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SPECIES STRUCTURE AND SEASONAL DISTRIBUTION OF LEPTOCEPHALI IN THE EASTERN INDIAN OCEAN (110° E.)

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RÉSUMÉ

A titre de contribution à l'Expédition Internationale en Océan Indien, le C.S.I.R.O. (Cronulla, Australie) et le Centre O.R.S.T.O.M. de Nouméa (Nouvelle-Calédonie) ont effectué, d'août 1962 à août 1963, une série de croisières saisonnières le long du méridien 110° E entre les latitudes 9° S et 32° S. Au programme des prélèvements figuraient une centaine de traits de midwater trawl Isaacs-Kidd de 5 pieds dans la couche 0-200 m. Une fraction remarquable des récoltes a consisté en une collection de 761 leptocéphales, classés dans cette étude en 9 familles, 43 genres et 62 espèces; deux congridés, Ariosoma mauritianum *(Pappenheim) et* Gnathophis habenatus *(Richardson), dominaient néanmoins et représentaient 75 % de l'ensemble des prises. La diversité spécifique est particulièrement élevée de 9° S à 12° S. On peut répartir les leptocéphales de la présente collection en deux groupes principaux: un groupe tropical composé de murénidés, d'ophichthidés, de certains congridés et de quelques autres espèces, dont les adultes viendraient pondre au nord de 14° S, à 100 m, dans des eaux de température moyenne mais relativement peu salées et un groupe subtropical-tempéré comprenant surtout des congridés provenant d'une aire de ponte située à l'ouest de Perth, dans des eaux de température moyenne mais de salinité plus élevée. Les courants saisonniers nord et sud provoquent aux latitudes moyennes un recouvrement partiel des deux groupes. Les plus grandes abondances ont été observées en hiver aux deux extrémités de la radiale; il s'agissait alors de spécimens de petite taille. C'est aux latitudes moyennes, au printemps, en été et en automne, qu'ont été récoltés les grands leptocéphales et les formes métamorphiques. Les larves mesurant moins de 25 mm ont, dans une large mesure, échappé à la capture. La composition faunistique de la zone étudiée ressemble étroitement à celle du sud-ouest Pacifique ou, cependant, l'influence tropicale est plus marquée.*

ABSTRACT

A detailed seasonal investigation of the 110° E. meridian from 9° S. to 32° S. was conducted by the C.S.I.R.O., Cronulla, Australia, and the Centre O.R.S.T.O.M., Nouméa from August 1962 to August 1963 as part of the International Indian Ocean Expedition. This survey included about 100 hauls by 5 ft. Isaacs-Kidd midwater trawl through the upper 200 m along the meridian.

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A conspicuous part of the resultant catch was a diverse collection of 761 leptocephali, referred here to 9 families, 43 genera and 62 species. The two congrids: Ariosoma mauritianum *(Pappenheim) and* Gnathophis habenatus *(Richardson), however, dominated to the extent of 75 % of the total catch. Species diversity was greatest at about 9° S. to 12° S. The collection contains essentially a tropical component of muraenid, ophichthid, certain congrid and other species, whose adults spawn north of about 14° S. at 100 m in water of moderate temperature but low salinity; and a subtropical-temperate component consisting mainly of congrid species originating from a spawning area west of Perth in water of moderate temperature but relatively high salinity. The two components overlap at intermediate latitudes as a result of the seasonal movement of these waters southwards and northwards respectively. Larvae were most abundant, but smallest, during midwinter in the far north and south, while larger larvae and metamorphic forms occurred generally at intermediate latitudes during spring, summer and autumn. There was considerable escapement of small larvae of less than 25 mm from the IKMT. The species structure of larvae in this area is closely similar to that of the southwest Pacific although in the latter area there is a stronger tropical influence.*

I. *INTRODUCTION*

The attention of oceanographers and marine biologists of some 20 nations in recent years has been centred on the Indian Ocean, under the sponsorship of the S.C.O.R.-U.N.E.S.C.O. International Indian Ocean Expedition, in a major co-operative effort to expand the hitherto meagre knowledge of this important region. At the commencement of the research programme in 1959-1962 preliminary studies of this area were made in order to formulate more precisely the exact future scope of the expedition. The Australian contribution to these preliminary studies was in the form of 10 general cruises in the southeastern part of the Indian Ocean (east of 95° E.) by the naval vessels HMAS *Diamantina* and HMAS *Gascoyne.* The oceanographic programme was directed by the C.S.I.R.O. During these cruises the general hydrological and biological conditions were determined. Important upwelling south of Java during the southeast monsoon (Wyrtki, 1962b: 218) and a high nett biomass (Tranter, 1962: 116) were demonstrated for this area.

These preliminary observations were later expanded by a more detailed examination of the area and during August 1962-August 1963 six cruises were made to sample more particularly the waters along the 110° E. meridian from about 9° S. to 32° S. These six cruises were as follows:—*G4/62* (August 19-September 16, 1962); *Dm4/62* (October 15-November 13, 1962); *G1/63* (January 17-February 17, 1963); *Dm1/63* (March 28-April 27, 1963); *Dm2/63* (May 6-June 3, 1963); *Dm3/63* (July 9-August 11, 1963). In addition a short cruise *(Dm3/62)* was made along the 110° E. meridian between 32° S. and 43° S. in September-October, 1962. Data for all cruises appear in the relevant C.S.I.R.O. Oceanographical Cruise Reports (1965a-d; 1966a-b; 1967). Each cruise, except the latter, occupied a series of stations from 32° S. northwards along 110° E. to about 9° S., returning southwards along the same meridian to 32° S. Although a small number of stations were not placed precisely on 110° E. the east-west variation from this meridian of longitude was in general small and for the purposes of this study all are assumed to have been on 110° E.

By this pattern of sampling the oceanic waters of the southeast Indian Ocean were examined along 2000 nautical miles of the 110th meridian ranging from close to Java to about 1200 miles southwest of Perth, over depths of not less than 1200 m to 7500 m (Sunda Trench). Sampling during the year-long period occurred in all months with the exception of December, 1962. Each of the six major cruises lasted for one month, and successive cruises were separated by intervals of about one month. This scheme resulted in the southern limit being sampled more frequently (i. e. each month) than the northern limit (i. e. every two months) and intervening latitudes

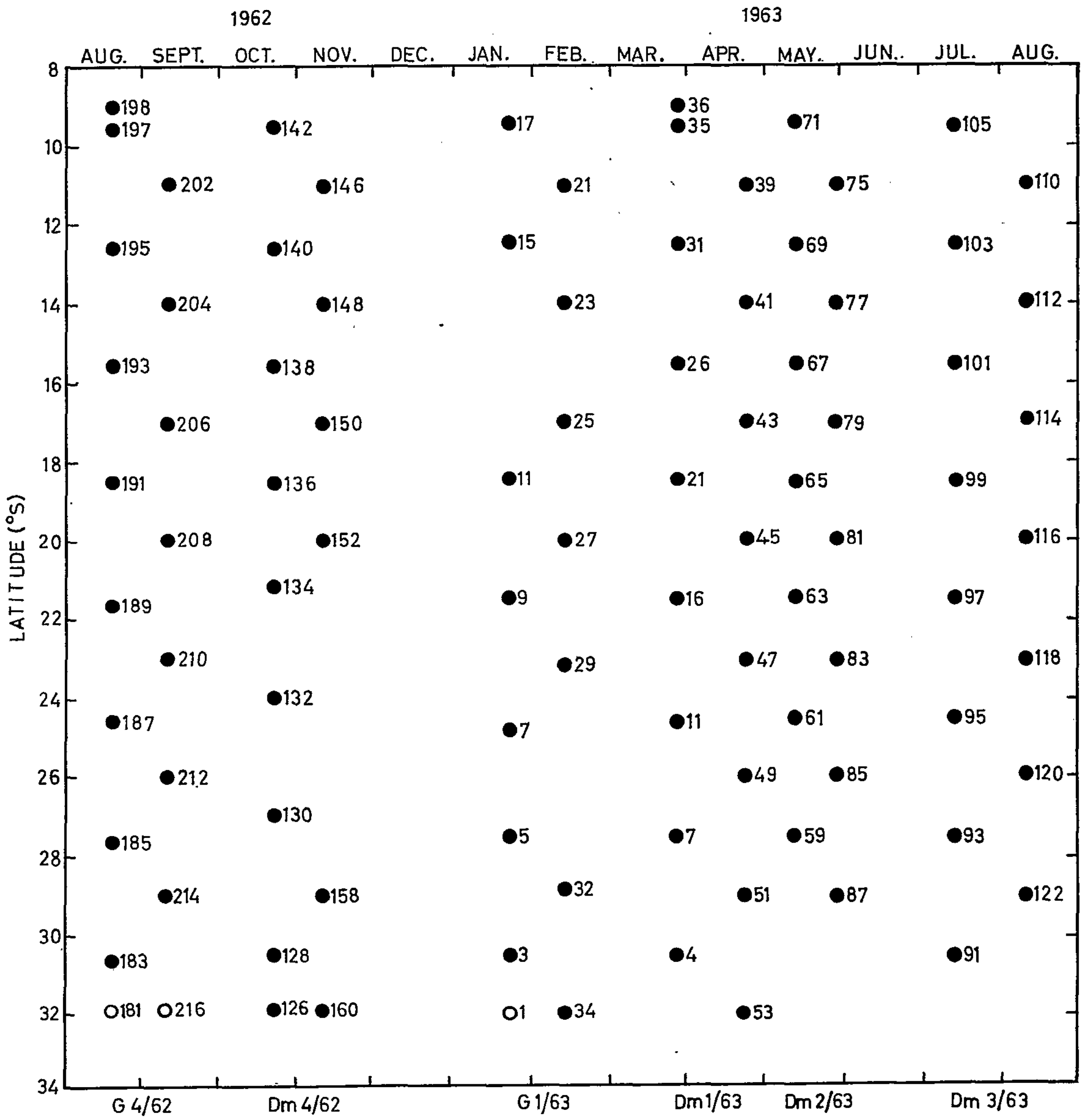

Fig. 1.— Position and times during 1962-1963 of the IKMT hauls along 110°E. Open circles indicate day stations.

were therefore sampled at intermediate periods with the frequency of sampling increasing towards the south. Results of the programme have been evaluated here with the lack of December sampling and the more infrequent northerly sampling in mind.

On the 1962-1963 cruises listed above French biologists from the Centre O.R.S.T.O.M., Nouméa, were responsible for the micronekton programme in which a 5ft Isaacs-Kidd midwater trawl was used to make regular, oblique hauls through the upper 200m along 110° E. The average maximum depth of the hauls was 210m and ranged from 120m to 400m. Tows were made at about 10 p. m. although some day stations were also occupied. Further details of the nature of this gear, its shipboard handling and the collecting and storing of samples, are available elsewhere (e. g. C.S.I.R.O. 1965a : 10-11). The latter account also sets out details of standardisation procedures and the handling of the micronekton. The distribution in latitude and time of the IKMT micronekton stations along 110° E. during the six cruises is shown here in Figure 1.

A large collection of micronekton resulted from these hauls. On 96 occasions eel-larvae appeared in the catch and for the whole programme comprised a total of 761 larvae, referable to at least nine families of eels and 62 species, representing about 5 % of the purely micronektonic organisms occurring in the total catch. These hauls were analysed in detail for systematic composition and the latitudinal and seasonal occurrence of eel-larvae in this part of the Indian Ocean during 1962-1963 determined from these results.

The analysis of the 96 samples involved the initial sorting of the leptocephali to species. This task was based mainly on systematic studies presented elsewhere (CASTLE, 1963a-1967) and which were made from an examination of a large collection of leptocephali taken in the southwest Pacific and from off Perth, Western Australia and assembled from the collections of various institutions. Reference may be made to these papers for the systematic details necessary for the recognition of the major taxa discussed in the present account. These previous systematic studies point out that correlative work on eel-larvae and their adults is not yet so greatly advanced that larval forms encountered in collections can always be immediately recognized and named. This situation stems from an inadequate knowledge of adult systematics as well as a lack of the relatively rare metamorphic growth stages which can be so valuable in linking larval types with adults. Despite the above difficulties, the larval characters of the most important eel families are now sufficiently firmly established to enable the sorting of collections at least to the familial level. The characters which thus define larvae of the various families may occur only in the larvae (for example, the festooned or swollen nature of the intestine of ophichthid leptocephali) or they may be also found in the adult (for example, the reduced or absent caudal fin in adult ophichthids).

Diversity in larval eels below the familial level is manifested more often then not in two major ways. Firstly, in any particular family, larvae can be grouped according to the abundance and distribution of melanophores, a character which seldom remains after metamorphosis. Other characters, such as the position of origin of the dorsal fin, the structure of the caudal, the presence of sensory pores on the head, may also be features of the adult, and often confirm the groupings recognized by consideration of the nature of the pigment. I believe that such characters in leptocephali partly define larval genera. Secondly, within each of these generic categories, so defined, there are usually subdivisions based on the numbers of myomeres (or number of vertebrae, as commonly expressed in the adults). These subdivisions based on myomere numbers are clearly at a lower taxonomic level than genus and are regarded to delimit species. It has been adequately shown elsewhere that myomere number in eels (as well as in other groups of fishes, including sharks) usually has a characteristic range in each species.

Although it is thus possible to recognize genera and species in sorting a collection of eel larvae, the definitive identification and correct nomenclature of these categories often cannot be achieved. This is mainly due to inadequate knowledge of metamorphic forms which usually show characters of larvae and adults by which larvae can be assigned to their correct genera, and also to insufficient records of vertebral counts in adult species. There is at the same time the inadequacy in adult systematics imposed by lack of broad comparative studies on Indo-Pacific eels in general. In the diverse tropical families such as the Ophichthidae and Muraenidae as well as in such poorly-known essentially deep-water families as the Nettastomatidae, many generic limits are not yet firmly established. In these also, the amount of variation of diagnostic characters in most species has not been adequately observed to place the systematics of the adults on a reliable basis. In general, diversity of larvae in certain families appears to be greater than that of adults, suggesting that there remain new forms of adults to be described. This interesting situation no doubt results in part from the relative ease by which larvae are collected compared with adults. The inadequacies outlined above, although a considerable restriction to the definitive nomenclature of many of the various forms of larvae recognized in the present collection, does not greatly interfere with the intention of this paper. Rather, it is mainly concerned with the seasonal and geographical relationships of a series of species independent of what these species may be formally called. The solution of problems of nomenclature, where these occur, largely awaits revisionary taxonomic studies on adults.

JESPERSEN's definitive study (1942) on leptocephali of Indo-Pacific species of the genus *Anguilla* dealt in part with larvae collected off the west coast of Sumatra. My recent papers (CASTLE, 1936b *et seq.*) discuss the systematics, growth and distribution of certain larval species collected west of Perth. As far as I can determine these are the only studies which record eel-larvae from the eastern Indian Ocean. The large collection made during the 1962-1963 cruises is therefore of considerable interest, not only for the information it provides on the seasonal and spatial distribution of eel-larvae, but because it is the first major systematic collection of leptocephali from this hitherto largely unknown area. As such it might be expected to give a lead to the systematic composition of the adult eel-fauna of this region.

In my previous papers dealing with eel-larvae in Australasian waters I discussed the species structure in the southwest Pacific (including the waters around New Caledonia, the Solomon Islands, the east coast of Australia, and the New Zealand area). Some systematic comparisons may now be made between faunas of the eastern Indian Ocean and the southwest Pacific. No detailed year-long study of a specific meridian of longitude in the southwest Pacific had been made before I wrote my earlier papers so that the eel-larvae of the two areas cannot be quantitatively compared. Nevertheless, some information on the relative abundance of larvae of the various species in the southwest Pacific is available. Detailed studies now being made of certain areas of the southwest Pacific by the Centre O.R.S.T.O.M. are expected to provide much comparable information on the seasonal occurrence of leptocephali and other organisms.

