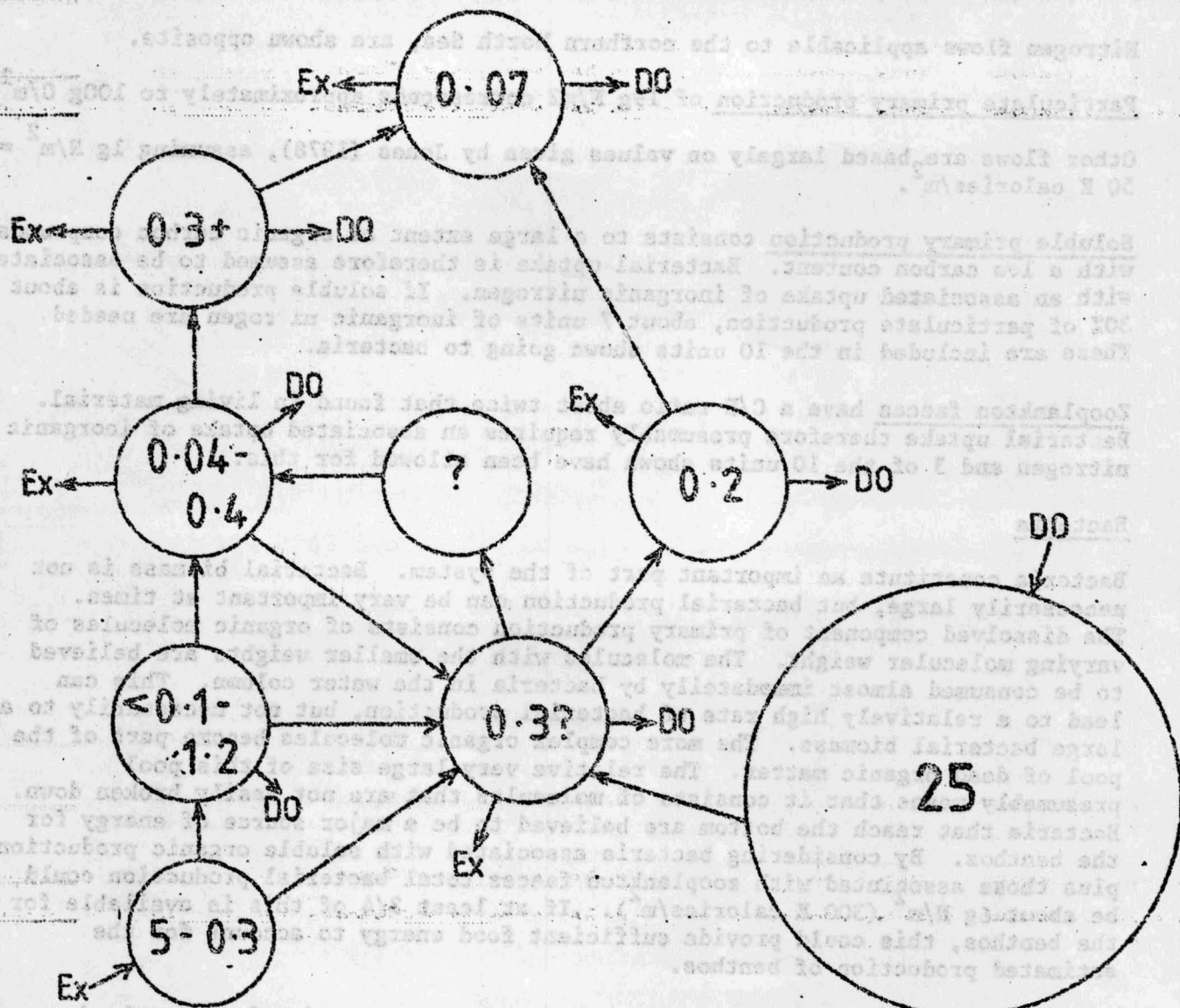
For simplicity, nitrogen in the marine ecosystem can be subdivided into 9 compartments. Living matter makes up a simple web, consisting of two food chains (pelagic and benthic), linked at the top by apex predators (such as adult demersal fish) and at the bottom by bacteria.

Dead material occurs as inorganic nutrient and organic matter. Both are found in the water column and in the bottom sediments. Dead organic matter occurs both as soluble and as particulate material.

A small selection of references from the very extensive literature on community dynamics is given at the end of the paper.

COMPONENTS OF THE ECOSYSTEM

2. Nitrogen Levels (northern North Sea)



Nitrogen levels are detailed in Table 1 and summarised above in units of gN/m^2 .

Important points to note are:

- living matter makes up 1% or less of the total (Fenchal and Jorgensen 1977 give 2% as a general figure);
- by the end of the spring bloom, the inorganic nitrogen concentration in the top 40m has dropped by nearly $5g N/m^2$. After the end of the bloom the increase in living plant and animal material is not more than about $2g N/m^2$ however. The remaining $3g N/m^2$ is presumably distributed between the bacterial food chain and the pool of dead organic matter.

Nitrogen Flows

Nitrogen flows applicable to the northern North Sea, are shown opposite.

Particulate primary production of 19g N/m^2 corresponds approximately to 100g C/m^2 .

Other flows are based largely on values given by Jones (1978), assuming $1\text{g N/m}^2 = 50\text{ K calories/m}^2$.

Soluble primary production consists to a large extent of organic carbon compounds with a low carbon content. Bacterial uptake is therefore assumed to be associated with an associated uptake of inorganic nitrogen. If soluble production is about 30% of particulate production, about 7 units of inorganic nitrogen are needed. These are included in the 10 units shown going to bacteria.

Zooplankton faeces have a C/N ratio about twice that found in living material. Bacterial uptake therefore presumably requires an associated uptake of inorganic nitrogen and 3 of the 10 units shown have been allowed for this.

Bacteria

Bacteria constitute an important part of the system. Bacterial biomass is not necessarily large, but bacterial production can be very important at times. The dissolved component of primary production consists of organic molecules of varying molecular weight. The molecules with the smaller weights are believed to be consumed almost immediately by bacteria in the water column. This can lead to a relatively high rate of bacterial production, but not necessarily to a large bacterial biomass. The more complex organic molecules become part of the pool of dead organic matter. The relative very large size of this pool presumably means that it consists of molecules that are not easily broken down. Bacteria that reach the bottom are believed to be a major source of energy for the benthos. By considering bacteria associated with soluble organic production, plus those associated with zooplankton faeces total bacterial production could be about 6g N/m^2 ($300\text{ K calories/m}^2$). If at least $3/4$ of this is available for the benthos, this could provide sufficient food energy to account for the estimated production of benthos.

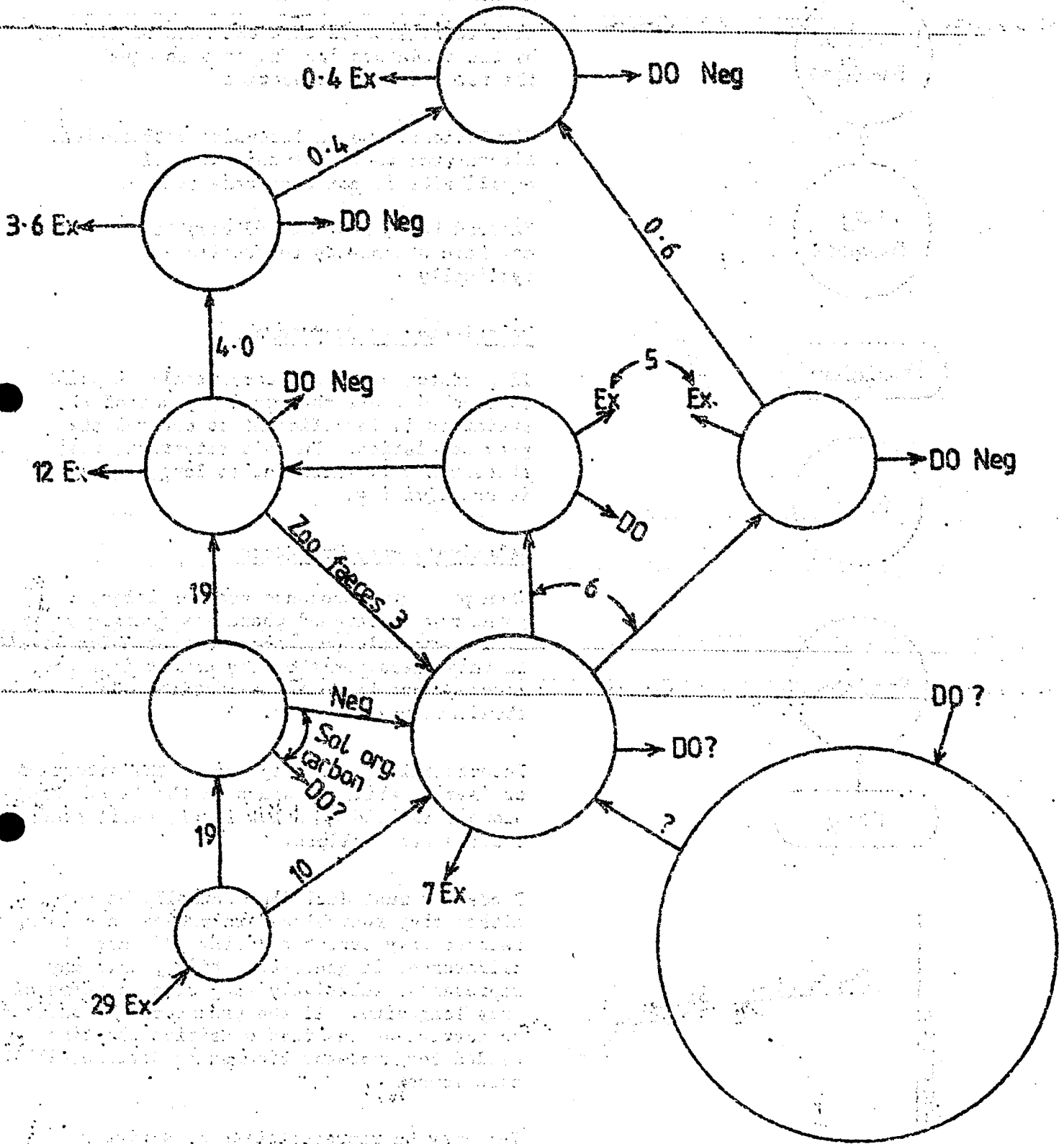
Adult demersal fish receive food energy from two sources i.e. via the pelagic food chain (2 steps) and via the benthos chain (also 2 steps).

Recycling

All nitrogen within the ecosystem must eventually be recycled. Animal and bacterial excretion within the water column recycles nutrient that can be utilised directly by plants. Animal and bacterial excretion within the sediment releases nutrient that cannot be used by plants until it is made available by upwelling. In the North Sea, zooplankton and fish alone excrete about $16\text{g N/m}^2\text{ yr}$ which is a little more than one half of the $29\text{g N/m}^2\text{ yr}$ that flows to the inorganic nitrogen pool. In the central Pacific, where much of the bacterial production occurs within the water column, the proportion of nitrogen recycled directly to the plants may be much larger (Cushing 1979).

COMPONENTS OF THE ECOSYSTEM

3. Nitrogen Flows (Northern North Sea) (Units $g/N/m^2/yr$)



Neg - Negligible = <0.1

MODELLING ENERGY FLOW 1. SOME PROPERTIES OF A SIMPLE FOOD CHAIN

The Concept of Stability

Here it is assumed that the rate of feeding by the predators just happens to equal the rate of prey production.

Simulations, and an extensive mathematical literature, show that this kind of equilibrium is not necessary stable.

Instead both predator and prey biomasses may have a tendency to oscillate cyclically.

Relatively Few Predators

If predator biomass becomes small, a point is reached where the grazing power of the predators is insufficient to control the prey population. In this situation, prey abundance will increase, so long as its food is not limiting.

