The decline of the herring stocks and the gadoid outburst

D. H. Cushing

Fisheries Laboratory, Lowestoft,
Suffolk NR33 0HT, England

The gadoid outburst in the sixties occurred as the various herring stocks in the North Sea were in decline and it was tempting to assume that the two events were related. An enquiry was made into the possible mechanisms by which such a succession might take place, but they are difficult to substantiate. Indeed, until it is known how populations stabilize themselves it might prove difficult to understand how they compete.

Introduction

Between the late fifties and middle sixties the stocks of autumn spawning herring in the North Sea declined considerably. With a succession of good year classes spawned from 1962 onwards, the stocks of gadoids have increased. Andersen and Ursin (1977) have used a multispecies simulation model which suggests that the gadoid outburst was associated with the decline in herring and mackerel; in particular they show an inverse relation between stocks of herring and mackerel and those of Norway pout and sand-eel. It is a large and complex model in which eleven commercial species are grouped in four compartments and within any one, food is shared. Then any excess of food due to exploitation of one stock is shared amongst the others and then the recruitment of one of them may increase. In this paper some mechanisms are explored.

The decline of the herring stocks

Burd (1978) described the state of the stocks of herring in the three ICES areas of the North Sea, IVa, IVb and IVc, since 1919 (Fig. 1). There are three groups of spawning herring in the North Sea, Downs, Dogger and Buchan (Cushing and Bridger, 1966); since the middle sixties, a Shetland group has been identified, but its relation with the Buchan stock remains indeterminate. I shall refer to this group as Buchan/Shetland despite the fact that the traditional Buchan spawning grounds have been abandoned since the sixties.

The stock in IVc represents the Downs stock almost exclusively; during the period 1946–1953, it was reduced to about half of the pre-war level, between 1954–1958 to one-seventh and in the years 1962–1970 to one-twentieth. This stock declined sharply during the second world war when there was no fishing and the decline may have been due to a natural decline in recruitment; an alternative explanation is that, in 1946

and 1947, the drifters fished close to shore on abundant post-war stocks but did not sample the older fish offshore. Burd's wartime samples are based on the age distribution of catches in 1946 and 1947. The stock in IVb represents the Dogger stock and from 1930 onwards up to one-third may have comprised Downs spawners. Between 1935 and 1950, the stock was abundant but it declined by half during the fifties, to one-quarter in the years 1958–1966 and from 1968 onwards it was reduced to one-thirtieth of that in the
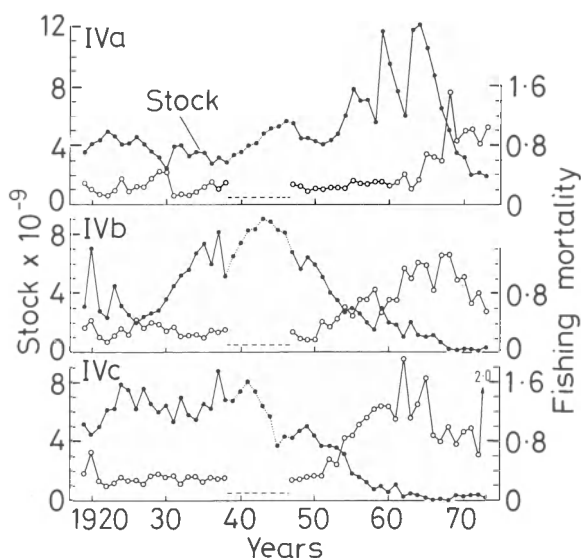

Figure 1. Trends in stock in numbers (●——●) and in fishing mortality (o——o) in the ICES sub-divisions IVa, IVb and IVc from 1919 to 1973; the stock in IVc represents the Downs stock, that in IVb the Dogger stock (with a proportion of the Downs stock) and that in IVa the Buchan stock (which may have included a Shetland component from the late sixties onwards) (Burd, 1978).

peak years. The stock in IVa represents the Buchan/Shetland stock, which may include components of the Dogger and small parts of the Downs stocks; this group increased to high levels between 1952 and 1966, after which they declined considerably, reaching pre-war levels in 1969.

The Downs and Dogger stocks were well reduced before 1962, early enough to initiate a gadoid upsurge. The Buchan/Shetland group increased until the mid-sixties after which it declined, but the peak production of this group was reached in 1965, after the gadoid outburst had started. All North Sea autumn and winter spawning herring stocks have declined, probably under the stress of heavy fishing, but the three groups of stocks decreased at different periods.

The gadoid outburst

The increase in gadoids is shown in the following record of high year classes in the sixties, each of which is much larger than any predecessor before 1962: cod, 1963, 1964, 1965, 1966, 1969, 1970, 1974 (Daan, 1978); haddock, 1962, 1967, 1974 (Jones and Hislop, 1978); and whiting, 1962, 1967, 1974 (Jones and Hislop, 1978). Cod spawn mainly in the central and southern North Sea in March (Daan, 1978) although spawning

grounds exist in the north (Fig. 2a, b). Their nursery ground lies on the Danish and German coasts between July and the following February (Fig. 3 and 4). Haddock spawn in the northern North Sea in spring and their nursery extends across the northwestern North Sea off the Scottish coasts (Anon., 1976). Young whiting tend to live in the southeastern and central North Sea, young cod in the southern and central North Sea and young haddock in the northern North Sea (Anon., 1977): the early and crucial part of each life history is restricted to distinct and particular regions.

Two possible causes of the gadoid outburst

Although the causes of the gadoid outburst remain unknown, the large increases in recruitment could be due to the *release of food* at an early stage in the life cycle or to *relaxed predation* at any stage before recruitment.