II. LATITUDINAL AND SEASONAL ABUNDANCE OF LARVAE

Leptocephalids were a very prominent part of IKMT hauls along 110° E. although the proportion they formed of the total catch in each haul varied considerably with latitude and time-of-year. It soon became clear during the programme that this part of the eastern Indian Ocean is a rich area for eel-larvae, despite the almost entire absence of previous records of leptocephali and the relatively small known adult fauna. Leptocephali appeared in 96 of the 102 IKMT hauls.

The tables set out in Section IV list these hauls together with certain station data. Their positions during the six major cruises are plotted in Figure 1 so that they may be related to other figures illustrating the distribution of larvae and hydrological conditions during August 1962-August 1963. The longitude is assumed to be 110° E. and the time of the haul 10 p. m., unless otherwise stated. Further station data, if required, are available elsewhere (C.S.I.R.O., 1965-1967). The total numbers of larvae in each of these hauls are listed in the penultimate right-hand column of the tables. As trawling time varied standardisation was achieved by correcting the observed number of larvae per haul to same time-of-hauling which in the present programme was set at 83 minutes; corrected numbers of larvae appear in italic figures in the extreme right-hand column of the tables. Other columns detail the exact systematic composition, a subject which is discussed at length in later sections of this paper. The present section considers the annual and latitudinal distribution of the eel-larvae as a whole, regardless of systematic composition.

A study of Section IV (b) shows that more southerly hauls, around 25° S. to 32° S. contained more larvae than those made in the north, with a notable meagreness of larvae from 13° S. to 20° S. To express these broad observations graphically the abundance of larvae at various latitudes during 1962-1963 is plotted in Figure 2 (as individuals per standard haul) and Figure 3 (as dry weight in mg. of larvae per standard haul). Dry weight has been calculated from the

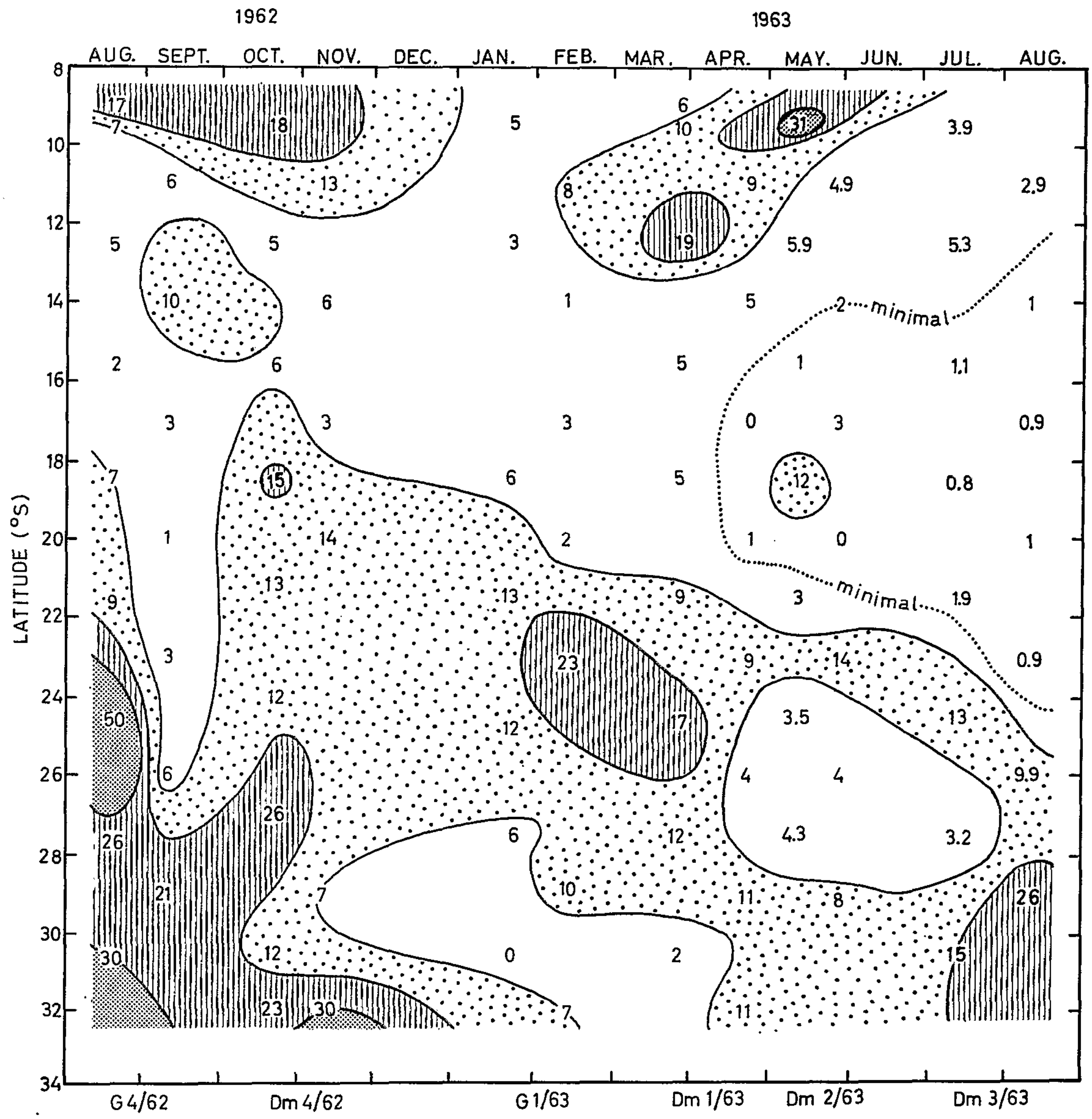

Fig. 2. — Numbers of leptocephali occurring along 110°E. during 1962-1963. Figures given are numbers per standard haul.

wet volume x 60, where the latter is the conversion factor for leptocephali (C.S.I.R.O., 1965a: 132). Numbers of larvae per standard haul are also plotted in Figure 6 (c), taken as average number for hauls at each position of latitude throughout the year. The abundance of larvae at various latitudes may therefore be compared with numbers of species at these latitudes (Figure 6 (a) and (b)) thus giving an indication of the diversity of the catch. Biomass of the larvae bears a direct relationship to dry weight (biomass $= \frac{\text{dry weight} \times 1000}{79}$ — figures supplied by M. Legand, Centre O.R.S.T.O.M.) so that biomass can be calculated for each standard haul, but its graphical expression would not differ essentially from that shown in Figure 3. The

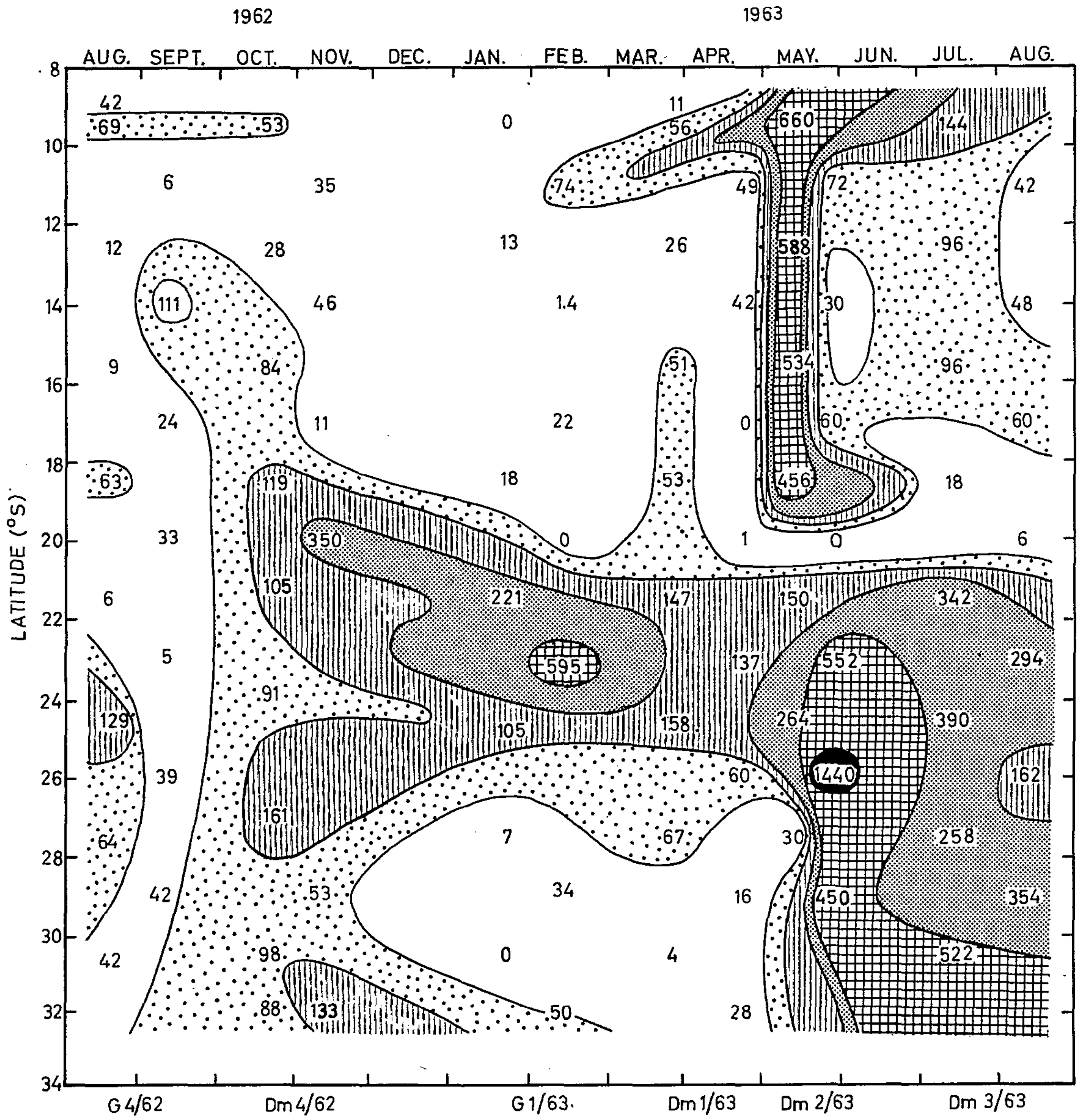

Fig. 3. — Biomass (dry weight) of leptocephali along 110°E. during 1962-1963. Figures given are mgm. per standard haul.

number of larvae per standard haul for each species is not known, but the percentage that larvae of two most important species in the collection (Family Congridae) contribute to each haul is also shown in Figure 6 (d). The latter figures have been calculated from uncorrected values of numbers of these species per haul, but the percentages should presumably (within limits) be independent of sample size. Actually, as will be shown in Section III, the IKMT is differentially selective, favouring eel-larvae of a certain size (and therefore in some cases of identity). Hauls run for a greater time would probably show increasing bias towards such larvae.

Larvae were most numerous in hauls made south of 23° S. during July to November and here reached a maximum of 50 per standard haul (Figure 2). Smaller secondary peaks occurred in the area immediately south of Java in August to December and March to June where numbers

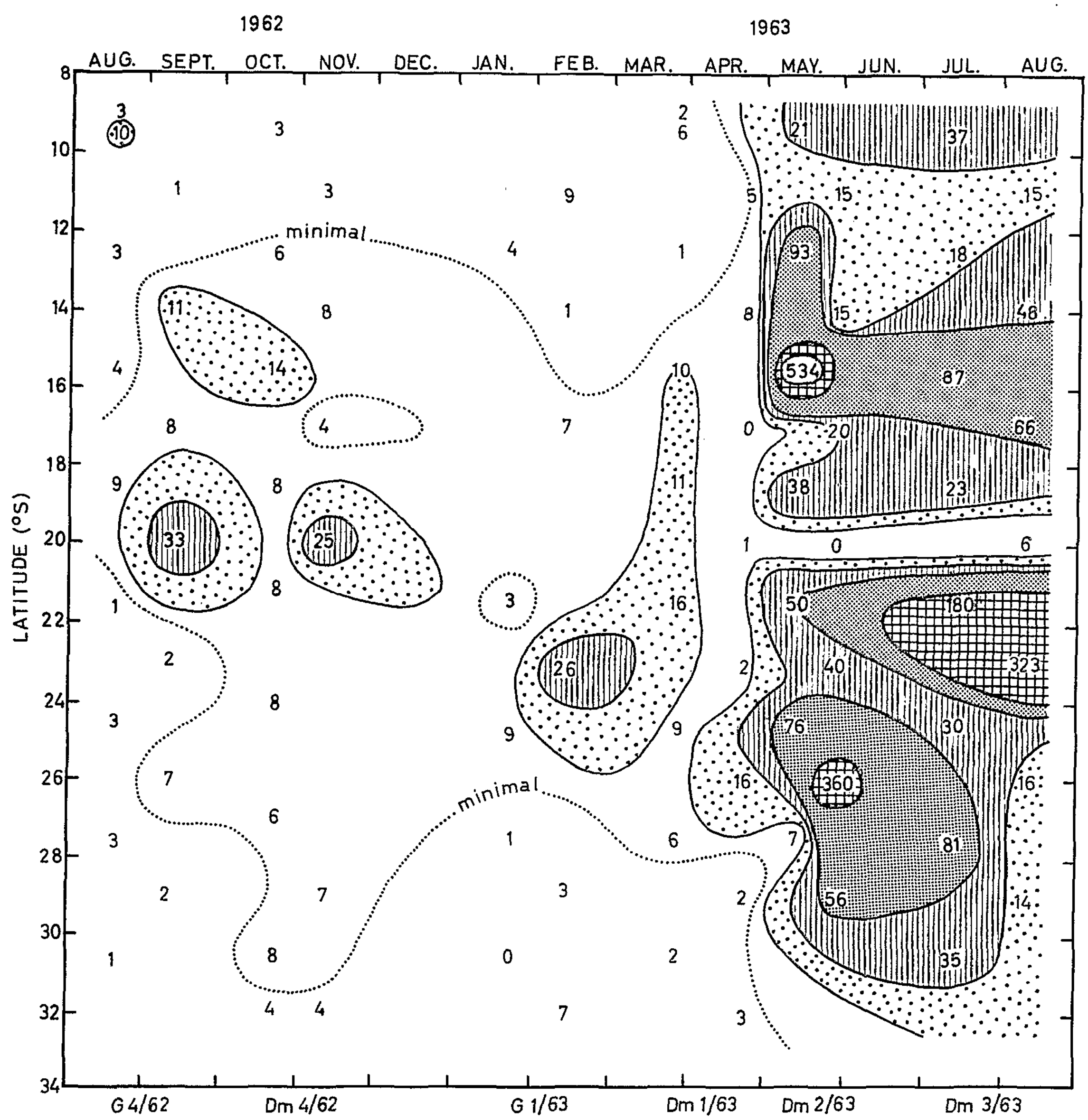

Fig. 4. — Average weight of leptocephali per standard haul along 110°E. during 1962-1963. Figures given are mgm.

reached 32 per haul. During the period October to April larvae were also moderately abundant in latitudes of 17° S. to 26° S. and here reached 23 per haul. There was a broad belt of minimal occurrence from 13° S. to about 20° S. throughout the year (Figure 2) where larvae seldom occurred in greater numbers than 10 per standard haul, usually much fewer.

Biomass (as expressed by dry weight) of larvae was greatest mainly from late May to August south of 20° S. and during May from 9° S. to 20° S., reaching peaks at 10° S. during May, at 26° S. during late May and at 23° S. in mid-February. There was a broad belt of high biomass south of 20° S. throughout the year (Figure 3).

It is clear when comparing Figures 2 (number) and 3 (weight) that positions and times of greatest larval numbers do not always coincide with those of greatest biomass. This discrepancy immediately suggests that there was a difference in average size of larvae occurring at times and in areas of maximum numbers and maximum biomass. To provide an approximate indication of larval sizes the average size of larvae per standard haul was therefore calculated from $\frac{\text{biomass.}}{\text{no. of larvae}}$. These average sizes are plotted in Figure 4. There is of course a possible error inherent in this method of expressing size of larvae since smaller larvae are likely to be relatively less bulky and therefore relatively lighter than longer larvae. However, even if this were so it would serve to accentuate the discrepancy. That is, if size were expressed in terms of length, rather than weight, the differences shown in Figure 4 between areas where average size was low and those where average size was high would be accentuated.

