1. INTRODUCTION

The serranid Subfamily Epinephelinae comprises about 159 species of marine fishes in 15 genera (Fig. 1), commonly known as groupers, rockcods, hinds, and seabasses. These species are of considerable economic value, especially in the coastal fisheries of tropical and subtropical areas. It has been estimated that 90% of the world's harvest of marine food is derived from artisanal fisheries, and groupers are a major component of the artisanal fisheries resource. Although groupers are usually the most expensive fishes in local markets, separate catch statistics are not reported for most species, and landings are often summarized as "serranids" or "groupers." This lack of species-specific catch data is due, in part, to the difficulty of identifying many of the species. For example, two of the most important commercial species, "*Epinephelus guaza*" (of the Mediterranean and Atlantic Ocean) and *E. tauvina* (of the Indo-Pacific region) are often misidentified. The importance of correct species identification should be obvious to every biologist and is certainly appreciated by intelligent farmers and taxonomists. It is essential for the proper management of a fishery resource to correctly identify the species concerned.

The purposes of this grouper catalogue are (1) to provide a means of identifying the various species, (2) to present a synopsis of the literature on the biology and fisheries of these species, and (3) to present a new generic-level classification of the groupers.

The Indo-Pacific groupers (110 species) were revised by Randall and Heemstra (1991), and that work is incorporated in the present catalogue. Heemstra (1991) completed a taxonomic revision of the 14 species of groupers that occur in the eastern Atlantic Ocean and Mediterranean Sea. The results of this revision are also included in the present catalogue. The reader is advised to consult these two revisions for taxonomic details.

Our treatment of the American groupers was greatly facilitated by the excellent revision by C.L. Smith (1971). With a few exceptions, we recognize the same species as Smith did. Where we differ with Smith, we have given additional data and a detailed explication of our taxonomic conclusions. The first author (P.C.H.) did the research on American groupers and accepts full responsibility for any errors concerning these species.

1.1 Habitat and Biology

Groupers are bottom-associated fishes found in the tropical and subtropical waters of all oceans. Most species occur on coral reefs, but some live in estuaries or on rocky reefs. Groupers are generally associated with hard (rocky) bottoms, although juveniles are found in seagrass beds, and adults of a few species prefer sandy or silty areas. Some species occur in depths of 100 to 200 m (occasionally to 500 m); however, the majority inhabit depths less than 100 m, and juveniles are often found in tidepools.

As the major predators of the coral-reef ecosystem, most groupers feed on a variety of fishes, larger crustaceans, and cephalopods . A few groupers (e.g., *Paranthias* spp., *Epinephelus undulosus*) have long, numerous gill rakers and are thus adapted for plankton feeding. Adults of many species (e.g., *Plectropomus* spp., *Variola louti*) are primarily piscivorous, and they are usually seen cruising the reef or shallows in search of their prey. Most groupers are ambush predators, hiding amongst the coral and rocks until an unwary fish or crustacean goes by, then catching their prey with a quick rush and snap of their jaws. The large head and mouth of the typical grouper enables it to suck in a large volume of water (and the prey) in less than a second. The numerous inwardly-depressible sharp teeth are well adapted for seizing the prey and preventing its escape from the mouth. Some groupers have been observed following moray eels (and occasionally other fish) as they forage over the reef, in order to catch the small fishes and crustaceans that are frightened from their hiding places by the eels.

Except for occasional spawning aggregations, most species are solitary fishes: and tagging studies have shown that groupers are generally resident on a particular reef for long periods of time (often years). This site specificity and the relatively slow growth rate of groupers make them particularly vulnerable to over-fishing. In addition, some groupers use localized spawning sites to which they migrate from distances of several kilometres; and these sites are often exploited by local fishermen who catch large numbers of fishes during the brief spawning period of 1 or 2 weeks. This removal of a considerable number of reproductively active fish from the population may be detrimental to sustained yields of the fishery. Although an individual male may spawn several times during the breeding period, there is no evidence to suggest that females spawn more than once a year. Some species (e.g., *Epinephelus akaara*) spawn in pairs, others (e.g., *E. striatus*) spawn in large aggregations.

Judging from the few species that have been studied, groupers are protogynous hermaphrodites. The gonad lies ventral and slightly posterior to the swim bladder. The ovary is in the form of a bilobed sac that unites posteriorly to form a common ovi-

