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LARVAL DEVELOPMENT IN FOUR SPECIES OF INDO-PACIFIC CORAL TROUT *PLECTROPOMUS* (PISCES: SERRANIDAE: EPINEPHELINAE) WITH AN ANALYSIS OF THE RELATIONSHIPS OF THE GENUS

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ABSTRACT

Larval development of *Plectropomus leopardus*, *P. maculatus*, *P. areolatus* and *P. laevis* was determined from specimens captured in Australian waters. Larvae are readily identifiable as epinepheline serrands by body shape, head spination and fin spine development. *Plectropomus* larvae are distinguished from other epinepheline larvae by structure of the pelvic spine, supraocular and preopercular spines, fin meristics, and pigment. The four species are distinguished primarily by pigment, number of pectoral rays, and to a lesser extent, by proportions of spines. Polarity for 12 character states was assigned after study of their ontogeny. This information was used to construct a phylogeny of epinepheline genera for which information on ontogeny was available. This led to the hypothesis that *Plectropomus* is the primitive sister group of other studied epinephelines and that *Cephalopholis* is distinct from *Epinephelus*.

The Indo-Pacific serranid genus *Plectropomus* Oken is composed of seven species (Hoese et al., 1981; J. E. Randall, in press) and is the fourth most speciose genus of the tribe Epinephelini (sensu Johnson, 1983) after *Epinephelus, Cephalopholis* and *Mycteroperca*. Commonly called coral trout, *Plectropomus* species are important medium to large predators on coral reefs (Goeden, 1978). *Plectropomus maculatus* is occasionally trawled (Hoese et al., 1981). Coral trout are highly valued sport and commercial fishes throughout their ranges.

Little is known of the early life history of any *Plectropomus* species. Neither eggs nor larvae have been described, and there is only one published study of spawning seasonality (Goeden, 1978). However, this is not unusual for Indo-Pacific epinephelines. Of the 11 genera of Indo-Pacific epinepheline serranids (Table 1) development has been completely to partially described for only a few species of *Epinephelus* (Mito, 1966; Ukawa et al., 1966; Mito et al., 1967; Fourmanoir, 1976; Chen et al., 1977; Tseng and Ho, 1979; Hussain and Higuchi, 1980; Leis and Rennis, 1983) and an unidentified *Cephalopholis* (Leis and Rennis, 1983). The larva identified as *Cephalopholis*? by Fourmanoir (1976) appears not to be of that genus but some other epinepheline. The larvae identified as *Epinephelus* by Nellen (1973) are in fact anthiine serranids. Development of American and eastern Atlantic epinepheline serranids is reviewed by Kendall (1979; 1984) and Johnson and Keener (1984). I have examined incomplete series of two as yet unidentified epinepheline larvae and larval series of *Epinephelus* and *Cephalopholis* from northern Australia to provide comparative material.

The status of *Cephalopholis* is controversial. Students of the American ichthyofauna generally regard *Cephalopholis* as a subgenus of *Epinephelus* (Smith, 1971; Johnson, 1983; Kendall, 1984) while those who study Indo-Pacific species consider *Cephalopholis* to be distinct from *Epinephelus* (Randall and Ben Tuvia, 1983; Randall, in press). I retain *Cephalopholis* as distinct from *Epinephelus* because of differences between their larvae (see Relationships, below) which seem to warrant a reassessment of the status of the genus.

I propose here to describe the larval development of four species of *Plectro-*

Table 1. Merisitic characters of Indo-Pacific serranid genera of the tribe Epinephelini. All genera but *Variola, Cephalopholis, Epinephelus* and *Plectropomus* are probably monotypic. From radiographs (numbers in parentheses indicate number of species x-rayed) and Randall and Ben Tuvia (1983). All have 24 vertebrae (10 + 14)

Genus	Dorsal fin	Anal fin	Pectoral fin	Pre-dorsal bones	Number interneural spaces with dorsal fin pterygiophores (not predorsals)
*Aethaloperca** (1)	IX,17–18=26–27	III,8–9	17–18	1–2	16–17
Anyperodon (1)	XI,14–16=25–27	III,8–9	15–17	2	17
Cephalopholis† (7)	IX,14–17=23–26	III,8–9	16–21	2	15–16
Cromileptes (1)	X,17–19=27–29	III,10	18	2	17–18
Epinephelus (14)	XI–XII,12–18=23–29	III,7–9	16–20	2	16–18
Gracila (1)	IX,15=24	III,9–10	19	2	15
Plectropomus (6)	VII, 11=19	III,8	14–18	1	14
Promicrops† (1)	XI,14–16=25–27	III,8	19	2	17
Saloptia‡ (1)	VIII,11=19	III,7–8	14–15	1	14
"*Trisotropis*"§ (1)	XI,19–21=30–32	III,10	18–19	2	17
Variola (1)	IX,13–15=22–24	III,8–9	16–18	2	15

* Not recognized by Johnson (1983), presumably synonymized with *Cephalopholis*.
† Considered by Johnson (1983) a subgenus of *Epinephelus* after Smith (1971).
‡ Not recognized by Johnson (1983), presumably synonymized with *Plectropomus*.
§ Following Johnson (1983), this monotypic genus should be renamed because *Trisotropis* is a junior synonym of *Mycteroperca*.

pomus from material collected in Australian waters and to compare *Plectropomus* larvae with other epinepheline larvae for both identification and relationships.

Materials and Methods

The larvae used in this study came from light traps, plankton tows and midwater trawls from several sources (see Acknowledgments). The principal collecting areas were the Great Barrier Reef off Townsville (19°S) and near Lizard Island (14°S), and the Australian northwest continental shelf near Port Hedland (20°S). Larvae were fixed in 5–10% formalin-seawater or ethanol. Approximately 130 *Plectropomus* larvae were available, but many were extensively damaged and were either entirely or partially unsuitable for descriptive purposes. For this reason the numbers of larvae used for each count or measurement are not equal.

Larvae were examined under a dissecting microscope and measured using its ocular micrometer. Measurement was to the nearest micrometer unit, which varied from 0.015 to 0.128 mm, depending on magnification. Some larvae were stained with alizarin or cleared and stained following the method of Dingerkus and Uhler (1977) as modified by Fritzsche and Johnson (1979) and Potthoff (1984). Drawings were done with the aid of a camera lucida.

Terminology and measurements generally follow Leis and Rennis (1983). Fin spine terminology follows Johnson and Keener (1984). Pectoral fin ray counts include all rays from both fins. If one fin was too damaged to be counted, I assumed both fins had the same count. Unlabeled lengths are body length. Percentages are of body length unless otherwise stated. All pigment referred to is melanin.

Material Examined.—Specimens are lodged in the Australian Museum, Sydney (AMS) and CSIRO Division of Fisheries, Hobart. All but two AMS lots are from the Great Barrier Reef. All CSIRO and two AMS lots (I.25122-001, 25123-001) are from northwest continental shelf of Australia.

Plectropomus maculatus AMS I.23220-003, I.22553-003, I.23513-003, I.23759-004, I.23511-003, I.24209-003, I.24555-001, I.23573-002, I.24207-007, I.24208-007, I.24643-001, I.25122-001, I.6110; CSIRO L1, L2, L3, L4, L5, L6, L7, L8, L9.

Plectropomus leopardus AMS I.24209-006, I.23752-003, I.23591-003, I.23596-004, I.24212-001, I.24759-001, I.23761-001, I.23573-003, I.23578-001, I.23580-003, I.23577-001, I.23581-001, I.23737-001, I.23592-001, I.23531-003, I.21495-007, I.23594-001, I.23785-001, I.23760-001, I.23113-017, I.23098-023, I.24209-004, I.24209-002, I.24209-005, I.23742-002, I.24208-006, I.24208-005, I.23764-005, I.23123-013, I.24210-001, I.25116-001; CSIRO L10.

Plectropomus areolatus CSIRO L11, L12; AMS I.25123-001.

Plectropomus laevis AMS I.24747-001, I.24509-002, I.24515-001, I.24528-001.

Table 2. Selected characters of larvae of three Indo-Pacific serranid genera of the tribe Epinephelini. Data on *Epinephelus* include published descriptions of *E. tauvina* and *E. akaara* (see Introduction for citations)

Species examined	*Plectropomus* 4	*Epinephelus* >6	*Cephalopholis* >5
Pelvic spine	3 ridges; spines of primary ridge strongly enlarged and recurved, one specimen with a few bifurcate spines (metamorphic?)	4 ridges; spines of primary ridge recurved or not, about 25% of specimens with some bifurcate spines	4 ridges; spines of primary ridge strongly to slightly enlarged and recurved, about ½ of specimens with some bifurcate spines
Supraocular ridge* (Fig. 2)	forms late (3.7 mm); 2–4 weak spine points; serrations weak	forms early (3.0 mm); single strong spine point; serrations coarse	forms early (3.0 mm); single strong spine point; serrations coarse
Preopercular spines			
Upper limb (Fig. 1A)*	1 (rarely 2) until 15 mm, then up to	1–3 (≥2 after 8 mm)	1–9 (≥2 after 8 mm)
Lower limb (Fig. 1B)*	6 (4 after 7 mm)	1–3 (≤2 until 10 mm)	1–4 (≤2 until 11 mm)
Serrations on some lower limb spines	no	yes	yes
Some spines on lower limb antrorse	yes*	no	no
Posterior 1 or 2 dorsal spines form first as soft ray(s)	no	yes	yes
Size (mm) at which all dorsal spines present (number)	7.3–7.7 (VIII)	13.5–16.0 (XI)	9.4–11.1 (IX)
Size (mm) at which all anal spines present	following settlement >22.5 but <37	prior to settlement 16–18	prior to settlement >11 but <16
Tail melanophores*	None or ventral series of 14–21. Reduce in number with age to 0. No dorsal shift to lateral position.	Single enlarged ventral melanophore which shifts dorsally to mid-lateral peduncle at about 6.5–7.5 mm.	Ventral series of 15–23. Reduce in number with age to 1–4 and shift dorsally to lateral peduncle from <6.5 to 8 mm, depending on species.
Scales	None present in largest larvae (18.2 mm)	Forming in specimens as small as 18.5 mm	Forming in specimens 16.5–17.3 mm

* Indicates a character which changes with growth.

