

Larval development of the oral brooding cardinalfish *Apogon rueppellii* (Teleostei: Apogonidae) in Western Australia

Francisco J. Neira*

Abstract

Late stage eggs and the development of the planktonic larvae of the oral brooding apogonid, *Apogon rueppellii*, are described and illustrated using material collected in the Swan Estuary, in south-western Australia. The eggs (2.2-2.5 mm) are nearly spherical and contain the embryos coiled with the tail covering the right eye. The larvae examined (5.5-16.3 mm) are pelagic, lightly pigmented, have a moderately deep body, a compact, coiled gut which extends to about midbody, a large, conspicuous gas bladder and 24 myomeres. *Apogon rueppellii* larvae are unique among previously described apogonid larvae in that they hatch in an advanced postflexion stage, possessing a yolk sac, functional mouth, developed eye and completely formed second dorsal, anal and caudal fins. The first dorsal and pelvic fins form during their short planktonic life and individuals settle at about 16 mm. It is suggested that both the advanced stage of development at hatching and short planktonic life contribute to maximize their survival and retention within the estuary. Comparisons with similar taxa and the early life history of other oral brooding apogonids are also presented.

Introduction

Most representatives of the perciform family Apogonidae are known to incubate their eggs orally (Breder and Rosen 1966, Leis and Rennis 1983, Thresher 1984). This type of incubation has been reported to be carried out predominantly by males and, in some instances, both sexes, after which the parent(s) may or not temporarily guard the newly-hatched larvae in their mouths (Ebina 1932, Smith *et al.* 1971, Chrystal *et al.* 1985). While most published accounts on oral brooding in this family have been restricted to reports of the occurrence of this reproductive specialization in several species (e.g. Hale 1947, Garnaud 1950, Fishelson 1970, Charney 1976, Omori and Takahashi 1980, Kuwamura 1983), only a few have also included a description of the eggs and larvae (Ebina 1932, Allen 1975).

The cardinalfish *Apogon rueppellii* is very abundant in marine coastal embayments and estuaries of the west coast of Australia. Its distribution extends from Albany in south-western Australia to Arnhem Land in the Northern Territory (Hutchins and Thompson 1983; Hutchins and Swainston 1986). The members of the large population of this species found in the Swan Estuary typically have a one year life cycle and breed within the middle and upper regions of this estuary between December and March (Chubb *et al.* 1979, Chrystal *et al.* 1985, Neira *et al.* in press). Individuals are sexually mature between 45 and 49 mm and the males brood from 50 to 230 fertilized eggs for about two weeks until the hatching of the larvae (Chrystal *et al.* 1985).

*School of Biological and Environmental Sciences, Murdoch University, Murdoch, Western Australia 6150.

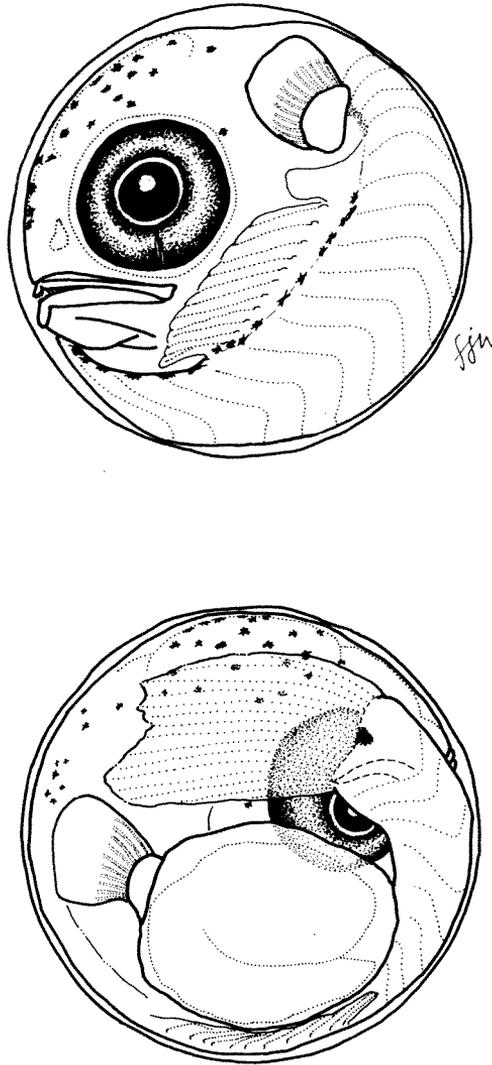


Figure 1. Lateral views of a 2.3 mm diameter late stage egg of *Apogon rueppellii* removed from the mouth of a 45.9 mm male.

