THE BIOLOGICAL EFECTS OF UPWELLING IN THE SEA WITH SPECIAL REGARD TO FISHERIES

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ABSTRACT

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This article is worked out on the basis of a theme given by the evaluation committee in connection with the present author's doctorate. The article gives a brief survey of the physical background for upwelling and the most important upwelling areas in the world oceans and deals primarily with the effects of upwelling on production of organic matter and its conversion to higher forms of life. The more direct effects of upwelling, e.g. on behaviour and mortality of fish are also discussed.

INTRODUCTION

In some restricted areas of the world oceans, especially along the west coasts of continents at subtropical latitudes, prevailing winds drive the surface layer water seawards. The water transported offshore s replaced by deeper nutrient rich water. This process is called upwelling. Such areas of coastal upwelling are biologically the richest parts of the oceans, and large fish populations live there. They are found particularly in the eastern boundary currents of the subtropical anticyclones, e.g. off Peru, California, Northwest and Southwest Africa. Extensive coastal upwellings also occur in other areas, e.g. in the Arabian Sea, the Bay of Bengal and around the Antarctic continent.

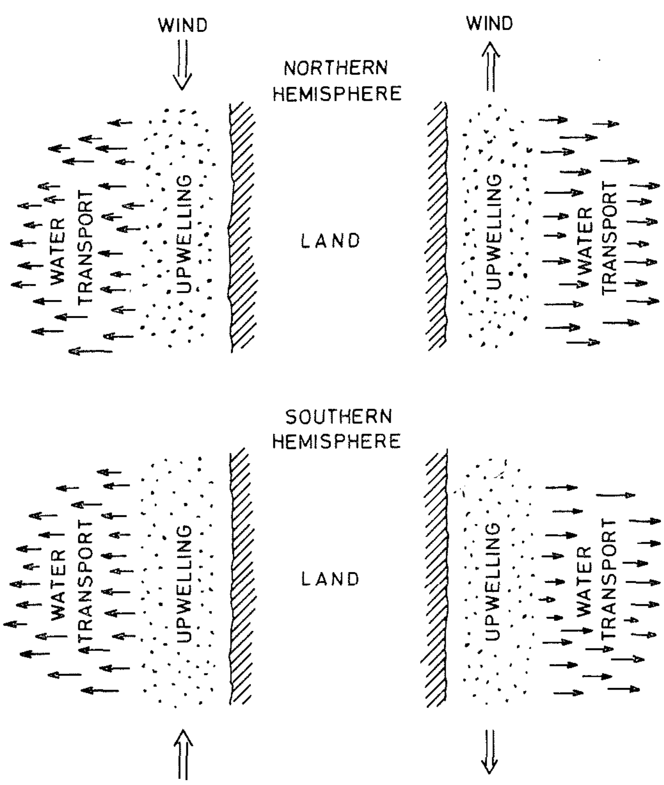

Fig. 1. Upwelling in relation to the wind direction along a coast line in the northern and southern hemisphere.

Recently, much concern has been devoted to the fishing potential of areas of high primary production (upwelling areas). The FAO's Advisory Committee on Marine Resources Research, has pointed out that comparative studies should be promoted of sea areas where good data on primary production and fisheries statistics coincide, particularly in some upwelling areas, e.g. off Peru and off Southwest Africa, in order to answer two specific questions: (1) what is the magnitude of fish stocks at the second and third trophic levels in the main upwelling areas, and (2) what is the relation between fish stocks and primary production in each or any of the upwelling areas (ANON. 1967).

PHYSICAL BACKGROUND AND IMPORTANT AREAS OF UPWELLING

GENERAL

When prevailing winds blow along coastlines, they may cause upwelling as indicated in Fig. 1. Also the great wind systems of the atmosphere, the cyclones and anticyclones, bring about large-scale eddy-systems in the oceans. Two subtropical anticyclones are generally found in all oceans, one north and one south of the equator. Fig. 2 illustrates the surface water currents in the world oceans where also the great eddy-systems are indicated. The most important upwelling areas are found at the eastern boundaries of the currents. In the western boundary currents upwelling does not occur to the same extent because the former are more narrow and intense with higher velocities than the eastern boundary currents where the water also tends to have a somewhat lower salinity (CUSHING 1969). The currents

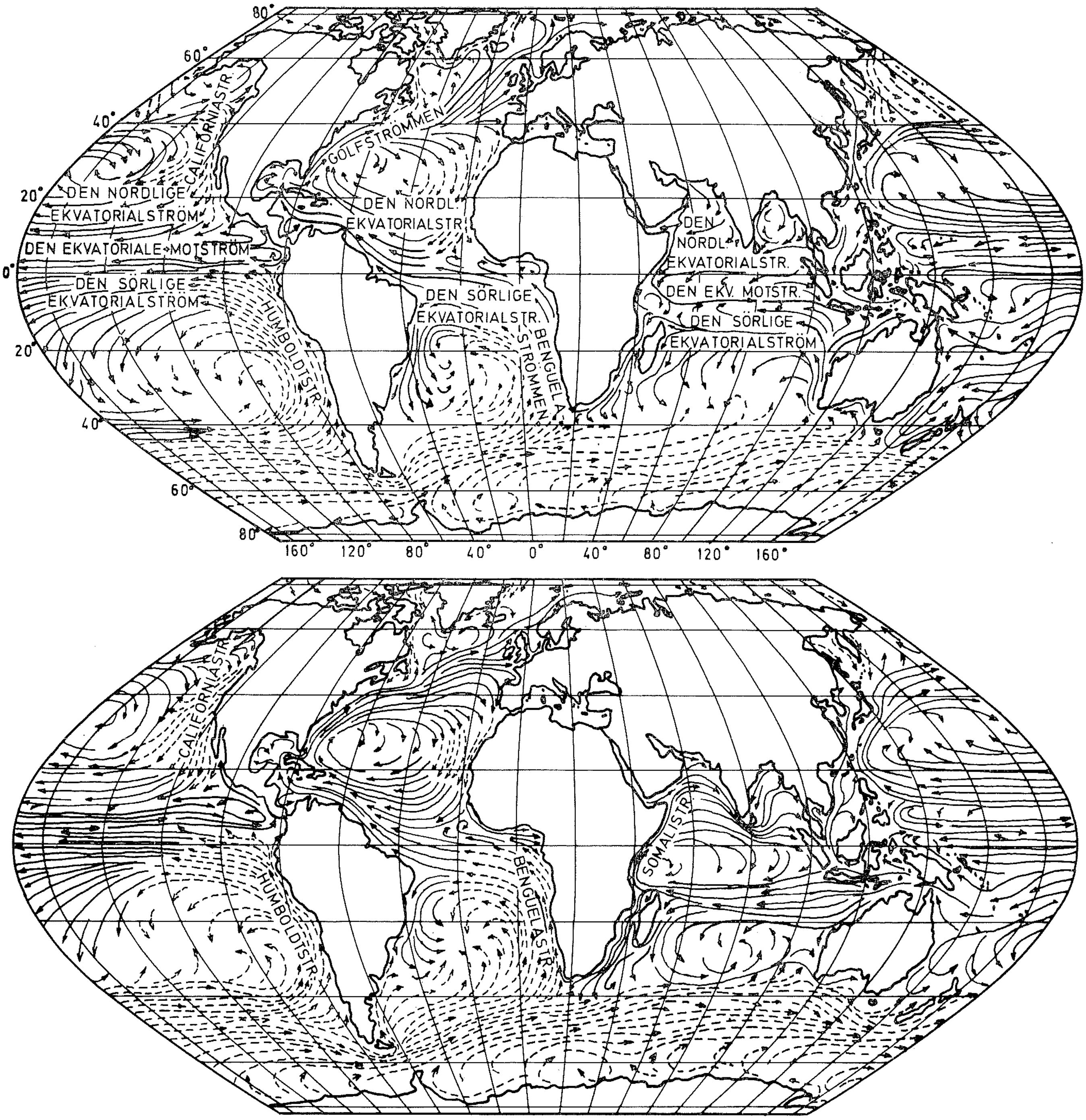

Fig. 2. Surface water currents of the oceans in January (top) and July (below).

