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THE DISTRIBUTION OF SOME PLANKTON ANIMALS IN THE ENGLISH CHANNEL AND APPROACHES

III. THEORIES ABOUT LONG-TERM BIOLOGICAL CHANGES, INCLUDING FISH

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(Text-figs. 1–6)

In previous contributions (Southward, 1961, 1962) it has been suggested that some of the changes that have taken place in the macroplankton population of the western English Channel during the past 58 years might have been caused by relatively small fluctuations in environmental factors, leading to a shift of distributional boundaries. The well known rise in sea temperature during the period, and a deduced change in emphasis of water movements (but not in the basic pattern), were quoted as likely factors. However, other theories involving more fundamental deduced changes, such as large-scale alterations in water movements or loss of fertility of the water, have been put forward in the past. In this contribution the various biological and other changes that have been observed in the area are briefly described and then the theories summarized and compared critically with one another.

I am indebted to Dr F. S. Russell, Dr D. J. Crisp, Dr D. H. Cushing, Mr A. C. Burd, Mr N. A. Holme and my wife for critical discussions of the theories. Mr R. J. H. Beverton and Dr D. H. Cushing have read the manuscript and made valuable suggestions.

THE CHANGES

The most obvious changes were biological, affecting plankton, bottom fauna, intertidal fauna and both pelagic and demersal fish.

Macroplankton

As already discussed in Part II there was a general reduction in the occurrence of north-western species; for example, some, like *Meganyctiphanes norvegica* seem to have disappeared from the Western Basin of the Channel after 1930, and others, such as *Aglantha* became very scarce. Inshore off

Plymouth an abundant population of chaetognaths, in which *Sagitta elegans* was usually dominant, was replaced in 1931 by an almost equally abundant mixed population in which *S. setosa* was dominant. After 1935 the total chaetognath population declined and has remained at a relatively low level ever since (Russell, 1930–39). Today, though *S. elegans* and *S. setosa* can be found off Plymouth, the latter is usually dominant or alone present inshore while *S. elegans* is more of an offshore form (Southward, 1962).

Accompanying the decrease of north-western forms there appears to have been a marked increase in south-western forms, not noticeable so much in relative numbers as in length of stay, most of the autumn and winter seasons being dominated by them. With the change in species composition of the macroplankton, the total catch of organisms in the 2 m stramin ring trawl became very much reduced, particularly after 1935. Accompanying the reduction in macroplankton, there was a decline in the numbers of non-clupeoid young fish (post-larvae up to a few weeks old) as sampled by the 2 m net, first slightly from an annual average of 1827 (sum of monthly averages) in 1924–30, to 1416 in 1931–34, then drastically to 481 in 1935–38 (Russell, 1930–39). During 1931–34 only the summer-spawning species were affected, but after 1935 the spring-spawning species also suffered. Since then the decline appears to have continued, and in 1958–60 the average of all non-clupeoid young fish (not determined to species) was a mere 112 (see Part II, Tables 4, 5, 6). Coincident with the decline in young of demersal fish there was a large increase in numbers of pelagic eggs of pilchard, first commented upon in 1934, and very abundant by 1936; since then these eggs have occurred through most of the year instead of only occasionally in summer and autumn (Russell, 1930–39; Corbin, 1949, 1950). Clupeoid larvae also became more abundant, particularly in May, June and July, when all were almost certainly pilchard; however, the slowly hauled 2 m net is not a good method of sampling such larvae in the daytime (cf. Russell, 1926*b*, 1928) and the numbers have fluctuated too widely to demonstrate the full extent of the increase.

Fisheries

It is well known that the commercial fishery for herring off Plymouth failed completely after 1935, when more than 80% of the catch consisted of fish over 6 years old (i.e. the 1927/28 year class or earlier) (Kemp, 1938). Recent examination of the evidence indicates that there was a steady decline in recruitment of young fish to the commercial stocks after the last good year-class of 1925/26, becoming severe after the 1927/8 class and virtually absent after the 1931/32 spawning (Figs. 1 and 2; Cushing, 1961).

During the 1930's and since there have been many records of the occurrence of rare warm-water species of fish in the area (Russell, 1953). By the early 1950's there had been an increase in the proportion of warm-water species of demersal fish on the Plymouth trawling grounds worked by the Laboratory's research vessels, compared with 1919–22 (see Appendix: unpublished records of the late Dr G. A. Steven). Of the species less common in 1950 than earlier, most were northern forms.

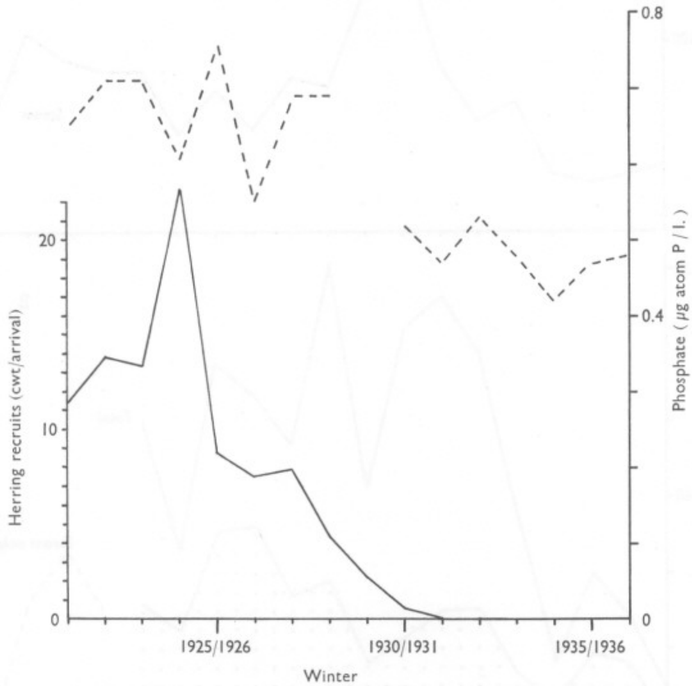

Fig. 1. Values of herring recruited to the Plymouth fishery, taken back to the season of hatching (—), and values for the winter maximum of inorganic phosphate (---). From data tabulated by Cushing (1961).

Benthos

The macrofauna of the shell-gravel community between Plymouth and the Eddystone showed a decrease in numbers in 1950 compared with 1925 (Holme, 1953), and it seems possible that a general decline in biomass occurred, although no comparable figures are available. Many species that were common or not rare around Plymouth in 1925 are now absent or very rare in the area, though some are still found off Falmouth or Mounts Bay or farther to the west (Holme, 1961). Some of these forms are of northern distribution or are stenothermal species with low optima, but a few are of more general distribution. A somewhat similar group of species is found in the north-western parts of the North Sea (Holme, 1961; Ursin, 1960).

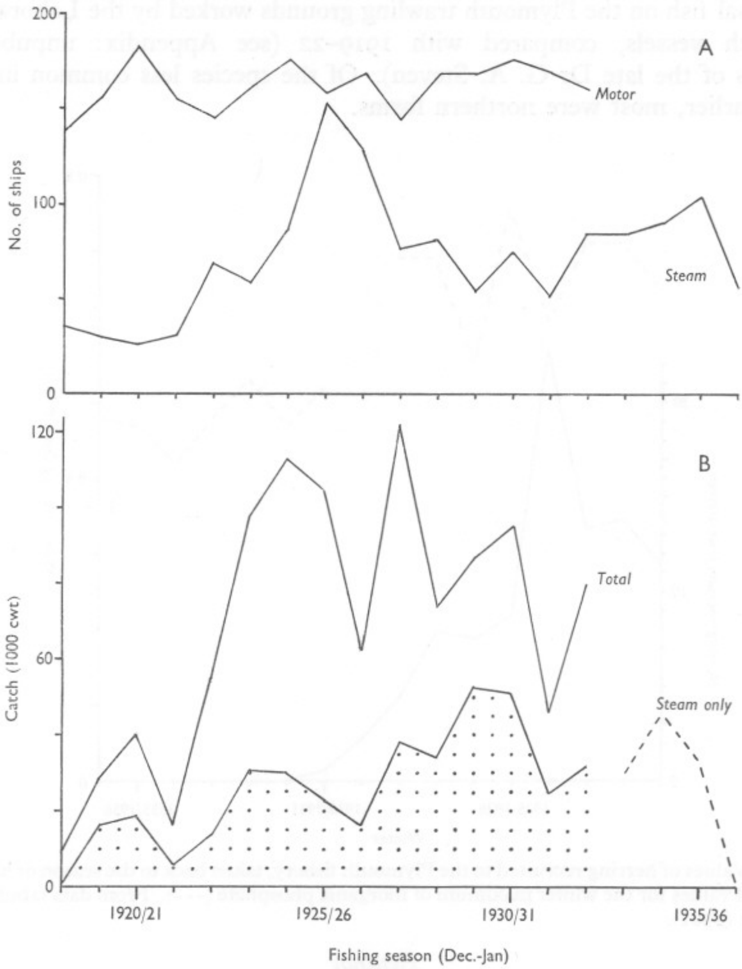

Fig. 2. The Plymouth herring fishery; seasonal data. A, the number of motor-boats and steamers engaged; B, the total landings of herring (—) and the proportion caught by the steamers (▦). From data given by Ford (1935) and Kemp (1938).