Release of food

The gadoid outburst started in 1962 with the strong haddock year class hatched in the northern North Sea. Because the herring in that region did not decline until 1965 (indeed the stock level remained at a high level
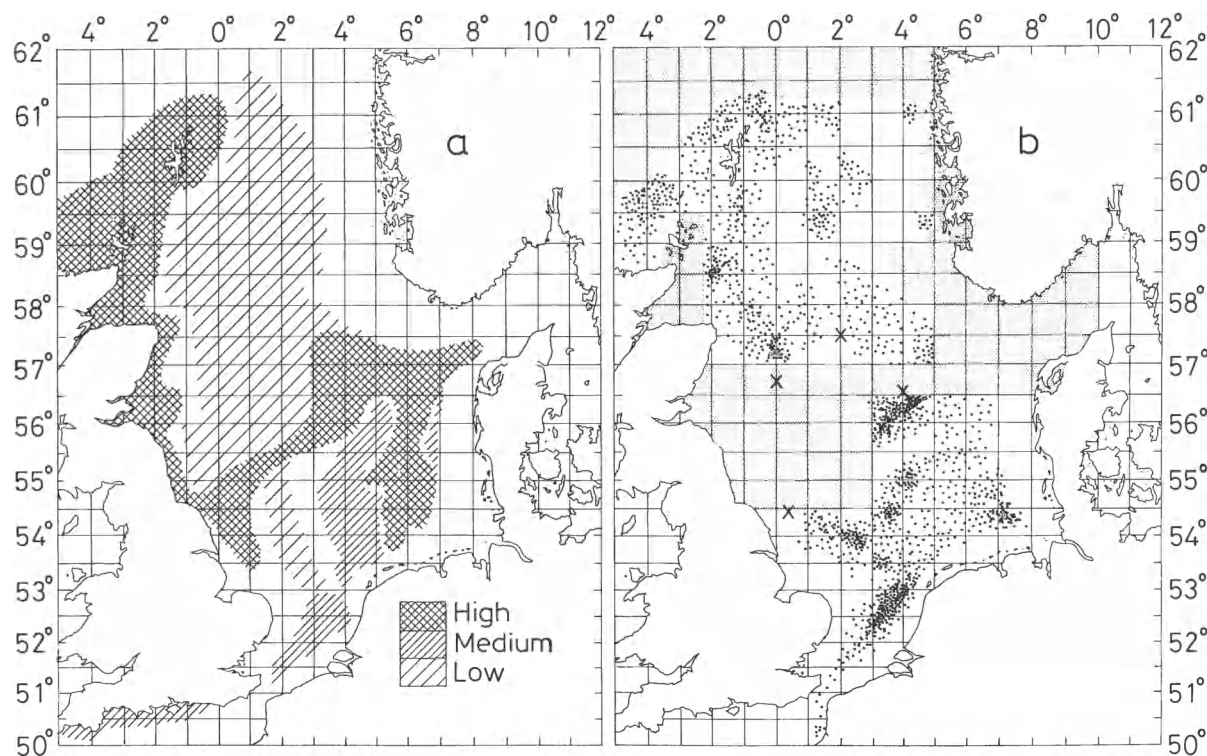

Figure 2. The spawning grounds of the cod in the North Sea (a) spawning activity in the beginning of the 20th century (Anon., 1909) (b) distribution of cod eggs based on information collected after 1945. The stippled area was not surveyed and the crosses mark the spawning centres identified by Graham (1934, Fig. 24). Redrawn after Daan (1978, Figs 43 and 44).
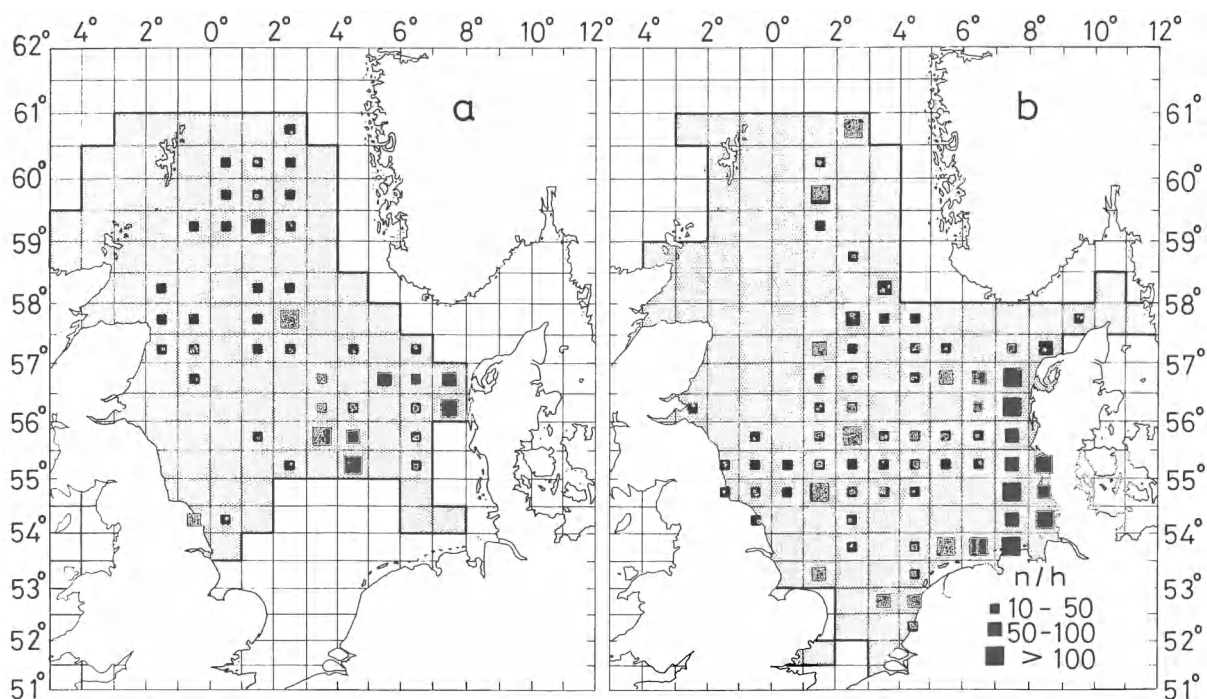
Figure 3. The distribution of young cod (a) average density (number per hour fishing) of 0-group cod taken during research vessel surveys in June and July 1969–1974 (b) average density (number per hour fishing) of I-group cod taken during research vessel cruises in February 1965–1974. Redrawn after Daan (1978, Figs 46a and b).

until 1968), the release of food from herring must have been restricted to the central and southern North Sea. As the herring food there has been well studied, the following organisms would include those released:

7–12 mm larvae; crustacean eggs, nauplii and some juvenile copepods; 12·5–42 mm postlarvae; small copepods (*Pseudocalanus, Temora, Microcalanus*); 42 mm+ (whitebait); *Eurytemora,* cyprids, decapods and small fish; adults; *Calanus* and smaller copepods in the thirties; euphausiids, sand-eels, *Oikopleura* in the twenties (Hardy, 1924; Savage, 1931; 1937).

Hardy showed that larval and postlarval herring take *Pseudocalanus* in preference to *Calanus*; indeed, when *Calanus* were as abundant as *Pseudocalanus* in the water, there were none in the guts of postlarval herring. Larval cod feed on *Calanus* nauplii initially and upon the copepodid stages of *Calanus* as postlarvae (Jones, 1973). In the Southern Bight of the North Sea, however, where *Calanus* is absent, larval and postlarval cod feed on *Pseudocalanus* (Last, 1978). Herring of the Dogger and Buchan/Shetland groups spawn five to six months before the cod and they would have drifted nearly to the eastern nursery ground by the time the cod larvae hatched. Hence larval food released by the Dogger and Buchan/Shetland groups would not be available to the cod population unless it were through the overwintering zooplankton population, as suggested by

my colleague Mr. D. J. Garrod. The decline of larval herring in the Southern Bight of the North Sea would have released *Pseudocalanus* for larvae and postlarvae in the main feeding area between the Dogger and Fladen, the larger stages of *Calanus* would have been released by the decrease in adult herring.