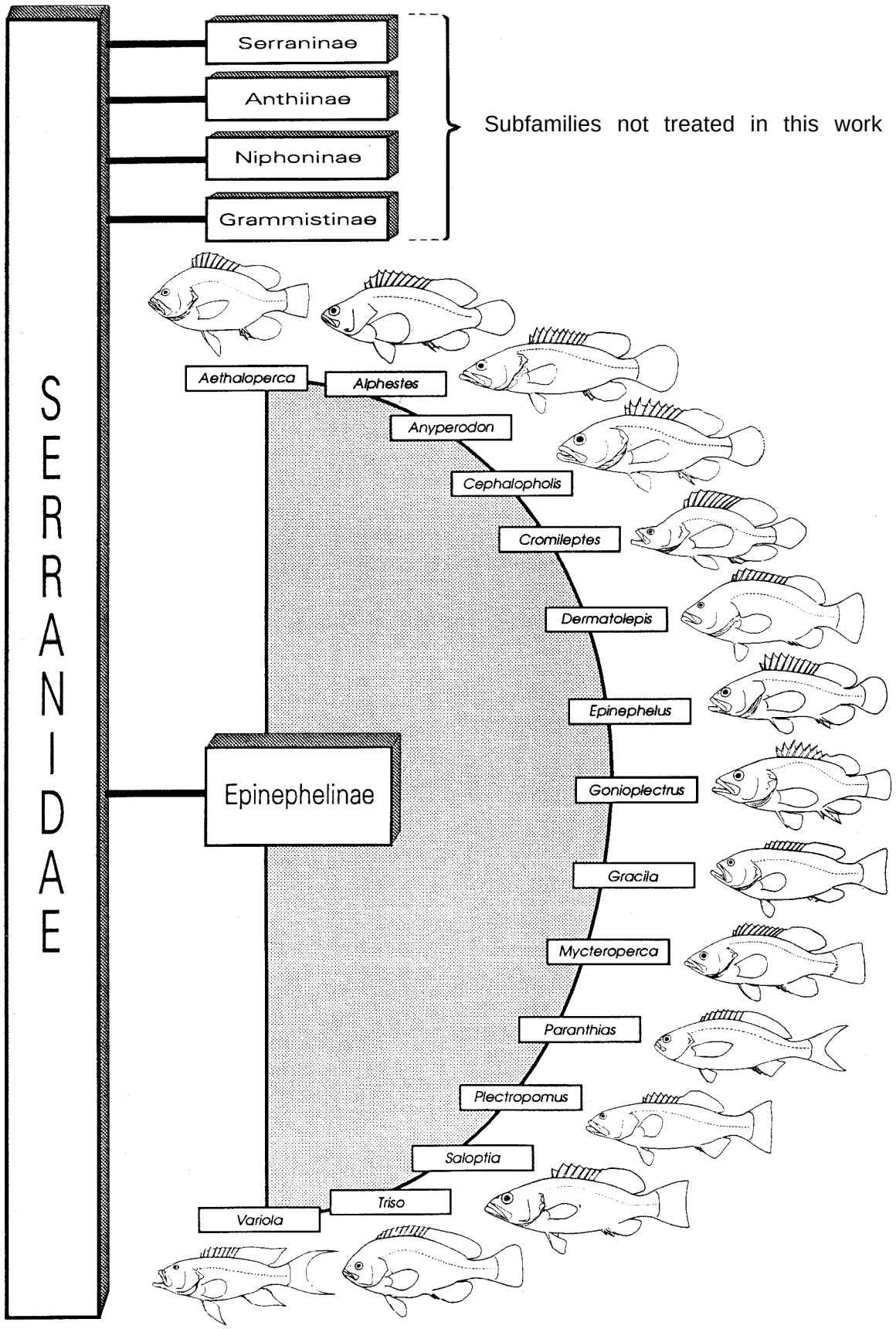
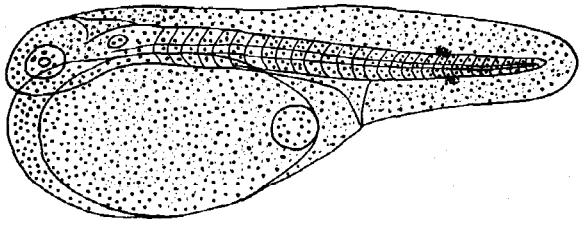


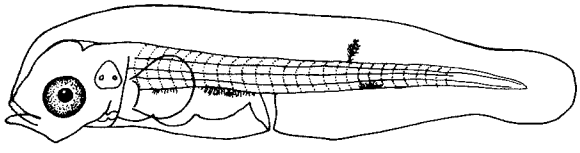
Fig. 1 Classification of the Family Serranidae

duct. In a mature female, numerous oocytes are arrayed in lamellae surrounding a central lumen, with spermatogenic tissue in small dormant crypts on the periphery of the lamellae. After spawning as a female for one or more years, the grouper changes sex and thereafter functions as a male. At sexual transition, the oocytes degenerate, the spermatogonia proliferate, and the ovary is transformed into a functional testis. Evidence of the ovarian origin of the testes are the remnants of oocytes and the ovarian lumen, which can be seen in cross-sections of the testes. This protogynous mode of reproduction is complicated in certain species by the 'occurrence of some large females that do not change sex and some small males that are mature at the same size as the smallest females. An exogenous (behavioural) inducement of sexual transformation, as opposed to an endogeneous (size) threshold, is indicated by 1) the sexual transition occurring over a broad range of size (age), and 2) the presence of females older than the age at which transition is completed for the population.

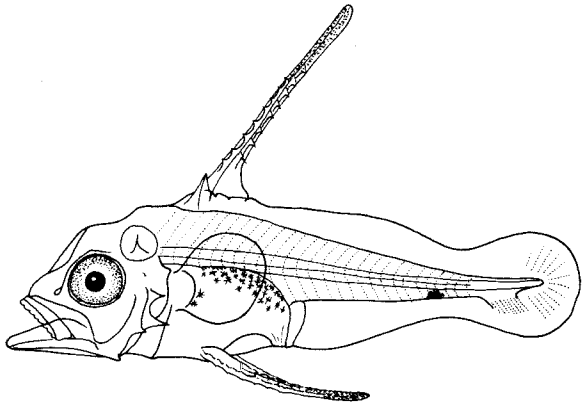
The available information on the larval development of some 29 species of groupers was summarized by Kendall (1984) and Leis (1987). The fertilized eggs are pelagic, spherical, transparent, 0.70 to 1.20 mm in diameter, with a smooth chorion, colourless unsegmented yolk and a single colourless oil globule 0.13 to 0.22 mm in diameter. Newly hatched larvae of *E. septemfasciatus* (Fig. 2) are 1.85 mm TL, and first feeding begins on the third day after hatching (2.6 mm TL). Grouper larvae are characterized by their "kite-shaped" body'(greatest body depth at origin of dorsal fin), second dorsal-fin spine and pelvic-fin spines greatly elongated, with 3 or 4 serrate longitudinal ridges, well-developed head spination (with prominent spines on the preopercle and supraocular ridge), and dense pigmentation on the dorsolateral surface of the body cavity. In laboratory reared specimens, the pelagic larvae of *E. akaara* transformed to the benthic juvenile stage at 25 mm TL, 25 or 26 days after hatching (Mito et al., 1967). But in *E. septemfasciatus,* the transformation occurred at 31 mm TL, and the pelagic larval period lasted 60 days (Kitajima et al., 1991). In view of the shallow water bottom-associated habitat of adults and juveniles, the relatively long-lived pelagic larvae of groupers may provide the mechanism by which many species have attained their wide geographic distributions.