Intertidal organisms

Between the early 1930's and the late 1950's there was a marked increase in the occurrence or abundance of southern forms on rocky shores (Crisp & Southward, 1958) and a decline of at least one northern form. More recently the possible northward spread of another southern form has been detected (Carlisle & Tregenza, 1961) and the process may be continuing.

Environment

Changes in the environment were generally less obvious than the biological changes. The fact that northern seas were warming up was well known in the 1930's (e.g. Kemp, 1938), but less notice was taken of the possibility that the English Channel also was becoming warmer, though it had been suggested by Lumby (1935) and Scherhag (1937). Only recently with a longer period of records available was it appreciated that a rise of temperature had occurred

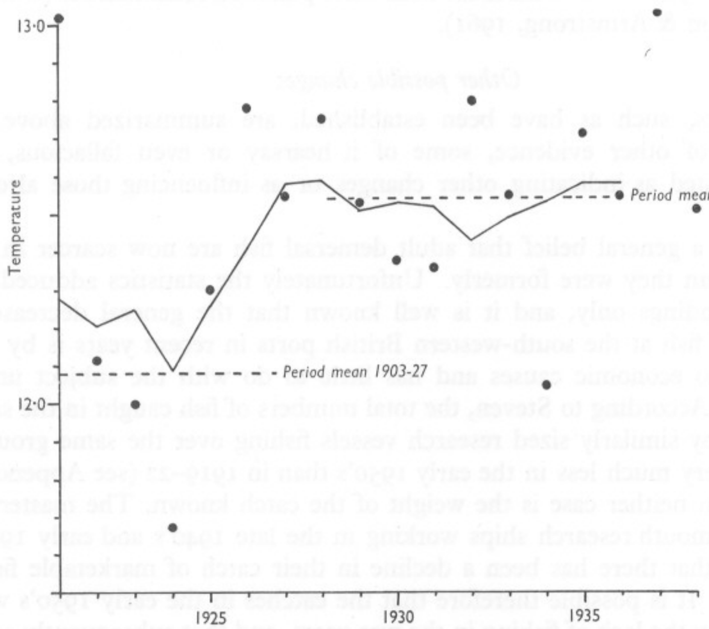

Fig. 3. Variations in the annual mean sea-surface temperature at E1. The dots show the actual annual means, the solid line the five-year running means: the period means are also shown (from data tabulated by Southward (1960)).

near Plymouth, of the order of half a degree Centigrade, and somewhat more to the south-west and west (Smed, 1952; Southward & Crisp, 1954; Bowden, 1955; Cooper, 1958; Southward, 1960). The running means of annual temperature at E1 suggest a steepening of the rise during the 1920's when some of the major biological changes began (Fig. 3). It is worth noting that a more pronounced rise in temperature (also in salinity) in the Skagerrak and Kattegat was accompanied by increases in the southern element of the fauna (e.g. Brattström, 1941; Dahl, 1953).

A more widely known change in the English Channel is the decline in the winter maximum of phosphate (Cooper, 1938, 1955*a*). At station E1 the average for 1932–35 was about 25% below that for the period 1923–30, and a slightly smaller fall (19%) was found in mid-Channel (station E 2). Although now regarded as a declining trend (Cushing, 1961) this change was once believed to be sudden and to have taken place mainly in 1931 (Kemp, 1938) (see Fig. 1).

A more subtle change in the environment has been associated with the change in plankton. It has been found that echinoderm larvae develop better in water in which a community of north-western forms had been living ('elegans' or 'western' water) (cf. Russell, 1935) than in water obtained from inshore off Plymouth or from areas with other plankton communities (Wilson, 1951; Wilson & Armstrong, 1961).

Other possible changes

The facts, such as have been established, are summarized above. A good deal of other evidence, some of it hearsay or even fallacious, has been suggested as indicating other changes or as influencing those already noted.

There is a general belief that adult demersal fish are now scarcer in the Channel than they were formerly. Unfortunately the statistics adduced are often of landings only, and it is well known that the general decrease in landings of fish at the south-western British ports in recent years is by and large due to economic causes and has little to do with the subject under discussion. According to Steven, the total numbers of fish caught in the same size trawl by similarly sized research vessels fishing over the same grounds were not very much less in the early 1950's than in 1919–22 (see Appendix). However, in neither case is the weight of the catch known. The masters of the two Plymouth research ships working in the late 1940's and early 1950's assure me that there has been a decline in their catch of marketable fishes since then. It is possible therefore that the catches in the early 1950's were improved by the lack of fishing in the war years, and that subsequently overfishing has caused a further decline (cf. E. S. Russell, 1942). The same argument would not apply to the early 1920's, as the Channel fishing industry was not so heavily curtailed in the First World War.

There appears to have been a very big increase in the abundance of cuttlefish (*Sepia officinalis*) in the Channel during the past forty years, possibly as part of the trend towards an increase in southern forms. According to the unpublished trawl records of R. S. Clark and E. Ford, the species was very rare in 1921–22, whereas in 1958–61 it could be obtained in large numbers off Plymouth and was taken well up Channel.

There are some beliefs concerning detrimental acts in relation to the herring fishery, mostly perpetrated by 'foreigners': (*a*) destruction of spawn on the bottom by trawling, also disturbance of spawning grounds and dispersal of shoals: Ford (1933) records this controversy and the landing of trawled herring at Plymouth; (*b*) heavy fishing activity or general overfishing of a comparatively small stock of fish; for example, as Dr Cushing informs me, there are no statistics of landings at French ports from the Plymouth grounds, but they are believed to have been heavy.

We know now that the stock of herring was a comparatively small one maintained by a few good years of survival of the young. Hence there was a distinct possibility of overfishing, particularly in 1926 when a great increase in fishing effort brought about a very disproportionate increase in that part of the catch landed at Plymouth (Fig. 4). Most of this extra effort was due to steam drifters from other ports, the local motor fleet remaining fairly uniform.

THEORIES

The theories which attempt to explain these changes fall into two groups according to whether a change in fertility of the water is assumed or not.

Chemical control

Theories under this heading lead off from one another to form a group of interlocking hypotheses (Cooper, 1955*a*, *b*). They start with the view, perhaps inevitable in the 1930's and before the other changes were established, that the decline in macroplankton, young fish and winter phosphate represented a real decrease in the fertility of the sea off Plymouth. At the simplest (Kemp, 1938; Harvey, 1950) it is suggested that a decline in available phosphate meant a lower level of primary production; as a consequence the zooplankton crop was less and hence there was less food for macroplankton and fish. In the absence of food the predators either declined in number (demersal fish) or 'went away' (herring). To develop the theory beyond this stage demands a series of assumptions. It is first of all assumed that there is a steady loss of phosphate to deep water in the ocean, and that to maintain a high level in coastal waters requires an influx of water of higher phosphate content (Cooper, 1955*a*, 1958). Such water could come only from deep in the ocean, by up-welling of cold water (Russell, 1936; Kemp, 1938). In the north-east Atlantic area any up-welling of the usual sort is unlikely since the prevailing winds blow onshore, and up-welling must therefore be produced by energy transferred from elsewhere, for example by internal waves caused by sinking of cold water in the Arctic (Cooper, 1955*a*). It is assumed that such processes occur infrequently, chiefly during cold winters in the Arctic, and that one or two years' contributions may influence the phosphate levels of the continental shelf waters for a decade (the apparent oceanic influx of the autumn of 1921 in the English Channel is quoted as an example, but we cannot tell if it carried any phosphate). During such a period it is assumed that a commercial fishery may first arise and flourish and then decline again afterwards.

