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Development of Eggs, Larvae and Pelagic Juveniles of Three Indo-Pacific Ostraciid Fishes (Tetraodontiformes): *Ostracion meleagris*, *Lactoria fornasini* and *L. diaphana*

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Abstract The eggs, larvae and pelagic juveniles of *Ostracion meleagris*, *Lactoria fornasini* and *Lactoria diaphana* were identified from reared and field collected specimens from Hawaii, Japan, Australia and the eastern Pacific. Eggs are large and pelagic with limited chorion ornamentation and a cluster of oil droplets. At hatching, larvae are well developed, rotund, and enclosed in a dermal sac. The sac disappears and dermal plates form prior to notochord flexion. Larvae of the three species can be distinguished by their pigment patterns and development of the carapace of ossified dermal plates. Eggs of the three species could not be distinguished. The larval stage ends at a small size (<6 mm) but the juveniles may grow to a substantial size while remaining pelagic. *L. diaphana* matures and spawns while pelagic in the eastern Pacific.

The four genera of Indo-Pacific ostraciid fishes are *Ostracion* (about 8 species), *Lactoria* (3 species), *Rhynchostracion* (1 species) and *Tetrosomus* (1 species) (Tyler, 1980). Litttle is known of the early life history of these fishes. Aboussouan and Leis (1984) reviewed the early life history of Indo-Pacific ostraciids, and noted that a complete developmental series had not been described for any species. The eggs or early larval stages of a number of unidentified Indo-Pacific ostraciids have been illustrated or briefly described, although occasionally misidentified (Delsman, 1930; Sanzo, 1930; Mito, 1962, 1966; Watson and Leis, 1974). The only identified Indo-Pacific ostraciid larvae to be described previously are the yolk-sac and preflexion larvae of *Ostracion meleagris* (Leis and Rennis, 1983). However, Aboussouan and Leis (1984) stated that *Lactoria* and *Ostracion* have pelagic eggs and that *Lactoria*, *Ostracion* and *Tetrosomus* have pelagic juveniles that may reach relatively large sizes before settlement. In ostraciids the transition from larval to juvenile stage is complete when the caudal fin forms. From that point the pelagic juveniles resemble miniature adults with the exception that carapace spines form during the pelagic juvenile stage (Leis and Rennis, 1983).

In this paper we use laboratory-reared and field-captured specimens to describe the egg, larval and pelagic juvenile development of *Ostracion meleagris*, *Lactoria fornasini* and *Lactoria diaphana*.

Materials and methods

The reared larvae used in this study were from two sources: Miyake-jima, Japan and Kaneohe Bay, Hawaii. The Miyake-jima specimens were reared at the Tatsuo Tanaka Memorial Biological Station from eggs scooped by SCUBA divers into plastic bags from spawning pairs of *Lactoria fornasini*. Spawning behaviour of this species is described by Moyer (1979, 1984), and some of the same harems studied by Moyer supplied the eggs for our study. Eggs were obtained from plankton tows in and near Kaneohe Bay, Oahu and were reared at the Hawaii Institute of Marine Biology.

Four rearings were conducted at Miyake-jima from eggs captured on 3, 8 and 9 August 1979 and 1 June 1981. Eggs and larvae were reared in unaerated seawater and were periodically removed for preservation. No attempt was made to feed the larvae and none survived longer than eight days after hatching. Specimens from all four rearings are included in the descriptions. The sea temperatures on collection dates in 1979 and 1981 were 27°C and 23–23.5°C, respectively. Temperatures in the rearing containers were 25.3–29.4°C in 1979, and 22.3–25.1°C in 1981.

A number of rearings were carried out in Hawaii but because ostraciid eggs were never abundant in the plankton tows, few were available for any rearing experiment (see Leis 1977, 1978 for methods). Larvae were occasionally observed to feed, but none lived longer than unfed larvae (5 days). Larvae were preserved at irregular intervals. Temperatures varied from 25–29°C.

Larvae were obtained from plankton tows and midwater trawls in a variety of areas (see material examined).

A series of *Lactoria fornasini* larvae from the June 1981 Miyake-jima rearings was cleared and stained for bone and cartilage by the methods of Dingerkus and Uhler (1977) as modified by Potthoff (1984).