The figure clearly shows that the largest larvae in all latitudes (except at about 20° S.) occur in May to August, reaching maxima in May at 15° S. and 26° S. and in June-August at 23° S. Much smaller peaks of average size occur at about 20° S.-23° S. at other times of the year. It is important to stress that the major peaks represent *few*, *large* larvae. Small larvae, on the other hand, occur in greatest numbers from 9° S. to 14° S. from August to April, from 21° S. to 32° S. during August-September and in the south from November to April. Although these observations apply to all species taken together, they refer more especially to two species, the congrids *Ariosoma mauritianum* (Pappenheim, 1914) and *Gnathophis habenatus* (RICHARDSON, 1848) since these predominate in the catch, particularly in more southerly latitudes.

In general therefore, larvae are most abundant north of 12° S. during spring and early autumn, and south of 22° S. during spring and late summer, where they are also smallest. Largest larvae in low numbers occur in intermediate latitudes during the winter. The significance of these observations in relation to the life histories of the species in the collection is discussed in Section VII.

Note: Eel-larvae are markedly gelatinous organisms and suffer considerable loss of weight on preservation. Work is currently in progress on this important consideration and preliminary studies show that the action of formalin reduces the weight of eel-larvae by about 10 %. Biomass or weights of larvae as given above must therefore be appreciably less than the true values. Present figures must be regarded as minimal estimates only.

III. SIZE SELECTIVITY OF NET AND GEAR

A conspicuous feature of the collection of leptocephali made by the 5 ft. Isaacs-Kidd midwater trawl during the present series of cruises was that very small larvae of less then 25mm were infrequent in the hauls. Figure 5 (a) shows the size-frequency of all eel-larvae in the total catch while Figure 5 (b-c) indicates in detail size-frequencies of the two most important species, *Ariosoma mauritianum* and *Gnathophis habenatus*. The relative absence of larvae of less than about 25mm total length is clearly shown in these figures.

Aside from the rather exceptional case of *Anguilla anguilla* (L.) which has a larval life of up to three years, most species of eels probably exist as larvae for a year or less. We may assume therefore, that the 1962-1963 sampling period encompassed the whole larval life of the species in the collection (either as one or more year classes), and that early stages were not missed because of trawls being made too late. There are then two implications of the scarcity of very young larvae in the collection: (a) that the IKMT inadequately sampled the very early stages of the population, and (b) that spawning and early growth of larvae occurs outside the spatial limits of the hauls (that is, either below the 210 m average maximum depth of the hauls or to the west or east of the 110° E. meridian.

Firstly, the oblique nature of the hauls ensured that the whole of the upper 200m was sampled and therefore even if the very youngest stages occurred in specific depths of the upper 200m, they would have been sampled by the IKMT. Secondly, available records of eel-larvae from other parts of the world suggest that early growth (and probably spawning) of eels takes

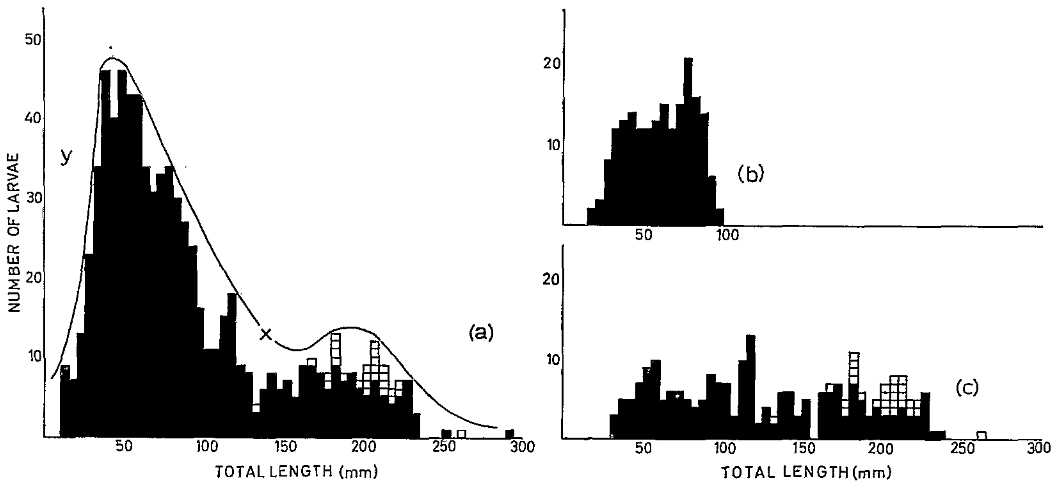

Fig. 5. — Length-frequency polygons of leptocephali:— (a) total larvae; (b) *Gnathophis habenatus*; (c) *Ariosoma mauritianum*. Open squares indicate metamorphic specimens of *A. mauritianum*. x— catching ability of the IKMT; y— probable escapement of young larvae from the net.

place in the upper 300m. Metamorphic stages may occur in very much deeper water. For example, Bruun (1937: 16, fig. 6-7), discussing the vertical distribution of larvae of *Synaphobranchus*, shows that larvae of *S. kaupi* Johnson, 1862 in the Atlantic occur most frequently at 125m-225m depth, while metamorphic larvae occur at 1200m-2500m. Castle (1963b : 25 & 41) shows that that very small larvae (5mm-10mm) of the congrids *Gnathophis habenatus* and *G. incognitus* Castle, 1963 occur in the upper 200m of the Tasman Sea off Sydney (34° S.). Spawning and early growth of most eels is undoubtedly associated with specific hydrological conditions which often characterise the upper 200m, probably those of temperature and salinity. The precise hydrological requirements, of course, may differ from species to species. I have also recorded (1963b: 27) very small larvae (9mm-18mm) of *G. habenatus* taken by larval fish trawl in the upper 100m about 40 miles west of Rottnest Island, off Perth. This is some 300 miles east of the 110° E. meridian, but it is possible that spawning and early growth of this species takes place over a much wider area than indicated by earlier investigations and may indeed encompass 110° E. at this latitude.

In consideration of the above it therefore seems likely that it is the limitation of the IKMT which accounts for the relative absence of very small larvae in the present collection, and not because hauls failed to sample areas where these were present. This view is supported by similar results for mesopelagic fishes (Legand, personal communication). Individuals of these less than about 20mm in total lengths were also less frequent in the hauls. In the case of eel-larvae, the IKMT appears to select leptocephali of 25mm-60mm most effectively (Figure 5). The net becomes much less efficient for retention of smaller specimens because of their « escapement » and for larger specimens because of their « avoidance » of the net.

The curve « x » fitted to the size-frequency polygon (Figure 5) would theretore represent very approximately the catching ability of the IKMT and fairly well expresses the decrease in relative number of larvae larger than about 60mm consequent from natural mortality. Two segments of the total population in the water mass sampled by the net during all of its hauls throughout 1962-63 are therefore absent from Figure 5. These are (a) the very numerous small larvae less than about 25mm which, because of their small size, « escape » from the net (represented by the area « y » and equal to about 25 % of the total theoretical number in the water mass filtered), and (b) the unknown number of very large larvae that « avoid » the net (represented by an area above the right hand portion of curve « x »). Avoidance of the net is possibly not as great in eel-larvae as in other micronektonic organisms of a comparable size because of their relatively weak swimming ability. Active escapement must also be offset by the greater ease by which eel-larvae may be entangled in net meshes.

The secondary maximum at about 200mm is probably formed by a mixture of nearly full-grown and metamorphic larvae. The latter reach about 240mm at full growth but contract in length during regressive metamorphosis. This means that there would tend to be more individuals at less than maximum larval size than there would be if growth were linear at this stage of life.

From these observations it is concluded that considerable modification of Figures 2-4, representing the abundance and size of the eel-larvae, are required in order to express more accurately the temporal and spatial distribution of the larvae. With the knowledge that most of the larvae escaping from the IKMT were very small ones, and that small larvae mostly occur in late August-October north of 14° S. and south of 20° S. (cf. Figure 3) the difference shown in Figure 2 between areas and times of minimal and maximal occurrence would be greatly accentuated. Furthermore, if the IKMT sampled very young larvae efficiently there would also be an effect on the systematic composition of the catch. An increase in the numbers of larvae of species which reach relatively small maximum sizes at full growth could be expected in the hauls.

IV. CHECKLIST OF SPECIES

Section II discussed the abundance of all larvae (from latitude to latitude and from month to month during the year) regardless of systematic composition. However, the collection was a very diverse one and there were considerable differences between the abundance of the various species occurring in the collection. Before such matters are discussed it is necessary to outline the systematic composition of the collection.

A total of 62 species, 43 genera and nine families were recognized in the collection. In Section IV (a) below, the various species collected are listed in systematic form against the stations at which each occurred. Each of the 62 species is assigned a code number (although one species is indeterminate because of the small size of the specimens, it is also coded, giving a total of 63 categories). In Section IV (b) below, selected station data are set out for the 102 IKMT stations of the seven cruises. The species occurring at each of these stations are listed in the right-hand columns by their code numbers as assigned in Section IV (a), and the composition of the catch of each station can therefore be found by checking back to the species list in Section IV (a). The seven most abundant species in the collection (a species has been regarded as « abundant » if its total number of individuals was 20 specimens or more—a purely arbitrary distinction) are listed separately from the remainder in the right hand columns and the number of individuals of each of these species occurring at each station is given. Specimen numbers of the remaining species at each station are also listed as « others ». In this way the total catch, and its systematic composition at each station, may be determined from the tables. The seven most abundant species were *Ariosoma scheelei*, *A. mauritianum*, *Leptocephalus scalaris*, *Gnathophis habenatus* and *Scalanago lateralis* (all Family Congridae); *Nemichthys scolopaceus* (Nemichthyidae) ; *Serrivomer samoensis* (Serrivomeridae).

IV (a). **List of species and stations.**

CONGRIDAE

(1) *Ariosoma scheelei* (Strömman, 1896)—34 specimens (total lengths 28.6mm-178.9mm) : Stations G4-185-62, G4-197-62, G4-198-62, G4-202-62, Dm4-138-62, Dm4-140-62, Dm4-146-62, Dm4-148-62, Dm1-31-63, Dm1-35-63, Dm1-39-63, Dm1-41-63, Dm2-59-63, Dm2-61-63, Dm2-65-63 Dm2-71-63, Dm2-83-63, Dm3-103-63.

(2) *Ariosoma mauritianum* (Pappenheim, 1914)—245 specimens (total lengths 33.9mm-238mm) : Stations G4-183-62, G4-185-62, G4-187-62, G4-189-62, G4-195-62, G4-197-62, G4-198-62, G4-202-62, G4-204-62, G4-206-62, G4-210-62, G4-212-62, G4-214-62, G4-216-62, Dm3-104-62, Dm3-106-62, Dm3-108-62, Dm4-126-62, Dm4-128-62, Dm4-130-62, Dm4-132-62, Dm4-134-62, Dm4-136-62, Dm4-138-62, Dm4-140-62, Dm4-142-62, Dm4-148-62, Dm4-152-62, Dm4-160-62, G1-7-63, G1-9-63, G1-15-63, G1-29-63, G1-32-63, G1-34-63, Dm1-7-63, Dm1-11-63, Dm1-16-63, Dm1-21-63, Dm1-26-63, Dm1-39-63, Dm1-47-63, Dm1-49-63, Dm1-53-63, Dm2-59-63, Dm2-65-63, Dm2-67-63, Dm2-69-63, Dm2-71-63, Dm2-85-63, Dm2-87-63, Dm3-91-63, Dm3-93-63, Dm3-95-63, Dm3-97-63, Dm3-101-63, Dm3-103-63, Dm3-105-63, Dm3-120-63, Dm3-122-63.

(3) *Ariosoma anago* (Temminck & Schlegel, 1842)—2 specimens (total lengths 50.1mm-212.3mm): Stations Dm1-41-63, Dm2-71-63.

(4) ? *Alloconger anagoides* (Bleeker, 1864)—6 specimens (total lengths 97.2mm-207.0mm): Stations G4-198-62, Dm4-138-62, G1-21-63, Dm1-31-63, Dm1-39-63.

Adult unknown:

(5) *Leptocephalus scalaris* Castle, 1964—25 specimens (total lengths 31.5mm-223.4mm): Stations G4-191-62, G4-198-62, Dm4-140-62, Dm4-142-62, Dm4-152-62, G1-9-63, G1-17-63, G1-21-63, Dm1-26-63, Dm1-35-63, Dm1-36-63, Dm1-47-63, Dm2-63-63, Dm2-65-63, Dm2-67-63, Dm2-85-63, Dm3-95-63, Dm3-118-63.

(6) *Gnathophis habenatus* (Richardson, 1848)—196 specimens (total lengths 15.6mm-106.6mm): Stations G4-181-62, G4-183-62, G4-185-62, G4-187-62, G4-189-62, G4-212-62, G4-214-62, G4-216-62, Dm3-102-62, Dm3-104-62, Dm3-108-62, Dm4-126-62, Dm4-128-62, Dm4-130-62, Dm4-132-62, Dm4-158-62, Dm4-160-62, G1-5-63, G1-29-63, G1-32-63, G1-34-63, Dm1-4-63, Dm1-7-63, Dm1-11-63, Dm1-49-63, Dm1-51-63, Dm1-53-63, Dm2-59-63, Dm2-87-63, Dm3-91-63, Dm3-93-63, Dm3-95-63, Dm3-120-63, Dm3-122-63.

(7) *Gnathophis incognitus* Castle, 1963—18 specimens (total lengths 13.1mm-97.5mm): Stations G4-189-62, G4-212-62, Dm4-134-62, Dm4-140-62, G1-5-63, G1-9-63, Dm1-7-63, Dm1-51-63, Dm2-87-63, Dm3-110-63.

(8) *Conger wilsoni* (Bloch & Schneider, 1801)—1 specimen (total length 86.9mm): Station G4-193-62.

(9) *Conger cinereus cinereus* Rüppell, 1828—2 specimens (total lengths 44.0mm-45.7mm): Stations Dm2-69-63, Dm2-71-63.

(10) *Scalanago lateralis* Whitley, 1935—28 specimens (total lengths 12.0mm-83.2mm): Stations G4-183-62, G4-185-62, G4-187-62, G4-216-62, Dm3-104-62, Dm4-126-62, Dm4-130-62, Dm4-132-62, Dm3-95-63, Dm3-120-63, Dm3-122-63.

Adults unknown:

(11) *Leptocephalus stenorhynchus* Castle, 1964—2 specimens (total lengths 46.7mm-116.2mm): Stations Dm4-152-62, Dm1-31-63.

(12) *Leptocephalus geminus* Castle, 1964—6 specimens (total lengths 40.3mm-148.2mm) : Stations Dm4-136-62, G1-21-63, Dm2-65-63, Dm2-71-63, Dm3-103-63.

(13) *Leptocephalus* cf. *L. geminus* Castle, 1964—2 specimens (total lengths 88.3mm-115.2mm): Stations G4-187-62, Dm3-114-63.

(14) *Uroconger ?braueri* Weber & de Beaufort, 1916—11 specimens (total lengths 12.0mm-129.9mm): Stations G4-198-62, Dm4-142-62, G1-21-63, Dm1-16-63, Dm1-31-63, Dm1-41-63, Dm2-75-63, Dm2-83-63, Dm3-105-63.

Others:

(15) ?—1 specimen (total length 70.9mm): Station Dm4-146-62.

(16) ?—2 specimens (total lengths 83.7mm-84.9mm): Stations Dm2-79-63, Dm3-105-63.

(17) ?—3 specimens (total lengths 49.9mm-54.8mm): Stations Dm1-36-63, Dm2-71-63.

(18) ?—1 specimen (total length 68.1mm): Station Dm1-47-63.