Attractive as these theories may seem, there are many objections to them. The most serious is that we cannot in fact say whether there was any fall in primary production. As already noted (Part II) the winter phosphate level has very little relationship to total production (including fish) during the year. To determine total production one must know, among other things, the rate of turnover of nutrients (for references, see Cushing, 1959). A reduction of the standing crop of macroplankton and the numbers of young fish can just as well indicate increased predation by larger animals.

Furthermore the theories assume that there is no movement of water masses between the time of phosphate maximum (January to February) and the period of abundance of spring- and summer-spawned young fish (March to July). The Plymouth inshore stations are not in the direct line of flow in the Channel (see Part II), but it is very unlikely that the water there remains constant for so long, although during the most critical part of the period the *type* of water movement may remain constant—e.g. the 'winter' type of circulation of Dietrich (1950), involving north-western plankton (Part II; see also Harvey, 1950).

A final objection to the chemical control theories may be found in the data on the herring fishery. Recent analysis suggests that the fall in recruitment of young fish began some years before the first signs of a decline in macroplankton, in fact only a few years after the start of the period of increased fishing effort and landings in 1921 (Cushing, 1961). Furthermore, the herring fishery off Plymouth was by no means a post-1918 phenomenon as suggested by some versions of the chemical control theory. An extensive fishery took place from before 1900 to 1914, but the fishing effort was less (mostly a sailing fleet gradually being motorized) and hence the peak landings were smaller than in 1922–35 when steam drifters dominated the scene (Fig. 4). The later period was the more 'successful' for economic reasons, and attracted more ships from other ports. It can be seen from the graph (Fig. 4) that after 1918 the peak annual catch by the local motor-fleet did not exceed the peak of the pre-1914 catch (e.g. in 1903) by the local sail and motor-fleet, though the overall average catch was obviously greater in the later period.

Whether the chemical control theory is correct or not, it is indisputable that before the change there was some association between a large standing crop of macroplankton, larger numbers of young demersal fish and high values of winter phosphorus (Russell, 1930–39). In particular, Harvey (1950) has noted a direct correlation between numbers of summer-spawned non-clupeoid young fish and the phosphate maxima the previous winter. However, the data show no correlation between phosphate and total numbers of young fish, nor even with spring-spawned non-clupeoid young fish. Since summer-spawned non-clupeoid young fish comprise only a small proportion of the total young fish in the year it seems questionable if they alone would suffer directly from any decline in fertility. An alternative explanation of this correlation is provided by Cushing (1961); his theory belongs to the biological group.

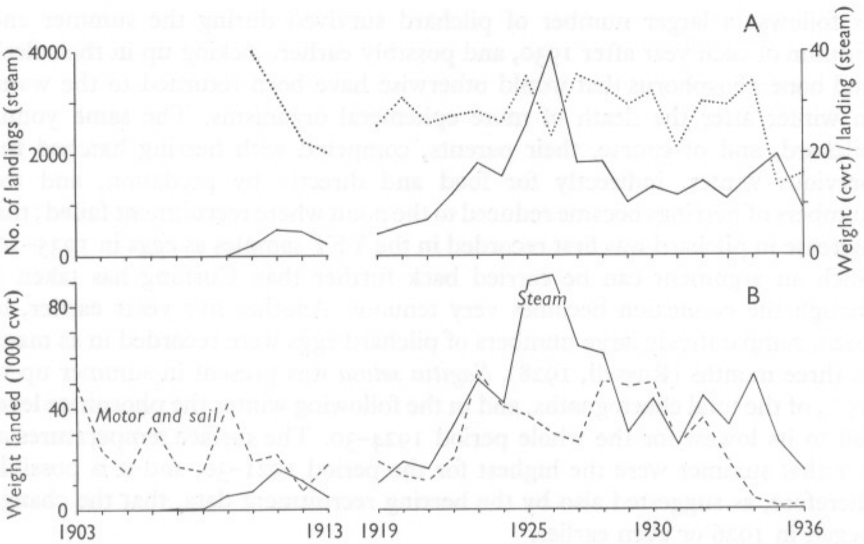

Fig. 4. The Plymouth herring fishery 1903–36, omitting the war years; data by years, as calculated in the annual return of fishery statistics. Each year includes the January figures for one season and the December figures for the next, but alternative information is not readily available. A, —, The number of landings by steamboats; · · · ·, the weight per landing by the same ships. B, —, the total weight landed by steamers; - - - -, the total weight landed by sailing craft and motor-boats.

Biological control by pilchard

In seeking an explanation for the decline in herring and increase in pilchard off Plymouth, Cushing (1961) was led to explore the numerical relationships of these fish and the phosphate values. Statistical analysis showed a significant correlation between the winter phosphate values and the abundance of both species; the numbers of pilchard eggs during the peak spawning (used as an index of adult fish)[1] were inversely related to the phosphate values the following winter; the number of herrings recruited to the fishery each year was related, not to the phosphate the winter they were spawned, but to the phosphate a year later. That is, both herring and pilchard were related to the same value of winter phosphate.

It is clear enough from the evidence presented by Cushing (1961) (see also Table 1) that a real increase in stock of mature pilchard occurred in 1935 and 1936 (Russell, 1930–39). Hence, allowing up to 5 years for pilchard to reach maturity then, it is suggested that in 1930–31 there began a period of greatly increased survival of young pilchard (at a stage too large to be caught by a slow-moving net). Cushing's explanation from this point may be summarized

[1] It is hardly necessary to point out that landings of pilchard from the English Channel are so small in proportion to the estimated stock that they provide no information as to changes in stock level (Cushing, 1957).

as follows: a larger number of pilchard survived during the summer and autumn of each year after 1930, and possibly earlier, locking up in their flesh and bone phosphorus that would otherwise have been returned to the water in winter after the death of more ephemeral organisms. The same young pilchard, and of course, their parents, competed with herring hatched the previous winter, indirectly for food and directly by predation, and the numbers of herrings became reduced to the point where recruitment failed; this increase in pilchard was first recorded in the YFT samples as eggs in 1935–36. Such an argument can be carried back further than Cushing has taken it though the connexion becomes very tenuous. Another five years earlier, in 1926, comparatively large numbers of pilchard eggs were recorded in as many as three months (Russell, 1928), *Sagitta setosa* was present in summer up to 25% of the total chaetognaths, and in the following winter the phosphate level fell to its lowest for the whole period 1924–30. The surface temperatures at E 1 that summer were the highest for the period 1921–30, and it is possible therefore, as suggested also by the herring recruitment data, that the change began in 1926 or even earlier.

Cushing mentions an alternative explanation of some of the data: that in some way herring declined, allowing the pilchard to increase and eventually gain the upper hand. Since the herring stock was small and the pilchard stock is now big, this interpretation is thought to be less likely. If ever it were to be considered there is always the possibility that an initial decline of the herring resulted from overfishing.

As a concomitant of Cushing's theory, the decrease in macroplankton and young of demersal fish is attributed to the increase in pilchard, by direct predation or competition for food, and the apparent correlation of young fish and phosphate is then indirect, via the pilchard.

The main objections to the pilchard control theory are that it does not explain all the changes. Furthermore, like the chemical control theory, it requires an assumption that the process takes place in a steady environment, with little or no water movement to disturb the relationships between fish and phosphate during the autumn (see p. 8), with the difference that during this period the trends in plankton and water movements are largely south-western in character (see Part II). No explanation is provided as to why the pilchard increased in 1930–31, though cyclic fluctuations in stock or a relationship to Dietrich's (1950) pattern of water circulation are discussed.[1] No account is taken of other pelagic or semi-pelagic perennial populations: sprat, horse-mackerel or cuttlefish for example. Finally, the theory does not explain the change in indicator species, particularly the replacement of *Sagitta elegans* by *S. setosa*. Although in this instance the former is associated with herring and

[1] In an earlier paper the increase in pilchard is attributed to increased survival of young due to the change in macroplankton and a lower number of coelenterate predators in summer (Cushing, 1957).

the latter with pilchard, it does not follow that a change in fish should cause a change in chaetognaths.