in the Indian Ocean are largely influenced by the monsoons, and therefore upwelling is more seasonal. The monsoon system is especially pronounced in the Arabian Sea and in the Bay of Bengal. Upwelling is known to take place off the Somali coast, at the Arabian coast and off the West and Southwest coasts of India. At higher latitudes upwelling usually has a temporary character, lasting only for a few days, and the biological effects of these types of upwelling are less pronounced.

As the water in subtropical regions is blown offshore at an angle to the coast, it is presumed to be moving towards the equator. Fig. 3 gives a schematic representation of the water movements and upwelling in the Benguela Current. About 100 km offshore a convergence is often found where the water sinks. A little farther offshore there is a divergence generating a secondary upwelling above the thermocline (Hart and Currie 1960). This cell of convergence is the region which Sverdrup (1938) called a dynamic

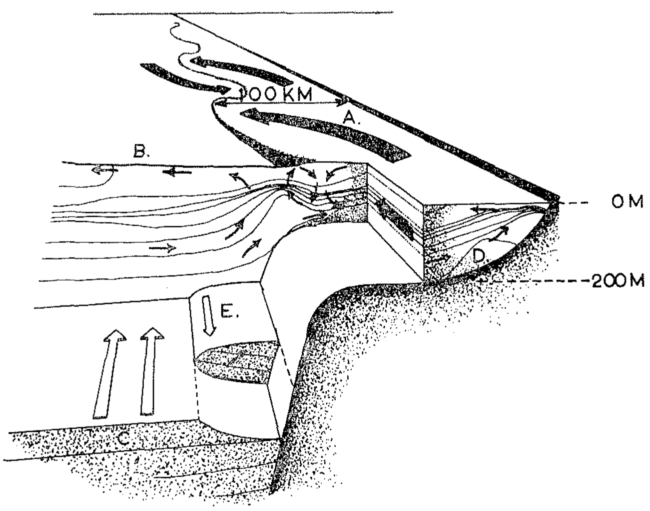

Fig. 3. The mechanism of upwelling in the Benguela Current off the western coast of South Africa, A) coastal water, B) oceanic surface layer, C) deep water, D) zone of upwelling and E) deep counter current. Adapted from HART and CURRIE (1960).

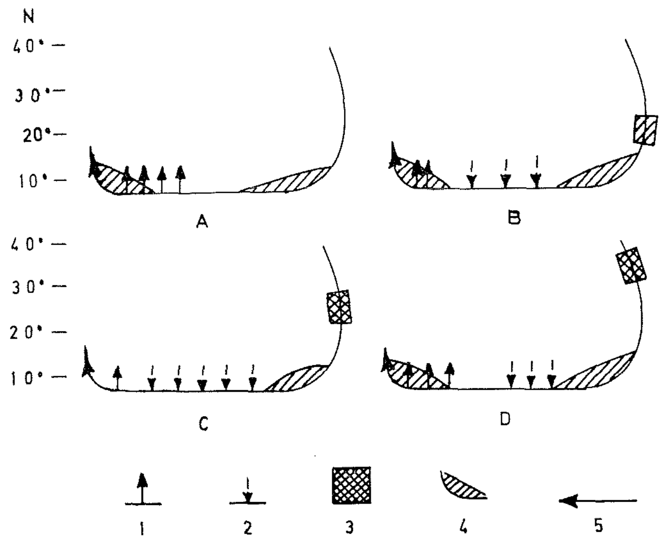

Fig. 4. Diagram of the seasonal movement cycle and upwelling, (A) winter, (B) spring, (C) summer, (D) autumn in an eastern boundary current and in an equatorial system in northern latitudes, 1) divergence, 2) convergence, 3) coastal upwelling, 4) extensive area of divergence and 5) current. Adapted from CUSHING (1969).

boundary. The depth of the upwelling systems appear to be shallow. In the Benguela Current it is about 200 m, and the current flowing towards the equator is compensated by a counter current below about 200 m flowing towards the pole.

Divergences are also found along the poleward boundaries of the subtropical anticyclones, especially at the western ends of the equatorial currents and along the equatorial boundaries of the southern anticyclones. Upwelling areas also are found in the equatorial currents, the most well-known being the Costa Rica Dome (WYRTKI 1966) at the root of the North Equatorial Current in the North Pacific. Analogous phenomena exist in the East Atlantic and in the East Indian Ocean. Fig. 4 illustrates the seasonal cycle of upwelling in an eastern boundary current and an equatorial system in northern latitudes (CUSHING 1969). The figure shows the movement of the coastal upwelling system towards the pole from spring to autumn as the subtropical anticyclones intensify and indicates the divergence areas along the equator. The divergence is most pronounced during the winter.

MAIN UPWELLING AREAS

In coastal upwelling areas sediments rich in organic matter are found, and these areas may be charted by mapping phosphatic deposits (TOOMS 1967). In Fig. 5 all major coastal upwelling areas have been charted by this method including some minor areas like those off the Malabar coast (India) and the coast of Ceylon. Also the Guinea upwelling, the area off Northwest Australia and the centre of upwelling off California are shown. The Benguela deposits off Southwest Africa extend round the Cape of Good Hope. The equatorial system is not indicated by this method. Data relating to the Indonesian areas and the Caribbean Sea are not included in the figure.

BIOLOGICAL EFFECTS

GENERAL

The biological effects of upwelling can be classified in two main groups:

1) the effects on production of organic matter and its conversion to higher forms of life, and
2) the direct effects on behaviour, mortality etc. of animal living in the areas. Both of these effects will have great influence on the fisheries.

The upwelling areas at low latitudes are characterized by a rather deep euphotic zone (down to 50 m below the surface), and production increases towards the surface as the water rises. The production cycle in an upwelling area resembles that in temperate waters (CUSHING 1969). Rising cool water, rich in nutrient originates from depths of less than 200 m, and contains a resident and sparse population of plants and animals, similar to that of temperate waters in early spring. In the euphotic zone the algae