Larvae were measured using the ocular micrometer of a dissecting microscope to the nearest 0.12–0.016 mm, depending on the magnification used. Definitions generally followed Leis and Rennis (1983) with the exception that body width was measured at the pectoral fin base even if the body width was greater elsewhere. All lengths are body length (i.e. for preflexion larvae, notochord length; for postflexion individuals, standard length). All measurements were of preserved material unless noted. Drawings were done with the aid of a camera lucida.

Material examined. AMS, Australian Museum, Sydney; NMFSLJ, National Marine Fisheries Service, La Jolla; ZUMC, Zoologisk Museum University of Copenhagen.

Ostracion meleagris (all from Hawaii) all AMS.—reared: I. 23813-037 to 055; field: I. 23570-039 to 044, I. 24754-005, I. 24755-002, I. 24757-001.

Lactoria fornasini all AMS.—reared: from Japan, I. 24753-001 to 027; from Hawaii, I. 23823-024 to 029; field: from Hawaii, I. 23570-031, I. 23598-022, I. 23812-005+004, I. 23820-016, I. 24754-001+002, I. 24755-001+002, I. 24756-001; from Australia, I. 23907-005, I. 24163-006.

Lactoria diaphana.—reared: from Hawaii, AMS I. 23813-030 to 036; field: from Hawaii, AMS I. 23570-032 to 038, I. 23812-006 to 008, I. 24583-007, I. 24754-003+004, I. 24755-003+004, I. 24758-001, I. 24760-001; from eastern Tropical Pacific, AMS I. 24761-001+002, I. 24762-001 to 004, I. 24780-001, I. 24781-001; NMFSLJ, ETP 20.022, ETP 30.118, ETP 60.020, ETP 60.145, ETP 60.159, ETP 70.014, CR 7205-J 20.127; from southwest Pacific, ZUMC CF 3585-4, CF 3587-7.

Results

Identification. Planktonic ostraciid eggs from Hawaii were first identified when ovarian eggs of *Lactoria fornasini* and *Ostracion meleagris* were found to conform in size, shape and chorion ornamentation with the planktonic eggs (Watson and Leis, 1974). Ripe ovarian eggs of *L. diaphana* were not available. No other pelagic fish eggs are known which possess the chorion ornamentation which characterizes *Ostracion* and *Lactoria* eggs (Fig. 1). This feature combined with the large size and slightly non-spherical shape of Indo-Pacific ostraciid eggs enables ready identification to family.

Ostraciid larvae with carapace plates formed cannot be confused with any other larvae with the possible exception of aracanids (which are presently unknown, Aboussouan and Leis, 1984). Prior to formation of the carapace plates ostraciid larvae might be confused with some lophiiform or tetraodontiform larvae and Leis and Rennis (1983) described how to distinguish these.

Identification of the reared eggs and larvae of *Lactoria fornasini* was assured because we obtained the eggs from spawning adults. Eggs and larvae of *Lactoria diaphana* were identified from specimens captured where this is the only ostraciid: in the tropical eastern Pacific (13–15°N, 126°W) more than 1,200 km from shallow water. Larvae of these species could be distinguished by pigment characters (see below). Once the pigment differences were established they were used to identify larvae from rearings and plankton samples in Hawaii.

Ostracion meleagris eggs could not be distinguished from the others. But, in a few rearing experiments, features of eggs were studied before hatching, and when the reared larvae from them were identified, the eggs were identified and described in retrospect. Pigment differences served to distinguish *O. meleagris* larvae from *Lactoria* spp. larvae (see below). We assembled a size series of these distinctively-pigmented larvae from reared unidentified eggs and plankton tows in Hawaiian waters, and identified them as *O. meleagris*. Three species of *Ostracion* have been recorded from Hawaii (Randall, 1972): *O. meleagris*, *O. whitleyi* and *O. cubicus*. *Ostracion whitleyi* is rare and there is but one dubious Hawaiian record of *O. cubicus* (Randall, 1972). Therefore, it is possible, but unlikely that we may have mistakenly included small larvae of *O. whitleyi* or *O. cubicus* in our supposed series of *O. meleagris*.