The change in macroplankton is better explained by the theory, put forward fully in Part II, of a change in communities and distribution boundaries as a result of a rise in temperature and a change in emphasis of water movements in the Western Basin. This is the simplest explanation of the macroplankton problem, and it is possible to account for the change in pelagic fish the same way: a decline in a northern form at its southern limits (herring) and an advance of a southern form (pilchard), the fish forming part of the ecological system in each case. It is then immaterial whether we say the pilchard increased first and crowded out the herring or the herring declined and the pilchard came in, because both changes must have occurred together and the end result was the same.

Biological control by temperature

The arguments for this theory as affecting the macroplankton population have already been presented (Part II). To bring in herring and pilchard is to complete the picture of the balance between two competing ecosystems being altered by rising temperature. From the evidence it appears that on the whole the change was quite gradual, as might be expected, taking place from 1926–36 at least. It is extremely fortunate that Dr Russell was making basic quantitative observations at the time and that some parts of the process were sufficiently abrupt to draw attention, otherwise we would have been completely in the dark about possible causative factors.

The apparently abrupt nature of some aspects of the change can be attributed in part to the sharpening effects of competition between pairs of closely related species of similar habits but of very different distributions (cf. Conover, 1956). The pilchard is so obviously adapted to succeed under warmer conditions: it spreads out its breeding period over a large part of the year and is able to take advantage of the lesser but more regular plankton production of warmer waters (cf. Qasim, 1956). The herring, on the other hand, was obviously a cold-water form with a short breeding period near the coldest part of the year. This meant that off Plymouth, as in other localities near the southern limit of its distribution, it was not well adapted to the cycle of plankton production, the larvae being hatched out after the autumn outburst of plankton, and well before the peak of production in the spring.

Furthermore, the herring appear to have been influenced directly by the falling temperature when shoaling (Ford, 1929) and it is possible to envisage spawning being delayed by a warm autumn to such an extent that recruitment failed (cf. Crisp, 1959). This idea gains some support from the correlation that can be shown to exist between annual mean surface temperature at E 1 and the figures for herring recruitment the same year (Fig. 5, $r = 0.78$, $P = 0.01$), and the absence of significant correlation with temperatures prevailing the year after the herring were hatched. Moreover, most of the increase in temperature has been felt in the autumn (Southward, 1960). But such a correlation need not be direct, and might be regarded as merely another aspect of pilchard/herring competition, the pilchard having been favoured by the higher temperatures.

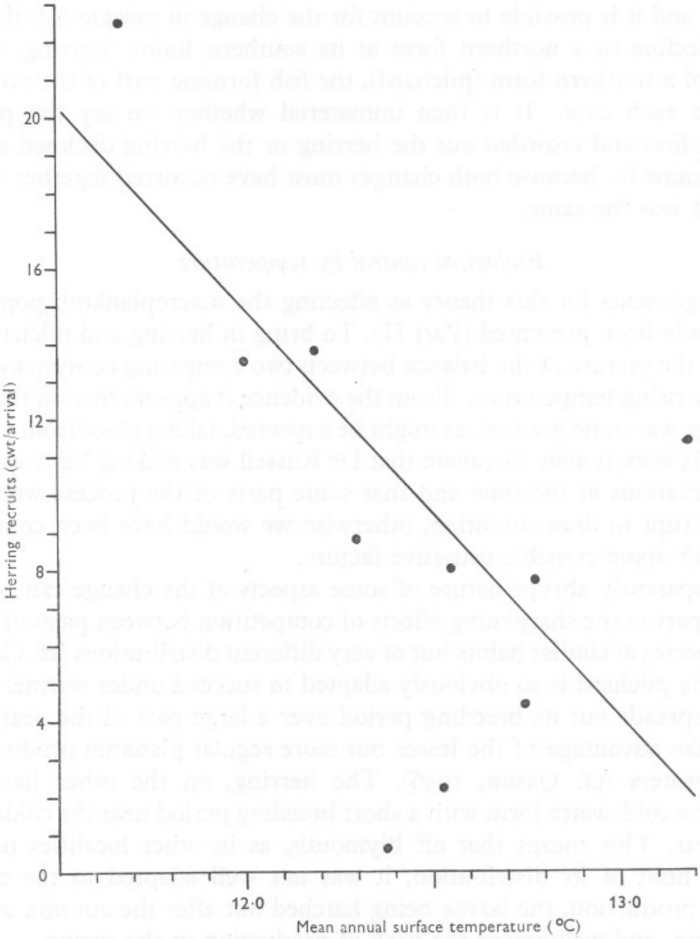

Fig. 5. Regression of herring recruitment for period 1921–31 (Cushing's data) on mean annual surface temperature at E 1.

The great advantage of the temperature control hypothesis is that it permits an explanation for all the other changes that have taken place. The increase of southern species in other habitats (demersal fish, cuttlefish, intertidal zone) and the decrease in northern forms (demersal fish, intertidal zone, and in part, benthos). The possible general decline in the biomass of the bottom fauna might also be explained by a slight change in the plankton production cycle in the water above, as suggested in Part II. A more efficient process with less violent seasonal fluctuation would mean less 'wastage' to the bottom during the peak spring outburst; the cycle in the English Channel off Plymouth is in fact more efficient than that in some other temperate localities (cf. Riley, 1956). If we allow for an increase in numbers of clupeoid fish, it is hardly surprising that another habitat dependent on the same primary production should suffer a loss of organic content.

Objections might be raised in connexion with the apparent abruptness of the plankton change in 1931, with the decrease in winter phosphate, and the matter of biological differences between sea waters. In Part II it was suggested that the changeover off Plymouth in 1931 was not necessarily sudden over the Western Basin as a whole. A very local extension of the boundary between the ecosystems, as part of a gradual change over several years, would be seen as an abrupt change at a single station. A slight increase in emphasis of the south-western influence would bring about a rapid change from *Sagitta elegans* to *S. setosa*, the latter being drawn into the anti-clockwise movement around the Western Basin from more easterly regions where it was normally dominant. This would occur as part of the normal seasonal cycle, at the start of the influx of south-western influence in the late summer and autumn (see Part II; Russell, 1933). It was the partial failure of *S. elegans* to return the following spring and in subsequent springs that was more significant. The change in dominant chaetognath was not really completed until after the slight regression of *S. elegans* and other north-western forms in 1935–36. Thereafter the decline of both *Sagitta* and general macroplankton might be connected with predation by pilchard.

With regard to the decline in phosphate, it has already been suggested that this might merely be an index of the changed ecosystem and not a loss of fertility, less of the phosphorus coming back into solution during the winter. When the apparent increase in numbers of pelagic fish is considered, it is obvious enough that part of the decrease in phosphate could be bound up in their bodies, as suggested by Cushing (1961), but the extent to which this would contribute to the decrease is, at the moment, debatable (see p. 20).

Finally, the biological differences between sea waters: this too may be connected with the different ecological systems. The so-called 'Western Water' was usually obtained from the central or northern parts of the Fastnet area inhabited by a typical north-western assemblage of macroplankton forms, with *S. elegans*, or *Aglantha* or similar forms, including the larvae of *Luidia sarsi* (Part II). During 1958–60, at the time of year when the samples were taken, this water was almost barren of crustacean or echinoderm larvae other than *Luidia*, and pelagic fish were practically absent. In contrast, the waters off Plymouth, which were not successful for laboratory rearing, were teeming with larval life, and had been for a month or so previously. Young fish of all descriptions, including sprat, and decapod larvae were present and the echo-sounder records showed an abundance of pelagic fish, although the large macroplankton predators found in the Fastnet water were sparse or absent. In other words, the unsuccessful water had already been inhabited by large numbers of small animals as well as by pelagic fish, while the successful water was comparatively fresh to the process of larval rearing. This difference might perhaps be sufficient to account for the experimental results which assume that some biologically active factor is present in the Fastnet water. There is then no reason to suppose that there was initially any more of this factor in the one water, merely that it had seen greater use in the other water. Nor does it follow that one water is 'better' than the other for the adult *Echinus*, since numbers of unmetamorphosed larvae can have little to do with numbers of adults. By a similar argument we might explain the evidence that Plymouth inshore water provided better rearing facilities before 1931, i.e. when a north-western community was dominant in the plankton. The north-western trend is then assumed to have been the stronger, at least off Plymouth, and the area would receive a greater proportion of 'less-used' water than it does today. Moreover, locally the relative scarcity of pilchard would reduce the rate of use, the stock of herring having fewer larvae, to judge from the YFT samples. At the same time the larger number of predators within the macroplankton such as *Sagitta* and *Aglantha* would tend to keep down the number of small larvae, though possibly not such big forms as *Luidia*, to a level that might even permit them to grow better.