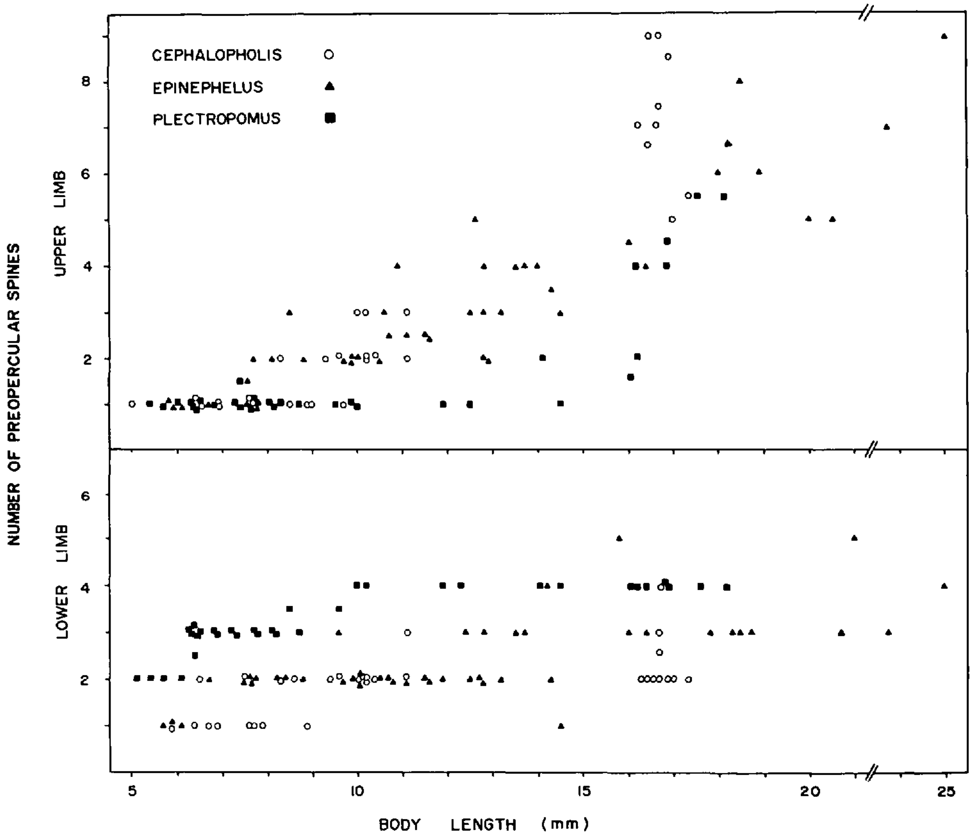


Figure 1. Development of spines on the preopercular outer border in larvae of three genera of epinepheline serranids. Number of spines on upper limb (upper panel); number of spines on lower limb (lower panel). Data from Indo-Pacific species including published descriptions of *E. akaara* (Ukawa et al., 1966) and *E. tauvina* (Hussain and Higuchi, 1980) and specimens examined in this study.

Results and Discussion

Identification.—Larvae were identified as epinepheline serranids by their characteristic head spination, kite-shaped body and elongate, ornamented dorsal and pelvic fin spines (Kendall, 1979; 1984; Leis and Rennis, 1983). Larger larvae were identified as *Plectropomus* by their fin meristics, particularly the dorsal fin counts of VIII, 11 and single predorsal bone. Only two genera of epinepheline serranids have these characters (Table 1): *Plectropomus* and the monotypic *Saloptia. Saloptia* is closely related to and perhaps synonymous with *Plectropomus* (J. L. B. Smith, 1963; my observations). *Saloptia* is presently known only from the Cook Islands, Samoa, Southern Japan and the South China Sea (Kyushin et al., 1982; Wass, 1984). Five species of *Plectropomus* may occur in northern Australia (Hoese et al., 1981), and because all larvae from the present study were from Australian waters, they were identified as *Plectropomus*.

The larger *Plectropomus* larvae were used to establish characters which enabled assembly and identification of series of smaller larvae. These characters included tail pigment, structure of the pelvic spine and head spination (Table 2, Figs. 1–3). The pigment pattern on the tail (no pigment or a series of small ventral

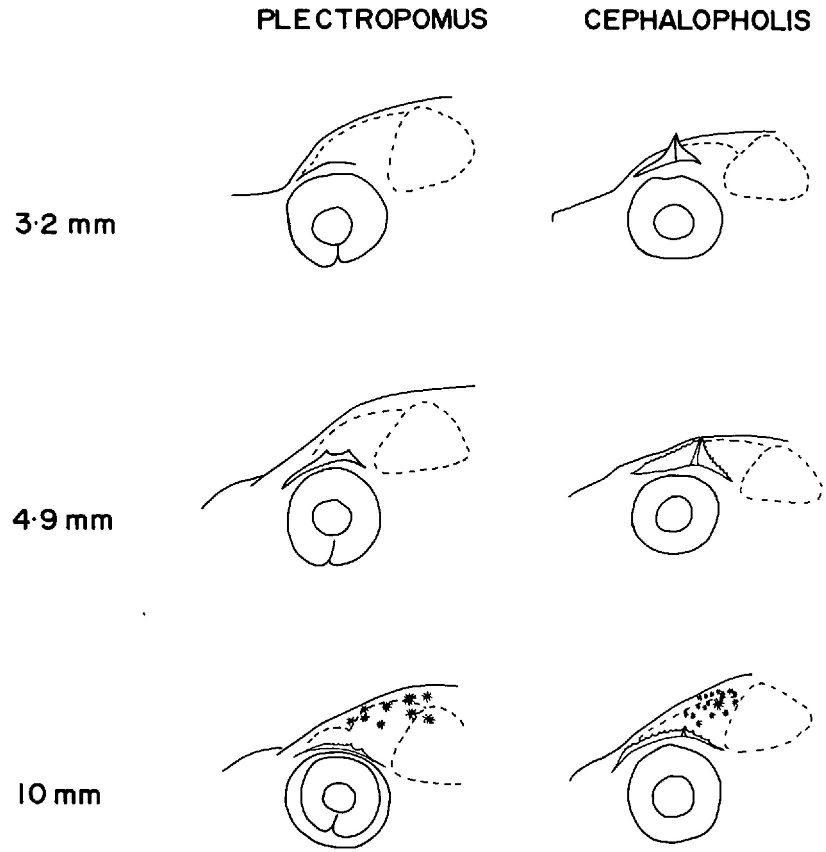


Figure 2. Development of supraocular ridge in *Plectropomus* and *Cephalopholis* (development in *Epinephelus* is similar to that in *Cephalopholis*). 3.2 and 4.9 mm specimens are *P. leopardus* from northern Great Barrier Reef; 10 mm specimen is *P. maculatus* from Australian northwest continental shelf. 3.2 and 4.9 mm specimens are *Cephalopholis* species A from northern Great Barrier Reef; 10 mm specimen is *Cephalopholis* species B from central Great Barrier Reef.

melanophores) was used to distinguish the larvae from *Epinephelus* which have a single large melanophore (Kendall, 1979; 1984; my observations). In addition, the ventral pigment on the tail does not shift dorsally in *Plectropomus* as it does in *Cephalopholis* and *Epinephelus*. *Plectropomus* larvae have three longitudinal ridges armed with spinelets on the pelvic spine. All American epinepheline genera, examined Indo-Pacific species of *Cephalopholis, Epinephelus* and the two unidentified genera have four ridges (Johnson and Keener, 1984; my observations). This character can be used to distinguish *Plectropomus* from other genera in larvae as small as 2.5 mm. The supraocular ridge of *Epinephelus, Cephalopholis* and the two unidentified genera forms at about 3 mm as a single spine point which quickly enlarges to a maximum at about 5 mm and gradually becomes indistinguishable from coarse serrations along the ridge at about 11 mm (Fig. 2). In *Plectropomus,* the ridge originates as a single, weak spine at about 3.7 mm. The spine enlarges only slightly and one or more additional spine points form from about 5 mm. Only weak serrations form and the multiple spine points can be distinguished in larvae as large as 14.5 mm (Fig. 2).

Very small *Plectropomus* larvae that had not yet developed head spination or

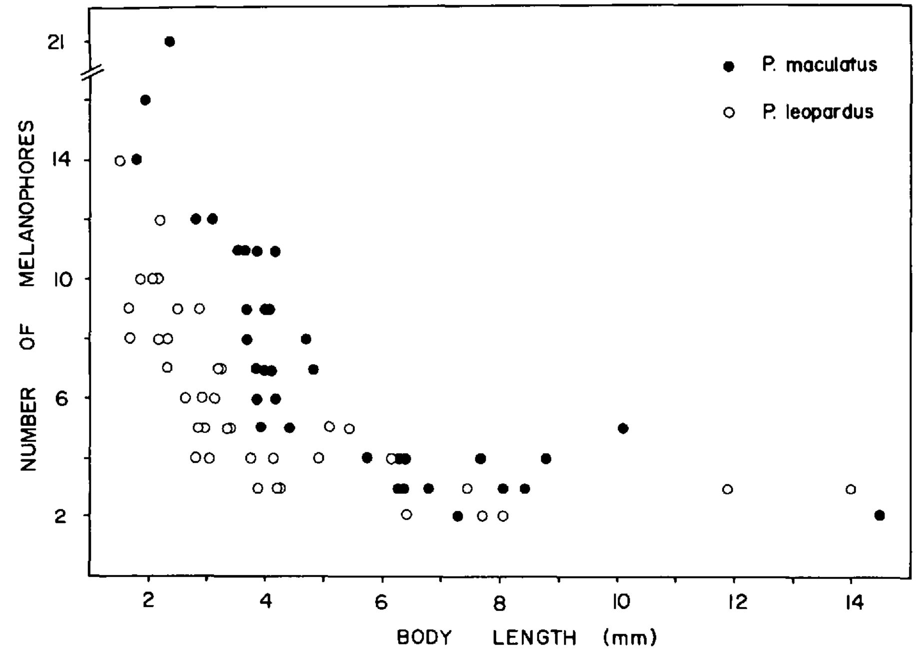


Figure 3. Number of ventral melanophores on tail (excluding exposed tip of notochord) in relation to body size in *Plectropomus leopardus* (open symbols) and *Plectropomus maculatus* (solid symbols).

ridges on the pelvic spines were distinguished from *Cephalopholis* and *Epinephelus* larvae solely by pigment: *Epinephelus* have a single enlarged ventral melanophore on the tail, and which distinguishes them from the others. Based on the smallest larvae identifiable by other means, it was established that *Plectropomus* and *Cephalopholis* larvae could be distinguished by ventral pigment. Two species of *Plectropomus* larvae had 12 or fewer melanophores ventrally on the tail (this number decreases with growth, Fig. 3), 1–3 melanophores on the ventral edge of the notochord tip and caudal anlage, 0–1 melanophores on the caudal fin fold and at least as many notochord edge melanophores as caudal fin fold melanophores. Most *Cephalopholis* larvae, in contrast, had more than 12 ventral melanophores on the tail, 0 or 1 notochord edge melanophores, more than 2 melanophores on the caudal fin fold, and more finfold than notochord edge melanophores. Each larva was scored giving one point for each *Plectropomus* character state and no points for each *Cephalopholis* character state. Larvae with a score of 0 or 1 were considered *Cephalopholis.* No larvae had a score of 2. A few of the smallest larvae had scores of 3 (because they had >12 melanophores ventrally on the tail, Fig. 3), and were considered to be *Plectropomus,* as were larvae with a score of 4. The two less common types of *Plectropomus* larvae lack tail pigment over the identifiable size range available as do larvae of the two unidentified genera. These could not be distinguished before spine formation.

