1. INTRODUCTION

This catalogue covers all of the presently known species of trichiuroid fishes, which includes 23 species of snake mackerels, snoeks, gemfishes, sackfishes, escolars, the oilfish and the domine (Gempylidae) and 32 species of cutlassfishes, hairtails, scabbardiishes and frostfishes (Trichiuridae) (Fig. 1). It is not a definitive work on the classification, biology and exploitation of the trichiuroid fishes, since many taxonomic problems remain and much of their biology is still unknown. It is intended as a review of what is known, and as an illustrated guide that can serve as a basis for future work.

A comprehensive review specifically for trichiuroid fishes has never been attempted. There are a number of recent revisions at the regional or family level (e.g.,Matsubara and Iwai, 1952; Tucker, 1956; Parin and Becker, 1972) but none on a global basis. The present work is based on recent extensive examination of specimens in museums and in the field by both authors, and is part of an on-going effort to revise both groups.

To avoid excessive literature citations, we concentrate on publications of specific relevance to the biology and fisheries of the species in question. Other important papers on systematics, anatomy, and distribution, as well as more general aspects of biology and fisheries, though omitted in the text, have been included in the bibliography.

1.1 Habitat and Biology

Trichiuroid fishes are voracious carnivores distributed chiefly in tropical and temperate seas at 50 to 1 500 (rarely 2 000) m depth.

Species of the Gempylidae are adapted to mesopelagic, benthopelagic, or pelagic life and most of them typically swim fast in pursuit of prey, but some species of *Diplospinus* and *Paradiplospinus* move slowly or drift while waiting to ambush prey. Species of the Trichiuridae are well adapted to benthopelagic life and typically catch prey by waiting in ambush.

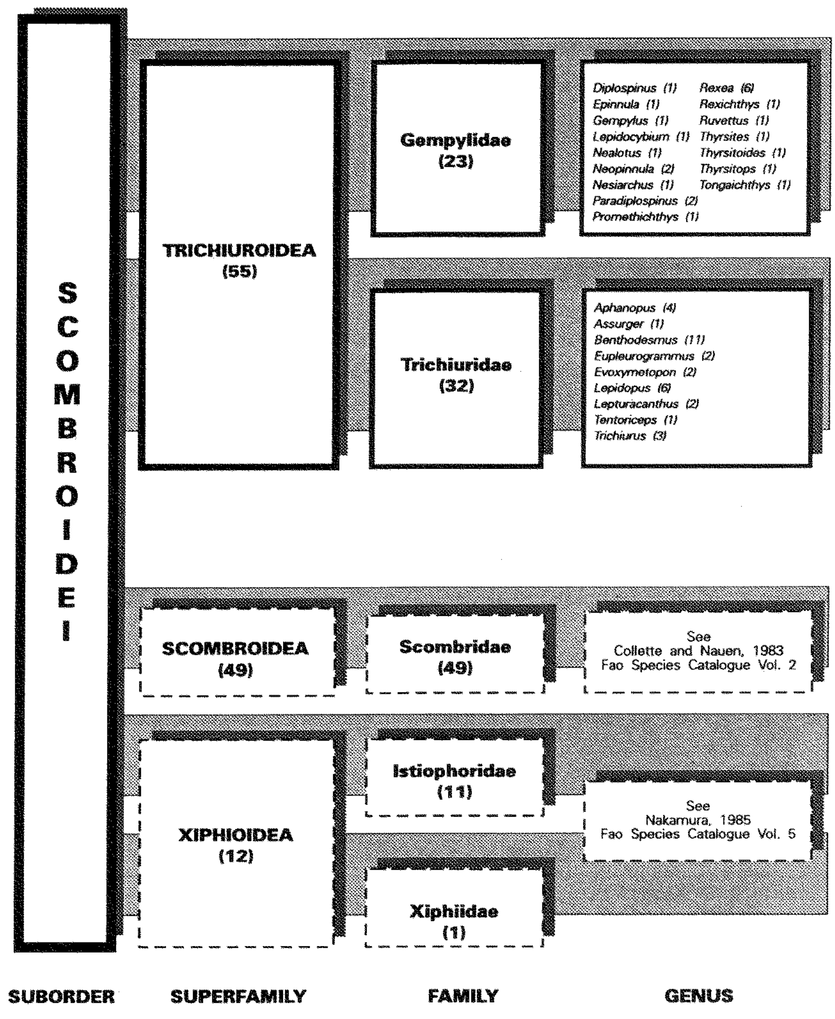

Fig. 1 Structure of the Linnean classification of the suborder Scombroidei (the families Sphyraenidae and Scombrolabracidae have also variously been included in the Scombroidei but are omitted here pending further clarification; see Collette et al., 1984, and Johnson, 1986). An alternative classification was given by Nakamura (1985) in which the billflshes (Istiophoridae and Xiphiidae) were placed in a separate suborder, the Xiphioidei