Before we can consider the application of the various theories, it is important to assess the true status of the pilchard in the area, the extent of its increase in abundance, its spawning, and ecological role in relation to herring.

THE STATUS OF PILCHARD AND HERRING IN THE ENGLISH CHANNEL OFF PLYMOUTH

The most obvious indices to the changed status of pilchard off Plymouth are those used by Cushing (1957, 1961): the length of the spawning period and the numbers of adults calculated from the abundance of the eggs.

Spawning of pilchard

Although pilchard have always spawned in the Western Basin as far as records go back, the present length of season and abundance of eggs seems unprecedented. In 1948 for example, pilchard eggs were found every month in the routine YFT's taken off the Eddystone, except in February and August (Corbin, 1950). From the TTN surveys in 1958–60 it appears that spawning began in the Western Basin in February, when a few eggs and well marked shoals of fish were present to the south-west of Scilly. In March spawning intensity had increased and eggs were present over a large part of the western end of the Channel and in the Scilly–Lands End Passage. By

May pilchard eggs were found in the whole Western Basin and spawning had begun to spread through the narrows to the Eastern Basin. As spring gave way to summer spawning decreased at the entrance to the Channel, the region of greatest abundance of eggs shifting towards the south coasts of Devon and Cornwall and the more easterly parts of the Western Basin, though a patch of eggs of lesser abundance was found well clear of the entrance to the west. In October the pilchard eggs appeared to be restricted to relatively inshore water off the Devon and Cornwall coasts, and to the south-west of Ushant.

TABLE 1. OCCURRENCE OF PILCHARD EGGS AT THE PLYMOUTH INSHORE STATIONS

Mostly from oblique hauls of the 2 m stramin ring trawl at the Eddystone or E1; based on Russell, 1926*a*, 1930–39; Corbin, 1949, 1950; Southward, 1962; supplemented by personal communications by F. S. Russell.

Year	J	F	M	A	M	J	J	A	S	O	N	D
1924	*n*	*n*	*n*	+	–	–	+	*n*	*n*	*n*	*n*	*n*
1925	*n*	*n*	*n*	+	–	–	–	–	*n*	*n*	*n*	*n*
1926	*n*	*n*	*n*	–	–	+(+)	++	–	+(+)	*n*	*n*	*n*
1927	*n*	*n*	*n*	–	–	–	+	–	–	–	–	–
1928	–	–	–	*n*	*n*	*n*	*n*	*n*	*n*	*n*	*n*	*n*
1929	*n*	*n*	*n*	–	–	–	–	–	–	–	*n*	*n*
1930	*n*	–	–	–	–	–	–	–	–	–	+	–
1931	–	–	–	–	–	–	–	–	–	–	–	+
1932	–	–	–	–	–	–	–	–	–	+	–	–
1933	–	–	–	–	–	–	–	–	–	+	+	–
1934	–	–	–	–	–	–	–	–	+	–	–	–
1935	–	–	–	+	+	+	++	++	++	++	+	–
1936	–	–	++	++	++	++	++	+	++	++	*n*	–
1937	–	–	–	+	++	++	++	++	+(+)	+	+	+
1938	–	–	–	+(+)	++	++	++	+(+)	+(+)	+	+(+)	+
1947	–	–	–	+	++	++	++	+	+	+	+	+
1948	+	–	+	+	++	++	+	–	+	+	+	+
1957	–	+	+	++	(++)	++	(++)	(+)	(++)	+	(+)	*n*
1958	*n*	–	(+)	*n*	*n*	(++)	++	*n*	++	++	(+)	*n*
1959	–	–	*n*	+	(++)	(++)	(++)	*n*	(+)	(++)	*n*	*n*
1960	–	–	*n*	++	*n*	*n*	(++)	*n*	*n*	*n*	*n*	–
1958–60*	–	+	+	*n*	+	+	+	*n*	*n*	+	+	+

–, Absent
+, Present } as monthly averages
++, > 1000 per haul } as monthly averages
(+), Present } as single samples
(++), > 1000 per haul } as single samples
n, no samples

* From high-speed sampler surveys in the Western English Channel.

At the end of the year some slight spawning was still taking place in inshore waters off Plymouth, but, unlike 1948, this activity did not continue into January.

Cushing's (1957) data for April–September, 1950, is in agreement with this summary, as are the YFT samples. Off Plymouth in 1957–60, the spawning period extended from February to November inclusive, with a peak activity (more than 1000 eggs per YFT haul, or 0·25 per m^3) from March or April to October. Quite similar seasonal changes in pilchard egg production were found from 1935 to 1938, though, particularly in 1935, the first year of abundant pilchard eggs, the season began a little later than in recent years. Before 1934 pilchard eggs were very rarely recorded at the Eddystone though sometimes more frequent at E 1 and E 2 (Russell, 1926*a*). Off Plymouth from 1924 to 1934 the occasional appearances of eggs were recorded mainly in the second half of the year, from July or September to December, but only once in April and June.

Adult pilchard are recorded as having been caught off the Cornish coast as early as the 16th century (Couch, 1840), and statistics are available back to 1870 (Cushing, 1957). Traditionally it has always been regarded as an autumn fishery, although there appears to have been some oscillation in the actual dates. Couch (1822) says 'fishing begins towards the end of July, and terminates about the time of the autumnal equinox; but in the memory of persons now living it commenced at the period at which it now ceases, and continued until Christmas'. Later, the same author noted that the main fishery had returned to the later period (Couch, 1865). Much of the earlier evidence of spawning is doubtful. For the period around the turn of the century it appears from Clark (1920) and from Cunningham (1889), that spawning was regarded as occurring from April to October, with a peak in June and July, but that it took place to the south of the Eddystone, i.e. towards E 1 rather than at the usual inshore stations sampled by Russell in 1924–38 (L 4, L 5, Eddystone). If these reports are correct the change in the period of breeding since then is about one or two months extra both at the beginning and end of the season, and an extension of peak spawning from 2 to 6 months. However, the intensity of spawning was obviously never great, few eggs being reported from tow-nettings although 'running' fish were caught at times (Cunningham, 1889, 1893, 1895). Similarly, in 1921–22 there appear to have been few occurrences of pilchard eggs in the Petersen young-fish trawl (unpublished records R. S. Clark & E. Ford), an instrument which has somewhat greater theoretical catching power than the 2 m stramin YFT.

As far as the more inshore stations and earlier periods are concerned we have to rely almost entirely upon hearsay. There are persistent references to a second spawning taking place close inshore, in the warm autumn according to Couch (1865), in December and January, or even February and March[1] according to Dunn (quoted by Cunningham, 1889). This second spawning was said to be distinct from the offshore spawning which took place in April and May (Couch, 1865) or May and June, even August (Dunn, quoted by Cunningham, 1889), and was not necessarily produced by the same fish (Couch, 1865). Cunningham did not believe the spawning periods were separate, his own records of ripe adults extending from June to November. Nevertheless, comparison with the egg distribution found in recent years, and the admittedly unsatisfactory echo-sounder data from the 'Sarsia' cruises, suggests that the fishermen were perhaps aware of a real difference that the

[1] But was there confusion with sprat eggs?

scientists missed through lack of ships and samples. In some recent years there has been a reduction of spawning intensity at the Plymouth stations in August, marking in 1958–60, a transition from an overall offshore spawning and shoaling in the Western Basin to a more inshore spawning and shoaling later in the year. The evidence obtained with the more satisfactory echo-sounding equipment on the W.F.A. research vessel 'Madeline' during 1961 (personal communications Mr J. P. Bridger), would appear to support this idea.

