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Population Fluctuations and Recruitment in Marine Populations [and Discussion]

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Population fluctuations and recruitment in marine populations

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This paper is not concerned with the effect of oil pollution as such, but sets out to consider the range of natural variation and the extent to which this might mask the effects of other factors such as possible pollutant effects.

To detect the effect of a pollutant (or a change in fishing effort) it is necessary to allow for natural variations, both random and periodic. Some examples are given to illustrate the extent of natural variations, in a variety of marine populations.

For Arcto-Norwegian cod, information is available on catches from about the middle of the last century to the present day. Large catches are about 3–6 times the size of small catches. The difference between large and small catches is about equal to the mean catch. Further, the time taken to change from a small to a large catch level is very variable.

The Greenland cod provides an example of a stock that increased very considerably due to a northerly increase of the limits of distribution of the species. This increase was associated with a warm period in the North Atlantic and with increased catches.

Many fish stocks and in particular many species of pelagic fishes, exhibit much larger fluctuations in stock size, e.g. the Hokkaido herring, the Japanese sardine, the Bohuslan herring, the Atlanto-Scandian herring and the Califonian anchovy and sardine. Fluctuations also occur in invertebrate species and evidence is given of changes that have occurred in North Sea phytoplankton and zooplankton.

The Peruvian anchovy provides an example of a stock that decreased very considerably, due partly to fishing and partly to changes in the hydrographic régime that caused the fish to become more available for exploitation.

Fluctuations in fish stocks are primarily due to fluctuations in recruitment. The factors affecting recruitment are not yet fully understood but are known to be determined during the first year of life and probably during the larval or early juvenile stages. Whatever the mechanism, however, it is the variations in recruitment that determine a very large part of the variations in adult fish stocks and hence it is variations in recruitment and the causes of these that are important.

In conclusion, the examples show that natural communities can exhibit large natural fluctuations, of varying periodicity, in the long term. Apart from incidents where there is gross pollution, an effect of pollution can therefore only be convincingly demonstrated for those species for which background information is available for a long enough period to allow for long-term periodicity as well as for short-term and irregular variability.

INTRODUCTION

A characteristic of natural populations of animals and plants is that they are subject not only to short-term variation but also to longer-term cyclical trends, often of an irregular nature. Because of this, the effect of, for example, the introduction of a pollutant into the environment or of a change in fishing effort cannot be assessed on a short-term basis but can only be assessed after taking account of the natural variation. Only where it can be argued that a population level, after the introduction of a pollutant, is significantly different from what it would have been if the pollutant had not been introduced, can it be concluded that the pollutant has had a significant effect on the population.

FLUCTUATIONS IN POPULATION SIZE AND FLUCTUATIONS IN RECRUITMENT

A characteristic of commercially important marine teleosts is that the life cycle is divided into a number of stages during which the individuals are dependent on very different food sources and are subject to very different environmental factors. For example, the North Atlantic haddock is a species that spends much of its adult life feeding on small, and usually relatively inactive, organisms on or close to the sea bottom. For much of the first year of life, however, this species leads a pelagic existence, starting with a larval stage spent to a large extent in the top 50 m of water, and followed by a juvenile stage during which feeding is characteristically on species of zooplankton in midwater. It is only towards the end of the first year that feeding on the sea bottom begins and the typical adult way of life is assumed.

For most commercially important fish species, it is now reasonably well established that fluctuations in population size are primarily due to fluctuations in the early life history and hence in recruitment (i.e. the numbers of 'recruits' produced annually). Fluctuations in stock size are therefore very largely due to events that occur during the early larval and juvenile stages and are generally less dependent on events that influence the size of the adult stock.

Causes of recruitment are uncertain. What is known is that in general, recruitment is not directly dependent of the size of the spawning stock, but appears to be dependent on other factors, frequently environmental in origin, that affect the fish during the early larval and juvenile stages. Attempts to find correlations between the year class strengths, either of different species in the same area, or of similar species in different areas, have generally led to non-significant correlations (Dragesund 1971; Hennemuth *et al.* 1980; Jones 1977).

SOME THEORETICAL CONSIDERATIONS OF THE EFFECTS OF NATURAL VARIATION

The simplest situation is that depicted in figure 1. This illustrates a hypothetical situation in which a population shows no variation at all, and that initially is constant at the level AB. At time t_1 it is assumed that the population is perturbed in some way, with the result that during the interval from t_1 to t_2 the population declines as depicted by line BC. From time t_2 onwards, the population size remains at a new level CD. In an idealized situation like this, all that is required to detect the effect of the perturbation is a single estimate of population size before t_1 and a single estimate after t_2.

In practice, the situation is not as simple as this owing to natural variations in population size. Figure 2, for example, shows a situation similar to that in figure 1 but with random variations in population size superimposed on the average levels. Thus before time t_1 population size fluctuates about level AB and after t_2 it fluctuates at the level CD. In order to detect the effect of the perturbation, it is necessary to take sufficient samples before t_1 and sufficient samples after t_2 to detect the change in average level by using appropriate statistical techniques. The number of samples required to detect a given difference in levels can be calculated from information obtained from a preliminary sampling programme.

An additional complication is that in addition to short-term fluctuations, there may be long-term cyclical fluctuations in population level. Figure 3, for example, shows a situation in which the average population size is subject to a long-term cyclical fluctuation. Figure 4 shows the situation most likely to be encountered in practice, where there is a long-term cyclical variation with short-term variations superimposed. In order to detect the effect of a perturbation, it is necessary not only to have an estimate of short-term variation, but also a sufficiently long time series of data to allow for the long-term trend.