This paper describes the planktonic larval stages of *A. rueppellii* from material collected in the Swan Estuary, in south-western Australia. It also compares some aspects of the oral brooding of *A. rueppellii* with those of other apogonids and discusses the significance of this reproductive specialization in an estuarine embayment.

Materials and Methods

Collection of larvae

Larvae of *Apogon rueppellii* were obtained from surface plankton samples collected between January 1986 and April 1987 in the middle and upper Swan Estuary (Lat 32°04'S; Long 115°44'E), in south-western Australia (see Neira and Gaughan 1989 for details of collection methods).

Material examined

A total of 81 larvae, ranging in body length (BL) from 5.5 to 16.3 mm, were examined to describe the changes in pigmentation, morphometrics and meristics. Ten larvae were deposited in the Australian Museum, Sydney, under the catalogue number 1.27027-001.

Measurements and counts

Larvae of *A. rueppellii* were measured to the nearest 0.01 mm using a dissecting microscope fitted with an eyepiece micrometer. Terminology and body measurements of larvae follow Leis and Rennis (1983). All measurements except body length (BL, mm), i.e. the standard length in all specimens, are expressed as a percentage of body length. Myomere counts and ray counts of paired fins were made on the left side of the body. Pigment refers to melanin. Drawings were done with the aid of a drawing tube fitted to the dissecting microscope.

Thirty specimens were cleared and double-stained following the technique of Potthoff (1984), to count fin rays and vertebrae and to determine the sequence of bone ossification. The term "ossified" refers to structures stained positively for bone.

Results

Identification

Larvae were identified as belonging to the family Apogonidae by the presence of two separate dorsal fins, the presence of 24 myomeres and a prominent swim bladder (Miller *et al.* 1979, Leis and Rennis 1983). Larger specimens were identified as those of *Apogon rueppellii* by the dorsal and anal fin counts of VII+I,9 and II,9-10 respectively (Munro 1960). Embryos close to hatching, obtained from late stage eggs removed from the mouth of a 45.9 mm male captured in the upper Swan Estuary, were used in the initial assemblage with the early planktonic larvae. More advanced larvae were linked in a series using pigmentation and fin development.

Description of late stage eggs

Eggs of *A. rueppellii* prior to hatching are spherical and slightly ovoid and measure between 2.2 and 2.5 mm in diameter (mean = 2.3 mm; SD = 0.08; n = 20). Embryos possess a yolk sac, developed eye and developed anal, second dorsal and caudal fins. All eggs examined had the embryos coiled, with their tails covering the right eye (Figure 1).