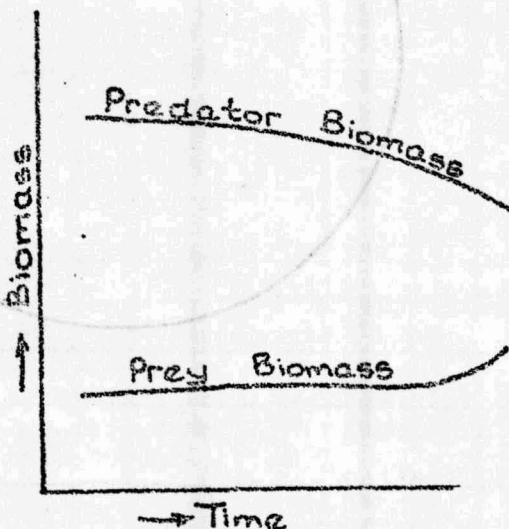
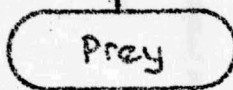
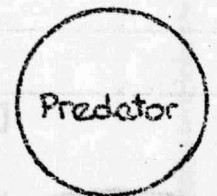
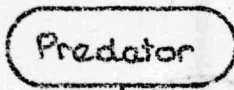
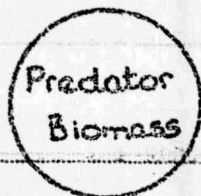
Relatively Many Predators

When predator abundance becomes large, a point may be reached where its grazing power is able to hold prey abundance at a low level. In this situation the prey cannot increase, however much food it has, until predator abundance has declined.

Theoretically, this represents the situation of 'semi stability' shown on the left. Prey biomass is held at a low level, until predator biomass has declined.

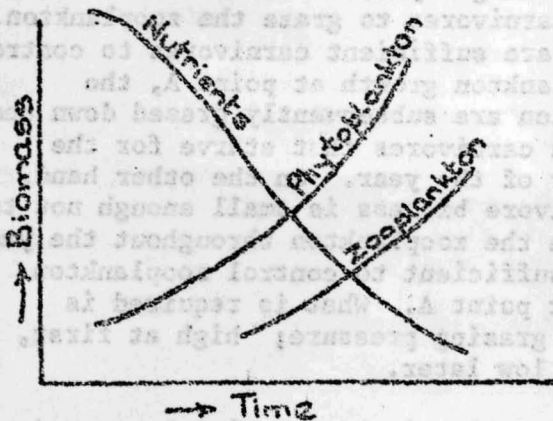
Predators must decline eventually because either they themselves are preyed on or simply because they starve and die. Because of differences in generation times, this may represent a relatively long time in terms of prey longevity. If the predators are adapted to survive at low food densities the time needed for predator biomass to decline will be even longer.

This may be representative of a winter situation in temperate waters. It is hardly representative of a summer situation however. During the productive period various adaptations are evident which have the effect of counteracting or avoiding this kind of situation.



MODELLING ENERGY FLOW 2. THE SPRING BLOOM AND THE TENDENCY TO 'OVERPRODUCE'

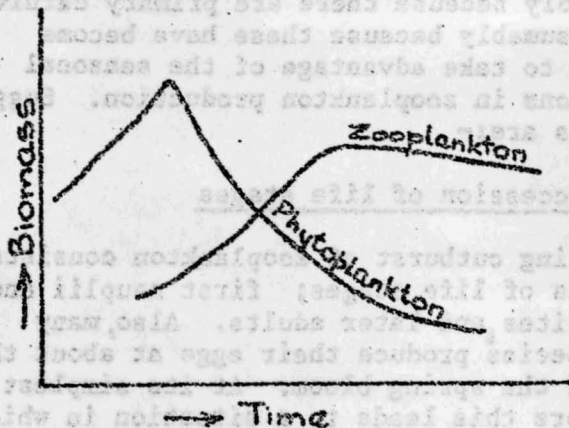
Primary production in the North Sea is not a steady-state process. Instead, it is dominated by seasonal variations in the availability of light and nutrients and a striking theoretical feature of such a system is a tendency to 'overproduction' of the top trophic level.



Beginning of the Spring Bloom

Simulation of the beginning of the spring bloom is comparatively simple. Nutrients start at a relatively high level and are rapidly depleted. Phytoplankton biomass starts from a low level and grows exponentially at first until growth is checked by nutrient limitation. Zooplankton biomass also starts from a low level and also grows exponentially at first until growth is checked by the depletion of phytoplankton.

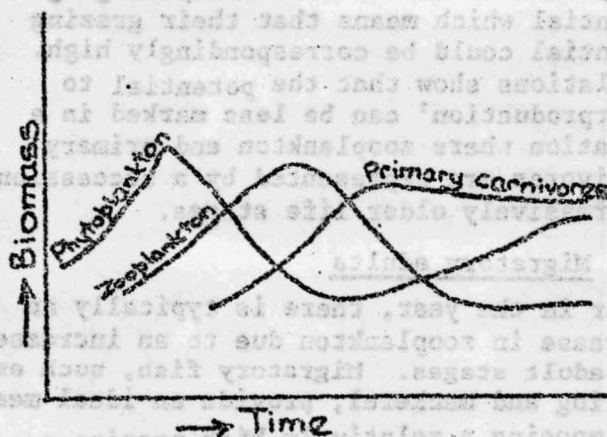
In the North Sea, phytoplankton biomass attains about 1.2 g N/m^3 at the end of the bloom on average. Actual biomasses are very variable however and sometimes reach 5 g N/m^3 (Steele & Henderson 1977).



End of the Spring Bloom

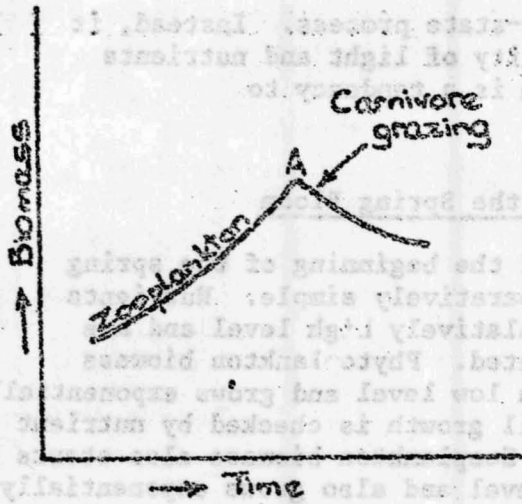
Theoretically, zooplankton biomass can achieve a relatively high biomass at the end of the spring bloom. In the North Sea, the maximum biomass is about 0.7 g N/m^3 but individual sample values up to twice this amount have been recorded (Steele & Henderson 1977).

Theoretical simulations of the spring bloom frequently lead to a zooplankton biomass large enough to graze the phytoplankton to a relatively low level. Phytoplankton cannot then recover until the zooplankton have decreased to some extent.



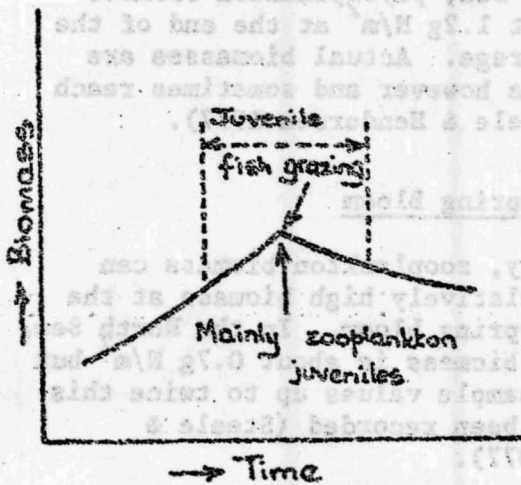
If there are higher trophic levels the theoretical outcome is still the same, i.e. the tendency is for the biomass of the top trophic level to become large enough to graze down and, 'hold down' the biomass of its prey. In the diagram, primary carnivores graze zooplankton down to a low level, permitting phytoplankton to increase until it is nutrient limited.

Predation on Zooplankton - simple theory



To prevent 'overproduction' of zooplankton, for example, it is necessary to impose an appropriate level of predation on the zooplankton at point A. The interesting feature of the simulations is that this cannot necessarily be achieved theoretically, simply by introducing a particular biomass of pelagic carnivores to graze the zooplankton. If there are sufficient carnivores to control the zooplankton growth at point A, the zooplankton are subsequently grazed down and it is the carnivores that starve for the remainder of the year. On the other hand, if the carnivore biomass is small enough not to overgraze the zooplankton throughout the year, it is insufficient to control zooplankton growth at point A. What is required is variable grazing pressure; high at first, becoming low later.

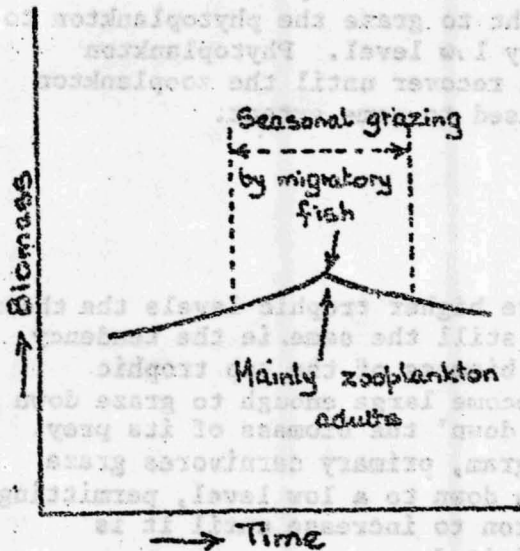
Predation on Zooplankton - what happens in nature



An 'overproduction' of zooplankton followed by fall-out to the sediment may have been the situation in former times when the North Sea petroleum reserves were being formed. This is not the situation today, however, presumably because there are primary carnivores and presumably because these have become adapted to take advantage of the seasonal variations in zooplankton production. Suggested examples are:-

3.1 Succession of life stages

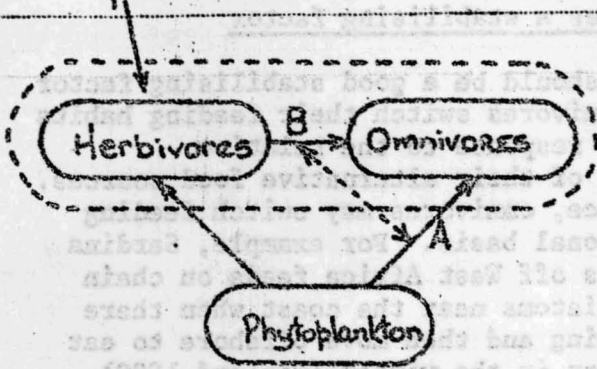
The spring outburst of zooplankton consists of a series of life stages; first nauplii and copepodites, and later adults. Also, many fish species produce their eggs at about the time of the spring bloom. At its simplest therefore this leads to a situation in which there is a succession of zooplankton life stages, coinciding more or less with a succession of fish life stages. Fish larvae and juveniles have a relatively large growth potential which means that their grazing potential could be correspondingly high. Simulations show that the potential to 'overproduction' can be less marked in a situation where zooplankton and primary carnivores are represented by a succession of progressively older life stages.



3.2 Migratory adults

Later in the year, there is typically an increase in zooplankton due to an increase in the adult stages. Migratory fish, such as herring and mackerel, provide an ideal means of imposing a relatively high grazing pressure on these zooplankton for a relatively short period of time.

Zooplankton

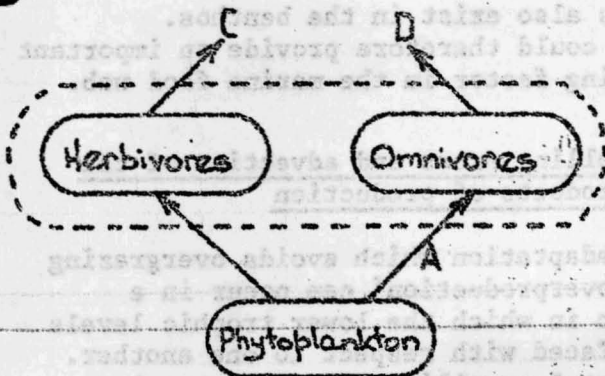


3.3 Omnivory in zooplankton

Another important adaptation is omnivory. Omnivores have the capacity to switch feeding from one trophic level (A) to another (B).