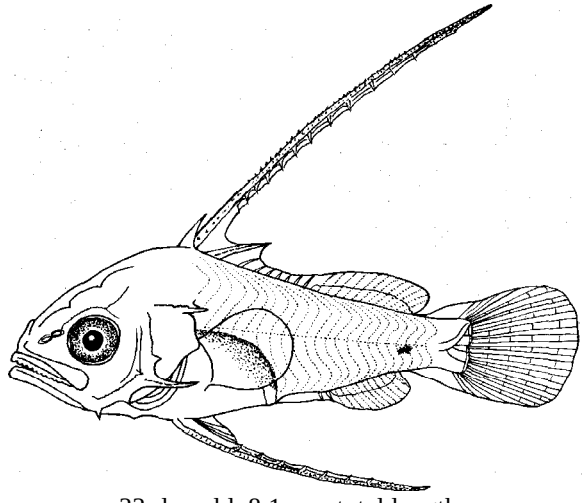
newly hatched larva, 1.85 mm total length



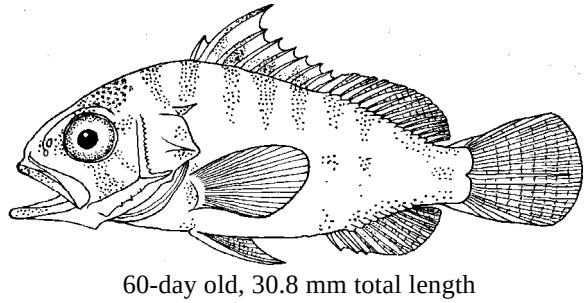
postlarva, 3-day old, 2.60 mm total length



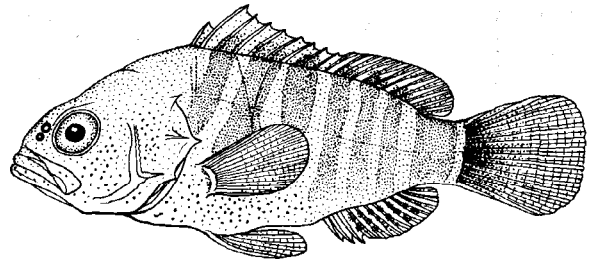
25-day old, 4.8 mm total length



33-day old, 8.1 mm total length



60-day old, 30.8 mm total length



75- day old, 49.3 mm total length

Fig. 2 Larval Development stages of Epinephelus septemfasciatus (after Kitajima et al., 1991)

1.2 Fisheries

Groupers are of considerable importance in the commercial, sport, and artisanal fisheries of tropical and subtropical seas. A few species are used in aquaculture. *Epinephelus coioides, E. malabaricus, E. akaara, E. striatus, E. septemfasciatus, Cromileptes altivelis,* and *Mycteroperca microlepis* have been spawned in captivity. Several species are commonly used in cage-culture operations.

The protogynous mode of reproduction in groupers presents problems for fishery management. Male groupers (which are produced by sexual transformation of old females) are usually larger, older and less numerous than females; and the commercial, sport and subsistence fisheries are often biased (by means of hook size and fishing techniques) towards the capture of large adults. Hence, males are caught in greater proportion than they exist in local populations. The reproductive consequences of this sexually selective fishing may differ from the consequences of non-selective fishing in gonochoristic species. Bannerot et al. (1987) discuss the problems inherent in stock assessment and management of grouper fisheries.

Groupers contribute substantially to the world commercial fish catch, with over 97 000 t landed in 1990 (Table 1). In addition, these statistics greatly underestimate the total catch, because most groupers are caught in artisanal fisheries, which do not report catch statistics. This under-reporting of grouper catches is indicated by the fact that, despite the much greater size and reef area of the Indo-Pacific region, more groupers are reported in commercial fisheries statistics from the Atlantic Ocean than from the Indian and Pacific oceans combined. The largest commercial catch of groupers is reported from the Caribbean area (Table 2, FAO Fishing Area 31).

From 1981 to 1990 there has been a trend of increasing landings of groupers (Table 3). This is generally true for all species or categories reported, except for *Epinephelus morio* from the Gulf of Mexico which appears to be in decline.

1.3 Classification of the Family Serranidae

The composition and phylogenetic relationships of the Family Serranidae were discussed by Johnson (1983, 1988): Kendall (1984), and Leis (1986). Johnson (1983) proposed that the Serranidae comprises three subfamilies: Serraninae, Anthiinae and Epinephelinae. He further divides the Epinephelinae into 5 tribes: Niphonini, Epinephelini, Diploprionini, Liopropomini, and Grammistini. Johnson (1988) hypothesized that the Diploprionini, Liopropomini, and Grammistini constitute a monophyletic group that is most closely related to the Epinephelini, and that this group of four tribes is the sister taxon on the Niphonini. An alternative classification that does not contradict the phylogenetic relationships proposed by Johnson is adopted here. In our scheme the Family Serranidae is divided into five subfamilies: Serraninae, Anthiinae, Niphoninae, Epinephelinae, and Grammistinae (Fig. 1). The Grammistinae includes the tribes Grammistini, Diploprionini, and Liopropomini.

Table 1
Reported world catch of groupers in metric tons by area in 1990 (FAO, 1992)

Species	Main Areas				
	Pacific Ocean	Atlantic Ocean	Mediterranean and Black Sea	Indian Ocean	Total
E. aeneus		2 169 F	414 F		2 583 F
E. akaara	166				166
E. analogus	18				18
*E. marginatus**		1 261 F	3 308 F		4 569 F
E. morio		2 964 F			2 964 F
E. striatus		201			201
E. touvina	199				199
Epinephelus spp.**	21 786 F	43 241 F	3 547 F	16 767 F	85 341 F
Mycteroperca spp.		1 100 F			1 100 F
Total	22 169 F	50 936 F	7 269 F	16 767 F	97 141 F

* catches for *E. marginatus* were previously reported as *E. guaza*
** not elsewhere included
F = FAO estimate from available sources of information

Table 2
Reported world catch of groupers in metric tons by FAO Fishing Areas in 1990 (FAO, 1992)