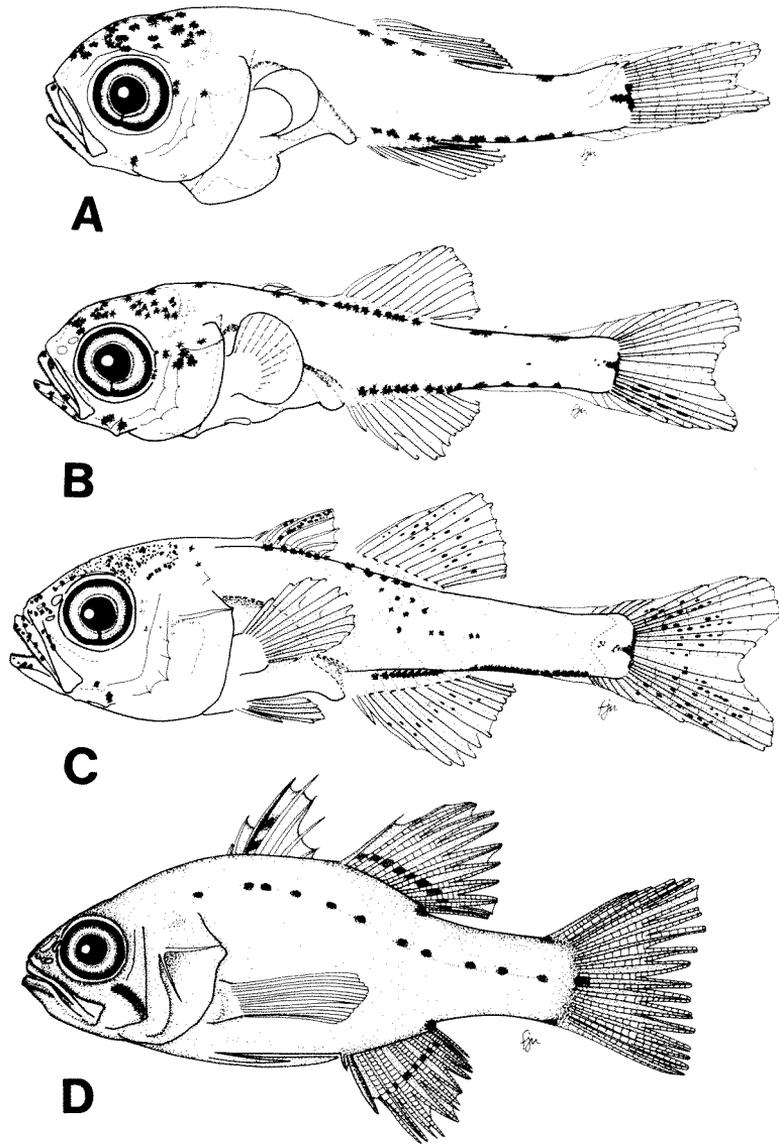


Figure 2. Larvae and juvenile of *Apogon rueppellii* from the Swan Estuary. (A) newly-hatched 6.0 mm larva with yolk sac. (B) 7.3 mm larva with developing pelvic fins. (C) 11.3 mm larva. (D) 30.0 mm juvenile. Larva illustrated in A and those in B and C were collected in the upper estuary in February 1986 and January 1987, respectively. Juvenile illustrated in D was caught in the middle estuary in October 1986.

Description of the planktonic larvae

Apogon rueppellii larvae (Figure 2) are moderately deep bodied and have a compact, coiled gut which extends to about midbody, a large, conspicuous gas bladder and 24 myomeres (range = 23-25, mean = 24, SD = 0.46, n = 25). Larvae hatch from orally brooded eggs at sizes between 5.5 and 6.4 mm with a yolk sac and the notochord already flexioned (Figure 2A). Remnants of the yolk sac are reabsorbed by 6.8 mm (Figure 2B). The mouth is functional in the newly-hatched larvae and presents canine-like teeth along the premaxilla and dentary. The head length and body depth remain about one third of the body length during development, whereas the preanal length increases from about 50.0% in newly-hatched larvae to around 59% in older larvae (Table 1). There is no gap between the anus and the origin of the anal fin. Scales appear by 12.0 mm and settlement occurs at sizes over 16.0 mm.

At hatching, the maxilla and premaxilla are the only bony structures which are ossified. The vertebral elements and the haemal and neural spines start to ossify shortly after hatching and are completely ossified by 8.0 mm.

Development of fins

Fin development is summarised in Table 2. At hatching, larvae possess the complete set of elements on the second dorsal, anal and caudal fins (Figure 2A). The rays of the pectoral fin start to form sequentially from dorsal to ventral by 6.9 mm and all (15-17) rays are present by 10.2 mm. The buds of the pelvic fins appear by 6.9 mm and all (1,5) elements are formed by 7.7 mm. The first dorsal fin start to appear at about 6.8 mm and the seven spines are present by 8.5 mm (Table 2).

