

## A SURVEY OF THE PELAGIC FISHERIES OF THE WORLD

## Part I: GENERAL CONSIDERATIONS

By

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## INTRODUCTION

It has been a great privilege to be asked to open the discussion on the World Pelagic Fisheries in the symposium arranged by Dr. G. L. Kesteven as part of the proceedings of the Singapore Inaugural Meeting of the Indo-Pacific Fisheries Council. The literature on the subject is very extensive, and scattered in many books, journals and periodicals published in the five continents. Owing to the shortness of notice for the preparation of the paper, it has not been possible to review any but a fraction of the literature on the subject, and no one is more conscious than myself of the incompleteness and inadequacy of the paper presented. I hope, however, that the more salient features of the subject have been touched upon in this brief review, and that these will lead to a fruitful discussion. I should like to take this opportunity to offer my sincerest thanks to Dr. G. L. Kesteven, F.A.O. Regional Representative (Fisheries) for every encouragement and for readily placing at my disposal a list of bibliography on the subject which he had prepared, and to my colleague, Dr. N. K. Panikkar who, at very short notice, was able to get together a considerable part of the locally available literature at Madras and to prepare a general connected account of the biology of pelagic fishes from his own and my notes on the subject.

The paper is presented in two parts: (1) General considerations of the pelagic environment as influenced by latitude, climate, currents, tides, and the biological and physico-chemical contents of the sea and their influence on fish and fisheries; (2) Biology of pelagic fishes, chiefly of the shoaling forms such as herring, mackerel, horse-mackerel, flying fish, so far as is known and has been possible to gather in the short time at our disposal.

*Geographical divisions of the oceans.* The pelagic region of the oceans is a part of the marine bio-cycle of the world which may be divided geographically into two main divisions, viz (1) the Atlantic with its connections in the North and the South with the Arctic and Antarctic waters respectively, and the associated partially land-girt seas—the North Sea, the Baltic Sea, the Mediterranean Sea,

the Gulf of Mexico and the Carriibbean Sea, and (2) the Pacific and Indian Oceans with their connections in the South with the Antarctic, and with a northern connection for the former Ocean with the Arctic by the Behring Sea. The Red Sea, the Arabian Sea, the Bay of Bengal and the Andaman Sea, the China Sea, the Sulu Sea, and the Java, Sunda, Arafura, Banda and Celebes Seas of the East Indies and the Japan and Yellow Seas are more or less land-bounded.

*Oceans of the world as a continuous domain for marine organisms.* The oceanic mass of water thus constitutes for marine organisms a single continuous domain whose populations are, as a rule, of greater density in the upper strata of water than the lower, and exhibit in the former a greater diversity of form and organisation. With the exception of a few of the higher forms of life such as the seals, whales, dolphins, turtles, snakes, which have secondarily adapted themselves to life in the sea, the majority of sea organisms have the ocean as their original home. This marine domain or bio-cycle has been estimated to have about 300 times the habitable space provided by the terrestrial and fresh water bio-cycles together. It may be broadly divided into the primary and secondary biotic divisions based upon the physical nature of the sea or upon the nature of the biota.

*Physical and biological divisions of the oceans.* The two primary divisions of the oceans are (1) the benthic including all the ocean floor and (2) the pelagic including the whole mass of water. Although this article deals specifically with the latter division, the physical and biological continuity of the marine domain or bio-cycle makes it necessary that the characteristic features of both the divisions be taken into account if the significance of factors affecting pelagic fisheries is to be fully understood. The pelagic division is further sub-divided into the Neritic and the Oceanic regions corresponding to the littoral and the abyssal sub-divisions of the benthic, in reference to the depths to which light penetrates the neritic and oceanic regions and to the extent and depth of the continental shelf. These are not, how-

ever, absolute divisions as depth of penetration of light in the neritic region may be affected by the turbidity conditions of the sea and the extent of the continental shelf may be correlated with the geological formation of land masses and the extent of terrigenous deposits brought in by rivers.

