

**MONOGRAPH ON BOTHID LARVAE
(PLEURONECTIFORMES – PISCES)**

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1. P R E F A C E

It was perhaps the progressively dwindling resources of the land and the search for new frontiers that forced man to turn to the ocean for food and wealth. The many voyages, exploratory surveys and expeditions undertaken with a view to satisfying the enquiring mind in the early days have now been transformed into valuable clues for potential living and non-living resources. His knowledge on the systematics of plants and animals over the past few centuries has helped him to identify and exploit the commercially important groups successfully. The binomial nomenclature adopted by taxonomists all over the world since the time of Linnaeus has helped in a big way to prepare distribution charts of target species for their effective exploitation. For understanding and estimating the production potential of an ecosystem properly, it is essential that the status of target species together with their relationship with other biotic communities in the system be known intimately up to the species level.

In recent times, however, a lack of appreciation for taxonomic work is discernible in scientific circles. This has persuaded scientists to concentrate on areas other than systematics. However, new concepts of the conservation and management of biodiversity and related problems have clearly indicated the great relevance and importance of taxonomical work. The experience gained in the classification and cataloguing of marine organisms for over a century has helped the taxonomists to understand the inter and intra species relationships in the food chain and other aspects of the ecology of different communities.

The data collected during the International Indian Ocean Expedition have served to highlight the production potential of the Indian Ocean in terms of zooplankton biomass. But the production potential of the target species can be ascertained only if the systematics and distribution pattern of the plankton communities are studied in detail. In the case of fish, the prediction of a fishery depends on the survival and abundance of larval forms and the environmental conditions in which they live. Most of the fishes have planktotrophic larvae. Their presence in the plankton indicates the occurrence of the adult species which constitute the fishery. They also function as indicator organisms. Where the larval life is protracted as in the case of flat fishes and eels, the larvae are transported to far off places by the prevailing currents helping the distribution of

species over a wider area which is very much restricted in the case of adults living on the ocean floor. The larval forms, apart from deriving food from the plankton, offer themselves as food for other planktonic and nektonic organisms.

The identification of larval forms of fishes, more especially certain groups to specific levels, has been difficult and has created some confusion among larval taxonomists, mainly on account of the absence of connecting links between different stages in the larval history and the adults, as well as paucity of their number in the plankton as reflected in the collections. According to Dr. Ahlstrom, an eminent ichthyoplankton taxonomist, "utter confusion and chaos prevailed in the literature pertaining to larvae of flat fishes, particularly bothid species" (personal discussion, 1977).

It was in this context, that the decision to study the taxonomy of the larval forms of bothid flat fishes available in the plankton collected during International Indian Ocean Expedition 1960-65 from the Indian Ocean was taken up. The scarcity of larval material in the IIOE collections, the faulty preservation which led to the mutilation and dismembering of parts of the specimens as well as non-availability of connecting links between various stages have been serious handicaps in the preparation of a descriptive document on the larvae of flat fishes from the Indian Ocean. However, study of the larval forms from the Indian Ocean has been made possible due to the availability of material from the Naga Expedition (1959-61) from the Gulf of Thailand and South China Sea, placed at the disposal of the present author through the good offices of Dr.E.H. Ahlstrom, from the collections maintained at the Scripps Institute of Oceanography, U.S.A.

Larvae of bothid flat fishes belonging to 9 genera and 24 species have been identified and described, of which 16 species are reported for the first time from the Indian Ocean. Attempts have also been made to correlate the environmental parameters and their influence on the distribution pattern of different species.

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2. INTRODUCTION

2.1 Scope and purpose of the study

Effective utilization of marine resources depends upon the accurate knowledge of their occurrence, relative abundance and distribution which in turn depends on the environmental characteristics prevailing there. The new dimensions added to oceanographic research such as the remote sensing facilities, seasats, manned submersibles and others have substantially improved the quality of ocean studies. The pioneering works of a few individuals or institutions in the latter half of the nineteenth century and early half of the twentieth are being expanded and developed by the collaborative attempts on a global basis. The International Indian Ocean Expedition (IIOE) 1960-65 is an evidence of one such collaborative multinational attempt. Many earlier expeditions and exploratory surveys in the marine environment had enabled fishery scientists to collect, identify and catalogue a large number of organisms including fishes. Nevertheless, even the systematic and careful investigation on fish and fisheries for over a century had succeeded in identifying and classifying only about 50 per cent of the fishes and their larvae in the Pacific and the Atlantic. Yet, this knowledge has helped them to make highly significant contributions towards understanding the factors influencing wide variations in the brood strength of commercially important food fishes in the American and European waters. Similar studies have not yet materialised in the Indian Ocean. The International Indian Ocean Expedition 1960-65 was more or less a crash programme to collect as much basic data as possible so that important and fundamental oceanographic research in these waters could be taken up and conducted at a much faster pace than would have been possible otherwise.

In recent years there has been an unfortunate tendency to neglect studies relating to taxonomy under the false notions that such studies are not relevant or fashionable for providing material for immediate benefits. But this apprehension is absolutely wrong and baseless because without an accurate knowledge of the exact species composition and their incidence it will not be possible to assess the potential resources of an area, map them and manage them for the benefit of mankind. Ecological studies will be inaccurate and meaningless if the species

contained in a community of an ecosystem is not identified correctly. The importance of taxonomy in ocean search was demonstrated significantly in the recent discovery of vent community assemblages.

The prediction of a fishery depends among others, on the knowledge about the survival of larval forms. Hence identification of ichthyoplankton naturally becomes a strenuous, but unavoidable exercise. Our basic information on the fish eggs and larvae started with G.O Sars in 1865. Initially the progress was tardy, but it soon gained momentum and ended in the identification of eggs and larvae of most of the European food fishes. The absence of similarity between the larvae and adults has made ichthyoplankton identification complex and confusing. The rarity of specimens in the plankton added to the problem considerably. This is particularly so in the case of tropical fishes. The zooplankton analysis of the IIOE samples has made it clear that unless special surveys are conducted to collect fish eggs and larvae, a large percentage of the fish larval population will continue to remain unknown.