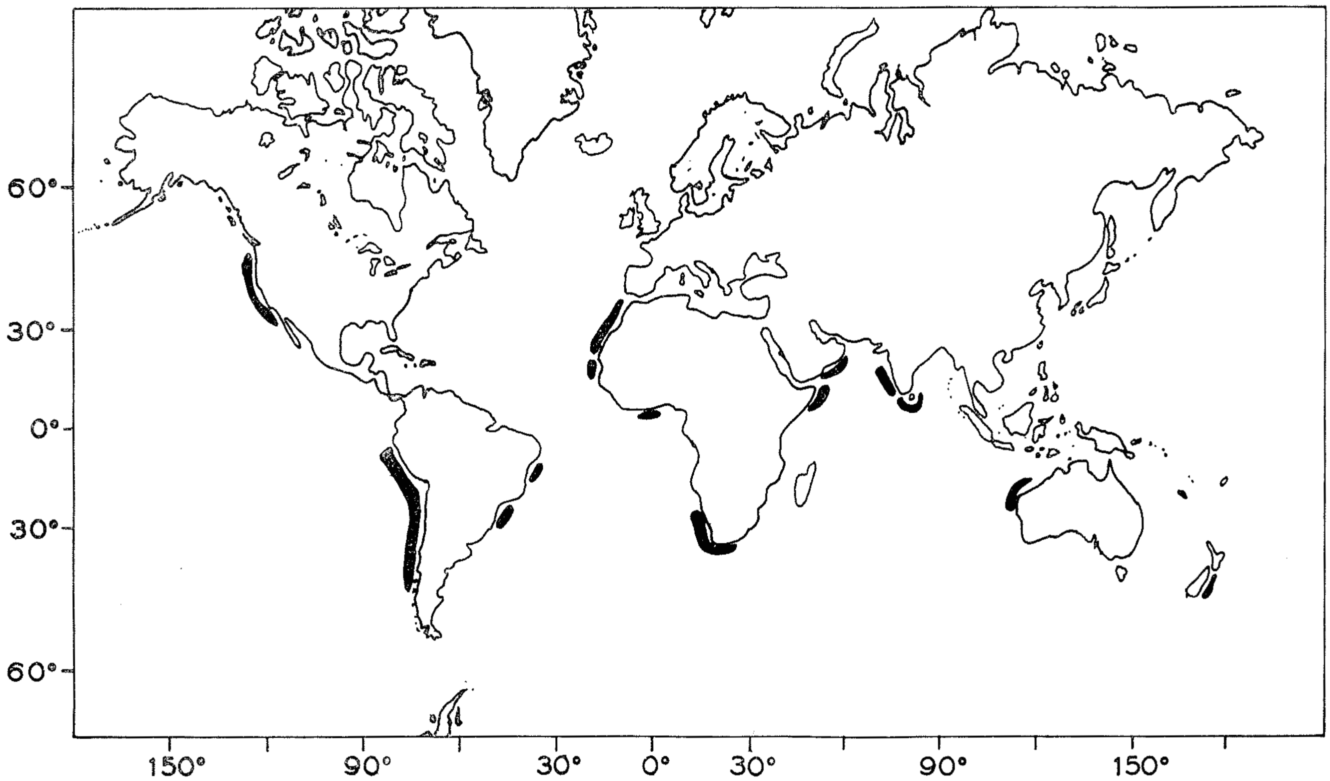

Fig. 5. Distribution of phosphatic deposits. Adapted from TOOMS (1967).

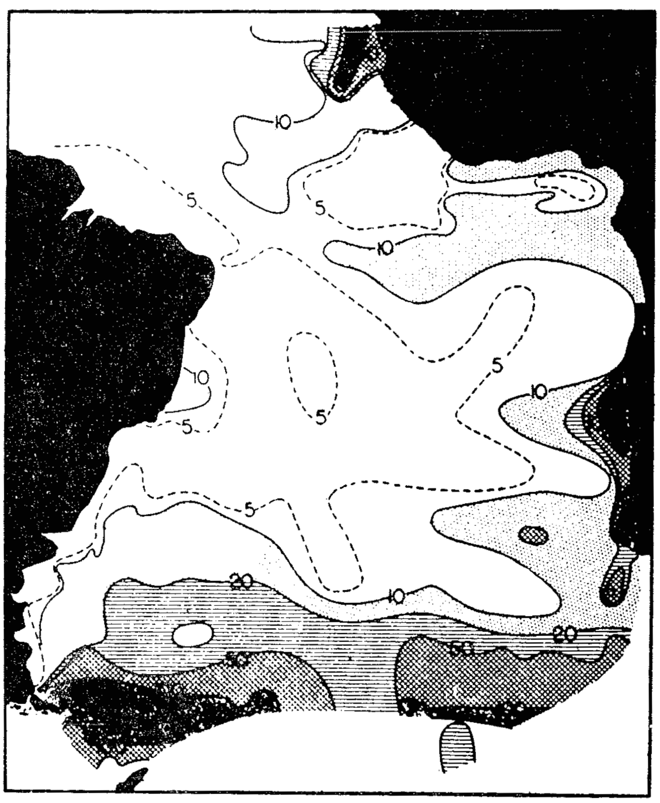

Fig. 6. The concentration of total plankton (micro- and nanno-plankton) in the South Atlantic from surface to 50 m. The numbers on the curves represent thousand of individuals per liter. Reproduced from SVERDRUP, JOHNSON and FLEMING (1943).

start to divide as in temperate waters in spring. The increase in animal production is caused by increasing plant populations and must follow plant production in time. A delay in animal population by as much as half a generation may occur. This delay allows for the production of large stocks of plants and later of animals.

In upwelling areas where the rate of upwelling (vertical movement of water) is slow, of the order of one meter per day, the production increases slowly from the bottom of the euphotic zone. From the one to the five per cent light level the increase in production appears to be very slow, but it increases exponentially as upwelling proceeds. Because the depth of the euphotic zone is many times the distance of daily upwelling, the peak production is reached near the surface, not far from the point of upwelling (CUSHING 1969).

Vertical circulation and high productivity in the coastal upwelling areas lead to considerable decomposition of organic matter on the seabed of the continental shelf. This results in an enrichment of nutrients in the subsurface water layers which are brought back to the lighted layers (the euphotic zone) where the plants respond with luxuriant growth. On the basis of data from the Meteor expedition much higher standing stocks of phytoplankton were demonstrated

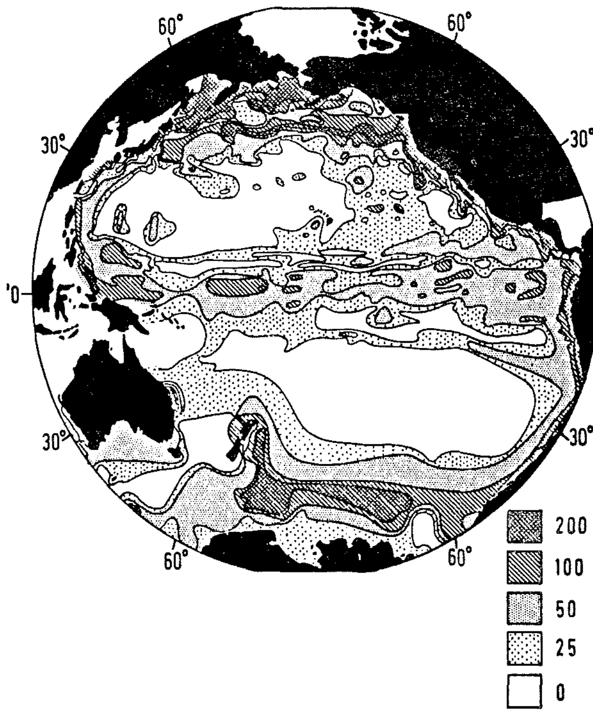

Fig. 7. Distribution of zooplankton in the upper layers of the Pacific (ml/1000 m^3 displacement volume). Adapted from REID (1962).

along the West African coast than along the east coast of South America (HENTSCHEL 1928), reflecting the location of the coastal upwelling areas in the South Atlantic. High values were also found along the equatorial belt and around the Antarctic continent (Fig. 6).

