

Stability and variability in the marine ecosystem

Erik Ursin

The Danish Institute for Fisheries and Marine Research, Charlottenlund Castle,
DK-2920 Charlottenlund, Denmark

Abstract

The abundant literature on changes diverts attention from the basic stability of marine life and its causes. Density dependent mortality of juvenile fish and buffering mechanisms within the demersal and pelagic phases of the ecosystem are the main subjects of the paper.

Introduction

When a marine biologist discovers that something has changed or oscillates he is inclined to write a paper on it. When he finds that everything is as usual there is no instigation to write. He is looking for changes. There is an extensive literature on variability, but not much on the fundamental stability of marine ecosystems. We shall consider three points: (1) annual recruitment to fish stocks, (2) buffer systems taking the edge off critical situations and, (3) the stability of total fish biomass.

Annual recruitment to fish stocks

Scores of papers are being written on year class strengths in fishes. Many are simply descriptive: which year classes were outstanding and which were not. Others try to relate year class strength to physical or biological factors. One effect of all this literature is to divert attention from the fact that many species maintain a remarkably stable recruitment considering the enormous reduction in numbers from the egg stage until maturity.

In 1963-75 cod (*Gadus morhua*) year classes in the North Sea varied by a factor six from the smallest to the biggest year class (Table 1). A remarkably small variation considering that a cod spawns between half a million and five million eggs per year, extremely few of which can survive until adult size. When the cod's life comes to an end it must have produced – on an average – one mature female and one mature male. Only extremely small deviations from the number of two are feasible if the species shall retain approximately its present abundance as, apparently, it has done for at least 150 years. This replacement of one pair of mature fish by another must even occur within a wide range of mortality of the mature stock. When the stock is heavily fished the average mature female may lay, say, two million eggs in its short lifetime. With low fishing intensity it may manage to lay perhaps forty million eggs. Yet the number surviving until maturity at different

stock size levels varies so little that nobody has demonstrated that it does vary at all. The important thing to know is not why year class 1966 is twice as big as year class 1967. What we need know, and do not know, is how between two million and forty million eggs are being reduced by six or seven size orders to between one and ten survivors until maturity.

Imagine a marksman shooting with a rifle at a small target 200 metres away. Suppose he hits the target every time, but he does not always hit the black mark. Fishery biologists studying his results will be much concerned about why the bullets do not pile one on top of the other like Robin Hood's arrows, but sometimes hit a little to the left, sometimes a little to the right. The amazing fact that they all hit the small target escapes them.

The marksman analogy is not quite appropriate. We have to look for something analogous to a radar guided missile which is set on an approximate course and adjusts the course repeatedly on its way towards the target. Crude adjustments first, minor adjustments later. We know very little about the regulating mechanisms at work. Fish larvae die quickly when starving whereas adult fish can starve for months without apparent ill effects excepts a weight loss. Very likely, one of the first crude adjustments of the year class size is through an increased starvation mortality when larvae are more abundant than food resources permit. Much work is being done along these lines at present, experimental as well as theoretical (Beyer & Laurence 1978). This adjustment must be a crude one because food resources vary too, so that high mortality could occur also with a low density of larvae.

There is an interesting point, however. It was mentioned above that the necessary reduction of numbers for cod is six or seven size orders. Cod is a fish with many eggs. Herring (*Clupea harengus*) for instance, have fewer eggs. The eggs are bigger and the herring is a smaller species. The necessary reduction is two or three size orders less than for cod and the low mortality of young herring may be due to differences in the starvation risk. It was probably R. Jones (1973) who first advanced the sensible idea that if an animal is constructed to grow at an enormous rate it is probably poorly adapted to situations when fast growth is impossible. A young cod or haddock (*Melanogrammus aeglefinus*) grows to 1000 or 10000 times the hatching size in three months and stands a great risk of dying because of lack of food at some stage within these three months. Smaller species with moderate food requirements can be expected to have a better survival. It becomes sensible that the size of fish eggs varies little with species size: small species with a slow growth need fewer eggs to lose.

These are considerations relating to the early stages of the fish's life, but it is incredible that the final adjustment of recruit numbers occurs as early as that. We are at a loss for a general description of the finer adjustment. Yet, in certain cases there are patterns to be seen. North Sea plaice (*Pleuronectes platessa*) are a good example.

Plaice spawn in the southeastern North Sea and the pelagic larvae are at metamorphosis carried with the water into the vast estuarine areas known as the Wadden Sea, a region with extensive tidal flats reaching from Denmark to the

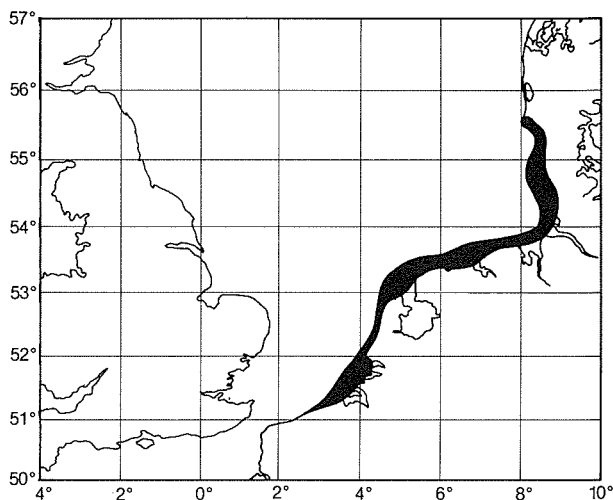


Fig. 1. North Sea with the Wadden Sea – an important nursery ground for plaice – indicated.

Netherlands (see Fig. 1). The young bottom stages remain about half a year on the tidal flats and in the associated deep channels. Later, they move seawards in a way which has been described as a two-dimensional diffusion with the coast as a reflecting barrier (Beverton & Holt 1957). The inshore area where plaice must spend the first months of their demersal life is small, only 5 percent of the area of the southern and central North Sea, the habitat of the older plaice.