As noted by Leis (in press), a potential problem exists with the identity of *Lactoria diaphana*. In the eastern Pacific what is known as *L. diaphana*

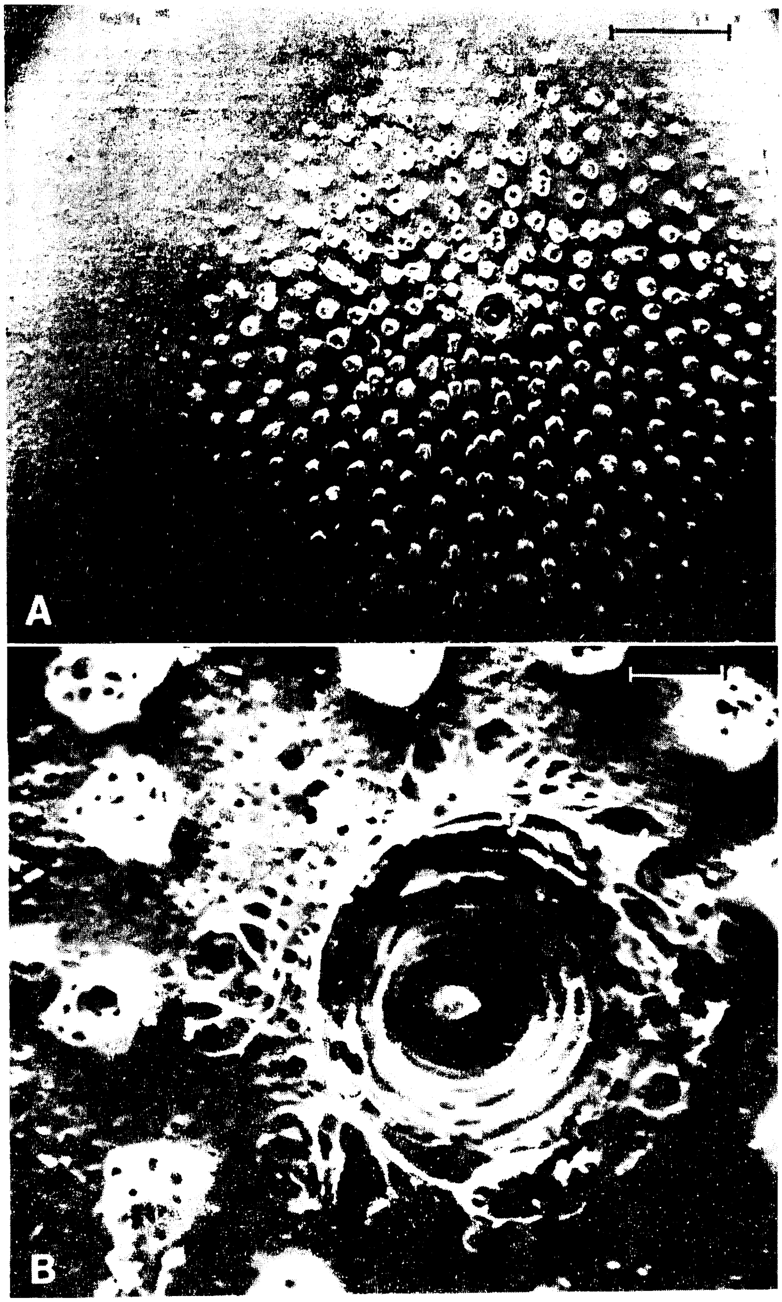

Fig. 1. Scanning electron micrograph of chorion ornamentation of an unidentified ostraciid egg from Hawaii. A, whole field of ornamentation (scale bar 100 μm). B, detail of centre of field showing micropile and some ornamentation (scale bar 10 μm).

matures and spawns pelagically and is generally considered an oceanic, pelagic species (e.g. Thomson *et al.*, 1979). In the western Pacific, *L. diaphana* spends a major portion of its life in benthic association with reefs or soft bottoms in shallow to moderate depths (e.g. Masuda *et al.* 1975, Moyer 1979, 1984). *Lactoria diaphana* in the west does remain pelagic to a large size (>100 mm, see below). However, we have no direct evidence of spawning before settlement in the west.

Table 1. Some characters of ostraciid eggs. Measurements in mm. (n) number examined, (x) mean, (s) standard deviation, (*) patch present but not measured.