Species	FAO Fishing Areas											
	27	31	34	37	41	47	51	57	61	71	77	87
E. aeneus			2 169F	414F								
E. akaara									166			
E. analogus												18
*E. marginatus**	194		1 067F	3308F								
E. morio		1 164			1 800F							
E. striatus		201										
E. tauvina									199			
Epinephelus spp. *		28 140F	12 240F	3 547F	2 566F	295	12 717F	4 050	5 386	15 102E	886 F	412
Mycteroperca spp.					1 100F							
Total	194	29 505F	15 476F	7 269F	5 466F	295	12 717F	4 050F	5 757F	15102F	886F	430

Table 3
Reported world catch of groupers in metric tons for the years 1981 to 1990 (FAO, 1992)

Species (Area reported)	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
E. aeneus (Mediterranean and Atlantic)	1 000	889F	960 F	1 729F	1 621F	1 181	1 289F	2 679	2 596F	2 583F
E. akaara (Hong Kong)					135	210	401	164	150	166
E analogus (Colombia)	50	10	3	40	33	58	58	25	24	18
*E. marginatus** (Mediterranean and Atlantic)	1 796	1 443	1 939	4 098	4 320	3 748	3 799	3 946	4 346F	4 569F
E. morio (Cuba, Mexico, Brazil)	13 226	11 598	3 535	3 611	3 791	3 748	4 170	4 019F	4 456F	2 964F
E striatus (Colombia and Cuba)	391	414	398	370	491	361	363	287	305	201
E. tauvina (Hong Kong)					108	126	353	246	160	199
Epinephelus spp. ** (all areas)	51428F	57599F	51 150F	62 510F	62 056F	63 682F	66 124F	76 850F	75 862F	85 341 F
Mycteroperca spp. (Brazil)	884	793	984	942	2 117	1 126	1 228	1 073F	1 100F	1 100F
Total	68 775F	72 746 F	58 969F	73 300F	74 672F	74 240F	77 785F	89 289F	88 999F	97 141 F

* catches for E. marginatus were previously reported as *E. guaza*
****** not elsewhere included
F = FAO estimate from available sources of information