The Wadden Sea consists of a system of sand and mud flats showing various degrees of submersion during the tidal cycle and with a different fauna. Shrimps (*Crangon crangon*) abound on certain flats and prey upon the young bottom stages of plaice (Bergman *et al.* 1976). It is likely that the area really suited to young plaice is small relative to the numbers of metamorphosing plaice. These grow faster when they are few (Tåning 1945, Rauck & Zijlstra 1978). This can be due to a scarcity of food or perhaps, at high densities the young plaice spread into less suitable areas. Anyway, as might be expected under such conditions, the year class strengths are levelled out during the stay in the Wadden Sea: Rauck & Zijlstra (1978) found that numbers of recently metamorphosed plaice fluctuated more than after some months in the Wadden Sea.

This means of regulating year class strength is probably quite efficient. Plaice recruitment varies less than recruitment to most other fish stocks in the North Sea, as illustrated in Table 1 which shows relative year class strengths in 1963-75 for 11 species which have been made subject of intensive investigation by the countries around the North Sea. The figures are from ICES Working Group reports except those for Norway pout (*Trisopterus esmarki*) (Jones & Hislop 1978) and the first data set for mackerel (*Scomber scombrus*) (Hamre 1978). The strongest year class of each species has been assigned a value 100 to improve comparability. A pattern emerges even though data are missing in some years for several species.

Haddock recruitment shows a remarkable instability. Whereas plaice recruitment varied only by a factor 5 the haddock figures varied by a factor 100. One gets

Table 1. Recruitment variation in North Sea fishes 1963-1975. Numbers adjusted to a value of 100 for the most outstanding year class of each species. 'Ratio' is the ratio between the numbers in the strongest and the weakest year classes.

Year class	Gadoids					Flatfishes		Clupeids		Sand-eel	Macke-rel	
	Cod	Had-dock	Whit-ing	Saithe	Norway pout	Plaice	Sole	Her-ring	Sprat			
1963	52	1	14	17	4	100	100	100			10	
1964	49	1	26	23	6	29	21	53			26	
1965	70	2	30	18	0.5	28	11	47			43	
1966	63	12	37	50	7	25	11	66	59		62	
1967	20	100	100	51		21	18	65	62		10	
1968	19	6	33	55	2	27	9	36	37		16	
1969	82	2	30	29		32	26	78	41		100	100
1970	100	14	33	29	45	25	6	62	20	100	9	12
1971	18	21	68	30	7	20	14	41	19	21		17
1972	35	4	90	40	16	62	19	19	46	47		4
1973	31	21	63	100	100	40	18	47	91	28		15
1974	51	40	92	27	38	25	7		100	86		11
1975	27	9	37	50	18	37	22		79	41		4
Ratio	6	100	7	6	200	5	17	5	5	5	11	25

a suspicion that there is no stabilizing mechanism whatever in North Sea haddock. A lot of eggs and larvae die of course, so that survival is never catastrophically high, but there is apparently no stage in the haddock's life when the carrying capacity of its habitat is severely limiting in the North Sea although there was a slight indication of food scarcity in 1967 (see below). Conditions may be different elsewhere. Cod for instance, one of the stable species in the North Sea, fluctuates as much in the northeast Atlantic and the Barents Sea as haddock does in the North Sea (ICES 1973). This is probably what can be expected if the distribution of a fish is limited by low temperatures in the larval stages. Whichever stock size may be maintained due to occasional good yearclasses in warm years, recruit numbers may go down to virtually zero in cold years. West Greenland cod presents a case of such temperature dependent survival, Fig. 2.

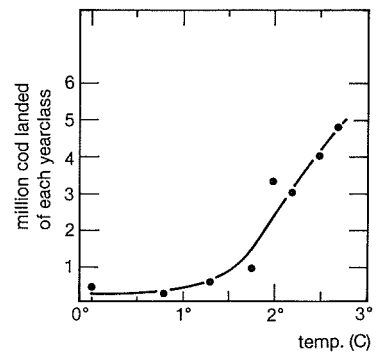


Fig. 2. West Greenland. Yearclass strength of cod as a function of surface temperature during the larval and post-larval stages (Hansen & Hermann 1953, redrawn).

It is interesting that haddock is unique among North Sea fishes in showing cyclic biomass changes (Sahrhage & Wagner 1978). An outstanding year class tends to start a three year cycle because most spawners are three years old. Several such cycles have been noticed in the present century. The most persistent started with a good year class in 1952 and remained discernible in 1964. Such cycles can exist only in the absence of appreciable density dependent young fish mortality.

Comparing plaice and haddock it must be remembered that the recruitment regulation in plaice works one way only. It can reduce an outstanding year class, but it cannot improve on a year class which is a failure. A similar regulating mechanism for haddock would have to make haddock a rare fish in the North Sea, because the strongest year class in the period 1963-75 could then be only 5 times the strength of the weakest year class whereas it was in fact 100 times stronger.

Imagine a fish species whose weak year classes produce as many recruits as a weak year class of plaice or cod, but with no regulating mechanism cutting off the top of an outstanding year class. The carrying capacity of the whole North Sea would then be tested, and the ecosystem even endangered when an outstanding year class occurred. Such catastrophic propagation does not seem to occur and even heavily stunted populations, so often seen in American and European lakes, are scarcely known among marine species. It is difficult to see how evolution has managed to avoid it, but anyway, there has been a long time to accomplish it. The sea is several hundred million years old, whereas the age of lakes is often counted by thousands of years only. They have not achieved the balance and stability of the marine environment.