NEMICHTHYIDAE

(19) *Nemichthys scolopaceus* Richardson, 1848—44 specimens (total lengths 30.0mm-402.5mm): Stations G4-185-62, G4-193-62, G4-206-62, G4-208-62, G4-214-62, G4-216-62, Dm4-128-62, Dm4-134-62, Dm4-136-62, Dm4-138-62, Dm4-150-62, Dm4-160-62, G1-7-63, G1-9-63, G1-11-63, G1-25-63, G1-27-63, G1-29-63, G1-34-63, Dm1-4-63, Dm1-7-63, Dm1-11-63, Dm1-21-63, Dm1-31-63, Dm1-35-63, Dm2-61-63, Dm2-67-63, Dm2-71-63, Dm2-75-63, Dm2-85-63, Dm2-87-63, Dm3-112-63.

(20) *Borodinula infans* (Günther, 1878) or *B. gilli* (Bean, 1890)—3 specimens (total lengths 47.9mm-194.2mm): Stations Dm4-128-62, Dm1-11-63.

Adult unknown:

(21) *Leptocephalus attenuatus* Castle, 1964—4 specimens (total lengths 73.1mm-163.4mm): Stations Dm4-136-62, Dm4-150-62, Dm4-152-62, Dm1-21-63.

SERRIVOMERIDAE

(22) *Serrivomer samoensis* Bauchot, 1959—25 specimens (total lengths 12.1mm-65.0mm): Stations G4-195-62, G1-11-63, G1-15-63, G1-15-63, G1-21-63, G1-27-63, Dm1-21-63, Dm1-26-63, Dm1-39-63, Dm1-45-63, Dm1-47-63, Dm2-65-63, Dm2-67-63, Dm2-77-63, Dm2-79-63, Dm3-103-63, Dm3-120-63.

(23) *Serrivomer bertini* Bauchot, 1959—8 specimens (total lengths 24.8mm-58.9mm): Stations G4-185-62, G4-214-62, Dm4-130-62, Dm4-160-62.

(24) *Serrivomer* sp.—2 specimens: G1-25-63, Dm3-97-63.

CYEMIDAE

(25) *Cyema atrum* Günther, 1878—5 specimens (total lengths 12.1mm-27.9mm): Stations Dm4-132-62, G1-5-63, G1-34-63, Dm1-53-63, Dm3-122-63.

NETTASTOMATIDAE

(26) *Nettastoma ?parviceps* Günther, 1877—1 specimen (total length 87.2mm): Station G1-17-63.

Adult unknown:

(27) *Leptocephalus rostratus* Schmidt, 1909—1 specimen (total length 191.2mm): Station Dm3-114-62.

(28) *Leptocephalus* cf. *L. rostratus* Schmidt, 1909—5 specimens (total lengths 37.8mm-75.3mm): Stations G4-185-62, Dm4-132-62, Dm4-160-62.

(29) *Leptocephalus* cf. *L. dolichorhynchus* Lea, 1913—1 specimen (total length 120.5mm): Station Dm4-160-62.

(30) *Leptocephalus stylurus* Lea, 1913—4 specimens (total lengths 37.5mm-95.6mm): Stations G4-189-62, G4-202-62, Dm4-126-62, G1-32-63.

Others:

(31) ?—3 specimens (total lengths 28.8mm-54.0mm): Stations G4-189-62, G1-23-63, Dm2-61-63.

(32) ?—3 specimens (total lengths 31.4mm-92.2mm): Stations G4-206-62, Dm1-21-63, Dm1-47-63.

(33) ?—1 specimen (total length 57.2mm): Station G1-29-63.

(34) ?—5 specimens (total lengths 13.2mm-38.6mm): Stations G4-214-62, Dm3-106-62, Dm4-128-62, Dm3-116-63.

MURAENIDAE

(35) *Gymnothorax* sp. (102-109 myomeres)—15 specimens (total lengths 26.1mm-56.5mm): Stations G4-198-62, Dm4-140-62, Dm4-142-62, Dm4-146-62, Dm4-148-62, G1-17-63, Dm1-31-63, Dm2-75-63.

(36) *Gymnothorax* sp. (125-133 myomeres)—4 specimens (total lengths 13.3mm-88.7mm): Stations G4-197-62, Dm1-31-63, Dm1-39-63.

(37) *Gymnothorax* sp. (139 myomeres)—1 specimen (total length 53.5mm): Station Dm1-35-63.

(38) ?*Rabula* sp. (198 myomeres)—1 specimen (total length 68.9mm): Station Dm1-35-63:

(39) *Anarchias* sp. (119-124 myomeres)—2 specimens (total lengths 52.2mm-56.1mm). Stations G4-204-62, Dm2-71-63.

(40) *Uropterygius* sp. (98 myomeres)—1 specimen (total length 38.9mm): Station Dm2-69-63.

(41) *Uropterygius* sp. (113 myomeres)—1 specimen (total length 44.1mm): Station G4-204-62.

(42) *Uropterygius* sp. (119-125 myomeres)—3 specimens (total lengths 20.0mm-64.9mm): Stations G4-198-62, G4-202-62, Dm4-142-62.

(43) *Uropterygius* sp. (137 myomeres)—1 specimen (total length 60.8mm): Station G4-195-62.

OPHICHTHIDAE

(44) *Ophichthus* sp. (154-164 myomeres)—3 specimens (total lengths 71.0mm-84.7mm): Stations G4-198-62, G1-21-63, Dm1-36-63.

(45) ?*Muraenichthys* sp. (125 myomeres)—1 specimen (total length 34.7mm): Station G4-187-62.

(46) ?*Muraenichthys* sp. (145 myomeres)—1 specimen (total length 38.1mm): Station G4-183-62.

(47) ?*Myrichthys* sp. (108 myomeres)—1 specimen (total length 38.8mm): Station Dm1-31-63.

(48) ?*Myrichthys* sp. (119-123 myomeres)—7 specimens (total lengths 43.7mm-63.5mm): Station Dm1-31-63, Dm1-36-63, Dm2-71-63, Dm3-110-63.

(49) *Myrophis* sp. (129-134 myomeres)—2 specimens (total lengths 27.8mm-70.0mm): Stations Dm4-140-62, G1-21-63.

(50) *Myrophis* sp. (143-144 myomeres)—2 specimens (total lengths 59.9mm-72.5mm): Stations G1-7-63, G1-17-63.

(51) *Myrophis* sp. (151-161 myomeres)—4 specimens (total lengths 77.8mm-89.2mm): Stations G4-197-62, G4-198-62, Dm1-31-63, Dm1-41-63.
Others:

(52) ?—2 specimens (total lengths 68.4mm-72.6mm): Stations Dm4-150-62, Dm2-63-63.

(53) ?—1 specimen (total length 173.1mm): Station G1-1-63.

XENOCONGRIDAE

(54) *Kaupichthys hyoproroides* (Strömman, 1896)—5 specimens (total lengths 32.9mm-62.9mm): Stations G4-198-62, G4-204-62, Dm4-146-62, Dm1-31-63.
Others:

(55) ?—1 specimen (total length 56.0mm): Station Dm3-99-63.

(56) ?—3 specimens (total lengths 38.2mm-61.0mm): Stations Dm4-146-62, G1-29-63, Dm1-31-63.

MORINGUIDAE

(57) *Moringua macrochir* Bleeker, 1855—1 specimen (total length 23.2mm): Station G4-187-62.

(58) *Moringua* sp. (106 myomeres)—1 specimen (total length 40.2mm): Station Dm4-146-62.

Others:

(59) ?—1 specimen (total length 23.9mm): Station Dm4-132-62.

FAMILY UNKNOWN

(60) ?—1 specimen (total length 67.7mm): Station G4-204-62.

(61) ?—1 specimen (total length 75.6mm): Station G4-204-62.

(62) ?—6 specimens (total lengths 22.1mm-48.9mm): Stations Dm4-162-62, Dm1-31-63.

(63) ?—3 specimens (total lengths 44.3mm-64.5mm): Stations Dm1-39-63, Dm2-69-63, Dm2-71-63.

IV (b). **List of stations and species**

Cruise	Station	Date	Lat. S.	Depth m	Species and number of specimens								Total	Standard haul
					1	2	5	6	10	19	22	others		
G 4/62	181+	19/8	31°58′	210				1					1	
	183	20/8	30°42′	290		7		13	5			46:1	26	30
	185	21/8	27°42′	245	1	13		7	3	1		23:2, 28:1	28	26
	187	22/8	24°30′	210		14		24	6			13:1, 45:1, 57:1	47	50
	189	23/8	21°45′	205		5		1				7:1, 30:1, 31:1	9	9
	191	24/8	18°30′	230			1						1	7
	193	25/8	15°33′	200						1		8:1	2	2
	195	26/8	12°34′	195		1						43:1	5	5
	197	27/8	9°30′	180	1	3					3	36:1, 51:1	6	7
	198	28/8	9°07′	170	2	1	1					4:1, 14:2, 35:3, 42:1, 44:1, 51:1, 54:1	14	17
	202	7/9	10°58′	200	2	4						30:1, 42:1	8	6
	204	9/9	14°00′	310		6						39:1, 41:1, 54:1, 60:1, 61:1	11	10
	206	10/9	17°00′	190		1				1		32:1	3	3
	208	11/9	20°00′	300						1			1	1
	210	12/9	23°00′	260		3							3	3
	212	13/9	26°00′	200		4		2				7:1	7	6
	214	14/9	29°00′	260		5		15		1		23:3, 34:1	25	21
	216+	15/9	32°00′	200		1		2	1	1			5	—
Dm 3/62	102	25/9	32°00′	400				6					6	5
	104	26/9	33°24′	200		3		5	1				9	10
	106	27/9	36°12′	200		1						34:2	3	3
	108	28/9	39°00′	200		1		2					3	3
	110												0	
	112												0	
	114	1/10	44°36′	200								27:1	1	1
	115		43°12′										0	

+Day station

Cruise	Station	Date	Lat. S.	Depth m	Species and number of specimens								Total	Standard haul
					1	2	5	6	10	19	22	others		
Dm 4/62	126	16/10	31°57′	200		7		16	1			30:1	25	23
	128	17/10	30°30′	200		1		7		1		20:1, 34:1	11	12
	130	18/10	27°00′	200		15		5	1			23:2	23	26
	132	19/10	24°00′	200		6		4	1			25:1, 28:1, 59:1	14	12
	134	20/10	21°20′	200		3				2		7:7	12	13
	136	21/10	18°30′	200		6				3		12:1, 21:1	11	15
	138	22/10	15°30′	200	1	2				2		4:1	6	6
	140	24/10	12°38′	200	1	1	1					7:1, 35:1, 49:1	6	5
	142	25/10	9°30′	200	6	1	4					14:1, 35:1, 42:1, 62:1	15	18
	146	4/11	11°00′	200	1							15:1, 35:5, 54:1, 56:1, 58:1	10	13
	148	5/11	14°00′	200	1	1						35:2	4	6
	150	6/11	17°00′	200						1		21:1, 52:1	3	3
	152	7/11	20°00′	200		12	1					11:1, 21:1	15	14
	158	10/11	29°00′	200		6		2					8	7
	160	11/11	32°02′	200		5		16		1		23:1, 28:3, 29:1	27	30
G 1/63	1+	18/1	32°00′	220								53:1	1	—
	3	19/1	30°31′	190									0	
	5	20/1	27°30′	270		4						7:1, 25:1	6	6
	7	21/1	24°50′	270		6				4		50:1	11	12
	9	22/1	21°30′	150		5	1			1		7:3	10	13
	11	23/1	18°30′	260						2	2		4	6
	15	25/1	12°30′	180		1					2		3	3
	17	28/1	9°20′	200			1					26:1, 35:1, 50:1	4	5
	21	8/2	11°00′	200			1				1	4:1, 12:1, 14:2, 44:1, 49:1	8	8
	23	9/2	14°00′	250								31:1	1	1
	25	10/2	17°00′	195						2		24:1	3	3
	27	11/2	20°00′	195						1	1		2	2
	29	12/2	23°10′	250		18		1		1		33:1, 56:1	22	23
	32	14/2	28°55′	250		1		7				30:1	9	10
	34	15/2	32°00′	180		1		3		3		25:1	8	7
Dm 1/63	4	30/3	30°30′	150				1		1			2	2
	7	31/3	27°30′	220		2		4		1		7:1	8	12
	11	1/4	24°36′	170		9		1		1		20:2	13	17
	16	2/4	21°30′	225		8						14:1	9	9
	21	3/4	18°30′	210		1				1	1	21:1, 32:1	5	5
	26	4/4	15°30′	200		1	1				3		5	5
	31	5/4	12°30′	210	1					1		11:1, 14:1, 35:1, 36:1, 47:1, 48:1, 51:1, 54:2, 56:1, 62:5	17	19
	35	6/4	9°30′	196	2		1			1		4:1, 37:1, 38:1	7	10
	36	7/4	9°00′	196			2					17:1, 44:1, 48:1	5	6
	39	19/4	11°00′	196	1	2					1	4:2, 36:2, 63:1	9	9

+Day station

Cruise	Station	Date	Lat. S.	Depth m	Species and number of specimens								Total	Standard haul
					1	2	5	6	10	19	22	others		
	41	20/4	14°00′	230	1							3:1, 14:1, 51:1	4	*5*
	43	21/4	17°00′										0	
	45	22/4	20°00′	240							1		1	*1*
	47	23/4	23°00′	240		6	1				1	18:1, 32:1	10	*9*
	49	24/4	26°00′	190		3		1					4	*4*
	51	25/4	29°00′	196				9				7:1	10	*11*
	53	26/4	32°00′	196		1		5				25:1	7	*11*
Dm 2/63	59	9/5	27°30′	196	1	1		3					5	*4.3*
	61	10/5	24°30′	160	1					1		31:1	3	*3.5*
	63	11/5	21°30′	195			1					52:1	2	*3*
	65	12/5	18°30′	200	2	4	3				1	12:1	11	*12*
	67	13/5	15°30′	200		1	1			1	2		5	*1*
	69	14/5	12°30′	200		1						9:1, 40:1, 63:1	4	*5.9*
	71	15/5	9°27′	175	4	1				1		3:1, 9:1, 12:2, 17:2, 39:1, 48:4, 63:1	18	*31*
	75	26/5	11°00′	195						2		14:1, 35:1	4	*4.9*
	77	27/5	14°00′	195							1		1	*2*
	79	28/5	17°00′	196							2	16:1	3	*3*
	81	29/5	20°00′	190									0	
	83	30/5	23°00′	200	3							14:1	4	*14*
	85	31/5	26°00′	210		1	2			1			4	*4*
	87	1/6	29°00′	215		3		3		1		7:1	8	*8*
Dm 3/63	91	11/7	30°30′	200		1		12					13	*15*
	93	12/7	27°30′	196		2		1					3	*3.2*
	95	13/7	24°50′	200		3	1	3	2				9	*13*
	97	14/7	21°30′	190		1						24:1	2	*1.9*
	99	15/7	18°30′	220								55:1	1	*0.8*
	101	16/7	15°30′	220		1							1	*1.1*
	103	17/7	12°30′	220	2	1					2	12:1	6	*5.3*
	105	18/7	9°30′	160		1						14:1, 16:1	3	*3.9*
	110	3/8	11°00′	200								7:1, 48:1	2	*2.9*
	112	4/8	14°00′	195						1			1	*1*
	114	5/8	17°00′	120								13:1	1	*0.9*
	116	6/8	20°00′	200								34:1	1	*1*
	118	7/8	23°00′	240			1						1	*0.9*
	120	8/8	26°00′	196		2		4	6		1		13	*9.9*
	122	9/8	29°00′	190		13		10	1			25:1	25	*26*

V. THE SYSTEMATIC COMPOSITION OF THE COLLECTION

One of the conspicuous features of the collection set out above is the large number of forms (45, or 70 % of the total) which cannot be referred to their adult species. Of these, 18 can be identified to genus (at least tentatively), seven to already described species of *Leptocephalus* (the adults of which are unknown) and 20 are as yet undescribed forms. This situation clearly reflects the relatively poor state of knowledge of the growth stages of eels in general, particularly those of the Indo-Pacific area.