The highest standing stock of zooplankton is found at the upwelling areas (Fig. 7). Outside these, the standing stocks are rather low, and REID (1962) did not find more than 0—25 ml zooplankton/1000 m^3 measured as displacement volume in the upper 150 m of the open Pacific, except in the equatorial belt. In the coastal upwelling areas the standing stocks were more than ten times higher. At the divergences of the subtropical anticyclones a relatively wide band of zooplankton was observed along the equator; the eastern dense patches coincided with zones of divergences in the South and the North Equatorial Currents. Also in the open Atlantic the standing stocks of zooplankton are only about one tenth of that found in the coastal upwelling areas according to recent data given by KINZER (1969).

UPWELLING AND ANNUAL PRIMARY PRODUCTION

Attempts have been made to estimate primary production in the world oceans. STEEMANN NIELSEN and JENSEN (1957), RYTHER (1969), KOBLENTS-MISHKE, VOLKOVINSKII and KABANOVA (1968) have assigned specific levels or ranges of primary production to different parts of the oceans. Although the approach was somewhat different in each study, in general the agreement between the three was fairly good. RYTHER (1969) has summarized their results, and the conclusions are given in Table 1:

1) Annual primary production in the open sea varies, mainly between 25 and 75 g of carbon fixed per square meter per year, and an average value of 50 is listed in Table 1. This is believed to be true for roughly 90 per cent of the oceans.
2) Higher levels of primary production occur in shallow coastal waters, i.e. within the 200 m depth contour. The mean value for this region is estimated to be 100 g of carbon fixed per square meter per year. In addition, certain offshore waters are influenced by divergences and other hydrographic features which bring nutrient-rich water into the euphotic zone. The primary production in these offshore areas is comparable to that of the coastal zone. Their total area is difficult to assess. RYTHER considered the coastal zone including some offshore areas of high primary production to be 9.9 per cent of the world oceans.
3) In the areas of coastal upwelling primary production normally exceeds 1 and may exceed 10 g of carbon per square meter per *day* during periods of active upwelling. However, upwelling does not persist throughout the year in all areas; for ex-

Table 1. Provinces of the oceans according to their levels of primary organic production.

Province	Percentage of ocean	Area (km^2)	Mean productivity (g of carbon/m^2/yr)	Total productivity (10^9 tons of carbon/yr)
Open ocean	90.0	326.0×10^6	50	16.3
Coastal zone+	9.9	36.0×10^6	100	3.6
Upwelling areas	0.1	3.6×10^5	300	0.1
Total				20.0

+ Includes offshore areas of high productivity.

ample in the Arabian Sea where the process is seasonal and related to the moonson winds. For all areas of coastal upwelling throughout the year it is probably safe, although somewhat conservative according to RYTHER, to assign an annual value of 300 g carbon per square meter per year. Again their total area is difficult to assess. RYTHER suggested that the coastal area of upwelling amounts to about 0.1 per cent of the world oceans.

An estimate of the total primary production of carbon per *day* in upwelling areas has also been carried out by CUSHING (1969). The approach was different from RYTHER's, and the value obtained by CUSHING was at least two times higher than RYTHER's figure. The total area of coastal upwelling was considerably larger in CUSHING's estimate because of a different method of calculating the extent of the upwelling areas.

UPWELLING AND TROPHIC LEVEL EFFICIENCY

The trophic levels of food chains in the sea are given in Table 2. Numerous attempts have been made to estimate the production in the sea of fish and other organisms of potential food value to man, e.g. GRAHAM and EDWARDS (1962), SCHAEFFER (1965), KASAHARA (1966). These estimates, for the most part, are based on estimates of primary organic production rates in the open ocean (STEEMANN NIELSEN and JENSEN 1957) and various assumed trophic-dynamic relationships between photosynthetic producers and the organisms of interest to man. Included in the latter are number of steps or links in the food chain and the efficiency of conversion of organic matter from each trophic level to the next.

One factor to be considered in this context is the size of the producer organisms. It is generally agreed that the characteristics of the phytoplankton organisms change from large microplankton to the much smaller nannoplankton as one moves from coastal to offshore oceanic waters. Since the size of an organism is essential in relation to its potential use to man, the following relationship exists: The larger the plant cells are at the beginning of the food chain, the fewer are the trophic levels required to convert organic matter to a useful form. The oceanic nannoplankton cannot be effectively filtered from the water by most of the common zooplankton crustacea, as for instance some of the euphausides. The microzooplankton, e.g. some protozao and larval nauplii of microcrustacea, arc the primary herbivorous of the open sea. Of considerable importance in the carnivorous zooplankton in the open sea are the chaetoghnaths. Some tunas, the dolphins and squids are all top carnivorous.

Table 2. Trophic levels.

0.	*Phytoplankton*	(net particulate production)
1.	*Herbivorous*	(feeding on plants: Zooplankton, some fishes, e.g. clupeoids)
2.	*Carnivorous*	1st stage (feeding on animals: Some of the zooplankton, fishes and mammals).
3.	*Carnivorous*	2nd stage (feeding on animals: Fishes and mammals)
4.	*Carnivorous*	3rd stage (feeding on animals: Fishes and mammals, e.g. tuna and dolphins)

Data are available from some upwelling areas for estimating the potential yields (per year) at various trophic levels (SCHAEFFER 1965), but for most of the areas the available data are insufficient to convert the standing stock of zooplankton into estimates of production. Different estimates have resulted from differences in the choice of the number of trophic levels and the ecological efficiencies.

RYTHER (1969) examined the three provinces of the ocean listed in Table 1 and made the following considerations:

1) A food chain consisting of five trophic levels between the photosynthetic organisms and man would seem reasonable for the oceanic province.

2) The phytoplankton in the coastal zone may be large enough to be filtered and consumed directly by the common crustacea zooplankton such as copepods and euphausids. The larger animals of the coastal province (those directly useful to man) are certainly the most diverse with respect to feeding type. Some molluscs and some fishes are herbivorous. Many others, including most of the pelagic clupeoid fishes, feed on zooplankton. Another large group, the demersal fishes, feed on bottom fauna which may be anywhere from one to several steps removed from the phytoplankton. If the herbivorous fishes are excluded (since these occur predominantly in the upwelling provinces), RYTHER assumed that the average food organisms from coastal waters represent the end of at least a three step food chain between phytoplankton and man.

