THE CLUPEOID RESOURCES OF TROPICAL SEAS

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INTRODUCTION

The world catch of fish from the sea has doubled in the last decade, rising from $24 \cdot 1 \times 10^6$ tons in 1958 to $49 \cdot 7 \times 10^6$ tons in 1968 (Anonymous, 1969); in this period the catch of clupeoid fish has expanded at an average annual increase of $11 \cdot 8 \%$ from $7 \cdot 2$ to $20 \cdot 5 \times 10^6$ tons, which is significantly greater than the $6 \cdot 3 \%$ annual increase for other sorts of fish. Much of the increased exploitation has fallen upon the clupeoid stocks of lower latitudes; during this period the catch of high latitude herrings (*Clupea* spp.) has increased only from $3 \cdot 2$ to $4 \cdot 0 \times 10^6$ metric tons annually, while the clupeoids of warmer seas have sustained a fourfold increased rate of exploitation from $4 \cdot 0$ to $16 \cdot 0 \times 10^6$ metric tons annually. The clupeoid catch is mostly used industrially in the production of fish meals and oils and the increased catches have been in response to an expanding demand in world markets for these products; thus, as the percentage of the world catch composed of clupeoids has risen, so has the percentage of the total world catch which is used industrially; in 1948 only $7 \cdot 7 \%$ was so used, rising to 13% in 1958 and to $35 \cdot 6 \%$ in 1968. The warm-water clupeoids contributed very largely to this spectacular increase in industrial production. About $4 \cdot 66 \times 10^6$ tons of fish meal were manufactured in 1968 to which the catches of *Sardina*, *Sardinops*, *Sardinella*, *Brevoortia*, and *Engraulis* contributed $3 \cdot 05 \times 10^6$ tons, while high latitude fisheries for *Clupea* contributed only $0 \cdot 76 \times 10^6$ tons; the remaining $0 \cdot 85 \times 10^6$ tons were made up of non-clupeoid species.

There is no indication that the industrial demand in the developed countries of the world for fish meal, fish oil, and solubles will decline; indeed, forecasts indicate an increasing demand for such products as industrial farming extends its scope, and as the range and use of formulated human foods requiring the use of proteins of high biological acceptability continues to increase. It seems probable that fish meal and more highly-refined fish protein concentrates will continue to be competitive with proteins of plant origin in at least part of the industrial protein market. There are also indications of considerable under-utilization of some tropical clupeoid

stocks and while, to be sure, no second event to rival the boom-years of the Peruvian fish meal industry can be looked for, significant growth in catches may reasonably be anticipated for several decades.

It has seemed appropriate, therefore, to review briefly what is known of the biological basis of tropical fisheries for clupeoids; the term 'tropics' is here interpreted very loosely and fisheries will be discussed in latitudes as high as is necessary to explain the biology of low latitude species and their exploitation.

SYSTEMATICS AND DIVERSITY OF FORM

The clupeoid fish are small teleosts which are relatively 'unevolved' and typically are less than 20 or 30 cm in length; they have no barbules and are frequently laterally compressed, with a series of hard scutes along the ventral surface of the body. Most are soft-bodied, difficult to handle, and covered with rather deciduous scales. Most species are greyish or silvery in colour and usually the only patterns on the body are those for counter-shading, making them inconspicuous in the sea; related to their inconspicuous coloration is their very frequent habit of occurring in schools, sometimes very large ones. Their flesh is often very oily, and the oil content normally varies seasonally, even in low latitude species. According to Berg's classification, the Order Clupeiformes includes many fossil suborders as well as several suborders containing living members as diverse as the herrings and the salmon-like fish. The suborder Clupeoidei includes several groups of families of herring-like fishes: the Elopoidae and Albuloidae, containing carnivorous, large, silvery tropical sea fish; the Alepocephaloidae, containing small abyssal and bathypelagic fish; and the Clupeoidae, with which we are concerned in this review, and to which reference is intended by the general term 'clupeoid'. There are two Families of living clupeoids: the herrings and their relatives of the family Clupeidae, and the anchovies of the family Engraulidae. The herrings are larger, more diverse in form, and extend into higher latitudes than the smaller anchovies, which are characterized by their very long maxillae and lack of a lateral line. Many members of both families have reduced dentition and an abundance of filamentous gill rakers. The great majority of the several hundred species of clupeoids occur in warm or tropical seas. While only a single genus (*Clupea*) is important in high latitudes and the cold temperate regions, in the warm temperate mid-latitudes there are approximately 10 important genera, dominated by *Sardina*, *Sardinops*, *Engraulis*, *Brevoortia*, *Ethmidium*, *Opisthonema* and others. In low latitudes more than 25 genera occur, many of which are important.

The general rules governing the diversity of animal life in high latitudes and low, in eutrophic and in oligotrophic regions, and in stable and in varying environments, have been demonstrated in many animal groups. It is evident that clupeoid fishery resources follow similar rules with regard to variation in their diversity; in high latitudes where the oceanographic regime varies widely from winter to summer, and where there is a spring bloom of diatoms followed by a peak of zooplankton, there are relatively few species of clupeoid fish. In low latitudes, where the seasonal changes in food supply and the level of the standing crop of food is lower, the diversity of clupeoids is

high. This latitudinal trend is broken, in the tropics, in situations where local seasonal upwelling occurs; here, a few species of clupeoids may occur in great abundance, their biomass dominating the total fish biomass of the area; it is in such situations that the great clupeoid fisheries of low latitudes occur and which, moreover, are based to a considerable extent upon species which are specialized phytoplankton-feeders.

Not all zoogeographical regions have, at similar latitudes, a comparable diversity of clupeoids; the paucity of the tropical marine fauna of the Gulf of Guinea compared with the equatorial regions of the western Atlantic is well known (e.g. Ekman, 1953) as is, in general, the even greater diversity, habitat for habitat, of the Indo-Pacific equatorial region than the Atlantic. The clupeoids appear to follow the same patterns with the consequence that all types of clupeoid ecology do not occur in all tropical oceans. The menhadens of the western boundary currents of the Atlantic and the bonga of the tropical regions of the eastern Atlantic are extremely close to each other both morphologically and in their ecology, and it is not clear why there are no *Brevoortia*-like fish in the truly tropical regions of the western Atlantic, nor why menhaden or bonga-like forms are not widespread in the shelf regions of the western Indo-Pacific, where conditions would appear to be extremely suitable for their development. With this possible exception, the western parts of the Indo-Pacific region include the richest diversity of clupeoid ecology and this area is particularly rich in the large number of predacious *Ilisha*-like forms which occur there, while at the other end of the scale the west African region of the eastern tropical Atlantic exhibits a very reduced diversity of clupeoid ecology; here there are no round herrings (*Dussumeria*), there are no gizzard shads (*Dorosoma*), and there are no toothed anchovies (*Lycengraulis, Lycothrissa, Coillia*). Only a single species of predatory herring (*Ilisha africana*) occurs in the eastern Atlantic, compared with the many genera, including tens of species, of this ecological type in the western Indo-Pacific.

ECOLOGY

TOLERANCE OF LOW SALINITIES

With few exceptions, clupeoids occur over or near the continental shelves and frequently their habitat is strictly coastal; associated with their neritic distribution is a rather widespread tolerance of low salinities, though not all species are euryhaline. Within single genera, such as *Sardinella*, a rather wide range of tolerance to salinity changes may occur. The tropical Atlantic *S. aurita*, for example, is extremely stenohaline, tolerating only a very small range in the salinity of its environment; Postel (1955) shows that it does not occur in water with a salinity lower than 35‰, so it does not enter estuaries and avoids those parts of the coast which are much influenced by terrestrial run-off. In the Gulf of Guinea it is confined to rather restricted parts of the coastline. On the other hand, *S. cameronensis* occurs mainly in the Bights of Benin and Biafra, where mixed-layer salinities regularly fall as low as 20‰; *S. eba*, the third West African congener, occurs widely along the tropical coastline where it frequently enters estuaries and coastal lagoons. A similar series of congeneric species with stenohaline and euryhaline habits

could probably be demonstrated for the same genus around the coasts of India (i.e. among *S. longiceps, S. gibbosa, S. albella, S. sirm,* and *S. fimbriata*) and elsewhere in the tropical seas.

The euryhaline species of both tropical and temperate latitudes include shad-like forms which are anadromous, entering fresh water and frequently penetrating far up rivers during their spawning migrations, as well as species which do not regularly migrate between brackish and marine environments. The most familiar shads are the species of *Alosa*, which enter rivers in large spawning runs on the North American continent. These, together with the gizzard shads (*Dorosoma*) and the alewives (*Pomolobus*) are replaced in the Indo-Pacific region by river-ascending shads of the genera *Hilsa* and *Macrura*. In the tropical Atlantic there appear to be no important shad-like fishes in the large tropical rivers of western Africa. This is perhaps another facet of the general poverty of the tropical Atlantic marine fauna compared with that of the Indo-Pacific, and one which invites consideration of planting such species to enrich the fauna available for fisheries.

Among the anchovies of the family Engraulidae, several genera occur only in tropical fresh waters. Perhaps the most important of these are species of *Lycengraulis*; for example, *L. grossidens* occurs in western South America from Venezuela to Rio de Janeiro, where it is important in local markets, and ascends quite small streams. Another member of the same genus (*L. limnichthys*) occurs only in Lake Maracaibo in Venezuela. The genera *Pterengraulis* and *Hildebranchichthys* are also found in the Amazon basin and Venezuela where, again, they are very commonly caught in local indigenous riverine fisheries. Turning to the herring-like species of Clupeidae, we find a rather smaller number which are adapted purely to low salinity environments; there are, of course, some cases in which anadromous shad-like forms have become landlocked and invaded fresh waters within recent times, the best-known example of which is the invasion of the Great Lakes of North America by the alewife, *Pomolobus aestivalis*, whose range previously included only the rivers between Nova Scotia and North Carolina. In South American rivers, the genus *Rhinosardinia* is restricted to fresh water, while in West Africa the little *Pellonula vorax* does not descend below upper estuarine conditions. In the Indo-Pacific region, species of *Pterothrissa, Microthrissa,* and *Pellonula* are among those restricted to waters of very low salinity, or to riverine conditions. Land-locked species may represent important fishery resources. In Lake Tanganyika, in the African Rift Valley, two small clupeoids are abundant, namely, *Stolothrissa tanganicae* and *Limnothrissa miodon*. Hickling (1961) describes the fishery in the open lake for the first of these two species, which is a pelagic, zooplankton feeding fish that can be attracted in enormous numbers to lights at night, and whose potential catch has been estimated at more than 1.0×10^5 tons annually.

SCHOOLING HABITS

One of the most significant characteristics of clupeoids from a behavioural and also from a fisheries viewpoint is their occurrence in dense and often very large schools which containing many hundreds of thousands of fish may weigh up to more than 100 tons in some cases. Such large schools generally occur in the open ocean rather than in restricted brackish waters and fre-

quently have a shape and type of behaviour which is diagnostic and which enables an experienced fisherman to identify them. This may be done either by direct observation from a fishing vessel, by observation from a light airplane, or by the use of hydro-acoustical instruments, such as echo-sounders and sonars. The specific diagnosis of a school is generally made on a combination of factors. Its size, the depth at which it is swimming, the shape it makes in the water, the manner in which the individual fish break the surface (if this occurs), and the colour of the mass of fish as they glint in the sun, may all be taken into account. Furthermore, at night, the schools of some species may be readily visible and identified even at some depth in clear water when there is significant bioluminescence from the plankton; under these conditions the individual shoals may appear as large balls of green fire deep in the water—a sight once seen, never to be forgotten.