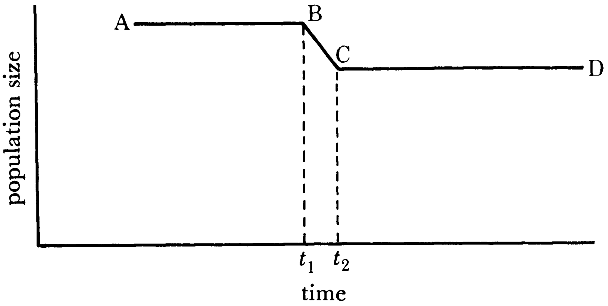

Figure 1. Simple situation in which a stock stabilized at level AB is perturbed and becomes stabilized at a new level CD.

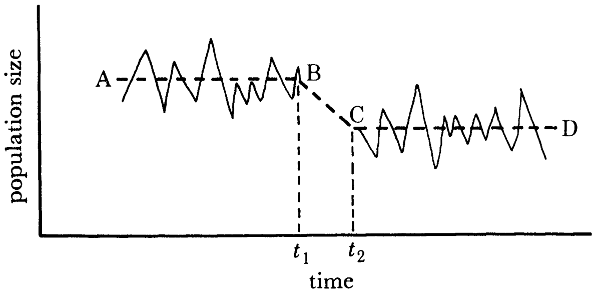

Figure 2. Similar situation to that shown in figure 1 but with random fluctuations in population size superimposed on the average levels.

The system can be said to have been perturbed if the mean population levels after t_2 (i.e. CD) are different from what they would have been if the perturbation had not occurred (e.g. EF).

Examples of variations in marine populations

Because of the importance of knowing something about natural variations in populations, the remainder of this paper is concerned with examples, for some populations for which reasonably long time series exist.

Arcto-Norwegian cod

The Arcto-Norwegian cod provides a good example of a species for which there is a relatively long historical catch record. Before the last war, Arcto-Norwegian cod were traditionally caught by line vessels during an annual fishery for pre-spawning fish in the vicinity of the Lofoten

Islands. Data from Rollefsen (1954) have been used to calculate total catch from information about numbers caught and the average masses of individual fish for the period 1880–1945. Details are given in table 1 for selected years representing an approximate sequence of large and small catches in the fishery. After the war, trawling for cod extended throughout the northeast Arctic and catches from 1946 to 1978 in table 1 are taken from I.C.E.S. (1970, 1981).

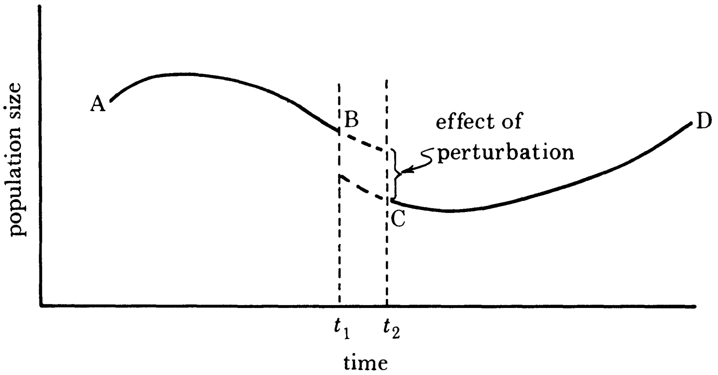

FIGURE 3. Similar to figure 1 but with population size subject to long-term cyclical variation. A perturbation over the period from t_1 to t_2 displaces the two parts of the cycle relative to each other.

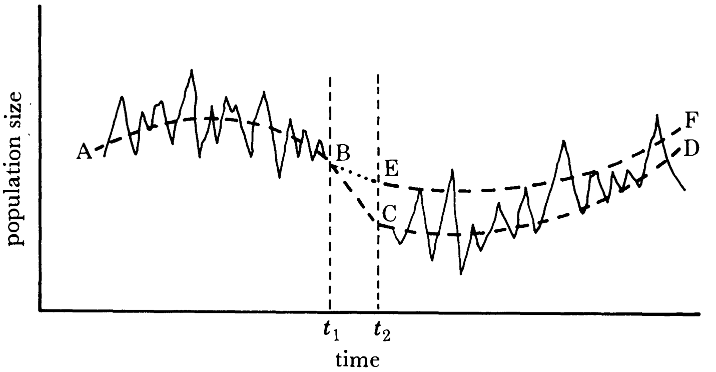

FIGURE 4. Situation normally encountered in practice in which population size is subject to both long-term cyclical variation and also short-term random variations. A perturbation during the period from t_1 to t_2 causes the post-perturbation mean level (shown by CD) to be different from what it would yave been in the absence of perturbation (shown by EF).

These data are also plotted in figure 5. Estimates of weights landed (table 1) show that over the post-war period, the yield has fluctuated between about 450 kt and about 1300 kt so that large catches are about three times the size of small catches. The ratio has, if anything, been greater for the pre-war period, when the fishery was essentially a line fishery at Lofoten.

For the entire post-war period the average catch is 809 kt. Also to a first approximation, the difference between the large catches and the small catches is about 850 kt, which is about equal to the average catch. The time taken to change from a small to a large catch is variable, the most rapid change being from 1965 to 1969 when the catch changed from 445 to 1197 kt in only 4 years.