1.4 Illustrated Glossary of Technical Terms and Measurements

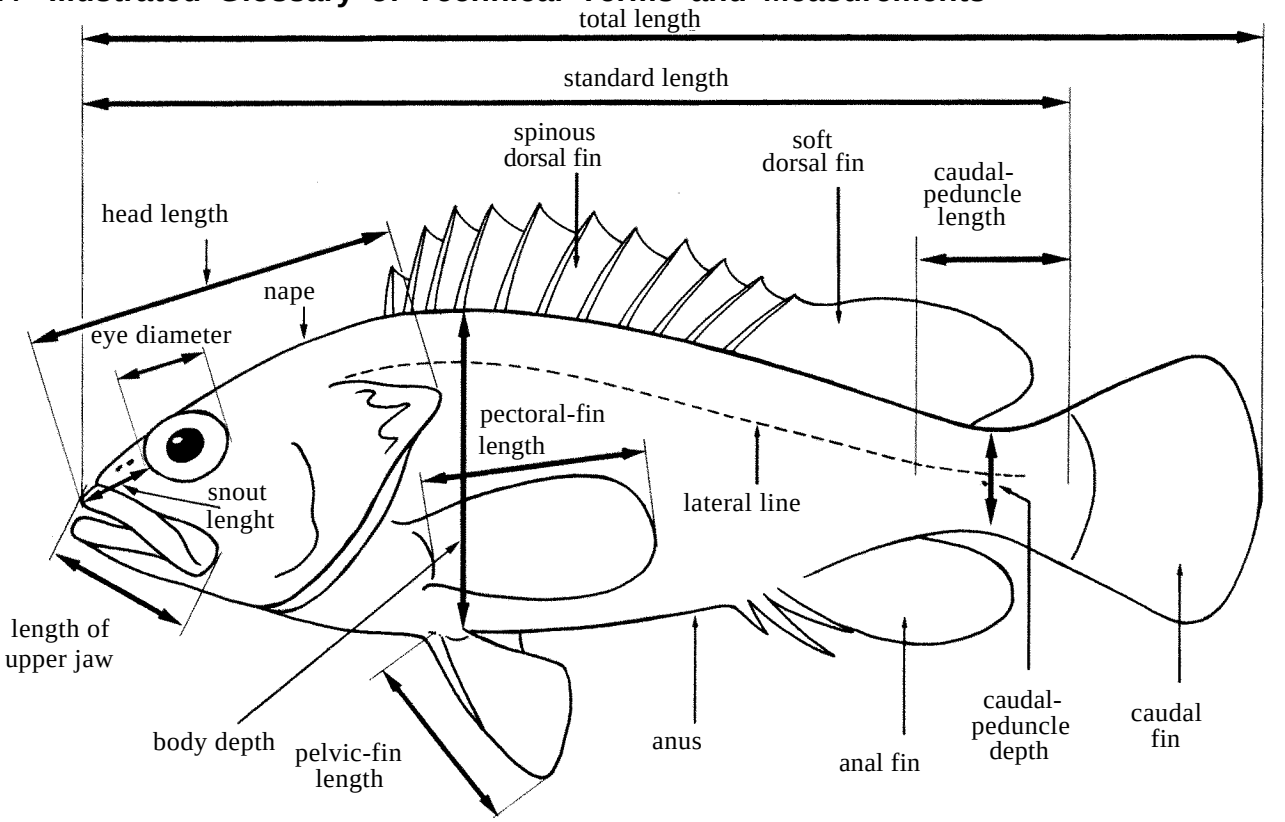


Fig.- External morphology and measurements

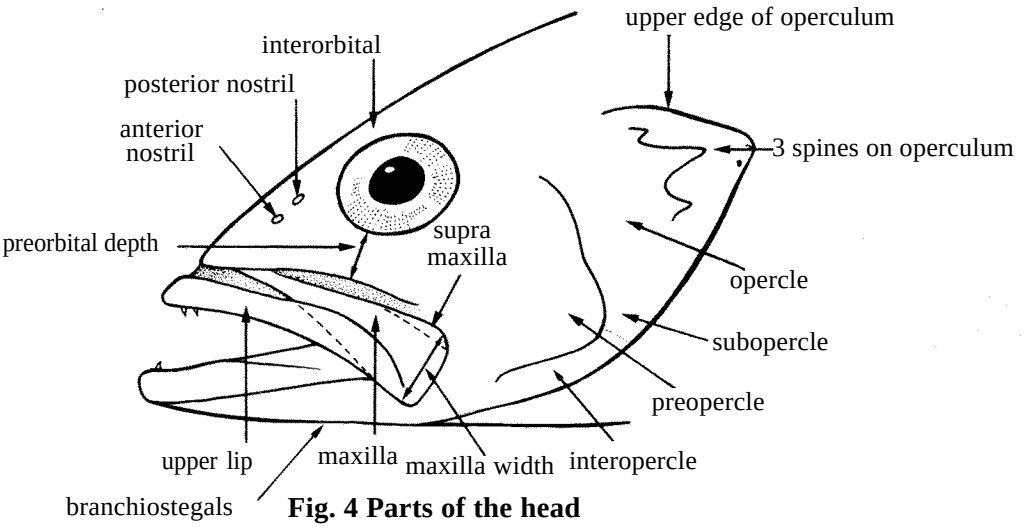


Fig. 4 Parts of the head

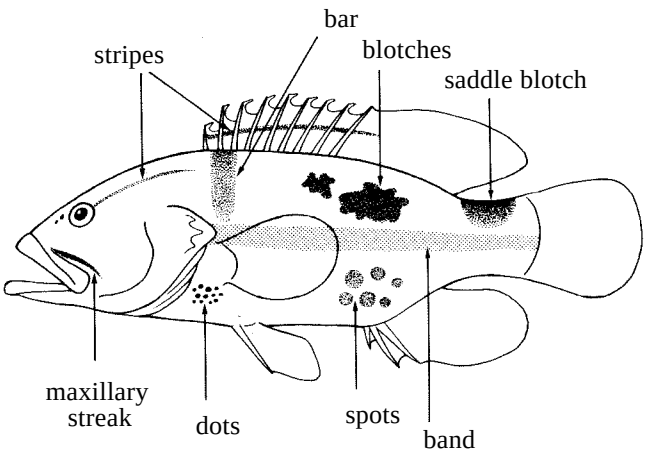


Fig. 5 Colour markings

Anterior - Towards the head or front end of the fish.

Antrorse - Curved or pointing anteriorly.

Axil - The inner side of the base of the pectoral or pelvic fins.

Band - An elongate colour marking, approximately 1 or 2 eye diameters in width (Fig. 5).

Bar - An elongate colour mark with vertical or near vertical orientation (Fig. 5).

Belly - The lower part of the body from the pelvic fins to the anal fin.

Blotch - A colour mark, larger than the eye and usually with irregular or indistinct borders (Fig. 5).

Body width - The greatest width (thickness) of the body, usually occurring at the base of the pectoral fins.

Branchiostegals - Ray-like bones supporting the gill membrane that seals the underside of the gill cavity (Fig. 4).

Canine - A prominent, conical tooth (sometimes curved) that is distinctly larger than other teeth in the jaws.

Caudal fin - The tail fin (Fig. 3). The shape of the caudal fin is distinctive for many species of groupers (Fig. 6). The **caudal-fin length** is the length of the longest caudal-fin rays.

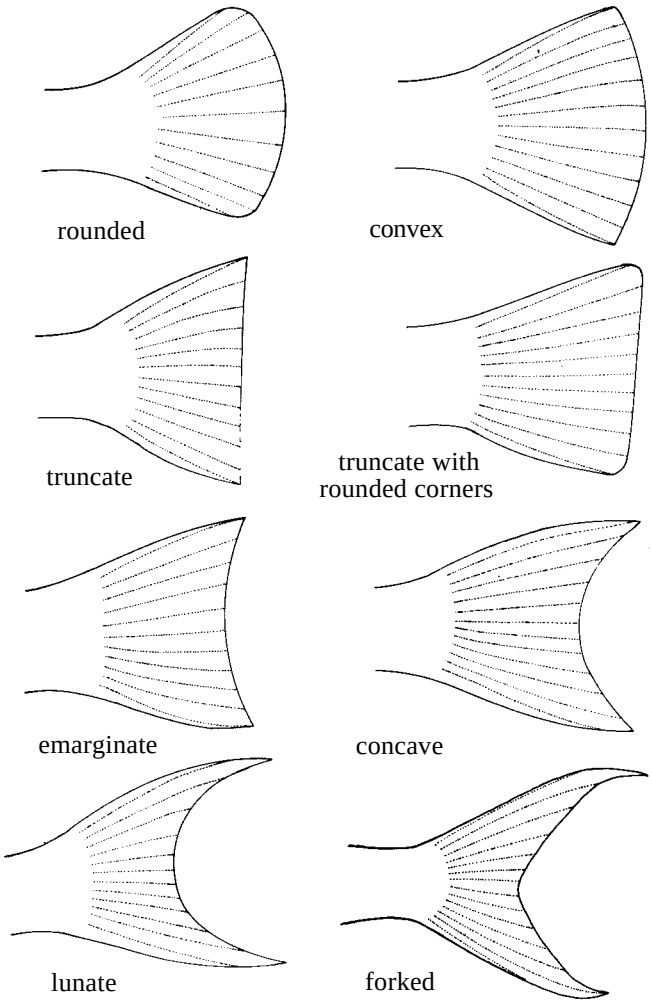


Fig. 6 Types of caudal fins

Caudal peduncle - The part of the tail that joins the caudal fin to the body. The **caudal-peduncle length** is the horizontal distance from the rear end of the anal fin base to a vertical at the caudal-fin base (Fig. 3). The **caudal- peduncle depth** is the least depth of the peduncle (Fig. 3).

Caudal vertebrae - Vertebrae that bear a haemal spine ventral to the vertebral centrum (Figs 7 and 8).