In the Gulf of Guinea, canoe fishermen recognize bonga, *Ethmalosa dorsalis*, by their habit of flipping on their sides and breaking the surface when feeding—each fish sending up an individual little splash, these splashes being rather widely scattered across the area occupied by the school; when not feeding, *Ethmalosa* at sea are distinguished rather easily from the several species of *Sardinella* which are found in the same region, since the golden glint of each individual fish gives a reddish tinge to the whole shoal when it is seen from far off (Postel, 1955). On the other hand, *Sardinella* in the same region normally form a dark bluish 'stain' at the surface, and the schools are apparently far more compact and closer to the surface so that they break it in a manner resembling the beat of rain on water; this is quite unlike the way *Ethmalosa* breaks the surface (Postel, 1955). The migrating shoals of the western Atlantic species of menhaden (*Brevoortia* spp.) have a very characteristic form and are seen dark against the background of the sea surface from the small spotter aircraft used by the fishery of the eastern seaboard of the United States; migrating shoals of thread herring (*Opisthonema* spp.) in the same region can usually be distinguished by the spotters from the menhaden which they are seeking. Shoals of *Brevoortia* and some species of anchoveta have another important diagnostic character in shallow-water feeding areas, where mud 'boils' covering several hectares of sea surface are formed by the activity of the fish; such boils are easily seen by spotter aircraft which may direct fishing vessels onto them.

The function of the schooling habit in clupeids is to be found in the relationship between predator and prey; not only are aggregations of individuals more difficult for a more widely dispersed predator species to locate but, once located, incorporation within a tight school protects the individual fish by means of the visual confusion it offers to the predator. Discussing the schooling of small fishes in open environments which are the prey of larger, more solitary predators, Brock and Riffenburgh (1960) showed that there is an "encounter advantage" in schooling which expresses the fact that by random searching a predator has a smaller chance of encountering an aggregated than a dispersed prey. On the other hand, once encountered, a large school may be at a detection disadvantage compared with a small school—it is easier to detect, once the predator is in its general area. Once the final contact between predator and prey has been established, and ignoring the problem of visual confusion of the predator, it may be assumed that a smaller percentage of a large school will be required to satiate a predator so

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that the individuals within it have a better chance of escaping at each encounter.

The capture of a small fish by an active, visual predator involves a complex behaviour pattern on the part of each; the predator must visually identify its prey, follow it during its escape activities, and finally take it. This pattern of predation cannot occur if the initial identification of the prey individual can be prevented, and this is perhaps the main function of tight schools of fish normally preyed upon by other fish (Hunter, pers. comm.). Anybody who has attempted, with a small hand net, to capture one goldfish from a tank full of goldfish or one bird in an aviary full of fluttering birds, knows how much easier this task becomes as the number of individuals, from which the captured individual has to be selected, is progressively reduced. There are many observations which indicate the correctness of this supposition and which demonstrate that very frequently the prey individuals which are successfully captured are those which do not, for some reason or other, remain within the coherent pattern of the school, but stray to one side; the initial dash of a predator into the thick of a school may not be so much intended to capture an individual prey as to break up the coherence of the school and to separate one or more individuals from it by their flight reaction, and subsequently to capture them. The behavioural patterns within clupeoid schools are rather rigid, are effective in passing information rapidly from individual to individual concerning the whereabouts of predators, and probably result in the tightening of the school under attack to prevent individuals being cut out of its pattern. Clupeoid schools are usually more or less on the move; during their passage through the water, a densely packed school may leave a trail as distinct as that left by a flock of sheep crossing an untrodden meadow. In the wake of a large shoal of anchovies, for instance, one may see the effect of intense and massive filtration upon the plankton content of the water and also a train of oil droplets rising to the surface resulting in a fish-oil slick. The functions of the schooling habit among clupeoids and its advantages for the species compared with a dispersed type of distribution, are probably various, but it seems certain that the most important is that of making the task of a predator more difficult.

Many tropical species apparently perform duel vertical migrations; this has been well demonstrated for the North Atlantic herring *Clupea* (e.g. Brawn, 1960), and has also been shown for a number of tropical species, such as *Sardinella aurita* off the coast of Ghana (Probatov, 1959). It is also apparent from sonar observations of some species, including the Californian anchovy, *Engraulis mordax* ,that shoals may disperse at night into small groups of fish (Smith, pers. comm.), and it has been suggested that in this way the groups of anchovies act at night, during their feeding activities, as predators in the predator/prey model of Broch and Riffenburgh (Hunter, pers. comm.). At dawn the small parties of perhaps five to ten individuals coalesce and the schools reform.

The seasonal migrations of clupeoids have an important effect upon the fisheries, particularly upon unmechanized fisheries which must by their nature be restricted to certain locations. The European–Scandinavian herring, *Clupea harengus*, is a particularly well-documented example of a migrating clupeoid in high latitudes, as is the Indian oil-sardine (*Sardinella longiceps*) in the tropical seas. Mass migrations of such species frequently result in the

fishery being strongly seasonal in nature and this is of particular importance where the nature of the social and economic structure of the fishery prohibits its operating over long distances, and so following the migrations of the species to whose capture it is specialized. It may be a question of waiting for the return of the fish each year along their accustomed migration routes, rather than migrating with the fish, as did the traditional fishery for the North Sea herring in the British Isles in which the Scottish fishing boats, and the girls ashore who cleaned the herring for the salting-down process, followed the fishery progressively southwards during the year from Scotland to East Anglia. Factors such as this are important, but are often neglected, in fisheries development plans in the tropics.

FEEDING REGIMES

With a few, but interesting, exceptions the clupeoids are microphagous, that is, their food is of small particle size. Predominantly, they are plankton-feeders, but they include a number of important species whose diet is particularly dominated by phytoplankton; they tend, therefore, to be rather 'low' in the food web in the sea, being close to the primary producers and this, of course, has significance in the very great productivity of clupeoid fisheries.

Leaving aside the few macrophagous forms such as the wolf-herring (*Chirocentrus*), the tarpon (*Megalops*), the ten-pounder (*Elops*), and the ladyfish (*Albula*) which are large, active fish-eating predators that are ecologically and systematically rather distinct from the true clupeoids, several clupeoid genera contain species whose adults have a diet in which relatively large crustaceans and small fish figure largely; these are the exceptions to the general rule of microphagy within the clupeoids. They include: the small, tropical, large-toothed, anchovy-like forms such as *Lycengraulis*, *Lycothrissa*, and *Coilia*; a number of genera of soft, very flattened herring-like forms having upturned toothed mouths, such as *Ilisha*, *Pristigaster*, *Opisthopterus*, *Raconda*, *Pliosteostoma*, and *Odontognathus*, all of which are restricted to low latitudes (e.g. Peterson, 1956). Some species of the thread herring, *Opisthonema*, and the warm-temperature shads of the genus *Pomolobus* have similar diets but are not so restricted to the tropical zone. The great majority of the clupeoids, on the other hand, have a diet which is based on zooplankton, mainly copepods and other small crustacea, and in which the adult fish occur often in more organized and denser schools than do the macrophagous genera mentioned above. These are characterized by the boreal species of *Clupea* and *Sprattus* whose ecology is well known on the coasts of Europe and North America. In the tropics there are several genera so close to *Clupea* in form and ecology as to be commonly known as tropical herrings; most species of the wide-spread genus *Sardinella* (Vijayaraghavan, 1953; Bainbridge, 1963) fall into this category, as do *Harengula*, *Clupeoides*, *Jenkinsia*, and *Lile*. The tropical round-herrings, widely distributed in the Indo-Pacific also have diets based mostly on macrozooplankton and have a very generalized form of dentition; these include *Dussumeria*, *Spratelloides*, and *Etrumeus*. The smaller tropical anchovies (*Anchovia*, *Anchoa*, *Anchoviella*, and *Setipinna*) appear in general to have an unspecialized zooplankton diet as do many of the brackish water forms such as the warm-temperate shads *Alosa* and the tropical West African *Pellonula*.

The species which have a purely phytoplanktonic diet, or at least a diet in which phytoplankton appears to be the preferred component, feed by filtering large diatoms and other phytoplankters from the water by means of elongated gill rakers which form a filtration sieve. Though few in number, from a fisheries point of view these species are some of the most interesting, both because of their occurrence in great quantity and also because they represent the most efficient possible utilization of the results of primary production. The small anchovies *Engraulis ringens* and *Cetengraulis mysticetus* in the eastern Pacific (Bayliff, 1963), the menhadens (*Brevoortia* spp.) in the western Atlantic (Deevey, 1956; Darnell, 1958), the West African bonga *Ethmalosa fimbriata* (Bainbridge, 1960) and the Indo-Pacific thread herring *Opisthonema libertate* and oil-sardine *Sardinella longiceps* (Peterson, 1956; Nair, 1960), all fall into this category.

In a special category are the gizzard shads *Dorosoma* of tropical and mid-latitudes which, as their common name implies, utilize a strong gizzard, or muscular portion of the alimentary canal, to grind mud taken from the bottom of estuaries and shallow shelf areas, so as to utilize benthic diatoms. In this, their ecology resembles that of the grey mullets (see Thomson, 1966).

EASTERN ATLANTIC

In the eastern Atlantic the latitudinal range of tropical conditions in the ocean is rather small and is clearly separated by frontal regions from the eastern boundary currents (Canary, Benguela) to the north and south; within the tropical region—which corresponds approximately to the area known as the Gulf of Guinea and to the Guinea Current—there are smaller numbers of clupeoid species than in any other tropical area. High rates of primary production occur only in two situations: first, as Bainbridge (1960) has shown, there are very large standing crops of phytoplankton and very high rates of carbon fixation in shallow coastal lagoons and estuaries, throughout most of the year; secondly, off Ghana and the Ivory Coast there is an area of coastal upwelling, where high rates of primary production occur seasonally in August and September, and where enrichment also induces high standing crops of planktonic biota, which are different in specific composition from those of estuaries and lagoons. The centres of production of clupeoid fish, and hence of activity in fishing for them, follow the same pattern. In the estuaries and on those parts of the continental shelf over which estuarine conditions occur at least seasonally, *Ethmalosa fimbriata* forms the object of very important local fisheries; in the Ivory Coast–Ghana upwelling region, there are large and important canoe fisheries for the 'herring', *Sardinella aurita*, and also a recently developed industrial fishery for this and for *S. eba*. Also of interest to the West African fisheries is *Ilisha africana*, which is not so restricted to eutrophic areas and which occurs throughout the whole region and is a regular component of the demersal trawl catches on the West African continental shelf.

Ethmalosa fimbriata is both superficially and anatomically extremely similar to the western Atlantic menhadens (*Brevoortia* spp.), although Monod (1961) has shown by his anatomical study of the two species that this resemblance is rather a matter of convergence than of very close systematic

relationship. Be that as it may, almost all that is known of the ecology of the American menhadens may be said to apply in general to *Ethmalosa*, which is a strong, active, filter-feeding clupeoid and attains a total length of approximately 40 cm. Bainbridge (1960) has shown that *Ethmalosa* obtains its food by passive filtration of phyto- and to a lesser extent microzooplankton with very little selection from the natural plankton communities by a detailed comparison of stomach contents and the catch in plankton nets hauled around the feeding school from which the fish were caught. Shoals of bonga are rarely found in clear water or far from estuaries or lagoons. In the Gulf of Guinea they occur in two regions: one, in the west, from Liberia to Senegal where many small rivers debouch and extensive estuarine and lagoon systems occur; the other, in the east, centred on the Niger Delta with its enormous lagoon systems and on the estuaries of the Cross and Cameroon Rivers. Although small populations occur off virtually every river mouth throughout the tropical region, bonga resources of importance occur only in these two major centres. *Ethmalosa*, like *Brevoortia*, spawns at sea (Bainbridge, 1960) and eggs and larval stages of this species have not been found in estuaries; however, within a few weeks of being spawned, the juvenile fish move into the estuaries in very great numbers and live there and in the lagoon systems, until they are approximately 10 cm in length, when they begin to migrate between the sea and the estuaries with a migration pattern similar to that of the adults (Salzen, 1958; Bainbridge, 1960). As Bainbridge (1960) has shown, there is a cycle of productivity and of standing crop of diatoms in these estuaries related to the tidal cycle; in brief, during periods of neap tide and small scour blooms of diatoms, principally *Coscinodiscus*, which appear to be flushed out in the intervening periods of spring tides and heavy tidal scour. The movements of *Ethmalosa* between the estuaries and the open shelf appear to be related to this cycle; during the neap tides and high crops of diatoms, the fish move into the estuaries to graze, returning to the shallow shelf areas outside the estuaries during periods of spring tides (Longhurst, 1960). Spawning appears to be more or less continuous throughout the year, although it is perhaps interrupted in June, July, and August by the effects of the rainy season when, due to the greatly increased flow from local run-off of the very heavy rains, 'neap tide' conditions scarcely occur in the estuaries. It is probable that a spawning peak occurs at the height of the dry season in January and February. As a result of this pattern, except during the rainy season when they appear to be flushed out, there are broods of young *Ethmalosa* from an inch or two in length constantly in the estuaries (Salzen, 1958); these juveniles appear to be restricted to the shallow parts of the estuaries where they fall easy and abundant victims to the fishing traps and to the large flocks of fish-eating birds, principally terns (*Sterna*), which also live in the estuaries especially during the dry season which is contemporaneous with the northern winter.