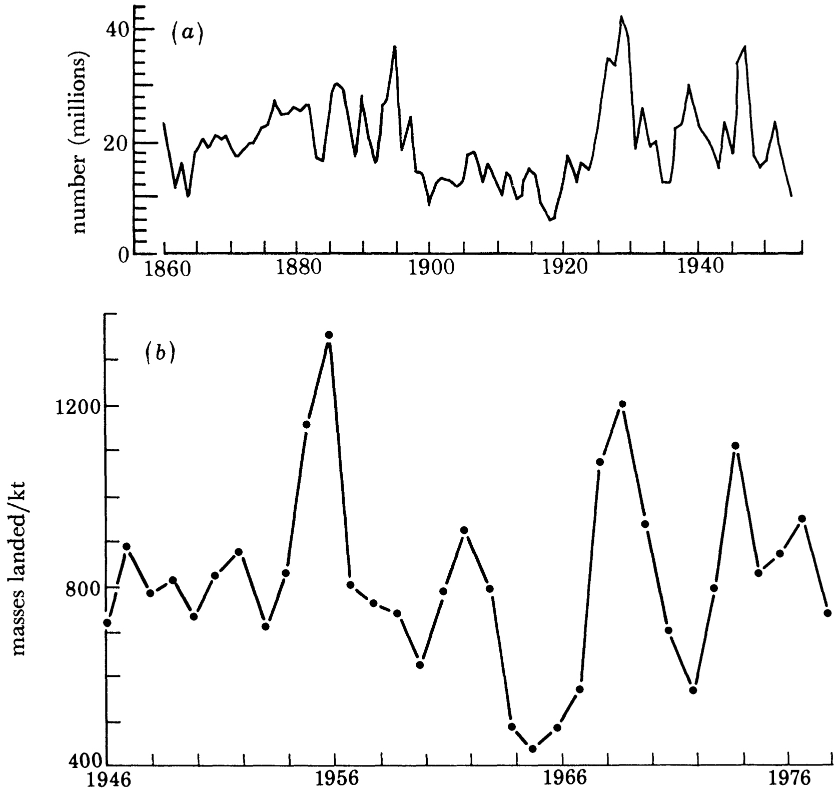

FIGURE 5. Fluctuations in the landings of Arcto-Norwegian cod. (*a*) Numbers landed in the Lofoten fishery from 1860 to 1955; (*b*) masses landed in the whole of the northeast Arctic cod fishery for the period 1946–1978.

TABLE 1. ARCTO-NORWEGIAN COD NORMINAL CATCHES FOR SUB-AREA I PLUS DIVISIONS II*a* AND II*b*

year	numbers caught (millions)	average mass kg	catch kt	year	catch kt	year	catch kt
1880	26	2.6	68	1946	706	1960	622
1892	17	2.9	49	1947	882	1961	783
1895	38	2.1	80	1948	774	1962	909
1900	10	3.2	32	1949	800	1963	776
1906	19	2.0	38	1950	732	1964	478
1918	6	2.9	17	1951	827	1965	445
1929	42	3.2	134	1952	877	1966	484
1935	14	4.0	56	1953	696	1967	573
1939	30	3.8	114	1954	826	1968	1074
1945	20	3.6	72	1955	1148	1969	1197
				1956	1343	1970	933
				1957	793	1971	689
				1958	769	1972	565
				1959	744	1973	792
						1974	1102
						1975	892
						1976	867
						1977	905
						1978	699

Sources of data: 1880–1945, Rollefsen (1954), for successive high and low years; 1946–59, I.C.E.S. (1970); 1960–76, I.C.E.S. (1981).

Pelagic fisheries with long historical records

There are four pelagic fisheries in particular for which relatively long historical records are available. These are the Norwegian or Atlanto-Scandian herring, the Swedish or Bohuslan herring, the Japanese sardine and the Hokkaido herring. Detailed catch statistics are not available but information is available showing an alternation of good and bad periods in the fisheries. These records are summarized in figure 6, which is taken from Cushing & Dickson (1976).

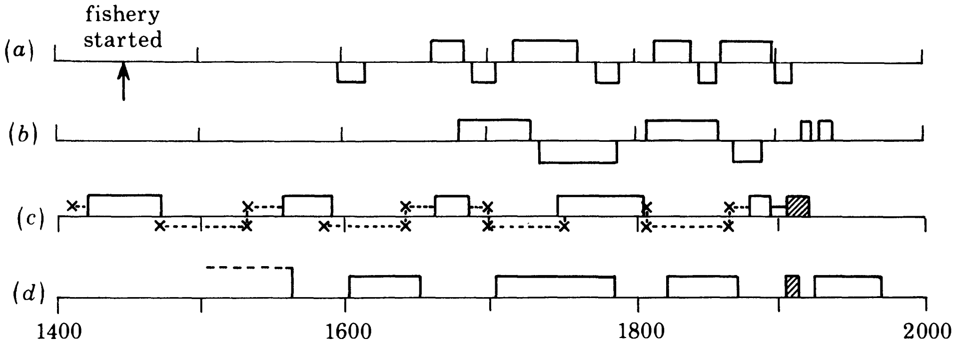

FIGURE 6. Periods of good and bad years for four pelagic fish stocks (from Cushing & Dickson 1976). (*a*) Hokkaido herring; (*b*) Japanese sardine; (*c*) Bohuslan herring; (*d*) Atlanto-Scandian herring.

Records of the Hokkaido herring fishery extend back to 1447 and information is given by Cushing and Dickson (1976), quoting Uda (1952, 1957). Figure 6 shows an alternation of poor periods and good periods in the fishery for several hundred years.

For the Japanese sardine there are records of similar fluctuations for good and bad periods since the beginning of the 18th century (Cushing & Dickson 1976, quoting Uda 1952, 1957).

The Bohuslan or Swedish fishery is for overwintering North Sea herring on the Bohuslan coast. Catches show a periodicity of about 110 years (Cushing & Dickson 1976).