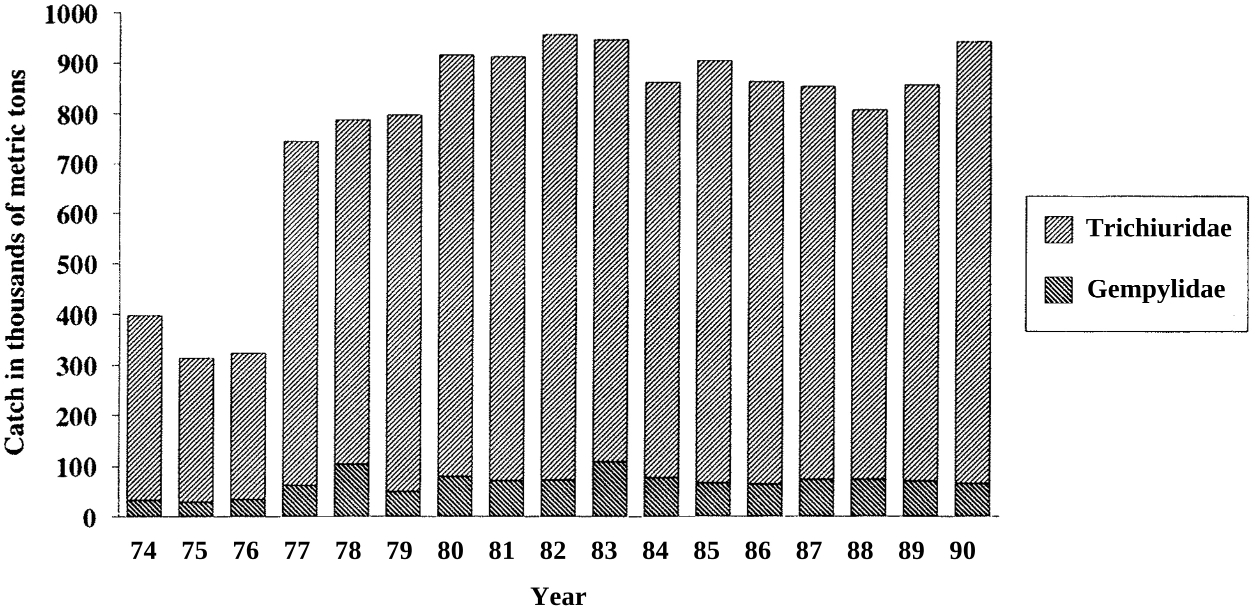

Fig. 2 Cumulative commercial landings of Gempylidae and Trichiuridae from 1974 to 1990 (from FAO, 1978,1980,1982,1992)

1.2 Fisheries

Landings of snake mackerels and cutlassfishes have contributed substantially to fisheries. In 1990, there was a total catch of 942 663 t reported globally and the catch appears to have been approximately stable for the last 10 years (Fig. 2) from a minimum of 805191 to a maximum of 956 640 t (FAO, 1992). This is likely to be an underestimate since many species are not reported, and much of the catch of trichiuroid fishes occurs in small scale fisheries and as bycatch that may go unreported. Trichiuridae contributed between 87 and 93% of the total catch of both trichiurid arid gempylid fishes in the period 1974 to 1990 (Fig. 2)

The exploitation of trichiuroid fishes varies widely among species and throughout their range (Fig. 3). They are caught by trawls, coastal set nets, shore seines and various types of angling gear. *Trichiurus lepturus* is the most important trichiuroid fish in fisheries (Table 1). *Thyrsites atun* is the second most important commercial species (Table 2), and also an important fish for sport fishing in South Africa. Other species such as *Lepidopus caudatus* and *Rexea solandri* are exploited on a smaller scale (Tables 3 and 4).

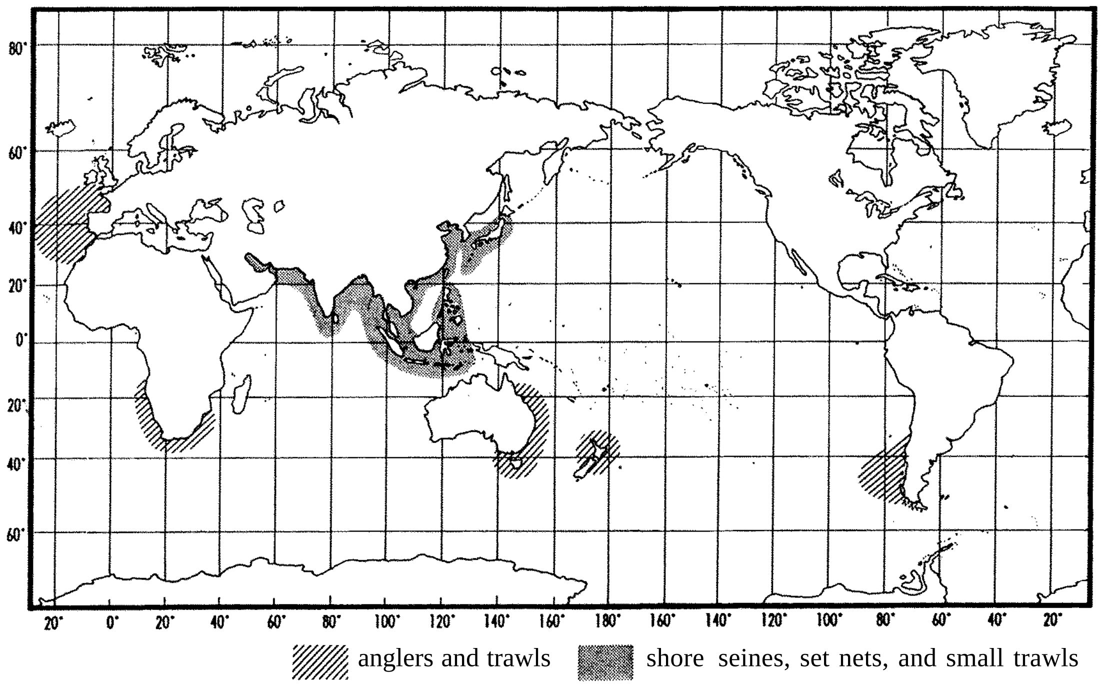

Fig. 3 Main fishing grounds for gempylids and trichiurids

Table 1
Catch in metric tons of *Trichiurus Lepturus* by country and year (from FAO, 1978,1980,1982,1992)

Year	China	Korean Republic	USSR	Japan	Total*
1973	?	124 200	24 500	41 600	251 307F
1974	?	66 391	40 710	39 262	292 296F
1975	?	120 078	22 152	32 423	214 375F
1976	?	75 555	33 414	30 563	188 237F
1977	392 515	72 032	42 530	28 035	596 733F
1978	387 164	86 065	24 090	28 085	574 470F
1979	437 206	120 723	21 174	30 518	647 815F
1980	473 315	119 980	54 467	37 805	748 716F
1981	499 012	147 677	9 415	35 097	751 486F
1982	493 373	121 960	66 838	35 948	785 643F
1983	451 772	152 633	54 494	34 851	735 415F
1984	450 030	145 413	24 570	33 602	693 448F
1985	458 723	127 608	48 190	32 037	710 344F
1986	406 403	107 561	85 261	30 195	673 920F
1987	393 606	113 446	72 339	31 883	650 222F
1988	365 730	104 392	68 376	30 912	617 616F
1989	416 202	102 399	68 114	29 806	682 818F
1990	497 733	99 460F	80 626	31 506	752 711F

*- all other countries also included; F - FAO estimate from available sources of information

Table 2
Catch in metric tons of *Thyrsites atun* by country and year (from FAO, 1978,1980,1982,1992)