The fisheries for *Ethmalosa* follow the adult fish and are clearly dependent upon their pattern of migration; despite considerable effort to mechanize and modernize these fisheries by local fishery agencies and F.A.O., they remain to this day in an unmechanized state throughout most of West Africa. This is understandable because of the nature of the resource and of the environment of the fishery; it is scattered throughout a multitude of

estuaries, lagoons, and inaccessible creeks and the fishermen live in thousands of small fishing villages and hamlets, most of which are accessible only by canoe or small launch and few of which are near a road.

This is a canoe fishery and some very fine canoes are deployed in it. The gear is of three kinds: most commonly, very large cast-nets are used during the day when the schools can be readily observed; in Sierra Leone, cast-nets of up to 18 ft in radius are used from seven-man canoes in which the caster (with two or three nets) stands in the bow, paddled by five paddlers, while the canoe is commanded by a captain who steers from the stern. The skill of these teams is quite extraordinary and one cannot but be impressed by the uncanny skill of the caster, who stands erect in the bow of a heaving canoe in a turbulent estuarine ebb-tide and throws a net which is undoubtedly one of the largest cast-nets developed anywhere in the world; on one occasion I counted as many as 250 *Ethmalosa* of 25 to 30 cm long in the catch from a single cast of such a net. More recently, small drift-nets have been used at night to take bonga in Sierra Leone, and the Ghanaian round-haul or 'ali' net, together with the typical Ghana canoes, has been introduced by migrant Fanti fishermen into the western bonga fisheries. In the fisheries of the eastern Gulf, particularly in Nigeria, the gear does not appear to be so evolved and smaller canoes and smaller cast-nets are the general rule; however, the small drift-net from two-man canoes at night is very commonly used in this region.

In Lac Nokoûe, in Dahomey, and in other eastern lagoon systems which have only very small or frequently-closed entrances through the beach, land-locked races of *Ethmalosa* appear to have developed; the species normally matures at about 21 or 22 cm in length and many adults attain at least 30 cm: however, in these lagoons the populations contain very few individuals longer than 12 cm in total length, and maturity first occurs at less than 10 cm. These populations are heavily fished by the lagoon fishing villages.

The *Sardinella* fisheries of the tropical West African coast are based upon two species, *S. aurita* and *S. eba*. These fisheries are concentrated in three regions: first, in the central upwelling area off Ghana and the Ivory Coast; secondly, in the frontal region, off Senegal and Casamance, between the Canary and Guinea Currents; and thirdly, in the frontal region between the northern Benguela Current and the tropical water of the Bight of Biafra, from Cape Lopez south towards the central Angola coast. In each of these areas, in the mid 1960s the total catch of *Sardinella* by canoes and small fleets of industrial sardine purse seiners was of the order of 50,000 tons (Zei, 1969). The composition of the landings between *S. aurita* and *S. eba* varies considerably from season to season and from place to place within these fisheries. *S. aurita* is quite unlike any of the other tropical east Atlantic clupeoids in form and ecology, being a long herring-like fish, very round in section. From the combined work of Postel and his associates in the French-speaking West African nations, of Johnson and others in the Ghana fisheries, and of the U.S.S.R. exploratory fishing surveys, there has now been built up a fairly satisfactory model of the biology and distribution of *S. aurita* off West Africa (Postel, 1959). It seems that this species alternates between periods spent in demersal schools in the offshore areas below the thermocline and others spent in surface waters and closer to the coast (Boradatov and Karpechenko, 1958). The species arrives off the coast of Ghana at the same time as the seasonal upwelling between June and late September; it

feeds heavily during this period, as Bainbridge (1960) has shown, largely upon *Calanoides carinatus*, a copepod that dominates the zooplankton during the upwelling; while it is at the coast, *Sardinella aurita* is present in dense schools which can be seen at the surface and which are composed of maturing individuals. Spawning occurs towards the end of the upwelling period, after which the fish return to the deeper sub-thermocline waters farther offshore, and where they again occur in large demersal schools, that rise into mid-water and disperse slightly at night.

The dependence of the fishery upon the upwelling phenomenon and the consequent behaviour of the *Sardinella* is very clear, and in the rare years in which the upwelling fails, so does the fishery. In 1968, the rainy season in Ghana continued intermittently from June until October, and was not interrupted, as is usually the case, by a 'little dry season' caused by a high atmospheric pressure system, itself caused by a coastal upwelling process; in this year, too, the fishery was a complete failure (Kwei, pers. comm.). It may also be supposed that the 1968 year-class would have a high degree of probability of failure.

The same pattern is seen off Senegal and probably occurs also to the south of Cape Lopez, though this is less well-documented. The Soviet work to the south of Cape Verde (Boradatov, Karpechenko, Probatov and Biryukov, 1959) has shown that the schools are aggregated in the frontal region from July to September and include both one- and two-year old fish. During this period there is relatively little feeding, though the gonads mature rather rapidly and subsequently the fish move inshore to spawn. During the period of maturation, there are daytime demersal schools similar to those described by the Russians off Ghana and these show the same diurnal vertical migration. Movement towards the coast appears to take place in the mixed layer and Postel (1959) describes the schools immediately to the south of Cape Verde peninsula over the shallow parts of the continental shelf as being round in form when seen from above, dark in colour, fast moving, and breaking the surface like rain; he suggests that a school 15 or 20 m in diameter will contain 20 to 30 tons of fish and the largest will include about twice this quantity. The schools here foresake the surface and descend deeper in the mixed layer during the middle of the day; at this time they are easily located with a simple echo-sounder.

During the upwelling season off Ghana, when the onshore spawning movement brings such shoals to the surface and near to the coast, a seasonal herring fishery develops in the string of small fishing towns almost the whole length of the coast of Ghana; based on the great Ghanaian surf-canoes with their rounded section and high sheer at either end, the herring are taken by simple, round-haul nets worked from single canoes. Set around a 'breezing' shoal of herring, the net is not pursed completely, but by means of a great commotion in the middle of the set, the fish are induced to 'gill' themselves, and the net with its enmeshed catch is loaded back aboard the canoe. The fish can only be removed by spreading the net on the beach, and so canoes can make only a single catch on each trip. Paddled by eight or ten men with three-pronged paddles these canoes are a fine sight going out through the heavy surf common on the Ghana coastline; attempts to substitute the canoes with inboard-engined surf-boats have failed because of the difficulty of getting these up the steep beaches—the canoes can easily be 'walked' up because of

their rounded line from stem to stern. A mechanization scheme based on outboard motors has, however, been extremely successful, not in reducing the crew number but in increasing the number of trips which can be made in one day and, since under sail the canoes could not get very close to the wind, in giving greater freedom of selection of fishing grounds.

Especially in the francophone ports of West Africa, a number of small fleets of French sardiniers have developed in the last decade; using round-haul nets, these vessels fish mostly for *S. aurita* and *S. eba*, and their catches make up a major part of the *Sardinella* landings of Senegal and the Ivory Coast. About 30 sardiniers operate from the port of Abidjan, for instance, taking around 25×10^3 tons of sardines annually.

There are also *S. aurita* fisheries in the Levant Basin of the eastern Mediterranean Sea, and Rifaat (1960) describes the *Sardinella* fisheries off the Nile Delta during the period before the closure of the Aswan High Dam. During the Nile flood (from August to December) thin, spent sardines moved from the east into the region immediately before the delta. They fed heavily and their fat content increased rapidly, e.g. in *S. aurita*, from 6·4% to 31% of the body weight within this three-month period. After the flood receded and the standing crop of zooplankton diminished the sardines moved away into deeper water. This Egyptian fishery, like that off the coast of Israel, was dominated by *S. aurita* but also included smaller quantities of *S. eba* and *S. granigera*. Now, however, since the closure of the new Nile dam, the annual flood no longer reaches the sea and the fishery appears to have become greatly diminished. In the tropical West African region *S. aurita* is present in small quantities below the thermocline virtually the whole length of the coast (Longhurst, 1964; Williams, 1968). The relation between these small and presumably isolated schools to the populations in the main fishing areas off Senegal, Ivory Coast–Ghana, and Congo–Angola is not known.

S. eba is a deeper and flatter fish than *S. aurita*. It can be found almost everywhere between Mauritania and Angola, except perhaps in the region of the Niger Delta and the Cameroons, where it is replaced by the closely related species *S. cameronensis*, itself also deeper and flatter in form than *S. aurita*. Much less is known of the biology and distribution of these two species than of *S. aurita*. Although they are widely distributed and present everywhere along the coast they are evidently more abundant in the eutrophic regions of Senegal, Ivory Coast–Ghana, and Congo–Angola, where they may at times rival the landings of *S. aurita*; in 1966, for example, nearly 50% of all the landings of the sardine boats from Abidjan were made up of *S. eba* (Marchal, 1967).

S. eba, and presumably also *S. cameronensis*, has a rather catholic diet based upon available zooplankton and to a much greater extent than *S. aurita* the juveniles penetrate into estuaries and lagoons in the same manner as do those of *Ethmalosa fimbriata*. Wherever there are trap fisheries for juvenile *Ethmalosa*, an important component in the catch is contributed by juveniles of *Sardinella eba*, and in the fisheries for adult *Ethmalosa* a certain percentage of adult *Sardinella eba* are normally included in the take; in places where *Ethmalosa* is not abundant, such as the western coast of Nigeria, the rather sparse stocks of *Sardinella cameronesis* form the basis of small fisheries operating either with drift-nets at night, or round-haul nets from large canoes during the day. As with *S. aurita*, both of these species

are also taken at some places and at some times of the year in rather large numbers by the big, highly-evolved beach-seines which are such a feature of the West African scene.

In the eastern boundary currents to the north and the south of the tropical area, the fisheries for *Sardinella* are replaced by fisheries for temperate sardines; in the Canary Current this boundary occurs off Mauritania, to the north of which *Sardina pilchardus*, the European sardine, is the main clupeoid fish taken. In the south, the division between the warm-water and the cool-water clupeoid fisheries is around Mossamedes, to the south of which the South African pilchard (or sardine) (*Sardinops ocellata*) is the dominant species. Although not a strictly tropical species, it seems worthwhile to pay some attention to this South African fish both because this occurs off a country with a 'tropical' economy but also because of some interesting features of the results of heavy exploitation of *S. ocellata* which have become evident in recent years. There appear to be two populations of the South African sardine, one centred at Walvis Bay off southwest Africa and the other off St Helena Bay in the Cape Province of South Africa; tagging shows that although there is limited interchange of individuals between these populations, on the whole they are reproductively isolated one from the other (Stander and Le Roux, 1968). In each region the fish appear to concentrate along the boundary between the upwelled Antarctic Intermediate Water of the Benguela Current, and more offshore oceanic water, and it is in this region that there are major fisheries during the winter months when the fish are feeding actively upon the diatom bloom in the upwelled water. Stomach analyses have shown that volumetrically phytoplankton dominates the diet in a ratio of approximately 2 to 1, the phytoplankton utilized being mainly large diatoms, and the zooplankton mainly calanoid copepods. The work of De Jager (1960) and his associates in southern Africa has shown that in summer the stocks disperse from the coastal upwelling areas to spawn offshore; this occurs over a wide region and in two main periods, from August to October, and from January to March. Large fish spawn during the first of these periods and smaller fish during the second. Stander and Le Roux (1968) have recently reviewed the history of the fishery for sardines at Cape Town which began in 1943 and which has recently shown indications of serious problems (Table I). The catching capacity of the purse seine fleet has continued to increase from a total hold capacity of 4.8×10^3 tons in 1950 to 11.7×10^3 tons in 1965, yet the catch has in recent years began to decline from peak landings of more than 400×10^3 tons in the years of 1962 and 1963. There have been considerable fluctuations in the percentage of individuals smaller than the length at which first maturity is reached, from year to year; this is due to variation in recruitment of the various year classes and the success of spawning; however, there has been a tendency since the mid-1950s for the percentage of juveniles in the landings to rise from values of less than 10% to above 50% in recent years. A general trend towards a decline in population size as a result of a failure of a number of year-classes to provide sufficient recruits led to a very sharp reduction in pilchard landings subsequent to 1963. By 1969 (Stander, pers. comm.) the fishery for *Sardinops* at Cape Town was reduced to only 50×10^3 tons or about one-eighth of its peak production, while about 250×10^3 tons of anchovy were taken. In 1963 abnormally high water temperatures, more than 4° C higher than usual, off