For the Atlanto-Scandian (or Norwegian) spring spawning herring, Cushing & Dickson (1976) show an alternation of good and bad periods from 1500 to 1968.

Cushing & Dickson (1976) comment on the extent to which the fluctuations in these fisheries have happened to coincide. In particular it has been well known for a long time that good periods in the Norwegian spring fishery have tended to coincide with poor periods in the fishery for Bohuslan herring. Beverton & Lee (1965) point out that the periods of the Norwegian spring herring fishery were correlated with the periodicity of ice cover north of Iceland and have suggested that this implies a link with climatic events.

To a first approximation, peak catches for the Japanese sardine fishery tend to coincide with those for the Norwegian spring herring fishery and to alternate with those for the Bohuslan herring.

Cushing & Dickson (1976) refer to data from Zupanovitch (1968) on the records of Adriatic sardine since the sixteenth century (table 2). It appears that the Adriatic sardine experienced a periodicity like that of both the Japanese sardine and also the Norwegian herring.

Another pelagic species for which a relatively long time series is available is the Pacific mackerel, and Troadec *et al.* (1980) give details of catches of commercial landings from 1926

Table 2. The periods of good and poor fishing in the Adriatic sardine and Japanese sardine stocks (Cushing & Dickson 1976)

(+ and − signs indicate positive and negative deviations from the mean, respectively.)

Japan	Yugoslavia
1500–1600	1533^{++}–1588^{++}
$1680–1730^{+}$	$1670–1730^{+}$
$(1716–1724^{+++})$	$(1718–1725^{+++})$
$1736–1789^{-}$	$1730–1780^{-}$
$(1760–1780^{---})$	(1775^{---})
1830^{+++}	$(1830–1840^{+++}$
$(1880–1884^{---})$	$(1878–1882^{---})$
$1917–1921^{+}$	$1919–1921^{+}$
$1929–1939^{+++}$	$1929–1940^{++}$
$1941–1957^{-}$	$1946–1955^{-}$

Table 3. California: commerical landings (kilotonnes) of Pacific mackerel (Troadec *et al.* 1980)

(Figures for 1926–1966 from Kramer (1969), and for later years from *F.A.O. yearbook of fishery statistics*, vol. 42 (1977).)

year	U.S.A.	Mexico†	total
1926	2	—	—
1927	2	—	—
1928	16	—	—
1929	26	—	—
1930	8	—	—
1931	6	—	—
1932	6	—	—
1933	32	—	—
1934	52	—	—
1935	67	—	—
1936	46	—	—
1937	28	—	—
1938	36	—	—
1939	37	—	—
1940	55	—	—
1941	36	—	—
1942	24	—	—
1943	34	—	—
1944	38	—	—
1945	24	—	—
1946	24	(1)	—
1947	21	(3)	—
1948	18	(0)	—
1949	23	(2)	—
1950	15	(4)	—
1951	15	(2)	—
1952	9	(2)	—
1953	3	(2)	—
1954	12	5	17
1955	11	10	21
1956	23	13	36
1957	28	(16)	—
1958	13	(1)	—
1959	17	(1)	—
1960	17	(3)	—
1961	20	6	26
1962	22	3	25
1963	18	10	28
1964	12	9	21
1965	3	9	12
1966	2	5	7
1967	1	1	2
1968	1	0	1
1969	1	0	1
1970	0	0	0
1971	0	1	1
1972	0	0	0
1973	0	0	0
1974	0	0	1
1975	0	2	2
1976	0	2	2

† There are no records of Mexican landings before 1946. Parenthesized figures for years after 1946 refer to combined landings of mackerel and jack mackerel.

to 1976 (table 3). This species is distributed throughout the region of the California current and has been subject to varying degrees of exploitation throughout this period. They were first caught for canning in the 1920s in California and until the 1960s catches were mostly in the range 20–40 kt per year. The peak catch was 67 kt in 1935. Since 1963 the fishery has collapsed, and directed fishing for mackerel has been prohibited in California since 1970.

The Californian sardine and anchovy

There are three stocks of sardine and anchovy in the California current region, which is an upwelling zone extending along the west coast of North America from Vancouver Island to the southern tip of Baja California (Mexico) (Troadec *et al.* 1980).

Of the various stocks it is the northern stock of sardine that is most important of the sardine stocks and the one that has been most intensively studied. For the anchovy, the central stock is larger than the other two combined, and has been the main object of commercial interest and scientific study in recent years (Troadec *et al.* 1980).

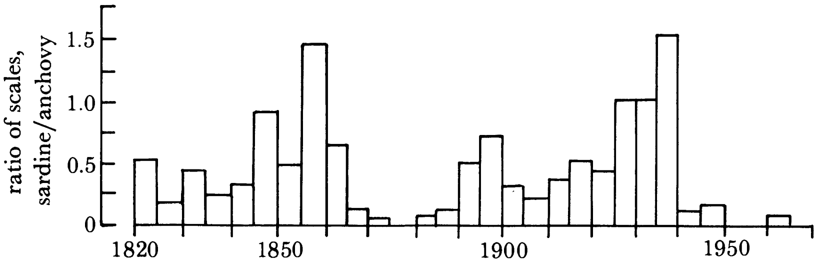

FIGURE 7. Ratios of sardine to anchovy scales in anaerobic sediments off the coast of California (from Soutar & Isaacs 1974).

Historical records of the relative abundances of these and other species in the same area have been studied by Soutar & Isaacs (1974). This was done by noting the abundance of sardine and anchovy scales in anaerobic sediments, and this has provided information on the relative abundance of these species over a period of about 150 years.