The closest the North Sea has been to a catastrophe due to excessive recruitment may have been when the most outstanding haddock year class ever recorded appeared in 1967, accompanied by strong year classes of the two smaller gadoid species whiting and Norway pout. The total stock of these three species varied in the years before about 300 000 tons, but reached in 1968-69 about 1.5 million tons of which the 1967 haddock year class accounted for perhaps 800 000 tons (Andersen & Ursin 1977, Ursin 1977). These figures must be considered on the background of a total fish stock of 8 or 9 million tons. Thanks to many years of Scottish investigations the size-at-age of North Sea haddock is quite well known. We can therefore see which influence the high numbers had upon the growth of the 1967 year class. Fig. 3, based on data kindly placed at disposal by R. Jones, shows the variation of size-at-age in 1959-73 with data for the 1967 year class plotted in. This year class had a slow growth, but not excessively so. It seems that the slow growth is restricted to the pelagic young stage which in haddock lasts about one year. In the 1967 year class it lasted a year and a half (R. Jones, personal communication). If the size-at-age entries are accordingly moved half a year to the left one finds quite an ordinary growth rate for the demersal stage.

This is remarkable because these haddock must have at least doubled the stock of demersal feeders for several years. Another remarkable thing is that even though pelagic haddock to some extent exhausted their own food resources there was apparently no similar growth retardation in other pelagic fish stocks. Even though

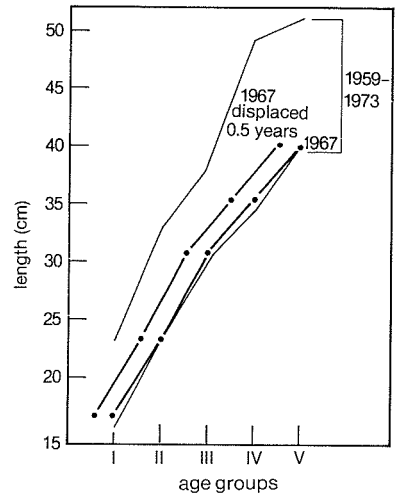


Fig. 3. Growth rate variation in North Sea haddock, showing the situation of the exceptional yearclass 1967 (Andersen & Ursin 1977).

there is a considerable overlap of prey species found in the stomachs of haddock and other fish, it can have been only their own favourite species that the young haddock managed to graze down, or the peak of spawning may have been reached at a different date than for the other species.

In other words, the ecosystem is sufficiently buffered to swallow even such a disturbance as the haddock shock. The buffering is a major problem of marine ecology and is discussed in the following paragraphs.

Buffers in the ecosystem

When K.P. Andersen and the present author first tried to model the North Sea ecosystem (Andersen & Ursin 1978, read at a symposium in 1975) there was experienced more variation in the model than is known from nature. For instance, the excessive haddock year class of 1967 soon grazed down the benthos. Haddock as well as other demersal feeders suffered poor growth in the model. In nature, there was no conspicuous impact of these billions of haddock, as already mentioned.

Another occasion when the model showed an unrealistic response was the reduction of the mackerel and herring stocks from 6 million tons to 2 million tons in a few years (see below). These species feed mainly on zooplankton which often amounts to about 95 percent of their food. It was estimated that 50 percent of all zooplankton consumed in the North Sea was consumed by these species when their biomass was high.

Therefore a bloom of zooplankton might have been expected when the mackerel and herring stocks were reduced to one third in the course of a few years. And indeed, such a bloom occurred in the model. However, when the model was presented at the ICES North Sea Symposium in 1975 there was also presented a zooplankton paper (Colebrook 1978) showing convincingly that there was not the slightest irregularity to be seen in 1964-67, when the pelagic fish stocks were so

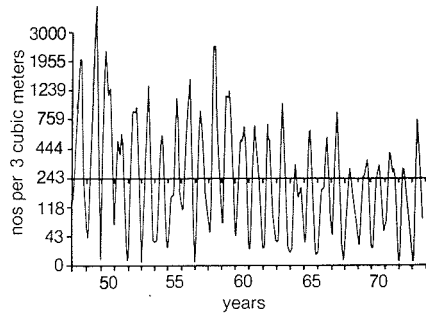


Fig. 4. Abundance of *Pseudocalanus* in an area in the northern North Sea (Colebrook 1978).

suddenly reduced. Fig. 4 illustrates Colebrook's results for a copepod, *Pseudocalanus*. One immediately notices the seasonal variation and a decline through the entire period of observation. The decline may or may not be due to some unnoticed gradual change in sampling technique. Anyway, it is not our concern at the moment, but there is no irregularity in the middle sixties.

This discrepancy between hypothesis and nature caused considerable worry. The only remedy we could think of was to introduce a predator among the plankton animals and let herring and mackerel eat both the predator and its food. We thought that it might do the trick, and it did. There were three plankton species in the model. According to their size they could be a euphausiid, a large copepod and a small copepod. They all ate phytoplankton and small amounts of zooplankton and benthos larvae. The food size preferences of the 'euphausiid' was now changed drastically to make it a ferocious predator upon copepods and upon its own young. The copepods were allowed to propagate a little faster in order to supply the food for the new predator. In the next computer run the output was almost as usual up to the moment when the removal of herring and mackerel began. From then on the difference was remarkable: nothing appreciable happened. The plankton predator became slightly more abundant and ate more of the copepods. Its own juveniles became relatively more abundant and therefore suffered more predation mortality. This reduced the predator recruitment, copepods increased again, the predator ate them, and so on. The desired buffer had been introduced.

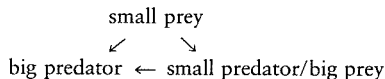
A similar arrangement was introduced for the benthos. Also here, there were three species: one of meiofauna, weighing about 1 microgram, a small polychaete of about 10 mg and a large bivalve or something similar, weighing about 2 g. They all ate detritus, as for instance copepod feces and dead copepods, and phytoplankton which had sunk to the bottom or had been brought down by turbulence. The big species was transformed into a crab by changing its food size preferences. The system now remained stable even when the 1967 year class of haddock made its impact upon the benthos. The haddock and other demersal fish showed normal growth in spite of a doubling of the total demersal stock.