		Chorion diameter				Diameter of chorion patch		Number of oil droplets	Melanophores in dermal sac of embryo	Condition of eggs
		major axis		minor axis						
	n	x	s	x	s	x	s			
Lactoria fornasini	31	1.78	0.04	1.61	0.05	0.56	0.11	8–18	none	preserved
	1	1.75		1.60			*	6	none	live
Lactoria diaphana	13	1.79	0.06	1.67	0.06	0.59	0.05	10–12	none	preserved
Ostracion meleagris	9	1.77	0.11	1.62	0.09		*	3–9	present in late stage embryos	live

Given this possible difference in life history it is conceivable that two closely-related species are involved (see Leis (1978) for a similar situation in *Diodon*). This is relevant to the present study because if two species are involved, our Hawaiian material identified as *L. diaphana* may contain both species. However, we could detect no differences between larvae identified as *L. diaphana* from Hawaii and the eastern Pacific.

Development. Eggs and larvae of all three species are very similar in development and morphology. For this reason, a general description of development is given which applies to all species. This is followed by species diagnoses and remarks.

Eggs (Table 1, Figs. 1, 2). The eggs are pelagic, slightly ovate and colourless (Fig. 1). The yolk is unsegmented and there is one (rarely two) cluster of 3–18 small (0.05–0.15 mm diameter) clear, yellowish oil droplets. The number of oil droplets tends to decrease with age as droplets coalesce. The chorion is smooth except for a circular field of small, hollow bumps centred around the micropile and located at the more acute pole of the egg (Fig. 1). The long axis of the egg is 0.1–0.3 mm longer than the short axis. The embryo is free to rotate inside the chorion, so its orientation relative to the micropile changes. Characters of the eggs of the three species are summarized in Table 1.

The following description of development is based on *L. fornasini* eggs from Miyake-jima, but aside from the times and some details of pigment as noted, it applies equally well to *L. diaphana* and *O. meleagris*. Development is generally similar to that in *Diodon* and *Ranzania* and the description utilizes the terminology of Leis (1977, 1978). *Lactoria fornasini* eggs hatched 89–93 hours following fertilization. Elapsed time following fertilization is given for available preserved specimens of *L. fornasini*.

Early stage (Fig. 2A, fertilization to blastopore closure 10 min, 40 min, 12 hrs): Little differentiation is evident during this stage. Just prior to blastopore closure, the embryonic axis is vaguely visible, and the oil droplet cluster is located opposite the embryo at the edge of the germ ring. Rarely there are two oil droplet clusters. No pigment is present.

Middle stage (Fig. 2B, blastopore closure to separation of tail bud from yolk: 24 hrs): The 24 hr old eggs have the tail bud just separate from the yolk and optic vesicles present. The oil droplets are clustered near the tail tip. No pigment is present.

Late stage (Fig. 2C, D, separation of tail bud from yolk to hatching: 36, 48, 60, 72, 84, 89 hours): The vesicular dermal sac is first visible at 36 hrs and becomes increasingly inflated with time. The pectoral fin buds are present at 48 hrs as are the exhalent gill pores. The mouth is open at 84 hrs. A few melanophores appear on trunk and branchial region at 36 hrs, and pigment spreads with time. At hatching, scattered, small melanophores cover dorsal and lateral surfaces of head, trunk and yolk sac. There are no melanophores in the vesicular dermal sac in *Lactoria* spp., but scattered melanophores in the sac are present in *O. meleagris*. *Lactoria fornasini* may have a single ventral melanophore on the tail, *L. diaphana* has a few lateral melanophores on the tail, and the tail of *O. meleagris* embryos becomes heavily infested with melanophores. Pale yellow pigment covers the trunk and head from 60 hrs. A small melanophore is present posteriorly on the eye by 60 hrs. A second, anterior melanophore is present by 84 hrs. The eye is uniformly but lightly pigmented at 89 hrs just prior to hatching.