3) It is in the upwelling areas that food chains are the shortest. This is partly due to the large size of the phytoplankton, but also to the fact that many of the phytoplankton species are colonial in habit, forming large gelatinous masses or long filaments. Some of the most abundant phytoplankton in the upwelling region off Peru are of these types. Such aggregates of plant material can be eaten by large fishes without any special feeding adaption. In addi-

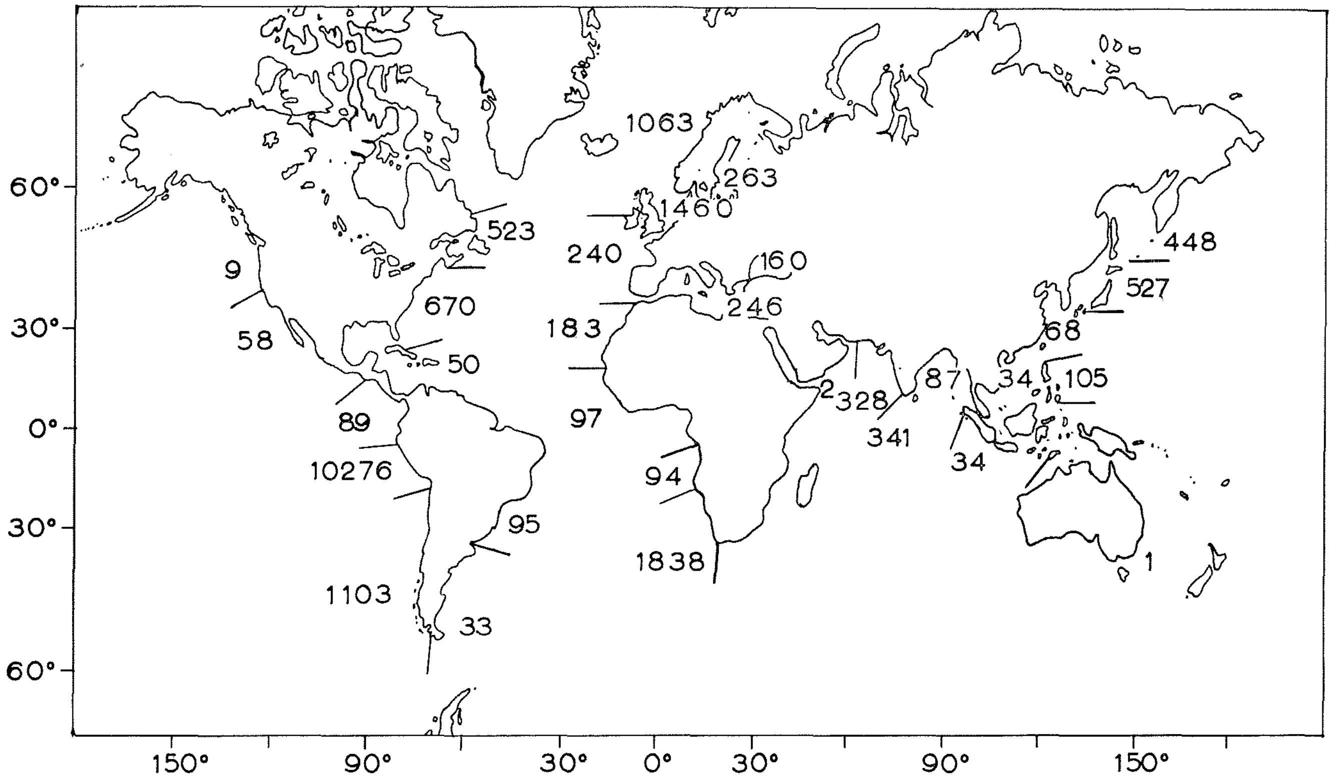

Fig. 8. Catches (in thousands of metric tons) of clupeoids (herring, sardines, anchovies etc.) in the world oceans, 1968 (FAO1969).

tion, several clupeoid fishes (sardines, anchovies, menhaden, etc.) do have gill rakers specially modified for removing the larger phytoplankton from the water. It is of little doubt that many of the fishes in the upwelling regions are direct herbivorous for at least most of their lives. According to SANCHEZ (1966) it is some evidence that juveniles of the Peruvian anchovy (*Engraulis ringens* Jenyns) may feed on zooplankton, but the adults are predominantly, if not exclusively, herbivorous. Also in other upwelling areas, e.g. the Gulf of Panama, anchovy feed on phytoplankton. In some upwelling regions, such as in the Arabian Sea, the feeding habits of fish are not well known. As a working compromise RYTHER assigned the upwelling province a one and a half step food chain.

EFFECTS ON FISHERIES

The principal economic value of the upwelling regions to man is connected to the large concentrations of fish of commercial importance. A significant element of these resources consists of clupeoid fishes with short food chains and their predators, such as bonito, yellowfin tuna and cormorant and other producers of guano. An impression of the magnitude of the clupeoid resources may be obtained from catches in different regions of the oceans in 1968. The highest catches by far were obtained in the upwelling region off Peru (Fig. 8), amounting to about 10.2 millions tons, mainly anchovy (*Engraulis ringens* Jenyns). The second important region was off Southwest Africa where 1.8 million tons were caught, mainly South African pilchard (*Sardinops ocellata* Pappé). Catches in other upwelling areas, e.g. off Northwest Africa and in the Arabian Sea were remarkably low, and it is likely that the potential resources are considerably higher than indicated by the catch figures. Productive areas of clupeoids outside the upwelling areas are, the North Sea and the Norwegian Sea.

The commercial catch of Peruvian anchovy in late 1960s has varied between eight and ten million tons. Anchovy are also the principal food of the guano birds, and various estimates of the amounts of fish consumed by these birds have been published. The estimates vary between 2.5 and 4.0 million tons. It has been estimated that at least 12 million tons of anchovy can be removed in a year from the coastal waters off Peru by birds and man, and this is equal to about one fourth of the world production of marine fish in 1968. The Peruvian anchovy are caught within a narrow strip along the coast constituting no more than about 0.01—0.02 per cent of the world ocean surface.

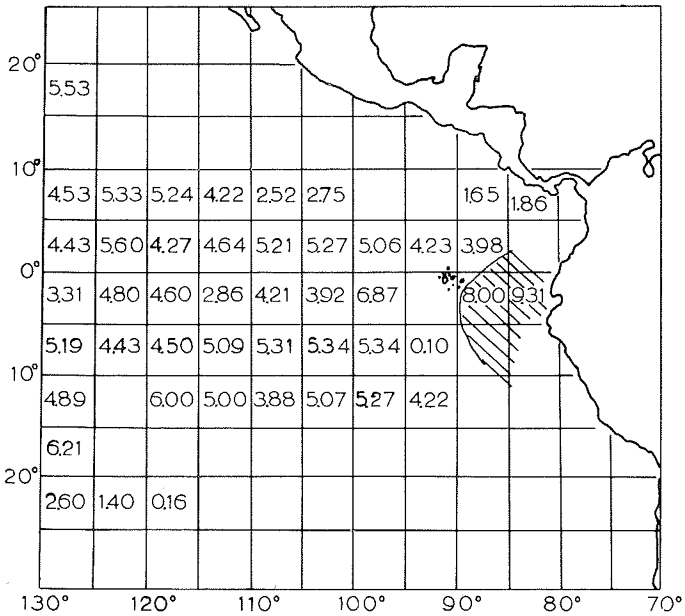

Fig. 9. Distribution of hook rate, i.e. catch/100 hooks of the Japanese long-line fishery for tuna and billfish in the eastern Pacific in 1961. Adapted from FORSBERGH and JOSEPH (1964).