Flat fishes, though they form only a relatively small percentage of the total fish population, still occupy a significant position in the list of highly preferred food fishes. According to Suda (1973), the potential benthic fishery resource of the entire Indian Ocean is as high as 7×10^6 tonnes and only a negligible fraction is currently being exploited. The flat fishes like most other benthic animals have planktotrophic eggs and larvae so well synchronised over the evolution with the most favourable physico-chemical and biological factors of the environment to ensure maximum dispersal and survival within their distributional range. Yet the egg and larval mortality is so high that many adult population with an annual average biomass of millions of tonnes are being maintained by a survival rate as low as 0.01 per cent. This suggests that small changes in the survival rate often reflects wide fluctuations in the adult stock size (Murphy, 1961). Variations in the biotic and abiotic factors of the environment at micro and macro levels are largely responsible for bringing about such high rates of mortality. The success of a fishery in any area is, therefore, intimately linked with the hydrobiological properties of the water bodies, density and quality of available larval food, especially during the spawning season (Lasker, 1981).

The extensive plankton collection of the IIOE has served to highlight the production potential of the Indian Ocean in terms of zooplankton biomass and regions of high productivity. These samples as far as they could be analysed also yielded substantial information on the systematics, ecology and distribution of certain major taxa constituting the zooplankton and have been published by various authors. Nevertheless, we are still at the fringe of the problem and the volume of work yet to be done necessarily demands careful selection of groups to be studied on a priority basis.

For reasons given above, and because of the economic importance of the 200 nautical mile limit gained by the nation with the declaration of EEZ, it was decided to select the fish larvae of the Indian Ocean for detailed study. Since this is a vast group, an attempt has been made in the present study to concentrate on the larvae of flat fishes of the Indian Ocean particularly on account of the fact that their taxonomy, morphology and distribution still remain to be worked out realistically.

The identification of larval forms of fishes, more especially certain groups to specific levels has been difficult and has created more confusion among larval taxonomists, mainly on account of the absence of connecting links between different stages in the larval history as well as paucity of their number in the planktonic populations as reflected in the collections. According to Ahlstrom, an eminent ichthyoplankton taxonomist, "utter confusion and chaos prevailed in the literature pertaining to larvae of flat fishes, particularly bothid species" (Personal discussion, 1977). It was, therefore, decided to take up the taxonomy of bothid larvae available in the IIOE samples. The scarcity of larval material in the IIOE collections, the faulty preservation which led to mutilation and dismembering of parts of specimens as well as non-availability of connecting links between various stages of growth have been a serious handicap for the preparation of a descriptive document on the flat fish larvae for the Indian Ocean.

The success of the present study of the larval forms of the Indian Ocean has been due to the availability of the material from the Naga Expedition also from the Gulf of Thailand and the South China Sea collected during 1959-61, placed at the disposal of the present author through the good offices of Dr.

E.H.Ahlstrom from the collections maintained at the Scripps Institute of Oceanography, U.S.A.

Ahlstrom has stated (1959, 1971) that the eggs and larvae are distributed mainly in the upper layers of 100-150 metres and could be collected by filtering the water column using a plankton net. He has also reported that there was no evidence of larval movement through the thermocline when they performed diel migrations. The plankton collected during IIOE should therefore contain most of the fish eggs and larvae of that region because the stratum sampled reaches up to 200 metres in deep waters and up to a few meters above the sea bed in the shallow region.

The availability of the extensive samples collected during the IIOE has also enabled a fairly detailed study of the larval distribution and abundance correlating it with certain major hydrographical parameters to assess the suitability of the environmental conditions of the different water bodies in the Indian Ocean and adjacent seas. As already mentioned, the larval phase is important for the benthic communities for their dispersal over wide areas. From the fishery point of view, a knowledge of the areas of larval abundance is important to locate new fishing grounds. Knowledge of larval taxonomy will also eventually pave way to take up studies on fluctuations in larval survival and predict the success of the fishery.

2.2 LARVAE OF FLAT FISHES

Development of the current concepts

Fishes have gained more acceptance among human beings than any other animal community on account of their omnipresence as well as their importance as an item of food in many parts of the world, from very early days of human history. The high density of human population prevailing in the coastal areas all over the world, could in a way, be related to the quantity of fish landings. Besides their importance as nutritious item of food, some human communities even worship them as devine. Thus, the Hindus, for example, regard fish as the first, of the ten incarnations of God.

In India the information about fishes dates back to the third millenium B.C. (Hora, 1956). Nath (1966) states that fish remains with out marks have been obtained from excavations at Mohanjodaro and Harappa of the Indus Valley civilization indicating their use as food. According to Hora (1951) King Somesvara was the first to record the common sport fish of India, grouping them into marine and freshwater forms. But a systematic study emerged only centuries later. It is now claimed that Aristotle (384-327 B.C.) is the father of ichthyology.

It is reported that the whole of aquatic environment holds about 20,000 species of teleosteon fishes out of which the flat fishes constitute only about 520 species (Nelson, 1976). According to Cohen (1973) the Indian Ocean contains about 3000 to 4000 species mostly living in inshore and coastal waters. The flat fishes contribute only a very small percentage of the fish population. They are a peculiar assemblage of fishes, the true phylogeny of which still remains obscure. They are generally known as flounders when their lower jaws are prominent or as soles when the rounded snout projects beyond the small curved mouth. Depending on the position of the eyes, they are designated either as dextral or sinistral flounders or soles. They range in size from a few cm in length to about 2.5 m and weighing a few gram to about 200 kg. They are also peculiar in that during their life they occupy two ecological niches, the adult living buried in or on the bottom feeding on detritus or other members of the bottom community while the larval forms lead a planktonic life in the pelagic realm. The larval life may be

short or protracted and vary with species. The adults have asymmetrical bodies with eyes on one side and invariably without a swim bladder or if present contained in a calcareous encasement. The larvae are symmetrical and often possess a swim bladder.

The flat fishes are found in almost all seas, mostly confined to the continental shelf area, some occur in the deep waters, estuaries, rivers and even in springs, several miles inland. Along the Indian coast, about 89 species assignable to 26 genera and five families have been reported.