No differences could be found between pre-

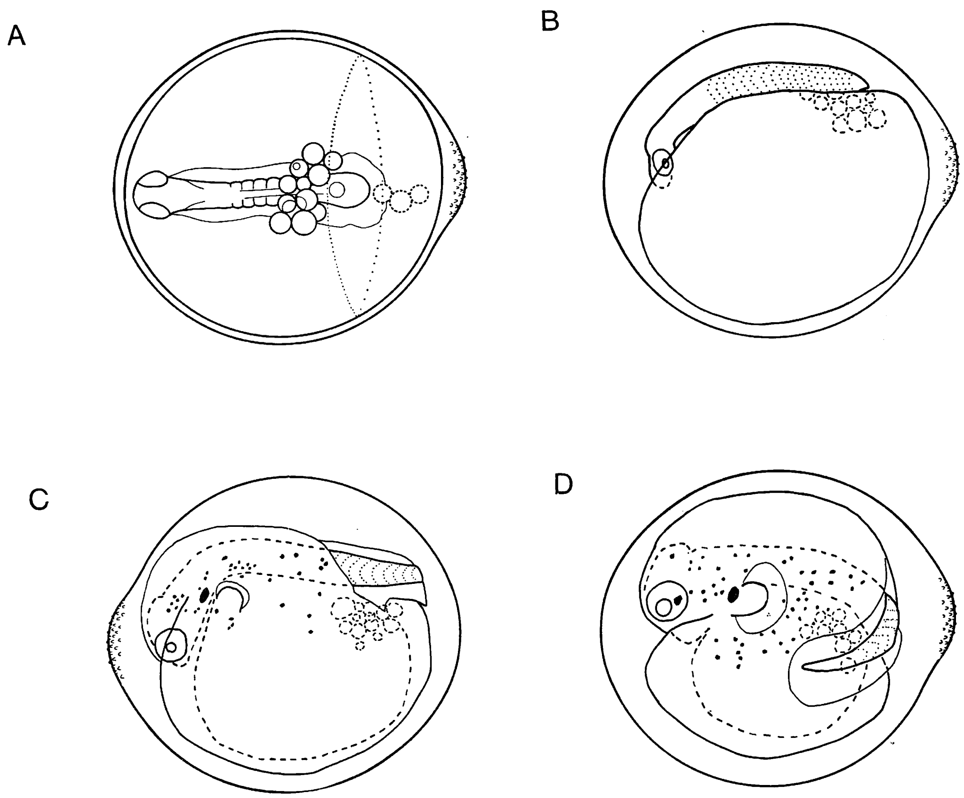

Fig. 2. Development of ostraciid eggs. A, early stage egg of *Ostracion meleagis* from Hawaii from plankton tow (live). Eggs of *Lactoria fornasini* from Miyake-jima (preserved): B, middle stage egg, 24 hours after fertilization; C, late stage egg, 48 hours after fertilization; D, late stage egg, 72 hours after fertilization.

served *Lactoria fornasini* eggs from the Miyake-jima rearings and preserved *L. diaphana* eggs from the eastern Pacific (Table 1). In spite of the fact that rearing of ostraciid eggs obtained from plankton tows in Hawaiian waters resulted in larvae of *O. meleagris*, *L. diaphana* and *L. fornasini*, it was never possible to reliably predict which larva would result from which egg. Nor was it possible in retrospect following rearing experiments to use measurements or other characteristics of the eggs to detect differences between the three species. The data on live eggs (Table 1) were derived from Hawaiian eggs studied when captured and then reared so the larvae could be identified. The apparent difference in oil droplet number between species (Table 1) is probably an artifact of oil droplet fracture in preserved eggs. The differences in pigmentation noted are only useful for the final 24–36 hours of incubation.

Larvae (Table 2, Figs. 3, 4, 5). The body is deep and wide, and always deeper than wide (Fig. 3). Ostraciid larvae are rotund throughout development. The head and trunk are a ball-like unit initially enclosed by a dermal sac and later by a hard carapace. The tail is relatively long, constituting 35–40% of body length (BL) until about 2.5 mm BL after which the tail rapidly decreases in actual and relative length to as little as 6% BL in a 4.1 mm *L. diaphana* just prior to notochord flexion. Following flexion, the tail begins to slowly increase in relative length (Table 2). Accurate myomere counts are difficult or impossible due to pigment and the dermal sac. Postanal myomeres are easily distinguished only in early larvae, and become progressively more difficult to count.

The head is large (to 44% BL). The snout is short and blunt until it begins to elongate slightly following flexion (Table 2). At hatching, the

Table 2. Morphometric and meristic data for larvae and pelagic juveniles of *Ostracion meleagris*, *Lactoria fornasini* and *Lactoria diaphana*. Measurements in mm. (x) mean, (s) standard deviation, (n) number of larvae examined. Larvae between broken lines were undergoing notochord flexion.