At this point we must consider the suggestion of Cushing (1957) that there might be a relationship between pilchard shoals and the pattern of water movements shown by Dietrich (1950), the spread of eggs and shoaling in the spring representing the winter clockwise movement, while the autumn inshore shoals on which the traditional Cornish fishery is based might be connected with the anticlockwise (summer) movement. At the time of Cushing's observations there was no evidence for the late autumn. The 1959–60 and 1961 evidence already quoted suggests some measure of agreement with this hypothesis, the decrease in egg production off Plymouth in the transition period coinciding with the changeover point to the south-western influence (summer circulation, cf. Dietrich, 1950; Part II). There is, however, no sign in these data of a 'return' of the shoals from up Channel postulated by Cushing (1957), and it is much more likely that the apparent movement of shoaling and spawning from the Western Basin to the Eastern Basin represents differences in the habits of fish resident in the various parts of the Channel. From the rather incomplete evidence available it could be suggested that there are at least two such groups of pilchard in the Western Basin. A 'western' group spawning along the northern side offshore in the spring, and apparently avoiding the south-western water present to the south side; and a 'south-western' group spawning along the path of the south-western trend in late summer and autumn and inshore along the Devon and Cornish coasts from autumn to the end of the year, and apparently avoiding the more obvious area of north-western influence (see Fig. 6). These hypothetical groups show a considerable measure of agreement with the fishermen's observations, and it might even be suggested that two races of pilchard with different spawning habits and possibly different migratory routes were involved. If so then the later-spawning south-western group, of possibly Biscay origin, is perhaps adapted to life in the warmer south-western water. This group is certainly the group of the traditional drift and seine net fishery, but from relative abundance of eggs it would appear to be much inferior in numbers of adults to the 'western' group. The latter group which spawns earlier might perhaps be adapted to cooler conditions found in the north-western water off Scilly and along the north side of the Western Basin in the spring. The increase in stock of pilchard since the 1930's could be regarded as largely an increase in this western group in response to the warming up of the water, which permitted an essentially warm-water species to extend its range or to increase its abundance greatly.

If these rather hypothetical suggestions have any factual basis, then the 'western' group is hardly fished at all by the traditional autumn fishery, though there are suggestions that its importance in total landings of pilchard has increased in recent years. However, to explain the change in the seasonal pattern of pilchard eggs at the Plymouth inshore stations requires an increase in abundance of both hypothetical groups.

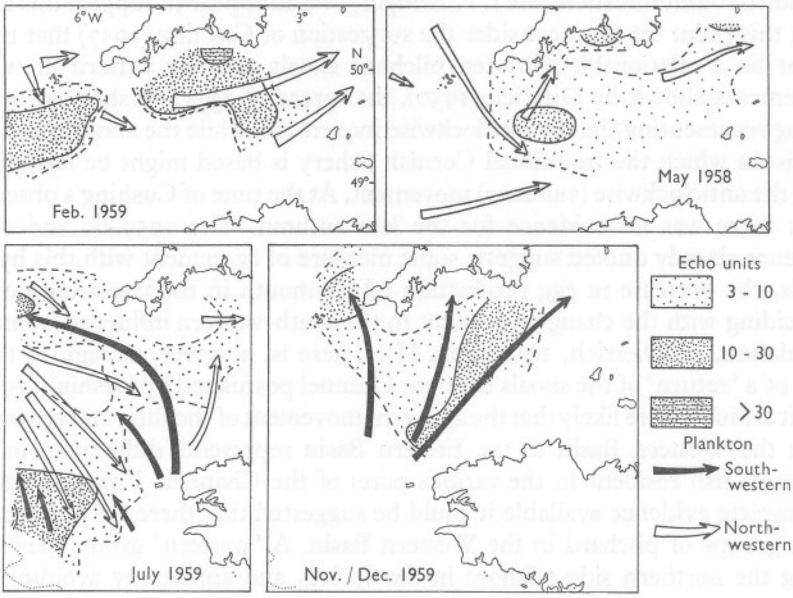

Fig. 6. Distribution of pelagic fish shoals and plankton, summarized from charts in Southward (1962). The fish are shown as echo-units for dry paper Graphette or MS 26*b* sounders (15 kc/s). Except for July, only one of the opposing plankton trends is given, to avoid confusion.

Increase in abundance of pilchard off Plymouth

It is not difficult to estimate the numbers of mature pilchard from the numbers of eggs, but such an estimate will be on the conservative side since predation cannot be calculated. For the English Channel as a whole Cushing (1957) gives an estimate of 10^{10} adult pilchards (within the range of error of $\times 2{\cdot}2$, $\times 0{\cdot}45$), which were spread out over an area of $9{\cdot}3 \times 10^{10}$ m^2, or just over one fish (2 or $\frac{1}{2}$) to each 10 m^2 surface. From Hickling (1945), a mature pilchard weighs just under 90 g gutted. Ignoring the gut weight this gives us an estimate of 9·6 g pilchard/m^2 surface.

A similar calculation, using the same methods, has been carried out for the Plymouth area for the year 1957. The eggs found in each routine YFT haul were plotted on graph paper, a smooth curve drawn through the points, and a mid-monthly egg value read off. This value was multiplied by a factor representing the number of days in the month divided by the number of days needed to hatch out the egg (Cushing, 1957) at the mid-monthly temperatures already worked out for station E 1 (Southward, 1960). The sum for the months April to October (relatively few eggs are present in the remaining months of the spawning period) was 243,000 eggs per 4000 cubic metres (estimated YFT volume) per year. Allowing a fecundity of 76,000 eggs per female (Cushing, 1957), and a sex ratio of unity, this is equivalent to 6·4 adult fish per YFT. For an average depth of water of 72 m this gives an estimate of 1 adult fish to each 9 m^2 surface around Eddystone–E 1, or 10·8 g wet weight/m^2, surprisingly close to the value for the whole Channel in 1950.

Both of these estimates assume one complete spawning a year (Cushing, 1957). It is possible that a steady production of eggs takes place rather than that the same fish spawns completely more than once (cf. Andreu & dos Santos Pinto, 1956), but there are no observations for the English Channel pilchards. If we allow about one-sixth of the wet weight as dry weight, these estimates are equivalent to Harvey's guess of 1·8 g dry weight/m^2 for *all* pelagic fish, mature and immature, in the Channel (Harvey, 1950): obviously, a serious underestimate of pilchard abundance was made, in spite of allowance for the extensive pilchard shoals reported by Hodgson & Richardson (1948).

At the moment it is impossible to make any reasonable estimate of the immature fish, since we have no measurement of mortality. The minimum numbers required to replace the adults, allowing the present 3 years to maturity (Cushing, 1961) and the usual cube law of growth, must amount to 5·4 g wet weight/m^2. The final total of 16·2 g wet weight/m^2 is then an obvious underestimate.

A much less modest estimate of the numbers of immature pilchard can be based on a recent haul with a French type of sardine seine, taken off the Eddystone by the W.F.A. research vessel 'Madeline' (personal communication, J. P. Bridger). This suggests a value of 180 g wet weight/m^2 for shoaling fish just under 2 years old, and though allowance must be made for shoaling, it must be noted that only a small part of the shoal shown on the echo-sounder was captured, and that echo-sounder surveys may show similar shoals at intervals over thousands of km^2 of the Channel.

Before 1931 pilchard eggs were rare at the Eddystone and E 1, usually little more than a few hundred a year per YFT (Table 1). This indicates an increase in numbers of spawning fish of the order of 1000 times, giving an estimate of the previous population of about 0·016 g wet weight per m^2 surface. To this must be added any non-spawning migratory pilchard, but even then it is difficult to see how the population can have exceeded 0·2 g/m^2.

Abundance of herring off Plymouth before 1932

There are, of course, no egg counts for herring, and the larval abundance in the YFT is too low and variable to use. It is therefore necessary to work back by inference from the age-group composition of the shoals landed. The fishery failed[1] after 1935, when most of the fish were over 6 years old (Ford, 1933; Kemp, 1938), and 8 years after the year of hatching of the last successful year-class, that of 1927/28 (Cushing, 1961). This year-class will have entered the fishery in 1931/32 at the age of 4, and hence was almost completely removed by fishing and natural mortality in the further 4 years before the end of the fishery. This suggests a total adult mortality rate of at least 25% per annum, possibly more.[2] For the period just before this year class joined the fishery, i.e. while recruitment was still occurring, the landings averaged some 75,000 cwt per season, and hence the adult stock could be estimated as at least 300,000 cwt. However, since we have no means of estimating the proportion of fishing mortality and natural mortality, such a stock estimate must be viewed with caution.