2.3 Phylogeny of the group

Different authors have tried to find a suitable taxonomic position for this enigmatic group among fishes. Linnaeus in 'Systema Naturae' has assigned only a generic status among Pisces and included all the known flat fishes under *Pleuronectes* (Norman, 1934). But later revelations indicated that this arrangement was quite unreasonable. Cuvier (1817) raised them to the rank of a family under the division of sub-brachial malacopterygians, which included also Gadoids, Gobiescoids, Cyclopterids, Echineids and Ophiocephalids besides flat fishes. Agassiz (1842) placed flat fishes near Chaetodontidae and Scorpididae. Muller (1846) created a new order Anacanthini to include Pleuronectoids, Gadoids as well as ophidioids. It was Cope (1871) who first recognised flat fishes as a distinct order to which he applied the term Heterosomata, a name invented by Dumeril, who regarded them as related to the cods. In 1880, Gunther divided the order Anacanthini into two main divisions – Anacanthini Pleuronectoidei and Anacanthini Gadoidei. Gill (1887) suggested that “the Heterosomatous fishes may have branched off from the original stock or progenitors of Taeniosomous fishes”. This idea was not elaborately followed. Jordan and Goss (1889) just like earlier ichthyologists considered flat fishes as belonging to a single family Pleuronectidae but subdivided into seven subfamilies Hippoglossinae, Pleuronectinae, Samarinae, Platessinae, Oncopterinae, Soleinae and Cynoglossinae. Jordan and Goss distinctly recognised soles from flounders but stated that “the characters which mark them as a group seem no more important than those which set off one subfamily of flounders from another”. In 1893 Gill regarded Heterosomata as a suborder of Teleocephali, equal in rank to the Anacanthini, close to which it was placed. Holt

(1894) hinted its affinity with such deep-bodied fishes as *Platax* or *Dascyllus* or even with *Zeus*. Jordan and his collaborators have recognised Heterosomata as a suborder under Acanthopteri, in which it was placed near the ribbon-fishes (Taeniosomi) and the cods (Anacanthini). Jordan and Evermann (1898) included flat fishes in a single suborder, Heterosomata and recognised two distinct families Pleuronectidae and Soleidae. Pleuronectidae were further divided into three, Hippoglossinae, Pleuronectinae and Psettinae and the Soleidae into two – Soleinae and Cynoglossinae and stated that “Its near relationship is probably with Gadidae although the developed pseudobranchiae and the thoracic ventral fins indicate an early differentiation from the “anacanthine fishes”. Kyle (1900b) divided Heterosomata into two families Pleuronectidae containing four subfamilies namely, Hippoglossinae, Pleuronectinae, Hippoglosso-rhombinae and Rhombinae and Soleidae containing three subfamilies namely, Soleinae, Achirinae and Cynoglossinae as well as Solei-pleuronectinae and Incertae sedis. Boulenger (1902) considered that flat fishes were nearly related to Zeidae to which he gave the name Zeorhombi with *Amphistium* a fossil fish from upper Eocene in a division of the Acanthopterygii. Jordan and Starks (1906) have reported 11 species of sinistral flounders belonging to five genera and one family from the seas around Japan. Franz (1910), Hubbs (1915), Tanaka (1915) Kamohara (1936) added many species and genera to the Japanese sinistral flounders. Regan (1910) regarded Psettodes as the most generalised member of the Heterosomata. He was the first to draw attention to the perch-like characters of *Psettodes* and suggested that rest of the flat fishes had arisen from a form similar to *Psettodes*. In 1913 he placed Heterosomata as a specialised off shoot from the order Percomorpha. He proposed an entirely new classification of the group based on the study of anatomy particularly the osteology of a number of genera. He recognised two suborders for Heterosomata, Psettodoidea and Pleuronectoidea. The only family under Psettodoidea was Psettodidae and the other was divided into two main divisions, Pleuronectiformes and Solaeiformes which corresponded to the Pleuronectidae and Soleidae of Jordan and Evermann. The division Pleuronectiformes contained two families Bothidae and Pleuronectidae, each again contained 3 subfamilies Paralichthinae, Platophrinae and Bothinae under Bothidae and Pleuronectinae, Samarinae and Rhombosoleinae under Pleuronectidae. The division Solaeiformes contained two families Soleidae and

Cynoglossidae. Jordan (1923) following Regan raised the subfamilies to the rank of families. Even though Jordan (1923) placed Heterosomata near Anacanthini and Allotriognathi he stated that “the flounders and soles, having no spines and the ventral fins thoracic with an increased number of rays, should not be placed far from the percomorphous series”. Kyle (1921) was of opinion that Pleuronectidae cannot be derived from Psettodoidea and that Pleuronectiformes are polyphyletic in origin. This did not get recognition at that time. Regan (1929) omitted the suborders and divisions and recognised five families Psettodidae, Bothidae, Pleuronectidae, Soleidae and Cynoglossidae. The subfamilies of Bothidae and Pleuronectidae were retained but the South African genus *Paralichthodes* was removed from the subfamily Samarinae and placed in a separate subfamily Paralichthodinae. Norman (1934) did not disturb Regan’s latest arrangements which according to him was a perfectly natural one except for creating another subfamily to place dextral Pleuronectidae under Poecilopsettinae. According to Norman (1934) the sub-families of Jordan and Goss (1889) corresponded to the respective genera excepting the subfamily Samarinae and Oncopterinae, the members of which were unknown in their time. Thus, the order Heterosomata was regarded as containing 5 families namely, Psettodidae, Bothidae, Pleuronectidae, Soleidae and Cynoglossidae. Even though most of these authors held the view that Heterosomata has arisen from a common ancestor, Chabanaud (1934, 1936) agrees with Kyle (1921) in considering that Pleuronectidae cannot be derived from Psettodoidei and that the Pleuronectiformes are of polyphyletic origin. This view was also held by Berg (1940) and recognised Pleuronectiformes as an order under subclass Actinopterygii under class Teleostomi. He stated that there is no reason to apply the ‘rule’ of priority to taxonomical units higher than genera. He has followed Goodrich (1906, 1930) and has chosen the names coined after the name of the most distributed and best known family. Hence instead of Heterosomata, a name unintelligible both to the specialists and uninitiated, the name “Pleuronectiformes” was used. Berg divided the order into two suborders Psettodoidei and Pleuronectoidei. The suborder Pleuronectoidei is divided into two super families Pleuronectoidea including the family Bothidae and family Pleuronectidae and superfamily Soleoidea including family Soleidae and Family Cynoglossidae. The family Bothidae corresponds to Bothidae + Paralichthidae of Jordan and Scopthalmidae of Chabanaud. The family has three subfamilies