Unfortunately, there was not at that time the slightest evidence that the mechanism invented in the computer is realistic even though it had the desired effect upon the results. Soon after, however, predator exclusion experiments were published by several authors (critically reviewed by Arntz, 1981). Arntz (1977) did

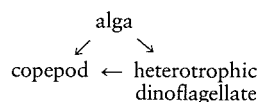
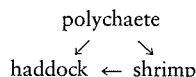
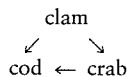
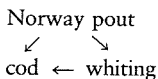
experiments with trays in the Kiel Bay of the Baltic. Each tray held a quantity of sediment with its natural fauna. Some trays were covered by netting to keep the fish, mainly cod, from grazing the benthos in the tray. Cod is the major consumer of benthos in the area. One purpose of the experiment was to measure the increase of the benthos in the absence of cod. Very little happened when the cod was kept away except that there were a few more crabs and gobies (small species, 5 cm) under the netting than in the uncovered trays. These experiments might have been designed to test the hypothesis on the buffering of the benthic-demersal phase of a marine ecosystem. Yet the test was incomplete. The hypothesis was not rejected, but it had not been tested whether the crabs and gobies actually controlled the infauna. It was shown only that the infauna remained stable in their presence.

However, working on tidal flats in the German Wadden Sea Reise (1978) fenced three types of areas: (1) uncovered; (2) covered by coarse netting to keep birds and other big predators out; (3) covered by fine netting to keep also small predators (crabs, shrimps, gobies) away. The areas covered by coarse netting remained almost unchanged entirely in accordance with Arntz' results. Under the fine netting the infauna bloomed. After three months the numbers of polychaetes, lamelli-branches, etc. were 4-10 times higher than in the uncovered controls. As a test of the buffer hypothesis this design is excellent and obviously, the hypothesis still cannot be rejected. One should not overlook, however, that a change in the infauna under a finemeshed screen might be caused by a sheltering effect of the screen itself. More recently (Klein Breteler, 1980) there has been described a similar buffering system in the plankton although under laboratory conditions. A stable production of copepods was maintained through several generations in a three species culture of a copepod, an alga and a heterotrophic dinoflagellate. When copepods were kept with algae only, the system sometimes got out of control because the algal concentration became excessive. In the three species culture this did not occur. Copepods consumed both algae and dinoflagellates and the latter consumed algae. Dinoflagellates increased in number when the copepods were too few to keep their food stocks down. The control of algae would pass to the dinoflagellates whose increased population would be grazed off again as soon as copepods became plentiful.

Such observations suggest a replacement of the traditional food chain (for inst., algae → copepods → herring → cod) which is unstable, by a food web of triangular meshes each containing a prey species, a predator species and a species which is predator to the first, prey to the latter. Thus:



where the arrows indicate predation. Likely examples are:



In practice, each position is probably occupied by several species. For cod read for instance 'cod and turbot' and for shrimp or crab read 'shrimps, crabs and gobies'. The two predators of a triangle may prefer food of different sizes. It makes little difference if whiting eat smaller Norway pout than cod do. When there are many cod they will eat quantities of whiting such that the Norway pout which would have been consumed by these whiting are left to grow into a suitable size for cod to eat them. Increased numbers of large cod lead to a reduction of whiting biomass and to an increased production of Norway pout, a species with a rapid turnover. This with the apparent effect that the predators, cod, produce some of the food they consume. The following figures (in units of 1000 tons, from Ursin 1982) calculate the effects of reducing the fishing mortality coefficient upon North Sea cod from 0.75 to 0.40:

	$F = 0.75$	$F = 0.40$	Difference
Fish consumption by cod	464	1025	561
Total fish production	8694	8995	301
Surplus consumption by cod			<u>260</u>

Conclusions from a simple inspection of the quantities of fish consumed by cod would be misleading. The stabilizing effect of the triangular foodweb system is such that about half the fish in the cod stomachs would never have been produced if the cod had not been there to consume them.

A different stabilizing mechanism is discussed by Jones (1979) who considers the role of displaced animals in the system. There are probably always some which due to disease or because they inhabit less suitable localities are more likely to be eaten than others. This means that predators have easier access to food when their own stock is small because they can feed more on easily accessible displaced, perhaps even dying or dead, animals. When the predator stock increases the depletion of prey stocks will not increase proportionally because the predator must rely on less displaced or even fully established prey, difficult to catch. This reduces predator growth rates and accordingly, food requirements. The risk that a predator extinguishes its own prey would be much reduced if this mechanism is of considerable importance. It may be possible to test the displacement hypothesis by comparing for instance the number of parasites in prey animals in fish stomachs and in potential prey animals in the sea. Counting all prey in fish stomachs as dead because of predation as in the calculation above may overestimate the influence of predators upon the size of prey stocks.

Stabilization also occurs in connection with prey switching which is the phenomenon that abundant prey is consumed disproportionately often. It occurs in feeding experiments (Murdoch *et al.* 1975) but is difficult to ascertain in nature.

The stability of fish biomass

The replacement of depleted stocks by other species and the mechanisms underlying such replacement are subjects of high actuality in recent years. Daan (1978) reviews the situation and concludes that clear cases of replacement of a depleted stock by another stock are difficult to find, possibly in some situations because of insufficient

information. Reasonably clear cases are so few that they may be accidental.

The problem is perhaps that ecologically, fish are not a unit. They may be replaced by invertebrates depending on the same food resource. Jellyfish and squid are obvious examples and indeed, there are several reports on increased squid catches when fish catches decreased because of high fishing mortality (Daan, 1978).