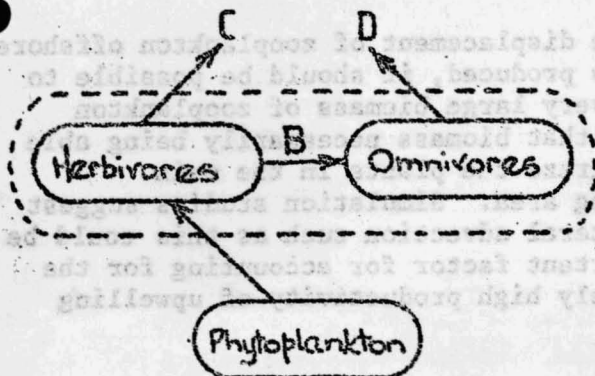
Seasonal variations in omnivory could lead to significant variations in the grazing pressure on the herbivore component of the zooplankton.

Omnivores as herbivores



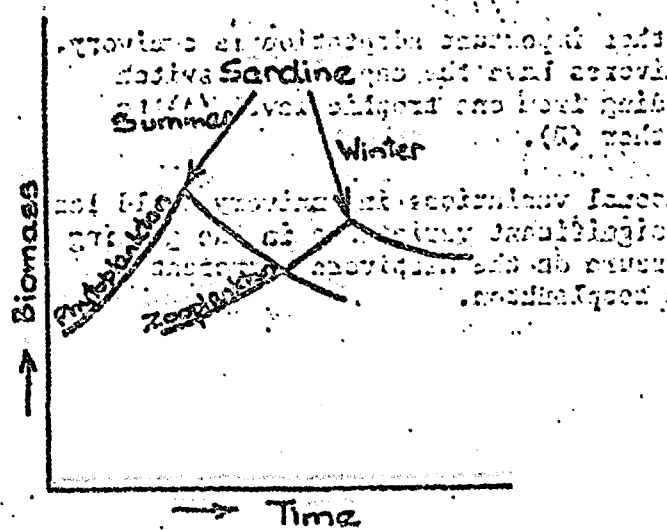
As long as omnivores acts as herbivores (Flow A) there is a maximum of grazing pressure on the phytoplankton. This depicts a situation of maximum grazing pressure on phytoplankton and maximum tendency for zooplankton biomass to increase.

Omnivores as carnivores



If omnivores act wholly as carnivores (Flow B) grazing pressure on the phytoplankton should be reduced to a minimum. This depicts a situation of minimum grazing pressure on phytoplankton and minimum tendency for zooplankton biomass to increase.

Omnivory as a stabilizing factor

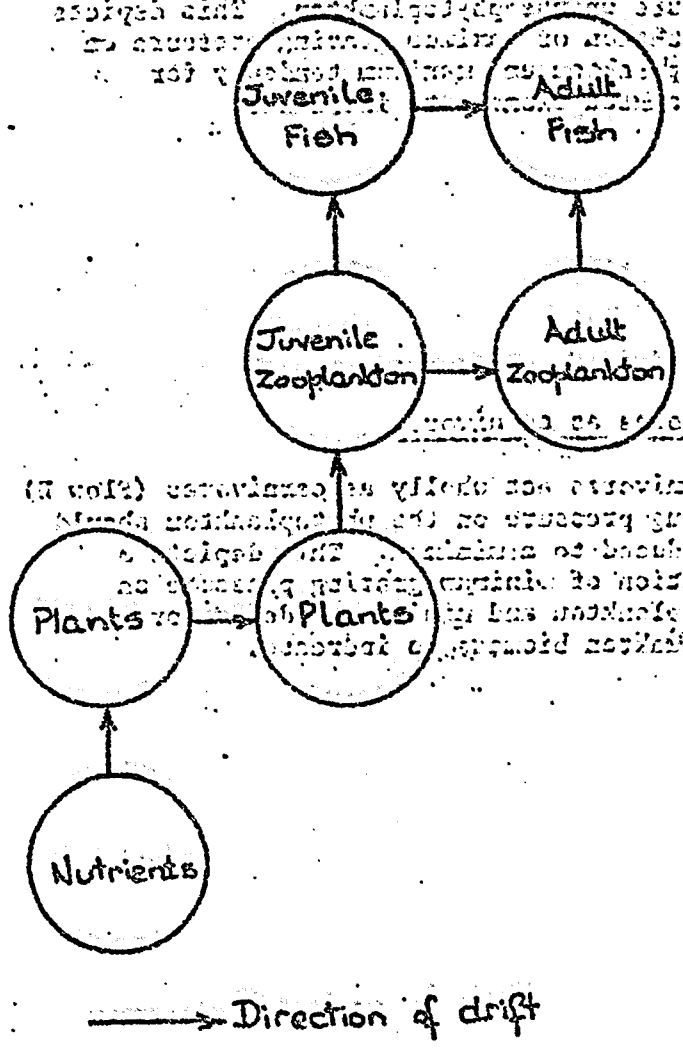


Omnivory should be a good stabilizing factor if the carnivores switch their feeding habits in direct response to the relative abundance of their alternative food sources. In practice, omnivores may switch feeding on a seasonal basis. For example, *Sardina pilchardus* off West Africa feeds on chain forming diatoms near the coast when there is upwelling and then move offshore to eat zooplankton in the winter (Nieland 1960).

Simulations show that this is not likely to be such an effective way of achieving perfect stability. However it should still have a considerable capacity to reduce the amplitude of seasonal fluctuations in zooplankton.

Omnivores also exist in the benthos. Omnivory could therefore provide an important stabilizing factor in the marine food web.

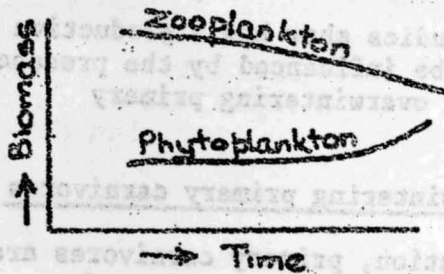
Upwelling areas and advection of the products of production



Another adaptation which avoids overgrazing due to 'overproduction' can occur in a situation in which the lower trophic levels are displaced with respect to one another. In a coastal upwelling area for example, such as that off the coast of N.W. Africa, primary production is most intense close to the coast whilst the greatest zooplankton biomass is near the edge of the shelf. (Blackburn 1976)

With the displacement of zooplankton offshore as it is produced, it should be possible to have a very large biomass of zooplankton without that biomass necessarily being able to overgraze the plants in the main upwelling area. Simulation studies suggest that lateral advection such as this could be an important factor for accounting for the relatively high productivity of upwelling areas.

MODELLING ENERGY FLOW 4. THE AUTUMN BLOOM

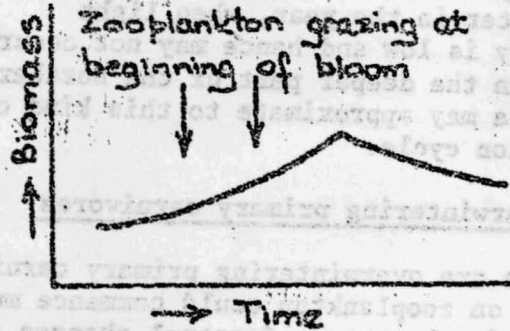


Beginning of bloom

An autumn bloom can occur if zooplankton biomass has declined (or been reduced by grazing) to a level at which phytoplankton growth is possible. An adequate nutrient flow is also necessary.

Increase in phytoplankton biomass

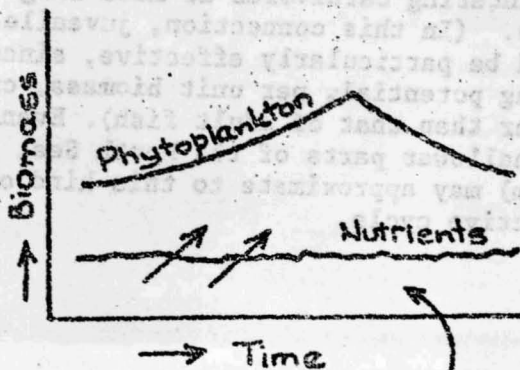
The autumn bloom is likely to differ from the spring bloom because of the existence of a not inconsiderable biomass of zooplankton. Because of zooplankton grazing, the peak in phytoplankton production is likely to be much smaller than the peak attainable during the spring bloom.



An important implication is that a small phytoplankton increase in autumn, may be an indication of just as big an increase in primary production, as a much bigger peak in spring.

Nutrient availability at the beginning of the bloom

At the beginning of the spring bloom, there is typically a high concentration of inorganic nutrients. At the beginning of the autumn bloom on the other hand the nutrient concentration in the euphotic zone is likely to be low.



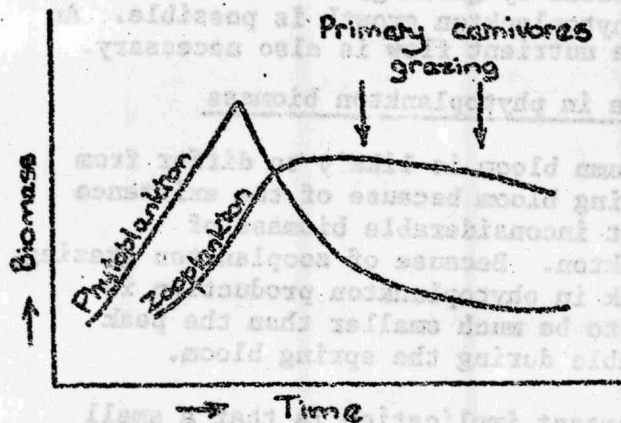
Nutrient re-cycling must compensate for low nutrient concentration

Simulations suggest that to make the productivity of the autumn bloom as large as that of the spring bloom, it is necessary to compensate for this, by increasing the rate of nutrient recycling in the autumn. The increase in temperature, that takes place in the North Sea between spring and autumn might be one way of achieving this.

The Autumn Bloom (continued)

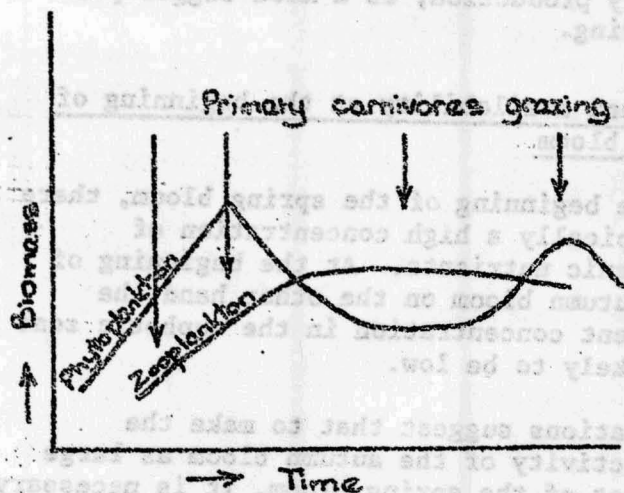
Primary carnivores

Simulation studies show how a productive system might be influenced by the presence or absence of overwintering primary carnivores.



Without overwintering primary carnivores

In this situation, primary carnivores are produced after the spring blooms of phyto- and zooplankton. Zooplankton biomass becomes theoretically large, relatively early in the cycle, and then declines gradually. An autumn bloom may not be possible until later in the year, when light intensity is low and hence may not occur. Events in the deeper part of the northern North Sea may approximate to this kind of production cycle.