-Paralichthyini (Miocene to Recent); Bothini (Lower Eocene to Recent) and Rhombini (Scophthalmi). Family Pleuronectidae corresponds to Hippoglossidae + Pleuronectidae + Samaridae + Rhombosoleidae of Jordan. Otoliths occur in Paleocene of England. It is divided into five subfamilies, Pleuronectini, Poecilopsettini, Paralichthodini (Paralichthodes Gilchrist), Samarini and Rhombosoleini. The family Soleidae corresponds to Achiridae + Soleidae + Synapturidae of Jordan (Eocene – Upper Lutetian – to Recent).

Hubbs (1945) revised the classification of sinistral flounders, and taking into consideration the works of Norman and Hubbs, Matsubara (1955) again revised the classification of sinistral flounders from the Japanese waters into 45 species belonging to 18 genera, 8 subfamilies, two families and two suborders. Amaoka (1969) reported that even this is not up to date because the conclusions were arrived at by studies based on external characters. According to Amaoka, the phylogenetic relationship of the Heterosomata has not been properly understood on account of the poor osteological studies. Amaoka has made a comparative study of the cranium, orbital bones, gill rakers, branchial apparatus, urohyal, vertebral and other accessory bones, caudal rays and caudal skeleton and has arrived at the conclusion that flatfishes are polyphyletic in origin, a view proposed by Kyle (1913) and supported by Chabanaud (1934, 1936). He has drawn up a phylogenetic scheme for the sinistral flounders and related flat fishes based on the study of the morphology of Japanese flounders. He recognised four large genetic stems Psettodes stem, Citharoides stem, Paralichthys stem and Bothus stem. These four stems are so distinct that they could be considered as four families namely, Psettodidae, Citharidae, Paralichthyidae and Bothidae. He further stated that Heterosomata is not a natural group derived from a single stock as a generalised percoid as Norman and Hubbs have suggested, but sprung off from different stocks among the ancestral percoids much earlier than that extending to percoid.

Hensley and Ahlstrom (1984) have reviewed the existing literature on the evolution of pleuronectiform fishes. They have considered the Regan (1910, 1929), Norman (1934). Norman's model and classification with the modifications of Hubbs (1945), Amaoka (1969), Futch (1977) and Hensley (1977) represent the most recent detailed, hypothesis for pleuronectiform evolution, referred to as

the “Regan-Norman model and classification”. In the light of new information, this working hypothesis has been re-examined using, adult, larval and egg characters. They have stated that the “Regan-Norman model involved in an eclectic approach i.e. a combination of phyletic and phenetic methods. Although some of the groups currently recognised appear to be based on synapomorphies, many are clearly based on symplesiomorphies and were recognized as such by the authors. This search for horizontal relationships among pleuronectiforms using eclectic methods, with one exception, has been the only approach used in this group. The exception is the recent work of Lauder and Liem (1983) in which a cladogram for flat fishes is presented. However, these authors present this as a tentative hypothesis and admit the interrelationships expressed are still problematic. Most of the characteristics they use are reductive, few characters were analyzed, and the authors were understandably unaware of recent character surveys, since much of this information remains unpublished”.

Hensley and Ahlstrom (1984) have assumed that the Order Pleuronectiformes as monophyletic and the sister group is the remaining percomorphs. The information available at present, according to them, to hypothesize the multiple origins for flat fishes. This demands inclusion of a great deal of convergence. They recommend in depth study of the group before offering a new hypothesis of inter-relationships.

Intergeneric relationships for the family Bothidae based on larval characters have been examined by Fukui (1997) using cladistic analysis in order to obtain cryptic information among adult systematics. He has recognized 16 morphological characters to establish his observations.

Asterorhombus and *Engyprosopon* except sp. 2 of the subfamily Bothinae are sister groups for the subfamily Taeniopsettiniae (Fukui 1997). *Arnoglossus* is not monophyletic, because Atlantic-Mediterranean *Arnoglossus* has not a synapomorphy, string-like elongated dorsal fin ray (char. 8) which Indo-Pacific *Arnoglossus* including *A. tenuis* shares, and monophyletic group A2 for Indo-Pacific *Arnoglossus* excludes Atlantic-Mediterranean *Arnoglossus*. *A. tenuis* and other species also are not monophyletic in Indo-Pacific *Arnoglossus*,

because *A. tenuis* has not two synapomorphies, rostrum above snout and larger metamorphosis size (char. 5 and 6) which other Indo-Pacific species share. Amaoka (1969 : 125) mentioned that *Arnoglossus tenuis* may represent a distinct genus owing to their adults having close-set and scarcely enlarged anterior teeth, gill rakers without serrations, and lower meristic counts (e.g. scales in lateral line 48-57) etc. Hensely (1986) also mentioned that *Arnoglossus* is not probably monophyletic on the basis of adult characters, although the reason was not given. Fukui (1997) feels that re-examination of adult systematics is necessary in *Arnoglossus*. Simultaneously, more effort should be used to examine the larvae of Indo-Pacific *Arnoglossus* species which are not known, because some species resemble *A. tenuis* in having the characters as shown above (e.g. *A. macrolophus* (as *A. tapeinosoma*) Norman, 1934 ; Amaoka, 1971b. Amaoka *et al.*, 1992 ; Arai and Amaoka, 1966). Since *Engyprosopon* is a presence or absence apomorphy, larval cleithral spines (char. 12), it seems that this genus is not monophyletic. Hensley and Ahlstrom (1984) mentioned that the subfamily Taeniopsettinae may not be monophyletic on the basis of adult characters. However, it is shown that three genera of *Taeniopsetta*, *Engyophrys*, and *Trichopsetta* for which larvae are known are monophyletic in the present analysis.