		Body length		Snout to anus length		Head length		Snout length		Eye diameter		Body width		Body depth		Fin rays			
		x	s	x	s	x	s	x	s	x	s	x	s	x	s	D	A	P	C
Ostracion meleagris																			
Reared:																			
Age (days)																			
0	15	2.05	0.11	1.29	0.06	0.54	0.07	0.07	0.04	0.21	0.03	0.64	0.09	1.13	0.10	0	0	0	0
1	7	2.12	0.15	1.28	0.05	0.54	0.06	0.09	0.02	0.25	0.02	0.75	0.10	1.10	0.02	0	0	0	0
2	2	1.90	0.02	1.18	0.14	0.51	0.04	0.14	0.04	0.24	0.06	0.67	0.05	0.85	0.13	0	0	0	0
3	3	1.68	0.11	1.09	0.15	0.56	0.02	0.12	0.02	0.29	0.01	0.71	0.14	0.86	0.12	0	0	0	0
4	3	1.84	0.11	1.23	0.14	0.57	0.09	0.12	0.06	0.30	0.02	0.76	0.13	1.01	0.10	0	0	0–8	0
5	5	1.98	0.22	1.19	0.05	0.66	0.07	0.15	0.02	0.31	0.02	0.71	0.04	0.92	0.07	0	0–7	6–9	0
Field:																			
Size class																			
1.5–2.0	7	1.77	0.14	1.34	0.19	0.62	0.09	0.13	0.03	0.26	0.06	0.75	0.13	0.96	0.10	0	0–7	0–9	0
	1	2.31		1.69		0.88		0.28		0.39		1.32		1.51		7	9	11	0
	1	5.00		4.54		2.05		0.58		0.83		3.84		4.10		9	9	11	10
	1	9.03		7.81		4.01		1.28		2.05		7.17		7.30		9	9	11	10
Lactoria fornasini																			
Reared:																			
Age (hours)																			
0	6	2.23	0.08	1.43	0.08	0.51	0.06	0.10	0.04	0.24	0.02	0.77	0.06	1.27	0.09	0	0	0	0
12	3	2.03	0.20	1.40	0.02	0.42	0.08	0.08	0.03	0.25	0.03	0.71	0.08	1.17	0.07	0	0	0	0
24	6	2.11	0.14	1.32	0.05	0.57	0.02	0.14	0.02	0.26	0.02	0.81	0.04	1.21	0.11	0	0	0	0
36	3	2.05	0.03	1.25	0.03	0.54	0.11	0.16	0	0.29	0.01	0.73	0.10	0.97	0.06	0	0	6–8	0
48	3	2.01	0.02	1.18	0.02	0.54	0.04	0.14	0.03	0.28	0.01	0.73	0.05	1.10	0.10	0–2	0–3	7–8	0
60	3	1.94	0.08	1.17	0.07	0.59	0.07	0.15	0.03	0.29	0.03	0.88	0.04	1.06	0.05	0–3	0–4	7–8	0
72	3	1.89	0.05	1.09	0.06	0.54	0.03	0.13	0.03	0.31	0	0.64	0.07	1.07	0.08	4–6	6	9	0
84	3	1.97	0.05	1.15	0.09	0.51	0.06	0.12	0.04	0.30	0.01	0.71	0.06	1.02	0.01	4–6	5–7	10–11	0
96	7	2.20	0.18	1.38	0.07	0.63	0.06	0.16	0.02	0.31	0.02	0.93	0.11	1.14	0.10	0–6	0–6	8–10	0
108	3	1.90	0.06	1.05	0.06	0.49	0.09	0.14	0.03	0.30	0.02	0.67	0.09	0.87	0.08	5–6	6–7	9–10	0
120	3	1.84	0.05	1.00	0.06	0.56	0.02	0.13	0.03	0.29	0.02	0.81	0.05	1.01	0.11	3–5	4–6	7–9	0
144	2	1.67	0.16	1.05	0.06	0.45	0.04	0.11	0.02	0.31	0.01	0.65	0.04	0.99	0.01	5–7	6–8	9–9	0
192	2	2.28	0.01	1.35	0.05	0.63	0.05	0.14	0.01	0.31	0	0.91	0	1.05	0.11	3–4	6–7	10	0