The area normally fished over was that of the spawning shoals from Dodman Point to Bigbury Bay (Ford, 1933) but it is likely that the fish lived and fed in a much larger area. As an estimate we can take the area from Lizard to Start Point, extending as far out into the Channel as station E 1. Thus, taking the estimate based on apparent total mortality, we have approximately 15,000,000 kg or 1.5×10^9 g herring distributed over 1200 square miles or 0.3×10^9 m^2. Allowing another 50% for juveniles without intervening mortality this comes to 7·5 g wet weight/m^2 surface, or including the very small population of pilchard then present, a possible total clupeoid population of 7·6 g/m^2.

From the two sets of calculations, which are admittedly based on insufficient data, it would appear that clupeoid fish off Plymouth are now at least twice as abundant as they were before 1930–35, and possibly very much more than twice.

Increase in clupeoid fish and decrease in phosphate

Cushing (1961) has suggested that some, if not all, of the decrease in winter phosphate at station E 1 is locked up in the increased population of pilchard. Between 1921–30 and 1931–38 there was a fall of approximately 0·2 μg/atom P/l.; this is equivalent to 0·446 g phosphorus/m^2 surface.

There is no exact information for the total phosphorus content of pilchard, but we can estimate between 0·4 and 0·8 g for a wet weight of 90 g. From Vinogradov (1953) the tissues may contain up to 0·5% phosphorus; the bone is approximately 45% mineral of which 95% is calcium phosphate, and may

[1] The failure of the Plymouth herring fishery does not imply the total absence of herring, particularly in inshore waters. A few specimens were trawled on the Looe–Eddystone grounds by M.B.A. vessels in 1960–62, most usually in the first half of the year. Those examined were all spent or recovering spent, with more than 4 winter rings on the scales. They may be representatives of a local inshore group or may perhaps be stragglers from farther east (e.g. Gt West Bay where herring are taken each winter) or from the north Cornish coast (St Ives). They are probably not from the Irish (Dunmore) fishery (personal communication Mr A. C. Burd).

[2] Cushing (1961) has guessed a mortality of 0·20 based on that calculated for the Dunmore group by Mr A. C. Burd.

constitute some 5% of the wet weight (cf. Alexander, 1959 on freshwater fish). From this estimate the decline in phosphate would be the equivalent of 5–10 adult pilchard per 10 m^2 surface, whereas the egg calculations show a present density of only 1 per 10 m^2 and the above inexact estimates have suggested an increase in clupeoids of at least two times, possibly more. However, it is clear from Cushing's statement of his hypothesis that the difference in phosphate is regarded as locked up in the younger age groups, for which no reliable estimate can be made at present.[1] Nevertheless, the heavy catch of immature fish taken by the 'Madeline' gives food for thought and shows the need for more direct investigation of pilchard abundance.

Some consideration must be given to the increase in abundance of cuttlefish. Although the cuttlebone is largely calcium carbonate, the tissues contain some 0·2% phosphorus and the animal is six times the weight of a pilchard (personal communication, Dr E. J. Denton). We cannot easily estimate the abundance of these animals, since many probably escape the trawl, but their increase must have withdrawn some of the phosphorus from circulation particularly as they live through the winter, post-spawning mortality occurring late in the spring (in May 1961 hundreds of recently dead specimens were seen floating at the surface in the Channel off Dover).

Effect of pilchard as predators

Although the inshore fish can eat phytoplankton at times (Swithinbank & Bullen, 1913; Hickling, 1945; personal observations) it seems that in general pilchard are part-selective macroplankton feeders (Massuti, 1955; see also Radovich, 1952, and Hand & Berner, 1959, on the Pacific sardine), as are other clupeoids such as herring, sprat and anchovy (Hardy, 1924; personal observations). The stomach contents of the latter two species are often stratified, suggesting that different food organisms may be selected at different times, and it is worth noting that *Sagitta* (sp. indet.) is often preferred, over a hundred being found in a single 1-year-old sprat.

In 1935–38 inshore Cornish pilchard were feeding mainly from March to October, with at least 1 g wet weight food per stomach from April to July: that is, heavy feeding corresponded with the peak of the breeding season off Plymouth (Hickling, 1945). Hence the adult fish in one YFT area off the Eddystone might be capable of eating say 6 g wet weight in one meal. The total macroplankton standing crop, as estimated by the YFT, can reach as much as 25 g wet weight per standard $\frac{1}{2}$ h haul in April, during the peak plankton

[1] Dr Cushing suggests (personal communication) that the difference in phosphate could be accounted for by only ten 6-month-old pilchard per m^2 surface, which is equivalent to 0·14 per m^3 of water. Recently some fast tows of the 2 m stramin ring trawl were made off Looe at the end of June. The total catch of young clupeoids, almost certainly all pilchard, varying in age from a few days to an estimated two months (20 mm length), was of the order of 0·4–0·8 per m^3. This density would indicate that there was no great improbability in the number of 6-month-olds required by the pilchard control theory.

outburst in 'good' years before the main pilchard breeding season begins (e.g. in 1955, see Part I), but in most years may be less than 2 g wet weight per YFT at the same time. On average therefore we can say that off the Eddystone the adult pilchard should be capable of reducing the crop of macroplankton by at least half each day, and it is hardly surprising that the samples between April and October show an inverse correlation between numbers of pilchard eggs and most other macroplankton organisms. The same relationship seems to apply over most of the Western Basin when pilchard are spawning (e.g. March 1958, Part II; or compare Russell, 1926*a*).

As noted by Harvey (1925) long ago, a rise in temperature will be accompanied by a significant increase in the metabolic rate of the organisms, and, as Kinne (1960) has recently shown, will lead to increased food consumption by fish. It is possible that the metabolic rate of herring is higher at a given temperature than pilchard, following the general rule among poikilotherms of differing geographical distribution (e.g. Fox, 1939), and hence the same rise in temperature might require a comparatively greater intake of food in these fish, perhaps reaching such a level that they might not be able to satisfy their needs from the crop available in a given time. Such a relationship would leave the herring at a great disadvantage compared with pilchard, and intensify the competition between them for food.

The effect of predators would be felt least by organisms such as decapod larvae, which are produced by relatively large bottom-feeding adults; these larvae, and of course pilchard eggs and young pilchard, constitute the bulk of the macroplankton captured in YFT hauls from April to October.

Finally, if clupeoid fish increased in abundance off Plymouth to the extent suggested during the 1930's, it is hardly surprising that the standing crop of macroplankton decreased, even of commoner species hardly likely to be directly affected by climatic changes. It is also not surprising that a decline in the numbers of the planktonic young of demersal fishes should first be shown among those species which spawn in late spring and summer, when pilchard breeding and feeding is at its peak. The subsequent decline in spring-spawned young fish is then, on this hypothesis, an index to greatly increased stocks of pelagic fish throughout the year.

CONCLUSIONS

Some assessment has already been given of the advantages and disadvantages of the various theories. The chemical control theory hardly fits all the facts now known, and at its full state of development is the most complicated; the pilchard control theory is simpler, but fails to account for many of the other biological changes, and does not, at the moment, provide a satisfactory explanation for the whole of the decline in winter phosphorus content.[1] Both of these theories assume little or no circulation of water. We are therefore left with

[1] See footnote p. 21.

the temperature control theory, which offers the simplest explanation yet of all the biological changes—or most of them—but is the least tangible as far as positive evidence for cause and effect is concerned. It is implicit in the temperature control theory that pilchard have increased in abundance, accounting for part at least of some of the other changes: the rise in temperature and the accompanying slight change in water movements seems to provide the best explanation for this increase.

The main points of the temperature control theory can be summarized as follows: (1) Rising temperature, increasing south-western influence, decreasing north-western influence. (2) Decline in northern forms and increase in southern forms in most habitats, including intertidal zone, plankton, and, in part, benthos. Possible smoothing out of the plankton production curve during the year. (3) Decline in species of fish of economic importance, both pelagic and demersal, most of them of northern distribution, and a corresponding increase in species of southern distribution but of less economic importance in Britain. In particular almost complete replacement of herring by pilchard, and a probable total increase in stock of pelagic fish. Increase in cuttlefish. (4) Decline in winter phosphate due to changes in (1), (2) and (3). The phosphate has not necessarily decreased but is kept in biological circulation longer. (5) Effect of increase in pelagic fish and possible smoothing out of plankton production curve detrimental to animals in other habitats, particularly benthos and macroplankton, apart from effects of change in communities under (1) and (2).