With overwintering primary carnivores

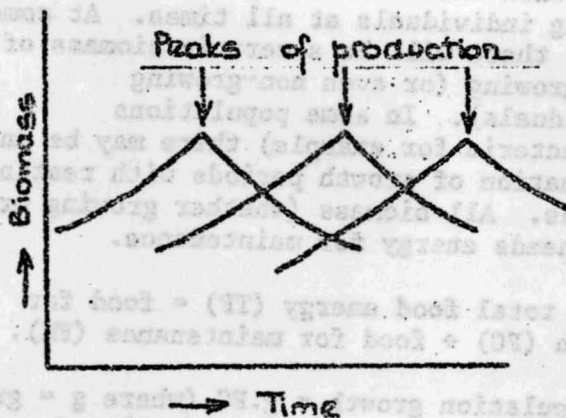
If there are overwintering primary carnivores, grazing on zooplankton could commence much earlier in the year. Seasonal changes in zooplankton biomass are theoretically less predictable and a peak (if recognisable) may occur relatively later in the year. An autumn bloom can be produced theoretically, provided the grazing potential of the overwintering carnivores is made large enough. (In this connection, juvenile fish should be particularly effective, since their grazing potential, per unit biomass, can be greater than that of adult fish). Events in the shallower parts of the North Sea, (<100m) may approximate to this kind of productive cycle.

MODELLING ENERGY FLOW 5. FEEDING STRATEGIES

Production, in a seasonally perturbed ecosystem, is likely to consist of a sequence of peaks of prey production. Predator feeding strategies might exhibit various adaptations therefore - ie:

4.1 Adaptation to feed at high prey density

One feeding adaptation would be to be adapted to feed at the peaks of prey production. This should provide the advantage of a high concentration of food. Possible examples are:

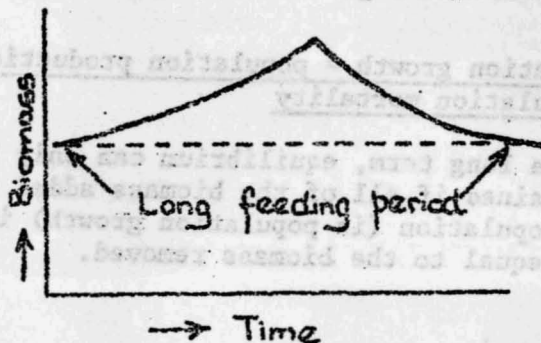


(a) Migratory feeding. Fish like herring and mackerel for example might be adapted to being in the right place at the right time ie migratory feeders could be adapted to benefit from predictable peaks in prey abundance that happen to occur seasonally in different places at different times.

(b) Opportunistic feeding. Other species may be able to take advantage of any temporary increase in prey abundance whether it was predictable or not, eg seasonal feeding on sandeels or euphausiids by demersal fish.

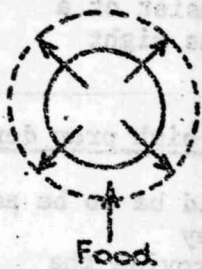
(c) Omnivory. Changing trophic level, enables an animal to exploit successive peaks in prey abundance and hence to benefit from an increased prey abundance for a prolonged period.

4.2 Adaptation to feed at low prey densities



An alternative strategy would be to be adapted to feed at low prey densities. This should provide the advantage of a longer feeding period. A possible example might be Norway Pout, which eats zooplankton at times when zooplankton abundance is too low for herring and mackerel feeding.

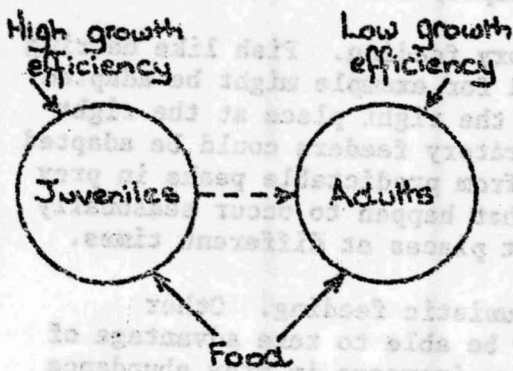
MODELLING ENERGY FLOW 6. TRANSFER EFFICIENCIES



Growth =
30% food

Growth efficiency of an individual and of a population

In rapidly growing individuals, particularly juveniles, assimilated energy can be converted into growth with an efficiency of as much as 30%. Yet, the growth efficiency of an entire population will be less than this.



There are several reasons, one being that no population consists wholly of rapidly growing individuals at all times. At some times, there will be a certain biomass of slow growing (or even non-growing individuals). In some populations (eg bacteria for example) there may be an alternation of growth periods with resting periods. All biomass (whether growing or not) needs energy for maintenance.

Thus, total food energy (TF) = food for growth (FG) + food for maintenance (FM).

If population growth = $g \cdot FG$ (where g = growth efficiency of growing individual). Growth efficiency of a population

$$= \text{population growth} / \text{total food consumed}$$

$$= g \cdot FG / (FG + FM) = g / (1 + FM/FG)$$

population growth efficiency must be smaller than individual growth efficiency therefore.



For equilibrium
production =
growth

Population growth = population production = population mortality

In the long term, equilibrium can only be maintained if all of the biomass added to the population (ie population growth) is just equal to the biomass removed.

TRANSFER EFFICIENCIES (Cont'd)

Effect of 'fluctuations' in biomass on transfer efficiencies

Fluctuation in biomass also tend to make transfer efficiencies small.

Effects on transfer efficiency

Under ideal conditions, the predators just take up the prey production. The process of energy transfer up the food chain, and hence transfer efficiency, should be relatively high in this situation.

Relatively few predators

There can be prey production that is not taken up by the next trophic level because there are not enough predators. Transfer efficiency is therefore reduced.

Food induced mortality

If there is food induced mortality that is not taken up by grazing, individuals may be lost (to higher trophic levels) by dying and falling to the bottom. This will tend to reduce transfer efficiencies to higher trophic levels.

Omnivory

Omnivory tends to counteract instability. However it does so at the expense of the transfer of energy to higher trophic levels.

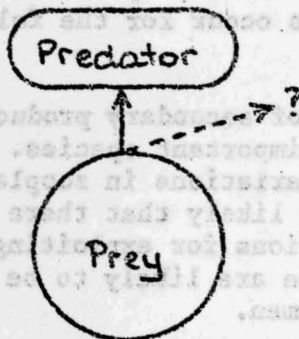
Consequences of fluctuation in biomass

An important consequence of fluctuation in biomass, or of any tendency towards this, is therefore to make the average rate of transfer of energy up the food chain smaller than it theoretically could be under ideal conditions.

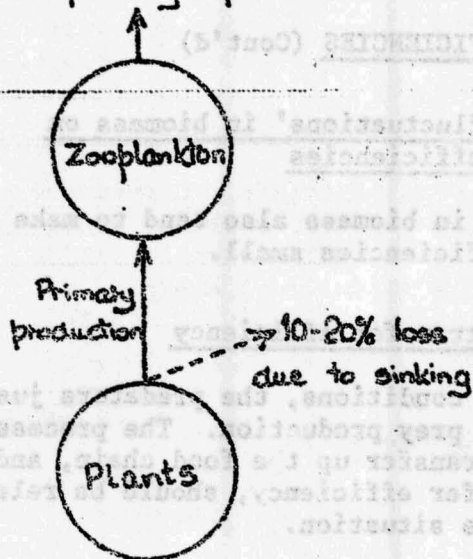
Energy for fish production

The energy available for fish production will depend largely on:

- (1) the rate of primary production;
- (2) the efficiency of transfer of energy up the food chain.



Secondary production =
15% primary production



Rate of primary production

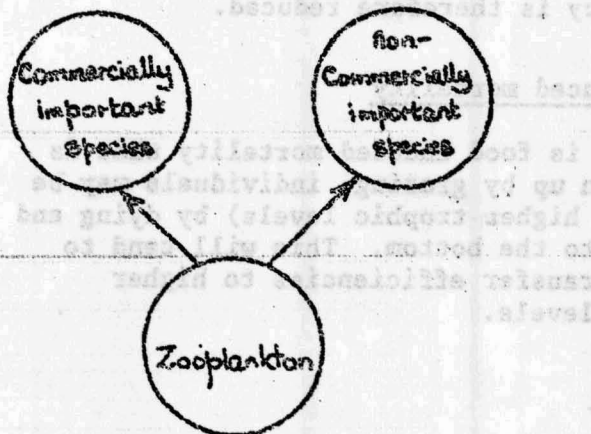
Seasonal variations in the relative concentrations of nutrients, phytoplankton and zooplankton, will tend to make the average rate of primary production smaller than it theoretically could be under ideal conditions.

Transfer of primary production to secondary production

The efficiency of transfer of primary production to secondary production depends largely on the extent to which all of the primary production is grazed. If, for example, 80-90% is grazed on average, the transfer efficiency of primary to secondary production could be about 15%.

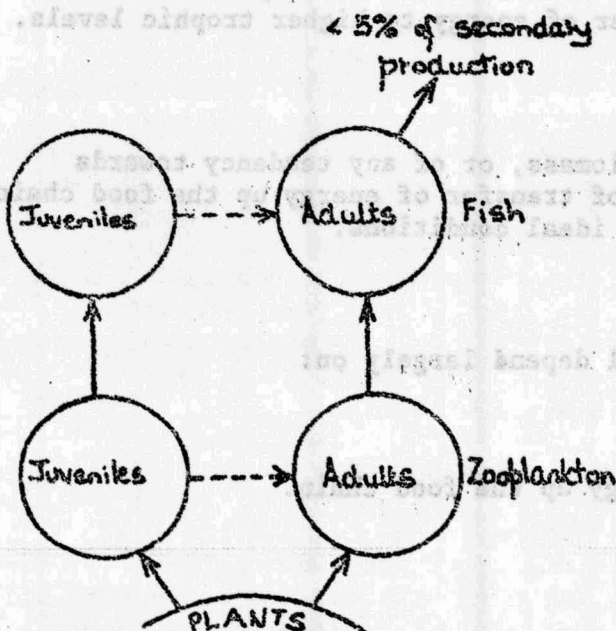
Transfer of secondary production into commercial fish production

The proportion of secondary production going into commercial fish production could be quite low. Losses occur for the following reasons:



(1) Consumption of secondary production by non-commercially important species. Because of the seasonal variations in zooplankton production, it is likely that there are a number of adaptations for exploiting it. Only some of these are likely to be due to species of importance to man.

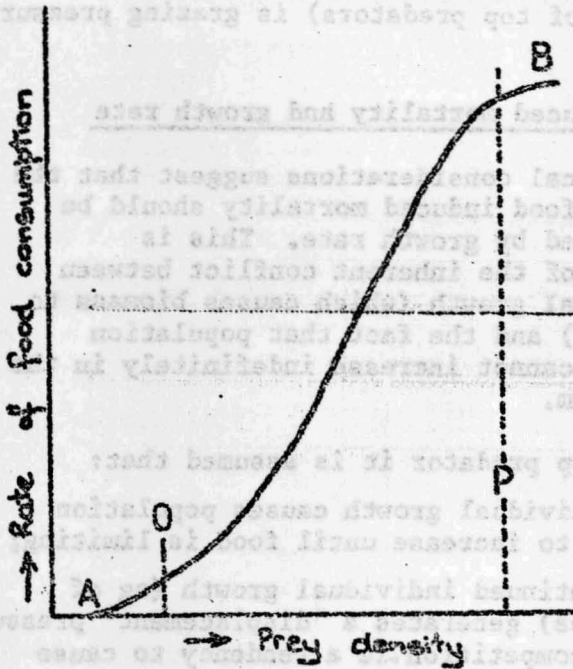
(2) A relatively large part of the secondary production consists of juvenile zooplankton that may be largely consumed by juvenile primary carnivores. If only adult fish production is considered, the proportion of secondary production converted to adult fish production may be as low as 5% or less.



Production of adult demersal fish

Demersal fish production depends partly on the pelagic food chain (for the early life history stages) and partly on the benthos food chain. It is interesting to note (Table 2) how, within the ICES and ICNAF areas, the proportion of demersal feeders in commercial fish landings, declines with decreasing latitude. This may be a consequence of the fact that the probability of bacteria and zooplankton faeces reaching the bottom, is something that is likely to decrease with increasing temperature.