*Physical and biological characteristics of the benthic divisions of the sea.*

Fishes of both the benthic and the pelagic divisions of the ocean have to depend for their sustenance on the organisms and organic substances produced in it either in the form of plants or animals or in the form of organic detritus. The benthic division from the shore to the abyss is usually covered by sedimentary terrigenous deposits, organic or pelagic oozes, and red clay. Except for the fact that the deep sea deposits, consisting of nutrient organic and inorganic matter, may be brought within the range of the neritic region by upwelling and currents in the ocean, the terrigenous deposits restricted to the configuration of the continental shelf seem to influence the greater productive capacity of the coastal region in reference to fisheries. Plants are the real sustainers of animal life in the sea in general, and the production and distribution of plants in the sea depend upon a great variety of factors chief among which are light and available nutriment in the biotic division in which they occur. The eulittoral zone of the benthic division which can support large attached plants constitutes only about two per cent of the sea floor, and even here unfavourable substratal conditions restrict the production of such plants.

The function of primary food production in the sea therefore devolves on the unattached floating plants, e.g. phyto-plankton—such as, algae, diatoms, flagellates, coccolithophores, etc. which occur in enormous numbers. The phytoplankton may be divided broadly into neritic and oceanic populations. As the conditions of salinity, temperature, turbidity and other environmental factors vary considerably in the neritic region as contrasted with the more stable conditions in the oceanic region, it may be supposed that phytoplankton production in the coastal belt may be adversely affected, but in actual fact the waters of the neritic region are believed to be fifty times more productive than the open oceanic waters (Lohmann, 1908) as substantiated by the abundant benthic and pelagic fauna in the former. The production of phyto-plankton is in general conditioned by light and latitude, and by available nutrients in solution. The source of these nutrients in solution in neritic or oceanic waters is the decomposing plants and animals brought down from land or present in

the sea. It has been shown that the periphytic bacterial population of pelagic waters has a tendency to follow closely the distribution of plankton ensuring thereby the thorough decomposition of dead planktonic organisms even before they have had time to sink to great depths and the regeneration of mineralized plant nutrients in the upper layers of water both in and below the euphotic zone. The upper layers of water have however a relatively poor concentration of nutrients as compared to the bottom layers, more particularly in the interface between mud and water, unless augmented with nutrients from the bottom by processes of vertical diffusion, convection overturn and upwelling.

*Biological characteristics of the oceanic regions of the pelagic division.*

The oceanic pelagic life is made up of animals independent of the bottom throughout their development (Radiolarians, Foraminifera, Hydromedusae, Siphonophores, Ctenophores, Chaetognaths, copepods and hyperines among crustacea, heteropods, pteropods, appendicularians, salps, pyrosomas, some sharks, a great number of bony fishes with air-bladder and some without, and the whales). The neritic pelagic includes, in addition to the above, animals which are dependent on the bottom during part of their existence (medusae with alternating generations, larvae of benthic animals, floating eggs of many fishes, water fleas, *Podon* & *Evadne* whose eggs sink to the bottom, and the ostracod *Philomedes* and numerous other free-living crustacea). Many cephalopods, most sharks and rays, many bony fishes of the neritic pelagic are included which rest at the bottom at night. The sea turtles, seals and walrus which belong to the pelagic region feed on benthic forms. The time and season of dependence on the bottom vary with different animals so that periodic changes in the composition of the neritic pelagic are much more pronounced than in the oceanic. The outer seaward boundary of the neritic pelagic is generally the 200 metre contour of the benthic region, and includes the banks as well as coastal waters. This boundary is the obvious result of dependence on the bottom. Inhabitants of the neritic and oceanic pelagic are usually mixed at the boundary, and currents carry neritic forms out and oceanic ones in, generally to their destruction, although the eels are a notable exception.

As the maximum production of phytoplankton is restricted to the lighted zone, animals of the pelagic region, whether adult or larvae, which permanently or temporarily live in it to feed on phyto- and zoo-plankton, will be restricted to the lighted zone. All true pelagic animals are independent of the bottom in that they have the ability to main-

tain themselves in open water without sinking. Some animals like the ctenophores never sink to the bottom, while many elements in the pelagic fauna are larvae of animals which spend their adult life in the benthic region. Where the pelagic or benthic period is very short the animals must be reckoned as benthic or pelagic respectively as the case may be. Mackerel which unquestionably belong to the pelagic region are known to spend part of the year resting on the bottom.