For the Pacific sardine, records from the Santa Barbara Basin show variations in the annual rate of scale deposition from 1 to about 15 scales per 1000 cm^2, compared with an intermediate rate of about 5. If we use scale deposition rate as an index of stock size this would suggest that stock size has varied by a factor of about 15.

In the case of the northern anchovy, also in the Santa Barbara Basin, the annual scale deposition rate per 1000 cm^2 has ranged from about 2 to 20, suggesting a variation in stock size by a factor of about 10. Figure 7 shows how the relative abundances of sardine and anchovy have varied, based on the ratio of numbers of sardine to anchovy scales in sediments off California.

In general, it appears that good and bad periods appear to coincide in the Norwegian herring, the Japanese sardine, the Adriatic sardine and also the Californian sardine fisheries. Cushing & Dickson (1976) concluded from this that there are common periodicities in a number of fish stocks that are widely separated geographically and that this might be indicative of a widespread effect of climatic change.

Post-war changes in various fish stocks

Since World War II, owing to a great increase in research effort on many stocks throughout the world, detailed information is available showing large changes in some fish stocks over relatively short times. For example, in the California current system, a most noticeable feature has been the decline of the California sardine and the coincidental increase in the anchovy catches (Smith 1972) (figure 8). For the sardine, catches fluctuated around a level of 500 kt during the 1930s and 1940s and then after about 1950 started to decline irregularly to extremely low levels by the mid-1960s.

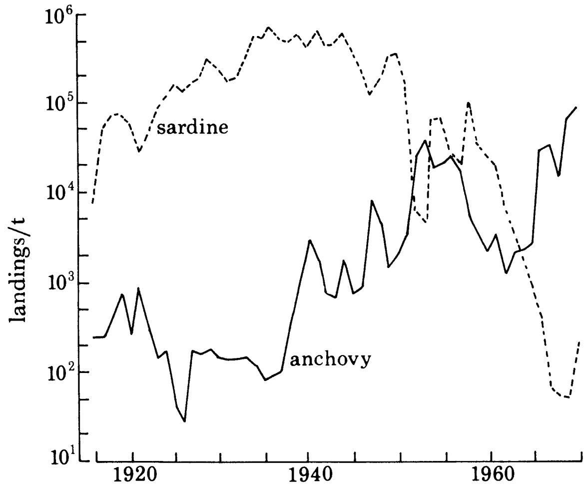

FIGURE 8. Annual catches of sardine in the California current system since 1916 (from Smith 1972).

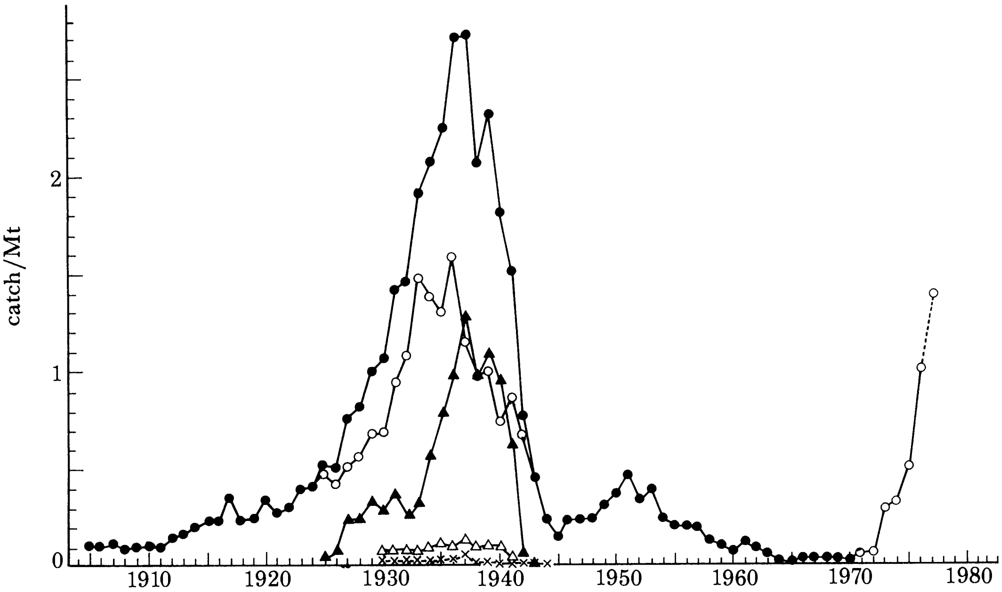

FIGURE 9. Fluctuations in the sardine catch from the far east (from Kondo 1980). ●, Grand total for the area; ○, around Japan; ▲, off Korean peninsula; △, off coast range; ×, off South Sakhalin.

For the anchovy, catches in the 1920s and 1930s were about 100 t and then started to increase in the 1940s to reach about 50 kt by the early 1950s. Between 1970 and 1976 catches have fluctuated irregularly between 73 and 210 kt (Troadec *et al.* 1980).

The sardine catch in the Far East also shows very considerable fluctuations. Figure 9, from Kondo (1980), shows how the total Far East catch rose from about 100 kt in 1905 to a peak of nearly 3 Mt in the late 1930s, only to decline again equally rapidly to about 200 kt in 1945.

Around Japan, sardine catches similarly rose to a peak in the late 1930s of about 1.5 Mt and again declined to a comparatively low level by the end of the war. These catches remained at a low level until the 1970s when they increased comparatively rapidly and within the space of only a few years reached 1.5 Mt again.