Temperate seas

The clearest case of fish stock replacement described so far is from the North Sea (Figs 5 & 6). The results are output from a multispecies assessment model, called 'the fishery model' by Andersen & Ursin (1977, § 6). Input data is as in Ursin (1978). The method is basically the same as virtual population analysis, but calculations are performed over short timesteps.

Herring and mackerel stocks were reduced in 1965-69 because of improved fishing techniques. Recruitment to most other stocks increased rapidly in the first few years after, and biomass rose steadily. (Biomass increases in the early sixties are mainly caused by the outstanding 1962 haddock year class). Total fish biomass, however, remained remarkably stable.

Fish production (Fig. 6) increased by about 50 percent. Food consumption by fish increased less so that the efficiency of food conversion ($100 \cdot \text{production}/\text{consumption}$) increased from 20 percent to 24 percent. Several of the replacement species are short-lived ones and replaced mainly a stock of old mackerel. A 'rejuvenation' therefore occurred and a higher conversion efficiency is not unexpected.

The size frequency distribution of North Sea fish changed little in spite of these marked changes in stock composition. The curves in Fig. 7 describe the situation before and after the great changes in North Sea fish stocks in the late sixties. The analysed periods are shaded in Fig. 5. The size classes are logarithmic, each being $\sqrt{2}$ times bigger than the preceding class. The ten commercially most important species were included and also dab (*Limanda limanda*) and long rough dab (*Hippoglossoides platessoides*) because they contribute considerably to the biomass. Fish less than one month old were omitted. The two North Sea curves in Fig. 7 are

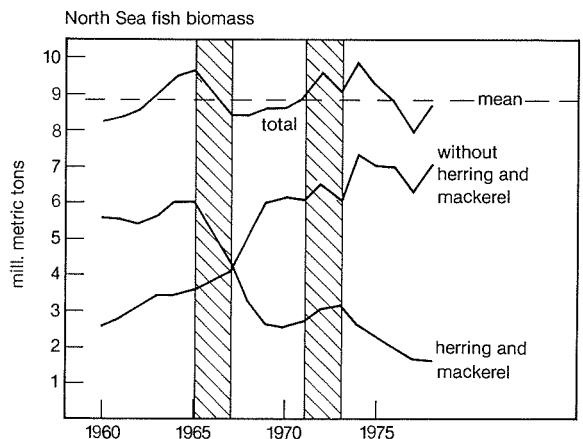
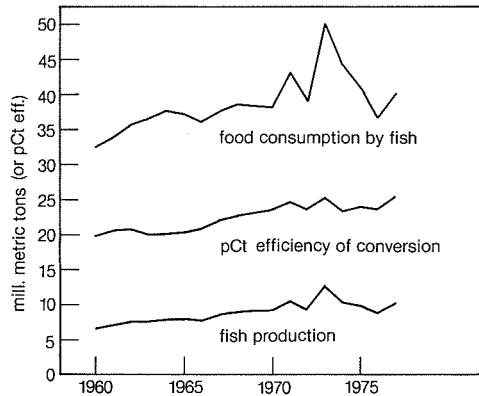


Fig. 5. North Sea. Estimated changes in fish biomass composition since 1960. Data for the shaded periods were used in Fig. 7.

Fig. 6. North Sea. Effects of changes in fish biomass composition.



remarkably similar in spite of great changes in species composition. The increased numbers of small fish are traceable, though. A not very conspicuous hump on the 1965-66 curve (indicated by an arrow) is due to the large stocks of herring and mackerel which were gone, more or less, in 1971-72. By and large, the stability of the size frequency distributions in spite of major perturbations is more remarkable than such changes as can be discerned. Moreover, the North Sea curves differ little from a similar curve (also in Fig. 7) for the Baltic, based on ICES working group assessments of the three most important species: cod, herring and sprat (*Sprattus sprattus*).

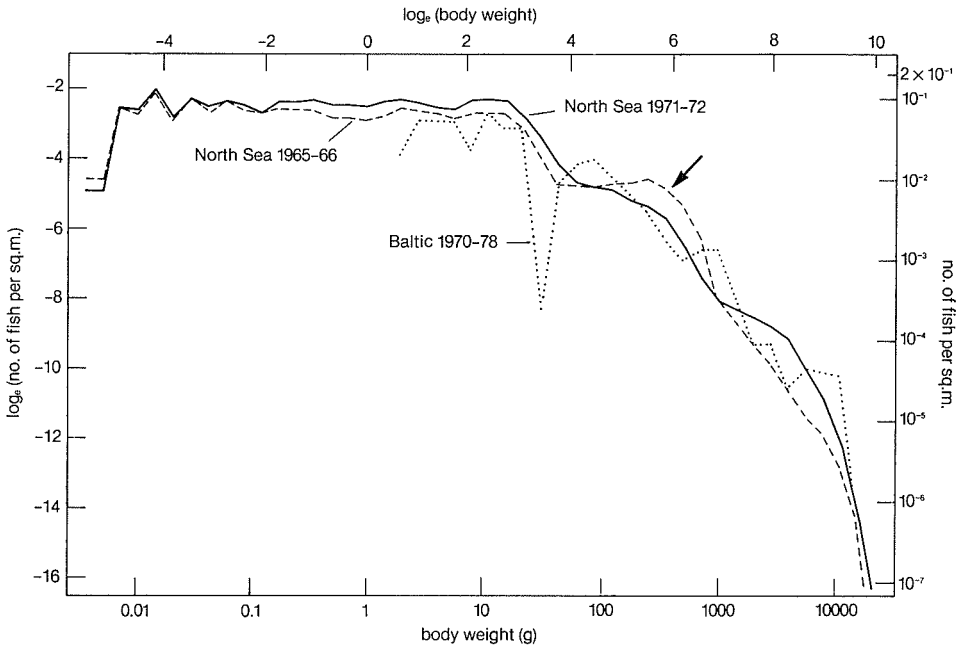


Fig. 7. Fish numbers as a function of body weight in the North Sea and in the Baltic.