Amaoka (1969) presented a scheme of intergeneric relationships for Japanese bothids based on adults characters. Amaoka's analysis was eclectic, e.g., a combination of phenetic and cladistic methods and did not include *Engyophrys*, *Trichopsetta*, *Grammatobothus*, *Lophonectes* and *Monolene* for which larvae are known. Fukui 1997 compared the two monophyletic groups based on larvae with Amaoka's scheme. He observed that *Asterorhombus* is taeniopsettine genera and the sister group for Indo-Pacific *Arnoglossus* (except *A. tenuis*) is *Laeops* and *Chascanopsetta*. However, the sister group for *Arnoglossus* is *Psettina* and the sister group for *Arnoglossus* and *Psettina* is *Asterorhombus* in Amaoka's scheme and stated that Amaoka's scheme is incorrect owing to his analysis being eclectic.

The classification of flat fishes followed in the present report is the one adopted by Ahlstrom *et al.*, (1984). They have divided the Order Pleuronectiformes into three sub-orders, Psettidoidei, Pleuronectoidei and

Soleoidei. The sub-order Psettodoidei contains only one family Psettodidae and the members are distributed in the waters of the Indo-Pacific and West African regions. The suborder Pleuronectoidei includes five families. The family Citharidae containing two subfamilies. Subfamily Brachypleurinae found in the waters of the Indo-Pacific region and Subfamily Citharinae in the Indo-Pacific, Mediterranean and West African regions. The family Scopthalmidae occur in the North Atlantic, Mediterranean and Black Sea. The family Paralichthyidae are found in the western and eastern Atlantic, eastern Pacific and the Indo-Pacific regions. The family Bothidae includes subfamily Taeniopsettinae found in the western Atlantic, eastern Pacific and the Indo-Pacific waters and subfamily Bothinae in the Indian, Pacific and Atlantic Oceans, Mediterranean Sea and the Southern Ocean waters. The Family Pleuronectidae has five subfamilies. Pleuronectinae found in the Atlantic, Mediterranean, Pacific and Arctic waters; Poecilopsettinae of the Indo-Pacific and Atlantic regions ; Paralichthodinae of the Indian Ocean off South Africa ; Samarinae of the Indo-Pacific region and Rhombosoleinae of New Zealand, Southern Australia and South American waters. The suborder Soleoidei contains two families Soleidae and Cynoglossidae. The Family Soelidae has two subfamilies Soleinae of worldwide distribution tropical to temperate waters and Achirinae of American coasts (some are found in fresh water). The Cynoglossidae has two subfamilies Symphurinae in the waters of the tropical-subtropical American coasts, Mediterranean, west Africa and Indo-Pacific and Cynoglossinae in the Indo-Pacific, Mediterranean, West Africa and Japan regions. Some are found in fresh water.

Many scientists have described different species occurring in different water bodies and also assigned appropriate position. The larval taxonomy, however, is more complicated, confusing in most cases and fragmentary in several instances. In general, it could be stated that the studies on developmental aspects of teleosts by G.O. Sars in 1804 has initiated the larval systematics. Notwithstanding the considerable amount of information on eggs and larvae of teleostean fishes of temperate and tropical waters, those relating to flat fishes are not up to the desired level. Apart from the monographic work on *Pleuronectis platessa* by Cole and Johnstone (1902) the morphological details are also contained in the works of Goodrich (1906, 1930), Moser (1981), Dunn (1984). But they are very few and far from complete.

The distribution pattern of adults and some larvae of flat fishes is contained in the reports of Bonde (1927), Bowman (1935), Thompson (1936), Thompson and Cleve (1936), Rapson (1940), Raymont (1947), Seshappa and Bhimachar (1955), Bishai (1960, 1961 a, b), Musienko (1961), Pearcy (1962), Pradhan and Dhulked (1962), Riley (1964), Rass (1965), Shuntov (1965), Haertel and Osterberg (1967), Pillay (1967), Yesaki and Wolotira (1968), Edwards and Steele (1968), McIntyre and Eleftheriou (1968), Hognestad (1969), Powles and Kohler (1970), Irvin (1974), Hoss *et al.* (1974), Balakrishnan and Lalithambika Devi (1974), Lalithambika Devi (1969, 1977, 1986, 1989 a, b, 1991, 1993).

Data on spawning and fecundity among flat fishes are not only rare but also incomplete. Some information is however, contained in the publications of Buchanan-Wollaston (1924), Yamamoto (1939), Chidambaram (1945). McHugh and Walker (1948), Arora (1951), Shellbourne (1953, 1956, 1957, 1962, 1963 a, b, 1964, 1965), Bagenal (1955 a, b, 1956, 1957, 1958, 1960, 1963 a, b, 1966, 1967), Marr (1956), Kuthalingam (1957), Simpson (1959, 1971), Rustad (1961), Torchio (1962), Barr (1963), Railey and Thacker (1963), Pitt (1964), Ryland (1964, 1966), Kashkina (1965), Bowers (1966), Riley (1966), Groot De and Schuy (1967), Holliday and Jones (1967), Kutty (1967), Mirnov (1967), Ryland and Nichols (1967). Nash (1968), Pozdnykov (1967), Wada (1970), Houde and Ramsay (1971), Yasunaga (1971), Lahaye (1972).