The Greenland cod fishery

The Greenland cod stock provides an example of a stock at the limit of its distribution which underwent considerable changes in size associated with changes in temperature. During the last century, cod is said to have been particularly numerous at west Greenland along the entire coastal region from Julianehab to Disko Bay, and this coincided with a period that must have been generally mild in the North Atlantic because some southern species of fish were observed at Iceland about that time. Then came a period of cooling and by the beginning of this century, corresponding with a cold period, the Greenland cod stock had dropped to a low level, and up to 1917 there were only small local fjord populations of cod in Greenland.

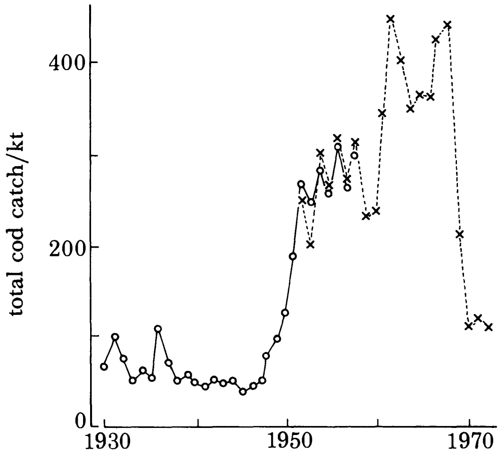

Figure 10. Catches of cod at West Greenland (1920–74) (from Beverton & Lee (1965) and Malmberg (1979–80)). ○—○, Greenlanders' catch; ×---×, international catch.

In the early 1920s, sea temperatures rose abruptly by more than 1 °C and large numbers of adult fish appeared off the southwest coast and penetrated as far north as latitude 72° N. An interesting feature of the growth of the Greenland cod stock at this time is that this was due to some exceptionally good year classes, rather than the result of gradual change. These good year classes occurred during a relatively small number of warm years starting in 1924, as illustrated by the good correlation between bottom temperatures in June on Fyllas Bank off west Greenland and the year class strength of cod in Greenland waters, over a temperature range up to 3 °C (Taning 1953). The build-up of cod is demonstrated by the increase in catch of Greenland cod between about 1920 and 1960, and over this period the catch increased from a negligible level to about 400 kt per year (figure 10). During the 1930s a permanent spawning stock was established in Greenland, and this was associated with a period of interchange of fish with Iceland.

The Peruvian anchoveta and El Niño

Off the coast of Peru there is a fishery for anchovy that is influenced by variations in the hydrography of the eastern Pacific known as the El Niño phenomenon. About once in every 7 years there is an irregular oscillation of the local hydrographic conditions, associated with a reduction in the degree of coastal upwelling and a considerable drop in the productivity of the region. The effect on the anchoveta is to reduce the area of distribution of the fish with a concentration of fish in those spots where plant production still continues. The shoals tend to occur at a greater depth than normal (up to 200 m) with some displacement to the south of the normal locality. These changes in the accessibility of the anchoveta population result in heavy mortality among the guano bird population. Figure 11 shows variations in the population of guano birds and also in the catch of anchoveta.

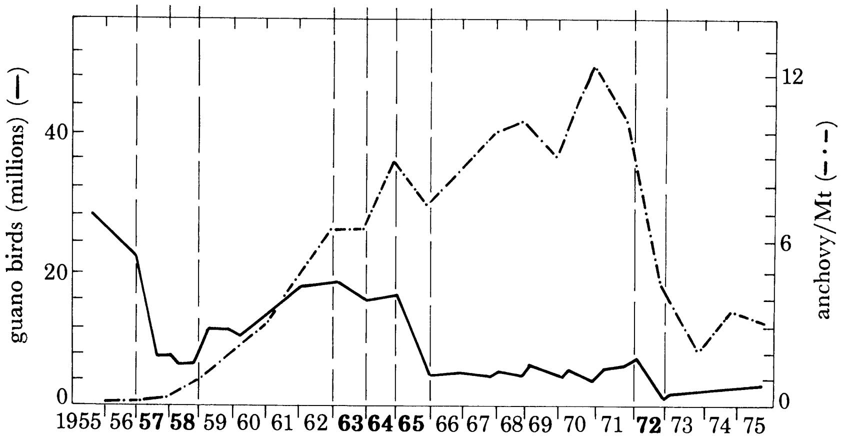

Figure 11. Fluctuations in the numbers of guano birds (—) and in the catches of Peruvian anchoveta (–·–) (from Valdivia 1978). Abnormal years are shown in bold type.

In the 1950s, catches of anchoveta were relatively small, but during the 1960s there was a gradual increase in catches until a peak of about 12 Mt was reached in 1970. Owing to El Niño conditions the fish became concentrated in an area close to the coast and the catch per unit effort remained high in relation to the abundance of fish. Fishing therefore continued to be profitable even though the total stock was being reduced very considerably. The result of the combination of poor recruitment and intense fishing on the highly concentrated adult stock was that the amount of fish left to form a spawing stock at the end of 1972 was only about 2 Mt.

During the first half of the 1970s there was a slow build-up in the stock aided by favourable recruitment in 1975 and this led to an increase in the stock to 10–12 Mt by the beginning of 1976. Another El Niño in 1976, however, led to the appearance of warm water along the coast during a large part of the year, causing the fish to concentrate once more in a narrow area close to the coast where feeding conditions appeared to be unfavourable since the normal diatom–zooplankton assemblage was scarce and dinoflagellates were unusually abundant. The result was that the stock available at the beginning of 1977 was lower then ever before at the beginning of any year, and a catch of about 1 Mt, which was taken in the first half of 1977, must have decreased the stock still further. Thus, although conditions during 1976 were different from the classical El Niño years of 1972 and 1957, the effect on the fishery was still disastrous.