Identification of *Plectropomus* larvae to species utilized meristic and pigment characters. Of the six species of *Plectropomus* reported from Australia, *P. oligacanthus* (which has 28–30 pectoral rays) was not considered because its presence in Australian waters is based on one old, dubious record (Hoese et al., 1981). The number of pectoral rays in adults (Hoese et al., 1981; Randall, in press) divided the remaining species into three groups: 32 pectoral rays, *P. maculatus* (91% of

Table 3. Distinguishing characters of larval *Plectropomus*

	leopardus	*maculatus*	*areolatus*	*laevis*
Ventral melanophores on tail (Fig. 3)*	0–14 decrease in number rapidly with size	2–21 decrease in number slowly with size	0	0
Dorsal melanophores on trunk/anterior tail (Table 4)*	0	0–4 present only between 2.8 and 5 mm	0	0
Size at appearance midbrain pigment	6.4–7.4	6.3	7–9 mm	?
Melanophore on pelvic membrane	absent	present in larvae >2.3 mm	absent	absent
Length spine at preopercular angle (Fig. 4)*	long	short	intermediate	long
Points on supraocular ridge (Table 4)*	3–4	2	2	2–3
Length of 2nd dorsal spine (Fig. 5)*	intermediate	intermediate	long	short
Pectoral fin rays (both sides)	32	32	30–32	34

* Indicates varies with size. Refer to figures or tables noted.

specimens) and *P. leopardus* (95%); 30–32 pectoral rays *P. areolatus* (25% = 30, 75% = 32); 34 pectoral rays *P. laevis* (95%). The four types of larvae in the collections (Table 3) were also divisible into three groups: two with 32 rays, identified as either *P. maculatus* or *P. leopardus*; one with 30–31 rays, identified as *P. areolatus*; and one with 34 rays, identified as *P. laevis*. Newly settled (20–22 mm) *P. leopardus* have no spots on the pelvic fins, and this corresponds to one of the larval types with 32 pectoral rays. Three of four young settled *P. maculatus* (37–57 mm) have the remains of a black spot on at least one pelvic spine and this corresponds to the spot present in the other larval type with 32 pectoral rays. On this basis, the larvae were identified as *P. leopardus* and *P. maculatus*, respectively. There were only five larval specimens of *P. laevis*. Certain distributional and abundance data support these identifications (see species accounts).

Development.—Development of the four *Plectropomus* species is generally similar, and differs among species only in minor detail. For this reason, a description of development as it applies to all species will be given first. This is followed by diagnoses and remarks for each species. Morphometric and meristic characters are given in Table 4. Reasonably complete developmental series were available only for *P. leopardus* and *P. maculatus*. Only six *P. areolatus* and five *P. laevis* larvae were available.

Morphology (Table 4, Figs. 6–10).—Larvae of *Plectropomus* are morphologically generally similar to other epinepheline larvae (Kendall, 1979; Leis and Rennis, 1983). The smallest available *Plectropomus* larvae have a coiled gut. The gas bladder is located over the anterior gut but is not conspicuous because it is obscured by pigment and is rarely inflated in day-caught larvae. The body is compressed and roughly kite-shaped and much deeper at the level of the pectoral fin base than at the level of the anus. However, as larvae approach settlement, body depth at these two levels is about equal. The head is large (to 43%), relatively

Table 4. Morphometric and meristic characters of *Plectropomus* larvae. Mean values in mm and parenthetically, standard deviation. If no standard deviation given, value is based on one individual only. Values separated by a dash indicate a range. d indicates damaged, blank indicates structure not present. Counts for pectoral fin are sums of both fins of each individual. Larvae between dashed lines are undergoing notochord flexion

Size class	N	Pre anal length	Pre dorsal length	Head length	Snout length	Eye diameter	Body depth at P_1 base	Body depth at anus
				Plectropomus leopardus				
1.51–2.00	4	0.99 (0.06)	0.74 (0.14)	0.56 (0.07)	0.16 (0.03)	0.26 (0.03)	0.60 (0.07)	0.47 (0.08)
2.01–2.50	7	1.11 (0.11)	0.76 (0.05)	0.71 (0.15)	0.22 (0.06)	0.31 (0.29)	0.72 (0.07)	0.45 (0.06)
2.51–3.00	6	1.57 (0.18)	1.20 (0.11)	1.10 (0.18)	0.36 (0.07)	0.39 (0.04)	1.07 (0.20)	0.70 (0.15)
3.01–3.50	6	1.62 (0.07)	1.23 (0.07)	1.10 (0.10)	0.34 (0.05)	0.39 (0.06)	0.98 (0.05)	0.68 (0.04)
3.51–4.00	2	1.94	1.48	1.42 (0.18)	d	d	1.16	0.90
4.01–4.50	3	2.29 (0.03)	1.66 (0.13)	1.64 (0.07)	0.61 (0.07)	0.49 (0.02)	1.47 (0)	1.06 (0)
4.90	1	2.58	1.94	2.00	0.66	0.59	1.72	1.09
5.01–5.50	2	2.96 (0.35)	2.04 (0.23)	1.87	0.69	0.59 (0.08)	1.86 (0.16)	1.36 (0.16)
6.01–6.50	2	3.03	2.80 (0.14)	2.64 (0.08)	0.79 (0.03)	0.69 (0.04)	2.11 (0.02)	1.62 (0.01)
7.43	1	4.10	3.00	3.12	0.84	0.81	2.66	1.88
7.70	1	4.48	3.52	3.35	0.98	0.81	2.39	1.81
8.06	1	4.58	3.42	3.29	1.10	0.97	2.90	2.19
11.91	1	6.80	4.74	5.16	1.35	1.23	3.81	2.71
14.10	1	8.30	8.33	6.02	1.55	1.42	4.64	3.74
16.01–16.5	3	9.35 (0.44)	6.23 (0.41)	6.42 (0.40)	1.75 (0.15)	1,68 (0.13)	5.12 (0.26)	4.27 (0.19)
16.51–17.0	2	10.57 (0.09)	6.79 (0.02)	6.66 (0.18)	1.83 (0.13)	1.80 (0.02)	5.44 (0.08)	4.62 (0.17)
17.81	1	10.63	7.43	6.98	1.92	1.79	5.76	4.80
18.20	1	11.02	7.43	7.05	1.92	1.92	5.89	5.38
				Plectropomus maculatus				
1.51–2.00	2	0.97 (0.04)	0.65 (0.02)	0.50 (0.04)	0.15	0.27 (0.01)	0.65 (0.02)	0.41 (0.10)
2.34	1	1.25	0.94	0.88	0.28	0.36	0.81	0.62
2.80	1	1.55	1.16	1.03	d	0.34	0.90	0.71
3.10	1	1.94	1.23	1.29	0.47	0.39	0.94	0.49
3.51–4.00	13	2.06 (0.20)	1.44 (0.16)	1.43 (0.16)	0.46 (0.06)	0.42 (0.03)	1.28 (0.12)	0.86 (0.09)

Table 4. Continued

Size class	N	Pre anal length	Pre dorsal length	Head length	Snout length	Eye diameter	Body depth at P_1 base	Body depth at anus
4.01–4.50	8	2.10 (0.23)	1.68 (0.09)	1.48 (0.08)	0.45 (0.01)	0.43 (0.01)	1.30 (0.07)	1.03 (0)
4.84	1	d	d	d	d	d	d	d
4.70	1	2.58	2.06	1.94	0.77	0.52	1.61	1.23
5.74	1	3.48	2.32	2.45	0.88	0.69	1.94	1.57
6.01–6.50	4	3.81 (0.18)	2.95	d	d	0.67 (0.03)	2.17 (0.16)	1.42
6.80	1	d	d	d	d	d	d	d
7.30	1	d	d	d	d	d	d	d
7.69	1	4.40	3.46	3.10	d	0.77	1.94	1.61
8.00–8.50	2	d	d	d	d	d	d	d
8.71	1	4.11	3.59	3.42	0.97	0.97	2.58	2.19
10.11	1	5.64	3.97	4.06	1.16	1.03	d	2.26
14.48	1	7.94	5.51	4.84	1.16	1.35	4.64	3.74
				Plectropomus areolatus				
6.26	1	d	2.84	2.58	1.09	0.66	2.09	d
6.40	1	d	d	d	d	d	d	d
6.92	1	3.87	2.97	2.81	0.77	0.65	2.58	1.87
7.30	1	4.32	3.10	3.00	0.90	0.70	2.58	1.74
9.61	1	6.00	4.06	4.00	0.91	0.90	3.29	2.39
10.00	1	d	d	4.10	1.28	1.02	d	d
				Plectropomus laevis				
4.71	1	2.58	2.19	1.68	0.65	0.61	1.29	0.97
4.84	1	2.39	1.87	1.74	0.63	0.56	1.48	1.23
5.00	1	2.58	1.87	1.80	0.65	0.55	1.55	1.10
5.74	1	3.03	2.26	2.26	0.90	0.71	1.94	1.29
12.49	1	7.43	5.55	5.25	1.94	1.29	4.19	3.16

Table 4. Continued

Size class	Length D spine 1	Length D spine 2	Length P_2 spine	Length preopercular angle spine	D	A	P_1	P_2	Points on supraocular ridge
Plectropomus leopardus									
1.51–2.00		0.34 (0.18)	0.36 (0.04)		0–I	0	0	0–I	0
2.01–2.50		0.88 (0.48)	0.89 (0.43)		I	0	0	I	0
2.51–3.00		2.06 (0.53)	1.99 (0.46)	0.09 (0.02)	I	0	0	I	0
3.01–3.50		2.31 (0.58)	2.06 (0.66)	0.11 (0.04)	I	0	0	I	0
3.51–4.00		3.03	2.74	0.23 (0.06)	I	0	0	I	0–1
4.01–4.50	0.09 (0.01)	5.38	3.77 (1.00)	0.36 (0.05)	I–III	0	0	I,2	1–2
4.90	0.11	5.30	4.71	0.44	III	0	0	I,2	2
5.01–5.50	0.14 (0.02)	d	4.68 (0.87)	0.47 (0.04)	III	0	0	I,2	2–3
6.01–6.50	0.19 (0.04)	7.05	5.89	0.69 (0.09)	III–IV+3–11	0–I,3–9	0–17	I,2–3	2–3
7.43	0.36	9.10	d	0.86	VI+11	II,9	25	I,5	2
7.70	0.25	10.25	7.43	d	VIII,11	II,9	31	I,5	3
8.06	0.28	d	6.26	0.86	VIII,11	II,9	32	I,5	3–4
11.91	0.70	d	d	0.97	VIII,11	II,9	32	I,5	3
14.10	0.52	d	d	1.00	VIII,11	II,9	32	I,5	3
16.01–16.5	0.65 (0.10)	4.97 (2.09)	4.58 (1.08)	0.65 (0.07)	VIII,11	II,9	32	I,5	—
16.51–17.0	0.58 (0.18)	3.97 (0.72)	4.18 (0.43)	0.81 (0.05)	VIII,11	II,9	32	I,5	—
17.81	0.45	6.02	d	0.77	VIII,11	II,9	32	I,5	—
18.20	0.84	3.46	3.84	0.77	VIII,11	II,9	32	I,5	—
Plectropomus maculatus									
1.51–2.00		0.16	0.11		0–I	0	0	0–I	0
2.34		1.41	1.90		I	0	0	I	0
2.80		1.84	1.81	0.04	I	0	0	I	0
3.10		2.84	2.58	0.09	I	0	0	I	0
3.51–4.00	0.06	4.39 (0.40)	3.74 (0.43)	0.23 (0.04)	I–II	0	0	I,0–2	1