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the coast of South West Africa, especially in May and June apparently caused a complete spawning failure and the decline in the pilchard fishery was consequently accelerated by the complete recruitment failure of the 1963 year-class. The catch from the northern population of *Sardinops* off southwest Africa continues higher, however, than that off Cape Town, with a quota in 1969 of $1{\cdot}0 \times 10^6$ tons for land-based processing and $0{\cdot}57 \times 10^6$ tons for floating processing plants. There are indications, again, of falling catches and

TABLE I

Statistics of the South African fishery for Sardinops ocellata *at Cape Town (adopted from Stander and Le Roux, 1968); weights in short tons.*

Year	Number of boats	Total hold capacity of fleet	Tons, total landings	Tons per hold capacity	Juveniles in catch %	Juvenile anchovies in research ship catches %	Anchovy commercial landings
1950	150	4,850	95,093	10·50	7·31		
1951	183	6,400	109,610	12·01	2·89	—	—
1952	197	7,260	187,424	22·23	12·31	—	—
1953	229	8,320	150,987	15·73	3·11	—	—
1954	225	8,470	97,336	11·07	0·92	—	—
1955	228	8,300	134,424	13·55	0·07	—	—
1956	222	8,210	84,156	8·02	6·29	6	—
1957	210	8,210	118,557	9·41	15·86	8	—
1958	201	8,480	214,528	22·15	53·15	33	—
1959	165	8,660	286,796	30·90	64·65	34	—
1960	143	8,310	350,361	42·16	51·86	81	—
1961	131	9,310	443,449	47·64	15·57	38	—
1962	122	9,840	452,735	46·01	30·62	60	—
1963	127	10,920	441,943	40·47	52·69	0	23
1964	126	11,350	282,301	24·87	52·55	96	95
1965	125	11,730	222,920	19·00	52·63	89	209

in 1969 the plants at Luderitz did not fulfil their quotas, and 250×10^3 tons of anchovies were processed. The apparent decline in the stock of pilchards is evident not only in commercial landings but also in the number of eggs taken in egg and larva surveys by research vessels, and in the catch rate of adults sampled by blanket-nets from research vessels during the same period.

The South African pilchard shares its environment with an anchovy (*Engraulis capensis*) which apparently has a very similar ecology; the distributional ranges, and the diet of the two species overlap very strikingly (Stander and Le Roux, 1968). and it may be presumed that in some way the populations of the two are in a dynamic balance so that their combined biomass equals what can be supported by the planktonic food-chain. Both include a small number of copepod species in the dominant components of their diet (*Calanoides carinatus*, *Centropages branchiatus*) and a number of diatoms are similarly common to the diet of each (*Nitzschia*, *Thalassiosira*, *Skeletonema*, *Chaetoceros*). There is some evidence that the stock of *Engraulis* has increased as that of the pilchard has decreased at Cape Town; in the routine blanket-net catches from South African research vessels the ratio of anchovies to pilchards has changed (Table 1) from approximately one anchovy to 15 pilchards in the mid-1950s to more than 10 anchovies for each pilchard taken in the mid-1960s; this led to the initiation of an anchovy fishery in 1963 out of Cape Town, which at first had limited success but now appears to be established. We shall meet similar examples of competition between sardine-anchovy species-pairs in the Indo-Pacific in considering the Californian and other fisheries.

WESTERN ATLANTIC

In the enormous warm-water area of the western Atlantic, which extends effectively from New England to Argentina, there is a less distinct division between tropical regions and the warmer parts of the western boundary currents than in the eastern Atlantic; in this whole area there are approximately 75 species of clupeoids—considerably more than in the eastern Atlantic. Of these, some dozen or so are significantly utilized in the warm-water fisheries.

The species which are exploited range from such small and relatively unimportant forms as the little anchovy, *Anchovia clupeoides*, which is common in the fish markets of the Caribbean and Brazil, to the very important fisheries for menhaden (*Brevoortia* spp.), which occur in relatively low latitudes and, although strictly outside the tropical area are so similar to the West African *Ethmalosa* fisheries as to be of interest to us here. There are no major fisheries in the western tropical Atlantic which depend upon anchovies of the family Engraulidae; there are, however, a number of local fisheries, similar to that for *Anchovia clupeoides* mentioned above, for rather less than a dozen species of anchovies. Among these are the bay anchovy (*Anchoa mitchilli*) which occurs from Cape Cod to Yucatan and is an inshore species, feeding on small zooplankton and having some commercial use in the manufacture of anchovy paste in the southern United States. *A. hepsetus* occurs from Chesapeake Bay through the tropical region to Uruguay and migrates along the eastern seaboard of North America in the summer where some $10-15 \times 10^3$ tons are taken annually; it is also abundant in the West Indies where it is the object of a number of small fisheries. On the eastern seaboard of South America *A. tricolor* occurs from Venezuela to Argentina, and is commonly found in fish markets throughout this region. About 13 species of the genus *Anchoviella* occur in the western tropical Atlantic and, of

these, two (*Anchoa perfasciata* and *A. elongata*) are fished to some extent in Central America and the Caribbean. The freshwater anchovies, *Pterengraulis atherinoides*, and several species of the genus *Lycengraulis* are important in inland fish markets of the Amazon Basin through to Venezuela. The major clupeoid fisheries of this area are based upon the Clupeidae. Leaving aside the fisheries for the Atlantic and Gulf shads, *Alosa sapidissima* and *A. alabamae*, and that for the river herring, *Pomolobus chrysochloris*, we find that there are two major fisheries for clupeoids to be considered: that for menhaden (*Brevoortia*) in the Gulf of Mexico and on the Atlantic seaboard of the United States and also off the southeastern coast of South America, and that for *Sardinella* off Venezuela and Brazil.

Two species of *Sardinella* appear to be important along the tropical eastern coast of South America; these are *S. anchovia* along the coast of Venezuela and *S. brasiliensis* which appears to replace it in the region of the Guianas. There has been considerable confusion in the literature as to the nomenclature of these species and both have on occasion been referred to as *S. aurita*, but it is doubtful whether they are conspecific with the West African species; *S. anchovia* also frequently appears in the fisheries literature under the name *Clupanodon pseudohispanica*. The major population of *Sardinella anchovia* is concentrated along the eastern coast of Venezuela between Margareta Island and the Gulf of Cariaco. The recent work of Simpson and Gonzales (1967), and Simpson and Griffiths (1967) have provided much information about this important species, which has produced landings generally fluctuating from 30 to 40×10^3 tons annually in the last decade, and reaching a high level of 44×10^3 tons in 1965. The life history of *S. anchovia* is very closely tied to the upwelling cycle in the eastern region of Venezuela. The fishery is mostly concentrated in the Gulf of Cariaco and it is this population which has been most studied; it is quite likely that other populations in more open sea regions have parallel relationships with local upwelling cycles. The Gulf of Cariaco is an east-west trending gulf, long and narrow with a relatively narrow entrance almost closed by a sill at 60 m depth. During the non-upwelling part of the year, water in the Gulf at depths greater than the sill depth are not replaced and frequently become anaerobic. The northeast trades reach their peak strength between December and April and during this time they displace much surface water from the Gulf which is replaced by an undercurrent across the sill; this replacement water upwells over much of the area of the Gulf and the resultant eutrophication and high standing crop of plankton coincides with the spawning peak of the Gulf population of *S. anchovia* (Simpson and Gonzales, 1967). At present the fishery is based almost entirely upon beach-seines which are extremely efficient and whose operation is frequently arranged so as to capture complete schools of fish. The maximum weight of these schools appears to be in the region of 400 tons but 60% of them contain less than 100 tons of fish and 90% of them contain less than 20 tons of fish. Although this beach-seine fishery is extremely efficient so far, there is no evident reduction in the catch/unit effort of this fishery. It has been possible to age *S. anchovia* by a study of scale annuli, and the age composition of the catch appears to be weighted heavily in favour of 2- and 3-year old fish which together comprise more than 70% of the total landings (Heald and Griffiths, 1967). First year fish of about 14 cm in total length are not fully recruited to the beach-seine

fishery. This fishery also takes small numbers of *S. brasiliensis* which are at the extreme northern limit of their range in eastern Venezuela and can readily be distinguished from the more usual species by their deeper bodies.

There are similar but considerably smaller fisheries for the anchovy *Cetengraulis edentulus* on the Peninsula of Araya, during the wet season from May to November when the sardine fishery is less active, and up to 5 thousand tons of anchovies may be taken which are used for the production of fish meal. The thread herring *Opisthonema oglinum* is taken in similar quantities in a number of localities scattered along the coast by small beach-seine fisheries, but is nowhere very important. The future of clupeoid fisheries in this region, considering the rather wide area over which strong seasonal upwelling occurs and which coincides with the distribution of *Sardinella anchovia* (ascertained by egg and larva surveys), appears to be promising. It is likely that the beach-seine fishery will be supplemented by a normal boat purse-seine fishery offshore since according to Simpson *S. anchovia* may, at present, only be exploited at the extreme periphery of its range; however, operations of U.S. fishery research vessels off the Venezuelan coast have not indicated abundant offshore stocks of *Sardinella* (Bullis and Thompson, 1968).

Further to the south, along the coast of Brazil, there is a fishery for *S. brasiliensis* in the southern part of that country between Santos and Rio de Janeiro. The age composition in these two places is known and it is evident that the stock of *S. brasiliensis* includes a much greater number of year-classes than does the population of *S. anchovia* in more tropical areas. At Rio de Janeiro, seven year classes may be detected in the population, but at Santos only three. It also appears that the Santos stock contains no mature individuals, but only juveniles and fish in the early stages of maturation; at Rio de Janeiro the stock includes all stages of maturity. It is not clear whether this indicates long migrations of the population, which would not be impossible, or whether the fishery is taking only the edges of two improperly understood stock distributions. On the face of it, perhaps the second interpretation seems more likely.

Seven species of *Brevoortia* are distributed in the western Atlantic. Of these, five occur in the Gulf of Mexico and along the Atlantic coast of North America, while two occur on the coast of South America. Of the five North American species, two (*B. tyrannus*, the Atlantic menhaden, and *B. patronus*, the Gulf menhaden) form the object of one of the major fisheries of the world and together yielded a yearly catch in excess of 1×10^6 tons in the early 1960s. Minor catches are made of the yellowfin menhaden, *B. smithii*, and the finescale menhaden, *B. gunteri*, the former off Florida, and the latter on the northern coast of the Gulf of Mexico. *Brevoortia* has an ecology extremely similar to that already described for *Ethmalosa fimbriata* in the Gulf of Guinea. All species appear to have a very fine filter basket formed of gill rakers and their food appears to be dominated, at least where they are available, by larger members of the phytoplankton community; it is supposed that the long seasonal migrations which the species undertakes are arranged to carry them into areas of diatom and dinoflagellate blooms. When not in such areas, their food consists of microzooplankton. Spawning occurs rather early in the year and the eggs are hatched in offshore waters; this may be as early as January and February in the southern part of their range on the western coast of Florida but further to the north during spring and early

summer. After some weeks growth, at about 1 inch in length, the larvae enter estuaries where they spend the rest of the summer (June, 1959, 1960), leaving them only at the onset of cold weather; while in the estuaries the juveniles form typical clupeoid schools and undergo much predation from fish-eating birds. Their dominant food during this period comprises estuarine diatoms. After spawning, the adult stocks move northward along the Atlantic coast from their rather deep wintering grounds off Florida and westward along the north coast of the Gulf of Mexico from the same general wintering area. The migration takes place in the upper mixed layer where they are extremely vulnerable to spotting from masthead lookouts or light aircraft, and are readily taken with large purse seines.