Food for an individual predator



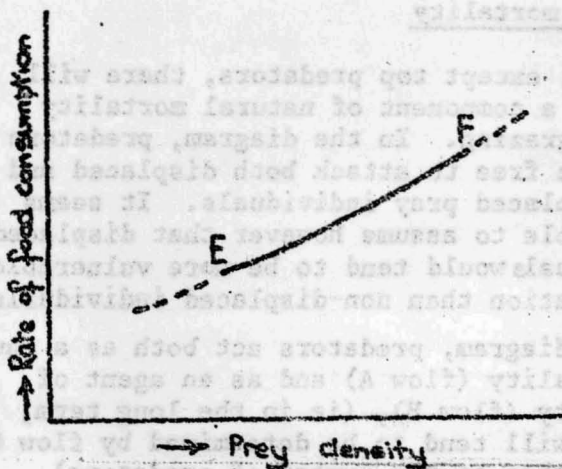
As prey density increases, experimental evidence shows that the rate of food intake by an individual predator can be expected to increase. (Curve A B).

At high prey densities ($> p$), a predator should be able to eat as much as it chooses ie food will be effectively unlimited. At low prey densities ($< p$) a predator will not be able to maintain itself even, and will be in danger of starving.

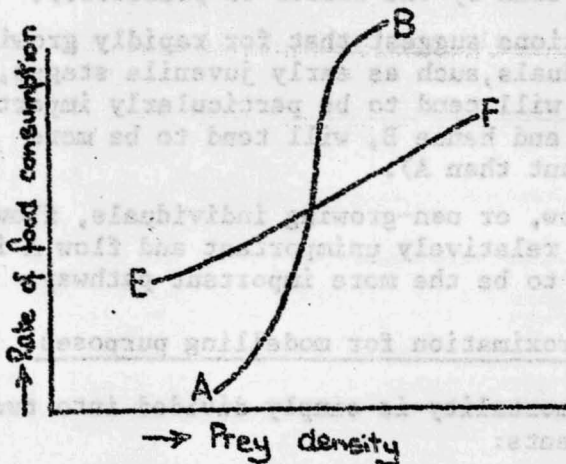
At very high prey densities, there will be more than enough food available for growth, maintenance and reproduction. Predator biomass should then be able to increase.

At very low prey densities, there will be insufficient food, even for maintenance, and predator biomass can be expected to decrease.

Food for a population



Theoretical considerations suggest that for an entire population, the relationship between prey density and rate of feeding is more likely to follow a curve such as E F than a curve such as A B. This is to be expected if the prey density is patchy (ie non-homogeneous). Thus, even at high prey densities, there may be some predators that happen to be in regions of low food density. Equally, even at low food densities there are likely to be some predators that happen to be in regions of high food density. The gradient of E F therefore is likely to be less steep than the gradient of A B.



Implications for stability

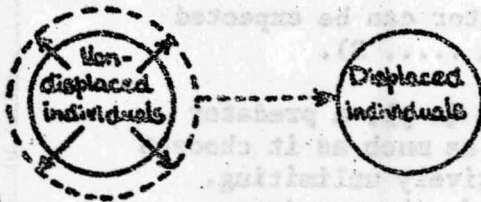
Simulations show that a much more stable food web can be obtained by using feeding response curves such as E F. This is because, when A B is used, relatively small variations in prey density have relatively large effects on predator responses. On the other hand, when E F is used, the predator response changes more gradually and stable solutions are found to be theoretically possible.

Patchiness is more likely to confer stability, than instability, on the ecosystem as a whole therefore.

In practice, complete stability is unlikely. Quite apart from seasonal perturbations, there may be variations in the degree of nutrient upwelling from one year to the next. The closest approach to stability may therefore simply be a situation in which the component parts of the ecosystem fluctuate cyclically and continuously.

MODELLING ENERGY FLOW 8. MORTALITY RATES

Natural mortality is likely to have two principal causes. One is food deprivation. The other, (except in the case of top predators) is grazing pressure from higher trophic levels.



Growth, when food becomes limiting generates a "displacement" pressure

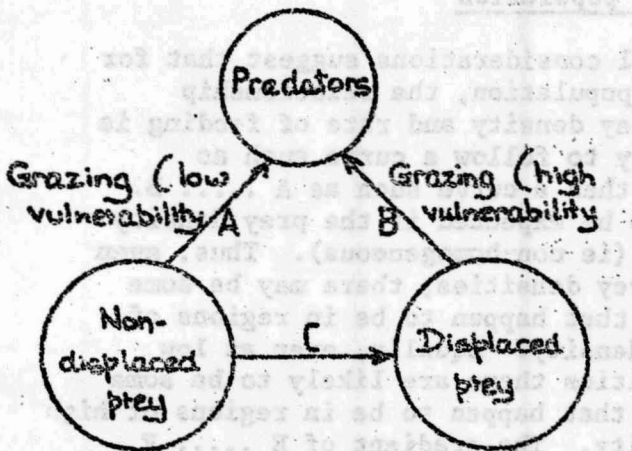
Food Induced mortality and growth rate

Theoretical considerations suggest that the rate of food induced mortality should be influenced by growth rate. This is because of the inherent conflict between individual growth (which causes biomass to increase) and the fact that population biomass cannot increase indefinitely in the long term.

For a top predator it is assumed that:

- (a) individual growth causes population biomass to increase until food is limiting;
- (b) continued individual growth (eg of juveniles) generates a 'displacement' pressure though competition, ie a tendency to cause some individuals, initially to lose condition, and ultimately to starve to death.

Grazing mortality



Animals that predators fail to eat and that fall to bottom

For all, except top predators, there will also be a component of natural mortality due to grazing. In the diagram, predators would be free to attack both displaced and non-displaced prey individuals. It seems reasonable to assume however that displaced individuals would tend to be more vulnerable to predation than non-displaced individuals.

In the diagram, predators act both as a cause of mortality (flow A) and as an agent of mortality (flow B), (ie in the long term, flow B will tend to be determined by flow C, rather than by the number of predators).

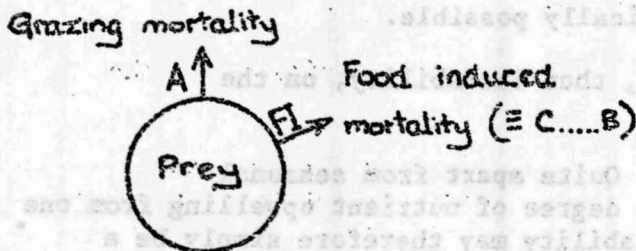
Simulations suggest that for rapidly growing individuals, such as early juvenile stages, flow C will tend to be particularly important (ie C, and hence B, will tend to be more important than A).

For slow, or non-growing individuals, flow C may be relatively unimportant and flow A is likely to be the more important pathway.

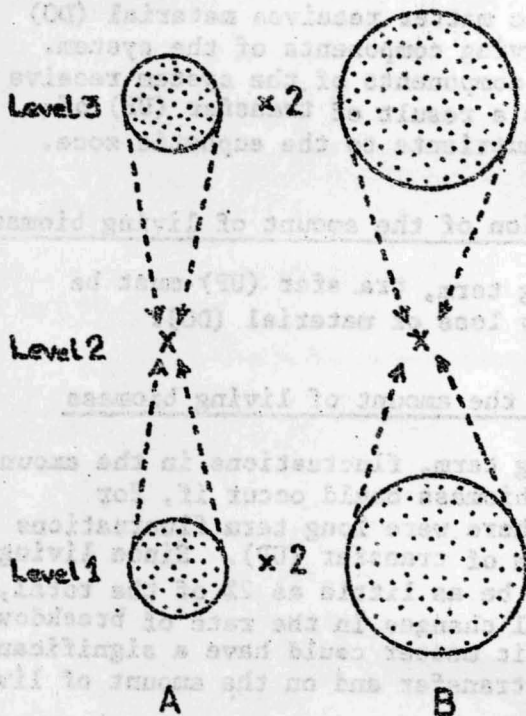
An approximation for modelling purposes

Here, mortality is simply divided into two components:

- (a) grazing mortality (A) is a function of prey/predator abundances;
- (b) food induced mortality (FI) is a function of food availability and prey growth rate (ie it is equivalent to B C combined).



MODELLING ENERGY FLOW 9. CHANGES IN BIOMASS AND ITS IMPLICATIONS



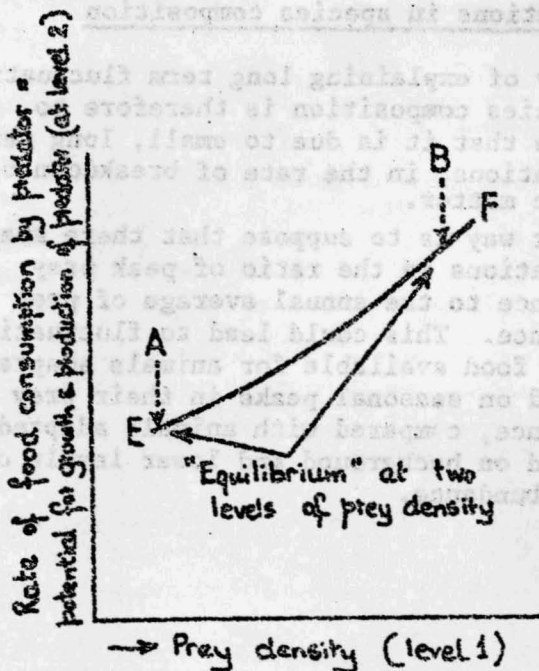
Long term changes in biomass have important biological implications. Consider for example a long term doubling of predator (level 3) and prey (level 2) biomass from the viewpoint of a single individual at level 2.

Each individual should encounter double the prey density when grazing. Individual rates of food intake should therefore increase.

Each individual at level 2 should encounter double the number of predators. Individual mortality rates should therefore increase.

Both A and B are theoretically possible in the long term. The difference is simply that each individual at level 2 could receive more food and hence could support more predators than before. (Note that this argument is independent of the absolute biomass of level 2.)

Long term increases in overall biomass should therefore be associated with increases in both growth and mortality rates.



Species composition and biomass

In the long term, a species may be able to respond to small changes in growth and mortality. For example, a small increase in mortality could be accommodated by a decrease in the proportion of adults and an increase in the proportion of juveniles.

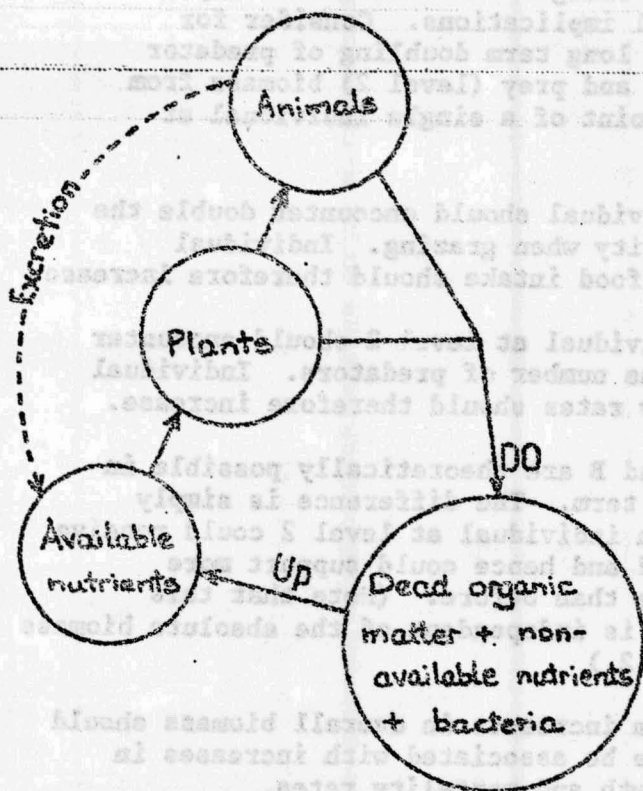
A large increase in growth and mortality on the other hand could easily lead to a change in species composition, ie at a low prey density one species may be favoured, whereas at a high density another may be favoured.