Table 4. Continued

Size class	Length D spine 1	Length D spine 2	Length P_2 spine	Length preopercular angle spine	D	A	P_1	P_2	Points on supraocular ridge
4.01–4.50	0.08	5.16	4.38 (0.63)	0.28 (0.05)	I–II	0	0	I,0–2	1
4.84	d	d	4.90	0.39	I	0	0	I	1
4.70	0.14	d	d	0.39	III	0	0	I,1	2–3
5.74	0.20	d	5.48	0.50	IV+11	I,9	16	I,2	2
6.01–6.50	0.20 (0.05)	d	6.58	0.58 (0.09)	V–VIII,11	II,9	20–21	I,4–5	2
6.80	0.23	d	d	d	d	d	26	d	d
7.30	d	d	d	d	VI+11	II,9	22	I,5	2
7.69	0.19	d	d	0.69	VIII,11	II,9	25	I,5	2
8.00–8.50	d	d	d	0.72	VIII,11	II,9	32	I,5	2
8.71	0.33	11.02	7.11	0.72	VIII,11	II,9	32	I,5	2
10.11	0.31	d	d	0.78	VIII,11	II,9	32	I,5	2
14.48	0.58	8.97	7.37	0.83	VIII,11	II,9	32	I,5	2
				Plectropomus areolatus					
6.26	0.17	d	d	0.59	IV+11	9	20	I,3	2
6.40	d	d	d	d	V+11	II,9	20	I,4	2
6.92	0.22	10.19	7.10	0.72	VI+11	II,9	31	I,5	2
7.30	0.23	11.20	7.42	0.73	VI+11	II,9	30	I,5	2
9.61	0.34	d	7.61	0.88	VIII,11	II,9	30	I,5	2
10.00	0.34	d	d	1.00	VIII,11	II,9	31	I,5	2
				Plectropomus laevis					
4.71	0.16	4.45	4.06	0.45	II	0	0	I	2
4.84	0.06	4.68	4.19	0.47	III	0	0	I,1	2
5.00	0.11	4.19	3.61	0.42	III	0	0	I,1	2
5.74	0.19	5.48	4.90	0.55	III+9	9	0	I,3	2
12.49	0.87	6.28	6.41	1.17	VIII,11	II,9	34	I,5	2–3

broad and extensively spined (see below). The mouth is very large. The maxilla reaches to the anterior edge of the eye at about 2 mm and well beyond mid eye at settlement. Small teeth are present on the premaxilla from about 3 mm, but no enlarged canines are present until after settlement. The snout is initially short and blunt, but becomes more elongate with growth. The eye is large. There are 24 myomeres with a typical formula of 10+14. No scales are present in any of the pelagic specimens.

The first spine to form on the head is at the angle of the preoperculum at about 2.5–3.0 mm. The spine grows rapidly (Fig. 4), becomes armed with small spinelets by about 4 mm, and reaches maximum relative length at about 6 mm (Fig. 4) when it reaches just past the border of the operculum, but not to the pectoral base. A small spine first appears on the upper limb of the preopercular border at about 3.2–3.7 mm. In most specimens, no more spines form on the upper limb until about 14 mm, but a 7.4 mm *P. leopardus* had a second spine on one side of the head. As many as six small spines are present in the largest pelagic specimens (Fig. 1, upper). A small spine forms on the inner border of the lower limb of the preoperculum at about 3.2 mm. The first spine on the outer border of lower limb of the preoperculum appears at about 3.9 mm. Additional spines are added with growth to a maximum of four in the largest specimens (Fig. 1, lower). Three of these spines become antrorse. Aside from the large spine at the angle, preopercular spines remain smooth and non-serrate. The spines at the angle and upper limb disappear at about the time of settlement, but those of the lower limb enlarge and become the antrorse spines of the adult.

The supraocular ridge becomes visible as a single weak spine at about 3.7 mm. Depending on species, the second weak spine of the ridge appears at 4.2–5.0 mm, and in some species, a third or more spines form (Table 4). Very fine serrations form along the ridge from 6–7 mm. The spines become progressively relatively smaller with growth, but are distinguishable from the serrations in larvae as large as 14.5 mm. In larvae approaching settlement (16–18 mm), the ridge is reduced and often subdermal. There are no spines and the serrations are weak and irregular.

The posttemporal spine first emerges at about 3.7 mm and becomes armed with small spinelets shortly thereafter. The supracleithral spine appears at about 5.7 mm, grows rapidly, becomes armed with small spinelets, and is longer than the posttemporal spine by 7.5 mm. The posttemporal spine is greatly reduced as larvae approach settlement, and both spines are absent in the smallest settled individuals.

A few less conspicuous spines form in *Plectropomus* as they do in other epinephelines (Kendall, 1979): these include the small subopercular and interopercular spines and opercular spination.

Fin development in *Plectropomus* differs in a number of ways from that in other epinepheline genera. Spine 2 of the dorsal fin emerges from the anlage at about 1.6–1.8 mm. It is smooth and enclosed in a membranous sheath in undamaged specimens. Serrations are present from about 2 mm and the first of the enlarged, recurved spinelets from about 2.3 mm. The spine grows rapidly, becoming markedly elongate and reaching maximum relative length at about 7–8 mm when it may attain 150% of body length (Fig. 5). Spine 2 is armed on the apex ridge with small spinelets and on the posterior lateral wings with enlarged, recurved spinelets. The number of enlarged, recurved spinelets increases with growth at least to 9 mm when 30 may be present on each wing. Dorsal spine 1 is present at about 4 mm with spines 3 through 8 forming sequentially (Table 4). Spine 3 of the dorsal fin is the second largest and increases in relative length with body growth, but it reaches a maximum of only 14.7% in *P. maculatus*. The eight

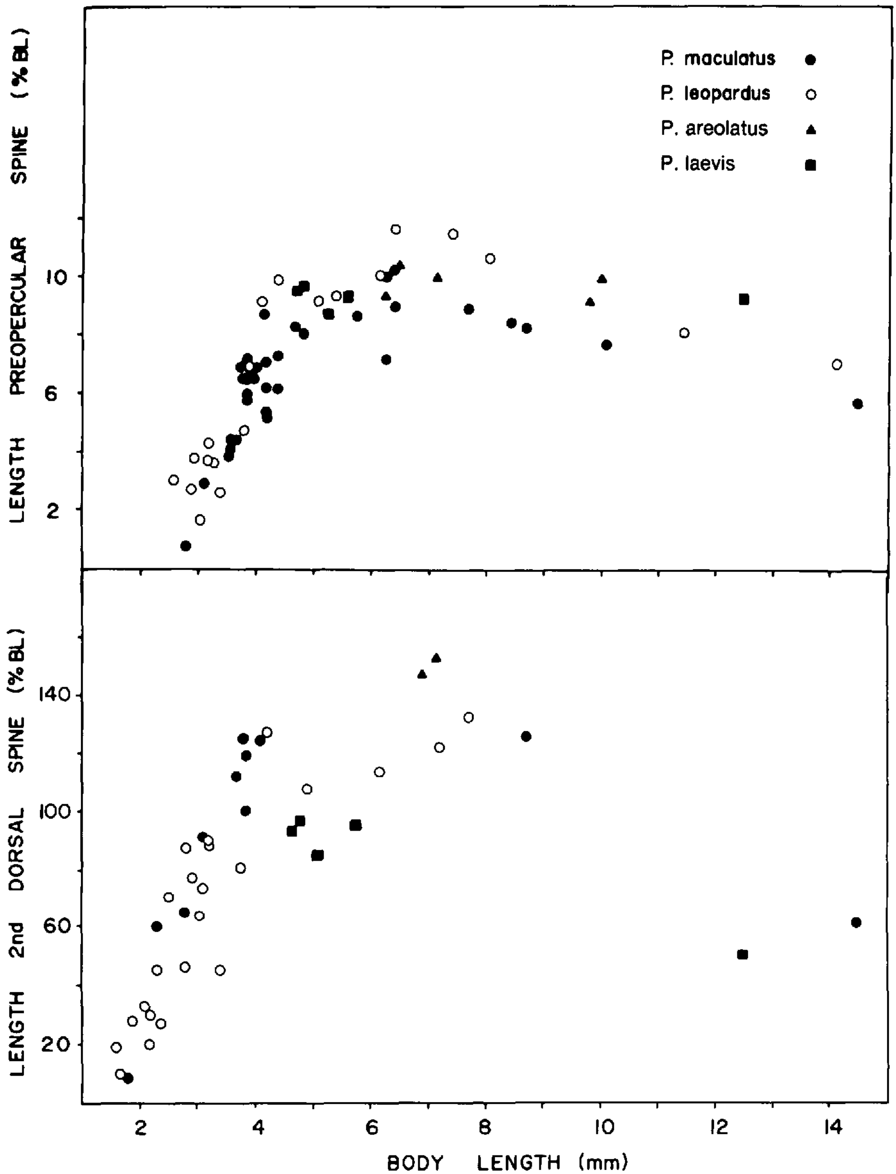


Figure 4. (Upper) Length of spine at angle of preopercular border (as percent of body length) in relation to body length in larvae of four species of *Plectropomus*.

Figure 5. (Lower) Length of dorsal fin spine 2 (as percent of body length) in relation to body length in larvae of four species of *Plectropomus*.

spines all form directly without passing through a soft ray stage. All spines are present by about 7 mm. All spines may become armed with at least weak apex or wing serrations, and spines 3 and 4 have enlarged, recurved wing spinelets by about 10 mm. Incipient soft rays are present at about 5.5 mm, and a full complement of 11 rays is present shortly thereafter. In larvae approaching settlement, the elongate dorsal spine 2 begins to erode distally, and becomes progressively shorter. Up to one-third of the spine may appear pitted and have sections missing at this stage. The smallest settled specimens have no elongate spines or ornamentation.

The soft rays of the anal fin form simultaneously with the soft dorsal rays. All rays are present before spine 2 of the fin forms at about 6 mm. Spine 1 forms shortly thereafter. These two spines become ornamented with serrations on the apex ridge and straight, recurved or bifurcate spinelets along the wings. Spine 3 forms from a soft ray but not until after settlement. A 22 mm settled *P. leopardus* has only two anal spines. The next largest specimen, a 37 mm *P. maculatus,* has a third spine that is flexible and appears to have just transformed from a ray.

The first, incipient caudal rays appear at about 4 mm, and notochord flexion takes place between 4.7 and 5.7 mm (Table 4).

The elongate pelvic spine develops in synchrony with dorsal spine 2 although it remains generally shorter (Table 4). Three ridges form along the length of the spine. In the terminology of Johnson and Keener (1984) these are ridges 1, 2 and 3+4. These ridges are evident in specimens as small as 2.5 mm. Ridge 1 develops enlarged, recurved spinelets. Ridges 2 and 3+4 develop small, straight spines with those on ridge 2 being somewhat larger. The pelvic soft rays begin to form at about 4 mm and all are present by 7 mm. The pelvic spine also becomes shorter through an erosive process as settlement is approached.

Incipient rays are present in the pectoral fin from about 5.5 mm and form sequentially from dorsal to ventral. A full complement of incipient rays is visible at about 7 mm.

The number of gill rakers increases with growth from about 15 total rakers on the first arch at 6–7 mm to 20–22 rakers at 12–14 mm. There is no indication of any differences between species in number of gill rakers during the larval period, so the differences between adults noted by Hoese et al. (1981) must result from later addition or loss of rakers.