A perusal of the literature concerning the larval descriptions of Bothidae would reveal that they are confusing than clear. Besides paucity of the materials, the number of publications is also rare. Unless some of the materials described are re-examined in the light of accrued knowledge on this group, it will be difficult to assess the parentage of these forms. Descriptions of larvae of bothids are also available in the papers of Cunningham (1891-92), Kyle (1897, 1913), Brauer (1906), Weber and Beaufort (1913), Regan (1916), Bowman (1923), Padoa (1931-56), Hubbs and Chu (1934), Uchida (1936), Brunn (1937 a, b), Kuronuma (1942), Gopinath (1946), Sparta (1948), John (1951), Jones and Menon (1951, 1953), Pantulu and Jones (1951), Nair (1952), Orton (1953, 1955), Deubler and Rathjen (1958), Jones and Pantulu (1958), Kalinina (1960),

Balakrishnan (1963), Mito (1963), Amaoka (1964, 1970, 1971a, b, 1972, 1973, 1974, 1976), Pertseva-Ostrumova (1965, 1971), Smith (1967), Houde, Futch and Detwyler (1970), Gutherz (1970), Russell and Neclademir (1971), Russell (1976), Yusa (1957, 1958), Ahlstrom and Moser (1976, 1981), Okiyama (1979), Sumida *et al* (1979), Moser (1981), Lalithambika Devi, (1981, 86, 89a, b, 91, 99), Dunn (1984), Ahlstrom *et al.*, (1984), Hensley and Ahlstrom (1984), Kendall *et al.* (1984), Fukui (1997), Lalithambika Devi & Rosamma Stephen (1998) and others.

Lack of a multidisciplinary approach in earlier works has made the detailed study of various forms severely restricted to a particular aspect to which attention was focussed. In many instances therefore, ecological conditions are not dealt with. Only some general information is available in the works of Bhimachar and George (1950), Ekman (1953), Ahlstrom (1954), Shelbourne (1957), Carruthers *et al.* (1959), Farris (1959), Bishai (1960, 1961), Fraser (1961), Laevastu (1961), Wyrski (1962, 1971 a, b), Brinton (1963), Knox (1963), Marshall (1963), Pantin (1963), Achieng (1964), Charnock (1964), Hall (1964), Jones (1964), Massmann (1964), Prasad (1964), Rice (1964), Rochford (1964, 1969), Foxton (1965), Bogrov and Rass (1966), Gallaghaer (1966), Panikkar and Jayaraman (1966), Ryther *et al.*, (1966), Bagenal (1967), Banse (1968), Kabanova (1968), Sharma (1968), Anon (1969 a, b, c ; 1970 a, b), Dwivedi (1969), Humphrey and Kerr (1969), Nazarov and Chepurnova (1969), Panikkar (1969), Lalithambika Devi (1969, 72, 77, 86, 89 a,b, 1993), Duing (1970), Kinne (1970), Voytov and Dementjeva (1970), Zoutendyk (1970), Balakrishnan and Lalithambika Devi (1970, 1974), Kimor (1971), Ahlstrom *et al.* (1976) Ozawa and Fukui (1986) and several others.

Fukui (1997) reviewed the early ontogeny and systematics of bothids of the world. Lalithambika Devi (1999) reported 23 species belonging to 9 genera from the Indian Ocean, their regional, seasonal as well as diurnal variations. She has also reported the biodiversity of these species in relation to environmental parameters such as temperature, salinity, dissolved oxygen and nutrients (Lalithambika Devi, 2000).

Generally speaking flat fishes except soles and flounders are not known to contribute substantially to the commercial fishery. This may partly be due to the uneconomic fish landings and partly due to lack of sufficient information regarding the food value of flat fishes.

3. MATERIAL AND METHODS

3.1 Material

During the International Indian Ocean Expedition (IIOE) major attention was given to the study of zooplankton along with some hydrography, meteorology and geology parameters. In order to maintain uniformity of sampling, a team of experts met at Cochin in 1961 felt the necessity for a standard sampling gear which led Currie (1963) to design the Indian Ocean Standard Net. The Indian Ocean Standard Net (IOSN) is a ring net, having a mouth area of one square metre and a length of 5 m. The filtering cone is made of nylon netting of 0.33 mm mesh. Tranter and Smith (1967) have stated that the filtering efficiency of the net is 0.96 initially and clogging has no significant effect in a standard haul and the volume of water filtered during a 200-0 m haul is approximately 192 m³. Hence it was recommended that the samples may be compared on the basis of catch per unit standard haul and not on the number in the volume of water filtered. A standard sample is defined as an IOSN collection of the plankton in the water column under 1 m², the stratum sampled being the upper 200 m in deep water and the entire water column where sounding is less than 200 m (IOBC Handbook, Vol. 1, 1969). But in the present study the number of larvae in the volume of water filtered has been adopted so as to include flat fish larvae contained in the plankton collections taken with nets other than IOSN during cruises of R.V. Blue Fin and R.V. Africana. Even though several ships participated in the IIOE, the zooplanktons were collected only by 17 ships belonging to nine nations, which were curated at the Indian Ocean Biological Centre in Cochin (India). There were 1927 samples out of which 1548 were taken using IOSN hauled vertically at a winch speed of 1 m/second from a depth of either 200m to surface or from bottom to surface. The collections were also preferred from above the thermocline to the surface. In some of the earlier cruises Indian Ocean Standard nets were not available and hence other nets were used. In some cases horizontal collections had to be resorted to because of the failure of winch. These are not included in the standard collections. The area covered by IIOE extended between 45°S and 25°N latitudes and 20°E and 125°E longitudes. The samples taken from 1927 stations were made only once. In some instances, stations fell within the narrow range of already worked out

stations but it was only accidental. The station list and the environmental data have been published in IOBC Handbook (1969, 1971).

As the participating scientists in the IIOE did not verify the methods of fixation and preservation, the condition of the preserved zooplankton material was not uniformly good. The samples were found in deteriorating stages in spite of the care taken at various levels. In the case of fish larvae, particularly those of flat fishes, the muscles of the larval body have been dissolved and the skeletal systems disarticulated. Many specimens were mutilated and damaged beyond recovery. Hence most of these larvae could not be used for studying morphometrics.

The major share of the zooplankton collections were made during 1962-64 period. Even though IIOE was the outcome of a co-operative venture, maximum advantages of such a cooperation was not achieved because of the insufficient coordination of the research vessels for simultaneous observations and coverage of stations in terms of space and time. Of the total 4198 one degree square in the Indian Ocean, Bay of Bengal occupies 6.265%, Arabian Sea 11.934%, Equatorial Indian Ocean 13.149%, South West Indian Ocean 17.065%, South East Indian Ocean 13.670% and South Central Indian Ocean 37.517% and the zooplankton collections as 18.46%, 22%, 19.62%, 16.89%, 10.49% and 12.48% respectively. Hence the Bay of Bengal region stands first in the density of observations and South Central Zone the last. This region has received only less attention. The Northern Indian Ocean up to 5°N including the Arabian Sea and the Bay of Bengal occupy nearly 18% of the total area sampled and this region was well sampled because 40% of the collections come from this region. When generalised interpretations were made, this fact was considered.