One way of explain long term fluctuations in species composition therefore is simply to postulate long term fluctuations in total living biomass.

FACTORS AFFECTING TOTAL LIVING BIOMASS

Interaction of living and dead matter

Dead organic matter receives material (DO) from the living components of the system. The living components of the system receive material as a result of transfer (UP) of inorganic nutrients to the euphotic zone.



Determination of the amount of living biomass

In the long term, transfer (UP) must be balanced by loss of material (DO).

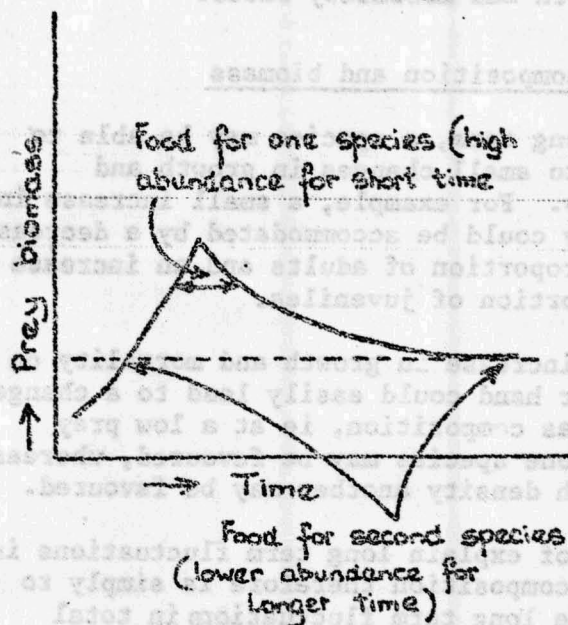
Changes in the amount of living biomass

In the long term, fluctuations in the amount of living biomass could occur if, for example, there were long term fluctuations in the rate of transfer (UP). Since living matter may be as little as 2% of the total, quite small changes in the rate of breakdown of dead organic matter could have a significant effect on transfer and on the amount of living biomass.

Fluctuations in species composition

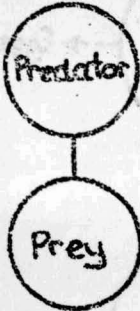
One way of explaining long term fluctuations in species composition is therefore to suppose that it is due to small, long term fluctuations, in the rate of breakdown of dead organic matter.

Another way is to suppose that there are fluctuations in the ratio of peak prey abundance to the annual average of prey abundance. This could lead to fluctuations in the food available for animals adapted to feed on seasonal peaks in their prey abundance, compared with animals adapted to feed on background and lower levels of prey abundance.



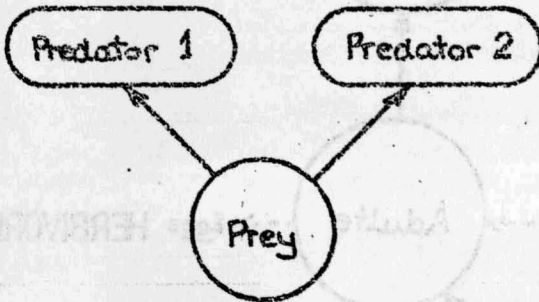
MODELLING ENERGY FLOW 10. SPECIES INTERACTIONS

The principal problem, when considering species interactions is to reconcile competition with co-existence.



Predator prey relationship

One kind of species interaction is the predator prey relationship. This represents a situation where the two species concerned occur at different trophic levels. It is easy to see that variations in the biomass of one, will influence the biomass of the other.

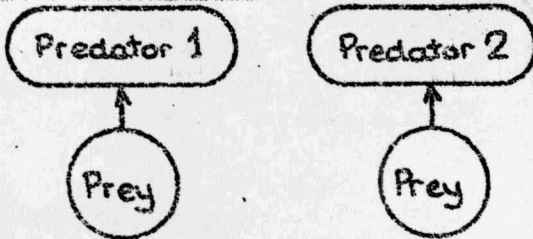


Species at the same trophic level

Where there are two or more species at the same trophic level, the question of food sharing arises. A satisfactory model must take account of the conflicting factors presented by competition and co-existence.

Competition

If two species simply share the same food, one will eventually become eliminated.



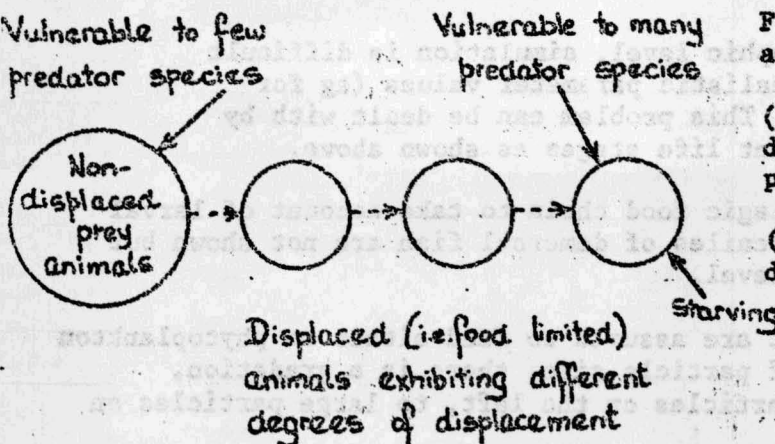
Co-existence

If the food is partitioned in such a way that the two species are completely independent, there may be no species interaction.

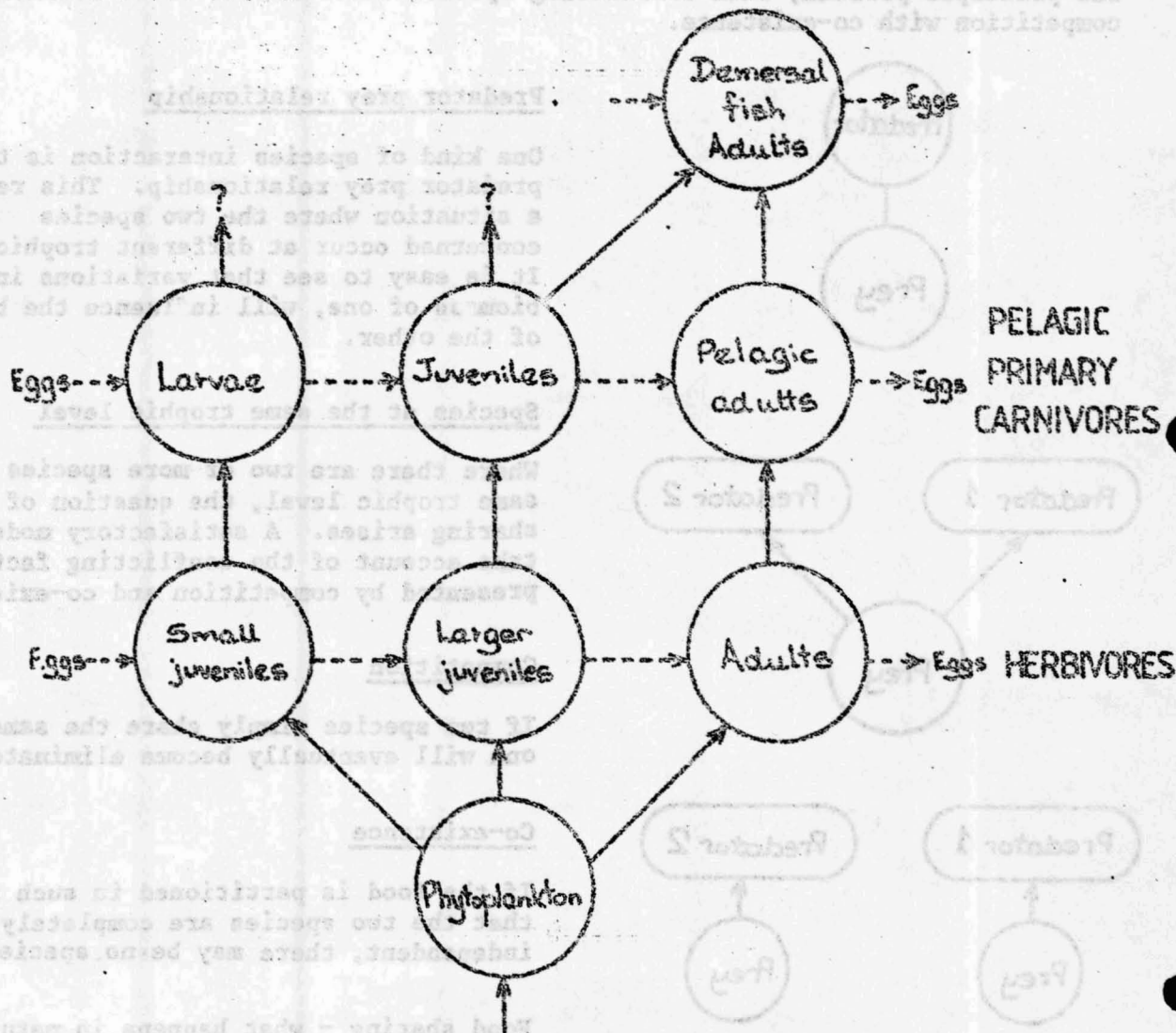
Food sharing - what happens in nature

Feeding strategies that permit food sharing are:

- (1) Adaptations leading to feeding on different levels of prey production (see previous page).
- (2) Feeding on displaced animals with different degrees of specialisation.



...that a relatively large part of the energy flow through such a system is through the larvae and juvenile components. This is likely because larvae and juveniles tend to graze on much larger...



An expanded food chain

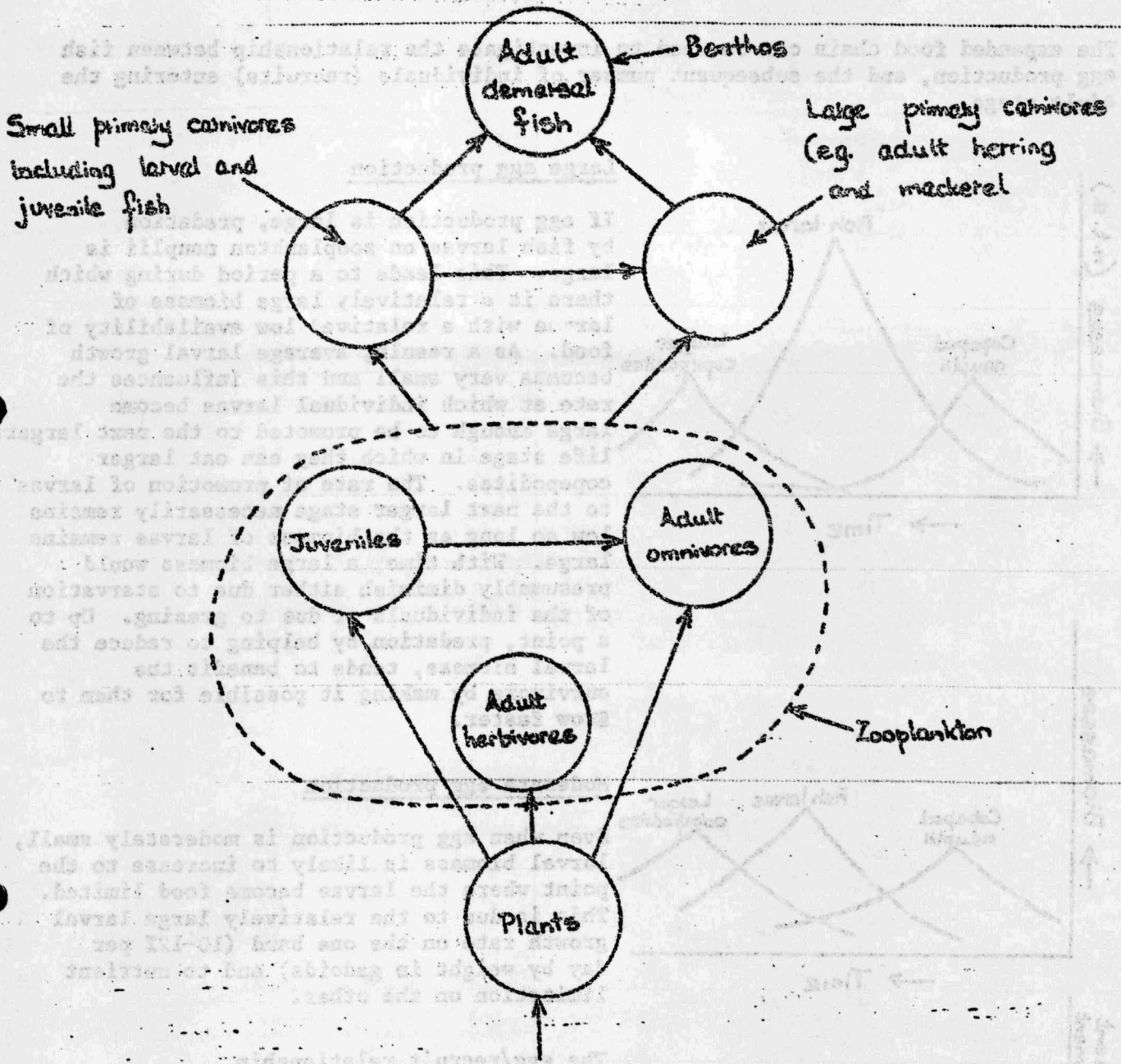
If there is only one compartment per trophic level, simulation is difficult because of the difficulty of choosing realistic parameter values (eg for individual growth and mortality rates). This problem can be dealt with by dividing each trophic level into different life stages as shown above.