It should not be forgotten that nothing plotted in Figs 5-7 is observed. It is all calculated. The actual information is on the age and size structure in the various populations. In order to calculate the biomass, consumption, etc. from such data a number of assumptions must be made (for instance, on natural mortality). The whole thing is nonsense if they are not realistic.

Yet, even if events in the North Sea are correctly described in the figures, we are left with the problem why a similar development has not been described from other seas. The increase of other stocks simultaneous with the decrease of herring and mackerel may be entirely unrelated except in time. This is one possibility. Another is that it is accidental that herring and mackerel in the North Sea were replaced by other fish species. If they happened to control the stocks of jellyfish by preying upon the fry of these, they might have been replaced by jellyfish of whose populations in the North Sea we know little. The replacement would not have been observed at all.

A third possibility is that the North Sea is one of the few areas in which we know all the major fish stocks. As late as in 1950 the large stocks of small, short-lived species (sprat, Norway pout, sandeels (*Ammodytes*)) were almost unknown in spite of the intensive research activity in the North Sea ever since 1880. The discovery of these stocks is mostly due to the extensive and varied fishery for processing which developed since 1950 (Popp Madsen, 1978).

There are extremely few places in the world from which a similar development as in the North Sea could be described if it happened. However, when Sherman (1978) finds that a rapid reduction of biomass of certain species in the Georges Bank area of the north-west Atlantic did not trigger an increase of other fish species except sand lance (= sandeel, *Ammodytes*), this is probably reliable because extensive stomach investigations (e.g., Maurer & Bowman, 1975) failed to disclose the presence of large, undiscovered fish stocks.

Upwelling systems

One case with some resemblance to the development in the North Sea is the reduction of anchovy (*Engraulis ringens*) stocks in Peruvian waters, apparently with replacement in part by other pelagic and perhaps also demersal species. Fig. 8, based on data from Arntz & Robles, 1980, and Valdivia, 1978, illustrates the situation, which is complicated by irregular penetrations of warm equatorial water. These imbalance the temperate ecosystem to which the anchovy belongs. The occurrence of such phenomena, known as El Niños, is indicated by arrows at the bottom of Fig. 8. One reason why full biomass replacement by other fish species did not follow the collapse of the heavily fished anchovy stock (yielding 10-12 mill. tons per year before the collapse) might be that the anchovy in a large part of its distribution feeds mainly on unicellular organisms whereas the replacing fish species are more carnivorous and therefore tend to introduce an extra trophic level into the system.

This is related to the much discussed subject of the food and feeding of anchovies. These have a choice of particulate and filter feeding (O'Connell, 1972). The widespread opinion (e.g. Rojas de Mendiola, 1971) that filtering anchovy may

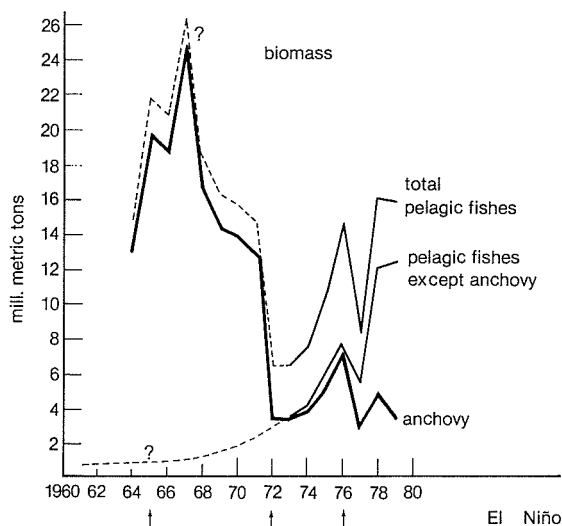


Fig. 8. The collapse of Peruvian anchovy and the supposed replacement by other pelagic fishes. Years with penetration of tropical water (the El Niño phenomenon) are indicated.

feed on phytoplankton was argued against by Cushing (1978), maintaining that anchovy, because they have a short gut, are not fit to deal with phytoplankton cells as is another clupeoid, the menhaden (*Brevoortia tyrannus*). On the other hand, the smallmeshed structure of the gills (King & Macleod, 1976) indicates small food particles. The apparent contradiction vanishes with recent observations on the importance of heterotrophic unicellular organisms as for instance naked flagellates in the marine ecosystem. Klein Breteler's (1980) observations referred to above are supported by field studies.

Sorokin (1977) showed that in Asiatic lakes and in the Japan Sea organic matter (probably particulate as well as dissolved) left over from a phytoplankton bloom gives rise to substantial production of heterotrophic unicellular organisms in the period after the bloom when nutrient concentrations are low and phytoplankton biomass and production remain at a low level until remineralization has taken place. Peinert *et al.* (in press) made similar observations in the Baltic so that, obviously, this is a widespread and important phenomenon.