Development of head spines

Spines on the head develop along the preoperculum and on the operculum and supracleithrum. Larvae hatch with two and three small spines along the anterior and posterior preopercular margins respectively. The posterior preopercular spines remain the same in length but increase in number throughout development. These spines merge into fine serrations along the preopercular border in larvae over 15 mm. The anterior preopercular spines disappear by 11.5 mm. A small supracleithral spine is visible by 7.0 mm and disappears by 12.0 mm. The single opercular spine appears by 7.5 mm and remains in juveniles (Figure 2D).

Pigmentation

Larvae of *A. rueppellii* are lightly pigmented and do not undergo significant changes in pigmentation after hatching (Figure 2). Internal pigment is visible on the dorsal surface of the swim bladder and gut in all planktonic larval stages prior to settlement. The head of newly-hatched larvae possesses scattered melanophores on the midbrain and snout. Pigment increases in these areas during growth and becomes particularly intense on the midbrain at the settlement stage. A melanophore at the angle of the lower jaw is present in individuals during development and remains in adults. The preopercular area remains relatively unpigmented during development until a dark pigmented patch develops underneath the eye in juveniles (Figure 2D).

Table 1. Morphometric measurements for larval *Apogon rueppellii*. Body intervals are expressed as a percentage of body length. n, number of individuals. Means and standard deviations (in parentheses) are given when n>1. Blanks indicate character is absent. Values with additional n (when n>1) indicate number of specimens in which character was observed and measured.

Body Length (mm)	n	Head Length	Eye Diameter	Body depth At P ₁ Base	Preanal Length	Pre-second Dorsal Fin Length	Pre-first Dorsal Fin Length
5.5	1	36.3	13.6	29.0	49.0	52.7	
6.0	3	32.8 (3.14)	14.2 (0.68)	29.4 (5.15)	51.6 (1.36)	51.6 (2.35)	
6.1	3	31.7 (2.05)	14.2 (0.77)	36.0 (0.00)	50.3 (1.54)	50.3 (0.77)	
6.2	4	31.8 (2.09)	14.3 (0.35)	34.6 (3.32)	50.4 (0.69)	50.0 (1.97)	
6.3	6	33.3 (2.24)	14.0 (0.59)	31.7 (4.49)	51.3 (2.37)	50.8 (3.04)	
6.4	1	31.2	14.0	37.5	50.0	46.8	
6.5	2	32.3 (1.54)	14.2 (0.38)	30.7 (3.07)	51.5 (2.30)	50.7 (1.54)	38.5
6.6	8	30.5 (0.50)	13.7 (0.25)	32.4 (0.73)	49.6 (1.00)	47.5 (0.73)	
6.7	7	30.9 (1.31)	13.7 (0.37)	31.6 (0.52)	49.5 (0.95)	48.2 (1.73)	34.3
6.8	7	30.2 (1.07)	13.5 (0.75)	29.6 (2.77)	49.8 (1.22)	50.6 (0.72)	36.7 (1.20) (n = 3)
6.9	7	30.6 (1.63)	13.2 (0.74)	29.6 (2.30)	49.7 (1.27)	49.9 (0.71)	36.8 (0.71) (n = 5)
7.0	4	29.6 (0.62)	13.5 (0.18)	31.4 (0.00)	49.3 (0.71)	49.3 (0.71)	35.7 (1.16) (n = 3)
7.1	1	30.9	11.3	25.3	50.7	47.9	35.2
7.2	2	34.0 (0.69)	12.5 (0.00)	27.0 (0.69)	53.5 (0.69)	52.7 (0.00)	40.3 (0.00)
7.4	1	33.8	12.2	25.7	55.4	52.7	39.2
7.8	1	33.3	12.8	25.6	53.8	52.5	38.4
7.9	1	31.6	12.6	25.3	53.1	51.9	36.7
8.3	1	34.9	10.8	25.3	55.4	50.6	37.4
8.4	1	33.3	10.7	27.4	54.7	52.4	40.5
8.5	1	34.1	11.7	28.2	60.0	55.3	41.2
9.4	1	36.2	11.7	27.6	55.3	53.2	38.3
9.5	1	33.7	10.5	25.2	55.8	52.6	35.8
9.7	1	35.0	11.8	24.7	54.6	53.6	42.3
10.3	1	33.0	11.6	28.1	54.7	50.5	40.7
11.0	1	32.7	12.7	27.3	52.7	55.4	42.7
11.2	2	32.1 (0.89)	12.7 (0.22)	30.4 (1.78)	57.6 (1.31)	56.2 (1.78)	41.1 (0.89)
11.3	1	33.6	12.4	29.2	53.1	56.6	43.4
12.0	3	35.6 (1.04)	12.5 (0.34)	29.7 (1.96)	56.9 (1.04)	54.7 (0.39)	39.7 (1.71)
12.1	1	35.5	12.4	30.6	56.2	52.9	38.8
13.0	1	30.0	12.3	34.6	59.2	56.1	40.0
13.2	1	34.1	12.5	30.3	58.3	56.8	39.4
13.5	1	34.8	12.9	33.3	59.3	58.5	40.7
13.9	1	33.1	12.2	32.3	53.9	55.4	39.5
14.5	1	34.5	12.4	31.0	57.9	59.3	42.0
16.3	2	36.5 (0.93)	12.2 (0.31)	31.2 (1.87)	57.5 (1.25)	57.5 (1.25)	40.0 (0.62)