In Table 1 is given an estimate of the demand for the released herring food by larval cod. Let herring die at 4% per day and grow at 5% per day for a period of 60 days; let cod die at 10% per day and grow in weight at 12% per day. The initial number of herring larvae before the decline was $30/m^3$ (Cushing and Bridger, 1966) and that of cod larvae after the gadoid outburst was $0·01/m^3$ (D. Harding, personal communication). The ratio of cod biomass after the outburst to that of herring before decline is very small. In other words, the decline of herring released more food than needed by the cod by a factor of more than three orders of magnitude. Hence the bulk of food must have been transferred to animals other than cod. Did the cod benefit from the very large increase of food to cod larvae in the Southern Bight in such a way as to affect the whole North Sea population?

There is no evidence that the outstanding year classes of cod originate on the spawning ground off Texel Island and nowhere else. From Daan's figures (Fig. 2a, b), this ground is of less importance than those around the Dogger or near the Aberdeen Bank. Dickson, Pope and

Table 1. The relative demand for food by cod and herring larvae in the Southern Bight of the North Sea

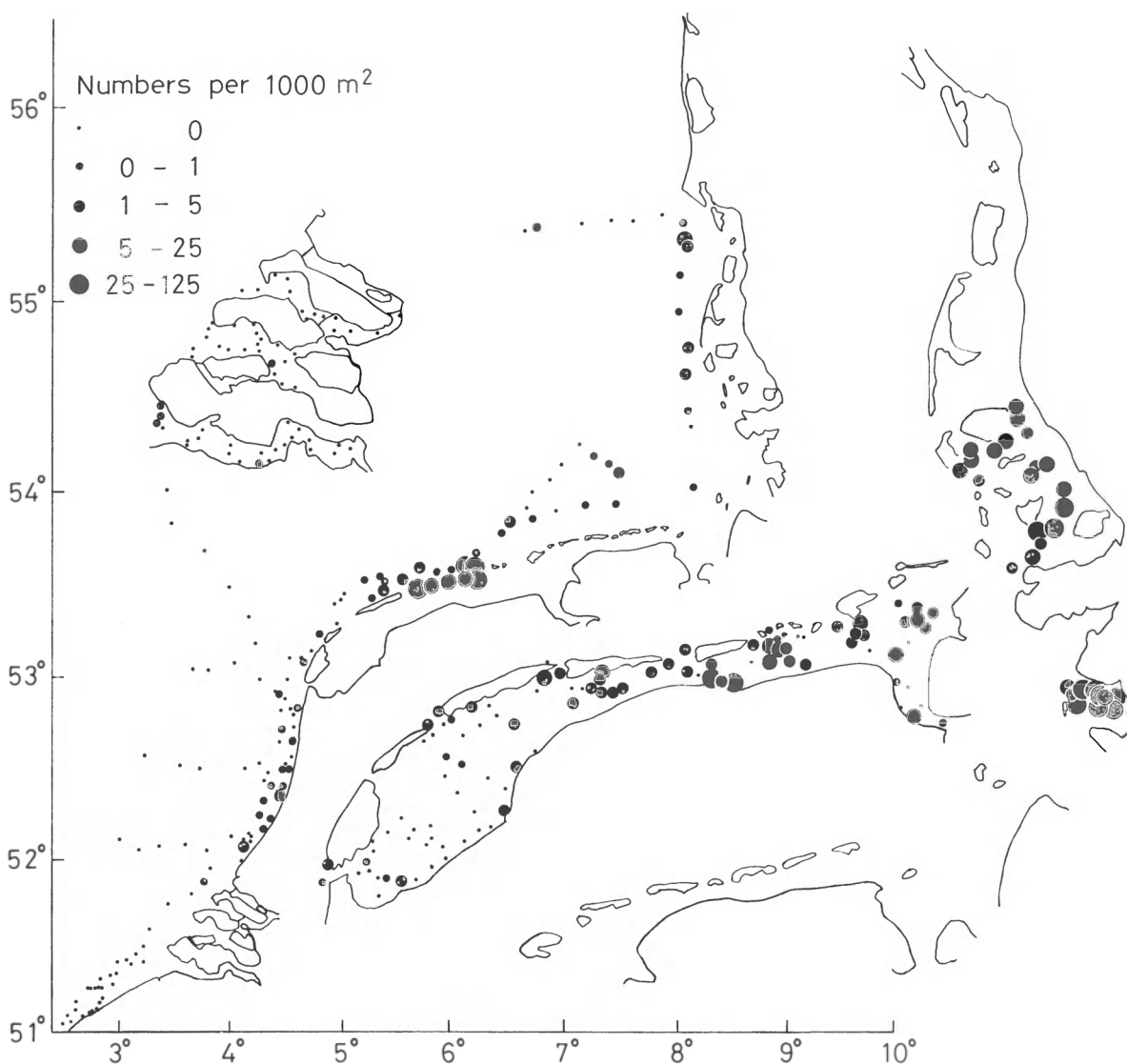| Days | No. of larvae/m^3 | | Ratios | | |
	Herring larvae before collapse of stock	Cod larvae after gadoid outburst	Herring: cod Nos.	Herring: cod wt	Cod: herring biomass
0	30·0	0·0100	3 000	1·00	0·00033
10	20·1	0·0037	5 432	0·50	0·00037
20	13·5	0·0014	10 140	0·25	0·00040
30	9·0	0·00051	18 000	0·12	0·00046
40	6·1	0·00019	33 300	0·06	0·00050
50	4·1	0·000069	61 500	0·03	0·00059
60	2·7	0·000026	115 800	0·015	0·00058

Figure 4. The distribution of juvenile cod (less than 17 cm in length) as determined from beam-trawl catches and expressed as numbers per 1000 m^2 in the Waddensea and along the continental coast in September and October 1970 (from Daan, 1978, Fig. 47b).

Holden (1974) have established a correlation between year-class strength and temperature on a line from the Spurn across the Dogger, which suggests that the spawning grounds around the Dogger originate at least part of the outstanding year classes.

Mature herring eat adult and copepodite stages IV and V of *Calanus* (Savage, 1937). Hence the decline of herring on the feeding grounds would have led to an increase in the natural mortality of large *Calanus* or its exploitation by another predator. Can the increase in cod be attributed to the increase in *Calanus* available in May and June after the decline of the herring stocks?

Cod do not feed on the larger *Calanus* until they are 15 mm in length (T. Wyatt, personal communication), i.e. after metamorphosis, and they start to feed on fish when they are about 30 mm in length. If the year class is determined during larval life (before 15 mm), the gadoid outburst was not affected by this release of food. If however, the growth of cod postlarvae were density dependent between the lengths of 15 and 30 mm (or, in effect, year-class strength were determined after the larval drift), then the addition of food would increase growth rate and perhaps decrease mortality rate and thence increase recruitment. Hence the mechanism of year-class determination is extended into the post-metamorphic part of the life cycle.