Year	New Zealand	South Africa	USSR	Australia	Japan	Total*
1973	2 800	600	?	900	10 600	22 200
1974	3 375	9 721	?	708	18 252	32 324
1975	2 503	10 619	-	807	10 568	28 124
1976	3 673	16 273	-	183	10 344	33 050
1977	4 697	18 724	-	84	34 379	59 248
1978	5 197	17 162	67 568	299	10 227	100 996
1979	6 970	11 676	18 700	177	5 802	44 669
1980	8 803	17 832	34 510	121	9 463	74 725
1981	22 392	14 454	10 062	199	14 549	63 104
1982	20 290	13 077	21 951	151	7 834	64 510
1983	21 578	9 135	60 907	173	8 668	101 548
1984	21 996	10 220	27 192	375	8 763	68 978
1985	17 340	11 269	27 091	395F	-	57 699F
1986	18 019	11 281	22 299	556F	-	54 258F
1987	27 024	14 504	3 963	710F	9 002	64 334F
1988	23 691	21 225	8 948	745F	5 989	63 065F
1989	20 498	16 485	12 960	397F	5 707	61 497F
1990	24 470	20 844	1 341	792F	4 502	54 445F

* - all other countries also included; F - FAO estimate from available sources of information

Table 3
Catch in metric tons of *Lepidopus caudatus* by country and year (from FAO, 1978,1980,1982, 1992)

Year	South Africa	Portugal	New Zealand	Total*
1973	?	7 500	-	7 500
1974	?	5 025	-	5 379
1975	?	5 610	-	5 736
1976	?	5 739	-	6 149
1977	?	9 060	1	22 884
1978	?	7 467	6	9 152
1979	127	4 555	5	4 770
1980	154	5 938	2	6 095
1981	620	5 935	1	6 556
1982	400	5 495	3	6 021
1983	608	6 864	1 213	8 710
1984	943	7 369	669	9 029
1985	1 312	6 266	967	8 548
1986	1 839	4 537	1 322	7 839
1987	3 201	7 336	1 304	11 846
1988	3 700	5 339	2 816	11 928
1989	9 439	5 491	1 562	16 615
1990	14 610	4 569	2 406	21 748

* - all other countries also included

Table 4
Catch in metric tons of *Rexea solandri* by country and year (from FAO, 1978,1980,1982,1992)

Year	Australia	New Zealand	Total*
1974	496	-	496
1975	655	-	655
1976	747	-	747
1977	2112	-	2 112
1978	2383	-	2383
1979	4542	423	4965
1960	3806	1035	4 841
1981	4750	3 006	7756
1982	3919	3822	7 741
1983	3046	3416	6462
1984	2796	5 336	8132
1985	2946	5429F	8375F
1986	4151	5208F	9359F
1987	5300	4099F	9399F
1988	5562	4935F	1097F
1989	4648	4035F	8691F
1990	5 912	4339F	10251F

* - all other countries also included
F - FAO estimate from available sources of information

1.3 Systematics and Zoogeography

Most authors (e.g., Nelson, 1984; Eschmeyer, 1990) recognize that the gempylids and trichiurids are closely related within the perciform suborder Scombroidei. They are here included in the superfamily Trichiuroidae which includes 25 genera and approximately 55 species (Table 5, Fig. 1). Also included in the suborder Scombroidei is the superfamily Scombroidea or tuna-like fishes (with one family, the Scombridae composed of 15 genera and 49 species, as reviewed in the FAO catalogue by Collette and Nauen, 1983) and the superfamily Xiphioidea or billfishes (with the families Xiphiidae and Istiophoridae as reviewed in the FAO Catalogue by Nakamura, 1985). However, Nakamura (1985) presented the billfishes as a separate suborder and offered evidence (Nakamura, 1989a,b) that they constitute a different “natural group” from scombroids and trichiuroids (Fig. 4). He hypothesized that the ancestors of trichiuroids were mesopelagic fishes that gave rise to mesopelagic gempylids which radiated into both benthic trichiurids and epipelagic tunas. An alternative view was presented by Parin (1988), who suggested that the common ancestors of trichiuroids were benthopelagic neritic forms that gave rise to both benthic trichiurids and mesopelagic gempylids. He considered that within the Gempylidae the benthopelagic species such as those in the genera

Table 5
Arrangement of the Trichiuroidea according to phylogenetic order (after Collette et al., 1984). Figures in brackets refer to the number of species

Phylum Chordata Superclass Gnathostomata Class Osteichthyes Subclass Actinopterygii Infraclass Teleostei Division Euteleostei Superorder Acanthopterygii Order Perciformes Suborder Scombroidei Superfamily Trichiuroidea	
Family Gempylidae (23)	**Family Trichiuridae (32)**
Genera *Lepidocybium (1)*	*Genera* *Aphanopus (4)*
Ruvettus (1)	*Benthodesmus (11)*
Epinnula (1)	*Lepidopus (6)*
Neoepinnula (2)	*Eupleurogrammus (2)*
Thyrsitops (1)	*Evoxymetopon (2)*
Thyrsites (1)	*Tentoriceps (1)*
Rexea (6)	*Trichiurus (3)*
Rexichthys (1)	*Lepturacanthus (2)*
Promethichthys (1)	*Assurger (1)*
Nealotus (1)	
Thyrsitoides (1)	
Nesiarchus (1)	
Tongaichthys (1)	
Gempylus (1)	
Diplospinus (1)	
Paradiplospinus (2)	