Economy in the use of hard skeletal matter such as lime, and silica, the absorption of large amounts of water in the jelly-like tissues, storage of lighter materials such as water of less salinity, fat, or even air in the tissues, the accumulation of fat, oil or air in the bodies or eggs are devices to help obviate the natural tendency of pelagic animals to sink. The bony fishes and the air-breathing sea vertebrates such as turtles, snakes, whales, sirenians, and seals of the pelagic region have solved their respective buoyancy problems in the pelagic region by the development of an air-bladder and by retention of their lungs. The retardation of sinking by changes in form is a widespread phenomenon among pelagic invertebrates. Flattened leaf-like form, suspensory bristles, long tentacles and appendages are among the means of suspension. Resistance to water produced by active muscular swimming is, however, the most widespread means of preventing sinking. In the fastest swimmers such as the blue shark and the mackerel every device calculated to reduce the resistance of the moving body to water is employed. The viscosity factor in water, which depends chiefly on temperature but less markedly on salinity is also of importance in reducing the rate of sinking. The pelagic animals of the Polar regions and of the oceanic depths with more or less identical viscosity conditions are, therefore, better able to suspend themselves in water than those of the tropical regions. The variation of viscosity with temperature may bear upon the fact that many pelagic organisms are smaller in warm seas than in cold, but notable exceptions to this have been recorded amongst diatoms (Wimpeny, 1936-37).

*Characteristics of plankton and nekton.* Free swimming forms of the pelagic which are independent of oceanic currents are grouped as nekton to distinguish them from the passively floating or suspended plankton, but no sharp distinction can be maintained between these two groups of animals. Such independence is reached only by certain fishes (tunny, bonito, etc.), cephalopods, reptiles and the homoiothermal marine mammals. Both plankton and nekton include predaceous and herbivorous forms and

cannot be distinguished on the criterion provided by food habits.

*Methods of procurement of food by pelagic animals.*

Special means of securing food are required by pelagic animals since their food differs from that of benthic animals. The predatory pelagic animals of this region, however, employ the usual methods of chase and capture. The basic food supply is provided by the phyto-plankton for a variety of organisms such as the pelagic protozoa, copepods and even larger animals like whales etc. The large plankton animals, from small metazoa to the size of pteropods, form the food of larger pelagic animals. A special apparatus for plankton collection has been developed convergently in the plankton feeders—which are divided into (1) those which feed by sticky tentacles, (2) those which produce a current of water which carries food, and (3) those which hunt actively. A divergent group of animals strains out living animals from a stream of water produced by themselves (Cladocera and copepods, salps and pyrosomas, the remarkable apparatus of appendicularians, the sieve-like strainers of the plankton-eating fishes such as herring or the giant sharks, and the baleen of the toothless whales).

*The permanent pelagic biota.*

Exclusively pelagic animals are the radiolarians, medusae, siphonophores, ctenophores, Chaetognatha, pelagic crustacea and Mollusca (Heteropoda and Pteropoda, *Ianthina* and *Phylliroe*), salps and appendicularians. Amongst these the pelagic copepod crustaceans predominate, comprising 90% of the whole fauna with schizopod, decapod and other forms in addition. Next come the pteropods, siphonophores and Chaetognatha while cephalopods and fishes are an important element. The microp plankton (constituting what is known as nanoplankton) and macroplankton also form part of this biota.

Wind and currents play a large part in the wide distribution of pelagic animals which remain in free suspension in water. Those endowed with feeble powers of swimming are no exception to this mode of distribution.

Among longer-lived animals aggregations appear which may be due to instinctive gregariousness as in schools of herring, mackerel, cod, etc. wandering to feeding or spawning grounds.

Composition of plankton varies with time as well as locality. It is usually composed of a great number of different animals but at a given place and

special time a single species may flourish to such an degree that it predominates to the extent of being termed a monotonous plankton. This is especially a phenomenon of the shallow seas more particularly of the colder waters lying over them.

There is difference in the composition of the surface plankton between day and night. At night numerous deep sea forms come to the surface even from great depths to return before day break. These are followed by predatory forms which live on them. The schools of herring come to the surface at night, remaining at considerable depths during the day. This suggests possible success in tropical latitudes of surface fishing by night and of deep-sea seining by day.