In view of the present inability to identify a high proportion of forms occurring in diverse collections of the type examined in this study, the value of proceeding further with detailed analysis may perhaps be questioned. It would seem more logical firstly to make as full a survey as possible of the eel-fauna of the eastern Indian Ocean and neighbouring areas so that a more complete picture of the adult taxa present would be available to which to refer any larvae collected in the area. Coupled with this would be a collection of metamorphic specimens to determine the generic characters of larvae and a review of vertebral counts upon which to base specific identifications.

Unfortunately there has been no opportunity to undertake such a wide ranging project and it is unlikely that such correlative information will become available for some time. As a result, an important part of the micronekton taken in the area could be left with little hope of elucidation as far as its definitive systematic composition is concerned.

The present author was thus faced with an extensive quantitative collection although definitive names could not be applied to many of the taxa present. Being aware of the possibility of recognizing familial, generic and specific categories, it was proposed to deal with this collection as a series of taxa whose relationships and distribution could be evaluated without final nomenclature. Fortunately, in this study, the important numerical components (i. e. 87 % of the total number of larvae) were able to be identified to species. The collection may therefore be usefully compared with those taken in other areas where these species occur.

The systematic studies on which this work is based have been mentioned above (CASTLE, 1963a *et seq.*). These reported on a total of about 70 species and more than 30 genera of eel-larvae from the southwest Pacific Ocean and a small area west of Perth. A number of larvae (belonging to at least 15 further species) whose familial identity could not be established at the time, were not treated in these reports. In the present account, on the other hand, all species occurring are considered. Many species from both collections have yet to be formally described but the present paper is not considered to be a suitable medium for such a lengthy systematic task. Description of these species will appear elsewhere.

The tables set out in Section IV (a) and IV (b) indicate a variety and abundance of leptocephali which must clearly originate from a systematically rich eel-fauna in this part of the Indian Ocean, an area which has not been closely examined for this group of fishes. At least nine of the dozen or more major families of eels whose larval characters are known are represented in the collection. Most notably absent are larvae of the Synaphobranchidae, Heterocongridae, Muraenesocidae and Anguillidae, all of which have previously been recorded from the eastern Indian Ocean as adults. The absence of the three former families is not especially surprising, since as well as being relatively small families compared with the Congridae, Muraenidae and others, their larvae are normally rare in collections. Anguillid larvae, on the other hand, have been shown to be abundant in the area of the Mentawei Deep, off the south coast of Sumatra during September-November (the Danish *Dana* Expedition collected more than 1200 anguillid larvae at all growth stages in this area during these months in 1929). However, as JESPERSEN (1942: fig. 60) has shown, no anguillid leptocephali were recorded by the *Dana* further eastwards than about 105° E., so that present collections were probably made beyond the normal area of occurrence of anguillid larvae in this part of the Indian Ocean.

On the systematic basis elaborated in Section I above, there appears considerable generic diversity, expressed in the recognition of 43 genera in the collection. This generic composition of the catch is set out in Figure 7 (a) and Table I. The figure shows the predominance of congrid genera, amounting to about 28 % (12) of the total number of 43; nettastomatids and ophichthids are also relatively important in the total (approx. 15 %). Further analysis of the catch (as expressed in Figure 7 (b)) indicates that, of the 62 species present in the collection, congrids are again the most important (29 %), with ophichthids (16 %) and nettastomatids (14.5 %) also relatively prominent parts of the total. When numbers of individual leptocephali for each species are considered (as shown in Figure 7 (c)) the Congridae assumes an even more conspicuous place in the composition of the collection—75 % (575) of the total of 761 larvae are congrids, more than half of which consists of the two species *Ariosoma mauritianum* and *Gnathophis*

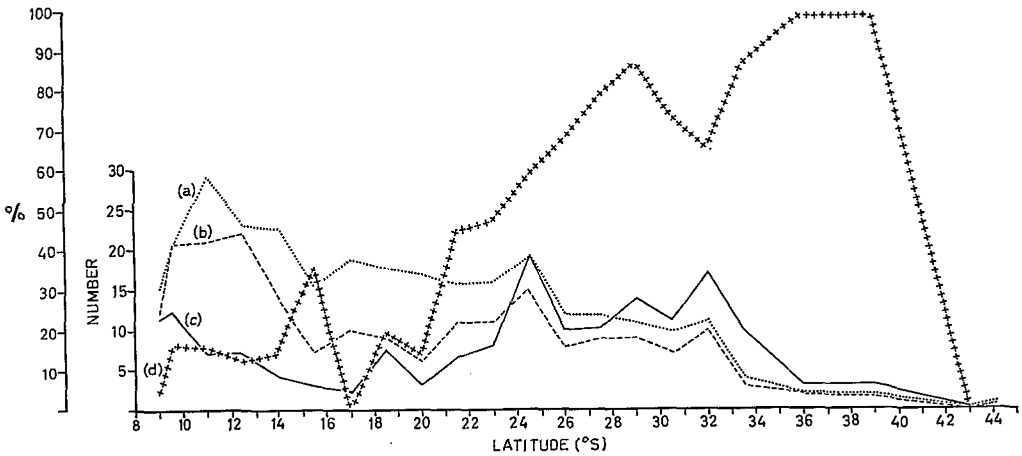

Fig. 6. — Latitudinal abundance of the various taxa along 110°E. throughout the year:— (a) theoretical number of species occurring at each latitude; (b) observed number of species occurring at each latitude; (c) number of larvae per standard haul (averaged for each point of latitude); (d) percentage of total catch contributed by *Ariosoma mauritianum* and *Gnathophis habenatus*. Left-hand scale (%) refers only to curve (d).

habenatus. These two species predominate more particularly in hauls made south of 23° S. where they make up an average of 50 % or more of the larvae in each standard haul. Figure 6 (a) shows their contribution to the catch at each position of latitude.

The relative abundance of the various taxa in the collection as expressed in Figure 7 cannot readily be explained in terms of the abundance of adults since insufficient is known about the eel-fauna of the eastern Indian Ocean. Records of eels from this area are scattered in the literature and no full species list is available although WHITLEY (1948: 12-13) records 13 genera and 19 species from the whole coast of Western Australia. Only two of these species were congrids. In previous studies of leptocephali collected during 1961-1962 by the Western Australian Museum, Perth, in a relatively small area off the coast of Western Australia near Perth, and presented elsewhere (CASTLE, 1963b *et seq.*), 13 genera and 16 species were recognized. WHITLEY (1948: 12-13) records 10 genera and 12 species from the same restricted area off southwest Australia.

It seems clear from these figures that considerable additions can be expected to the number of adult species known from the eastern Indian Ocean, particularly when more collections are made from the deeper waters and from tropical reef areas in the north.

The reasons for the overwhelming abundance of congrid leptocephali in the collection, particularly of *Ariosoma mauritianum* and *Gnathophis habenatus*, are not clear. Such abundance may well arise from the fact that congrid eels characteristically have a relatively long larval life of a year or more (as shown for *Ariosoma mauritianum* in the area—see CASTLE, 1964a: 12) and may therefore be more often encountered in plankton than would be larvae of families which typically have a more transient larval stage. Many congrid eels are known to spawn in the open ocean rather than in the more coastal shallower waters normally inhabited during their non-spawning life, and this characteristic may also account for the abundance of their larvae in the present hauls (which were made some distance from the coast). Furthermore, the greater frequency of trawling towards 32° S., that is, towards an area where the two species under discussion are known to be common (CASTLE, 1963a: 27; 1964a: 10-11), may also have contributed to the abundance of these two species in the collection. As a final comment on this matter, although no figures are available for the normal number of eggs carried by gravid females, there may possibly be a significantly greater fecundity in congrids than in eels of other

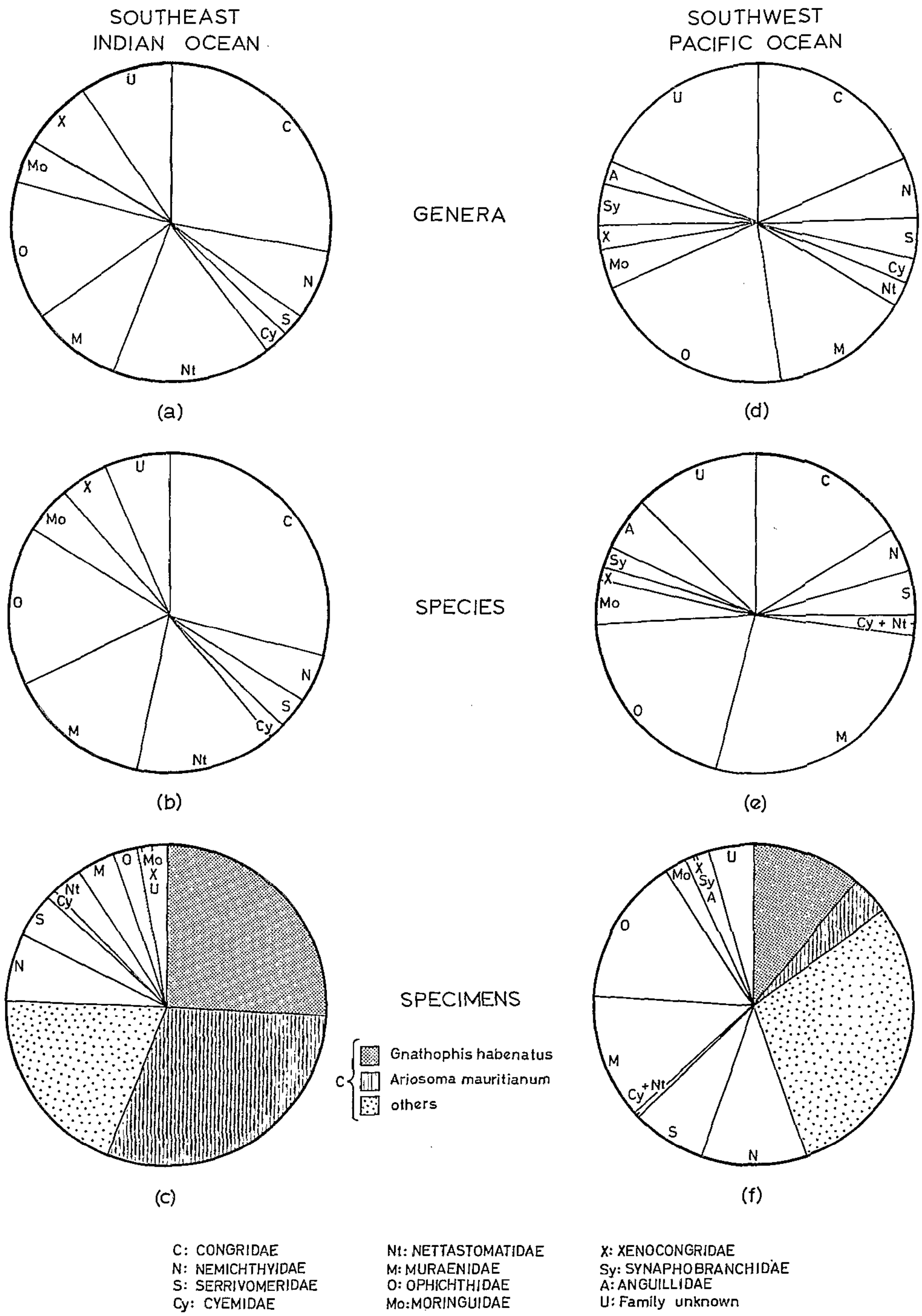

Fig. 7. — The systematic composition of the catch:— left: southeast Indian Ocean; right: southwest Pacific Ocean.

families. This might result in a greater abundance of congrid leptocephali in oceanic areas, and a consequent predominance in plankton hauls.

VI. THE RELATIONSHIP OF SYSTEMATIC COMPOSITION AND LATITUDE

An analysis of Section IV (b) shows that the number of species in hauls made along 110° E. from 9° S. to 32° S. varied considerably from haul to haul. The diversity of species was greatest at the northernmost limit of trawling, i. e. between 9° S. and 12°30′ S. Figure 6 (b) shows the species diversity along 110° E. Points on the curve (b) represent the actual number of species occurring at corresponding points of latitude as taken from the five or six hauls made at these latitudes (refer Figure 1) and listed in Section IV (b). For example, the greatest number of species (22) occurred at 12°30′ S., that is, at the position of Stations G4-195-62, Dm1-140-62, G1-15-63, Dm1-31-63, Dm2-69-63 and Dm3-103-63. At none of these individual stations, however, did the complete complement of species occur. The greatest number of species occurring at any one station was 12, at Dm1-31-63 (refer Section IV (b)).

In this northern region the average number of species per haul throughout the year was 5.5. Further southwards, between 15° S. and 20° S. there was a marked decrease in the average number of species per haul (2.5) although 10 species occurred in one haul at 17° S. Between 21° S. and 32° S. the average number per haul was 3.3, the maximum number of species occurring at any one series of stations was 15, and the maximum number in any haul was seven.

A closer study of Section IV (b) for the exact systematic composition of the catch at each station shows that there was considerable difference in the identity of the various species at each station along the meridian. For example, hauls made in the far north were richer in muraenids, ophichthids and certain congrids while congrids dominated southerly hauls. The species composition along 110° E. is plotted graphically in Figure 8 to illustrate these differences. Each horizontal line represents the extreme range of latitudinal occurrence of each of the 62 species present in the collection. The change in dominance of essentially tropical species (e. g. muraenids, ophichthids) in the north to congrids in the south can more readily be seen in the figure than from the tables in Section IV (b).

The plots of latitudinal distribution of many of the species have been constructed from only a few points, so that there may actually be gaps in the distribution of these species. The horizontal lines in the figure would not then be continuous. More information is clearly needed before such distributions can be finally determined.

If vertical lines are drawn on Figure 8 through each point of latitude it is possible to arrive at the theoretical species composition of larvae at each latitude. The theoretical or predicted number at each point of latitude is in all cases greater than the number of species observed to occur at these latitudes in the hauls. The predicted number of species along 110° E. is plotted in Figure 6 (a) and this may be directly compared with the actual number at each latitude (b). Greatest discrepancy between the two occurs at intermediate latitudes meaning simply that if distributions are continous as indicated in Figure 8, more species could be expected to occur at these intermediate latitudes. This anomaly might be explained by larvae occurring at greater depths here and beyond the limits of the IKMT hauls. In the far south and north actual species numbers more closely approach the theoretical.