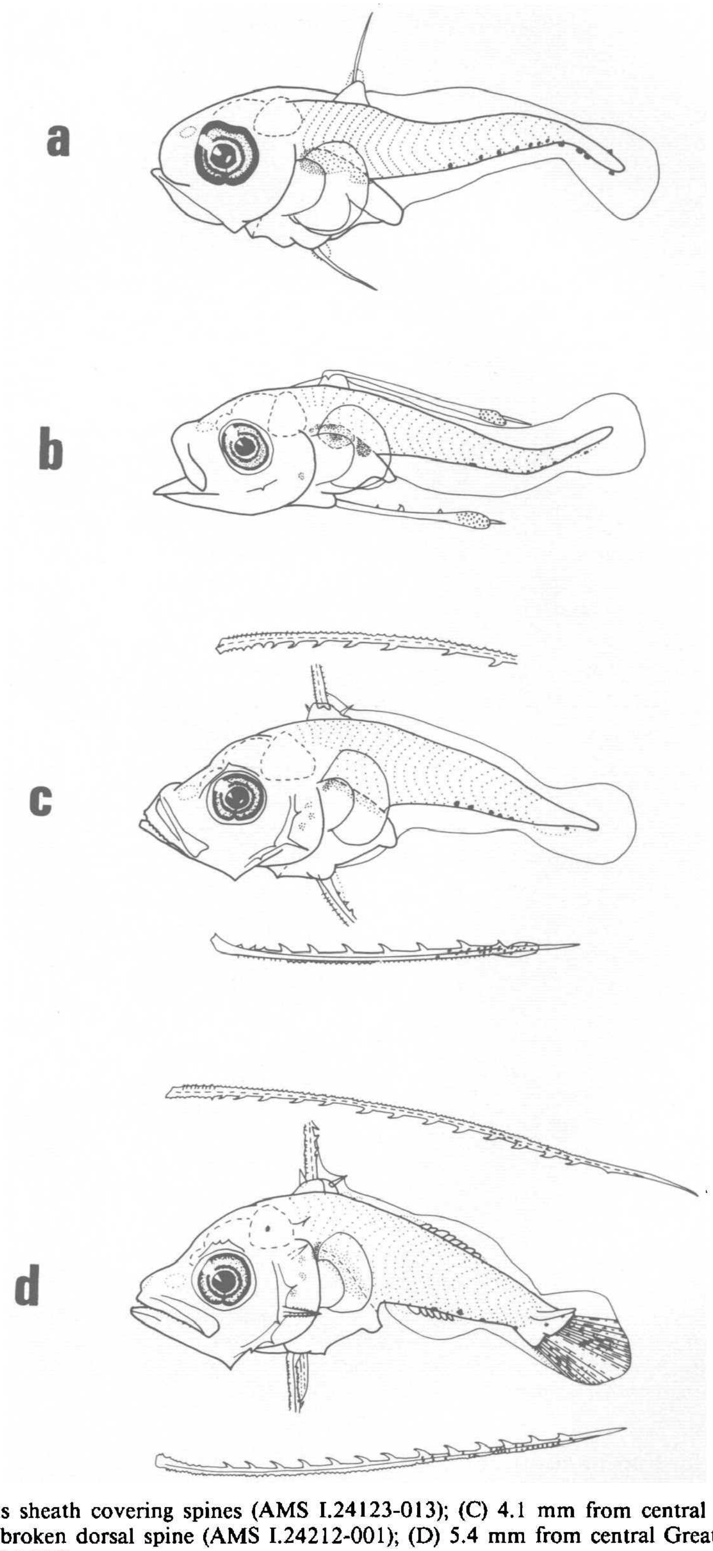
Pigment.—The gut and gas bladder are covered dorsally by a cap of pigment which may descend laterally as a solid sheet ventral to the pectoral base, or be restricted to a few individual melanophores along the dorsal edge of the gut (Fig. 10). A small group of internal melanophores is located on the anterior border of the gut. Gut pigment changes little with development.

Head pigment varies with species. In most species, pigment on the head is first evident as a melanophore on the ventral edge of the hindbrain at about 3 mm. This subsequently moves to the dorsal surface of the posterior hindbrain. Pigment dorsally on the midbrain appears at 6.5–9 mm depending on species, and reaches 12–14 melanophores per hemisphere before settlement. Some of these melanophores are retained for a time following settlement. The forebrain has up to 6 melanophores per hemisphere just prior to settlement.

In small larvae a sheath with a distal pigmented swelling covers the elongate dorsal and pelvic spines (Fig. 6). With growth, the pigmented swelling disappears and is replaced by scattered melanophores on the distal quarter of the spine. Many specimens lack this pigment but this may be the result of damage to the membranous sheath that covers the spine and that contains the pigment. Small (<5.7 mm) *Plectropomus* larvae may have 1–2 (rarely more) melanophores on the ven-

→

Figure 6. Development of preflexion and flexion *Plectropomus leopardus* larvae. Elongate second dorsal and pelvic spines shown detached to conserve space. In the detached pelvic spine, ridges 1 and 3–4 are shown in profile and ridge 2 is shown as if projecting out of the page. (A) 2.2 mm from northern Great Barrier Reef (AMS I.23531-003); (B) 3.4 mm from northern Great Barrier Reef—note



membranous sheath covering spines (AMS I.24123-013); (C) 4.1 mm from central Great Barrier Reef—note broken dorsal spine (AMS I.24212-001); (D) 5.4 mm from central Great Barrier Reef (AMS I.24209-002).

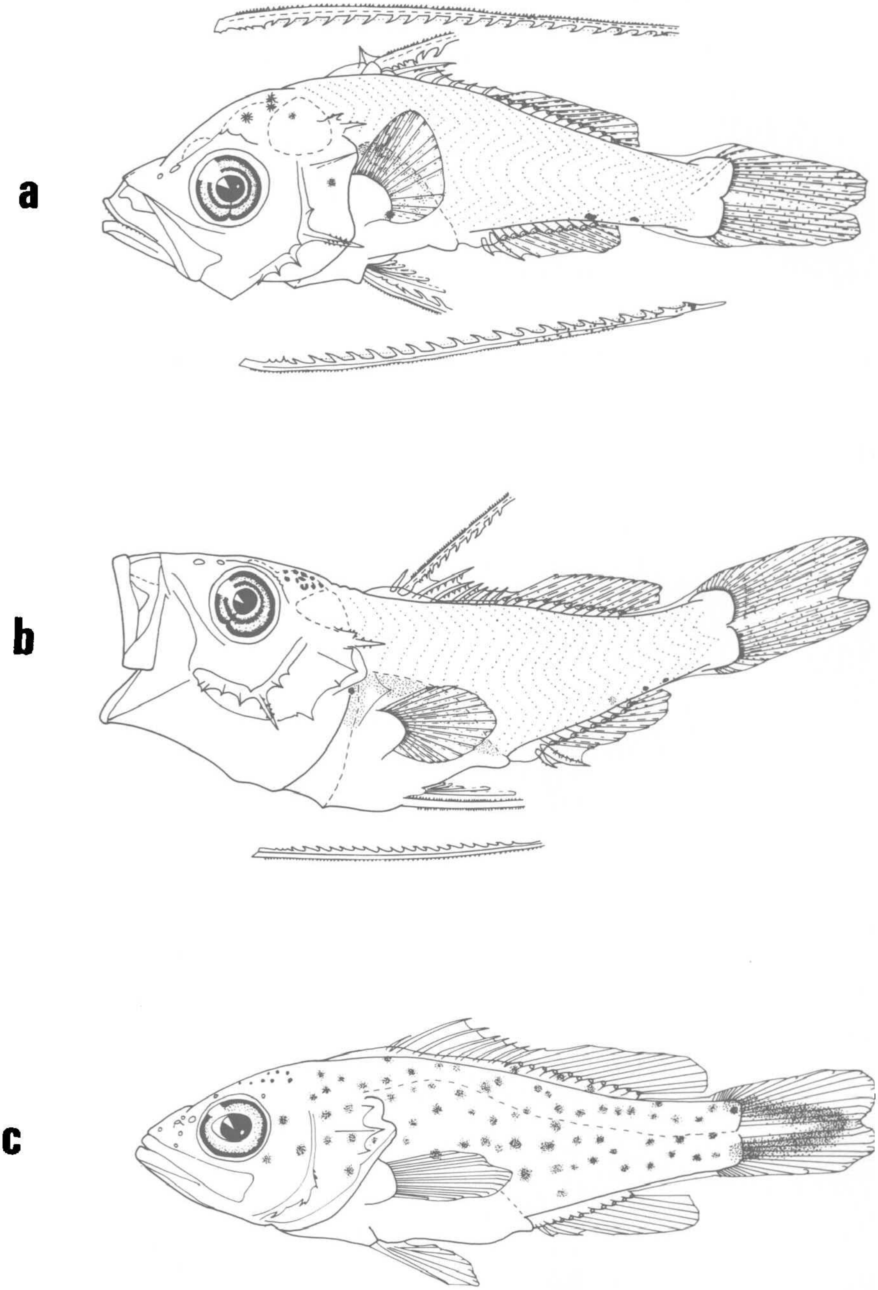


Figure 7. Development of postflexion *Plectropomus leopardus*. Spines arranged as in Figure 6. (A) 8.1 mm larva from central Great Barrier Reef (AMS I.24210-001); (B) 14.1 mm larva from central Great Barrier Reef—note broken spines and bifurcate spinelet (AMS I.24759-001): (C) 20 mm settled juvenile from southern Great Barrier Reef (AMS I.21495-007).

tral caudal fin fold in addition to those along the ventral edge of the notochord. The only other pigment found on fins of any *Plectropomus* during the pelagic period is a prominent melanophore on the pelvic fin of *P. maculatus*. This melanophore is found initially on the inner face of the pelvic spine at about 2.3 mm.

It moves onto the membrane between the spine and the first ray and remains there until at least 14.5 mm. Remnants of this spot are present in settled individuals.

Pigment on the tail, notochord, and posterior trunk varies with size but is species specific. *P. areolatus* and *P. laevis* lack tail or trunk pigment. *P. leopardus* and *P. maculatus* have a number of melanophores along the ventral edge of the tail. These decrease in number with age (Fig. 3) and in larvae of *P. leopardus* approaching settlement they may be entirely lacking. The anterior-most melanophore is often larger than the others. *P. maculatus* is the only species which may have dorsal melanophores in the posterior trunk/anterior tail region. These are present only from 2.8–5.0 mm, and 83% (20) of the specimens within this size range had 1–4 dorsal melanophores. A few melanophores along the ventral edge of the exposed notochord occur in preflexion larvae. In postflexion larvae (except *P. areolatus*), these melanophores may be found near the base of the caudal rays, but disappear before settlement.

Species Accounts

Plectropomus leopardus (Lacepède, 1802).—74 specimens, 1.5–18.2 mm plus settled individuals >20 mm, Figs. 6, 7.

Diagnosis (Table 5).—A series of melanophores along the ventral edge of the tail which decrease in number rapidly with growth (Fig. 3); no dorsal trunk or tail pigment; no melanophore basally on pelvic fin; elongate fin spines pigmented distally; dorsal spine 2 intermediate in length (Fig. 5); spine at angle of operculum long (Fig. 4); 3–4 points on supraorbital ridge (Table 4, Figs. 6 and 7); pectoral rays 32.