This shows a simple expansion of the pelagic food chain to take account of larval and juvenile stages. The larvae and juveniles of demersal fish are not shown but exist at the pelagic primary carnivore level.

Omnivorous zooplankton are not shown, but are assumed to feed either on phytoplankton or on juvenile zooplankton. In terms of particle size, there is a gradation, within each trophic level, from small particles on the left, to large particles on the right of the diagram.

Simulations show that a relatively large part of the energy flow through such a system is through the larvae and juvenile components. This is simply because larvae and juveniles tend to grow so much faster than adults.

11. AN EXPANDED FOOD CHAIN - 2



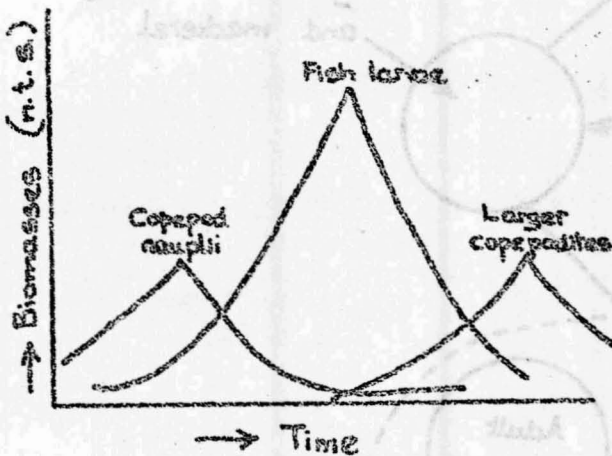
Food 'triangles'

More realistic than a linear food chain is the concept of food 'triangles', shown above for the pelagic system.

A theoretical advantage of such a system is that it confers a degree of 'elasticity' on the ecosystem that is not possible with a simple linear system.

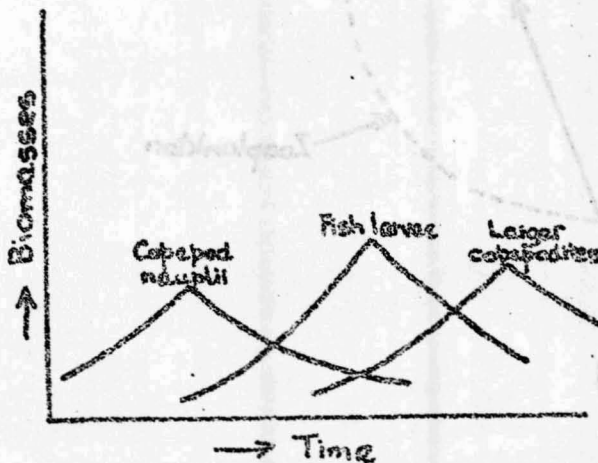
MODELLING ENERGY FLOW 12. THE FISH EGG/RECRUITMENT RELATIONSHIP

The expanded food chain can be used to investigate the relationship between fish egg production, and the subsequent number of individuals (recruits) entering the adult stage.



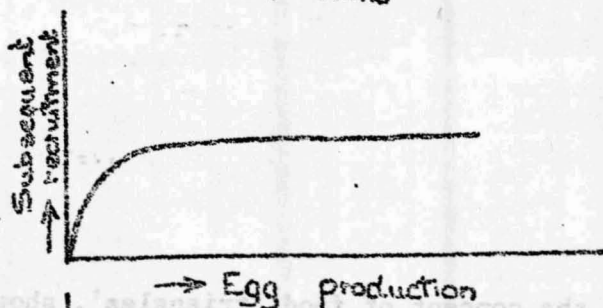
Large egg production

If egg production is large, predation by fish larvae on zooplankton nauplii is large. This leads to a period during which there is a relatively large biomass of larvae with a relatively low availability of food. As a result, average larval growth becomes very small and this influences the rate at which individual larvae become large enough to be promoted to the next larger life stage in which they can eat larger copepodites. The rate of promotion of larvae to the next larger stage necessarily remains low so long as the biomass of larvae remains large. With time, a large biomass would presumably diminish either due to starvation of the individuals or due to grazing. Up to a point, predation, by helping to reduce the larval biomass, tends to benefit the survivors by making it possible for them to grow faster.



Moderate egg production

Even when egg production is moderately small, larval biomass is likely to increase to the point where the larvae become food limited. This is due to the relatively large larval growth rate on the one hand (10-12% per day by weight in gadoids) and to nutrient limitation on the other.

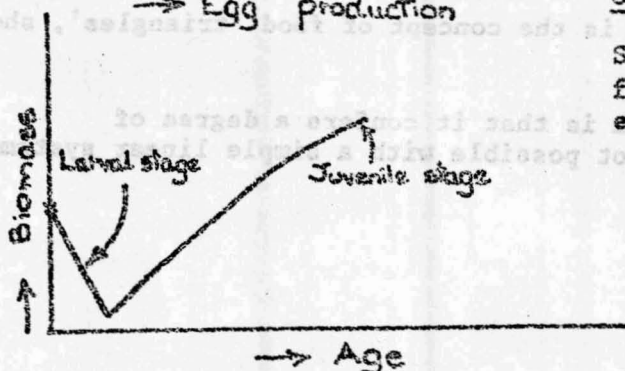


The egg/recruit relationship

Simulations suggest that average recruitment could be approximately constant over a relatively large range of egg production.

Change in biomass of a cohort

Simulations suggest that the biomass of a fish cohort decreases initially, before eventually increasing.



IMPLICATIONS FOR RECRUITMENT

The fish recruitment process presents particular problems for the following reasons:-

- (a) fluctuations in recruitment appear to be due to factors that operate during the larval and juvenile stages and that are apparently independent of the size of the adult spawning stock. As a result, adult stock size appears to fluctuate annually in a more or less random manner.
- (b) the fact that species co-exist seems to require that one species should not be able to increase its biomass arbitrarily at the expense of other species.
- (c) yet, the assumption of competition seems to require that all available food is taken up ie there should be no 'surplus' food to maintain the adults of a good year class, once it has been produced. The simulations suggest ways in which these factors might be reconciled:-

Recruitment with many species

In a multispecies situation, it is possible to vary recruitment within a closed system, of fixed size, by assuming that total recruitment is constant. A temporary expansion of one species should then be exactly offset by a temporary decrease of other species. To verify this hypothesis, recruitment data for all species are needed, and these do not yet exist. Such data as do exist however, do not support this hypothesis for the North Sea.

Recruitment and Primary Production

In a simple model, with only one fish species, it was found that recruitment was particularly sensitive to the rate of primary production.

Variations in total recruitment (for all species combined) might therefore be explained by postulating small variations in primary production ie an increase in primary production might not only cause overall recruitment to increase, but could also provide (temporarily) additional food for an increased biomass of adults.

The additional food needed for a large year class might also be accounted for, or partly accounted for, by postulating variations in the degree of omnivory.

A generalised stock/recruit relationship

Simulations, using the expanded food chain model show that recruitment tends to be practically independent of egg production at all levels of egg production other than those close to zero. This is a consequence of the potentially very large growth rates of fish larvae.

A stock/recruit relationship such as this has the advantage that population extinction, due to a random sequence of poor year classes should be extremely improbable. This cannot be said of a conventional stock/recruit relationship.

For moderate variations in adult stock size, the simulations support the hypothesis of 'constant recruitment' subject only to apparently random variations.

Implications for species replacement

In the northern North Sea, most of the zooplankton (by weight) consists of a single species (Calanus) and this is exploited by many predator species. To explain co-existence, each predator must be assumed to adopt a different feeding strategy. If one predator is eliminated, it is unlikely therefore that it would be wholly replaced by any other species at the same trophic level.

For example it is unlikely that a given biomass of a migratory species (such as herring) could be replaced by an equivalent biomass of a non-migratory species such as sprat or sandeel.

Implications for management

Implications for management are:

- (1) The yield per recruit approach appears to be a useful one for making short term calculations. Difficulties with this approach are that not enough is known about the ways in which recruitment, growth, and natural mortality are liable to change in the long term as fishing effort is changed.
- (2) In the long term, species interactions are most likely to be important to the extent that they may influence recruitment levels. Multispecies management may therefore be thought of as management that takes account of recruitment levels as well as of yields per recruit.

SUMMARY AND CONCLUSIONS

This paper summarises the results of simulation studies of a simple model of the marine ecosystem, with particular reference to factors affecting the production of the higher trophic levels in a seasonally perturbed ecosystem such as the North Sea. The principal conclusions are as follows:-

- (1) In young, rapidly growing animals, assimilated energy can be converted into growth with an efficiency of about 30%. Yet, transfer coefficients between trophic levels, may be very much smaller than this. There are several reasons for this:-
 - (a) Not all of a population consists of rapidly growing juveniles. There will also be slow growing (or non-growing) adults or resting stages, which require food, and yet contribute little if anything directly to production.
 - (b) Seasonal variations in the relative biomasses of adjacent trophic levels tend to generate seasonal variations in transfer efficiency. The net result is an annual transfer efficiency, that is lower than the theoretical maximum, (ie lower than the transfer efficiency when there just happen to be enough predators to exactly consume all of the prey produced).

In simple simulations, seasonal 'surges' of energy tend to cause 'overproduction' of the top trophic level, ie a biomass of top predators large enough to graze their prey down to a level at which they (the predators) subsequently starve.

This effect tends to be minimised in nature, by biological adaptations, or physical processes that prevent all trophic levels from being permanently present at the same time and place. As a result, although transfer efficiencies in nature are low, they tend not to be as low as those generated in simple simulation models.

- (2) The co-existence of several species, feeding on the same prey species, can be accounted for by assuming that each adopts a different feeding strategy eg:
 - (a) there could be migratory behaviour to exploit seasonal peaks of prey production, or non-migratory behaviour to exploit more sustained but lower levels of prey production;
 - (b) different degrees of specialisation for feeding on displaced individuals would permit food sharing;
 - (c) at times of seasonal peaks in prey abundance, there could be feeding by many species 'opportunistically' without this necessarily being associated with competition.