Muraenid larvae and the majority of the ophichthids appear to be restricted to the waters north of 13° S. while congrids such as *Ariosoma anago*, ?*Alloconger anagoides*, *Conger cinereus* and *Uroconger ?braueri* and others also have a northerly distribution, many of them not occurring south of 25° S. The presence of these diverse species (whose adults are all essentially tropical eels) accounts for the high average number of species in hauls taken between 9° S. and 13° S. However, added to these are species which occur almost throughout the whole range of trawling: *Ariosoma scheelei*, *A. mauritianum*, *Gnathophis incognitus*, and *Nemichthys scolopaceus*. These

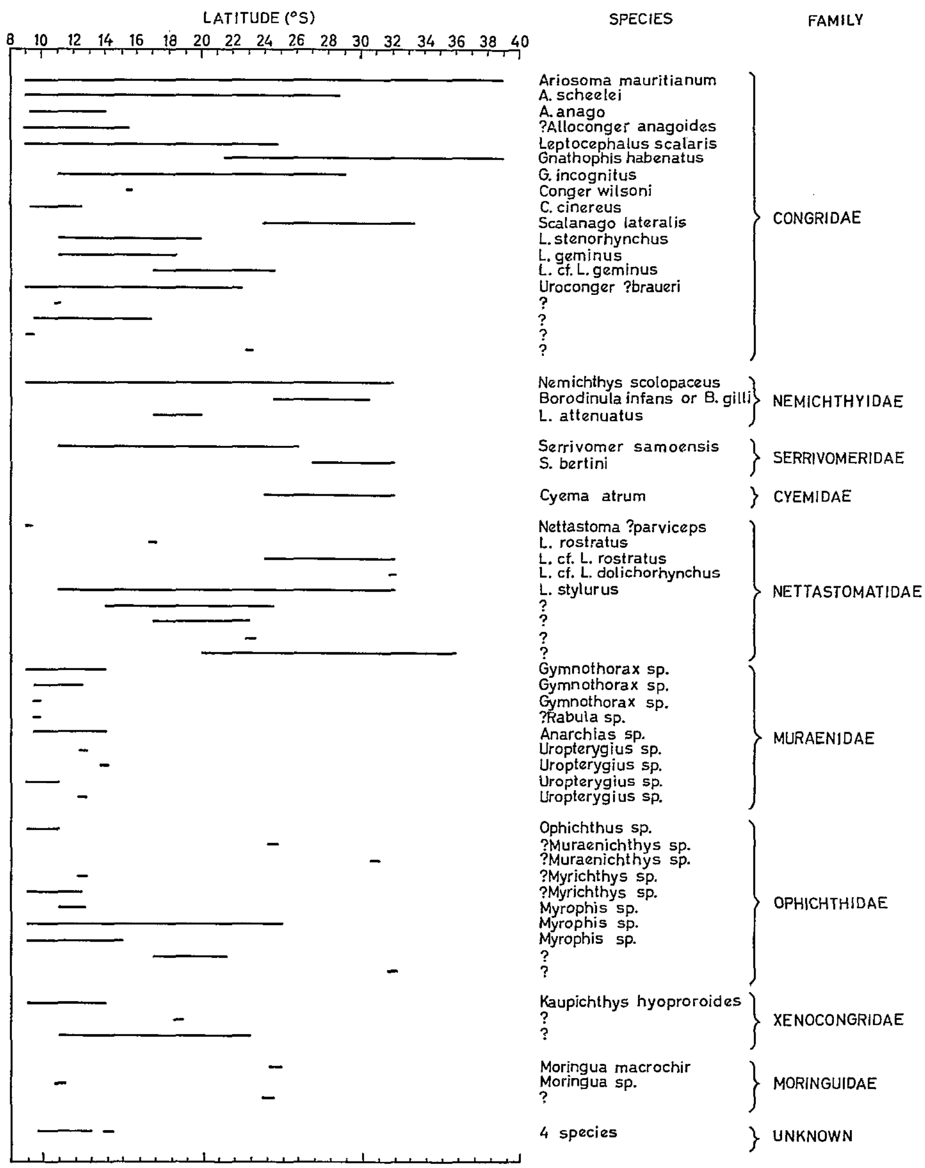

Fig. 8. — Latitudinal distribution along 110°E. of the 62 species occurring in the catch.

four species predominate in hauls made in the intermediate latitudes along 110° E. and appear to be widespread larval species, an observation noted in previous records (CASTLE, 1964, 1965) and suggesting the widespread occurrence of the adults.

South of about 24° S. the hauls are characterized by the species *Gnathophis habenatus*, *Scalanago lateralis*, *Borodinula gilli* or *B. infans* and *Serrivomer bertini*, but again superimposed on these are *A. scheelei*, *A. mauritianum*, *Gnathophis incognitus* and *Nemichthys scolopaceus*. The latitudinal range of seven of the most abundant species is plotted in Figures 9-14. (The latter also indicate the length-time relationship of individual specimens, a subject which will be discussed elsewhere in this paper).

Two species occur in hauls taken south of 21° S. in sufficient numbers and with sufficient regularity for them to be considered typically southern species. These are *Gnathophis habenatus* which occurred in 33 of the 44 hauls made at these southerly stations and *Scalanago lateralis* which occurred in 11 of these hauls. As I have noted previously (1963a: 36; 1964a: 29) both of these species probably spawn off Perth, Western Australia, and it appears from the present record, at least in their larval form, that these species are restricted to southern latitudes. Larvae of the two species of *Serrivomer* (*S. bertini* and *S. samoensis*) appear to be well separated latitudinally, the former occurring south of 26° S. (eight specimens), the latter (with a single exception), north of 21° S. (23 specimens).

VII. SEASONAL DISTRIBUTION OF THE SPECIES

A few species occurred in the collection in sufficient numbers for some comments to be made on their seasonal occurrence, latitudinal distribution at various times of the year, spawning of the adults, growth of the larvae and metamorphosis.

The most important of these is *Ariosoma mauritianum* of which there were 245 specimens ranging in total lengths from 33.9mm to 238mm and including partly-grown to metamorphic individuals. Previous studies on this species (CASTLE, 1964a: 12) suggested that adults spawn off Perth, Western Australia (as well as off Eastern Australia at about the latitude of Sydney). These previous collections from Western Australia contained very young specimens (11.1mm-19.1mm) collected in May and July, 1962 (that is, immediately before Cruise G4/62 of the present series), half-grown larvae collected in September-November, 1962 (at about the same time as Cruise Dm4/62) and full-grown larvae collected in February-April, 1962. The latter specimens are clearly members of the 1961 year-class. These observations show that spawning of *Ariosoma mauritianum* takes place here during March-April and that full-grown larvae are about a year old at the onset of metamorphosis.

The present collection confirms these observations. Figure 9 is a plot of total length against latitude of occurrence of 234 specimens of *Ariosoma mauritianum* with time (from August 1962-August 1963) indicated by various symbols to represent the six cruises. The figure shows that, in general, hauls made in latitudes of 25° S.-32° S. along 110° E. during August 1962 and July 1963 (i. e. cruises G4/62 and Dm3/63) were rich in relatively small (young) individuals. Such individuals were absent in the north at this time. At the same latitude in later months of the year larger specimens of up to 170mm total length occurred in the hauls. Concurrently, specimens of various sizes were found as far north as 9° S. Still later (January-April) from 22° S. to about 30° S. metamorphic individuals are common.

These observations are interpreted here as follows:—spawning takes place around 25° S.-32° S. in April-May, there is rapid growth to 40mm-50mm during midwinter with a movement outwards from the spawning area so that half-grown specimens may be trawled mainly during July-November at any latitude. Full growth is reached during the late summer and metamorphosis takes place in March-April in a broad area from 21° S.-27° S. The latter process may be initiated by the effect of increasing temperature and decrease in salinity that occurs by southward

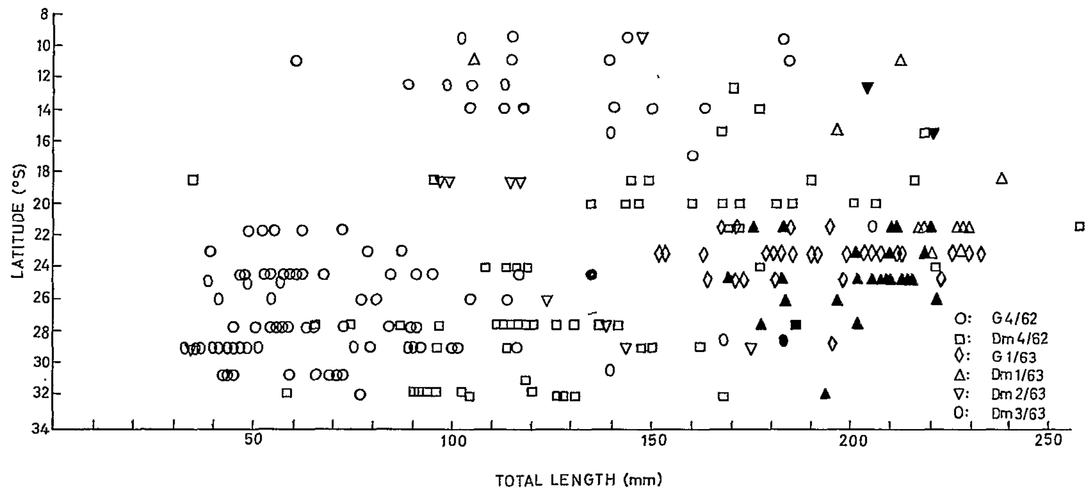

Fig. 9. — *Ariosoma mauritianum*: sizes of larvae along 110°E. The various symbols indicate the six cruises and hence time during 1962-1963. Black symbols indicate metamorphic larvae.

intrusion of tropical waters. Specimens collected at the same time of the year at more northerly stations are longer than those collected in the south. There would thus appear to be an early drift to the north where growth appears to be more rapid. The absence of full-grown or metamorphic specimens in the north suggests that full-grown specimens return to intermediate latitudes for metamorphosis, or that full-grown larvae move or are moved to some area or depth outside the limits of the investigation.

Contrasted with *Ariosoma mauritianum* is *Gnathophis habenatus*, whose length-latitude-time relationship is plotted in Figure 10. As indicated by the plot, spawning of adults takes place during mid-winter and full growth is reached by about March-May of the following year. The species is typically a southern one, the most northerly specimen recorded here is from 22° S. and the species may reach 39° S. However, the abrupt limit of northerly distribution at 24° S. of this species may only be a reflection of IKMT hauls being made too shallow. It is possible that larvae of *G. habenatus* may occur as far north as 15° S. but deeper than 200m., the larvae being associated with the deeper high salinity water mass moving northwards. The 24° S. limit appears to correspond almost exactly with the latitude at which this water mass moves below 200m. I have previously recorded (Castle, 1963a: 25-28) specimens from the southwest Pacific as far north as off Nouméa (22° S.) and from 43° S. (off Tasmania). Adults of the species are known to be gravid in early winter in New Zealand waters (Castle, 1963a: 24).

Scalanago lateralis (Figure 10) appears to be restricted to south of 24° S. and sizes of larvae suggest a spawning of the adults in June between 25° S. and 30° S., the larvae reaching full growth October-November. I have already discussed this species in a previous report (1964a: 28-29, fig. 9 E-H). Again, the apparent restriction of larvae of this species to south of 24° S. may only be the result of trawls being limited to the upper 200m. Larvae of *Scalanago lateralis* may be like those of *Gnathophis habenatus* in being associated with south Indian Central water, which moves deeper than 200m north of 24° S.

Ariosoma scheelei (Figure 11) is found as relatively small specimens in the north during winter, suggesting a northerly spawning area for this species. Some larvae move southwards to be found as 90mm-150mm specimens during early winter of the following year. Such observations accord well with those made on the distribution of the species in the southwest Pacific (Castle, 1964a: 5). It is interesting to note that only a single specimen of the species (85.8mm total length) was recorded in the latter study from close to Perth during August, 1961, while

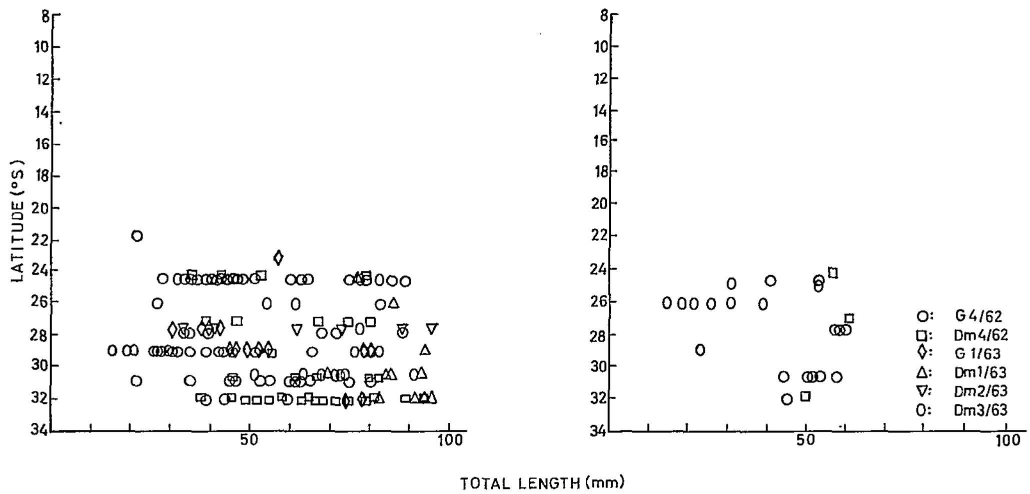

Fig. 10. — *Gnathophis habenatus* (left) and *Scalanago lateralis* (right): sizes of larvae along 110°E. The various symbols indicate the six cruises and hence time during 1962-1963.

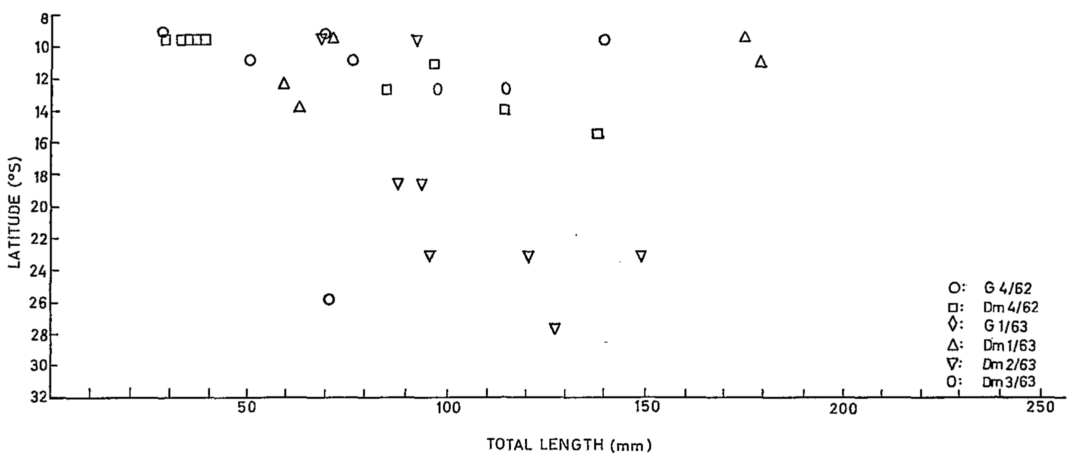

Fig. 11. — *Ariosoma scheelei:* sizes of larvae along 110°E. The various symbols indicate the six cruises and hence time during 1962-1963.

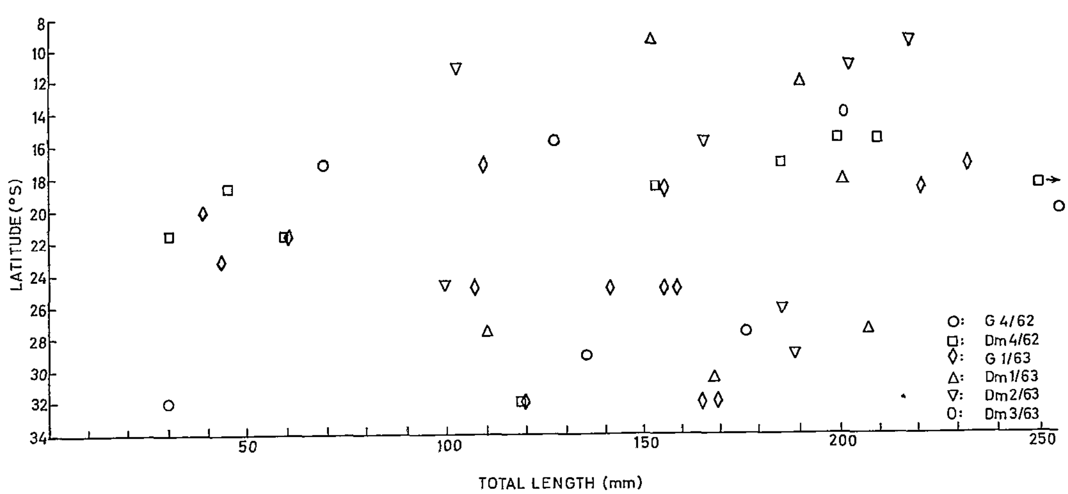

Fig. 12. — *Nemichthys scolopaceus:* sizes of larvae along 110°E. The various symbols indicate the six cruises and hence time during 1962-1963.