In the southern North Sea, food released by the loss of herring larvae becomes available for other fish larvae (such as plaice, sand-eels, etc) as well as gadoids, adult pelagic fish such as sprats and mackerel and also in large quantities to planktonic predators (copepods, ctenophores, jellyfish, pelagic polychaetes, etc). In the central North Sea the food released by adult herring becomes available to the same set of predators. Steele (1965) suggests that three quarters of the pelagic herbivores are taken by "other carnivores" and one quarter by pelagic fish. The thesis put forward by Andersen and Ursin (1977) might suggest that the released food could be taken by this sector equally as by the gadoids. Summarizing, the release of food by the decreased herring stocks might have had an effect on the post-metamorphic stocks of gadoid fish in the central North Sea.

Relaxed predation

Herring can only eat cod as larvae or post-larvae, i.e. up to 5 or 6 cm, and only the adults or near adults can take them. The potential predators would have been the adult herring of the Downs and Dogger stocks that declined in abundance during the late fifties and early sixties; the decline in the Buchan/Shetland stock was too late to start the gadoid upsurge. Adult herring of the Dogger stock do not live on the main cod spawning grounds in the southern and central North Sea in spring; they overwinter on the edge of the Norwegian deep water and from there they migrate to their feeding grounds in summer in the northern North Sea (Parrish and Saville, 1965). They may, however, take the small

proportion of cod larvae in the northern North Sea (Fig. 2). Hence the relaxed predation due to the decline of the Dogger stock could account for only a small part of the gadoid upsurge.

The adult Downs herring migrate northwards across the cod spawning ground off Texel to the Flamborough Off-ground in spring (Cushing and Bridger, 1966) and they could well take cod eggs and larvae from two cod spawning grounds on this migration. Hardy's records (1924) refer to < 10 gadoid larvae or postlarvae in April and May off Lowestoft and off Shields (including intermediate points) in 2000 herring stomachs. Savage's fuller study (1937) when the Downs stock was still abundant reveals 34 postlarvae in 1500 stomachs off Shields between 1930 and 1934 of which 9 were gadoids. In the same guts, 1588 sand-eels and 11 pleuronectids were found. In the spring herring fishery off Lowestoft, 1982 sand-eels were found in 200 herring stomachs. Each stomach content represents about a thousand encounters and the chance of encountering of a fish larva is (where the daily chance of encounter is $[(n/\text{gut})/n \cdot \text{guts}] \cdot 10^{-3}$) as follows:

Fish	Daily chance of encounter
Sand-eels	0·001060
Pleuronectids	0·000074
Gadoids	0·000006

During the spring, the pleuronectids in guts were ten times as abundant as the gadoids off Shields and around the Dogger sand-eels were nearly two hundred times as abundant. From our present knowledge of the stocks, these ratios do not represent stock ratios in the thirties; for example, the pleuronectid stock west of the Dogger was probably very much smaller than the cod stock. Hence the numbers of gadoids were underestimated by the stomach samples, not because the herring could not catch them, but perhaps because they did not properly coincide in space and time. The relaxed predation by the decline of herring around the Dogger and in the Southern Bight may not have had much effect on the growing cod larvae.

Juvenile and Dogger herring might take cod postlarvae as they drift towards the eastern nursery ground, including the Bløden Ground. The herring there are between 5 and 15 cm in length and as they grow larger than 15 cm, they migrate away into deeper water (Bertelsen and Popp Madsen, 1954). The Dogger and Buchan/Shetland herring move off northward in September and October on the edge of the Norwegian deep water. The Downs herring move away southeastwards in February reaching the Silver Pit and the Shields area in April (Cushing and Bridger, 1966).

There are two opportunities for predation (a) when the cod postlarvae arrive on the eastern nursery ground
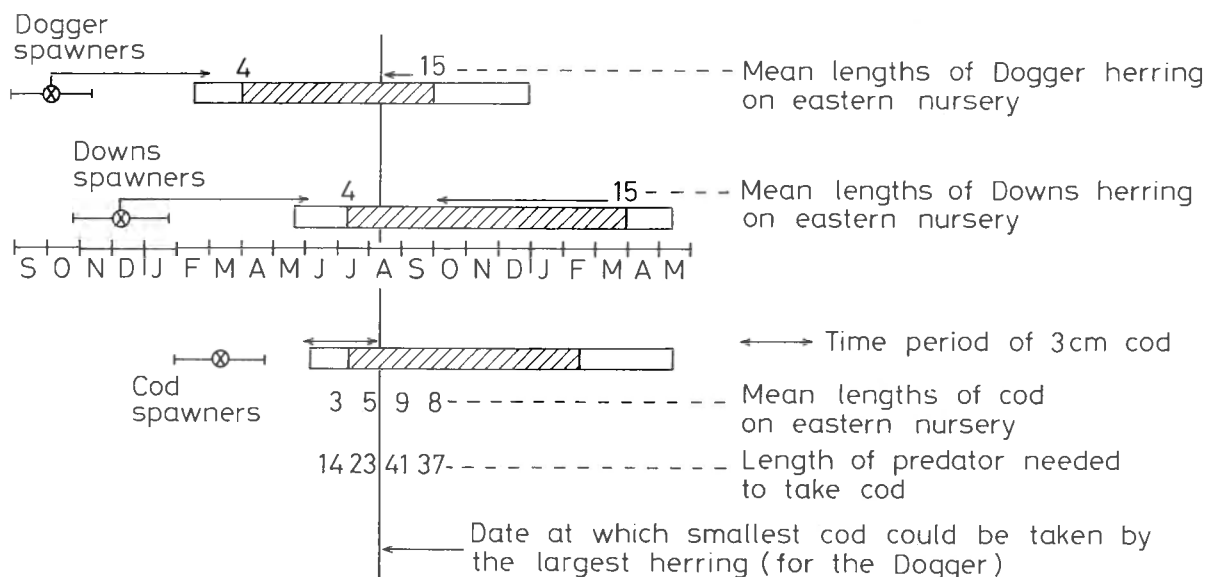
Figure 5. The temporal distributions of cod and herring (of the Downs and Dogger stocks) on the eastern nursery ground. The hatched rectangles represent the periods of life on the nursery ground (between 4 and 15 cm for herring). The circled crosses in horizontal bars represent the spawning seasons. The vertical line in early August represents the critical date later than which the growing 0-group cod could no longer be taken by I-group herring.

in July (b) when the juvenile herring leave in September or February. Figure 5 represents the appearance in time of different length groups of herring and cod on the eastern nursery ground. The spawning periods of cod and of both the herring stocks are shown. The times of arrival and departure from the nursery ground are given with some indication of the spread in time of the appearance of a particular length group. The mean lengths of herring at different times are also given as are those of cod from July to September (Graham, 1929).