Deep bays, fiords, lagoons of coral reefs operate like traps for plankton and destroy them. Oceanic and neritic plankton suffer in storms and are driven ashore in great masses.

The difference in density of marine populations in the oceanic and neritic regions is much greater than between those of the polar and tropical regions. This may be due to the greater food supply in shallow water brought about by the greater development of phytoplankton as a result of the accumulation of organic and inorganic deposits from land. The pelagic population is more or less self-sustaining, the food chain of which, from the smallest single-celled alga to the largest fish and toothed whales, is extensive and conditions the distribution of the larger forms of animal life. The mackerel fishery at the mouth of the English Channel depends on the amount of animal plankton, especially copepods; the appearance of the herring on the north coast of Iceland depends on the summer development of the copepod *Calanus*, and the complicated migration of the herring (except spawning migrations) and the movement of schools of whales seem to be dominated by their food supply. In open and warm seas the zooplankton lies at a deeper level on which large crustaceans and cephalopods feed which in turn form the food of the larger pelagic animals such as sperm whales.

*Effect of currents on the distribution of pelagic animals.* The pelagic habitat or biotope is influenced considerably by oceanic currents and eddies more particularly in the distribution of its inhabitants. Both passive and free swimming forms are affected by them. The study of surface currents has shown that they may form an open or closed circuit. A closed current returns its animals

through a wide range of temperature and environment as in the case of *Calanus finmarchicus* of the Norwegian Sea affected by the Gulf Stream. The closed circuits of the North and South Atlantic take about one to two years to return the plankton to its place of origin. The period is long enough to include several generations of short-lived plankton in addition to those larger animals with longer periods of development.

The non-circulating warm currents like the gulf stream or the Japan current and the cold currents like the Labrador current or Humboldt current or the Ojashie current provide different conditions of life for the pelagic animals which come within their range and, where warm and cold currents meet, the contrast in temperature and volumes of water which oppose may cause great mortality among plankton as it happens on many banks (New England, Agulhas, Spitzbergen and East Coast of Japan). This massive and extensive destruction of pelagic life may cause a temporary scarcity of life in that region but this provides an opportunity for the bottom fauna to thrive on the remains of the pelagic fauna, and for the phytoplankton to derive its nourishment from nutrients liberated by the disintegrating plankton which sink to the bottom. The plankton carried along by currents changes its composition as it goes along as a result of admixture from adjoining sources, but some of these have their characteristic plankton (index forms) by which the currents could be demarcated in the open ocean (cf. *Calanus hyperboreus* of the polar current north of Iceland and *C. finmarchicus* of the Norwegian Sea). Large numbers of animals are often found to accumulate at the borders of currents (*Salpa flagellifera* on the border of Benguela current and pteropods on the borders of great currents).

*Macroscopic floating algae constitute a pelagic benthos or pseudobenthos in surface waters.*

Algae provided with floating bladders (*Sargassum* of the North Atlantic and the Indo-Pacific, *Macrocystis* of the South Pacific) may be carried into a quiet whirl pool forming a special biotope of the pelagic (eddy of the Atlantic Sargasso Sea). The algae constitute the home of a number of littoral animals from the Caribbean Sea even when they reach the eddy area on the high seas. The changes from the littoral to the half pelagic life in the Sargasso eddy being so radical for many of the animals originally attached to the weeds, the fauna in the Sargasso Sea is poor in species but rich in individuals. The animals living on the weeds constitute a pseudobenthos. A number of unexplained faunal parallels exists between the fauna of the Sar-

gasso Sea and that of the Mediterranean Sea in the composition of the nannoplankton, in the forms of certain Radiolarians, Annelids, and Copepods. The Sargasso Sea is characterised by poverty of plankton, transparency of water, high temperature of water at depths between 200 to 400 meters in comparison to temperatures at corresponding depths in adjacent waters due probably to the greater density of surface water which is carried down to oceanic depths compensating in parts for the upwelling currents on leeward coasts.