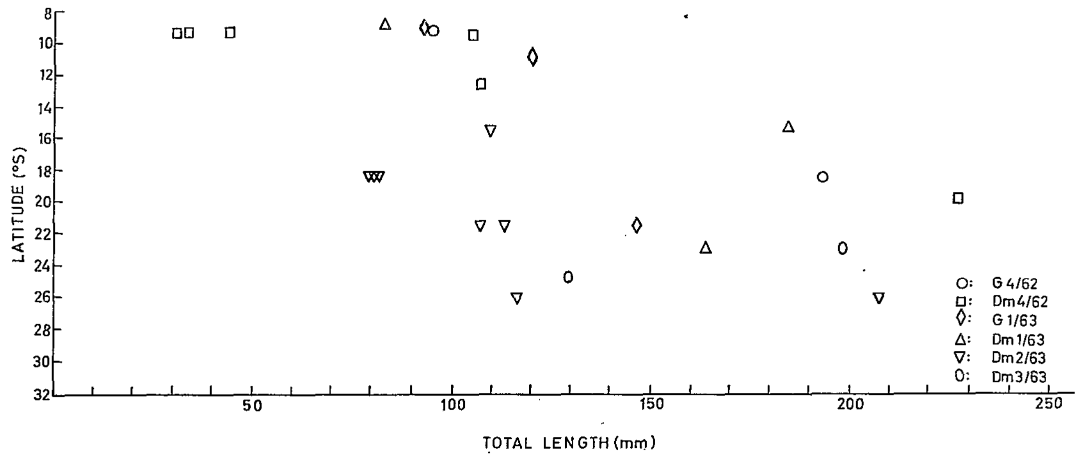

Fig. 13. — *Leptocephalus scalaris:* sizes of larvae along 110°E. The various symbols indicate the six cruises and hence time during 1962-1963.

47 specimens of *A. mauritianum* were trawled in the area also, suggesting the essential northerly distribution of *A. scheelei.*

There appears to be no observable pattern of seasonal movement in *Nemichthys scolopaceus* (Figure 12), whose larvae are widely scattered in the area. The smallest larvae seem to be located at intermediate latitudes along 110° E. but there are insufficient of these for the suggestion to be made that spawning of the adults takes place in this intermediate area. *Nemichthys scolopaceus* has a wide distribution in all oceans, both as adults and larvae, and it is likely that spawning is not restricted to widely disjunct localities.

Leptocephalus scalaris (Figure 13) is an essentially northern species, the adults of which probably spawn immediately to the south of Java during winter. At full growth the larva reaches at least 230mm and is one of the largest larvae in the present collection, being very bulky and not attenuate like the long larvae of *Nemichthys scolopaceus.* Larvae of *L. scalaris* appear to move southward during growth.

The two species of *Serrivomer* which occur in the collection, *Serrivomer samoensis* and *S. bertini* appear from Figure 14 to be clearly separated geographically. Larvae of the former, with one exception are possibly restricted to waters north of 21° S. while those of the latter appear only south of 27° S. However, this is not substantiated by Bauchot (1959: fig. 104-105) who shows that *S. bertini* is widely distributed as adults and larvae in the Central and Southwest Pacific while *S. samoensis* occurs as larvae in about 10° S. in the Pacific. However, this pattern of distribution may be related to the fact that similar hydrological conditions occur in different latitudes in the eastern Indian Ocean and the Southwest Pacific.

VIII. THE RELATIONSHIP OF HYDROLOGICAL FEATURES TO THE DISTRIBUTION OF THE VARIOUS SPECIES

With the exception of a few scattered observations on surface features the hydrological conditions of the eastern Indian Ocean were largely unknown in 1959 when the HMAS *Diamantina* began a series of cruises to investigate the area. Over the period 1959-1961 this vessel collected information on salinity, temperature, inorganic phosphate, extinction coefficient, water movements, plankton and other characteristics from a broad area extending from the Australian coast westwards to 85° E. and from the equator and Torres Straits southwards to beyond 40° S.

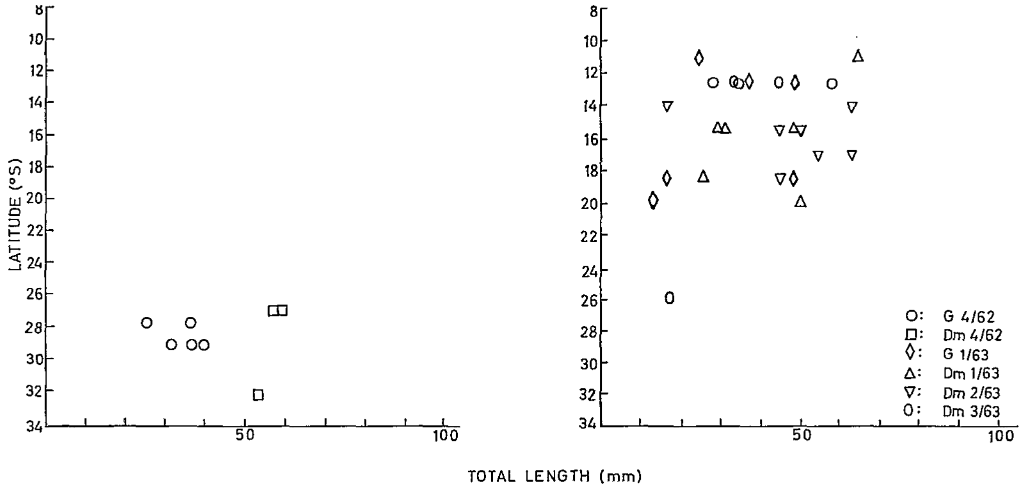

Fig. 14. — *Serrivomer bertini* (left) and *Serrivomer samoensis* (right): sizes of larvae along 110°E. The various symbols indicate the six cruises and hence time during 1962-1963.

These preliminary investigations determined the major hydrological features of this interesting area for the period of the southeast monsoon, that is, May-September, but some data were also collected for December-March. Some results of these investigations have been reported by WYRTKI (1962a, 1962b), ROCHFORD (1962, 1965) and TRANTER (1962), as well as in various cruise reports of the C.S.I.R.O. Australia.

The 1962-1963 programme along 110° E. provided more precise data on hydrological conditions in the area. These have been published in the various cruise reports of the programme (C.S.I.R.O., 1965-1967). HAMON (1965) has reported on water movements of the upper 1750m in the area and the currents across 110° E. from August, 1962 to August, 1963. Recently, ROCHFORD (1967) has studied in detail the hydrological structure of the upper 500m along 110° E. during 1962-1963. His account, which I was fortunately able to see in manuscript, has been of the greatest relevance to the present paper.

The above studies clearly demonstrate that the southeast Indian Ocean is hydrologically complex, and water conditions variable from season to season and from north to south. The hydrological characteristics of the area are considerably affected by the southeast monsoon blowing from this direction during May-September and by the northwest monsoon blowing in the opposite direction during December-March, particularly in the north. They are also greatly modified by the intrusion of various shallow and deep water masses of diverse origin from the north, west and south. Nevertheless, in broad view there are a number of distinctive features of the area which may be summarized here as relevant to the seasonal distribution of leptocephali.

On the surface the northern end of the 110° E. meridian (at about 9° S., immediately south of Java) is characterized throughout the summer by the high temperature (greater than 27.5 °C.) and low salinity (less than 34.00 $^{0}/_{00}$) water of the east-flowing Sumatra-Java Current. Although the surface temperature is high here it decreases rapidly with increasing depth due to the uplift of cooler waters arising in the south (ROCHFORD, 1967: fig. 1).

Immediately to the south of this current (10° S.-14° S.) surface temperatures are high throughout the year (greater than 26 °C.) and salinities low (less than 34.50 $^{0}/_{00}$) but the water moves to the west as the 90-mile wide South Equatorial Current. This current is supplied by water from the south, by marked upwelling (during spring) and from Timor and Java Sea water. It flows with high velocities of 30 cm/sec.-100 cm/sec. (16 miles/day-54 miles/day), although velocities in 200m are considerably less (27 miles/day maximum), and leaves the area near the Cocos-Keeling Islands to turn into the central Indian Ocean.

The high temperature, low salinity tropical waters spread southwards during late autumn and winter to as far south as 20° S. on the surface and during late summer and autumn to 26° S. in 100m-150m. Cooler (20°C.-22°C.), high salinity (greater than 35.90 °/oo) subtropical waters forming the West Australian Current between 110° E. and the Australian coast, flow northwards on the surface to 25° S. during the summer while subtropical high salinity water also flows northwards in 200m-300m to 12° S. in summer and 16° S. in winter. Waters deeper than 300m are variously influenced and need not concern us here since they are well outside the limit of the IKMT hauls. There appears to be little enrichment of the surface layers by nutrients, even during the spring period of maximum upwelling of deeper waters in the far north.

West of Perth across 110° E. eddy conditions may occur to some considerable depth (Wyrtki, 1962a: 4; Hamon, 1965: 270-271) although there is no apparent regularity in the time of appearance or direction of the eddy.

In general along 110° E. the effect of warm, low salinity tropical waters extends on the surface (and perhaps in deeper layers) to about 20° S., mainly during late autumn while cooler, high salinity subtropical waters reach 12° S.-16° S. during the summer and tend to flow deeper than the tropical waters intruding from the north. However, there is no distinct thermic barrier which can be drawn at a particular latitude between these two types of water.

The summary given above outlines very briefly the hydrological conditions obtaining along the meridian from August 1962-August 1963, and the main water masses responsible for the change in characters in various latitudes, depths and times of the year. It no doubt oversimplifies the complex pattern and reference should be made to the relevant papers for more accurate details. In relation to these features, some comments may be made on the factors limiting the distribution and movement of the eel-larvae. It should be noted again that the IKMT hauls were oblique so that the larvae present in each haul could have come from anywhere within the upper 210m which was the average maximum depth of sampling. The oblique nature of the hauls would not appear to be so critical in the south where the hydrological conditions changed only moderately with increasing depth although seasonal changes in the same area were more marked. In the north, however, particularly around 10° S.-14° S., temperature varied markedly with depth (from 25.5 °C. on the surface to 17.5 °C. in 100m during September 1962 and from 28.9° C. on the surface to 18 °C. in 100m during April 1963). Oblique hauls in 200m in this area would therefore mask any differences in vertical level taken up by larvae in this area. There is some suggestion from the present study that certain larvae may enter different water masses during their later larval life. It would therefore be of considerable interest to examine the vertical distribution of eel-larvae in selected areas to substantiate this suggestion.

There appear to be two major areas in which relatively small leptocephali appear at certain times of the year. These small leptocephali indicate the proximity of spawning areas of adults. Little is known of the growth rates of eel-larvae in differing physical conditions but larvae of less than 20mm-30mm probably would not be much older than a few weeks and therefore could not have moved far from the spawning area of their adults. These two areas are in the north, over the Sunda Trench and in the south, west of Perth. The northern area is apparently suitable in hydrological conditions, as well as in its proximity to areas of adult distribution, for the spawning of tropical species, especially those belonging to the Muraenidae, Ophichthidae and Congridae. Figures 2-4 indicate that small larvae in moderate numbers occur here during the spring period of maximum uplift of deeper waters. Temperatures here at this time are about 18 °C. in 100m but are very much higher on the surface (Rochford, 1967: fig. 18 & 23), while salinities are low (about 34.00 °/oo). Spawning of these tropical species probably takes place in 100m and thus occurs at relatively low temperatures and salinities. Much larger but fewer larvae occur here again in March during the autumn uplift and extend to the south to 20° S. with the tropical low salinity water mass (Rochford, 1967: fig. 18-19). The distribution of larvae closely follows that of the surface water and it is possible that older larvae may enter these waters from below. The young larvae must immediately be subjected to the strong westward-trending water movement of the South Equatorial Current which arises in this area of possibly 20 miles per day. The minimal occurrence of larvae in this area later in the year (January-March) suggests that larvae are moved from the spawning area by this current, although by entering the uppermost surface layers the larvae could effectively be moved eastwards during the reversal of surface movement of the northwest monsoon. Whether or not larvae could survive the markedly higher temperature in surface waters is unknown. There is again always the possibility that larvae may move to deeper waters and so have not appeared in the collection.

Small larvae of various species also occur west of Perth, mainly during late winter and early spring, indicating the location of a second major area in which essentially southern species spawn. The presence of eddy conditions across 110° E. in this latitude throughout most of the year undoubtedly influences the later distribution of larvae arising in this area. Water of relatively low temperature (18 °C.) and high salinity (35.50 ‰) occurs here during the winter spawning period of adults. Larvae commonly remain in this area during growth but apparently may also escape from it and appear in more northerly areas after May, undoubtedly under the influence of the northward-flowing South Indian Central water mass. At least one species which is common in the south however, occurs as relatively large larvae as far north as the Sunda Trench, its movement northwards possibly assisted by upwelling water *(Ariosoma mauritianum)*.

Between these important northerly and southerly limits lies a broad belt of warm, moderately saline water throughout the year. This seems to be an effective barrier to the further distribution northwards of essentially southern species and the movement southwards of tropical species, with the exception of a few species which occur along the whole length of 110° E., and which can obviously cross the belt of intrusive central Indian Ocean water. The presence of favourable northerly trending currents undoubtedly aids this movement.

The major limiting factors for eel-larvae along 110° E. therefore seem to be temperature and salinity, although the action of water movements may also determine the presence of larvae in any particular area and whether larvae may remain in this area throughout larval life. The northern limit of southern species and the southern limit of northern species seem to be determined by the limits of influence of cooler, high salinity subtropical waters and warm, low salinity tropical waters respectively. This is around 20° S. and agrees remarkably well with the division found in stomatopod larvae from material collected in the present series of cruises (MICHEL, 1968).

IX. COMPARISON WITH LEPTOCEPHALI COLLECTED IN THE SOUTHWEST PACIFIC

Studies on collections of eel-larvae have in the past been concerned essentially with the description and identification of the great variety of forms that are now known. The difficulties encountered in arriving at definitive identifications or even in distinguishing between genera and species have been a barrier to ecological studies despite the fact that eel-larvae have always been considered important in plankton collections. The situation has changed a little over recent years and at least a number of the more common species in the Atlantic and Indo-Pacific are systematically well-known so that there is a more reliable basis for ecological studies. The International Indian Ocean Expedition, for which collecting techniques and programmes were largely standardized and carefully designed, has enabled quantitative data on hydrological and biological conditions to be gathered from the Indian Ocean, so that the environmental conditions of eel-larvae, amongst other organisms, can be more reliably elucidated. The present study has by no means solved the earlier difficulties of identification posed by systematic studies. Rather it accentuates the fact that in some oceanic areas more forms of larvae are now known than adults.

There have been a number of systematic studies on eel-larvae which have dealt with features of the general biology of this group. LEA (1913) described a collection of eel-larvae from the Central Atlantic, while the many researches of SCHMIDT on the life-history of Atlantic *Anguilla* have become the basis for similar work on other genera. ROULE & BERTIN (1929) have examined the larvae of the Nemichthyidae in their intensive study of this group while BRUUN (1937) dealt with the Synaphobranchidae. The most exhaustive studies of specialized larval groups were by JESPERSEN (1942) on Indo-Pacific *Anguilla* and BAUCHOT (1959) on larval serrivomerids. There has thus been no study comparable to the present one, in its treatment of a general collection of eel-larvae in relation to seasonal hydrological conditions.

During 1956-1962 the Centre O.R.S.T.O.M., Nouméa conducted exploratory work to gather information on the hydrology, plankton and micronekton of a wide area of the southwest Pacific. A detailed seasonal investigation of a particular meridian, similar to that reported on here, was not included in these studies. I have previously reported on the bulk of the 550 leptocephali collected in this programme (CASTLE, 1963a-1967) but these studies are essentially descriptive. It is hoped that in the future more specific investigations in this area may be carried out to parallel the work of the six Indian Ocean cruises.

Even so, there are a number of comparisons which can be made here, particularly in relation to similarities of larvae from the two areas, spawning conditions and relative abundance of the various taxa. Many of the species recorded in the present paper also occur in the southwest Pacific. At least 25 species occur in both areas. The presence of small specimens of many of these indicates that spawning of the adults takes place in the Pacific, as well as in the Indian Ocean. There is a strong possibility of interchange of individuals between the two areas either by way of pelagic larvae and/or by the movement of adults, but whether this interchange is one-way or mutual, remains to be determined. Detailed studies of series of adults from the two areas would possibly provide the necessary information on this matter.

The leptocephali described from the southwest Pacific in my earlier accounts were collected in various ways (viz. by trawls, as beachcast specimens and from the stomachs of other fishes). Quantitative figures on the abundance of larvae at various latitudes in the Pacific from season to season similar to those determined from the present collection are therefore not available.