The Atlantic fishery, based upon *Brevoortia tyrannus*, started to decline from peak landings in 1956 when, to some extent, the fishing vessels either changed to other fisheries in the same region or shifted their effort into the Gulf of Mexico on to *B. patronus*. The last important year-class of *B. tyrannus* was that of 1958, which remained in the fishery and resulted in excellent catches until the year 1962 (Table II); since then production has declined.

TABLE II

Recent landings of menhaden in the western Atlantic: metric tons × 10^3.

	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968
	Brevoortia tyrannus + *B. patronus*									
United States Atlantic coast	658·1	550·4	587·0	585·7	384·7	302·0	318·9	233·6	210·2	251·3
Gulf	341·0	381·4	462·9	479·3	438·9	410·1	464·0	359·7	317·6	375·0
	Brevoortia pectinata + *B. aurea*									
Brazil			3·0	1·2	1·3	1·4	1·1	1·6	1·2	—

Off South America, southern Brazil, Uruguay and northern Argentina, there are small fisheries for *B. pectinata* and *B. aurea*, but they do not approach by an order of magnitude the importance of the North American *Brevoortia* fisheries. At Valparaiso, *B. pectinata* are taken to be salted or smoked for human consumption as are *Ethmalosa* in West Africa, while in North America the *Brevoortia* landings are used entirely for industrial purposes.

EASTERN PACIFIC

On the western side of the American continent the warm water of the Pacific Ocean, as in the eastern tropical Atlantic, spans a relatively small range of latitude. It appears that approximately 25 species of clupeoids occur abundantly. Numerically, these are dominated by 11 species of the genus *Anchoa* (several of which were considered as *Anchovia* by Meek); these are small, mostly zooplankton-feeding species, although *Anchoa starksi*, which occurs from El Salvador to Ecuador is also recorded as including abundant diatoms

in its diet. Some species have rather wide distributions, occurring throughout the tropical region, as, for instance, *A. naso* present from the tip of Baja California south to Peru; but several are rather restricted, for example *A. eigenmannia*, which occurs only between Costa Rica and Panama.

The trawl fisheries for shrimp in the Gulf of Panama and elsewhere along the western coast of Central America catch many species of clupeoid fish as a by-product; Peterson (1956) indicates the diversity of this fauna in which *Ilisha*-like fish are prominent. Local fisheries for a number of species, particularly of the genus *Anchovia*, supply the fish markets in coastal towns the length of the tropical coast. Recently, small-scale reduction plants have been established in Panama and Ecuador and are partly supplied by trash-fish, mainly clupeoids, from the shrimp fisheries, and partly by specialized fisheries—as in the Gulf of Panama—for the tropical anchoveta, *Cetengraulis mysticetus*, and for the thread herring *Opisthonema libertate*. The Panama fishery reached 65×10^3 tons in 1968, of which 12×10^3 were of thread herring, the remainder of anchoveta (Gulland, 1969).

Tuna boats, both of United States and Central American origin, for many years relied almost entirely upon *Cetengraulis mysticetus* for the live bait essential for their tuna fishing operations; as Peterson (1956) has indicated, one of the main fisheries for this species was in the Gulf of Nicoya and between 1939 and 1951 this species was virtually 'fished out' from this Gulf. Although it is possible that its disappearance (as indicated by the figures given in Table III) could have been the result of climatic changes, it is probably that the species was simply reduced below its survival point by the activities of the tuna bait-boats: it has subsequently been re-introduced successfully by the same boats back into the Gulf of Nicoya. *C. mysticetus* has a diet in which phytoplankton is extremely important; as Bayliff (1963) shows, the stomach is muscular and gizzard-like, a character it shares with other phytophagous clupeoids and with mullets. Centric diatoms such as *Coscinodiscus* form a

TABLE III

Statistics of the tuna bait-boat fishery for
Cetengraulis mysticetus *in the Gulf of Nicoya.*

Year	Total catch (scoops × 10³)	Mean catch rate (scoops/day)
1939	220·7	454
1940	25·3	186
1941	89·6	199
1942	19·2	258
1943	54·7	471
1944	23·5	165
1945	29·3	126
1946	90·2	279
1947	57·5	92
1948	7·1	44
1949	1·2	59
1950	—	0
1951	—	0

dominant part of the diet of young fish; adults tend, on the other hand, to feed on benthic diatoms such as *Melosira*, and Bayliff demonstrated that their stomach contents correspond well with the benthic diatom flora of their habitat. The population of *Cetengraulis mysticetus* in the Gulf of Panama has been studied by Howard and Landa (1958) who showed how rapidly its stock was turned over by reproduction and mortality. They found that although there was some spawning throughout the year this was at peak intensity in November and December and coincident with the annual period of upwelling. Bayliff showed that the size of first year fish and their abundance could be related to the strength of upwelling and population densities of adults. Reproduction occurs at the end of the first year of life when the fish have reached approximately 13 mm in length; in the second year, little more than another centimetre is added to the length of the fish, which this year reach maturity earlier than the yearlings and have an overall longer spawning season. The total population as sampled by the fishery may be comprised of more than 90% of first-year individuals (Table IV); this type of population structure appears to be typical of tropical clupeoid fish.

The eastern boundary currents which flow towards the tropical regions from the north and the south in the eastern Pacific Ocean each contain a pair of species, one sardine and one anchovy, which are the dominant clupeoids; in the south, off Peru and Chile, the anchovy is dominant and

TABLE IV

Percentage age composition of catches of Cetengraulis mysticetus *at a number of Central American locations* (*Barrett and Howard, 1961*).

Location	Year class I	II	III
Guaymas	77·7	22·3	—
Ahome	81·4	18·6	—
Banderas	83·8	16·2	—
Fonseca	33·5	54·5	12·0
Columbia	41·4	58·6	—
Ecuador/Peru	90·1	7·8	2·1

occurs in very great abundance, while in the north, in the California Current, the sardine was dominant until suppressed by fishing pressure, assisted by climatic changes which were in favour of the anchovy; at present, therefore, anchovies are dominant in both the Peru and California Currents. The eastern boundary current off Peru and Chile supports the largest single-species fishery in the world, and approximately 20% of all the world's landings of sea fish are taken by this fishery; this may be attributed to three factors, (1) the great quantity and high rate of carbon fixation by phytoplankton in the Peru Current, (2) the phytophagous habit of the anchovies concerned and hence the extremely abbreviated nature of the food chain, and (3) a relatively very high growth rate. Upwelling in the Peru Current is extremely strong and occurs for about 270 days each year over an area of about 0.5×10^6 km^2

(Cushing, 1968) at an average rate of 3×10^{12} cm³/sec (Wyrtki, 1966). As Cushing shows, about 155×10^6 tons of carbon may be fixed annually, a figure only exceeded for other coastal upwellings by that of the Benguela Current with 278×10^6 tons.

The anchovy (*Engraulis ringens*) of this region is very similar in general form to other members of the genus but is particularly distinguished by the occurrence of rather fine filaments on the gill rakers; these occur early in life compared with similar species elsewhere. This is related to the ecology of the species, whose diet is based upon phytoplankton, primarily diatoms, to a considerably greater extent than any other species of *Engraulis*. Investigations of *E. japonicus* and *E. anchoita* indicate that the diet of these widely separated species, one off Japan and one off Argentina, is rather similar; zooplankton dominates until the fish are 15 or 20 mm in length, after which phytoplankton becomes increasingly important in the diet, though apparently not to the same extent as in *E. ringens* off Peru. It is to be expected, however, that even this latter species in its early larvae stages will depend largely upon micro-zooplankton for its food.

Although it had been known for very many decades that theres was a large stock of *Engraulis* off the coast of Chile and Peru, it was not until 1940 that an industrial fishery was attempted; to a certain extent the reluctance to begin fishing this species was based on the supposition that the economy of the very important guano-producing birds of the Chile and Peru Currents depended upon the anchovy. It was supposed that the population of these birds was limited by food, even though in retrospect it is evident that the successful attempts of the guano administration of Peru to increase the population size of the guanay cormorants and of pelicans by statutory protection of the breeding populations and by increasing their available nesting sights by

TABLE V

Growth statistics of the Peruvian fishery for Engraulis ringens: *data derived from several sources.*

	Number of fishing boats	Number of reduction plants	Total landings (tons × 10⁶)	Fish meal production (tons × 10⁶)
1955	175	16	0·059	0·021
1956	220	27	0·119	0·031
1957	272	39	0·326	0·064
1958	321	53	0·737	0·121
1959	355	63	1·909	0·323
1960	654	89	2·944	0·553
1961	753	105	4·580	0·864
1962	1,090	120	6·275	1·120
1963	1,756	150	6·423	1·129
1964	1,836	155	8·863	1·548
1965	1,654	148	7·233	1·282
1966	1,670	144	8·530	1·466
1967	1,350	151	9·825	1·804
1968	1,172	120	10·263	1·922
1969	1,308	112	8·850	1·611

artificial means, indicate that the limiting factor for population size of these birds was not the amount of food available but rather nesting site limitation. As the tabulated data show, the commercial fishery which began in the early 1950s after an initial period of establishment grew very rapidly and soon placed Peru among the major fishing nations of the world. From landings of a few tens of thousands of tons in the mid-1950s, they had climbed in 10 years to more than 8 million tons per annum (Table V), while the number of boats and of reducing plants had increased in the same period by approximately an order of magnitude. The effect of this industrial expansion upon the economy of an underdeveloped country such as Peru has been very important. Throughout this period of expansion there has been a considerable amount of apprehension on the part of industrialists and biologists associated with the fishery as to the possible effect on it of the occurrence of El Niño conditions; during these incursions into the updwelling region of a layer of warm surface water the anchovies occur deeper than usual, remaining in the colder sub-thermocline water where they are unavailable to the populations of fish-eating birds; cormorants and pelicans are thus unable to dive far enough to catch fish successfully and emigrate and starve in very great numbers; the population dropped, during the last recorded severe El Niño, from about 16 million birds to perhaps 3 or 4 million birds. It was supposed that the reaction of the anchovies to El Niño conditions might have similar effects upon the success of the small bolicheros or purse-seiners used by the Peruvian fishery and this remained a spectre hanging over the development of this industry since it has been found that the seiners could not reach deeply enough to take fish under these conditions.

Recent studies on the population biology of the Peruvian anchovy show that the species occurs from northern Peru to central Chile, and seasonally further to the south, and that on the basis of meristic counts (Brandhorst, Careno and Rojos, 1965) at least three stocks occur, two off Chile and one off Peru; it is important to determine the degree to which the Peruvian stock, upon which most of the fishery is based, is independent of the southern stocks (Schaefer, 1967). Spawning occurs throughout the year south of Punta Aguja at 6° S, although two spawning peaks occur, one in October and the other, less important, in February or March; the young fish spawned in October begin to appear in the fishery as early as the end of the summer, while the young fish from the second spawning peak are recruited the following spring in July to September (Saetersdal and Valdivia, 1964). Recruitment to the fishery begins, early in the year, at 8 cm when the fish (at this time called peladilla) are about 5 months old, and is virtually complete in October at about 14 cms (Saetersdal and Valdivia, 1964); but, as Gulland (1969) points out, the time of greatest availability to the fishery does not correspond with expectation. In the period June–September when two year-classes are present in the fishery, apparent abundance is actually least, probably because of spawning-related behaviour of the fish and perhaps because the population has been heavily fished. Growth has been determined principally by the Petersen method, (Saetersdal and Valdivia, 1964) which gives good results only up to an age of 18 months; but from otolith studies Boerema et al. (1965) demonstrate that few fish survive beyond the second year of life. Growth is very similar to that of the tropical anchoveta Cetengraulis mysticetus discussed above, and a fork length of 13 cm is reached at the end of the first

year of life. Growth can be approximated to the von Bertalanffy equation which has constants of $k = 1 \cdot 7$ and $L_\infty = 15$ cm.

As Schaefer (1967) discusses in his review, the age structure of the exploited population appears to be getting younger and though, as he points out, it is difficult to identify year-class variation during the decade of the fishery, such variations between 1961 and 1966 appear to be rather small, and vary by a factor of less than $2 \cdot 0$; in high-latitude clupeoids, such as the North Atlantic herring *Clupea harengus*, year-class strength may vary by a factor more than 10 times greater.