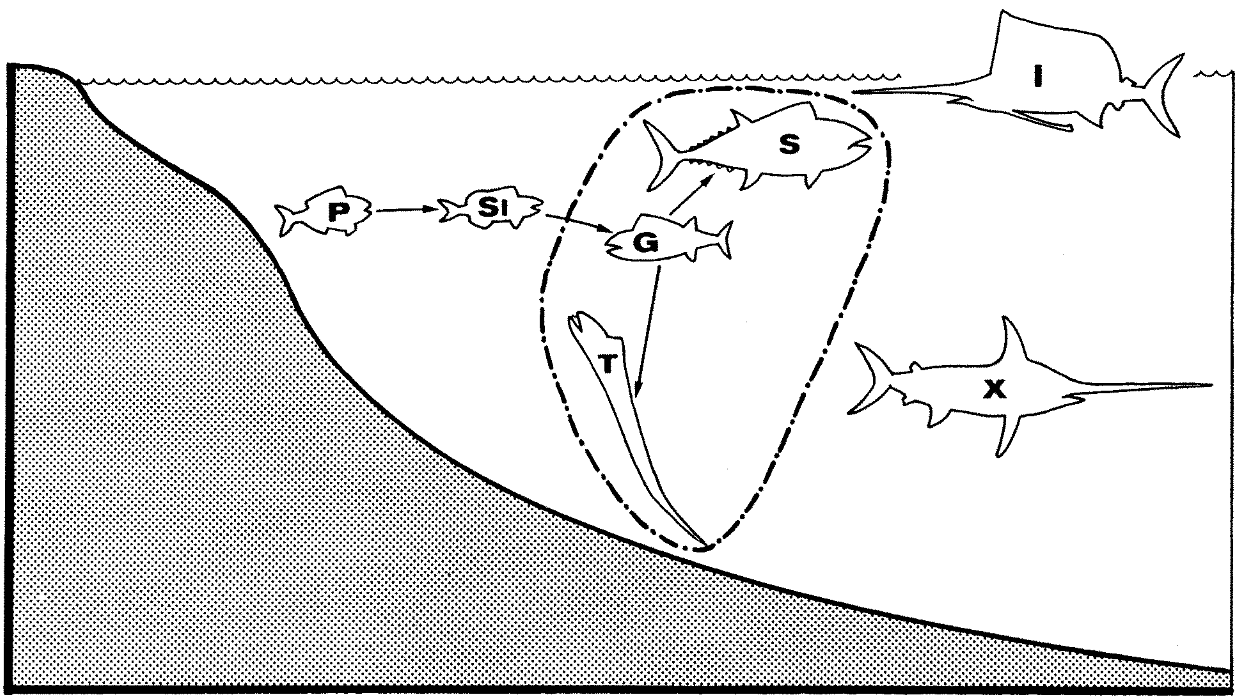

Fig. 4 Nakamura's (1989a,b) proposed phylogenetic relationships of certain scombroid fishes. The billfishes (I and X) are considered as an outgroup. P, hypothesized protopercoid; Si, scombrolabracids; S, scombrids; G, gempylids; T, trichiurids; I, istiophorids; X, xiphiids.

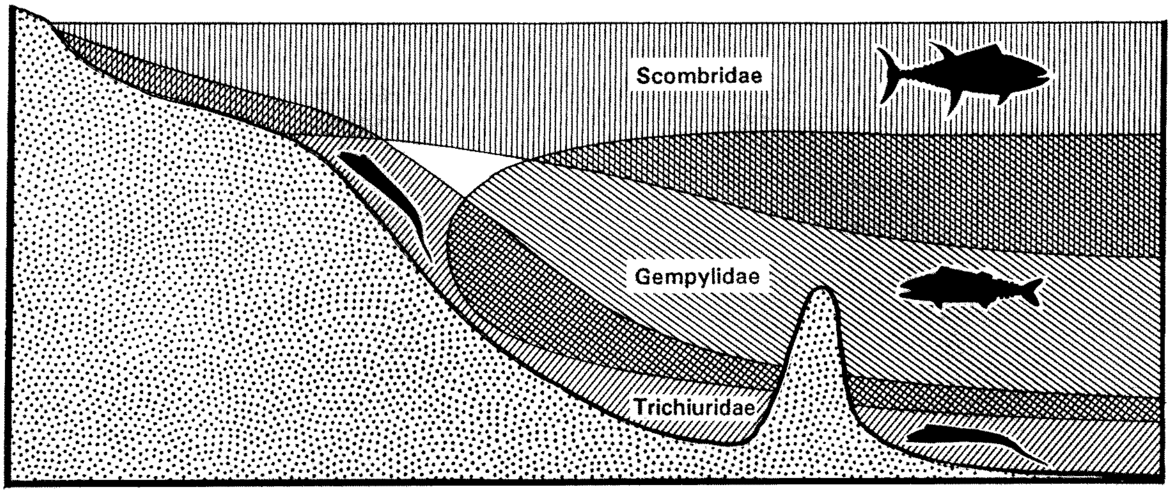

Fig. 5 Horizontal and vertical distribution of Scombridae (epipelagic), Gempylidae (mesopelagic and benthopelagic), and Trichiuridae (benthopelagic).

Lepidocybium, Ruvettus, and *Epinnula,* evolved first, followed by species of oceanic genera such as *Gempylus, Diplospinus,* and *Paradiplospinus.*

Nakamura (1989a,b,c; 1990c,d,e; 1991 a,b,c,d,e; 1992a,b,c) studied the correlation of certain morphological characteristics with habitat type of the Gempylidae, Trichiuridae and Scombridae. Scombrids are epipelagic (they inhabit the upper waters of the open ocean), trichiurids are benthopelagic (they inhabit the waters close to and some distance above the ocean bottom), and gempylids are either benthopelagic or mesopelagic (inhabiting the deeper waters of the open ocean) (Fig. 5). These habitat types are correlated with body form, body colour and markings, and shape of the lateral line, jaw teeth, tongue, nostrils, and, olfactory rosettes (Figs 6 to 11). There are 2 primary morphological and ecological forms in the 3 families of scombroid fishes studied by Nakamura (Fig. 6): 1) elongated body, slow-swimming and adapted to mesopelagic and benthopelagic habitats (Trichiuridae and trichiurid-like Gempylidae); and 2) fusiform body (streamlined), fast swimming and adapted to epipelagic life (Scombridae and scombrid-like Gempylidae). The cutlassfishes (Trichiuridae)