*The euphotic and dysphotic strata of the pelagic region.* The pelagic environment may also be considered in two different major strata:—

(1) The richly lighted euphotic stratum varying in depth, according to different authorities, from 0 to 100 metres, and (2) the weakly lighted dysphotic stratum varying in depth from 30 to 500 metres. The majority of shoaling pelagic fish belongs to the euphotic stratum while some species wander from the one to the other keeping track of the vertically moving plankton. The animal communities of the sea are extensive life zones comparable to the climatic zones of the continents, but in area, homogeneity of environmental factors, and the associated biota they surpass the latter. These communities may be subdivided into two main groups—of warm and cold waters corresponding roughly to the tropical and sub-tropical areas and the cold polar and temperate areas. The indistinct and ill-marked boundaries between these are determined by isotherms of surface water rather than by latitudes. But there has been some difference of opinion between authorities (Ortmann & Meisenheimer) as to the limits of these boundaries. According to the latter the tropical animal communities of the Atlantic and Indian Oceans are united around S. Africa but according to the former entirely separated by the South African continent.

*Division of the oceans into temperature belts.* The warm and cold regions of the sea can be sub-divided based upon the reactions of marine animals which seem to recognise an equatorial belt of water with a temperature above 25° C. as distinct from the relatively cooler waters lying on either side of this belt with a temperature range of 20° to 25° C. The colder waters around the poles with temperatures below 10° C. form a distinct belt from the less cold waters with a temperature range of 10° to 15° C. The North Atlantic region which has been better studied than others can be divided still further based on the distinctive animal communities designated as Arctic and Boreal. In the open

ocean itself temperature barriers with indistinct and varying seasonal boundaries exist in the regions affected by circulating or terminating streams of cold or warm water, and the pelagic animal communities associated with these seem to keep pace with these changes in boundaries.

*Seasonal periodicity in the pelagic biota and their composition in tropical & cold waters.* Seasonal periodicity which is so characteristic of the circum-polar waters seems to be lacking in the warm waters of the equatorial belt, but this has its advantages as well as disadvantages. The more constant warmth seems to keep the extensive propagation of a stenothermal animal community whose metabolism and growth are so accelerated as to quicken the process of succession in animal generations favouring mutations which give rise to a large number of genera and species. In colder waters, this variety which adds to the numbers of a generation is compensated for by a larger number of individuals of the few species that occur. Pelagic fisheries in the warmer waters therefore provide a larger variety of fishes which is no disadvantage from the commercial point of view, but present difficulties in the scientific interpretation of fisheries. The depth to which light penetrates in the tropics would presumably extend the vertical range of pelagic fisheries, suggesting the adoption of methods of catching fish different from those in vogue in colder waters, where the concentration of pelagic fish in surface waters is understandable. The following members of the pelagic communities in tropical seas indicate the great variety of forms which provide food for pelagic fish: Foraminifera (20 species as against 1 or 2 in colder seas), Siphonophora, geryonid Hydromedusae, charybdaeid Scyphomedusae, alcyonid Polychaeta, Copepoda (*Copilia*, *Euphausia*, *Sergestes* and *Lucifer* among Crustacea, the Heteropoda, Pteropoda and the pelagic *Ianthina* and *Phylliroe* among the molluscs, *Pyrosoma* *Salpa*, and *Appendicularia* among tunicates, the Exocoetidae among fish, besides a whole host of free swimming larvae of corals, echinoderms, molluscs, worms, crustaceans and fish.

The low temperatures of the colder waters seem to result in the reduction of fertility of animals although compensated for by the size of the eggs and in the suppression of the free-swimming larval forms which while retarding wider dispersal result in enormous over-crowding by the more successful members of the benthic communities. The Hydrozoa among Coelenterata, the Holothuroidea among Echinodermata and siliceous sponges among Porifera are among the groups of animals which seem to find favourable conditions of existence in the colder waters. The

higher crustacea apart from genera like *Acanthephyra* are usually absent, while copepods—many of them distinct from those in tropical waters—occur in enormous numbers of individuals favouring the growth of fish which mainly feed on them. The schizopods, hyperiids and pteropods are also characteristic of colder waters. The richness of diatoms in these waters explains the abundance of organisms like Radiolaria and Ciliata which use lots of siliceous skeletal material. A definite periodicity exists in the plankton of colder waters which are richer in plankton in the summer. Whether this production of plankton in colder waters over an entire year is greater than that of the tropical waters over a similar period is still unascertained, and the prevailing view, that the tropical seas are quantitatively poorer in plankton than the colder, based on somewhat meagre observations and vague generalisations, which holds the field, merits re-examination. In any case comparisons of the populations of pelagic regions of the tropical and colder seas appear to have been made on the basis of information obtained for the Atlantic Ocean only where difference in density of population may not be due to temperature alone. Moreover, the Indo-Pacific Seas, which are in more open communication with the Antarctic and Arctic Oceans and have a much longer coastline skirting them, broken by numerous bays, gulfs, rivers and estuaries, may possibly have as rich a pelagic fauna as that of the equatorial Atlantic.