Incidentally, it throws some light on a much used diagram from Colebrook & Robinson (1965) which has always puzzled this author. It shows (Fig. 9) in arbitrary units the average standing stock of phytoplankton and copepods in the north-western North Sea. With increasing light in the spring and after remineralization of nutrients during the winter there appears a spring phytoplankton maximum followed by a long period of low standing stock. The also conspicuous autumn maximum is supposed to be caused by an increase of nutrients in the photic zone after the autumn gales have disturbed the discontinuity layer formed in summer. Copepod stocks are low in winter when food is scarce, but increase rapidly, with a time lag, after the spring phytoplankton maximum. This is sensible, whereas at first it is surprising that copepod stocks remain at a high level all through the

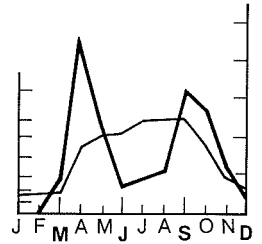


Fig. 9. Abundance of phytoplankton (heavy line) and copepods in an area in the North Sea. Arbitrary scales (Colebrook & Robinson 1965).

summer when phytoplankton is scarce (almost at winter level), only to decrease in the autumn when phytoplankton comes up again. When copepods do not show such a second mode as phytoplankton it is probably (Fransz *et al.*, 1978) because their predators (chaetognaths, jellyfish) have propagated during the summer with its high densities of copepods. The high, stable copepod numbers in summer become understandable when it is appreciated that there may be a large stock of heterotrophic, unicellular organisms on which copepods feed. The Andersen & Ursin (1977) model of North Sea population dynamics showed a drop in zooplankton in summer. This was known from the Colebrook & Robinson paper to be unrealistic, but could not be helped because there was nothing in the model to sustain a large copepod stock in the absence of large phytoplankton stocks, such as the heterotrophs might do.

The new importance attributed to unicellular heterotrophic organisms makes one wonder if the Peruvian anchovy might be replaced, neither by other fish species nor by copepods, but by naked flagellates forming with these and phytoplankton proper a predation triangle like those described above.

The hypothesis on heterotrophic protists as important controllers of marine ecosystems introduces an extra link in the trophic chain. If energy flows from phytoplankton to copepods and anchovy through the heterotrophs, then at least twice as much primary production is needed. This seems to be a smaller problem than might be expected because, coincidentally, in these years evidence is accumulating to the effect that the carbon-14 method in many cases grossly underestimated primary production.

The ecosystems discussed above are all labile and young systems. Most of the North Sea, for instance, was dry land some 20 000 years ago. Such systems seem to be characterized by a low degree of specialization and a high reproductive potential (much waste) making it possible for them to take advantage of a situation with improved survival rates of larvae. Obvious collapses of exploited stocks are few and limited to heavily schooling pelagic stocks, mostly or exclusively clupeoids. Phenomena of this kind were discussed at an ICES symposium in 1978 (Saville, 1980). Most other fishes of temperate seas and of subtropical upwelling systems appear to be to a large extent ubiquitous and 'opportunists'.

Tropical seas

Contrary to this, the demersal fisheries of the tropical Pacific interfere with an extremely old and highly specialized ecosystem, a situation discussed by Pauly (1979). The contrast to North Sea fisheries is striking. In these, large longlived demersal feeders as well as small shortlived pelagic feeders maintain large stock sizes in spite of heavy fishing mortalities. In the demersal fisheries of the Gulf of Thailand of which Pauly (l.c.) made a case study, both of these groups collapsed quickly under fishery pressure whereas large pelagic predators were reduced only to half their former stock sizes. Replacement of collapsed stocks occurred to a small extent only, and was effectuated by squid, crabs and only slightly specialized fishes, mainly flatfish. Table 2 compares virgin and exploited stock sizes as calculated by Pauly from trawl surveys. The observed development is ascribed to a high stabi-

Table 2. Changes in stock sizes of commercial species in the Gulf of Thailand, from Pauly (1979). Two significant digits retained.

Ecological group	Units of 1000 metric tonnes		
	Virgin stock	Exploited stock	<u>Exploited</u> Virgin
1. Large benthos feeders	150	1.3	0.0087
2. Small demersal prey	830	21	0.025
3. Intermediate predators	620	74	0.12
4. Large predators	21	5.3	0.25
5. Pelagic fishes	13	5.7	0.44
6. Flatfish	3.5	7.6	2.2
7. Squid and crustaceans	30	90	3.0
Depleted stocks (1-5)	1600	110	0.066
Replacing stocks (6-7)	33	97	2.9

lity and extreme efficiency of the unfished ecosystem in which reproductive potential is much lower than in temperate waters (less waste) and where prey stocks are already optimally exploited by predators. It is sensible to assume that interference by man may cause disaster to such a system.

The extent to which depleted stocks were replaced by invertebrates of no commercial value is not known. The increase of flatfish stocks seems to indicate an increased energy flow to the shelf bottom.

References

- Andersen, K. P. & E. Ursin, 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. — Meddr Danm. Fisk.- og Havunders., N. S. 7: 319-435.
- Andersen, K. P. & E. Ursin, 1978. A multispecies analysis of the effects of variations of effort upon stock composition of eleven North Sea fish species. — Rapp. P.-v. Réun. Cons. int. Explor. Mer 172: 286-291.