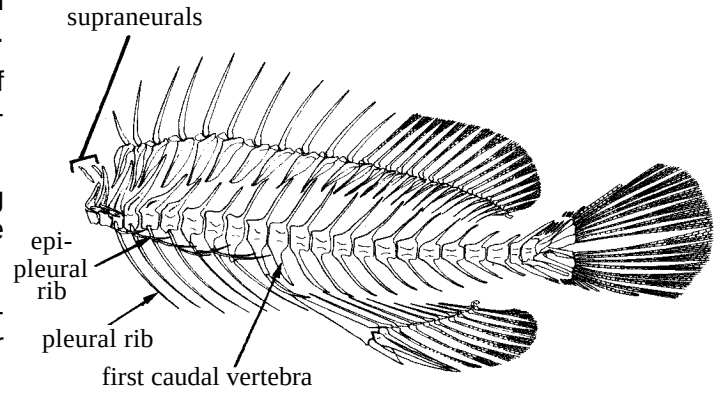


Fig. 7 Axial skeleton of *Epinephelus fasciatus*

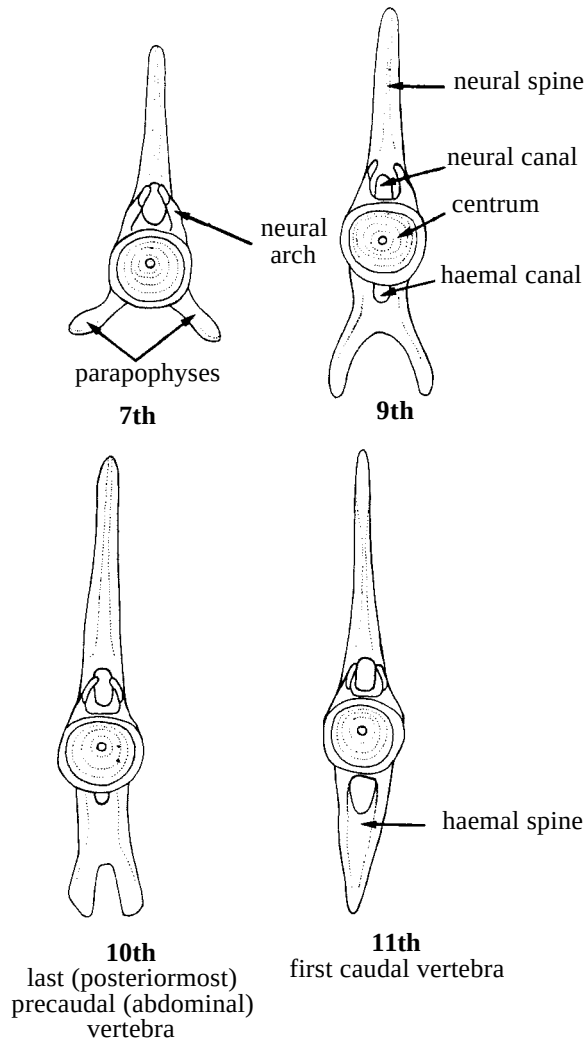


Fig. 8 Anterior view of vertebrae.

Compressed - Laterally flattened. A compressed fish (e.g., *Anyperodon*) has the body width less than half of the body depth.

Cranium - Bony part of the head, enclosing the brain; the skull. It is composed of many different bones (Fig. 9).

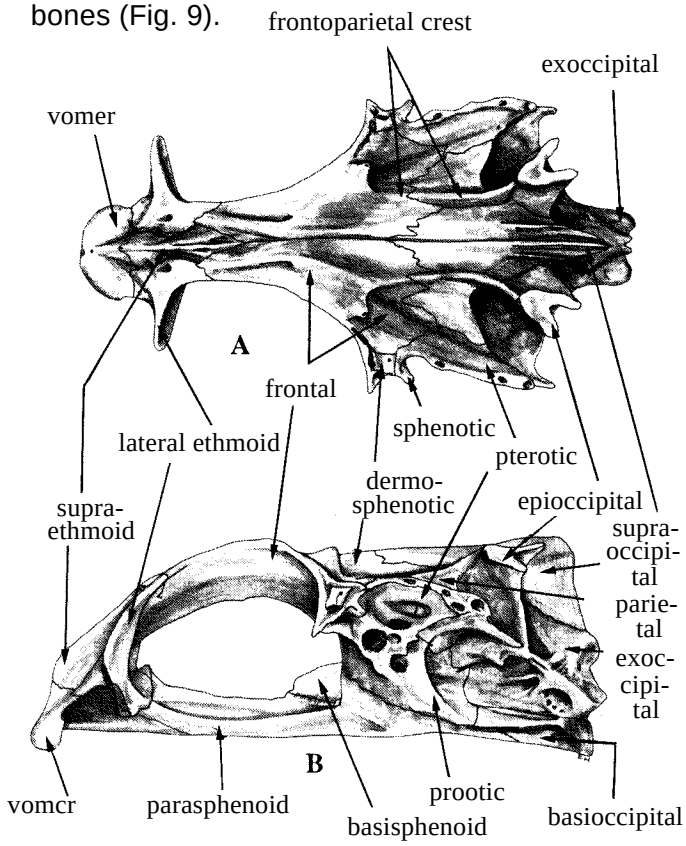


Fig. 9 Dorsal (A) and lateral (B) views of the cranium of *Epinephelus fasciatus*

Ctenoid scale - A scale with minute spines (ctenii) along the posterior margin. Ctenoid scales feel rough when the fish is stroked towards the head (Fig. 10).

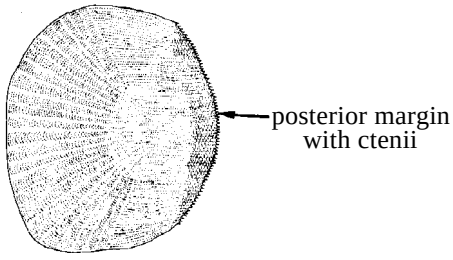


Fig. 10 Ctenoid scale

Distal - Away from the centre of the body or base of a fin.

Dorsal - On or towards the upper part of the fish.

Dorsal fin - The median fin on the upper part of the body (Fig. 3).

Dot - A colour mark about the size of a nostrils (Fig. 5).

Emarginate - Slightly concave (Fig. 6).

Epipieural ribs -Bones that attach on outside of upper surface of ribs (Fig. 7).

Eye diameter -The horizontal diameter of the fleshy orbit (eye opening) (Fig. 3).