(3) Overall recruitment (ie recruitment of all species combined) is thought to depend on:

(a) The level of primary production. A high level of primary production for example can account not only for an above average level of recruitment, but also (if only temporarily) for the increased food subsequently required by the increased adult stock.

(b) Variations in egg production alone (ie with spawning stock held constant) were found to have extremely little effect on the level of recruitment. Only as egg production approached very close to zero, was there any obvious decline in recruitment level.

(4) In the long term, species interactions are likely to be important to the extent to which they influence recruitment levels. Multispecies management may therefore be thought of as management that takes account of recruitment levels as well as of yields per recruit.

FRENCH ABSTRACT .

Ce memoire résume les conclusions tirées d'imitations d'un modèle de l'écosystème marin. On a développé ce modèle essentiellement pour être un instrument de programmation et un moyen de vérifier des idées sur le processus de la production marine pour voir si on peut faire accorder ces idées, en ce qui concerne la quantité, avec les observations reconnues.

On s'est attaché surtout aux facteurs qui touchent la production des poissons, le processus de recrutement, et la question des actions réciproques entre les différentes espèces. Voici les principales conclusions:

- (1) À cause des variations saisonnières de lumière et de la disponibilité des aliments nourrissants, l'écosystème de la mer du Nord est un système en régime non-permanent, c'est à dire que les propriétés de l'écosystème sont définies pour la plupart selon la dynamique au régime non-permanent plutôt qu' au régime permanent.
- (2) Les rendements du cycle d'alimentation sont sujet à être bien plus bas que les rendements de la croissance de l'individu à cause des difficultés à lier la consommation des carnivores à la production des proies dans un système qui varie selon les saisons. On estime qu' à l'état naturel, il y a beaucoup d'adaptations qui ont pour conséquence d'augmenter les rendements de déplacement au-dessus de ceux qui sont produits dans des modèles simples.
- (3) Le recrutement des poissons (pour toutes les espèces prises ensemble) est sujet à être presque indépendant de la production d'œufs de poisson (pourvu que la production d'œufs ne soit pas zéro).
- (4) On fait quelques propositions au sujet des moyens de faire accorder la coexistence de différentes espèces et le fait qu' on a observé que le partage des aliments est d'ordre général.

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TABLE 1

BIOMASS AND NITROGEN LEVELS IN THE NORTH SEA

			gN/m ²
Demersal fish	early 1960's	1.5 x 10 ⁶ tonnes ⁽¹⁾ wet weight	0.05
	late 1960's	3.0 x 10 ⁶ tonnes ⁽¹⁾ wet weight	0.10
Pelagic fish	early 1960's	10 x 10 ⁶ tonnes ⁽¹⁾ wet weight	0.3
	late 1960's	6 x 10 ⁶ tonnes ⁽¹⁾ wet weight	0.2
Benthos		1gS/m ² ⁽²⁾ , 5.6g dry wt/m ² ⁽³⁾	0.2
Zooplankton	winter (Av)	2-3 Kcal/m ² ⁽⁴⁾ (0.7g/m ² DW) ⁽⁴⁾	0.04 (0.07)
	summer (Av)	25 Kcal/m ² ⁽²⁾ (7g/m ² DW) ⁽⁴⁾	0.4 (0.7)
Phytoplankton	winter (min)	0.2 µg Chl a/l ⁽⁵⁾	<0.1
	spring (max)	2.5 µg Chl a/l ⁽⁵⁾ , (8), (11)	1.2
Inorganic	winter (max)	7 µg at N/1 ⁽⁶⁾ , 6 µg at N/1 ⁽⁹⁾	4-5 (10)
Nutrients	spring (min)	0.5 µg at N/1 ⁽⁶⁾	0.3
Soluble organic	winter (min)	5 µg at N/1 ⁽⁶⁾	3
Nitrogen	summer (max)	10 µg at N/1 ⁽⁶⁾	7 (11)
Sediment Nitrogen			25 ⁽⁷⁾

(1) Based on Data in Jones & Richards 1976

(2) from Steele 1974

(3) from Heip *et al.*, 1979

(4) from Adams (personal communication)

(5) from Steele and Henderson 1977

(6) from Butler *et al.*, 1979

(7) from Davies (personal communication)

(8) Martin & Hall 1975

(9) Dooley 1976

(10) Top 40m only

(11) Values up to 8 µg Chl/l can occur (Davies personal communication)

Conversion factors

Nitrate 1 µg at N/1 ≡ 0.7 gN/m² (for top 50m)

Chlorophyll spring 1 mg chl a/m³ ≡ 0.5 gN/m² (for top 50m)

" autumn 0.8 gN/m² (for top 50m)

Zooplankton 1 mg dry wt/m³ ≡ 0.01 gN/m² (for top 100m)

Fish 1 g wet weight ≡ 0.02 gN

TABLE 2

COMPARISONS OF THE LANDINGS OF PELAGIC AND DEMERSAL FISHES AT DIFFERENT LATITUDES:
 ICES REGIONS, LANDINGS IN 000s metric tons 1962-1976

Region/Sub Area	Pelagic	Demersal	% Demersal
Sub area I and II (No Arctic)	1451 ⁽³⁾	1364 ⁽⁴⁾	48)
Sub area V (Iceland)	495 ⁽³⁾	726 ⁽⁴⁾	59) 54
Region 2 (N Sea + Skagerrak)	2040 ⁽¹⁾	1005 ⁽²⁾	33)
Sub areas VI and VII	381	276	42) 36
Region 3	504	177	26

From Co-op. Res. Rep. Ser. B., 1971 and No. 85, 1979

ICNAF Regions

Landings (000s metric tons) 1970-1976

Sub Area	Pelagic ⁽³⁾	Demersal ⁽⁴⁾	% Demersal
1	6	100	94
2	13	154	92
3	159	607	79
4	414	452	53
5	409	239	37

(from ICNAF Statistical Bulletin Vols 20-26)

(1) including Sandeels, N Pout (613,000 tons)

(2) excluding Sandeels, N Pout

(3) including redfish

(4) excluding redfish

APPENDIX 1

Equations (1)

Animals (AN)

$$AN = AN + (AN(GAN-FIAN) + R_1 - R_2 - FEO) \Delta t$$

Phytoplankton (PH)

$$PH = PH + (PH(GPH-SINK) - 1.4 FEZH - 1.2 FEZO) \Delta t$$

Nutrients (NU)

$$NU = NU + (D.DOM + TEX - (1 + G). PH.GPH) \Delta t$$

Dead organic matter (DOM)

$$DOM = DOM + (FIM + PH (SINK + G.GPH) + 0.4 FEZH + 0.2 FEZO - D.DOM-FEB) \Delta t$$

(1) In these equations, the left hand side, is equivalent to the right hand side after an interval of time Δt has elapsed. Units are $mg/N/m^2$.

- see Appendix Fig. 1 for explanatory diagram

Notes on equations

Growth rate per unit biomass of animals (GAN)

$$GAN = \epsilon (FEAN-MA)$$

This represents total growth rate per unit biomass (ie somatic growth + growth of gonad)

Growth rate per unit biomass of phytoplankton (GPH)

$$GPH = MGPH (NU-NUTH)/(BN + NU - NUTH)$$

Food eaten by animals (FEAN)

$$FEAN = X (MGA/\epsilon + MA).AN$$

Influence of prey density on rate of food consumption by animals (X)

$$X = (PREY - PREYTH)/(B PREY + PREY - PREYTH)$$

Food induced mortality rate per unit biomass of animals (FIAN)

$$FIAN = MFAN (1 - X)$$

Excretion (TEX)

for any one animal group the rate of excretion (EX) is given by

$$EX = (FEAN - GAN.AN)$$

TEX = total excretion from all animal groups

Other terms

FEO = animal food eaten by other animals

FEZH = plant food assimilated by zooplankton herbivores

FEZO = plant food assimilated by zooplankton omnivores

0.4 FEZH + 0.2 FEZO = input of faecal nitrogen to pool of dead organic matter

FEB = food eaten by benthos

Bacteria

Bacteria are not included explicitly in the model. Bacterial action is allowed for by the parameters D and G (see Appendix 2).

R_1 = addition to animal biomass due to lateral transfer from younger life stages

R_2 = loss of animal biomass due to lateral transfer to older life stages (including transfer of eggs to youngest juvenile stage).

Egg production per unit biomass (GO)

$$GO = GAN.EG/(MGA)$$

$$R_1 = GO \cdot (\text{Biomass of adults})$$

For $i > 1$

$$R_i = X \cdot (\text{Biomass of juveniles of stage } i) / DUR$$

APPENDIX 2

Input parameters

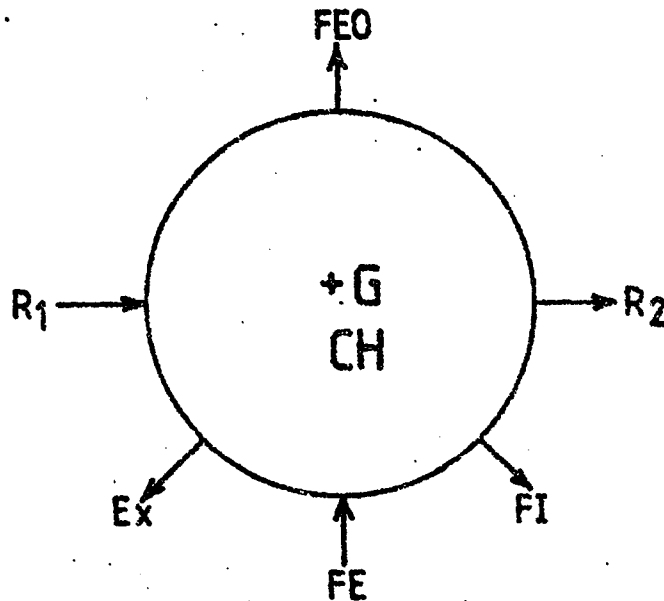
- D = rate of conversion of dead organic matter into nutrient available for plants. (Value varied seasonally from 0.3 to 0.6⁽¹⁾ to allow for temperature changes)
- G = rate of soluble organic production as a proportion of particulate primary production (value of 0.3 used).
- MGPB = maximum growth rate per unit biomass of phytoplankton, given unlimited nutrient (value varied seasonally from 75 to 150 to allow for temperature changes)
- MGA⁽²⁾ = maximum growth rate per unit biomass of animal material (including reproductive growth if an adult life stage)
- MA⁽²⁾ = annual maintenance requirements per unit biomass of animal material
- KN = nutrient level at which phytoplankton grow at half maximum rate (value of 0.7g N/m² used)
- BPREY⁽²⁾ = prey concentrations at which predator are able to eat at half of maximum possible rate
- ITE = nutrient threshold below which phytoplankton growth rate is zero (value of zero used)
- PREYTH⁽²⁾ = prey concentrations, below which predators cease to feed. (Mainly low values used just sufficient to prevent prey from being grazed to extraction)
- EG⁽²⁾ = proportions of MGA's converted into eggs
- DUR⁽²⁾ = durations of juvenile stages (in years)
- SINK = rate of sinking of phytoplankton
- ϵ = individual growth efficiency
- MFAN⁽²⁾ = Maximum food induced mortality rate for animals when there is no food

(1) all instantaneous rates in annual rates

(2) separate values for each category of animal material

APPENDIX FIGURE 1

PARTITIONING ENERGY FLOWS WITH RESPECT
TO BIOMASS OF A SINGLE ANIMAL LIFE STAGE



CH = net change in biomass due to operation of all factors

G = addition to biomass due to growth of individuals

FE = food eaten by biomass concerned

FEO = food eaten by predators on that biomass

EX = excretory loss term

FI = food induced mortality term

R₁ = biomass gained from younger life stages

R₂ = biomass lost to older life stages

$$FE = EX + G \quad \dots \quad (1)$$

$$CH = G - FI + R_1 - R_2 - FEO \quad \dots \quad (2)$$

OR

$$FE + R_1 = FEO + R_2 + FI + EX + CH \quad \dots \quad (3)$$