Schaefer uses as a unit of effort the catch per boat/ton/month to estimate the stock abundance of anchovies off Peru, and from his regression of effort on catch per unit effort obtains an estimate of the maximum sustainable yield of between $7 \cdot 7 \times 10^6$ metric tons per annum and $8 \cdot 1 \times 10^6$ metric tons per annum, depending on whether or not the calculations are corrected by a factor for increasing vessel efficiency during the period. He notes that the yields for the seasons 1964–65 and 1965–66 were very close to the maximum sustainable yield, and in fact may have exceeded it slightly. He, therefore, deduces that the fishery has now reached a point at which regulation is obviously essential to its continuing well being. It can also be estimated from a knowledge of the daily food intake of guano birds that the total stock of fish-eating birds on the coast of Peru consumes approximately $2 \cdot 5$ million tons per year and this, added to the sustainable yield estimate derived from the fishery, suggests that the total yield from the anchovy population could be in the order of 10 million tons if the birds were eliminated. Schaefer suggests that a minimal population of 3 million birds may be essential for their survival for the future in case the guano industry again became of greater importance than the fish meal industry; he bases his calculations on the population size at the time of reduction by El Niño; whether or not this is desirable is a matter for Peruvian economists to determine. Also, as Gulland (1969) points out, the relationship between anchovy stock size and the numbers of guano birds is probably rather complex. Although it was the case in the past it is not certain that the bird population is now size-limited by nesting sites. Although a careful study does not seem to have been made, there are indications that the bird populations are not recovering as fast from the most recent El Niño-related population collapse as they have in the past.

The great fishery for *Engraulis ringens* off Peru and northern Chile and the overwhelming dominance of this species in the pelagic ecosystem draws attention to the fact that in this region we again find an anchovy-sardine species pair. The sardine of the southeast Pacific Ocean, *Sardinops sagax*, forms the basis of a small fishery off northern Chile, where some 10×10^3 tons are taken annually; two species of *Ethmidium*, locally known as machete and machueol, give catches of about 20×10^3 tons in southern Peru. It would be extremely interesting to obtain historical data on the relative abundance of sardines and anchovies in the Chile–Peru region comparable with data from the sub-fossil record of California discussed below.

The clupeoid fisheries off California are of interest to us here even though they are prosecuted in mid-latitudes rather than in the tropics, because they are again based on a pair of species—one anchovy and one sardine—which have been studied in great detail and which show some interesting changes in

relative abundance because of an intensive fishery on only one of them, the California sardine. *Sardinops caerulea* of California is extremely similar to, and may be conspecific with, the Peruvian-Chilean species, while the California anchovy, *Engraulis mordax*, is distinguishable from the Peruvian anchovy principally by the number and length of its gill rakers which are fewer, shorter, and less well adapted to a diet based primarily upon phytoplankton. The growth rate and population structure of both these species is quite different from the Peruvian species; both grow considerably more slowly so that their populations include a greater number of year classes. While few individuals of *E. ringens* off Peru survive beyond 18 months of age, fish of 5–6 years old form a significant part of the population of *E. mordax* off California.

Briefly, the history of the decline of the sardine fishery of California is as follows: from its start, in the early part of the century, the fishery rose to a peak of sardine landings in the early 1940s; these then progressively declined
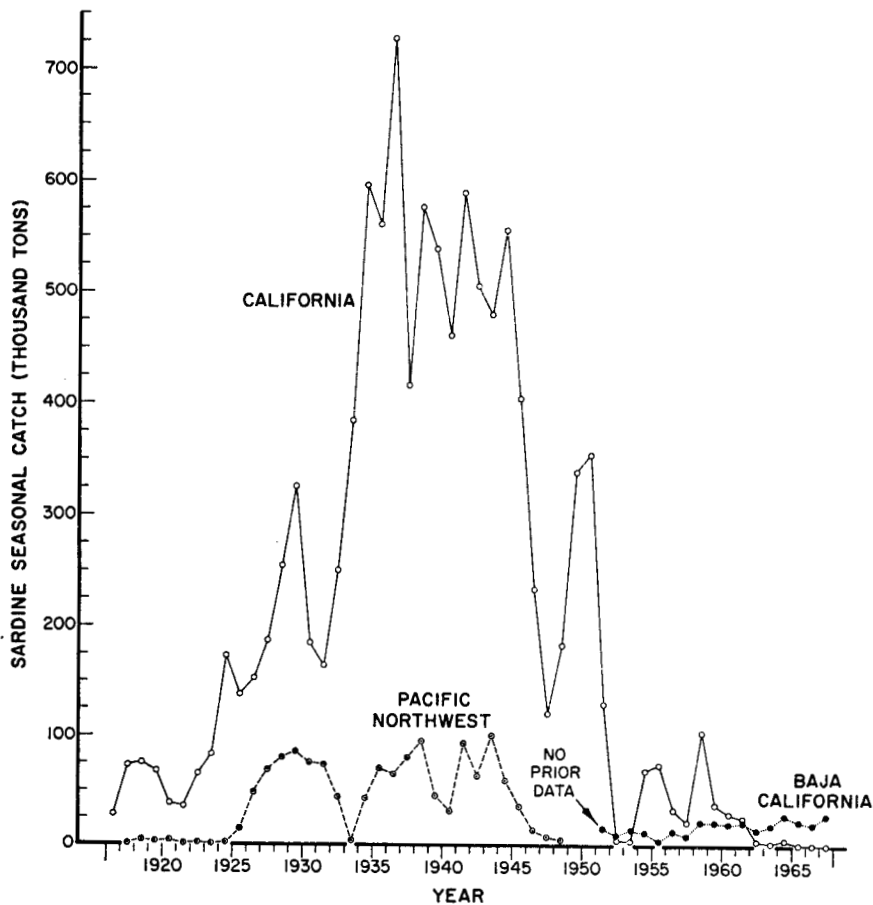

Fig. 1.—Annual catches in the fishery for Pacific sardine (*Sardinops caerulea*) in Oregon-Washington, California and Baja California, 1915 to present day (redrawn from Ahlstrom, unpubl.).

and with the exception of a minor resurgence in the late 1950s, continued until the present situation was reached (Fig. 1, Table VI). The fishery is now so small as to be negligible and a complete moratorium may be imposed on the fishing of this species off the State of California; this decline from landings of more than half-a-million tons in the early 1940s to a few hundreds of tons in the mid-1960s has had important economic effects upon the California fishing industry. Continuing egg and larval surveys in the California Current have confirmed that the decline in the landings has been a result of a declining total population of the northern race of the species which has now almost disappeared; the only remaining populations of any fisheries significance are isolated stocks in the Gulf of California and along the southern part of the west coast of the Baja California peninsula. As the stock of sardines declined, as indicated both by the catches of the fishing fleet and the findings of the egg and larval surveys (Fig. 2), so these latter indicated that the biomass of anchovies in the same region was increasing. By the mid-1960s it had become evident from these data that the biomass of anchovies had risen to such an extent that it had essentially replaced the original sardine biomass which had been present at the height of the fishery in the 1940s.

The reasons for the decline in the sardine fishery and the rise in the anchovy stock are certainly complicated but some very reasonable explanations which are probably near the truth have been put forward by Marr, Murphy and others. The models recognize certain basic ecological differences between the anchovy and the sardine in an environment unaffected by the fishery. The area over which the anchovy spawned in the early 1950s and presumably that over which it was generally distributed was more restricted than the spawning distribution of the sardine since the anchovy eggs and larvae occurred primarily along the coast, especially in certain regions in which there is strong and regular upwelling. The fecundity of anchovies, weight-for-weight, appears to be about twice that of the sardine and (perhaps more important) the year-class variation of the anchovy, as off Peru, appears to be much smaller than that of the sardine. The feeding ecology of the two species in the California Current, including that of their larvae, appears to be rather similar and it is likely that the two species are in competition for food, so that their total combined biomass, as Lasker (1970) has suggested, is probably food dependent and is thus limited by the total zooplankton production of the California Current. Finally, in general the anchovy appears to be a more northern species, its lower temperature limit for spawning being 2° C lower than that for the sardine. Anchovies spawn in water warmer than 11° C, while sardines spawn only at temperatures greater than 13° C. Two factors perhaps explain the decline of the sardine population and the rise of the anchovies; these are; first, the selective fishing pressure on the sardine, which was heavily sought by a fishery that almost neglected the anchovy; and, secondly, the beginning of the major decline in sardine stocks coincided with the start of an anomalous period in the California Current, from 1943 to 1957, of unusually cold conditions and of unusually strong and regular upwelling. These conditions might be expected to favour the anchovy at the expense of the sardine and to make it unlikely that abundant year-classes of the sardine would occur during this period; in fact, the only major year-class during this period resulted in a minor resurgence of the fishery during the late 1950s. The degree to which an increasing biomass of the anchovy
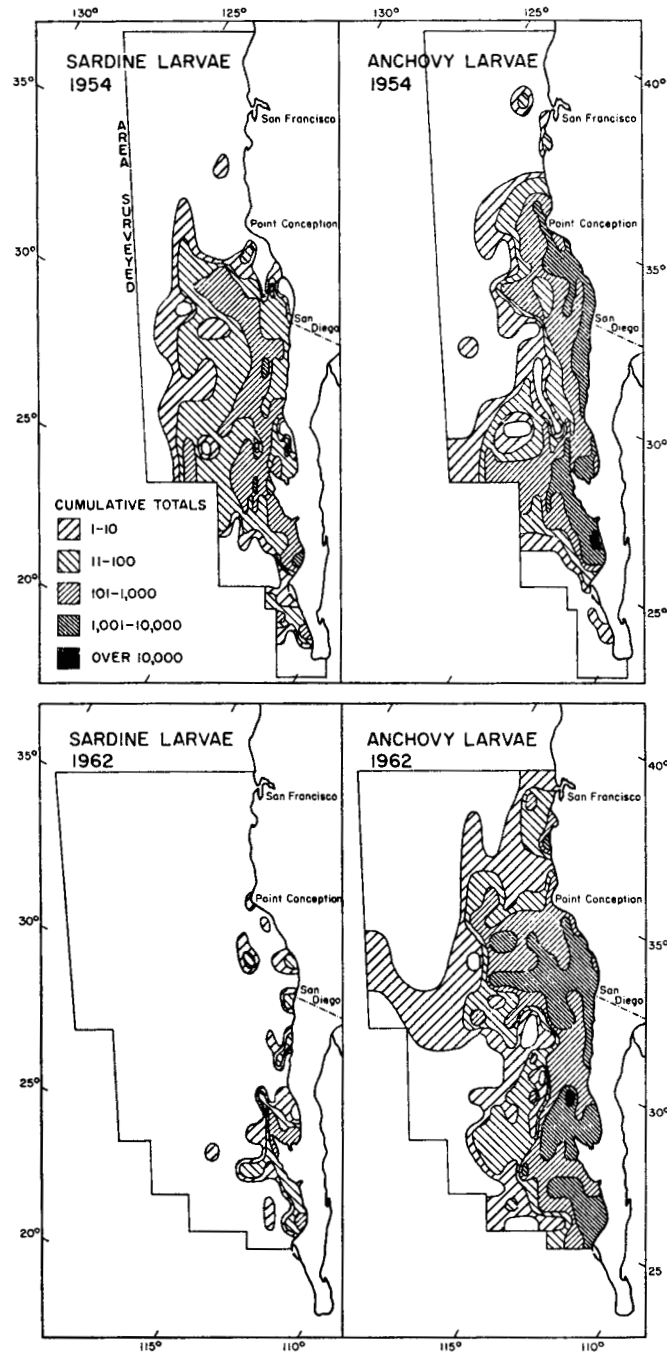
Fig. 2.—Relative abundance of sardine and anchovy larvae in ichthyoplankton surveys of the California Current in 1954 and in 1962 (Cal COFI data).

population has contributed directly, by competition, to the decline of the
sardine stocks is not clear, and it is now generally supposed that the anchovies
increased in number in response to the ecological vacuum left by the decline
of the sardine, rather than that the sardines declined because the anchovies
had become so abundant; this is indicated both by a lag in the biomass
response of the anchovy to the decline of the sardine (Murphy, 1966) and also
by failure to demonstrate decreased survival success as indicated by larval
length-frequency distribution of sardine larvae by many thousands of plank-
ton samples in which sardine larvae occurred alone, anchovy larvae occurred
alone, or the two occurred together (Isaacs, 1965); however, Gulland (in
prep.) has suggested that a relationship exists between the survival of sardines
to recruitment and the total spawning biomass of sardines and anchovies.