The flat fish larvae collected from the Gulf of Thailand and South China Sea during the Naga Expedition had to be studied in conjunction with the flat fish larvae of Indian Ocean collected during the IIOE without which it would not have given any satisfactory clue for the identification of many larval forms. The Naga Expedition covering the Gulf of Thailand and South China Sea organised by United States of America during 1959-61 was a cooperative venture of the Governments of the United States of America, Thailand and South Viet Nam.

The collections were mainly made on board R.V. STRANGER, a 325-ton research vessel of the Scripps Institute of Oceanography. The cruise pattern for the Gulf of Thailand consisted of five transverse lines, oriented roughly perpendicular to the coastlines, crossing the Gulf in north-easterly and south-westerly directions. The southern most line was from the Thai-Malaysian border near Kota Bharu towards Poulo Obi at the southern tip of the Indo-Chinese peninsula. The remaining four lines were parallel to the northern boundary. Hydrographic stations were spaced at 30 to 40 miles intervals along each line. The cruises conducted in the Gulf were reckoned as S1, S3, S5, S7, S9, and S9A and those of South China Sea as S2, S4, S6, S8, and 10 and S11. The first survey of Gulf of Thailand was timed to coincide with the transition between the end of the Southwest (SW) monsoon and beginning of the Northeast (NE). The cruise pattern for the South China Sea consisted of stations aligned along six lines perpendicular or nearly so to the eastern coast of South Viet Nam extending from nearshore to approximately 250 miles off shore. Temperature at various depths were recorded by reversing thermometers. Water samples for salinity, dissolved oxygen and phosphate were collected and estimated. The phosphate values were discarded because of their unreliability. Zooplankton was sampled by different plankton net tows. A circular net of 1 m diameter and mouth area of 0.79 m² having a mesh size of 0.65 mm in the body of the net and 0.3 mm at the cod end was towed along an oblique transect of the water column while the vessel moved at 1.5 to 2 knots with the net on the windward side, at all hydrographic stations and numbered as S1-1, S1-2, S1-3 etc. in each cruise. A 100 pound weight was shackled at a distance of 5-10 m below the net. The wire was paid out at 50 m/min until 200 m of wire was out, depending on the depth. The ship speed was regulated so that the wire angle was 45° with the vertical, to maintain uniform speed of the net through the water. The net was then retrieved at a constant speed of 20 m/min. The depth of haul was calculated from the amount of wire paid out multiplied by the cosine of the wire angle. The volume of water filtered was measured by a TSK Flow meter. The net usually strained about 300 to 400 m³ of water during a standard haul with 200 m wire out. The vertical plankton net used was Marotoku plankton net which is having a mouth diameter of 45 cm and a mesh size of 0.32 mm. The haul was made from 200 m when possible otherwise from bottom to the surface. The net retained smaller sized organisms than the 1 m net. A stramin net of 2.12 m mouth diameter and

1 mm mesh size was towed at night at surface behind the vessel with 100-200 m of wire out at a speed of 2-3 knots. Deeper oblique hauls of about 400 m were made at 6-8 stations per cruise in oceanic South China Sea area. The preserved plankton samples were split into two parts, one of the aliquots was kept at Chulalongkorn University, Bangkok, Thailand and the other at Scripps Institute of Oceanography.

The flat fish larvae of the Naga Expedition samples were placed at the disposal of the author for detailed study from the Scripps Institute of Oceanography and also from California Academy of Sciences, U.S.A.

The zooplankton collected during the IIOE and received at IOBC in the preserved condition were subjected to the following treatment as directed by Hansen (1966), UNESCO Curator. The preservatives used were 10 percent formaldehyde solution buffered with one per cent hexamethylene tetramine. The volume was determined by the wet displacement method (Hansen, 1966), the preserving fluid was drained off through a bolting cloth having the same mesh size as that of the net used for collecting the plankton. The last traces of water was removed by using a blotting paper. The plankton was then added to a known volume of fresh preservative fluid, the difference in volume was then noted as the displacement volume. The larger organisms, fish eggs and larvae were then removed from the whole sample. The remaining samples was then subsampled using Leas Plankton Fractionator (Wiborg, 1951) and Folsom Plankton Splitter (Mc Even *et al.*, 1954 ; Gopalakrishnan, 1972). A fraction of 3 to 5 ml of plankton depending on the total volume of the sample was sorted out in 5 per cent formalin kept in a petri dish to 79 defined taxonomic groups and ill defined forms in residue as per the approved scheme, using a camel hair brush. The organisms were counted using single as well as multiple tally counters and the number in the whole sample were estimated subsequently. The sorted material were preserved in separate vials in 5% buffered formaldehyde solution and stored in darkness. These were then sent to specialists all over the world as per assignment. The sorted groups of each sample were documented in printed scheme sheets and the copies are deposited at IOBC, Cochin and World Data Centre, Washington. The remaining portion of the sample was kept aside as

“Archives” at IOBC (now National Institute of Oceanography, Regional Centre), Kochi.

It was the untiring effort of 16 trained and dedicated scientific personnel for over 8 years to complete the whole process of sorting. The fish larvae, occupying the 79th position in the scheme of sorting, was then subsorted into major groups. The larvae of Pleuronectiformes (flat fishes) formed one of the subsorted groups among fish larvae. The bothid larvae were again subsorted from other flat fish larvae. Bothid larvae collected on board RV Africana and RV Blue Fin were helpful to fill the connecting stages.