The El Niño phenomenon has been known for a considerable time in Peru and has been principally associated with the mortality of seabirds. At times when there are hydrographic and meteorological indications of an El Niño, there have been numbers of bird carcasses strewn along the beaches. These usually in emaciated conditions and since their chief food is the anchoveta the implication is that they have died from a lack of this species. During the 1957–8 El Niño, for example, when the fishery was only just beginning, the number of birds fell from 28 million to 6 million (figure 11). There was a partial recovery in the 1960s, but during the 1970s the bird population fell to a very low level, presumably owing to the disastrous decline in the anchoveta stock.

The history of the Peruvian anchovy fishery provides an extreme example of the influence of meteorological and hydrographic conditions on a fishery. It is particularly unfortunate that at times when the fishery has been declining owing to recruitment failure, the adults should be concentrated so close to the coast as to make them extremely vulnerable to fishing.

Changes in North Sea phytoplankton

Although most of the data suitable for examining long-term fluctuation relate to fish stocks, some data are also available for other taxonomic groups. For example, continuous plankton records, reported in various papers from the I.M.E.R. laboratory at Plymouth, provide information about changes in North Sea phytoplankton since World War II. Reid (1977), for example, has concluded that in most areas of the northeast Atlantic Ocean, diatoms have declined in abundance in the last decade, while at the same time there has been an increase in phytoplankton colour. This refers to an unidentified green coloration of phytoplankton silks that may be due to the presence of organisms such as microflagellates, which may partially disintegrate in formalin leaving their chloroplasts in the silks. These would not be identifiable in the continuous plankton record samples. In particular, Reid (1975), referring to phytoplankton in the western part of the central North Sea, notes that before 1965, phytoplankton colour showed distinct spring and autumn blooms. After that date the productive season became longer, the distinction between the two blooms became less marked, and the autumn bloom declined in intensity. The diatoms decreased markedly after 1965 and this was associated with a drastic decline in the autumn bloom. Winter and summer diatoms almost disappeared and there was also a decline in the spring bloom.

The timing of the spring bloom has also changed. Glover *et al.* (1972) state that for the period 1948–69, the spring bloom of phytoplankton has occurred progressively later.

More recently, between 1970 and 1974, Colebrook *et al.* (1978) note that in the southern North Sea there has been a marked increase in the level of phytoplankton colour in January and February compared with the annual mean. They noted that the increase in these months was at least partly due to exceptionally early blooms of *Thalassiosira* and *Chaetoceros*.

Regarding particular species of phytoplankton, Colebrook *et al.* (1978) examined fluctuations in the abundance of seven species of *Ceratium* that occur regularly in samples from the North Sea. All but one species showed an advance in seasonal timing in the south and eastern parts of the North Sea. None of the species showed any consistent change in seasonal timing in the northwestern part of the North Sea.

Off the Dutch coast, Gieskes & Kraay (1977) examined changes in phytoplankton in connection with the increased nutrient discharge in the southern North Sea in recent decades. They note that in the southeastern North Sea, the mean phytoplankton colour between the years 1968 and 1972 was 1.7 times the average for the years between 1948 and 1952. Very close to the Dutch coast, however, the colour value increased by a factor of 2.4. This happens to be close to the estimate of the increase between 1950 and 1970 of the amount of suspended particulate organic matter in Dutch coastal waters according to de Jonge and Postma (1974).

Changes in North Sea zooplankton

Continuous plankton records from the I.M.E.R. laboratory also provide evidence of changes in the zooplankton. According to Glover *et al.* (1972), the total number of copepods and the zooplankton biomass in the North Sea have declined over the period 1948–69. Also the duration of the zooplankton season has fluctuated considerably, and has become progressively shorter over the period 1952–64. Regarding particular species, Colebrook (1978) concludes that *Pseudocalanus* declined from 1948 to about 1970 in all parts of the North Sea except for the northwestern North Sea, where it fluctuated about a constant level. To the west of the British Isles also it tended to decline.

Between 1970 and 1972, *Calanus finmarchicus* continued to decline in abundance, in contrast to *Calanus helgolandicus* in the southern North Sea, which did not show any systematic change in abundance (Colebrook *et al.* 1978).

From 1972 to 1977 in the eastern North Sea, euphausiids increased in abundance in continuous plankton records (Lindley 1979). The increase affected all five species, which normally occur in the area, but was not paralleled in other areas of the North Sea.

There have also been changes in the abundance of some fish larvae in the plankton. For example, over the period 1948–72 there has been a decline in the abundance of whiting, Norway pout, dabs and plaice. The downward trend of whiting started in 1964 whereas that for plaice has been general over the whole 25 year period (Coombs 1975). For whiting and sandeels there has been a shortening of the season during which the larvae have been caught and a delay in the time of the seasonal maximum abundance (Coombs 1975).

In the southeastern North Sea there was a decrease in diatoms in the mid-1960s and a decrease in copepods in the early 1960s, but these changes were much less dramatic than in other areas (Gieskes & Kraay 1975).

According to Robinson & Jonas (1981), zooplankton abundance was still below average in most areas of the North Sea in 1980. In particular, numbers of *Pseudocalanus elongatus*, *Paracalanus* spp., *Temora longicornis*, *Evadne nordmani* and pelagic molluscs were well below the long-term mean.

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Discussion

G. Conan (*C.O.B.–C.N.E.X.O., Brest, France*). Most of the fish populations described are heavily exploited ones. I wonder if some of the variability observed is not induced by man. Natural populations have developed life strategies that are no longer efficient if they are overexploited. The age distributions will show fewer adults and more juveniles than in unexploited ones. Consequently the age distrubutions and densities will be much more unstable than in natural unexploited conditions.