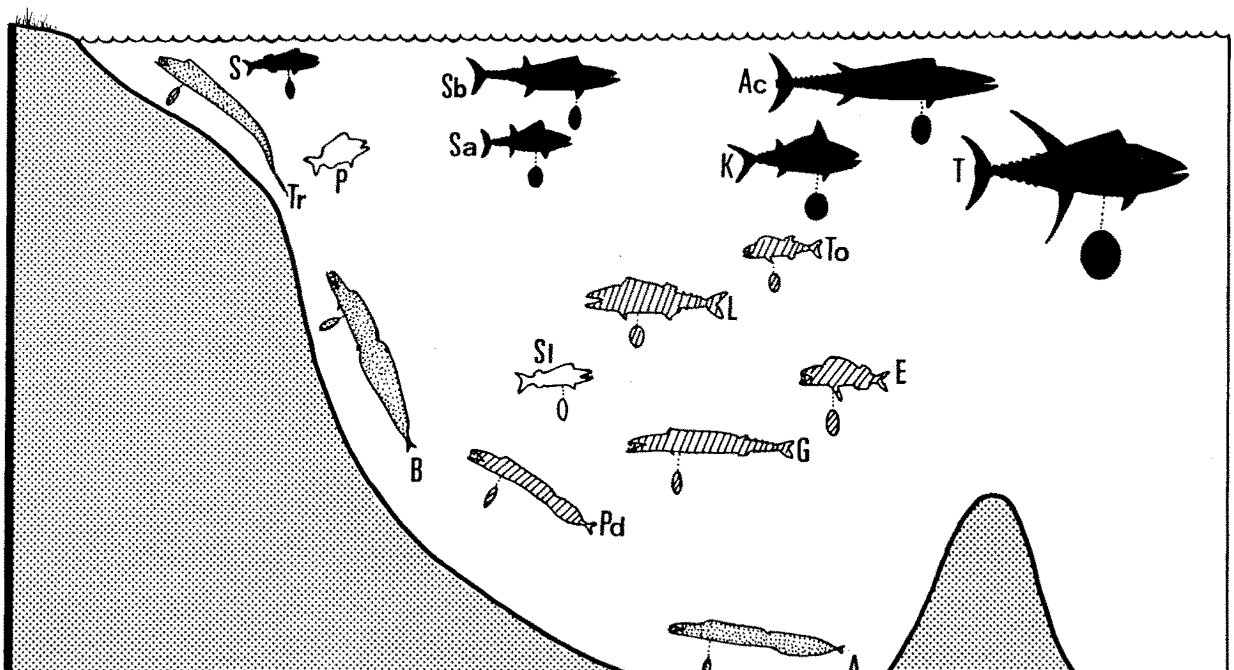

Fig. 6 Lateral and cross section body shape in relation to habitat type for certain scombroid fishes. Black figures represent scombrids, oblique lines gempylids, and stippled figures trichiurids. Genera are abbreviated as: A, *Aphanopus;* Ac, *Acanthocybium;* B, *Benthodesmus;* E, *Epinnula; G, Gempylus;* K, *Katsuwonus;* L, *Lepidocybium;* P, hypothesizcd protopercoid fish; Pd, *Paradiplospinus; S, Scomber;* Sa, *Sarda,* Sb, *Scomberomorus;* Sl, *Scombrolabrax;* T, *Thunnus;* To, *Tongaichthys;* Tr, *Trichiurus.*

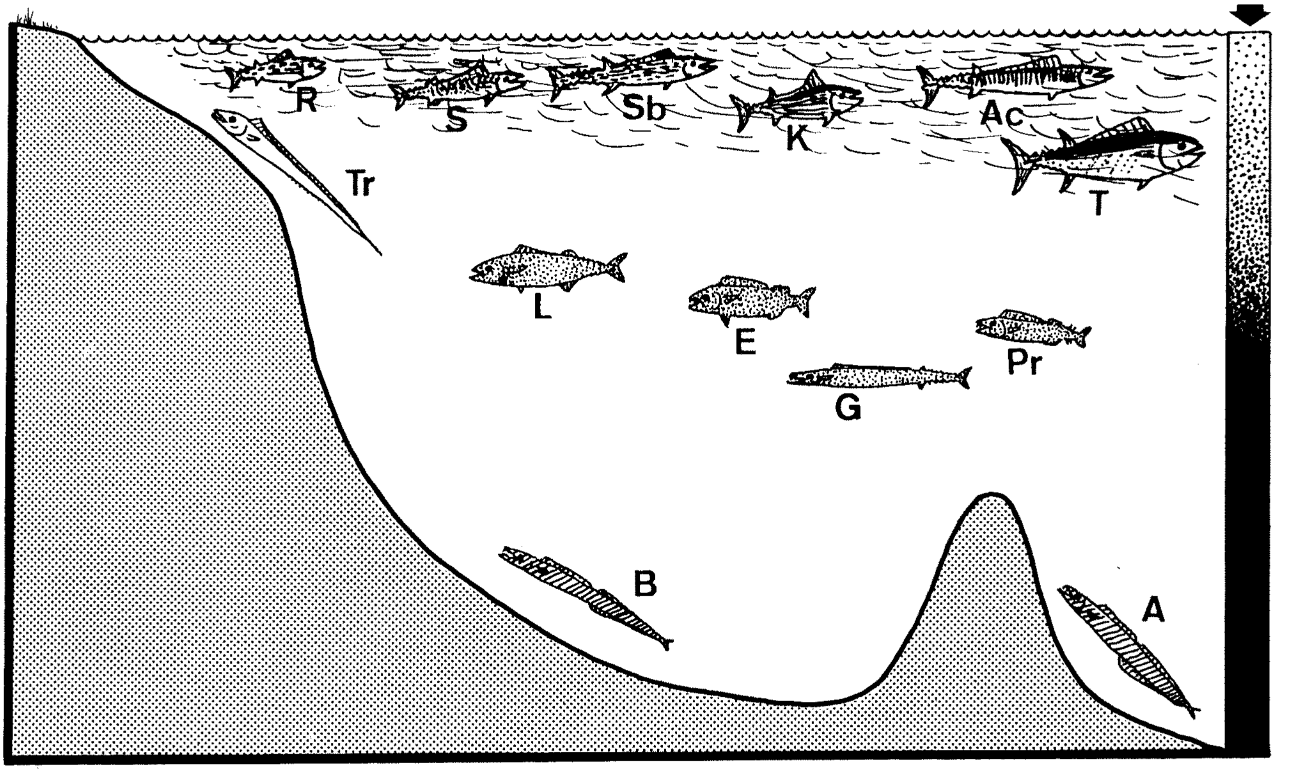

Fig. 7 Typical coloration with depth and decreasing light (direction of arrow). Stippling represents typically brownish gempylids, oblique lines represent dark coloration and tunas are counter shaded. Genus abbreviations as in Fig. 6 except: Pr, *Promethichthys;* R, *Rastrelliger*

represent one extreme of this ecological-morphological continuum in that they are elongate and exclusively benthic. At the other extreme, the tuna-like fishes (Scombridae) are fusiform and mostly epipelagic. The snake mackerels (Gempylidae) are intermediate with both elongate and fusiform body shapes and are both benthopelagic and mesopelagic. Body colour in these groups is also characteristic of their habitat type (Fig. 7). Tunas are counter-shaded (darker dorsally and silvery ventrally), gempylids are brownish or blackish consistent with their mesopelagic and benthopelagic existence, and trichiurids are dark coloured in deeper water and light coloured in shallow water. The pattern of the lateral line in the three families (Fig. 8) is also characteristic of the