Ursin (1973) reported that the average ratio of weight of predator to that of prey is 100:1; in length, this ratio is 4·57:1, provided that the proportionality constants of prey and predator are about the same. Beneath each length of young cod between July and September is given the length raised by a factor of 4·57, i.e. the average length of predator needed to take the cod. There is a critical date in early August, by which the cod have grown out of the attack range of any herring on the eastern nursery ground. Before that date, the Downs herring hatched in the same year are if anything smaller than the cod as they arrive on the nursery ground, despite the fact that the herring were hatched three to four months earlier. The specific growth rate of the cod larvae during the larval drift is 2 to 3 times greater (Cushing and Horwood, 1977). Before that critical date, the Dogger juveniles are not large enough to take the cod; only the very largest Dogger herring could take the cod as they arrive and because they represent the upper tail of the length distribution, there will not be enough of them.

After the critical date, the cod will have grown out of the predatory range of all the herring on the eastern nursery ground. The only place at which relaxed predation can then become effective is where the juvenile herring leave the nursery ground and migrate towards the feeding ground. The Dogger and Buchan/Shetland juveniles leave to the north and northeast in September and October, reaching the adult feeding ground in the following spring, where only a few cod larvae (in the northern North Sea) would be vulnerable. Because the Downs juveniles leave in spring and move towards the Silver Pit and the Shields area in April, they are the only potential predators of real importance, but the cod larvae were not recorded in the herring guts during the period of abundance in the Shields fishery, as noted in the section on release of food.

The relaxation of predation by the Downs herring might have allowed the gadoid larvae to increase in numbers on their way to the nursery ground. Of year classes hatched in the same year, the individual cod are bigger than the herring and herring of the previous year class are not quite big enough to exploit the cod effectively before the critical date. The real point is that the herring starts migrating at 15 cm in September and October and they reach that critical length too late. However, the larger I-group herring might still have taken the smaller 0-group cod and this represents the most likely form of relaxed predation that took place.
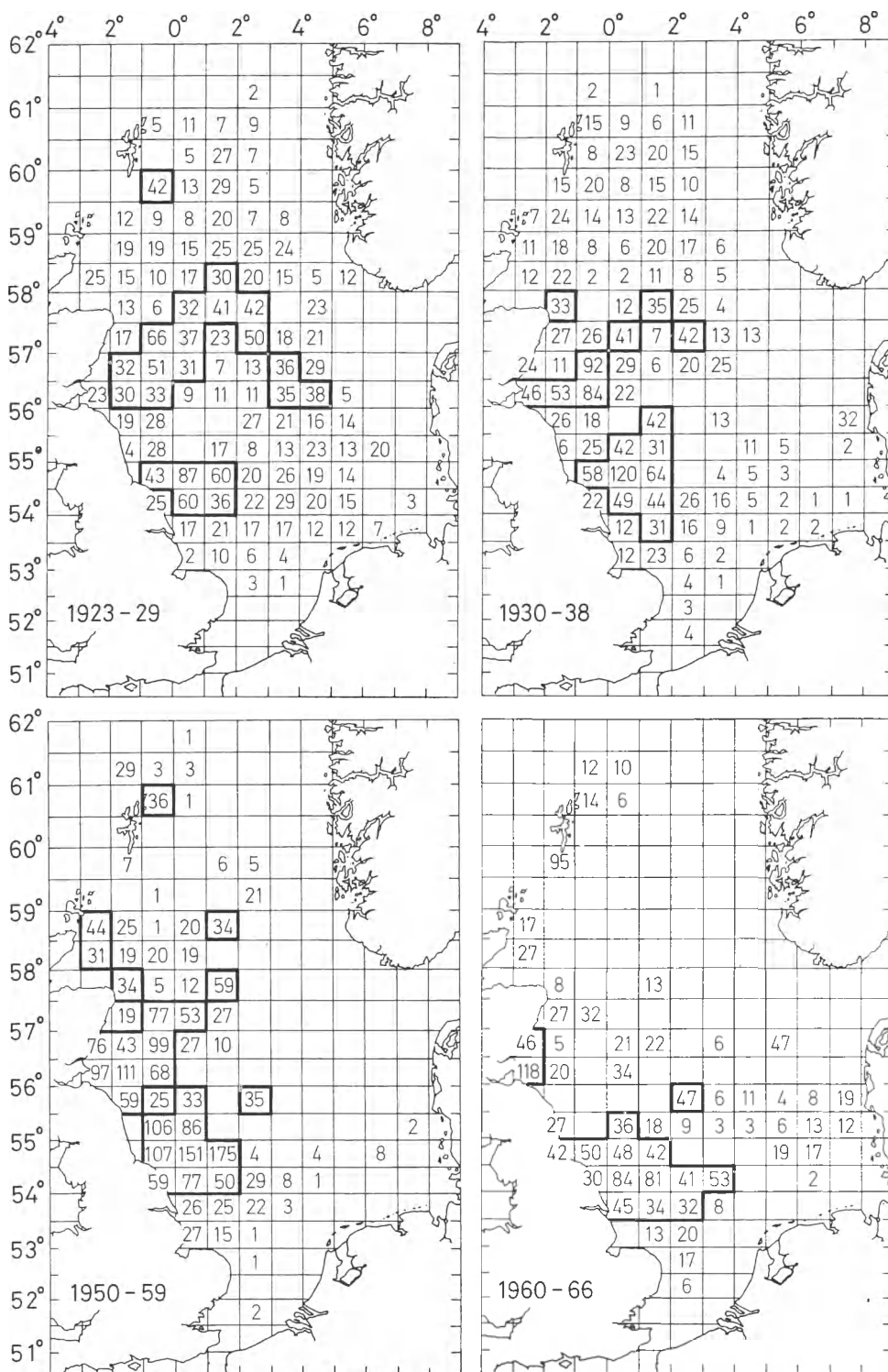
Figure 6. The spawning grounds of cod in the North Sea during four decades as indicated by the capture by British trawlers of the market category *large cod* in March. Catch rates are given in cwt/100 h fishing for those statistical squares in which the total catch was 250 cwt or more. Squares with mean catch rates of 30 or more cwt/100 h fishing are bounded by bold lines. From data held at the Fisheries Laboratory, Lowestoft.

A possible shift in the cod spawning ground in the North Sea

From Figure 2b there are four main cod spawning grounds, Aberdeen Bank, Middle Rough, Outer Rough and Southern Dogger (from the Flamborough Off-ground to just north of the Clay Deep). There are some differences between Graham's (1934, Fig. 24) distribution of spawning and Daan's (1978, Fig. 2b). The spawning patches on the Great Fisher Bank and Aberdeen Banks are in the same position but that on the Ling Bank has decreased. Figure 6 shows the average catch per unit effort by English trawlers in statistical squares in March (to indicate spawning grounds) by decades, 1923–1930, 1931–1939, 1951–1959, 1960–1966. In the course of time, the spawning grounds on the Aberdeen Bank, the Greater Fisher Bank and Ling Bank declined in importance and those around the west, north and east Dogger increased; that in the Southern Bight was not recorded because English trawlers did not fish for cod there. The cod spawning grounds may have shifted to the southward since the twenties and the gadoid upsurge was perhaps associated with such a re-distribution. Dickson et al. (1974) have shown that the increase in year-class strength was correlated with a decrease in temperature particularly near the western Dogger in March and April. The southerly shift of spawning may be associated with such phenomena.