The tail of newly-hatched larvae possesses melanophores on the ventral surface of the caudal peduncle and along the base of the anal fin. The melanophore at the centre of the caudal fin base is very conspicuous in all larvae and remains in juveniles (Figure 2). The melanophores which appear dorsally along the bases of the tail and second dorsal fin by 6.5 mm start to expand ventrally over the trunk and into the tail by 12.0 mm. A very distinct dark blotch forms at the base of the last soft ray of each of the second dorsal and anal fins by 15 mm and remains in juveniles. Shortly after, a series of small dark patches start to appear along the lateral line, finally becoming 9-11 in juveniles.

The second dorsal, anal and caudal fins are unpigmented in newly-hatched larvae. Scattered melanophores appear on the membranes of these fins by 6.5 mm and a distinct patch of melanophores form on the membrane which lies between the third and fourth spines of the first dorsal fin by 9.0 mm (Figure 2C). These patches and those on the base of the membranes of the dorsal and anal fins become very distinct in juveniles (Figure 2D).

Discussion

Larval development

Most of the larval development of *A. rueppellii* occurs inside the eggs which are incubated orally by adult males over a period of nearly two weeks (Chrystal *et al.* 1985). Unlike apogonid larvae previously described, those of *A. rueppellii* hatch in a stage which can be described as "late postflexion", i.e. with the notochord already flexioned and possessing remnants of a yolk sac, functional mouth, pectoral fin buds and the elements of the second dorsal, anal and caudal fins completely formed. The rays of the pectoral fins and the spines of the first dorsal fin form during their short planktonic life. Larvae of *A. rueppellii* show no apparent morphological specializations during their planktonic life and their exclusive features are consistent with the fact that most apogonid larvae are extremely variable not only in morphology but also in developmental patterns (Leis and Rennis 1983).

Similar taxa

Larval *A. rueppellii* are unique among other perciform larvae found in the Swan Estuary since they hatch possessing many adult characters. They can be easily identified by the short and light pigmented body, conspicuous, pigmented swim bladder, presence of two separate dorsal fins, fin ray counts, and the myomere number. Other characters include the dark pigmented patch at the centre of the base of the caudal fin and the absence of a gap between the anus and the origin of the anal fin.

Larvae of other representatives of Apogonidae occurring along the coast outside the Swan Estuary, namely the marine species *Siphamia cephalotes*, *Apogon victoriae* and *Vincentia punctata*, have not yet been described. With the exception of *S. cephalotes*, adults of the other two species have not yet been recorded in the Swan Estuary (Chubb *et al.* 1979, Loneragan *et al.* 1989). Adults *S. cephalotes* can be distinguished from those of *Apogon* and *Vincentia* by their possession of a luminous organ, a characteristic found only in the genus *Siphamia*, and the dorsal and anal fin counts of VI+I,8 and II,8 respectively (Munro 1960, Fraser 1972). In addition, the head spination of the larvae of a

Table 2. Fin ray development and vertebral counts in larval *Apogon rueppellii*. Vertebrate were counted only in cleared and double-stained specimens (denoted by *) in which vertebrae were clearly differentiated. Other blanks indicate character is absent. Pectoral and pelvic fin ray counts were made on the left side of the body. Procurrent rays are shown as dorsal/ventral elements.