Remarks.—The 11.9 mm larva (the only specimen of *P. leopardus* from northwest Australia) has a much longer dorsal spine 1 than expected from the two *P. leopardus* larvae closest in size to it (Table 4). This may be geographic or individual variation, but as the 12.5 mm *Plectropomus laevis* has a similarly large dorsal spine 1, this could be a normal developmental pattern. The shortage of specimens 10–15 mm long makes this difficult to evaluate.

P. leopardus larvae seem to have a longer preopercular angle spine than do *P. maculatus* larvae, but only in larvae larger than 4 mm (Fig. 4). Once again, the shortage of larger specimens makes it difficult to be sure.

The ventral melanophores of the tail decrease in number and size (Fig. 3) until only 0–2 very small melanophores remain on the peduncle of 16–18 mm larvae. About ⅓ of *P. leopardus* larvae this size lack pigment on the peduncle, and it is possible that such pigment is also lacking in *P. maculatus* larvae of similar size.

The 14.1 mm *P. leopardus* larva (Fig. 7) has some bifurcate spinelets on dorsal spine 2 and on one of the pelvic spines (the only *Plectropomus* larva to do so). This seems to be associated with transformation of the spine to the smooth adult form. This has also been noted in *Mycteroperca* (G. D. Johnson, pers. comm.).

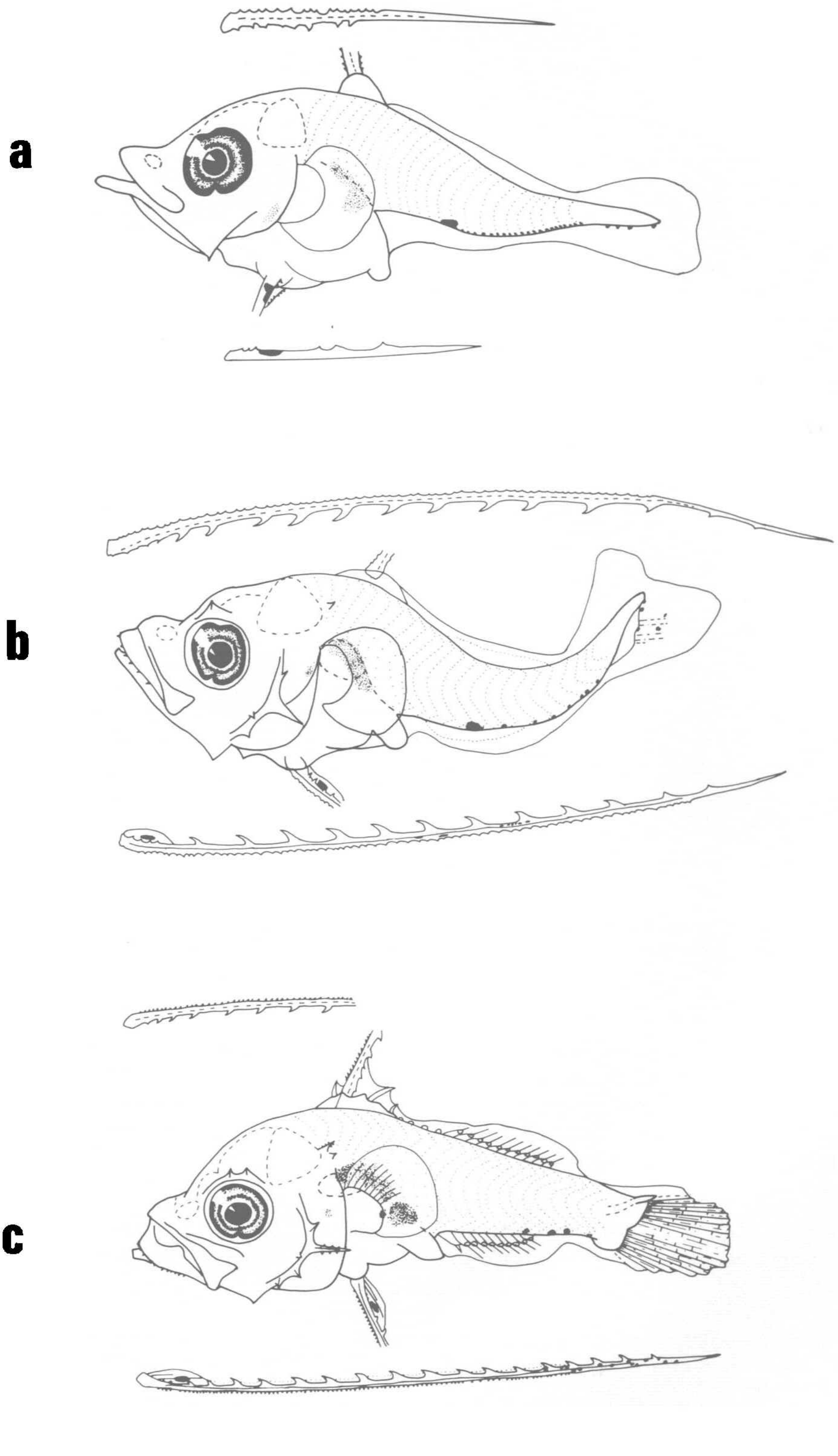
All the *P. leopardus* larvae but one were from the Great Barrier Reef lagoon where adults are "most abundant on mid-reefs and less abundant on outer barrier reefs and inshore reefs" (Hoese et al., 1981). The distribution of larvae is generally consistent with adult distribution.

Plectropomus maculatus (Bloch, 1790).—41 specimens, 1.8–14.5 mm plus settled individuals >37 mm, Figs. 8 and 9.

Diagnosis (Table 5).—A series of melanophores along the ventral edge of the tail which decrease in number slowly with growth (Fig. 3); 1–4 dorsal melanophores

Table 5. Character states of larval epinepheline serranids (P) indicates primitive, (D) indicates derived, (P/D) indicates both states encountered, (?) indicates assumed, see text for discussion of characters

Character		Genus					
		Cephalopholis	*Epinephelus*	*Gonioplectrus*	*Mycteroperca*	*Paranthias*	*Plectropomus*
1	Pelvic spine ridges	D	D	D	D	D	P
2	Number supraocular ridge points	P	P	P?	P	P?	D
3	Size supraocular ridge	D	D	D?	D	D?	P
4	Supraocular ridge serrations	D	D	D	D	D	P
5	Preopercular lower limb spine serrations	D	D	D	D	D	P
6	Preopercular lower limb antrorse spine	P	P/D	D?	P	P	D
7	Posterior dorsal spine formation	D	D	P?	D	D	P
8	Size at anal spine 3 transformation	P	P	P?	P	P?	A
9	Ventral pigment on tail	P	D	D?	D	D?	P
10	Mid-lateral pigment on peduncle	D	D	D	D	D	P
11	Number of predorsals	P	P	P	P	P	D
12	Elongate fin spine ornamentation	P	P	D	P	P	P


a
b
c

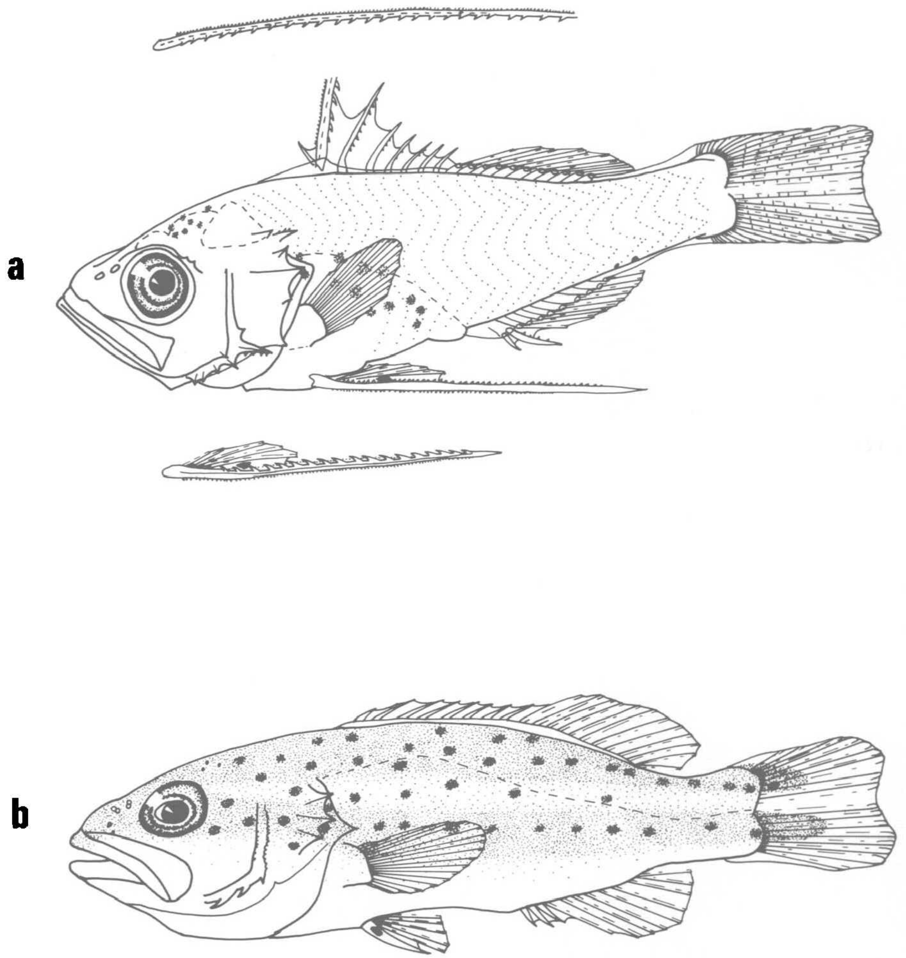


Figure 9. Development of postflexion *Plectropomus maculatus*. Spines arranged as in Figure 6. (A) 14.5 mm larva from central Great Barrier Reef (AMS I.24208-007)—note broken dorsal spine; (B) 40 mm settled juvenile from central Great Barrier Reef (AMS I.24643-001).

on anterior tail or posterior trunk in most larvae between 2.8–5.0 mm (Fig. 8); a prominent melanophore on pelvic fin basally in larvae >2.3 mm (Figs. 8 and 9); elongate fin spines pigmented distally; dorsal spine 2 intermediate in length (Fig. 5); spine at angle of preoperculum short (Fig. 4); 2 points on supraorbital ridge (Table 4, Figs. 8 and 9); pectoral rays 32.

Remarks.—A high proportion of the larvae of *P. maculatus* were badly damaged. The pelvic fin basal pigment was absent in four of the larvae >2.3 mm, but all these had badly damaged pelvic fins, so pigment absence could have been an

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Figure 8. Development of preflexion and flexion *Plectropomus maculatus* larvae. Spines arranged as in Figure 6. (A) 2.3 mm from northern Great Barrier Reef (AMS I.23573-002); (B) 4.1 mm from Australian northwest continental shelf (AMS I.25122-001)—note dorsal melanophore and that spines are from a 4.0 mm specimen; (C) 5.7 mm from central Great Barrier Reef (AMS I.24207-007)—note broken dorsal spine.