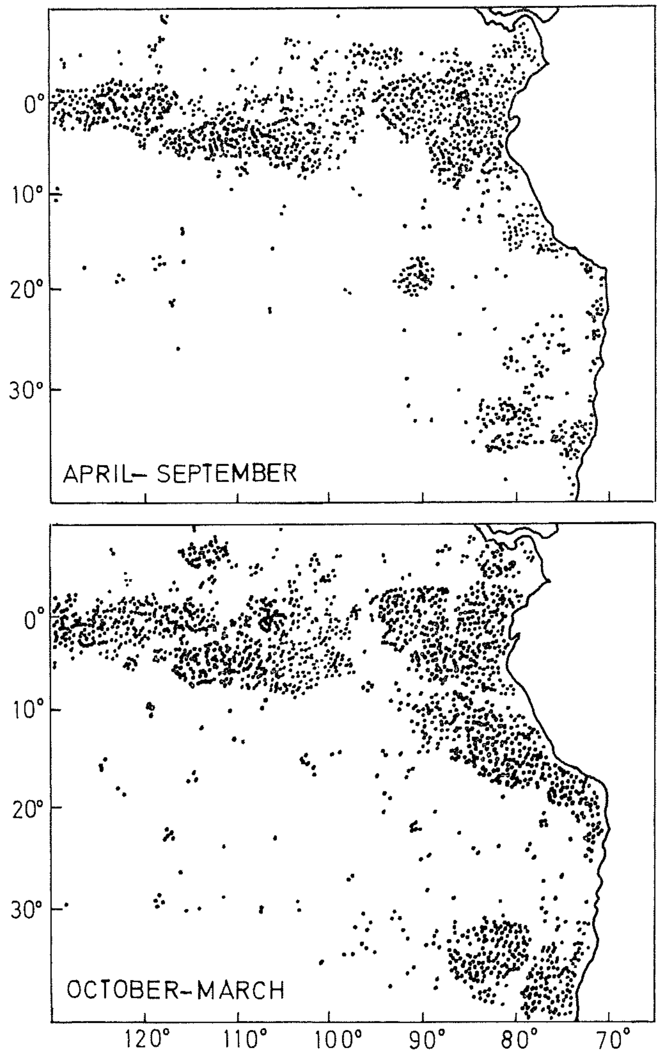

Fig. 10. Sperm whaling grounds in the eastern Pacific, 1761–1920. Each point represent the capture of one or more sperm whales (TOWNSEND 1935).

Other important commercial fish species living at or near the upwelling area off Peru are the hake and the tuna. In Fig. 9 is shown the hook rate of the Japanese longline fishery for tuna and billfish in the eastern Pacific in 1961 (FORSBERGH and JOSEPH 1964). Even though tuna and billfish were found over wide areas in subtropical and tropical waters, the highest abundance indices (indicated by the hook rate) were found along the coast off Peru within or close to the upwelling area. Also the distribution of whales, i.e. the sperm whale, is seen to correspond roughly with areas of upwelling including the divergences along the equator (Fig. 10).

In other upwelling areas it may be expected that animals of direct interest to man should be found in abundance. In the Benguela Current off Southwest Africa the pelagic fishes are already being increasingly exploited, and amongst them the South African pilchard take the first place. Next in the order of abundance are fishes as horse mackerel, hake and sharks. Shellfish also have their place among the economic resources of this current, and already there is a fishery for lobster. It is also possible that squid may some day contribute to a fishery in this area. The fertile waters of the Benguela Current with their abundant stocks of fish support enormous populations of sea birds. The value of guano deposits is also significant in this area. There are several herds of seals on the west coast of South Africa. These herds have been exploited commercially.

As in the Pacific, concentrations of tuna and whales in the Atlantic are found in or close to the areas of coastal upwelling and in the equatorial belt (Fig. 11). The potential resources of fish in other coastal upwelling areas along the west and northwest coast of Africa are not very well known yet, but according to recent investigations, pelagic fish species are abundant there.

Neither in the Indian Ocean are the distribution and abundance of fish sufficiently known. About 80 per cent of the marine fish catches of India are taken at the west coast. The bulk of it is caught from the Kerala and Mysore coasts. The main components of the catches by volume are the oil sardine (*Sardinella longiceps* Cuv. and Val.) and the Indian mackerel

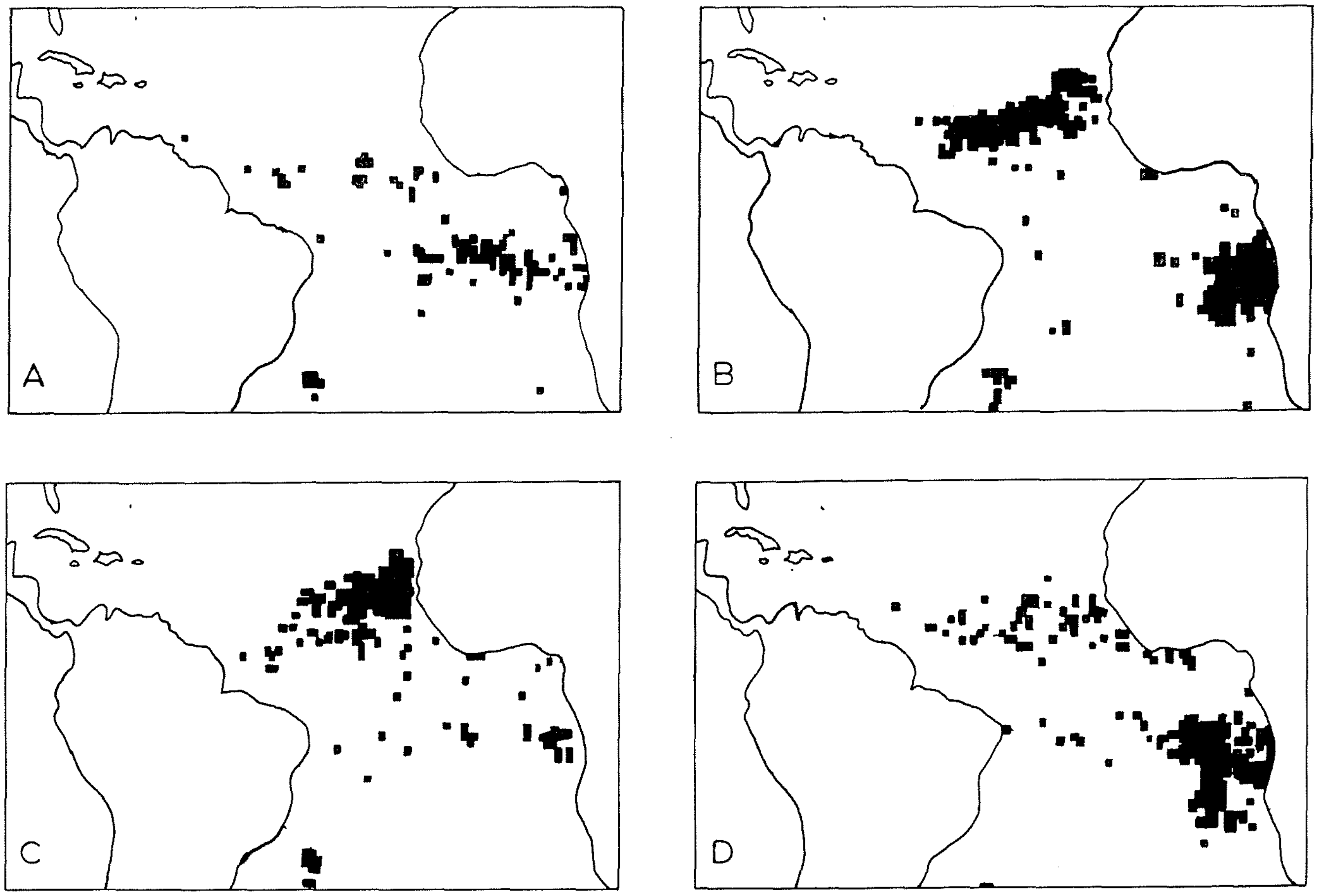

Fig. 11. Distribution of hook rate ,i.e. catch/100 hooks, of more than one tuna in central Atlantic. A) January–March, B) April–June, C) July–September and D) October–December. Adapted from POSTEL (1969).