Body Length (mm)	n	Dorsal Fin	Anal Fin	Pectoral Fin	Pelvic Fin	Caudal Fin Rays	Procurrent Rays	Vertebrae
6.3*	1	0+1,9	11,9	bud		9+8	2 / 2	24
6.5*	1	0+1,9	11,9	"		"	2 / 2	24
6.7*	1	0+1,9	11,9	"		"	2 / 1	24
6.7	1	0+1,9	11,9	"		"	2 / 2	
6.8*	1	11+1,9	11,9	"		"	2 / 1	24
6.9*	3	0-III+1,9	11,8-9	"	bud	"	3 / 1-3	24
6.9	1	11+1,9	11,10	3	"	"	3 / 3	
7.0*	2	III-V+1,9	11,9	4	"	"	2-3 / 3	24
7.0	1	VI+1,9	11,10	6	"	"	4 / 3	
7.1*	3	0-V+1,9	11,9-10	6-8	"	"	1-3 / 1-3	24
7.3*	1	11+1,9	11,9	6	"	"	3 / 2	24
7.5*	2	V-VI+1,9	11,9	8-10	"	"	3-5 / 4	24
7.7	1	VI+1,9	11,9	11	1,5	"	3 / 3	
7.8*	2	VI+1,9	11,9	10-12	"	"	4 / 3-4	24
8.0*	1	VI+1,9	11,10	13	"	"	5 / 5	24
8.1*	1	VI+1,9	11,9	13	"	"	4 / 4	24
8.1	1	VI+1,9	11,10	13	"	"	5 / 5	
8.2*	2	VI+1,9	11,9	9-11	"	"	4-5 / 3-5	24
8.5	1	VII+1,9	11,10	14	"	"	5 / 5	
9.0	1	VII+1,9	11,10	14	"	"	5 / 5	
9.4*	3	VII+1,9	11,9-10	13-15	"	"	6-7 / 6	24
9.5	1	VII+1,9	11,10	14	"	"	5 / 5	
9.6*	1	VII+1,9	11,9	13	"	"	6 / 5	24
10.2*	1	VII+1,9	11,9	15	"	"	7 / 7	24
10.2	1	VII+1,9	11,10	15	"	"	6 / 7	
11.0*	1	VII+1,9	11,9	15	"	"	7 / 7	24
11.3	1	VII+1,9	11,10	15	"	"	8 / 7	
11.4	1	VII+1,9	11,10	15	"	"	7 / 7	
11.5	1	VII+1,9	11,10	15	"	"	8 / 7	
11.7*	1	VII+1,9	11,10	15	"	"	8 / 7	24
12.0*	1	VII+1,9	11,10	15	"	"	7 / 6	24
16.3*	1	VII+1,9	11,10	17	"	"	7 / 7	24

species of *Siphamia* from eastern Australia (Leis and Bullock 1986), appear much more complex and developed than in any *Apogon* larvae.

Comparisons with other oral brooding apogonids

Apogon rueppellii is the only oral brooding teleost found in the Swan Estuary and the first apogonid which has been reported to exhibit such reproductive specialization within an estuarine embayment (Chrystal *et al.* 1985). G.R. Allen (Western Australian Museum, pers. comm), however, believe that other estuarine apogonids such as *Apogon ceramensis*, *A. hyalosoma* and *A. amboinensis*, which are found within the Indo-Australian Archipelago, may also incubate their eggs orally. Late stage eggs of *A. rueppellii* are spherical as in all apogonids for which eggs have been described except those of the northern Australian species *Apogon fusovatus* which produce spindle-shaped eggs (Allen 1985).

The number of eggs brooded by males *A. rueppellii* is considerably lower than that reported in most oral brooding apogonids (Table 3). This difference lies in the fact that fertilized eggs of *A. rueppellii* are much larger than most apogonid eggs previously described, a feature which, together with the volume of the buccal cavity of males, are the major factors limiting the maximum number of eggs they can incubate (Omori and Takahashi 1980, Chrystal *et al.* 1985). The largest eggs recorded to date in an apogonid (approximately 4.5 mm in diameter) were obtained from the mouth of a 95 mm specimen of *Vincentia conspersa* from southern Australia (Hale 1947).