The increase in all gadoids in the North Sea

Figure 7 shows the increase in gadoid biomass in the North Sea between 1959 and 1970 (Andersen and Ursin, 1977). All species increased in stock at about the same time and about the same rate. If the increase in cod was associated with the decline in the herring in the southern and central North Sea, we have to account for the increase in haddock which lives in the northern North Sea. The high haddock year classes occurred in 1962, 1967 and 1974 and even that in 1967 was hatched before any real decline in herring catches had occurred. Jones and Hislop (1978) have shown that the whiting and haddock year classes are correlated for a long period, yet the whiting tends to be an eastern and central North Sea species that potentially could have taken advantage of the decline in herring stocks. The increase in coalfish parallels that of the cod almost exactly, yet it lives on the northern shelf edge of the North Sea where the Buchan/Shetland stock was found during the sixties at the highest level of abundance. The Norway pout increased in stock during the same period at the same rate, and they live in the same region as the haddock.

Figure 8 shows the increase in the biomasses of the gadoid stocks on a logarithmic scale. The rates of increase are the same between stocks throughout the de-

cade which suggests a general gadoid upsurge across the whole North Sea and shelf area, rather than an increase in cod as the herring declined. As shown in Table 2, the coalfish and the cod march in step as do the haddock and whiting (the herring stocks in the southern and central North Sea are not included because they had already declined by 1959). The correlation between cod and coalfish is striking because the coalfish live on the northern shelf edge where herring were abundant during most of the sixties and yet the cod lives in the central and southern North Sea. Similarly the correlation between haddock and whiting, already noted, is of importance when it is recalled that they live in the northwestern and southeastern North Sea respectively; whiting lives in a region of herring decline and haddock in one of herring abundance. Lastly Brander (1977) has shown
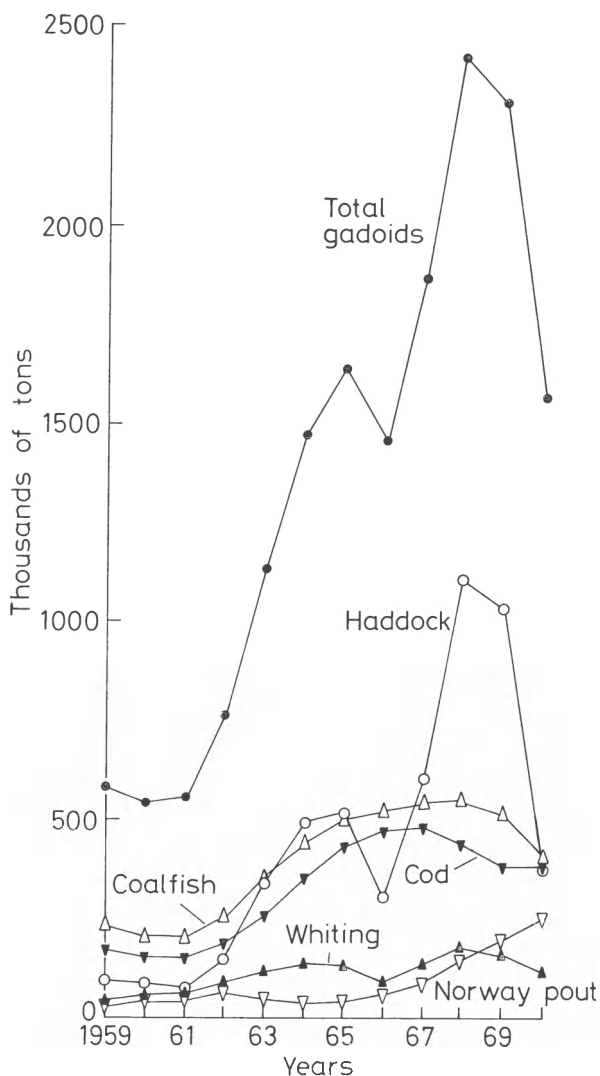

Figure 7. The gadoid outburst: biomass in thousands of tonnes, arithmetic scale.
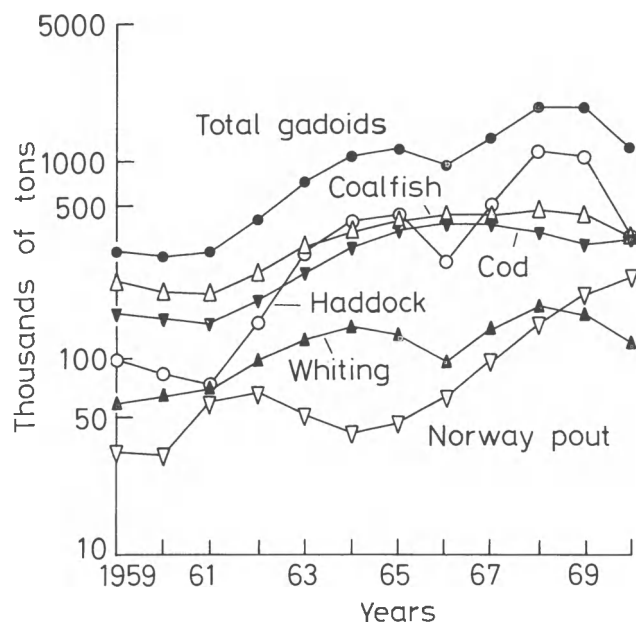
Figure 8. The gadoid outburst: biomass in thousands of tonnes, logarithmic scale.

that a gadoid upsurge occurred in the Irish Sea which probably started in the late fifties. There is no major industrial fishery in the Irish Sea.

The evidence seems to point to a more general explanation for the gadoid upsurge than the decline in herring stocks. Templeman (1971) has classified the year classes in gadoid stocks in the North Atlantic between 1940 and 1970; the quantities are based on catch per unit of effort or on cohort analysis and each year class of each stock was scored on an arbitrary scale of one to five. Figure 9 shows the total "reproductive potential" of all gadoid stocks in the North Atlantic which reached a peak in 1950 after which it declined. The recent period of warming also peaked at about that time and subsequently a period of deterioration followed, at least until 1971. The same pattern is shown separately in the northwest and northeast Atlantic. As the reproductive potential in the northeast Atlantic declined, it increased in the North Sea. Perhaps the gadoid upsurge in the

North Sea has a widespread origin, associated with climatic changes.

The increase in sand-eel stocks

Andersen and Ursin (1977) have suggested that the increase in sand-eel stocks was associated with the decline of herring and mackerel in the late sixties. Macer (1967) has shown that there are differences in growth rate and year-class strength between rather small areas in the North Sea and the same conclusion emerges from material taken in Canadian waters (Scott, 1968). Popp Madsen (1978) has shown that sand-eels do not migrate from the regions in which they spawn, e.g. Dowsing, southwest Dogger or the Danish coast. Each may comprise a distinct spawning group or stocklet.