There is also historical evidence (Soutar, 1969) from the occurrence of
scales of anchovies, sardines, and other pelagic species in the varved mud
sediments of several of the anaerobic basins in the Santa Barbara Channel
that similar shifts in biomass dominance cold water species associated with
the anchovy, and warm water species associated with the sardine, together
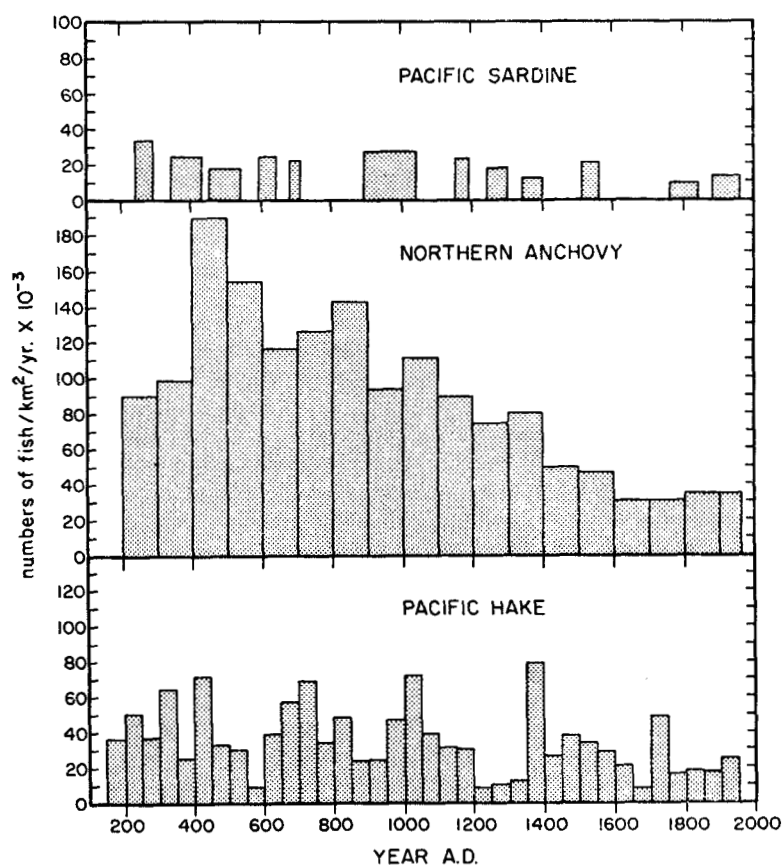

Fig. 3.—Abundance of hake, anchovy and sardine in the California Current at 34° N,
as deduced from sub-fossil fish scales in varved deposits in the anaerobic Santa Barbara
Basin (redrawn from Soutar, 1969).

with the two main species, had alternated during the many thousands of years during which the varved sediments were being deposited (Fig. 3). It seems very likely that this will prove to be a general phenomenon in such fisheries and the mechanics of the situation must certainly be understood; in particular, it is very important to be able to predict whether the situation is reversible, so that by proper management sardine stocks can be brought back in an area to replace those of the less valuable anchovies. It is unfortunate for the fisheries concerned that the less valuable species appears, from its ecology, to be likely to provide the basis of a more stable fishery than one based on the more valuable species; however, as Gulland (1969) suggests, the potential yield of the two-species system may be greater when it is in the anchovy phase. From the historical data, the potential yield of the sardine in the California Current was evidently considerably less than 1.0×10^6 tons but it seems probable that a sustained yield of up to 2.0×10^6 tons of anchovies may be achieved. A total spawning biomass of up to 4.0×10^6 tons is indicated by egg and larval surveys in the mid-1960s, and from values for the natural mortality rate derived from the age structure of the population Gulland suggests that about half the biomass can be removed annually.

INDO-PACIFIC

The central and western Indo-Pacific region encompasses a very large part of the tropical oceans stretching from the Red Sea to Madagascar, from the Chinese coast to Indonesia and Australia, and through the island archipelagos of the Pacific Ocean; this vast region contains a very great variety of ecological situations ranging from intense upwelling area off the desert coasts of the northwest Arabian Sea, through the oligotrophic oceanic regions of the central Pacific to the rich, shallow, brackish areas of the Indonesian archipelago where estuarine and mangrove conditions occur over very large areas. The Indo-Pacific region also contains the greatest number and diversity of species of clupeoids in the tropical oceans; along the mainland of Asia from China to the Red Sea, down the coast of eastern Africa, and through the Indonesian, the Philippine, and the Australian archipelagos the systematic diversity of clupeoids is baffling to the non-specialist: there are at least 11 species of *Sardinella*; rather similar to these are 15 or 16 species of *Harengula*, and a half-dozen species of *Clupeoides*; there are at least a dozen species of *Ilisha*, or forms very close to this genus, and the little fresh and brackish water herrings of the family Pellonulidae are represented by many genera and species; entering the rivers are a number of important shad-like clupeoids dominated by three species of *Hilsa*, and three species of the very similar genus *Macrura*; round herrings of the genera *Spratelloides* and *Dussumeria* are important and represented by several species each, as are gizzard shads of the genera *Dorosoma* and *Nematalosa*. Anchovies are represented perhaps most importantly by several species of the genus *Stolephorus*, but also by several *Setipinna*, *Lycothrissa*, *Coilia*, and *Thrissocles*.

CENTRAL PACIFIC

In the central Pacific region there appear to be no major clupeoid resources, since the main upwelling feature in this region, the divergence zone extending

along the equator almost the whole width of the Pacific Ocean does not appear to support big stocks of clupeoids, but is exploited by other groups of oceanic fish. At Hawaii, the only clupeoid resource of any consequence is an engraulid, the nehu (*Stolephorus purpurpus*) and this is mainly of importance as bait-fish for the live-bait boats of the skipjack fishery; live-bait is frequently in short supply and attempts have been made to substitute other species, even to the extent of the pond-rearing of African cichlid fishes for use on the bait-boats; Murphy (1966) describes the introduction of *Harengula vittata* from the Marquesas Islands to the Hawaiian archipelago, and although this appears to have been successful it has not solved the problem of the lack of live-bait. In most of the oceanic archipelagos and around oceanic atolls, shoals of clupeoids are abundant and many small anchovy-like genera in particular are familiar and important members of the fish fauna around coral reefs, but nowhere are these resources present in massive enough abundance to support important fisheries. It is, in fact, curious that these large shoals of anchovy-like forms are supported by the plankton production around oceanic reefs; the clarity of the water and the lack of phytoplankton blooms seems at odds with the occurrence of relatively abundant shoaling clupeoids.

WESTERN INDO-PACIFIC

Probably the most important clupeoid fishery of the western Indo-Pacific at the present time is that for the Indian oil sardine (*Sardinella longiceps*). Stocks of this species extend around the whole perimeter of the northern part of the Indian Ocean from the Gulf of Aden to the Bay of Bengal and also occur in the Indonesian archipelago and the Philippines. The landings of this important species in India have reached as much as 200 thousand tons per annum in some years, but the fishery is susceptible to irregular and large-scale fluctuations in resource availability (Table VII). For this reason, it has been studied intensively by fishery biologists in India, beginning in the early 1920s with the work of Hornell and his associates. As might be expected, the population over this vast area is divided into a number of probably reproductively isolated sub-populations, although these have so far been identified only by rather unsatisfactory meristic methods. Nair (1960) describes the main fishery for the species which is concentrated on the western coast of India, on the Kanar and Malibar coasts, where it is prosecuted within 8 or 10 miles of the shore by several different sorts of gear —gill-nets and drift-nets operated by canoes on which the freeboard has been extended upward by planking, and by large beach-seines. The shoals become available to the fishery towards the end of June, when populations of adults with mature gonads appear at the coast and progressively more northwards as the season advances; these fish have mature gonads and spawn during their first few months in the coastal region. As the season advances, a second wave of shoals arrives in the coastal regions and becomes available to the fishery; these are younger, immature fish and their availability reaches a peak during the months of October to December. By this time, the adults which arrived first have left the fishery which continues for a further couple of months into the new year. Approximately the same cycle of events is repeated annually on the east coast of India. The arrival of the first wave of adult sardines at the coast generally coincides with the onset of the southwest

monsoon; at this time there is a very strong seasonal bloom of phytoplankton, principally of the diatom *Fragillaria* spp. and it is supposed that the spawning migration is timed to coincide with this; the arrival of the second wave of such shoals, at a peak in October to December coincides with a second phytoplankton bloom. Nair (1960) has shown that the stomach contents of this species are dominated by phytoplankton, largely a single species of the diatom (*Fragillaria oceanica*) and dinoflagellates. He has suggested that the large and important fluctuations in the availability of the species from year to year may be dependent upon the nature and timing of the annual

TABLE VII

Landings of oil-sardine on the west coast of India, 1948–1968;
(from Panikkar and Jayaraman, 1967).

Year	Landings (metric tons × 10³)	Year	Landings (metric tons × 10³)
1948	1.2	1959	69·2
1949	0·3	1960	189·0
1950	34·4	1961	167·9
1951	17·2	1962	110·3
1952	13·9	1963	63·6
1953	51·8	1964	274·3
1954	33·9	1965	262·0
1955	30·4	1966	252·8
1956	7·4	1967	259·1
1957	191·5	1968	301·4
1958	123·3		

bloom of this diatom. Although the oil-sardine occurs throughout a very wide area of the western Indo-Pacific, nowhere else does it appear to form such large concentrations as those that occur on the west coast of India; in the Philippines and Indonesia, for instance, it supports minor fisheries in many localities, but nowhere is it the object of single-species fisheries of the magnitude of those on the Indian coasts.

From Indonesia and the Philippines to the Arabian Sea, a number of other species of *Sardinella* are the object of small, local multi-species fisheries; the most important species involved in these appear to be *S. gibbosa* and *S. albella*, which together form the basis of the choodai fishery of Palk Bay on the Indian coast each summer, when juveniles of both species are taken with cast-nets, gill-nets, and traps of various sorts. *S. fimbriata* and *S. sirm* join the above two species in local fisheries in the Philippines, in the Visayan Sea in Indonesia, along the north coast of the Arabian Sea, and along the north coast of the Australian continent. These are mostly zooplankton-feeders and where their diet has been investigated (as by Ronquillo, 1960, for a number of species in the Philippines) it is evident that they subsist upon a mixed diet, dominated by crustacea of various sorts, according to the relative availability from place to place and season to season. A number of fisheries for small anchovies have developed throughout this great region and these are apparently mainly based upon the genus *Stolephorus*. In the Philippines two

species (*S. commersoni* and *S. indicus*) are important, while in the Indian Ocean, as for instance at the Seychelles, *S. delicatus* appears to have some significance.

Besides the fishery for the oil-sardine, those for the various shads of the genera *Hilsa* and *Macrura* are also very interesting, and particularly that for *Hilsa ilisha* in India. Species of these genera occur in the river fisheries of Madagascar, off the eastern coast off Africa, of India, and in the East Indian archipelagos. The Indian fishery has been extremely well studied by the Pillays, husband and wife (see Pillay, 1958). They have shown that on morphometric and meristic grounds several stocks of *Hilsa* can be identified in the various river systems of the Indian subcontinent and this confirms the traditional ability of Indian fishermen and fish traders to distinguish fish of this species from different river systems in India by their taste, which as they point out, appears to be largely dependent on the fat content of the fish. Work on the genetic basis of the racial differentiation has been started by a study of the extent of individual serological variations in *Hilsa ilisha* of the Hooghly River. The distribution of the species extends from the Arabian Sea, including the Persian Gulf and the Red Sea, through the Bay of Bengal into the South China Sea and it occurs in estuarine areas and brackish lagoons throughout the whole of this area. Outside the spawning season the adult and maturing stocks are largely found in lower estuarine and inshore continental shelf regions of brackish water but do not occur significantly in the open ocean; during the breeding season the fish migrate upriver, and after spawning return to the estuarine region again, behaving like any other anadromous fish; as might be expected, in some of the major rivers such as the Ganges and the Brahmaputra, there are stocks which do not descend to the estuaries in the non-spawning season and these may be comparable with the lagoon-locked stocks of *Ethmalosa* already discussed for the coastal lagoons of the Guinea coast (p. 358). The stimulus for the upstream spawning migration depends upon the occurrence of flood-water, whether caused by the southwest monsoon or by the spring thaw in the northern mountains. In general, the upstream migration commences in the early spring and is over by the end of summer. Spawning of planktonic eggs occurs fairly high up the rivers some hundreds of kilometres from the estuaries which the adult fish have left, and juveniles descent progressively back to the estuaries and inshore areas, normally to reach the sea before they are one year old. The commercial catches of adult *Hilsa* usually include between three and five year-classes of adults and maturing fish. Fishing occurs primarily in shallow regions and especially in estuaries and the lower parts of riverine systems during the upstream migration of the fish. The main fishery season is, therefore, in the early part of the monsoon flood and varies from place to place and from river to river. A great many types of fishing gear and devices are used in the estuaries for the capture of *Hilsa*; cast-nets are thrown by men standing upon tiny platforms on a row of poles across the river while various forms of beach- and boat-seines, drift-nets, and gill-nets are worked off the mouths of the estuaries. The total catch of *Hilsa* for the Indian subcontinent in a successful year approaches 40×10^3 tons.