Gill arch - One of the 4 arches of bones that bear the gills. If the gill cover or operculum (Fig. 4) is lifted, the (outermost) gill arch is visible in the gill cavity (Fig. 11).

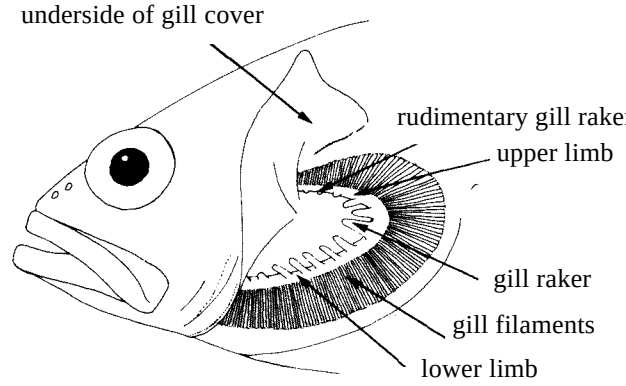


Fig. 11 First gill arch

Gill filaments -The soft, bright red filaments attached along the posterior (outer) edge of the gill arches (Fig. 11).

Gill rakers -The long bony protuberances along the anterior (inner) edge of the gill arches (Fig. 11). The **gill-raker count** is often given as two numbers (X + Y), where X is the number of rakers on the **upper (dorsal) limb** of the first arch, and Y is the number of rakers on the **lower (ventral) limb**, with, the raker at the angle (junction of upper and lower limbs) included in the lower-limb count. The range in number of gill rakers for a species is often given as follows: 7-9 + 16 -19 (which means there are 7 to 9 rakers on the upper limb and 16 to 19 rakers on the lower limb. **Rudimentary rakers** or **rudiments** (Fig. 12) are wider than long (high) and (unless indicated otherwise) are usually included in the gill-raker counts. If the rudiments are difficult to distinguish from intercalated bony tooth plates, the gill-raker count is of "developed" rakers only.

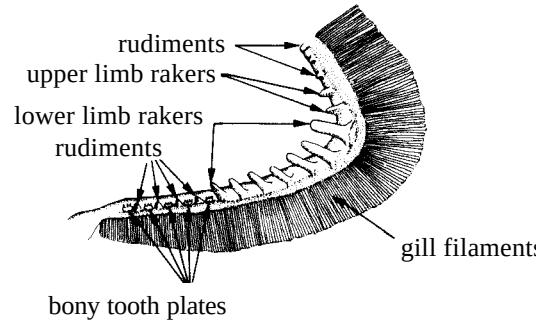


Fig. 12 Gill rakers and rudiments

Head length -The straight-line measurement from the front of the upper lip at the midline (with upper jaw retracted) to the posteriormost point of the operculum (Fig. 3).

Interorbital width - The least distance between the fleshy edges of the orbits (Fig. 4).

Lateral - Of or towards the side; opposite of "medial".

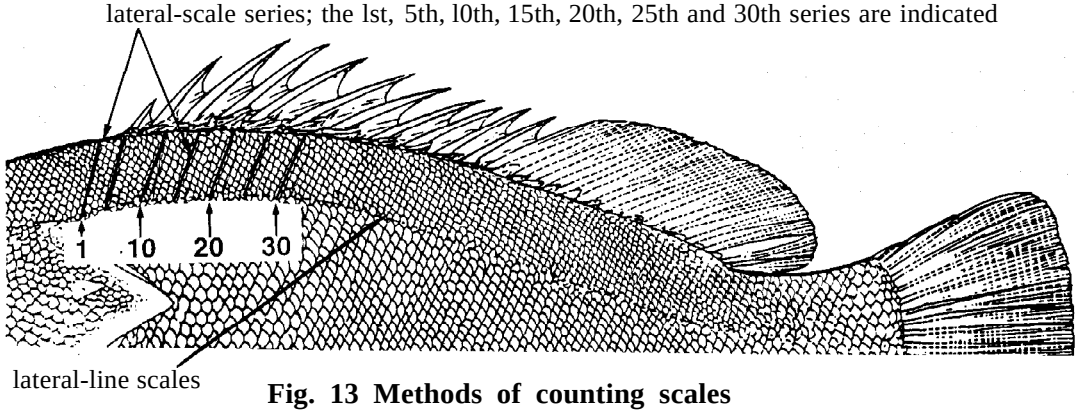


Fig. 13 Methods of counting scales

Lateral line -The series of pored or tubed scales that run from the upper end of the gill cavity to the caudal fin (Figs 3 and 13).

Lateral-scale series -The oblique series of scales that run above the lateral line from the upper end of the gill opéning to the base of the caudal fin (Fig. 13).

Lunate - Shaped like a crescent moon; deeply concave (Fig. 6).

Maxilla-The posterior, toothless bone of the upper jaw; partly covered by the upper lip when the mouth is closed (Fig. 4).

Maxillary streak - A dark streak along the edge of the maxillary groove (the groove below the eye that is hidden by the maxilla when the mouth is closed) (Fig. 5). Also called **moustache streak.**

Medial - Towards the middle or median plane of the body: opposite of "lateral."

Median fins - The dorsal, anal and caudal fins.

Nape - The posteriorpartof the top of the head (Fig. 3).

Opercle - The largest bone of the operculum (gill cover); mostly covered by skin and scales (Fig. 4).

Orbit - The fleshy eye opening. In live fish, the transparent cornea of the eye protrudes slightly through the orbit.

Palatines -The paired bones on each side of the roof of the mouth immediately posterior to the vomer. In most groupers, the palatines bear minute teeth which are visible on the roof of the mouth (Fig. 14).

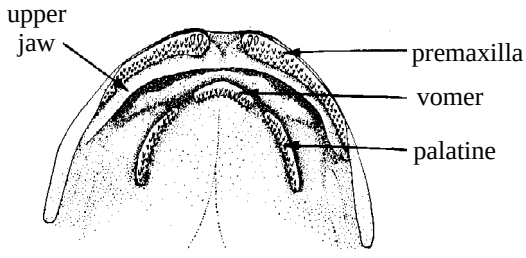


Fig. 14 Upper jaw and palate

Precaudal vertebrae - The anterior vertebrae which lack a haemal spine, but bear pleural ribs (Figs 7 and 8).