The richness of life in the pelagic region of the colder seas attracts a large number of birds, mammal predators such as penguins, whales, seals, etc.—a phenomenon little in evidence in the open warmer seas where abundant plankton such as is known in the Indian Ocean occurs, but here the corresponding surface feeders are the shark, the porpoises, etc.

Bipolarity or the similarity of the pelagic organisms of the Arctic and Antarctic waters has been observed in many groups of organisms but none of the explanations offered for this phenomenon can be said to have received universal approval. A compromise between the opposing views suggested is to treat the similarity between the polar faunas as primary and the differences as secondary.

*Conditions of pelagic life in virtually enclosed seas.* The smaller areas of the ocean such as seas, bays and gulfs appear for all practical purposes as separate areas with their distinctive temperature, salinity and biological conditions. The discharge of large rivers which controls salinity, latitude which determines the evaporation, and topography which may determine the

extent of exchange of waters between such isolated parts and the ocean are factors influencing the fauna. While in the polar sea salinity is decreased in summer by the melting of ice, in the tropical seas the increase in salinity in summer is due to increased evaporation. In the deep basins like those of the Baltic, the Mediterranean (Levantine and Ionian Seas), and the Red Sea, animal life becomes sparse owing to poverty of dissolved oxygen and richness of carbon dioxide. In certain seas like the Black Sea the fauna is affected still further by large amounts of hydrogen sulphide in solution as a result of inadequate circulation of water.

*Chemistry of sea-water in relation to plankton.*

Considerable advances have been made in recent years in our knowledge of the chemistry of sea-water in relation to the plankton and especially the factors which determine the productivity of the sea. In the earlier section reference was made to the effect of light, temperature and turbulence on the growth of phytoplankton. The second aspect which requires examination is the influence which the concentrations of nutrient salts in seawater have on the rate of growth and multiplication of the plant life that constitutes the phyto-plankton. When diatoms grow they utilize phosphates and the available nitrogen compounds—nitrates, nitrite, ammonium, uric acid, urea and probably amino acids—until these substances reach a concentration so low that plant life cannot grow and multiply in the normal manner. When only low concentrations of these nutrient salts are available the plankton production would be low. In the colder seas the burst of diatom activity in spring followed by the zoo-plankton peak results in the depletion of nutrients from seawater, but the inactivity during winter months results in accumulation and regeneration of nutrients which in their turn are used up during the succeeding spring. A cycle of this type does not exist in tropical waters owing to the absence of winter; consequently, the large annual variations in phosphates and nitrates observed in the colder seas are not encountered in the tropics. This does not mean that seasonal variations are totally absent. Changes in the direction of currents, winds and the upwelling of waters which they produce often result in seasonal variations which in their turn affect the plankton and fisheries.

In addition to nutrient salts small amounts of iron for plant pigments, silicates for the shells of diatoms, carbon dioxide for photosynthetic activity and probably other trace elements are essential for the growth of phyto-plankton.

The foregoing general considerations based on available data would seem to explain partly the pre-

sent distribution of pelagic fisheries of the world. The severity of northern climates, which does not help production of adequate agricultural crops, must have also contributed to the greater concentration on the part of the peoples of these climates on fisheries as an industry, and traditions of feeding and clothing changed only very slowly under compelling circumstances. The abundance of food in regions with highly developed agricultural, horticultural and livestock industries in certain tropical and sub-tropical regions seems

to have led to the relative neglect of coastal waters as sources of food. Almost the entire east coast of S. America (Brazil, Argentina, etc.), many parts of Africa, Asia and Australia provide examples of un-exploited or inadequately exploited waters for fisheries where food from agricultural and other sources has been available for a great majority of the populations. In these areas fisheries provide accessory food, not an important item of food as in the countries of the temperate and boreal regions.

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