- Arntz, W.E., 1977: Results and problems of an 'unsuccessful' benthos cage predation experiment. – In B.F. Keegan, P. O'Ceidigh & P.J.S. Boaden (eds): *Biology of Benthic Organisms*, pp. 31-44. New York.
- Arntz, W.E., 1981. Entwicklung von marinen Bodentiergemeinschaften bei Ausschluss von Räufern: Nur Artefakte? – *Meeresforsch.* 28: 189-204.
- Arntz, W.E. & A. Robles P., 1980: Estudio del potencial pesquero de interés para el complejo pesquero 'La Puntilla' (Pisco, Perú). – Programa Cooperativo Peruano-Alemán de Inv. Pesquera. Callao (mimeo).
- Bergman, M., B. Kuipers, P. Spliethoff & H. van der Veer, 1976: Garnalen en krabben als mogelijke predatoren van 0-jarige schol op het balgzand. – *Visserij. Voorlichtingsbl. Nederl. Vis.* 29: 432-438.
- Beverton, R.J.H. & S.J. Holt, 1957: On the dynamics of exploited fish populations. – *Min. Agric. Fish. Food, Fish. Invest.*, Ser. 2 19: 1-533. London.
- Beyer, J.E. & G.C. Laurence, 1980: A stochastic model of larval fish growth. – *Ecological Modelling* 8: 109-132.
- Colebrook, J.M., 1978: Changes of the zooplankton of the North Sea, 1948 to 1973. – *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 172: 390-396.
- Colebrook, J.M. & G.A. Robinson, 1965: Seasonal cycles of phytoplankton and copepods in the Northeastern Atlantic and the North Sea. – *Bull. Mar. Ecol.* 6: 123-139.
- Cushing, D.H., 1978: Upper trophic levels in upwelling areas. – In R. Boye & M. Tomczak (eds): *Upwelling Ecosystems*, pp. 101-110. Springer-Verlag.
- Daan, N., 1978: A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. – *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 177: 405-421.
- Franz, H.G., M. Ottema & P.A. Seip, 1978: Abundance and growth of fish larvae during the summer decline of copepod populations in Dutch coastal waters of the North Sea and possible interactions with jellyfish and ctenophores. – *ICES C.M.* 1978/L: 19, 9 pp. (mimeo).
- Hamre, Johs., 1978: The effect of recent changes in the North Sea mackerel fishery on stock and yield. – *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 172: 197-210.
- Hansen, P.M. & F. Hermann, 1953: Fiskeri og Havet ved Grønland. – *Skr. Danm. Fisk.- og Havunders.* 15: 1-128.
- ICES, 1973: Report of the ICES/ICNAF Working group on cod stocks in the North Atlantic. – *ICES Cooperative Research Report* 33: 1-52.
- Jones, R., 1973: Stock and recruitment with special reference to cod and haddock. (ICES Symp. on Stock and Recruitment, 1970) – *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 164: 156-173.
- Jones, R., 1979: Predator prey relationships with particular reference to vertebrates. – *Biol. Rev.* 54: 73-97.
- Jones, R. & J.R.G. Hislop, 1978: Changes in the North Sea haddock and whiting. – *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 172: 58-71.
- King, D.P.F. & P.R. Macleod, 1976: Comparison of the food and the filtering mechanism of pilchard *Sardinops ocellata* and anchovy *Engraulis capensis* off South West Africa, 1971-1972. – *Rep. S. Africa, Dept. of Ind., Sea Fisheries Branch Investigational Report*, No. 111.
- Klein Breteler, W.C.M., 1980: Continuous breeding of marine pelagic copepods in the presence of heterotrophic dinoflagellates. – *Mar. Ecol. Prog. Ser.* 2: 229-233.
- Madsen, K. Popp, 1978: The industrial fisheries in the North Sea. – *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 172: 27-30.
- Maurer, R.O., Jr. & R.E. Bowman, 1975: Food habits of marine fishes of the Northwest Atlantic. Data Report. – NE Fisheries Center, NMFS, Woods Hole (mimeo).
- Murdoch, W.W., S. Avery & M.E.B. Smyth, 1975: Switching in predatory fish. – *Ecology* 56: 1094-1105.
- O'Connell, Ch.P., 1972: The interrelation of biting and filtering in the feeding activity of the Northern anchovy (*Engraulis mordax*). – *J. Fish. Res. Bd. Canada* 29: 285-293.
- Pauly, D., 1979: Theory and management of tropical multispecies stocks. – *ICLARM Studies and Reviews* No. 1: 1-35. Manila.
- Peinert, R., A. Saure, P. Stegmann, C. Stienen, H. Haardt & V. Smetacek, (in press): Dynamics of primary production and sedimentation in a coastal ecosystem. – 16th European Marine Biology Symposium.

- Rauck, G. & J.J. Zijlstra*, 1978: On the nursery-aspects of the Waddensea for some commercial fish species and possible longterm changes. – Rapp. P.-v. Réun. Cons. int. Explor. Mer 172: 266-275.
- Reise, K.*, 1978: Predator exclusion experiments in an intertidal mud flat. – Helg. Wiss. Meeresunters. 30: 263-271.
- Rojas de Mendiola, B.*, 1971: Some observations on the feeding of the Peruvian anchoveta *Engraulis ringens* J in two regions of the Peruvian coast. – In John D. Costlow (ed.): Fertility of the Sea. II, pp. 417-440. New York.
- Sabrbhage, D. & G. Wagner*, 1978: On fluctuations in the haddock population of the North Sea. – Rapp. P.-v. Réun. Cons. int. Explor. Mer 172: 72-85.
- Saville, A.* (ed.), 1980: The assessment and management of pelagic fish stocks. – Rapp. P.-v. Réun. Cons. int. Explor. Mer 177: 1-517.
- Sherman, K.*, 1978: Ecological implications of biomass changes in the Northwest Atlantic. – ICES C. M. 1978/L: 24, 9 pp. (mimeogr.).
- Sorokin, Yu. I.*, 1977: The heterotrophic phase of plankton succession in the Japan Sea. – Mar. Biol. 41: 107-117.
- Tåning, Å. Vedel*, 1945: Forandringer af Rødspættebestanden i Vadehavet i Løbet af Krigsårene. (Plaice stock changes in the Wadden Sea during the war. (In Danish.)) – Naturens Verden 29: 193-203. Copenhagen.
- Ursin, E.*, 1977: Multispecies fish stock assessment for the North Sea. – ICES C. M. 1977/F: 42, 19 pp. (mimeogr.).
- Ursin, E.*, 1978: Continued exercises with a North Sea model for multispecies fish stock assessment. – ICES C. M. 1978/G: 47, 10 pp. (mimeogr.).
- Ursin, E.*, 1982. Multispecies fish stock and yield assessment in ICES. – In M.C. Mercer (ed.): Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59: 39-47.
- Valdivia, G.J.E.*, 1978: The anchoveta and El Niño. – Rapp. P.-v. Réun. Cons. int. Explor. Mer 173: 196-202.