(*Rastrelliger canagurta* (Cuv.)). These and other upwelling areas in the Northeast Indian Ocean will in the near future be subject to more intensive investigations in order to estimate the potential resources of fish in this region.

Much work has been carried out in the California upwelling zone during the past twenty years. However, at present this area is of minor importance with regard to yield of pelagic fishes. The stock of California sardine (*Sardinops caerulea* Girard) is at a very low level, but the anchovy (*Engraulis mordax* Girard) seems to have taken its place. There is also a fishery for Pacific hake (*Merluccius productus* (Aryes)) and some other species, but on the whole this area cannot be compared with the upwelling areas off Peru and South Africa.

Except for tuna and sharks, fishes characteristic of an upwelling area are usually not caught outside it. As the stocks are maintained within the area year by year, CUSHING (1969) found it reasonable to assume that an upwelling area is a biological unit. It is well known that the Pacific hake spawn in the early spring in the southern area of upwelling off California. According to ALVERSON (1969) the older fish appear off the coasts of Oregon and Washington in June (Fig. 12). As they live mainly in the deep water zone, i.e. below, 200 m, they may migrate north in the counter current. To spawn off Baja California the hake may return south in winter in the surface drift; perhaps at night when the hake are known to rise towards the surface. CUSHING has speculated about the drift of eggs and larvae as established by ALVERSONS's investigations. He suggested that eggs and larvae drift from Baja California and metamorphose fairly quickly to sink into the counter current which persists until the summer. Then the nursery area may lie at a middle depth off Central California, and CUSHING added that the fishes thus may live in the upwelling area all through their lives.

The Californian sardine, the Peruvian anchovy and the South African pilchard live in the coastal upwelling areas. These three species spawn near the point of upwelling. The greatest density of eggs of the Peruvian anchovy for instance are found within 150 nauticel miles off the coast (Fig. 13). Sardines, sardinella and anchovies live at or just above the

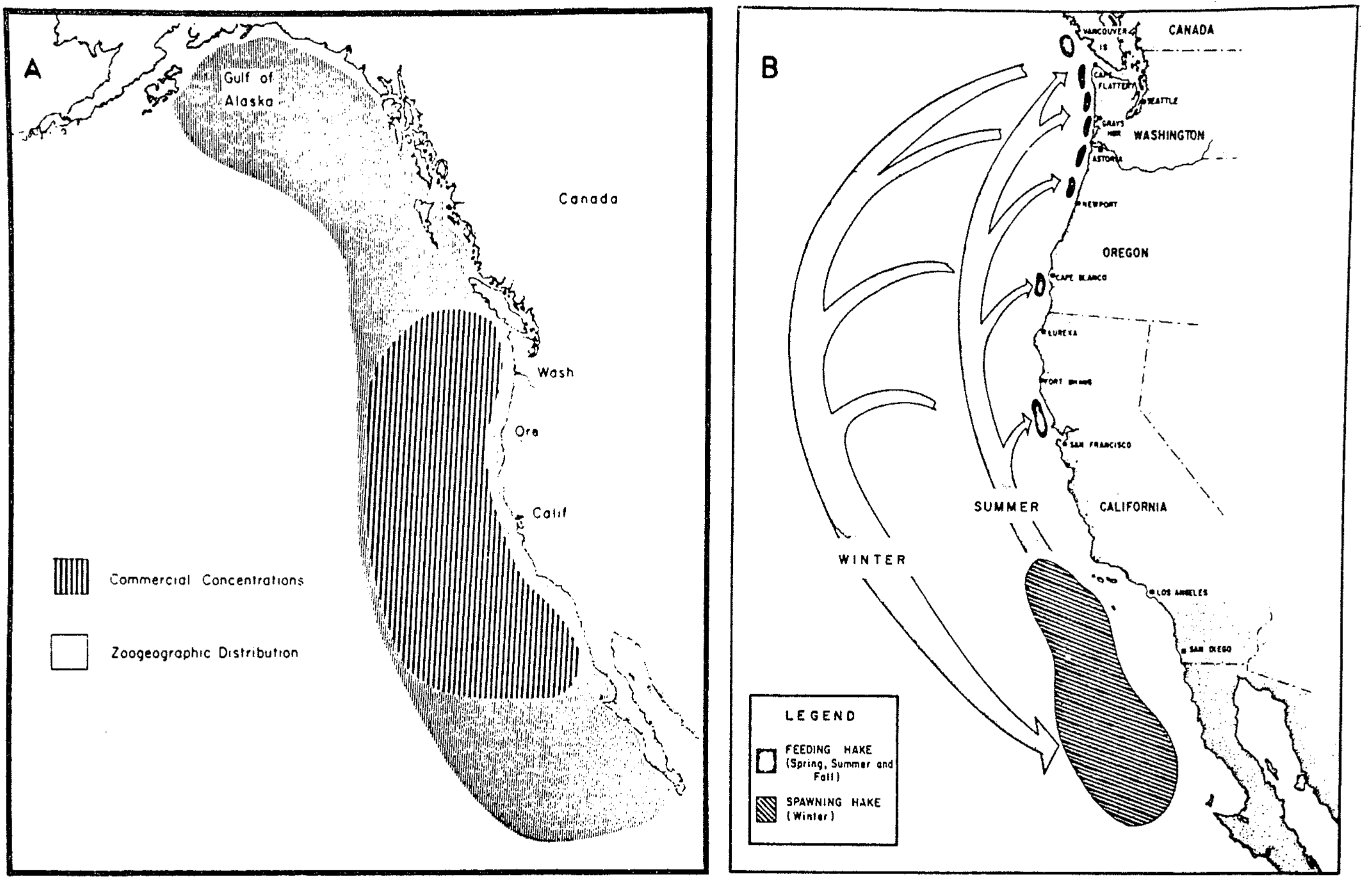

Fig. 12. Zoogeographic distribution of Pacific hake, A) showing area of commercial concentrations and B) annual migrations and distribution. Adapted from ALVERSON (1969).

thermocline. Below the thermocline live horse mackerel and close to the bottom hake; both perhaps depending to some extent upon euphausides.

Assuming that any upwelling area is a biological unit, it would be of special interest to estimate the potential yield of fishes in all upwelling areas. Using the values for primary production (Table 1) assigned to the three provinces and assuming different numbers of trophic levels as well as different ecological efficiencies in the three provinces, RYTHER (1969) calculated fish production in these three regions. The results are summarized in Table 3.

A variety of factors will affect the ecological efficiency, i.e. the transfer of organic matter between trophic levels. Since, in most cases, they cannot be quantitatively estimated, their total effect cannot be assessed. It is known only that the maximum potential growth efficiency is about 30 per cent, and that at least some of the factors which reduce this are more pronounced in low productive than in high productive areas. SLOBODKIN (1963) concluded that an ecological efficiency of about 10 per cent is possible, and SHAEFFER (1965) feels that the figure may be as high as 20 per cent. RYTHER used efficiencies of 10, 15 and 20 per cent, respectively to the oceanic, the coastal and the upwelling provinces (Table 3). It therefore is quite possible that the actual efficiency values are considerably lower than those used by

Table 3. Estimated fish production in the three provinces of the oceans.