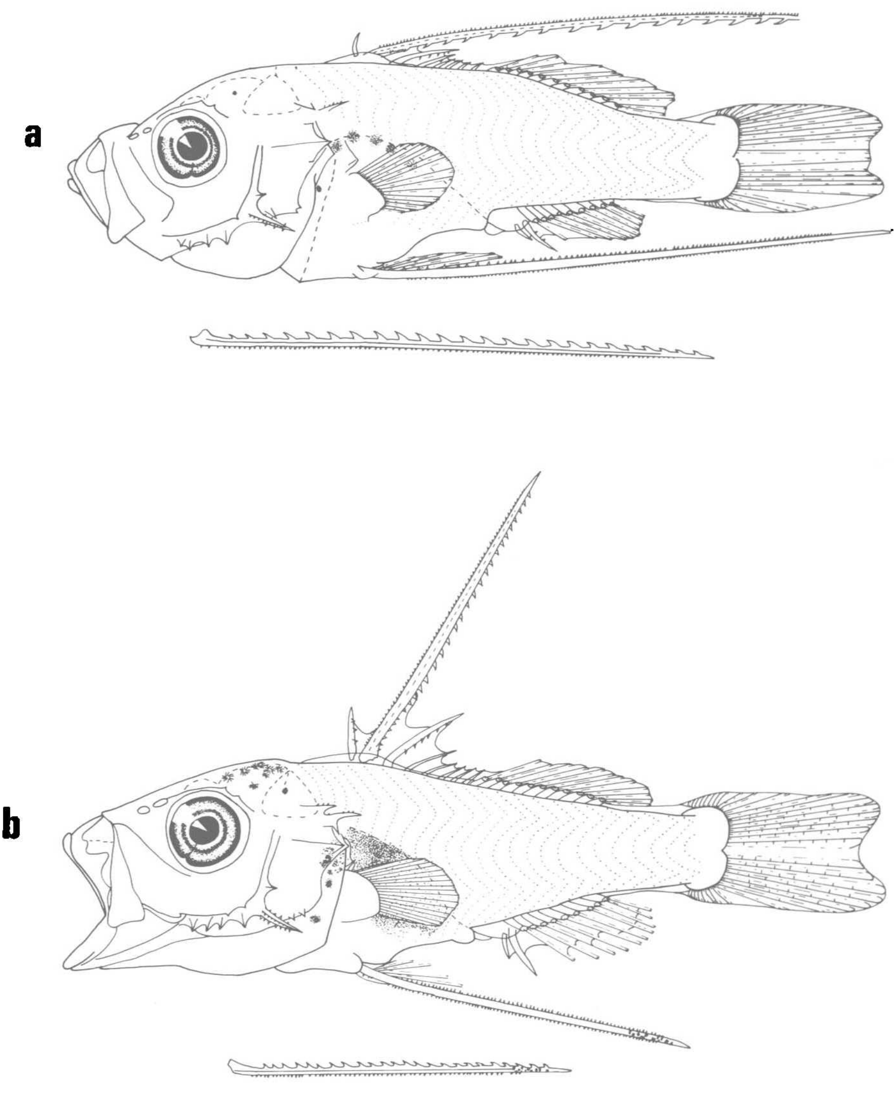

Figure 10. Larvae of two species of *Plectropomus*. Spines arranged as in Figure 6. (A) *P. areolatus*, 9.6 mm from Australian northwest continental shelf (AMS I.25123-001)—note broken dorsal spine; (B) *P. laevis*, 12.5 mm from central Great Barrier Reef (AMS I.24747-001).

artifact. Twenty of 24 specimens between 2.8 and 5.0 mm had dorsal trunk or tail pigment. However, geographic variation could be involved because 19 of the 21 specimens from northwest Australia had the pigment while only one of the three Great Barrier Reef specimens did.

The 10.1 mm specimen is only tentatively identified as *P. maculatus* (Table 4) because the pelvic fins are entirely missing. All other characters are consistent with an identity of *P. maculatus* with the possible exception of the presence of scattered melanophores on the snout and lower jaw. Similar pigment is often found in epinepheline larvae approaching settlement (Hussain and Higuchi, 1980), but it is absent on the larger (14.5 mm) *P. maculatus* larva (Fig. 9).

The two smallest larvae (1.80 and 1.94 mm) lack pelvic base pigment and are also only tentatively identified as *P. maculatus*. This identification is based on the absence of melanophores on the caudal fin fold and presence of 3 or 4 notochord tip melanophores. *P. maculatus* larvae <3.8 mm lacked caudal fin melanophores and had 3 or more notochord tip melanophores. In contrast, no *P. leopardus* larvae less than 2 mm had a combination of 0 caudal fin fold melanophores and 3 or 4 notochord tip melanophores.

The 4.7 mm *P. maculatus* had three spine points on the supraorbital ridge on one side and two points on the other, and the 7.4 mm *P. leopardus* had only two points on both sides. So, no single character of those used to distinguish *P. maculatus* from *P. leopardus* (Table 5) is completely reliable, and the characters should be used in combination. The basal spot on the pelvic fin is a good character in all but the smallest larvae, the number of tail melanophores is a good character between 2 and 5 mm, and the number of supraorbital ridge spine points is usually reliable in larvae >5 mm.

The reasons for identifying this larval type as *P. maculatus* are given in Identification. Distributional information supports this identification. *P. maculatus* were by far the most abundant (36 of 43 larvae) of the three types taken off northwest Australia where *P. maculatus* is the most abundant adult of the genus. On the Great Barrier Reef, *P. maculatus* is most abundant on coastal reefs (Hoese et al., 1981), and larvae of this type were generally captured closer to shore than were larvae of *P. leopardus*, a mid-shelf species.

Plectropomus areolatus (Rüppell) (Randall, in press, has shown that *P. truncatus* Fowler and Bean is a synonym).—6 specimens, 6.3–10.0 mm, Fig. 10.

Diagnosis (Table 5).—Tail entirely unpigmented; other pigment restricted or late to form; midbrain pigment not present until 7–9 mm; no melanophores on pelvic fin basally; elongate fin spines unpigmented (sampling damage?); dorsal spine 2 very long (Fig. 5); spine at angle of preoperculum of intermediate length (Fig. 4); two points on supraorbital ridge (Table 4, Fig. 10); pectoral rays 30–32.

Remarks.—Generalizations about *P. areolatus* larvae are tenuous due to the low number and limited size range of available specimens. Dorsal spine 2 seems to be longer in *P. areolatus* than in other species (Fig. 5), but this could be proven incorrect when more specimens become available. Larvae of *P. areolatus* are very lightly pigmented, but the lack of pigment on the elongate spines could be due to damage. The midbrain pigment is late in forming: the 6.9 mm and 9.6 mm specimens have a single melanophore on each midbrain hemisphere, but the 7.3 mm specimen has none. Although the postflexion *P. areolatus* larvae studied here had no tail pigment, it is possible that preflexion larvae do have tail pigment.

All *P. areolatus* larvae were from a single, relatively nearshore station off northwest Australia. Adult *P. areolatus* are apparently rare in both the Great Barrier Reef and off northwest Australia (Hoese et al., 1981; G. R. Allen, pers. comm.).

Plectropomus laevis (Lacepède), which is a senior synonym of *P. melanoleucus* (Lacepède), J. E. Randall, in press.—5 specimens, 4.7–12.5 mm, Fig. 10.

Diagnosis (Table 5).—Tail unpigmented, but some small melanophores may be present ventrally on exposed notochord tip; no melanophores on pelvic fin basally; elongate fin spines apparently pigmented distally; dorsal spine 2 short (Fig. 5); spine at angle of preoperculum long (Fig. 4); 2–3 spine points on supraorbital ridge (Table 4); pectoral rays 34.

Remarks.—The larvae are characterized by relatively short elongate spines, very sparse pigment and number of pectoral fin rays. The possibility remains that smaller larvae of this species and *P. areolatus* have ventral pigment on the tail which is subsequently lost. Again, the very small number of available larvae is a limitation.

All five larvae of this species were taken along the outer edge of the Great Barrier Reef continental shelf in the Coral Sea, and adults of *P. laevis* are most common on mid to outer shelf reefs in this region (Hoese et al., 1981).

Relationships

I have attempted to assign polarity to the characters of the larvae through an analysis of their ontogeny (Table 5): i.e., the direct method of Nelson (1978). The single exception is the predorsal bone number where evidence from other groups has been used (i.e., an outgroup comparison) because the ontogeny of the predorsals could not be adequately assessed.

The following phylogenetic analysis is based on published descriptions and observations made for the present study (PS). These are: *Cephalopholis:* Leis and Rennis, 1983; PS. *Epinephelus:* Mito, 1966; Ukawa et al., 1966; Kendall, 1979; Hussain and Higuchi, 1980; Johnson and Keener, 1984; PS. *Gonioplectrus:* Kendall and Fahay, 1979; Johnson and Keener, 1984. *Mycteroperca:* Kendall, 1979; Johnson and Keener, 1984. *Paranthias:* Kendall, 1979; Johnson and Keener, 1984. *Plectropomus:* PS.

Unfortunately, larvae of the other eight genera of the tribe Epinephelini are unknown, so they could not be included in the analysis. Larval series of Fourmanoir's (1976) *Cephalopholis*? and my two unidentified genera were too incomplete to permit their inclusion. The inclusion of *Gonioplectrus* is also based on a very incomplete series and conclusions regarding this genus should be interpreted with care.

My purpose here is to examine the relationships of *Plectropomus*. The characters used are listed below together with a justification for my assignment of polarity. The character state for each genus is given in Table 5.

1) Pelvic Spine Ridges. Four ridges is considered advanced. This is because in *Cephalopholis* the third and fourth ridges arise from a combined proto-ridge 3–4 and form later than ridges one and two.

2) Number of Supraorbital Ridge Points. Two or more points is considered advanced. The supraorbital ridge forms initially as a single point in all studied taxa. Subsequently, additional points form in some taxa.

3) Size of Supraorbital Ridge. A vertically enlarged supraorbital ridge is considered advanced. The enlarged supraorbital ridge of some epinepheline serranids (e.g., *Epinephelus*) is apparently derived from a small, single spine such as is initially present in all epinephelines.

4) Supraorbital Ridge Serrations. Coarse serrations on the supraorbital ridge are considered derived. The serrations on the ridges of all epinephelines are initially fine but become coarse with growth in some taxa.

5) Preopercular Lower Limb Spine Serrations. The presence of serrations is considered derived because the spines initially form without serrations in all epinephelines and subsequently develop them in some taxa.

6) Preopercular Lower Limb Antrorse Spines. Antrose spine are considered advanced. In *Plectropomus,* the only genus I studied that possess them, the antrorse spines are among the last to form on the preopercular border and form initially as normal spines. These give rise to the antrorse spines of the adult. G.

D. Johnson (pers. comm.) informs me that larvae of two American subgenera of *Epinephelus—Alphestes* and *Dermatolepis*—have antrorse preopercular spines. It is unclear if the single antrorse spine of adult *Gonioplectrus* is homologous to those of *Plectropomus.* The "large and serrate" lower limb spine of larval *Gonioplectrus* is not obviously antrose in Kendall and Fahay's (1979) illustration, but these authors speculate that the spine may give rise to the antrorse spine of the adult. I accept this speculation pending availability of specimens that might clarify the issue.