Figure 10a (Popp Madsen, 1978) demonstrates the trend in catch per unit of effort in recent years on the traditional grounds in the central and southern North Sea. Figure 10b shows the trends in catch per unit of effort on the Viking Bank and in the northern North Sea. Stocks on the traditional grounds were tending to decline and the fishermen discovered new ones in the early seventies. The increase in stock in the seventies observed by Andersen and Ursin (1977) may be only an exploration by the fishermen independently of the decline of herring and mackerel at the same time.

Discussion

This paper was stimulated by the multispecies model developed by Andersen and Ursin (1977) which suggested that the reduction of herring and mackerel stocks in the northern North Sea might be responsible for the increase in Norway pout and sand-eels, and by implication the more general gadoid outburst. The general thesis was that if the productivity of the North Sea has remained the same, the reduction of one fish stock must divert food to another, causing an increase in stock. The implication is that if industrial fisheries sustain themselves on protein, the protein system cannot be overexploited. They suggest that there were two ways of preventing the collapse of the North Sea herring

Table 2. Correlations between stock estimates of five gadoid species in the North Sea, 1959–1970 (stock estimates from Andersen and Ursin, 1977, Table 24).

Coalfish	Cod	Haddock	Whiting	Norway pout	
–	0·975**	0·814**	0·853**	0·414	Coalfish
		0·704**	0·765**	0·430	Cod
			0·933**	0·583*	Haddock
				0·524	Whiting
				–	Norway pout

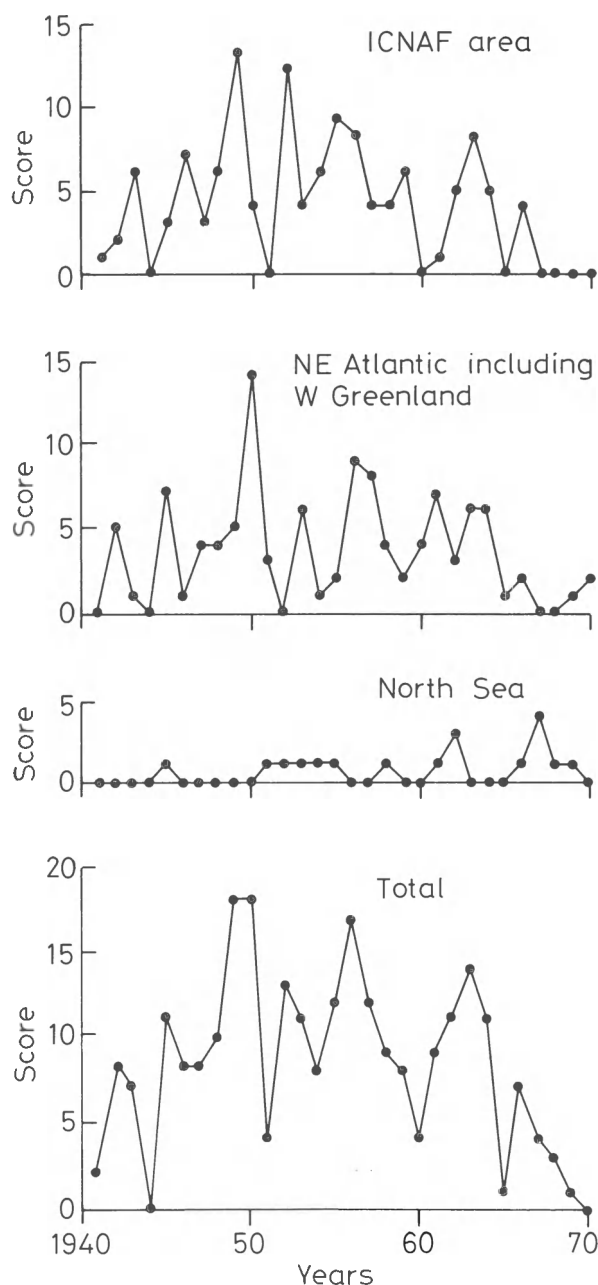* 5% level of significance, ** 1% level of significance.

Figure 9. The "reproductive potential" of gadoid stocks in the North Atlantic between 1941 and 1970 (after Templeman, 1971). Year classes of gadoid stocks were scored one to five and summed for each year. The scores are grouped for the whole ocean, the northwest Atlantic, the northeast Atlantic and the North Sea (Cushing and Dickson, 1976).
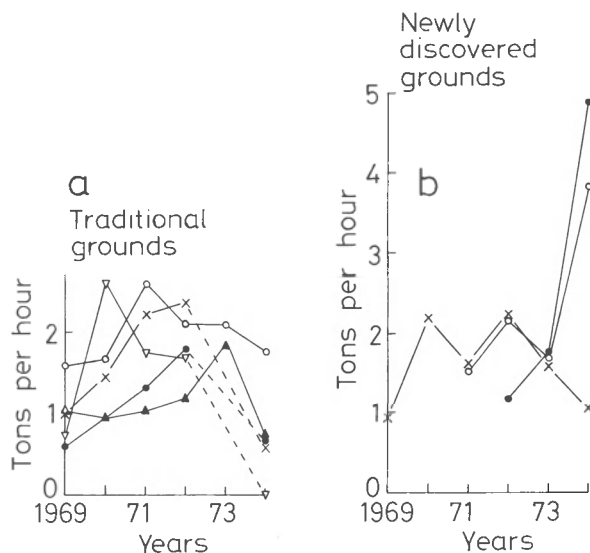

Figure 10. Changes in stock density (as catch per hour) of sand-eel stocks (a) on traditional grounds in the central and southern North Sea and (b) on more recently discovered grounds in the northern North Sea (Popp Madsen, 1978).

stocks, one to reduce fishing effort and the other to increase the effort in other North Sea fisheries. If the latter is true the changes in herring and mackerel stocks are linked to those in the gadoid ones.

The gadoid upsurge might be attributed to the decline of herring stocks by release of food to larval cod from the loss of larval or of adult herring. The most likely recipients of released food amongst the gadoids are the post-metamorphosis cod, but they would have to share the bonus with other predators three times as abundant as the original stock of herring and mackerel. The conclusion is not that the release of food cannot be substantiated, but that the crucial observations needed to justify the simulation model cannot yet be specified, particularly in terms of density-dependent growth amongst postlarvae.

Similarly, relaxed predation is hard to identify. The cod larvae might be eaten by adult herring (or adolescents on their way from the nursery ground) but they were much scarcer in the guts during the period of abundance than might have been expected. They could have been taken on the eastern nursery ground, but the cod were probably already too big when they arrived there. However, there may be an overlap between the distributions of I-group herring and 0-group cod, i.e. the larger herring could eat the smaller cod. Again the crucial observations needed to justify the simulation model cannot yet be specified.