R. Jones. The examples described were chosen because they extend back in time to a period when exploitation was not heavy. The variability then appears to have been just as great as it is nowadays.

M. V. Angel (*Institute of Oceanographic Sciences, Wormley, Surrey, U.K.*). Extending Dr Jones's comments about the El Niño, O'Brien has recently shown from a study of winds over the whole

Pacific that El Niños are probably generated by anomalous winds in the west Pacific, thousands of kilometres away from the Peruvian coast. A Kelvin wave is generated, which propagates along the Equator and turns clockwise when it impinges on the American west coast, depressing the thermocline and inducing the El Niño. In the open ocean, where physical processes so often force the biological processes, the ecologist studying the effect of an oil spill may be misled by the influences of events far outside his study area. Does this imply that past studies of this type have not been set in a broad enough context in time and space, and consequently have stood little chance of detecting long-term environmental impacts? And if so, how should this be remedied in the future?

R. Jones. I can only agree that studies should ideally be as broad as possible, both in time and space.

A. J. Southward (*Marine Biological Association, Plymouth, U.K.*). Radovich has suggested that stress due to overfishing, when added to natural changes, may push pelagic fish populations beyond the point of recovery rather than follow the classic Schaefer curve. He has suggested that the Californian Sardine consisted of four different genetic groups, and that overfishing wiped out the two northernmost stocks completely. Do any other species show signs of not following the Schaefer model, and could this explain the totality of the failure of the Plymouth herring in the face of the combination of environmental change and a great increase in fishing effort?

R. Jones. There are many pelagic fish stocks that have collapsed after a period of heavy fishing and environmental change. In each case the problem is to separate the relative importance of these two factors.

J. S. Gray (*University of Oslo, Department of Marine Biology and Limnology, Oslo, Norway*). I am not quite so pessimistic as Dr Jones. Many data sets show periodicities that can be correlated with climatic cycles such as hydrographic changes. Yet regular cycles are probably not common in marine data although we have a number of data sets from the Skagerrak area that show that a major change was initiated in 1970–71 and that this effect lasted for around 10 years. Recent work on long-term trends in microtines (Garsd & Howard 1981) shows that good prediction can be obtained by using a combination of pseudoperiodic cycles and superimposed large environmental influences. I feel that this approach is a sensible one and likely to be profitable on marine data.

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R. J. H. Beverton, F.R.S. (55 *Sandown Avenue, Swindon, U.K.*). Dr Jones's review of the long-term catch statistics of certain major fisheries is a salutary reminder of the inherent variability of fish populations. Nevertheless, I do not believe that the prospects of detecting effects of major oil spills on fish populations are quite as forbidding as that evidence might indicate.

There are several reasons why this is so. For one thing, the timescale over which the effect would be expected is a matter of a small number of years at most, and probably much shorter. Although some of the examples given by Dr Jones showed certain periods when even over, say, 3–5 years there was considerable variability, there were many other periods when this was not the case. Again, other kinds of fish populations show much less variability than the examples quoted by Dr Jones.

The more important reason is that one would make use of all the available biological and ecological knowledge to focus attention on these aspects of the life-history of the fish population in question most likely to be affected. I think we can discount mass mortality of adults; a whole population is rarely concentrated enough for a sizeable proportion of it to be exposed to even the largest spill, and the fish would probably swim away from it if they were. It is the egg, larval and juvenile stages that are potentially at risk, but neither the *Torrey Canyon* nor the *Amoco Cadiz* spills were located anywhere near the spawning or nursery grounds of major fish populations.

It would be a different matter, however, if these quantities of oil were to come ashore along the Dutch and German coasts in the summer, when a substantial part of the year's production of North Sea flatfish species are coming into very shallow water for the first few months of their demersal life. I do not know whether studies have been made of the effect of oil on O-group flatfish on sandy beaches, but if not, it would seem worthwhile to do so. Direct measures of mortality rates would be feasible, and there are enough data on this for a sharp increase above the normal to be detectable. Judging by what other speakers have said, abnormalities in growth, development, pigmentation and other indicators of stress would also be worth looking for.

R. JONES. I can only make the general observation that each incident must be examined on its own. I would agree that in some instances, useful conclusions might be possible from short time series. In others, it may not be possible to separate out the effects of long-term natural variability.

J. H. VANDERMEULEN (*Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada*). I found this presentation very illuminating, especially since the problem of separating out oil-related variability in fish stock from natural variabilities is of course very relevant to the Canadian and northwest Atlantic fishery. This is a well known problem, one that we come back to time and again, i.e. the masking of oil impact by inherent natural variability; usually the response is to study even further and in greater detail the variabilities that one may or might encounter.

I wonder, however, if there is not a possible alternate approach to this problem, and that is to focus instead on the occurrence of abnormal features in a fish stock for the purpose of impact assessment.

I offer this more by way of comment but what I am suggesting is that, rather than concentrating on normal features in fish stocks, one should instead look at abnormal features, such as the presence of broken back syndrome in larval fish, and the levels of certain enzymes known to be sensitive to the presence of contaminants, and so forth, and utilize those to assess impact, and not gross changes in populations or catches of fish. It would seem to me that such an approach offers three advantages, aside from the fact that it is much more direct. First, the incidence of such abnormal features in a normal non-contaminated fish stock should be relatively low, and therefore more amenable to statistical treatment than attempting total description of a fish stock. Second, it is independent of the true stock size and therefore dependent of the uncertainties plaguing fish stock assessment today. Third, it is the one category of properties that is bound to respond to the presence of a contaminant, be it petroleum hydrocarbon or heavy metal or polychlorinated biphenyl.