TABLE I.—Systematic composition of the catch of leptocephali in the Southeast Indian Ocean and Southwest Pacific Ocean.

FAMILY	GENERA (% total)		SPECIES (% total)		SPECIMENS (% total)	
	I.O.	P.O.	I.O.	P.O.	I.O.	P.O.
Congridae	27.9	18.4	29.0	16.1	75.5	41.6
Nemichthyidae	7.0	6.1	4.8	4.3	6.7	13.6
Serrivomeridae	2.3	4.1	3.2	4.3	4.6	7.3
Cyemidae	2.3	2.4	1.6	1.1	0.7	0.1
Nettastomatidae	16.3	2.3	14.5	1.1	3.1	0.2
Muraenidae	9.3	14.3	14.5	26.8	3.8	13.1
Ophichthidae	14.0	20.4	16.1	20.4	2.5	14.7
Moringuidae	4.6	4.1	4.8	4.3	0.4	1.9
Xenocongridae	7.0	2.4	4.8	1.1	1.2	1.2
Synaphobranchidae	0	4.1	0	2.4	0	0.1
Anguillidae	0	2.4	0	5.4	0	1.4
Unknown	9.3	18.9	7.0	12.7	1.3	5.2

Note: Indian Ocean figures calculated from data in Sections IV (a) and IV (b); Pacific Ocean figures from data presented in Castle (1963a *et seq.*). Refer to Figure 7.

More collections were made in tropical waters (around the north of New Caledonia i. e. 10° S. to 22° S.) than in more southerly latitudes thus introducing a bias towards larvae of tropical species. As my previous studies were spread over several papers I was not able to consider the systematic constitution of the collection as a whole in the same manner as possible here with the Indian Ocean collection. I have therefore included in Figure 7 (d-f) diagrams representing the percentage composition of the southwest Pacific collection in terms of genera, species and individual larvae. These figures may be directly compared with the similar figures constructed from the analysis of the Indian Ocean collection. Details are given in Table 1.

The figures show that congrid larvae were very much less dominant in the southwest Pacific collection (41.6 %) compared with that from the Indian Ocean (76.6 %). *Gnathophis habenatus* (10.9 %) was again the most prominent species but was by no means as common as in the Indian Ocean (25.8 %) collection. Larvae of *Ariosoma mauritianum* (3.8 %) were much less frequent 32.2 %), while those of *A. scheelei* (7.9 %) were slightly more prominent than in the Indian Ocean (3.9 %). *A. anago* appears to be a much more common larval species in the southwest Pacific. Muraenid and ophichthid larvae are much more typical of this latter area also. The presence of larvae of the Anguillidae in the southwest Pacific is notable, compared with its entire absence from the Indian Ocean collection, although, as already pointed out, the trawling programme here was problably placed outside the limits of distribution of anguillid larvae in the eastern Indian Ocan.

The differences in composition of collections made in the two oceanic areas, as indicated in Figure 7, are considerable but almost certainly do not reflect any fundamental difference in the structure of the eel faunas of these regions. Rather, these differences can probably be explained in part by two factors, both of which are related to the nature of the sampling.

The Pacific Ocean hauls were made largely by open plankton nets where the effect of « avoidance » of the net by large larvae is probably much higher than when an IKMT is used (Indian Ocean). Congrid larvae are generally of greater average size than those of many other eel families and the « avoidance » of congrids of the open plankton net, and hence their lesser importance in the whole collection, is likely to be greater. On the other hand « escapement » from the open plankton net for species average size is small (typically muraenids and ophichthids) is also likely to be less than from the IKMT.

Furthermore, the Pacific hauls introduce bias towards tropical species (e. g. muraenids, ophichthids) because they were generally made more frequently in tropical waters. As a result there is a greater importance of these species in diagrams 7 d-f (Pacific Ocean) compared with 7 a-c (Indian Ocean). More trawls made in subtropical waters along the east Australian coast would undoubtedly have greatly increased the proportion of congrids in the collection, particularly of *Gnathophis habenatus*, *G. incognitus* and *Ariosoma mauritianum.*

As previous systematic studies suggest, congrids typically spawn well out in the open ocean while muraenids and ophichthids probably do so in the shallow waters of adult distribution. The 110° E. meridian is located some considerable distance from the shallower waters off the west Australian coast and hauls made along it would therefore favour the collection of congrid larvae rather than those of more typically tropical families. It would seem that only the northernmost extremity of the 110° E. meridian, that is, immediately south of Java, would be a favourably placed area for spawning and early growth of muraenids and ophichthids but their larvae might be expected to occur over a much wider area, depending on the action of ocean currents.

X. GENERAL DISCUSSION

The historic studies made by Johannes Schmidt on larvae of the North Atlantic species of *Anguilla* and later by Jespersen (1942) on Indo-Pacific *Anguilla* larvae are the most informative works available on the early life-histories of eels. Other groups of eel-larvae have also been examined, but in much less detail than these definitive biological studies. Apart from these studies very little is known about quantitative aspects of leptocephalid distribution or the environmental characters associated with eel-larvae.

The Indian Ocean collection is therefore a valuable one in many ways. It is the first major systematic collection from the area and therefore provides a lead to the nature of the adult eel-fauna, which is largely unknown. It is also the first collection of eel-larvae to be taken in a quantitative manner along a strictly defined meridian of longitude. The section of the meridian examined passes along 2000 miles, through waters ranging from tropical to temperate, thus providing information on a wide variety of oceanic habitats. The year-long study provided also a unique opportunity for seasonal aspects of distribution to be examined. This is of particular interest since most eels probably have a larval life of a year or less and the study would therefore theoretically encompass the major part of the larval life of the species occurring along the meridian. Of perhaps greater interest in determining the nature of the environment of eel-larvae is that detailed hydrological information is also available from the examination of the 110° E. meridian, to be matched against the micronekton hauls.

Although the coverage of the Indian Ocean collection is unique in its extent and detail it would have been useful to have had information on the vertical distribution of larvae in the upper 200m-300m. It seems quite clear from the hydrological studies of ROCHFORD (1967) that these upper waters may be significantly stratified into distinctive water masses. It is certainly likely that many species may be restricted to particular layers, corresponding with such specific water masses.

It would also have been interesting to have had larval collections taken by other gear to fill the gap resultant from the relatively low efficiency of the IKMT for sampling larvae of small size. Such larvae are of particular value in locating spawning areas of adults.

In fact, the programme undertaken during the six cruises did include zooplankton sampling by other gear. Vertical hauls through the upper 200m were made with the Indian Ocean Standard Net and horizontal tows made simultaneously in 200m, 50m and 0m with Clarke-Bumpus Samplers. However, leptocephali in these samples, if any, have not yet been reported on.

Although not a serious shortcoming of the present investigation, complete definitive identifications of the minor species in the collection might also provide additional worthwhile zoogeographic information. Unfortunately, systematic studies on eel-larvae are not yet sufficiently advanced to complete this aspect of the present work. Finally, while it would have been useful to have had samples along the meridian during December 1962, this month does not appear to be a critical one in relation to the abundance and distribution of eel-larvae.

The species structure and abundance of eel-larvae along 110° E. shows wide variability according to latitude and time-of-year. This is associated with the variability of environmental factors, particularly those of temperature and salinity. Tropical through to temperate facies are exhibited from north to south and this is reflected in tropical dominance in the north, subtropical-temperate dominance in the south. Intermediate latitudes show a transitional fauna, but only when the whole of the upper surface waters is considered. Throughout the year the latitudinal extent of influence of these components depends upon the southward or northward movement of relevant water masses.

The proximity of the neighbouring Indonesian Archipelago to the northern limit of 110° E. appears to influence greatly the species structure of this area. Larvae occurring here are probably derived from adults of tropical eels which live along the Java coast or in offshore waters and spawn there or over the much deeper Sunda Trench. The contribution of adult eels from the coast of northwest Australia is probably weak since it lies rather far to the east. Most of the smaller specimens in northern hauls, however, are congrids and it is possible that only these spawn over the Sunda Trench while the muraenids and ophichthids do so in shallower waters.

Developing larvae of the latter may move out into the open ocean and appear in hauls made in the far north. The more southerly influence of the tropical component is mostly contributed to by tropical spawning congrids which typically inhabit the open ocean during larval life.

The strong westward movement of the South Equatorial Current, arising in the north of 110° E., must clearly determine the westward movement and dispersal of larvae of the tropical component in particular. This current, consisting of tropical low salinity water cuts across 110° E. at about 10° S. to 14° S., that is, in the exact position where species diversity along 110° E. is greatest. A westward dispersal of larvae from this area into the central Indian Ocean could thus be expected. It is certain that most species subjected to this current would reach Christmas Island and the Cocos-Keeling Islands. It is, however, a matter of speculation whether they would then be capable of further westward movement to enter the western Indian Ocean where metamorphosis might take place and the young become established. The distance from 110° E. to Mauritius, 3700 miles, is such a considerable one that it could only be crossed by larvae capable of a long pelagic life. Although the South Equatorial Current can have a very high velocity (over 50 miles per day) this is only at the point and time of its maximum development across 110° E. Its velocity further to the west is very much less and it seems unlikely that larvae could be transported westwards at greater than about 15-20 miles per day.

A recent newspaper report (« Eastern Province Herald », Port Elizabeth, South Africa, 25.1.69), which I have confirmed, has some bearing on this matter. This report concerns a bottle thrown from a ship into the sea « off the west coast of Australia » on 21.8.67. This object was retrieved in late January 1969 at Lawrie's Bay, 12 miles west of Port Elizabeth, a straight line distance from the 110° E. meridian of about 5000 miles. This represents a drift of approximately 10 miles per day for the 17-month period during which the bottle was in the ocean. However, taking into account the probable course of drift through the central Indian Ocean and southwards through the western Indian Ocean, the distance travelled is likely to have been appreciably more. The rate of drift was thus possibly somewhat higher than the 10 miles per day estimated. Whatever the precise figures are in this case, the report lends very definite factual support to the proposal that a movement westwards across the Indian Ocean is quite possible within the year-long larval life of certain eels, particularly congrids.

There is considerable similarity between the tropical eel-fauna of the Indonesian Archipelago and that of the western Indian Ocean. The South Equatorial Current may well have provided, and may well be providing, the pathway by which this similarity has developed, although movement of individual larvae or the gradual movement of species in the opposite direction, from west to east, could also occur. Amongst the many eel species which are known from both sides of the Indian Ocean are those of the genus *Ariosoma*. Although *A. anago* has been considered to be widely distributed in the western Indian Ocean, current studies indicate that it is *A. scheelei* and *A. mauritianum* which occur here. *A. anago* appears to be a Central and North Pacific species but has been confused with other species of the genus.

The southernmost part of the 110° E. meridian, west of Perth, delimits the centre of dispersal of the southern component in the collection. More typically southern species (mainly congrids), which probably inhabit as adults the shallow and offshore waters of the west Australian coast, spawn here and growth of their larvae takes place here also. The influence of this southern component to the north is that of the subtropical high salinity waters of this region, that is, the shallow West Australian Current and the deeper South Indian Central water mass. Spawning therefore probably takes place upcurrent of the area of adult distribution, although little is known of the distribution of eels along this part of the Australian coast. It is possible that larvae originating in this area, moving northwards, are turned to the west in intermediate latitudes into the central Indian Ocean. It would seem unlikely that they would be capable in one generation of crossing the considerable distance into the Western Indian Ocean and becoming established there as adult eels.

The collection also contains certain species which occur both in the north and in the south. These are almost exclusively larvae of deepwater species (e. g. *Nemichthys scolopaceus*, *Cyema atrum*, many of the nettastomatids) with one notable exception *(Ariosoma mauritianum)*. The latter is more characteristic of the south but occurs in moderate numbers in the far north suggesting that in its larval form at least, the species can tolerate water of varying temperature and salinity. The species is known to be widely distributed in the southwest Pacific as well as throughout the western Indian Ocean.

Knowledge of the distribution of eel-larvae in the southwest Pacific is now considerable. Many species occurring in the present collection are known also from the southwest Pacific although it seems clear that there are distinct spawning areas of the adults in each region. There may be some interchange of individuals between the two areas, either as larvae or as adults. However, adults of species common to the two areas are so poorly known in the eastern Indian Ocean that it is a matter of speculation just how similar they are to those of the southwest Pacific. Close comparison of adults might possibly give a lead to whether there is much interchange between these two oceanic areas. Tropical influence appears to extend less to the south in the eastern Indian Ocean than in the southwest Pacific, possibly due to the inhibiting effect of northward moving subtropical waters.

XI. SUMMARY

1. Eel-larvae (leptocephali) are abundant in subsurface waters of the eastern Indian Ocean, a hitherto poorly-known oceanic area for this group of fishes. The abundance of larvae is not reflected by a large adult eel-fauna, but this is undoubtedly because of insufficient knowledge and collections of adult forms in this area. The present collection of larvae is very much more diverse than the known adult fauna and suggests that considerable additions to this fauna can be expected.

2. The area showing the greatest diversity of species is that immediately south of Java, from which the tropical component of the collection originates and moves southwards along 110° E. during early winter, in company with moderate to high temperature, low salinity, tropical waters to about 26° S.

3. This tropical component is rich in larval muraenids, ophichthids, certain congrids, and others. These arise from a spawning of essentially tropical species at about 100m in water of moderate temperature (18 °C.) but low salinity (34.50 ‰) immediately south of Java during midwinter. The muraenids and ophichthids tend to remain in the far north where growth to metamorphosis is rapid, but other species, particularly congrids, are capable of longer larval life and move southwards. They appear later in the year in intermediate latitudes as sometimes very large larvae.

4. Larval diversity is very much less in southern latitudes of 24° S. to 32° S. where there is an almost complete dominance of two congrid species: *Ariosoma mauritianum* (Pappenheim) and *Gnathophis habenatus* (Richardson). These two species make up the major portion of the subtropical-temperate component of the collection which arises in a southerly spawning area west of Perth, again in waters of moderate temperature (18 °C.) but of relatively high salinity (35.50 ‰). Spawning of these southern species also takes place in midwinter and the developing larvae may move northwards to about 12° S. to 16° S. under the influence of the northward movement of the South Indian Central moderate temperature high salinity water mass.

5. There is thus a latitudinal overlap of northern and southern components in intermediate latitudes around 20° S. to 26° S. but the two are probably always distinct, though at different depths in the upper 200m-300m.

6. Also present in the collection are larvae of mainly deepwater species which may occur anywhere along 110° E. and thus seem independent of the influence of tropical or subtropical waters.

7. There is considerable escapement of very small larvae from the Isaacs-Kidd midwater trawl so that figures for biomass and larval numbers from hauls taken in the area by this gear must be viewed as minimal estimates.

8. Larvae are clearly smaller and more abundant in the far north and south of 110° E. during midwinter, indicating the proximity of these larvae to the spawning areas of the adults. Larger larvae of many species occur in intermediate latitudes during spring, summer and autumn. It is here that metamorphosis of *Ariosoma mauritianum* occurs, possibly initiated by changes in temperature and salinity of its environment, due to the intrusion of different water masses.

9. Biomass of eel-larvae is greatest during early winter at 26° S. but other maxima occur in early winter from 9° S. to 17° S. and at 23° S. during midsummer.

10. The seasonal and latitudinal distribution of eel-larvae along 110° E. and the location of spawning areas is largely governed by the location and movements of associated water masses, the main physical determinants being temperature and salinity. Eddy conditions may also determine whether the larvae of particular species remain in the spawning area throughout larval life.

11. There is an apparent strong dominance of the Congridae in the eastern Indian Ocean but this may only be a reflection of the location of hauls, congrid larvae being more characteristic of southern latitudes here. The Nettastomatidae, Muraenidae and Ophichthidae are also features of the area.

12. Comparison with samples made in the southwest Pacific shows that the tropical component extends further to the south in the latter area. This is no doubt related to a more southerly influence of tropical water masses in the Pacific as compared with the inhibiting effect of northward moving subtropical water in the eastern Indian Ocean.

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