The third possibility is that the gadoid upsurge is of climatic origin quite independent of the interactions between species in the North Sea. The timing of the event during a period of climatic deterioration, the similar events in the Irish Sea and the widespread nature of the increase amongst all gadoid species in different regions of the North Sea combine to support this thesis. If untrue one might have expected some part of the regional mosaic to stand out. However, the possibility that an independent gadoid upsurge was not assisted by the multispecies interaction cannot be ruled

out. Any climatic hypothesis of this type must rest in an increase of food to the gadoids (or decrease in their mortality) as for example expressed in the match/mismatch hypothesis of year-class generation (Cushing and Dickson, 1976). Such a hypothesis assumes that more gadoids were able to take more of the common foods, copepod nauplii, copepodites, etc, rather than somewhat uncommon fish larvae.

More generally, how does the interaction of fish populations affect their individual recruitments, despite the fact that under exploitation such interactions must be reduced to some degree? Before the industrial fisheries started, two million tonnes of fish caught might have eaten ten million tonnes of food. However, let us suppose that the magnitude of recruitment to the non-industrial fish stocks is unaffected by fishing and that the growth of individuals in the exploited adult stocks is density independent. The food released by exploitation of the human consumption fisheries is adult food, fish and crustaceans for cod, benthos for haddock, large plankton and small fish for whiting, and worms for sole and plaice. Because the density controls are unaffected, the food released goes elsewhere in the web; at the least, some worms may live longer. Fishing only affects the food web if the density-dependent controls in growth or mortality are affected or if recruitment is reduced by fishing, which may be very much the same thing. Then the problem of the industrial fisheries is really one of those stocks in which the control processes have been affected by fishing, the herring and mackerel, but not necessarily the gadoids.

Recruitment overfishing occurs when not enough eggs are produced by the parent stock and therefore the density-dependent controls are minimal. Such stocks would benefit directly by a transfer of food and recruitment might increase. A stock which does not suffer from recruitment overfishing would not benefit from such a transfer of food. To some degree exploitation isolates fish populations, because competition must be reduced (and indeed cannibalism), but to make them accessible to massive food transfers, they must be overexploited.

Andersen and Ursin (1977) suggest that changes in demersal and pelagic stocks are linked throughout the North Sea assuming no spatial or temporal segregation of stocks. Such segregation is investigated in this paper in terms of food release from and relaxed predation by the herring stocks before and during the gadoid outburst. Food might have been released from adult herring to postlarval cod and 0-group cod might have suffered less predation by I-group herring. However, we need to be able to put such information in quantitative terms in the stock and recruitment relationships of cod and herring. An alternative explanation, that the gadoid outburst was initiated by climatic factors is more general and requires a similar transfer of food, but not in quite so specific terms; in other words it could have been drawn from the planktonic reserve.

References

Andersen, K. P. & Ursin, E. 1977. A multispecies extension of 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.

Anon. 1909. Spawning conditions and spawning places of the gadoids. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 10: 44–87.

Anon. 1976. Fishing Prospects, MAFF Direct. Fish. Res., Lowestoft, 1975–1976. 59 pp.

Anon. 1977. Young Fish Surveys. Report of the Gadoid I-group Working Group. ICES CM 1977/F:19, 44 pp. (mimeo).

Bertelsen, E. & Popp Madsen, K. 1954. Young herring from the Bløden ground area. Annls biol., Copenh., 10: 155–6.

Brander, K. M. 1977. The management of Irish Sea fisheries – a review. Lab. Leafl., MAFF Direct. Fish. Res., Lowestoft, 36, 40 pp.

Burd, A. C. 1978. Long-term changes in North Sea herring stocks. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 172: 137–53.

Cushing, D. H. & Bridger, J. P. 1966. The stock of herring in the North Sea and changes due to fishing. Fishery Invest., Lond., Ser. 2, 25 (1): 123 pp.

Cushing, D. H. & Dickson, R. R. 1976. The biological response in the sea to climatic changes. Adv. mar. Biol., 14: 1–122.

Cushing, D. H. & Horwood, J. W. 1977. Development of a model of stock and recruitment. In Fisheries Mathematics, pp. 21–36. Ed. by J. H. Steele. Academic Press, London, 198 pp.

Daan, N. 1978. Changes in cod stocks and cod fisheries in the North Sea. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 172: 39–57.

Dickson, R. R., Pope, J. G. & Holden, M. J. 1974. Environmental influences on the survival of North Sea cod. In The Early Life History of Fish, pp. 69–80. Ed. by J. H. S. Blaxter. Springer-Verlag, Berlin & Heidelberg, 765 pp.

Graham, M. 1929. Studies of age determination in fish. I. A study of the growth rate of codling (Gadus callarias L.) on the inner herring trawling ground with a section on the relevant hydrography by J. R. Lumby. Fishery Invest., Lond., Ser. 2, 11 (2): 50 pp.

Graham, M. 1934. Report on the North Sea cod. Fishery Invest., Lond., Ser. 2, 13 (4): 160 pp.

Hardy, A. C. 1924. The herring in relation to its animate environment. Part I. The food and feeding habits of the herring with special reference to the east coast of England. Fishery Invest., Lond., Ser. 2, 7 (3): 53 pp.

Jones, R. 1973. Density-dependent regulation of the numbers of cod and haddock. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 164: 156–73.

Jones, R. & Hislop, J. R. G. 1978. Changes in North Sea haddock and whiting. Rapp. P.-v. Réun Cons. int. Explor. Mer, 172: 58–71.

Last, J. 1978. The food of three species of gadoid larvae in the eastern English Channel and southern North Sea. Mar. Biol., 48: 377–86.

Macer, C. T. 1967. Sand-eels (Ammodytidae) in the southwestern North Sea: their biology and fishery. Fishery Invest., Lond., Ser. 2, 24 (6): 55 pp.

Parrish, B. B. & Saville, A. 1965. The biology of the northeast Atlantic herring population. Oceanogr. Mar. Biol. Ann. Rev., 3: 323–73.

Popp Madsen, K. 1978. The industrial fisheries in the North Sea. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 172: 27–30.

Savage, R. E. 1931. The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. Fishery Invest., Lond., Ser. 2, 12 (3): 88 pp.

Savage, R. E. 1937. The food of North Sea herring, 1930–34. Fishery Invest., Lond., Ser. 2, 15 (5): 60 pp.

Scott, J. S. 1968. Morphometrics, distribution, growth and maturity of offshore sand launce (*Ammodytes dubius*) on the Nova Scotia banks. J. Fish. Res. Bd Can., 25: 1775–85.

Steele, J. H. 1965. Some problems in the study of marine resources. Spec. Publ. int. Commn N.W. Atlant. Fish., 6: 463–76.

Templeman, W. 1971. Year-class success in some North Atlantic stocks of cod and haddock. ICNAF environ. Symp., Bedford Inst., Dartmouth, Nova Scotia, 18–19 May 1971. Contrib. 7, 32 pp. (mimeo).

Ursin, E. 1973. On the prey size preferences of cod and dab. Meddr. Danm. Fisk.- og Havunders. (N.S.) 7: 85–98.