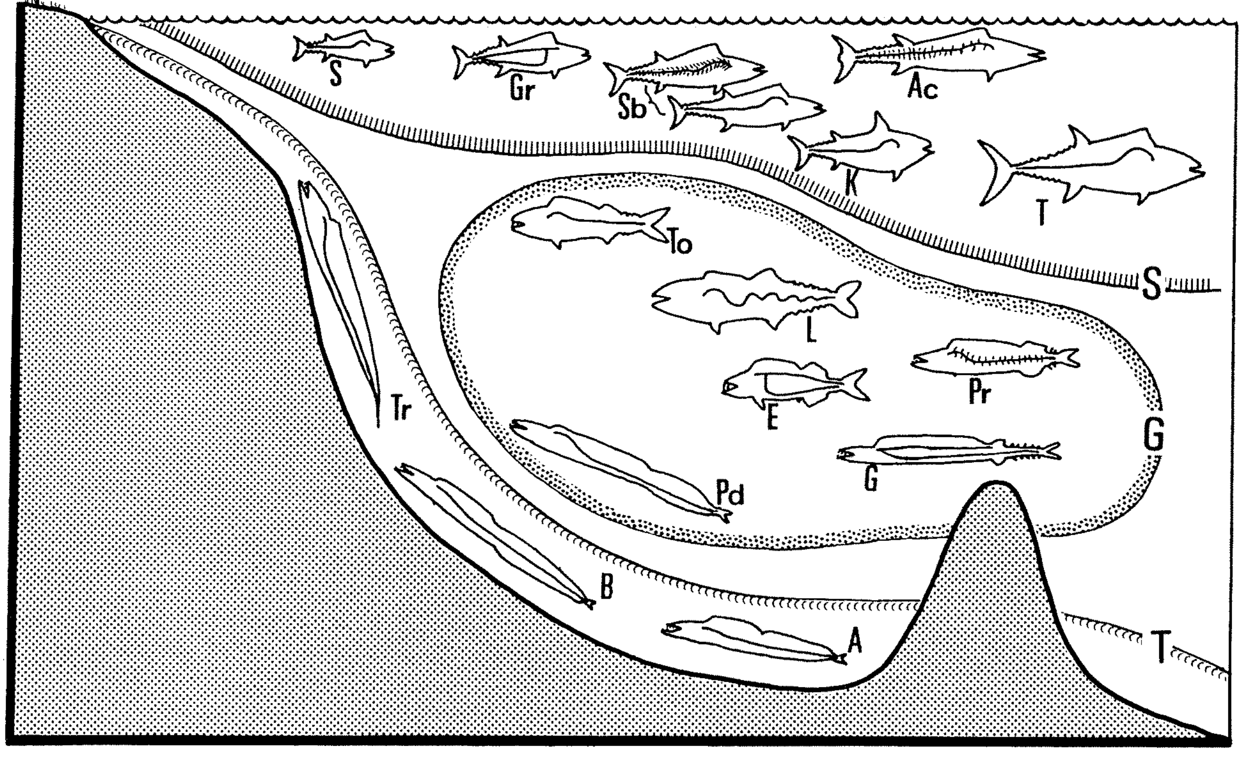

Fig. 8 Pattern of trunk lateral line in relation to habitat for Scombridae (S), Gempylidae (G), and Trichiuridae (T). Genus abbreviations the same as in Figs 6 and 7 except: Gr, *Grammatorcynus*

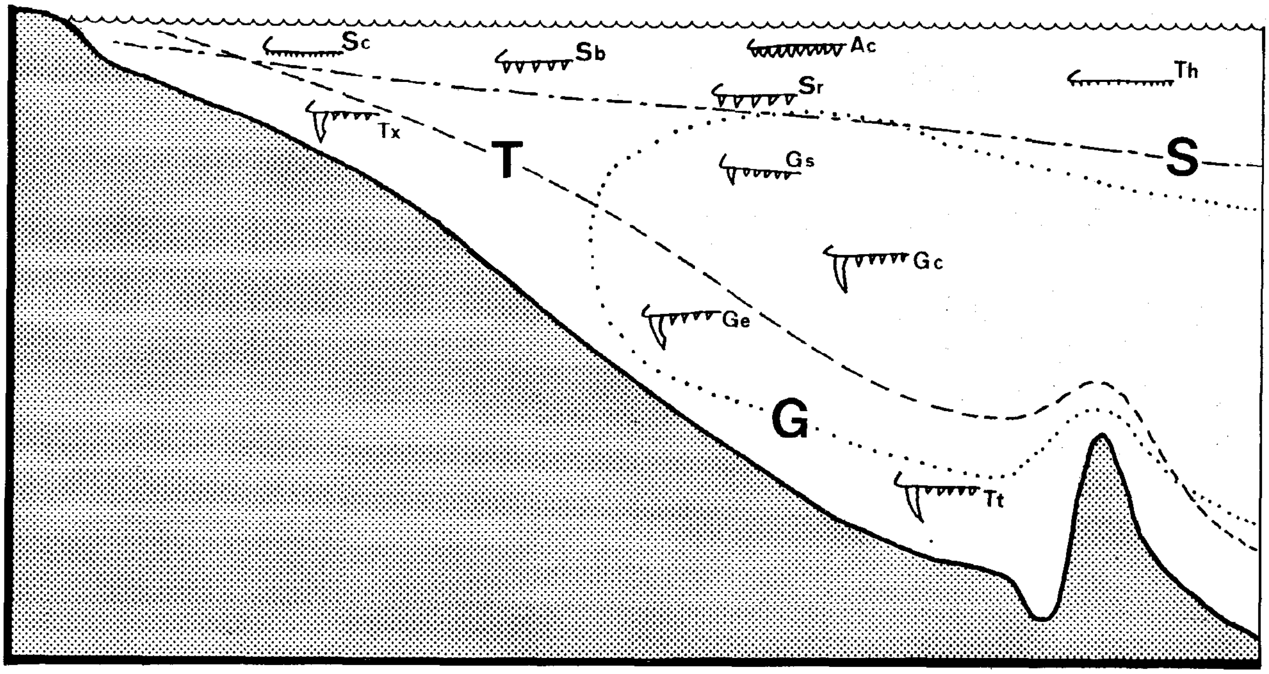

Fig. 9 Typical configuration of teeth in upper jaw in relation to habitat type for Scombridae (S), Gempylidae (G), and Trichiuridae (T). Abbreviations are the same as in Figs 6-9 except: Gc, compressed gempylids; Ge, elongate gempylids; Gs, semifusiform gempylids; Tt, trichiurids with tails; Tx, trichiurids without tails; Sc, Scombrini; Sr, Sardini; Th, Thunnini