Premaxilla - The paired, tooth-bearing bones of the upper jaw, mostly hidden by the upper lip (Fig.14).

Preopercle - The rounded or angular bone on the front part of the operculum; the posterior edge is exposed and usually serrate (Fig. 4).

Preorbital - The anteriormost and largest bone of the circumorbital bones that form the lower edge of the orbit (Fig. 4).

Pterygiophore - The series of 2 or 3 bones that support each of the spines and rays of the dorsal and anal fins (Fig. 15). Note that the distal element of each pterygiophore is between the left and right halves of its associated (following) fin ray.

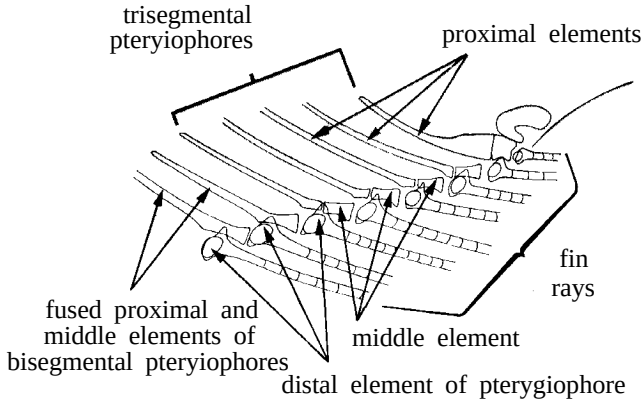


Fig. 15 Pterygiophores of the anal fin

Rays - The rigid or flexible struts that support the fins. **Soft rays** (usually just called "rays") are segmented, flexible and usually branched; the rays are also bilaterally paired (this bilateral structure is evident if the fish is cooked). **Spinous rays** (or fin "spines") are unsegmented, simple (unbranched) and pungent (stiff and sharp pointed). In the ichthyological literature, the fin spines are usually designated by Roman numerals and the soft-rays by Arabic numerals: D IX,1 4 (meaning that the dorsal fin has IX spines and 14 rays). The last ray of the dorsal and anal fins of groupers is usually split to its base and looks like two rays, but it is counted as a single ray because it is supported by a single pterygiophore.

Saddle blotch - A dark saddle-shaped blotch on the dorsal part of the body or caudal peduncle (Fig. 5).

Serrate - With a series of small points (serrae) like the teeth of a saw.

Snout -The part of the head in front of the eye (Fig. 3).

Spine - A sharp and stiff projection (see also rays).

Spot -A colour mark which is eye-sized or smaller, but larger than the size of the nostrils and usually with a regular or distinct margin (Fig. 5).

Standard length - The straight line distance from the tip of the snout to a vertical line passing through the base of the caudal fin (taken to be the point of flexure of the caudal fin) (Fig. 3).

Stripe - A narrow, oblique or horizontal colour marking, less than an eye diameter in width (Fig. 5).

Supramaxilla -A small elongate bone lying along the dorsal edge of the maxilla (Fig. 4).

Supraneural bones - Unpaired bones above the neural spines of anterior vertebrae between skull and origin of dorsal fin (Fig. 7). Also referred to as **predorsal bones.**

Synonym - An alternate name given to a particular species, genus, family etc. The oldest (senior) synonym that is given to a species is usually considered the valid (correct) scientific name for that species.

Thoracic -Pertaining to the thorax or chest region below the pectoral-fin base and in front of the pelvic fins.

Total length - The straight-line distance from the tip of the anteriormost jaw to a vertical line passing through the posterior tip of the longest caudal-fin ray (Fig. 3).

Truncate - Cut square; a caudal fin with a straight rear margin (Fig. 6).

Ventral - On or towards the lower part (underside) of fish.

Vertebrae - Bones of axial skeleton; divided into 2 sections, precaudal (abdominal) and caudal vertebrae (Figs 7 and 8).

Vomer - A median bone which lies on the roof of the mouth; often bears teeth (Figs 9 and 14).

1.5 Plan of the Catalogue

A classification of the Family Serranidae and a diagnosis of the Subfamily Epinephelinae are given, followed by remarks on the classification of groupers (Subfamily Epinephelinae), glossary of technical terms and measurements, aids to identification of groupers (keys to genera and species), and the information by genus and species (arranged alphabetically by genus and species). Since most species occur in only a single major region, the keys to species of the largest genera *(Cephalopholis, Mycteroperca* and *Epinephelus)* are divided into regional keys to shorten them and make them easier to use. Each genus account includes the type species and generic synonyms. For genera with more than one species, we also include a diagnosis and general comments on the habitat, biology, distribution and interest to fisheries of the included species. The information pertaining to species is divided into the following sections:

(1) Scientific Name: The reference to the original description and type locality of the species is given.

(2) Synonyms: Primary synonyms and alternate combinations of generic and specific names are listed.

(3) FAO Name: The FAO English name is considered the standard to be used for fishery purposes. This should avoid confusion caused by the existence of multiple names for the same species or the same name for several species. The FAO name is not intended to supplant the use of local names, but rather to serve as a worldwide reference. FAO French and Spanish names are given for each species.

(4) Diagnostic Features: Distinctive characters of the species are given as an aid for identification. These diagnoses should be consulted to confirm species identified using the illustrated key.

(5) Geographical Distribution: The general geographic range is given and illustrated on a map. The map shading includes known areas of occurrence and intermediate areas where a species is expected to be found.

(6) Habitat and Biology: Information on habitat, feeding preferences, age and growth, reproduction and behaviour is given for many species.

(7) Size: The maximum known size for each species is given.

(8) Interest to Fisheries: General information on the extent, type of fisheries and utilization is given. Detailed catch statistics (landings) are not available for all individual species.

(9) Local Names: Published local names are given. A local name is often applied to several species.

(10) Literature: Recent references that contain important information are given.

(11) Remarks: Taxonomic details and information that is not appropriate in the previous paragraphs are included here.

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