Such are the fisheries for various species of herring- and sardine-like clupeoids in the tropical region of the western Indo-Pacific; the main production, apart from the major fisheries for the Indian oil-sardine, is in the

coastal regions of southeast Asia, southern China, the Philippines and northern Australia, a region with a multitude of islands, great stretches of shallow continental shelves, and of innumerable estuaries, lagoons, and bays.

The occurrence of major fisheries throughout this region is dependent on the position of major upwellings together with their coincidence with large populations of people with a sea-going tradition. The locations of major coastal upwellings and regions of eutrophication have been identified piecemeal during the last several decades, and it has become evident that the most important are those along the coasts of Somalia and southwest Arabia during the southern monsoon (see, Banse, 1968) together with the shallower upwelling along the west coast of India during the same period of the year; in the Indonesian region, Wyrtki (1962) has described a dome-like phenomenon in the thermocline topography which induces strong up-welling to the south of Java. Cushing (1969) has recently reviewed these regions and quantified the annual amount of production in each region. The alternation of the northerly and southerly wind systems, and the complex geography of the monsoon regions of southeast Asia and the archipelagos are responsible for the occurrence of very many regions of minor upwelling, most of which are very little known for their biological or fisheries significance.

The occurrence of a major fishery for the oil-sardine (*S. longiceps*) on the Indian west coast and the absence of a fishery of such magnitude in Somalia and southern Arabia may be largely due to the pattern of distribution of the human population rather than that of the fish resources. Though it is little documented, there are indications of abundant stocks of clupeoid fish, including the oil-sardine and other species of *Sardinella* in the northwest Arabian Sea and it appears that the sparse population inhabiting the desert coast of southern Arabia are heavily dependent on these stocks for their protein supply and for a crude form of animal feed; cast-netted *Sardinella* are dried in the sun on the sand and used as camel-fodder in some areas, for instance. Only about 30×10^3 tons of *Sardinella* appear to be caught at the present day in the northwest Arabian Sea, or less than a tenth of that taken in good years on the west coast of India, although Cushing (1969) estimates about four times as much primary production off Somalia and Arabia as on the Indian coast. The estimate by F.A.O. of about 800×10^3 tons as the fishery potential of the northwestern Arabian Sea, most of which may be expected to be pelagic clupeids, does not therefore seem unreasonable. Direct fisheries exploitation of this region is urgently required for an under-standing of the future major fisheries of the world.

There are also indications (see Soerjodinoto, 1960) of major clupeoid resources associated with the Java–Sumatra upwelling region; the species involved here seems again to be the oil-sardine (*S. longiceps*) which is here known as lemuru. A minor fishery has developed for this species in the region of the Bali Straits, where the appearance of the fish, as on the west coast of India, is very seasonal; the season opens in September or October with the arrival of small fish, the larger fish arriving towards the peak of the fishing season in December and January at the height of the rainy season.

WESTERN PACIFIC

The North Equatorial Current on reaching the area of Indonesia and the Philippines, swings to the north and becomes a western boundary current

sweeping along the eastern coast of Asia, along the mainland of China, and passing Japan as the Kuroshio or Black Current. Comparable with the western boundary currents off the east coasts of North and South America, this current contains a resource of clupeoids in which several species of *Sardinella* dominate along the mainland of China while off Japan, in the rich boundary zone between the warm Kuroshio and the cold southward-flowing current Oyashio, there are important resources based upon another pair of species, one sardine and one anchovy, such as we have seen elsewhere (p. 371): in this area, the species involved are *Sardinops melanosticta* and *Engraulis japonicus*.

Along the southeastern coast of the mainland of China at the port of Hong Kong, information on the clupeoid landings are easier to obtain than elsewhere. They are dominated by a species known in the literature as *Sardinella aurita*, called at Hong Kong the golden sardine, but which is probably different from the species which bears the same name in the literature from the warm parts of the Atlantic and Mediterranean Seas; the ecology of the *S. aurita* of Hong Kong appears to be quite different from that, for instance, in the Gulf of Guinea. At Hong Kong, this species is not strongly related in its ecology to an upwelling region but has a similar ecology to the many other zooplankton-feeding *Sardinella* that occur in the western Indo-Pacific (Li Kwan, 1960). It is present in large numbers in schools off Hong Kong during winter from December to April although the fishing season for juvenile schools begins in May and ends in November, thus extending over the summer months. In spring, the shoals of adult *Sardinella* leave the Hong Kong region and pass towards the north where there is a fishing season for it off Formosa during the summer months. This is a relatively long-lived fish, about six to eight year-classes being present in the fishery. The 0-group fish occur close to the coast where the specialized fisheries for them occur in shallow water.

The fishery for adult *Sardinella* is by large purse-seiners which range from the coast; these seiners are big wooden sailing junks carrying four smaller boats or sampans: two of these shoot and haul the net, while the other two drive the shoals of *Sardinella* into the circle made by the seine. Elsewhere in the region the fishery for *Sardinella* spp. depends quite largely upon attraction to lights at night and although this is probably a very ancient fishery it can only have become as efficient as it is at present with the introduction of powerful incandescent gas lamps at the turn of the present century; in Indonesia, the same sort of fishing until a very few years ago was still carried out by primitive torches and it is quite likely that this technique continues to be used in out-of-the-way areas of the western Pacific archipelagos.

Li Kwan (1960) describes the various non-industrial fisheries then operating throughout the western tropical Pacific for 11 species of *Sardinella*, including *S. aurita* and *S. longiceps*. None of these are on a very large scale and typically several species are included in the catches—he speaks also of mixed-species schools, though the evidence for this is not very clear.

Further to the north, the Japanese clupeoid fisheries, although not tropical, are well enough investigated and understood to be worth discussing briefly here. The fishery for clupeoids has the common name of the 'Iwashi' fishery and is a multi-species fishery based primarily upon the sardine (*Sardinops*

melanosticta) and the anchovy (Engraulis japonicus) together with the round-herring (Etrumeus micropus); the addition of this third species to the Iwashi fishery places this region apart from those which we have already discussed in the eastern boundary currents of the Atlantic and Pacific Oceans. The Iwashi fishery reached a peak of more than $1 \cdot 1 \times 10^6$ tons, or 42% of the total fish landings in Japan, in the 1930s but has since declined to about half this figure; in the early 1960s it comprised only a little more than 10% of all fishes landed by the Japanese near-water fishing fleet. During the period of high catch and landings of the 1930s Sardinops made up the bulk of the landings, and the anchovy contributed only a few per cent. Fluctuations in the Iwashi fishery of Japan have been recorded in the half-millennium since the fishery was founded about the year 1500 (Uda, 1960); the present decline is the third such major decline recorded during this period. The decline in the sardine component of the Iwashi fishery in the last three decades has not been confined only to Japan, but has also occurred in the Soviet Far East, off Korea, and in the Yellow Sea.

The ecology of S. melanosticta appears to be very similar to that of other species of Sardinops discussed previously (Anonymous, 1969); distinct subpopulations based upon meristic characters have been recognized in the species; spawning occurs offshore and initially the post-larvae feed chiefly upon microcopepods and nauplii, progressively feeding upon larger micro-zooplankton. Subsequently, diatoms form an increasingly important item in the diet, although at no time does phytoplankton appear to be entirely dominant; however, during phytoplankton blooms, Yoshida (1955) found that diatoms figure rather largely in the diet; heavy feeding in spring coincides with the period of plankton bloom. During the period of abundant sardines in the 1930s it was known that the population undertook a complicated migration pattern around the Japanese Islands, although this can no longer be traced under present conditions of great scarcity of Sardinops; spawning apparently occurred and most of the stock originated near the southern tip of the island of Kyushu and the 0-group fish passed northwards along the Kuroshio Current to the Boso Peninsula passing their first year of life on this section of their migration pattern; in the following year the I-group migrated northwards during the summer to the island of Hokkaido and in the autumn of their second year of life migrated southwards again to winter around the Boso Peninsula. In their third year of life the same northward migration off Hokkaido occurred, but in this autumn these II-group fish passed rapidly southwards across the Japan Sea to the spawning area at the southern tip of the Island of Kyushu where they underwent their first spawning activity. In subsequent years the pattern of a northward migration to Hokkaido and Korea and a southern migration in the autumn to the Kyushu region was repeated. As the Sardinops stock declined during the 1930s to its present very low level, so the stock of anchovies appeared to increase and in the early part of the 1960s had risen from 9% of the landings from the Iwashi fishery in the early 1940s to almost 70% in the years around 1960. The remaining 30% of the catch is now comprised of juvenile and post-larval stages of all three species, together with a few other species not named here, which are together known under the commercial name of sirasu.

The distribution of Engraulis japonicus extends south to Formosa and somewhat north of the Japanese Islands but it appears that the main stock

is in the region of Japan. Ecologically, it is extremely similar to those species already discussed, feeding upon all available microplankton including small crustaceans and large plant cells; it is evident that we have here a situation extremely similar to that which we have discussed in greater detail in relation to the California Current and to the Benguela Current off the west coast of southern Africa (p. 373, p. 363). A multi-species fishery appears to be easily thrown out of balance so that the dominance of one species is replaced by the dominance of another and (in this case at least) the overall production of the fishery appears to decline concurrently with the change-over in dominance of one species to another. The historical record of the Japanese sardine fishery and the palaeontological record for the California sardine both indicate that these species pairs may fluctuate in abundance either relatively or absolutely (or both) without a heavy fishing pressure having developed on the preferred species; that fluctuations in relative or combined stock size can occur in unexploited populations does not, of course, suggest that under other circumstances the role of heavy fishing pressure in triggering the decline of a *Sardinops* population may not have been decisive, as it apparently was off California. In the South African, the Californian, and perhaps in the Japanese case, there is evidence which indicates that the recent declines have been triggered by fishing pressure on a population made vulnerable by climatic events.

The presence of a major sardine population off Japan only occurs when 'warm' oceanographic conditions obtain, that is, when the influence of the warm Kuroshio water is greatest around the Japanese islands. Uda (1960) shows how relatively good and poor decades in the last half-century are correlated with warm and cool oceanographic conditions and although it has been suggested (e.g. by Aikawa, 1943) that the heavy fishery which developed on the whole oriental sardine stock alone caused the decline, it seems more likely that the failure of recruitment in the years 1938–1941 were primarily caused by environmental changes. As Uda (1960) has pointed out, in the late 1930s the pattern of currents changed to such an extent around Japan that the migration patterns of the sardines were modified and spawning occurred in areas which would place the 0-group fish in a precarious situation with the onset of winter cooling. The changed location of the present centres of population (Nakai, 1960) tend to confirm the effect of environmental rather than fishery changes.

In the southern hemisphere in the warm temperate regions of Australia and northern New Zealand a similar pair of species *Engraulis australis* and *Sardinops neopilchardus* occur. Fisheries for both species in this region are trivial and only a few hundred tons at most are landed annually; the ecology of both, as they have been described by Blackburn (1960), appears to be rather similar to that of similar species discussed in greater detail previously and it is possible that these resources, which are certainly under-utilized, might support fisheries of some significance in the future.

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