The most obvious defects of this hypothesis, apart from its general vagueness and being based on a series of assumptions, though on less than the chemical control hypothesis, are: (*a*) we cannot properly measure the various biological changes, partly because of lack of earlier quantitative evidence, and partly because of present difficulties in obtaining quantitative evidence (e.g. pilchard); and (*b*) it is difficult to assess the effects of the biological changes on the level of phosphorus, and hence it is impossible to say with any certainty whether there has been any real change in basic fertility or not.

All the theories suffer from lack of basic data, and only further work or further biological changes will show which, if any, is the correct one. In particular, if facilities become available, it should be possible to assess the pelagic fish stocks more reliably with improved sonar gear, better nets and larger high-speed samplers. Estimates of total production in relation to chemical factors could be made for areas with typical north-western and south-western plankton.

It is obvious that continued vigilance is needed both in the English Channel and elsewhere,[1] to detect further changes in distribution or abundance.

[1] There have been several instances in recent years of an apparent spread of warm-water forms, including plankton and pelagic animals, to Scottish waters: e.g. Rae (1961), Colebrook, John & Brown (1961).

SUMMARY

Various biological and environmental changes that have been observed during the present century in the area of the western English Channel are briefly described, and then theories that have been put forward to account for them discussed and compared critically with one another.

At the moment, the rise in sea temperature and a possible accompanying change in emphasis of water movements offers the best explanation of all the changes. Such a theory is obviously applicable to the replacement of cold-water northern forms by warmer-water species that has taken place in many habitats (e.g. demersal fishes, pelagic fishes, intertidal zone). A decline in number of macroplankton animals, including the pelagic young of some demersal fish, can be regarded as another aspect of the temperature change, in part related to a shift in distributional boundaries, but also influenced by the replacement of herring by pilchard, which has apparently led to increased stocks of pelagic fish, and perhaps a higher level of predation throughout the year. It is suggested that the plankton production cycle may have become slightly smoother, and possibly a little more efficient, with less 'wastage' to the bottom-fauna, the biomass of which may also have suffered indirectly from the increased stocks of pelagic fish.

Some theories consider that the decline in winter maximum of phosphate-phosphorus that was observed in the 1920's–1930's represented a loss of fertility of the sea water, and was therefore the cause of the decline in herring and macroplankton. Such theories, of course, do not explain the other biological changes, and an alternative explanation is that the lower phosphate maxima are merely indices to the changed biological system, the difference being in circulation in the organisms with less returning to solution each winter. This does not imply a lower level of primary production, which is not necessarily closely related to the winter phosphate content of the water.

At the moment we cannot determine the extent to which the difference in winter phosphate is directly connected with increased stocks of pilchard, as suggested in other theories. All the hypotheses suffer from lack of basic data, and only further work or further changes will show which if any is the correct solution of the problem.

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APPENDIX

CHANGE IN COMPOSITION OF THE PLYMOUTH DEMERSAL FISH FAUNA

(Data compiled by the late G. A. Steven, assisted by Lt. Com. C. A. Hoodless, R.N.R. and A. D. Mattacola)

Table 2 compares the numbers of fish caught by two of the Plymouth research vessels during two periods separated by an interval of thirty years. For the earlier period records have been taken from the biological log kept by R. S. Clark & E. Ford of fish caught by S.S. 'Salpa' in 1919–22. During these years most of the inshore trawling grounds were visited, and hauls taken in all months of the year except April and June. The 130 hauls used to compile the table cover a total fishing time of 107 h, each varying from 25 to 105 min duration. The same places were visited by R.V. 'Sabella' in 1949–52, and trawled over for approximately the same times on as nearly as possible the same dates, the greatest difference between corresponding hauls being less than two weeks. 'Salpa' and 'Sabella' were approximately the same length, and although the former was a steamboat and the latter diesel, the trawling powers can be assumed to be reasonably similar, while the simple otter trawls were practically identical.[1]

TABLE 2. THE PLYMOUTH DEMERSAL FISHES

See text for full explanation

			Catch			
			1919–22		1949–52	
Change	Species	Distributional status	No.	No. of hauls in which present	No.	No. of hauls in which present
Not recorded in earlier period	*Pagellus centrodontus*	S	—	—	84	15
Increase 1:10	*Cepola rubescens*	S	1	1	66	36
	Merluccius merluccius	S	17	10	976	75
	Mullus surmuletus	S	4	3	122	30
	Trachurus trachurus	S	4	2	300	16
Increase 1:3	*Scophthalmus rhombus*	S	17	15	122	80
Some increase	*Conger conger*	S	25	17	63	47
	Lophius piscatorius	S	88	51	181	93
	Platichthys flesus	G	6	3	12	2
	Scyliorhinus stellaris	S	15	6	32	26
'Total disappearance'	*Molva molva**	N	18	15	—	—
Decrease 100:1	*Squalus acanthias*	G	2357	35	3	3
Decrease 10:1	*Capros aper*	S	71	26	2	2
	Trigla gurnardus	N	4952	106	90	69
Decrease 3:1	*Gadus merlangus*	G	6723	62	1731	74
	Limanda limanda	N	961	86	275	71
	Trigla lineata	S	268	87	67	59
	Zeus faber	S	775	117	234	68
Slight decrease	*Gadus callarias*	N	28	13	17	11
	Gadus luscus	S	473	12	352	19
	Microstomus kitt	N	181	72	166	80
	Pleuronectes platessa	N	162	65	134	54
	Raia spp.	—	908	111	742	107
	Scyliorhinus canicula	G	2255	72	1315	103
	Solea solea	S	168	71	114	72
No change	*Arnoglossus laterna*	S	1313	83	1435	127
	Callionymus lyra	S	9149	112	10711	130
	Gadus minutus	N	5679	68	6012	118
	Phrynorhombus sp.	S	65	27	64	38
	Scophthalmus maximus	S	39	28	32	31
	Solea variegata	S	145	45	142	64
	Trigla cuculus	S	4338	109	4577	124
	Total fish		41225		30220	

* This species has been taken occasionally off Looe by R.V. 'Sarsia', during prolonged (3 h) trawl hauls.

[1] Boards, 6 ft × 3 ft 5 in; footrope, 76 ft; headline, 60 ft.

It is of course impossible to compare the single pairs of hauls, since there can be so much variability in trawl catches. The total catches are therefore tabulated. It would appear that, although there was no drastic decline in numbers of fish caught, the species composition of the catch had changed considerably. This is clearly brought out in the table by allotting each species an arbitrary distributional status, based on International Council (1929–38), of north (N) or south (S), according to whether the major part of its geographical range is to the north or south of the English Channel. A few more generally distributed or cosmopolitan species are also indicated (G). Thus grouped, it is obvious that, in general, northern forms declined and southern forms increased between the two periods. Of the fish showing increases nine out of ten are southern forms, while ten out of fourteen of those showing a decrease are northern forms. Those species which have not changed significantly are almost all southern forms (five out of six). There are a few exceptions to this general rule. There were significant decreases in three southern forms, *Capros aper*, *Zeus faber*, and one species of gurnard; the two former species belong to the same family and appear to have similar habits—that of a 'reef fish' of relatively deep water, and may well be too stenothermal to tolerate the greater range of temperatures that accompanied the rise of temperature during the period (Southward, 1960). Similar arguments may apply to the gurnard (*Trigla lineata*) and to *Gadus luscus*, both of which have a very limited distribution compared with some of the other fishes; however, the changes in number of the latter species and of *Solea solea* appear to have been very small.

Only five of the species showing no marked change or an increase in number are of much commercial value. Their total numbers are very much smaller than those of the important commercial fishes that showed a significant decrease. It is unfortunate that so many of the species on which the British sea-fisheries are based are essentially cold-water forms, many of them near their southern limits in the Channel, and that social and economic causes prevent much utilization of the other, more abundant species taken in the trawl.