3.2 Methods

The bothid larvae from the IIOE and Naga Expedition collections were studied in detail. The numerical counts were assessed using microscope and the morphometric data with stage and ocular micrometer. The life history series were worked out by the serial method of working backwards from identifiable metamorphosed stages or post larvae to early stages. The larval forms were studied in three series wherever possible. First series were taken for morphometric data and presented in separate tables for each species. The specimens from the Naga Expedition collections were mostly used to take morphometric data because of the better condition. The locations from where flat fish larvae of the Indian Ocean as well as South China Sea and the Gulf of Thailand were designated by the respective station numbers with the accepted abbreviation of the ship prefixed to the number (IOBC Hand Book, 1969 and Naga Report by Faughn, 1974). The second series were used for differential staining for bone and cartilage using Alizarin Red and Alcian Blue to stain bone and cartilage respectively and enzyme trypsin solution for clearing flesh (Dingerkus and Uhler, 1977). The following procedure was adopted for staining ; washed the formalin preserved material in several changes of distilled water for 2 or 3 day, placed the material into a fresh mixture of 10 mg Alcian Blue and 90 ml of 95% ethyl alcohol and 10 ml glacial acetic acid for 24 to 48 hours, transferred to 95% alcohol (2 changes 2 to 3 hours in each change) and then through a series of 75%, 40% and 15% alcohol and distilled water 2 to 3 hours in each or until the specimen sunk. Placed the material in 30% aqueous solution of sodium borate, containing 1 gm of the enzyme trypsin, changed the solution

when it turned blue and repeated till bones and cartilages are clearly visible and the flesh colourless (2 to 3 weeks). The material was transferred to 0.5% aqueous KOH solution containing Alizarin Red S till bones became distinctly red and then transferred through 0.5% KOH-Glycerine mixture in the ratio of 75:25, 50:50, 25:75, 0:100 and stored in 100% glycerine to which a few crystals of thymol were added to prevent deterioration. The third series was used to study morphological peculiarities and drawings were made using Projectina Optik, Switzerland.

Finding that the method adopted by Moser and Ahlstrom (1970), Ahlstrom, Butler and Sumida (1976) and Moser, Ahlstrom and Sand Knop (1977) was more meaningful in describing fish larval period into 3 stages based on the flexion of the notochord which occurs during caudal fin formation, the same categorisation was also followed in the present study. The three stages recognised are preflexion, flexion and postflexion. In preflexion stages the notochord ends straight. In some flat fishes the initiation of caudal fin formation begins while the notochord is still straight. This phase of caudal formation is designated as “early caudal formation”. During the formation of caudal fin, flexion of the distal extremity of the notochord takes place and the process becomes complete when hypural plates are well formed. The flexion stages were conveniently subdivided into early flexion, mid-flexion and late flexion. Morphometric and meristic data were taken from specimens representing almost all the three stages. In the tables they are separated by broken lines. Body length of the larvae in preflexion and flexion stages were measured from tip of snout to the tip of notochord (NL) and in post flexion stages from tip of snout to the posterior margin of hypural elements, and denoted as standard length (SL).

In tables dealing with fin development, the dorsal and anal fins are shown as “forming” when the base of the fin ray is evident in the fin fold, but rays have not yet clearly appeared.

Terminology of other measurements taken are as follows:

- | | |
|-----------------------------|---|
| Snout to anus | - Horizontal distance from the tip of the snout through the midline of the body to the vertical through the anus. |
| Head length | - Horizontal distance from the tip of the snout through the midline of the head to the margin of the cleithrum preceding the pectoral fin base. |
| Snout length | - Horizontal distance from the tip of the snout to the anterior margin of the pigmented region of the eye. |
| Eye width | - Horizontal distance through the midline of the pigmented eye. |
| Eye height | - Vertical distance through the centre of the pigmented eye. |
| Body depth at pectoral base | - Vertical distance across the body at the pectoral fin base with or without dorsal fin pterygiophores and taken separately for statistical analysis. |
| Body depth at anus | - Vertical distance across the body at the anus with or without dorsal fin pterygiophores and taken separately for statistical analysis. |
| Caudal peduncle depth | - Vertical distance across the tail immediately posterior to the terminal dorsal and anal fin ray. |
| Caudal peduncle length | - Mid horizontal distance from the terminal median fin rays to the posterior margin of hypural elements. |
| Snout to pelvic fin origin | - Horizontal distance from the tip of the snout to the vertical through the origin of the left pelvic fin. |

The distribution and abundance of larvae were represented through charts. While preparing the data for distribution and abundance, the samples were compared on the basis of number per 1000 m³ of water filtered and represented by selected notations corresponding to the different grades of density. The grades of density selected are : 1-5, 6-10, 11-20, 21-40, 41-80 and above 80. Wherever the number of larvae, in the Naga samples could not be

assessed, their presence is indicated mostly by the sign '+'. These were included in describing seasonal as well as day and night variation but not indicated separately in the chart.

In order to understand the influence of the monsoon on the distribution and abundance of bothid larvae in the plankton, the samples taken during October 16 to April 15 (representing NE monsoon) and April 16 to October 15 (SW monsoon) were pooled together and presented in charts. Similarly the data were pooled to assess the day and night differences for which the samples taken during 0600 to 1800 hours were treated as day collections and the other as night. Graphs representing the relationship of bothid larvae to zooplankton biomass (displacement volume) and average number of larvae per 1000 m³ for Arabian Sea, Bay of Bengal, South West Indian Ocean, South East Indian Ocean, South China Sea and Gulf of Thailand were prepared and presented.

Since the sample size of the individual species were very small the seasonal as well as day and night variations for each species were presented in one and the same chart after assigning appropriate notations.

3.3 Statistical analysis

Statistical analyses of the morphometric data were done to express body proportions as 10⁻² of body length, or head length, mean, standard deviation and range and presented in tabular form. To study the distribution pattern the index, variance/ mean was employed. The index value of 1 represented random distribution, less than 1 spatial (uniform) and more than 1 contagious (patchy). Coexistence of species, pattern of distribution and dependence of bothid larvae with the prevailing hydrographic parameters were also studied using statistical methods. The coexistence was studied with the help of the matrix of correlation using Pearson's formula (Snedecor and Cochran, 1967). The multiple regression equation connecting larvae of bothids with maximum and minimum temperature, salinity, dissolved oxygen, and zooplankton biomass as well as the relative importance of each of the parameters to the abundance of bothid larvae were also presented.