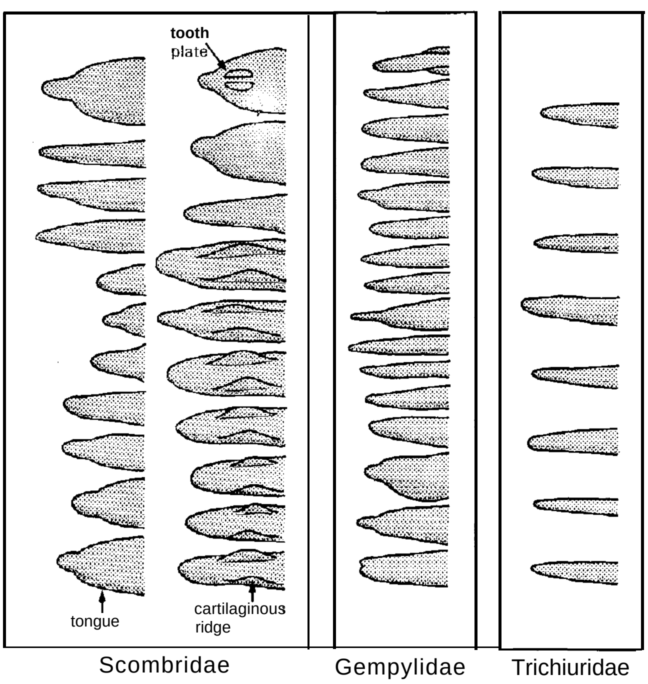

Fig. 10 Tongue shape for certain scombroid fishes. Scombridae top to bottom on left: ***Gasterochisma melampus, Scomber japonicus, S. australasicus, Rastrelliger kanagurta, Scomberomorus niphonius, S. koreanus, S. commerson, Acanthocybium solandri, Grammatorcynus bilineatus, G. bicarinatus, Sarda orientalis;*** **top to bottom on right:** ***Gymnosarda unicolor, Cybiosarda elegans, Allothunnus fallai, Auxis thazard, A. rochei, Euthynnus affinis, Katsuwonus pelamis, Thunnus albacares, T. tonggol, T. thynnus.*** **Gempylidae top to bottom:** ***Promethichthys Prometheus, Rexea solandri, R. prometheoides, Neoepinnula orientalis, Epinnula magistralis, Nealotus tripes, Nesiarchus nasutus, Thyrsitoides marleyi, Gempylus serpens, Paradiplospinus gracilis, Diplospinus multistriatus, Thyrsitops lepidopoides, Thyrsites atun, Lepidocybium flavobrunneum, Ruvettus pretiosus, Tongaichthys robustus.*** **Trichiuridae top to bottom:** ***Benthodesmus tenuis, Lepidopus caudatus, Evoxymetopon poeyi, Aphanopus carbo, Eupleurogrammus glossodon, Lepturacanthus savala, Tentoriceps cristatus, Trichiurus lepturus***

habitat type. The tunas have well developed lateral lines situated mostly on the upper sides which presumably is useful for detecting sensory stimuli in the upper waters of the open ocean. In contrast, trichiurids have their lateral line situated mostly on the lower sides which presumably is an adaptation to detecting sensory stimuli near the bottom of the ocean. Species of Gempylidae have lateral-line patterns similar to either trichiurids or scombrids depending on their habitat orientation. The swimming and feeding behaviour is also typical of these three families and their habitats. The tunas are fast-swimming predators with small, sharp teeth typidal for rapid grasping and ingestion of prey (Fig. 9). Their tongues are flat with cartilaginous ridges (Fig. 10) which serves to funnel water over the gills during their typically continuous, high-speed swimming. Nostril shape and shape of the olfactory rosette of tunas are also apparently adapted for their fast swimming mode (Fig. 11). Usually, the anterior nostril is small and round, the posterior nostril is a slit, and the rosette is rounded and often with an accessory sac. This ‘design’ decreases drag while water passes over the rosette and allows adequate olfactory function during continuous, fast swimming. Trichiurid fishes have dentition, tongues and nasal organs adapted to more sedentary benthic habits. Their teeth are long, sharp and often fang-like for seizing and holding prey during ambush predation. Their tongues are more slender and rounded and therefore not adapted to funnelling water over gills during swimming. They have a single, rounded nostril which serves as both incurrent and
rent pore and therefore passage of water over the