Province	Total primary production (tons of organic carbon)	Trophic levels (no.)	Efficiency (%)	Fish production (tons of fresh weight)
Open ocean	16.3×10^9	5	10	16×10^5
Coastal zone	3.6×10^9	3	15	12×10^7
Upwelling areas	0.1×10^9	$1^1/_2$	20	12×10^7
Total				24×10^7

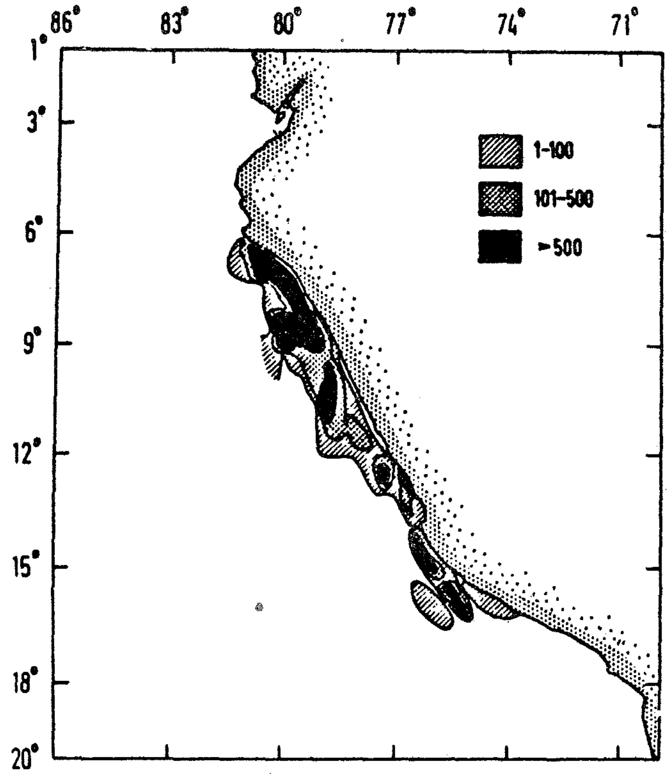

Fig. 13. Distribution of anchovy eggs off Peru in numbers per haul with a Hensen net (FLORES 1967, GUILLEN and FLORES 1967).

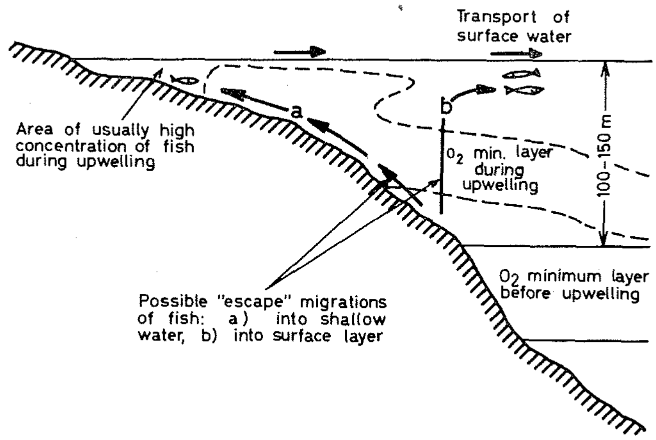

Fig. 14. Fish behaviour in the upwelling of oxygen minimum layer along the coast. Adapted from HELA and LAEVASTU (1962).

RYTHER. However, these calculations reveal several interesting features. The open sea, constituting about 90 per cent of the oceans is essentially a biological desert. It produces a negligible fraction of the world's fish catching. Upwelling regions totalling about or perhaps a little more than 0.1 per cent of the ocean surface produce about half the wordl's fish supply. The other half is produced in coastal waters and in the few offshore regions which have a comparably high productivity. RYTHER estimated that a total of about 240 million tons (fresh weight) of fish are produced annually in the sea. This is a rough figure subject to numerous sources of error, and it should not be considered significantly different from SCHAEFFER's (1965) figure of 200 million tons.

DIRECT EFFECTS OF CHEMICAL AND PHYSICAL CONDITIONS

A few of the more direct effects of upwelling on fisheries should also be mentioned. In some areas a distinct and shallow thermocline directly overlies a layer of water that is sometimes almost without oxygen. When this layer rises and invades the continental shelf, life on the bottom is affected. Pronounced oxygen minimum layers are found for instance in the Arabian Sea and in the Gulf of Guinea. When the oxygen minimum layers, which normally are found at depths of 100—150 m, rise along the continental shelf, the animals, including fish, move in front of it into shallow water or rise up into the surface layer (Fig. 14). However, the rate of upwelling can suddenly be intensified, and the oxygen replenishment apparently slowed down. In this case the oxygen minimum layer is brought close to the surface, and this may result in mass mortality of fish.

It has been observed (PANIKKAR and JAYARAMAN 1966) that an oxygen minimum layer along the coast of India is subject to movement, and that it comes fairly close to the surface near the west coast during the southwest monsoon. This may affect the fisheries for oil sardine and Indian mackerel. Similar phenomena, but not as striking as at the Indian coast, occur annually along the coast of West Africa. In the late 1950s dead fishes were reported floating at the surface of the western Indian Ocean. This may have been caused by an oxygen poor layer rising close to the surface in the deep ocean. Large scale effects of this kind are uncommon because animals are adapted to their environments, and effects of physical changes in the environment on fish stocks are exceptional. Therefore, such effects are most likely to occur where the environments are widely variable as in the western Indian Ocean.

A mass mortality of fish off the Somali coast in 1964 was reported by FOXTON (1965). This occurred during the monsoon period in August. FOXTON associated the mortality with temperature as exceptionally cold surface water (about 14—16° C) was found in the area, probably due to local upwelling.

The pulsation of warming and cooling in the eastern Pacific reaches an apogee every five to eight years.

Off the Northwest coast of South America it causes a phenomenon which has been named "El Nino", because it comes at Christmas time. The causes of the phenomenon is still uncertain, but its effect is a flow of warm tropical water over the normally cold upwelled water to a variable distance down the Peruvian coast. The effect of "El Nino" on fisheries and the guano birds is catastrophic. The birds cannot dive below the warm water to reach the fish, and they move down the coast to Chile, leaving all the young birds to die; "El Nino" produces a large scale change in the availability of anchovy, and it may affect the year-class of fish born in the following winter.

All examples quoted above illustrate changes in availability of fish caused by changes in the detailed structure of the upwelling systems. The upwelling process is sensitive to changes in wind direction and force, and such changes may induce fluctuations in the intensity of the upwelling. Phenomena such as "El Nino" and changes in the trade wind systems have great influence on the distribution and availability of fish stocks, and therefore they should be subject to detailed studies.

An annual sea fish production of 200—240 million tons of fish has been suggested, and about half of this production may be found in coastal upwelling areas. This clearly demonstrates the high potential resources of these areas. Great benefits to fisheries could be expected from a thorough understanding of the physical, chemical and biological processes in the upwelling areas. Therefore, more descriptive surveys are needed in most of the subtropical areas, such as the Indian Ocean and other upwelling areas, in order to extend our knowledge of the biological aspects of upwelling.

Production, however, is not equivalent to potential harvest. Firstly, man must share the production with other top level carnivorous. Secondly, man must take care to leave a large enough fraction of the annual production to permit utilization of the resource at something close to its maximum sustainable yield, in order to maintain fishery. Considering these factors, RYTHER (1969) found it unlikely that the potential sustained yield of fisheries is appreciably greater than 100 million tons, i.e. about 50 million tons from the upwelling areas. It is obvious that even if the yield can still be further increased, the resource is not inexhaustible.

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