Oral brooding has been reported in detail in the marine species *Apogon semilineatus* and *Sphaeramia orbicularis*, for which the eggs and larvae have also been described (Ebina 1932, Allen 1975). The sizes of the larvae of these species at hatching, i.e. 2.3 and 3.3 mm total length respectively, are significantly smaller than those of *A. rueppellii* (7.5-7.8 mm total length), a feature certainly associated with the smaller diameter of the eggs brooded by these marine apogonids (0.58 and 0.65 mm respectively; Ebina 1932, Allen 1975; Table 3). Moreover, in contrast to *A. rueppellii*, the larvae of these two marine apogonids hatch in a poorly-developed stage possessing a yolk sac and only the buds of the pectoral fins (Ebina 1932, Allen 1975). Newly-hatched larvae of *A. semilineatus* are retained in the mouth of the adult for some time after hatching (Ebina 1932). This parental care has never been reported in *A. rueppellii* and seems unlikely considering the large larval size and the advanced stage of development at hatching.

Oral brooding within an estuary

Most apogonids are strictly marine; only a few species inhabit brackish and fresh waters (Fraser 1972). In the case of *Apogon rueppellii*, which in Western Australia is represented by populations in coastal marine waters as well as estuaries (Chrystal *et al.* 1985), it is not known whether marine breeding habits differ from those reported here for an estuarine population. Oral brooding of eggs by male *A. rueppellii* within this estuary provides a high level of parental care and thereby compensates for the low fecundity of the females. Indeed, females of this species produce between 70 and 345 eggs, of which over 70% are retrieved by the males after their release (Chrystal *et al.* 1985). The chances

Table 3. Aspects of the reproductive biology of oral brooding apogonid species. Blanks indicate information not available. Size of brooders and that of larval size at hatching are assumed to be total length in those cases not stated in references. Sole figures in number of eggs carried are from only one specimen and those indicated by * were calculated from formulas. BL = body length.

Species	Location of Study	Brooders	Size of brooders (mm)	Number of eggs carried	Egg diameter (mm)	Larval size at hatching (mm)	Source
<i>Apogon affinis</i>	Venezuela	males and females	54.7-87.5	21,000	0.35-0.40	1.0	Smith <i>et al.</i> 1971
<i>Apogon imberbis</i>	Mediterranean	males		22,137	0.50		Garnaud 1950
<i>Apogon lineatus</i>	Yuya Bay, Japan	males	53.2-83.9	3,160-13,215*			Omori and Takahashi 1980
<i>Apogon maculatus</i>	Bahamas		56.5-60.5	75-100	0.16-0.34 ($x = 0.24$)		Charney 1976; Thresher 1984
<i>Apogon rueppellii</i>	Western Australia	males	45.0-85.0	70-280*	2.20-2.50 ($\bar{x} = 2.33$)	7.5-7.8 (5.5-6.4BL)	Chrystal <i>et al.</i> 1985; this study
<i>Apogon semilineatus</i>	Tateyama Bay, Japan	males and females	70.0-100.0		0.58-0.60	2.3	Ebina 1932
<i>Phaeoptyx conklini</i>	Bahamas		34.8-42.4		0.19-0.31 ($\bar{x} = 0.24$)		Charney 1976
<i>Sphaeramia orbicularis</i>	Palau Archipelago, USA	males	69.0-89.0	6,100-11,700	0.60-0.70	3.3	Allen 1975
<i>Vincentia conspersa</i>	Southern Australia		95.0	150	4.50		Hale 1947

of larval survival during their short planktonic phase are, on the other hand, enhanced by the fact that most of the larval development takes place within the egg. It thus seems probable that both the advanced stage of development of *A. rueppellii* at hatching and their short planktonic life contribute to maximize their survival and retention within estuaries, where conditions are much less stable than those at sea where apogonids are more abundant.

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