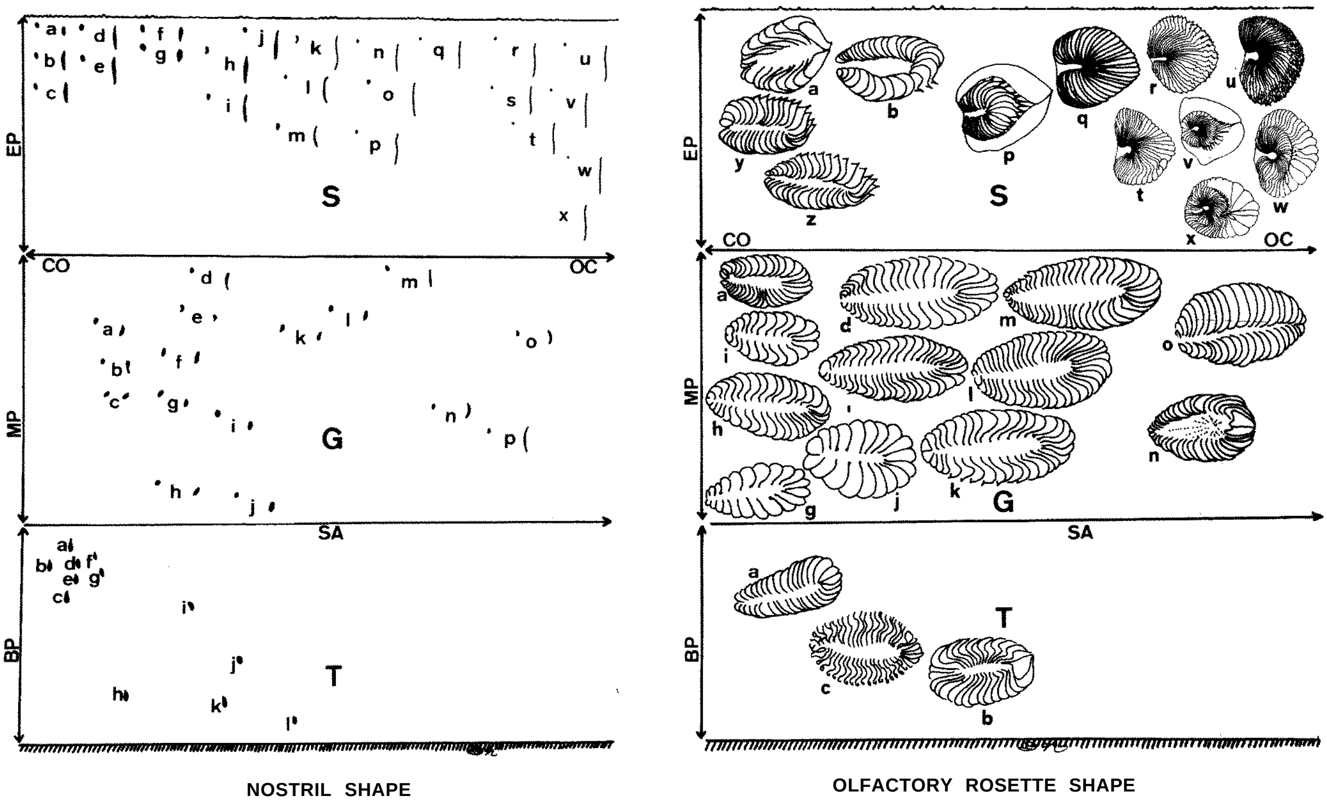

Fig. 11 Nostril and rosette shape arranged according to occurrence in epipelagic (EP), mesopelagic (MP), benthopelagic (BP), coastal (CO), and oceanic (OC) habitats and swimming ability (SA).
Scombridae (S): a, *Rastrelliger faughni*; b, *Scomber japonicus*; c, *S. australasicus*; d, *Grammatorcynus bilineatus*; e, *G. bicalinatus*; f, *Scomberomorus sinensis*; g, *S. queenslandicus*; h, *Cybiosarda elegans*; i, *Orcynopsis unicolor*; j, *Sarda orientalis*; k,*Auxis thazard*; l, *Gymnosarda unicolor*; m, *Gasterochisma melampus*; n, *Euthynnus affinis*; o, *Acanthocybium solandri*; p, *Allothunnus fallai*; q, *Katsuwonus pelamis*; r, *Thunnus tonggol*; s, *T. atlanticus*; t, *T. maccoyii*; u, *T. albacares*; v, *T. alalunga*; W, *T. thynnus*, x, *T. obesus*; y, *R. brachysoma*; z, *R. kanagurta*. Gempylidae (G): a, *Nealotus tripes*; b, *Rexea solandri*; c, *Rexichthys johnpaxtoni*; d, *Thyrsites atun*; e, *Thyrsitops lepidopoides*; f, *Promethichthys prometheus*; g, *Neoepinnula orientalis*; h, *Diplospinus multistriatus*; i, *Epinnula magistralis*; j, *Paradiplospinus gracilis*; k, *Nesiarchus nasutus*; l, *Thyrsitoides marleyi*; m, *Gempylus serpens*; n, *Ruvettus pretiosus*; o, *Tongaichthys robustus*; p, *Lepidocybium flavobrunneum*. Trichiuridae (T): a, *Trichiurus lepturus*; b, *T. gangeticus*; c, *Tentoriceps cristatus*; d, *Eupleurogrammus muticus*; e, *E. glossodon*; f, *Lepturacanthus pantului*; g, *L. savala*; h, *T. auriga*; i, *Lepidopus caudatus*; j, *Benthodesmus tenuis*; k, *Evoxymetopon taeniatus*; l, *Aphanopus carbo*

olfactory rosette is not strongly dependent on swimming movements. The olfactory rosette is more elongate in trichiurids than tunas but the relation of this shape with habitat type is not fully understood. Collectively, gempylids are intermediate between tunas and trichiurids in shape and configuration of teeth, tongue, nostrils and olfactory rosettes (Figs 9 to 11). Those that are fast swimming predators have short teeth, flat tongues and both rounded and slit-like nostrils. The more benthic-oriented gempylids have long, sharp teeth with fangs, relatively flat tongues and rounded nostrils.

Parin and Becker (1972) recognized three main ecological groups of trichiuroid fishes. The majority (33 species) are a group that are neritic or benthopelagic, dwelling above the bottom on continental shelves and slopes. The hairtails of the genera *Eupleurogrammus, Lepturacanthus* and *Tentoriceps* are usually found in shallow water from 20 to 200 m. Species belonging to *Lepidocybium, Neoepinnula, Rexea, Rexichthys, Ruvettus, Thyrsites, Thyrsitoides* and *Thyrsitops* of the Gempylidae, and *Assurger, Evoxymetopon, Lepidopus* and *Trichiurus* of the Trichiuridae are mostly confined to depths of 100 to 500 m at the continental shelf margin and at the upper part of the slope. Some are characteristically found on seamounts in the open sea, including the four commercially important species of trichiurids, *Trichiurus lepturus, Thyrsites atun, Lepidopus caudatus* and *Rexea solandri.*

The second group is comprised of 18 to 19 species found on the continental slope from 200 to 1500 m (rarely 2 000 m) and includes the gempylid genera *Nesiarchus, Paradiplospinus* and *Promethichthys*, and the trichiurid genera *Aphanopus* and *Benthodesmus. Aphanopus mik-. hailini* is found at depths deeper than all other trichiuroid fishes, having been reported from 1 350 to 2 000 m.

Most (perhaps all) of the benthopelagic trichiuroids of the continental slope develop in mesopelagic water masses. Postlarvae and juveniles of *Nesiarchus, Paradiplospinus, Promethichthys,*

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