7) Posterior Dorsal Spines Formation. It is considered an advanced condition if the posterior-most spines form initially as soft rays and subsequently transform into spines. Indirect formation of spines (i.e., spines forming from soft rays) is a specialized case of soft ray formation. Further, indirect formation results in an increase in number of spines over a basal level of 8–9 formed directly. In *Plectropomus* all eight spines form directly. In *Cephalopholis,* eight spines form directly and the ninth forms indirectly. In Indo-Pacific *Epinephelus,* all of which have 11 spines, nine spines form directly and an additional two form indirectly. The situation in American *Epinephelus* which have 9–11 spines, *Mycteroperca* with 11 spines, and *Paranthias* with nine spines, is unclear. Kendall (1979) stated that in *Epinephelus* species with 11 spines, the spines form as they do in Indo-Pacific species, but that in species with 9 or 10 spines, "no such transformation [of ray to spine] may occur." In *Mycteroperca* and apparently in *Paranthias* only one spine forms indirectly (Kendall, 1979). Johnson and Keener (1984) stated that in epinepheline serranids, the last two dorsal spines develop initially as soft rays, however, Johnson (pers. comm.) now believes this generalization is incorrect. For present purposes, I assume that what has been found in Indo-Pacific species applies: species with 11 spines have two indirectly formed spines and species with 9 spines have only one spine formed indirectly. American taxa, particularly those with 10 spines, should be re-examined.

8) Formation of Anal Spine 3. It is considered a derived condition for anal element 3 to transform from a soft ray to a spine following settlement. This is based on the observation that in *Plectropomus* the anal spines are weak and often flexible, which is clearly a derived condition for the Tribe. Delayed formation is viewed as a precursor of this condition. Other genera of the tribe Epinephelini have a strong anal spine 3 which transforms prior to settlement. Genera of the other tribes of the subfamily with the exception of *Liopropoma* and *Pseudogramma* either have fewer than three anal spines, or have not had the ontogeny of the anal spines described. In both *Liopropoma* and *Pseudogramma* anal spine 3 transforms from a soft ray prior to settlement.

9) Ventral Pigment on Tail. A single, enlarged melanophore is considered derived from a series of ventral melanophores. At least in *Epinephelus akaara* this pigment is derived from a series of ventral melanophores during the late yolk-sac stage (Mito et al., 1967) which is ontogenetic evidence that the series of ventral melanophores is a primitive character state. Additionally, the most common and widespread pigment pattern in preflexion percoid larvae is a series of ventral melanophores on the tail (Mito, 1966; Leis and Rennis, 1983). This includes other serranid subfamilies (Kendall, 1979). Therefore, *Epinephelus* spp. have the derived state of a single enlarged melanophore while *Plectropomus* spp. have only the primitive melanophore series. Lack of ventral pigment on the tail in two *Plectropomus* species is likely a specialized condition derived from an existing ventral series, and I expect that when very young larvae of these species are found, they will have some ventral pigment.

Cephalopholis spp. have the primitive pigment series and lack the advanced

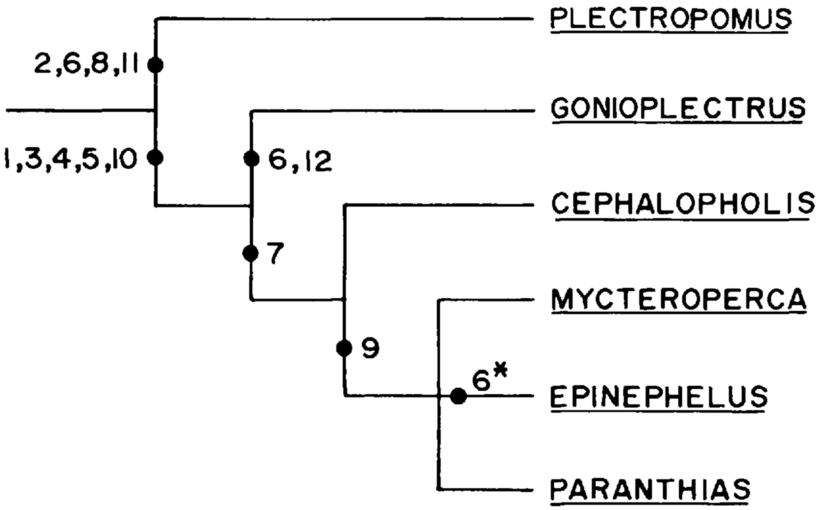

Figure 11. Phylogeny of the Tribe Epinephelini based on larval characters in genera for which larvae are known. Numbers refer to characters (see text and Table 5) and are located on branch which possesses the derived state. Note that character 6 occurs in three places, indicating conflict with the accepted classification. * indicates that the subgenera *Alphestes* and *Dermatolepis* both possess the derived character state (G. D. Johnson, pers. comm.) while *Epinephelus* does not. Therefore, it was considered inadvisable to include *Mycteroperca* and *Paranthias* as the primitive sister group of *Epinephelus*, although such a relationship could be inferred from the location of 6* in the cladogram.

enlarged melanophore, although there is some doubt about American species. Indo-Pacific *Cephalopholis* examined for this study had a ventral series of many melanophores which reduce in number with growth to 1–4 not particularly large melanophores. Reports of American *Cephalopholis* larvae imply that they have tail pigment similar to *Epinephelus* (Johnson and Keener, 1984; Kendall, 1984). Pigment in the two genera is similar after the mid lateral melanophore has formed via upward migration of the ventral pigment (see No. 10). However, it seems probable that prior to this, American *Cephalopholis* are similar to their Indo-Pacific congeners and also have the primitive pigment series and lack the enlarged melanophore. This is suggested by the subsequent discovery of a second ventral melanophore on the tail of the smallest *Cephalopholis* larva examined by Johnson and Keener (G. D. Johnson, pers. comm.).

10) Mid-lateral Pigment on Peduncle. A large melanophore mid-laterally on the caudal peduncle is derived from the ventral pigment of the tail via dorsal movement of the melanophore(s) in postflexion larvae and is considered the derived condition.

11) Number of Predorsal Bones. The presence of only one predorsal bone is considered derived. The single predorsal bone of *Plectropomus* is present as a cartilaginous structure by 10 mm. There was no indication of ontogenetic formation and loss of a second predorsal. Apparently, in *Epinephelus* the two predorsals form simultaneously (Johnson, 1983). Therefore, the polarity of this character could not be determined ontogenetically. Both Kendall (1976) and Johnson (1983) considered on the basis of outgroup comparison that the primitive number of predorsal bones in the serranids is three and that the epinepheline serranids are marked by a further loss of at least one of these. If this is correct, then the loss of a further predorsal is derived.

12) Elongate Fin Spine Ornamentation. The presence of raised ridges ex-

tending anteriorly from the small spinelets on the dorsal and pelvic spines is unique to larval *Gonioplectrus* and is therefore considered derived. The varied spine ornamentation found in other epinepheline larvae holds promise for phylogenetic studies within the tribe, but at present, the variety in ornamentation is too great compared to the number of species for which it has been described to perceive meaningful patterns or assign polarity to the character states.

Using the above characters, I constructed a larva-based phylogeny for members of the Tribe Epinephelini for which larvae have been described (Fig. 11). Some character states were assumed for *Gonioplectrus* and *Paranthias* (Table 5) because descriptions of development were incomplete. Therefore, the analysis is weak for these two monotypic genera. Character 6, antrorse spines on the preopercular border, occurs in three places in Figure 11 indicating a conflict with the proposed classification. Study of more larval specimens of *Gonioplectrus, Alphestes* and *Dermatolepis* (the two subgenera of *Epinephelus* which have antrorse spines on the preopercular border) when they become available might clarify this conflict. I felt it was better to leave as an unresolved tricotomy the relationships of *Epinephelus, Paranthias* and *Mycteroperca* (Fig. 11). One could argue that *Paranthias* and *Mycteroperca* should be combined into the primitive sister group of *Epinephelus,* but this appears unjustified because it would be based solely on one character (No. 6) the derived state of which occurs in only two subgenera of *Epinephelus.*

The position of *Plectropomus* as the primitive sister genus of all the other studied epinepheline genera (Fig. 11) is based on a high proportion of the characters used. If this hypothesis is correct, *Plectropomus,* not *Epinephelus,* should be considered closest to the generalized or ancestral epinepheline (C. L. Smith, 1971). Another interesting feature is the apparent close relationship of *Epinephelus, Mycteroperca* and *Paranthias,* all more closely related to each other than to *Cephalopholis,* based on larval characters.

Comparison of the larva-based hypothesis of *Plectropomus* relationships with those based on studies of adults is made difficult by a lack of clearly stated hypotheses for the latter. Previous treatments have suffered from nebulous definitions of the Serranidae in general and the Epinephelinae in particular. Jordan and Eigenmann (1890) considered *Plectropomus* in relation to American and European serranid genera and concluded it was most closely "allied" to *Acanthistius, Alphestes* and *Ellerkeldia* (=their *Gilbertia*), but also related to *Gonioplectrus* and *Hemilutjanus.* Further, *Alphestes* was considered intermediate between *Epinephelus* and *Plectropomus.* Only three of these proposed *Plectropomus* relatives—*Alphestes* (as a subgenus of *Epinephelus*), *Epinephelus* and *Gonioplectrus*—are included in the Epinephelini as currently conceived (Johnson, 1983). Johnson (1983) did not consider relationships within the Tribe. J. L. B. Smith (1949 and subsequent editions) placed *Plectropomus* in a separate family Plectropomidae. In contrast, he later considered *Plectropomus* closely related to *Saloptia powelli* which he described as a serranid (J. L. B. Smith, 1963). The two adult-based studies and the larva-based phylogeny seem to agree in proposing that *Plectropomus* is somewhat removed from most other epinepheline serranids, but little more can be ascertained from such a comparison.

In a clearly presented hypothesis based on study of American epinephelines (omitting *Gonioplectrus*) C. L. Smith (1971) considered *Cephalopholis* a subgenus of *Epinephelus,* and considered *Mycteroperca* more closely related to *Epinephelus* than either were to *Paranthias.* Smith's treatment of *Cephalopholis* is clearly at odds with the larva-based phylogeny, and is an indication that further work on epinepheline systematics is required. C. L. Smith's (1971) phylogeny is handicapped because it considered only American species. The present larva-based phylogeny is handicapped because relatively few species and genera could be included and also because very few characters were available after the first branch in Figure 11. This is an indication of the great similarity of the larvae of these more derived epinephelines. Further clarification of epinepheline relationships awaits description of the development of other epinepheline genera and phylogenetic studies of the adults. Based on what is known now, differences in larval development among congeners is relatively small, except in the case of spine ornamentation in *Epinephelus* and *Cephalopholis* (Johnson and Keener, 1984; this study). This should facilitate studies of relationships among genera, but will make studies of relationships within genera difficult.

Summary

Description of the development of four Australian species of *Plectropomus* (*leopardus, maculatus, areolatus* and *laevis*) shows that development differs among species only in minor items of pigmentation and spination (Table 3). *Plectropomus* larvae can be distinguished from larvae of other epinepheline genera by a number of characters (Table 2). An analysis of larval characters led to the hypotheses that *Plectropomus* is the primitive sister group of other studied epinephelines and that Indo-Pacific *Cephalopholis* is distinct from *Epinephelus* (Fig. 11).

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