Table 2. (Continued)

	n	Body length x	Body length s	Snout to anus length x	Snout to anus length s	Head length x	Head length s	Snout length x	Snout length s	Eye diameter x	Eye diameter s	Body width x	Body width s	Body depth x	Body depth s	Fin rays D	Fin rays A	Fin rays P	Fin rays C
Lactoria fornasini (continued)																			
Field:																			
Size class																			
1.5–2.0	6	1.76	0.09	1.07	0.06	0.49	0.06	0.10	0.02	0.27	0.03	0.72	0.08	0.92	0.09	0–7	0–8	0–10	0
2.1–2.5	4	2.23	0.15	1.74	0.20	0.77	0.19	0.20	0.04	0.40	0.06	1.14	0.20	1.32	0.25	9	9	10–11	0
	1	6.26		5.16		2.64		0.84		1.03		3.55		4.71		9	9	11	10
	1	6.90		5.55		3.16		1.10		1.68		4.19		4.97		9	9	11	10
	1	7.81		6.79		3.30		1.40		1.67		4.74		5.64		9	9	11	10
15.5–16.0	2	15.76	0.01	13.19	0	5.96	0.28	1.98	0.09	2.76	0.09	7.48	0.60	8.39	0.32	9	9	11	10
Lactoria diaphana																			
Reared:																			
Age (days)																			
0	1	2.31		1.28		0.62		0.08		0.23		0.70		1.33		0	0	0	0
4	1	2.03		1.17		0.55		0.14		0.31		0.94		1.01		0	0	0	0
Field:																			
Size class																			
1.51–2.00	15	1.79	0.09	1.13	0.08	0.55	0.06	0.12	0.04	0.29	0.04	0.77	0.08	1.02	0.11	0–4	0–5	0–9	0
2.01–2.50	11	2.22	0.13	1.40	0.23	0.73	0.14	0.19	0.05	0.32	0.07	0.93	0.17	1.18	0.14	0–9	0–9	0–10	0
2.51–3.00	7	2.75	0.18	2.27	0.26	0.96	0.10	0.29	0.04	0.48	0.05	1.40	0.28	1.78	0.22	0–9	8–9	9–11	0
	1	4.12		3.87		1.62		0.38		0.88		3.12		3.59		9	9	11	0
	1	4.19		3.81		1.81		0.56		0.81		2.90		3.74		8	9	11	8
	1	5.16		4.57		2.16		0.52		0.97		3.23		4.39		9	9	11	7
	1	5.48		5.16		2.26		0.77		1.03		4.00		5.16		9	9	11	9
	1	5.80		5.16		2.34		0.62		1.00		3.22		4.84		8	9	11	10
	1	6.73		5.96		2.56		0.77		1.15		3.84		6.02		9	9	11	10
	1	7.35		6.45		2.58		0.78		1.42		3.87		6.13		9	10	11	10
	1	9.99		8.79		3.22		1.15		1.92		5.64		7.69		9	9	11	10
	1	10.76		9.61		4.00		1.29		1.97		6.12		8.32		9	9	11	10
	1	11.90		10.88		3.97		1.29		2.06		6.13		8.96		9	9	11	10
12.51–13.00	2	12.75	0.09	11.46	0.08	4.36	0.18	1.54	0.18	2.37	0.09	5.64	0.18	9.68	0.81	9	9	11	10

mouth is open, but apparently functional only in *Lactoria* spp. The mouth remains small. The lips are fleshy and flare outward laterally when the mouth is open (Fig. 3). The eyes are incompletely pigmented at hatching, but become fully pigmented within 24 hours. The eyes become large (Table 2). The exhalent gill opening is restricted to a pore well before hatching.

The first structures to stain positively for cartilage are the cleithrum, branchiostegals, dentary, premaxillary and operculum in a one-day-old larva (i.e. the feeding, respiratory and locomotory structures; ostraciid larvae swim primarily with pectoral fins). The cleithrum, postcleithum, operculum and four branchiostegals are ossified in a four-day-old larva, at which time about 8 vertebrae are cartilaginous. In an eight-day-old larva the maxilliary, premaxillary, margins of the preoperculum, suboperculum, 6 branchiostegals, supracleithrum and portions of 6 vertebrae, are ossified and portions of the cranium and hyoid area are cartilaginous.

A large yolk sac containing oil droplets is present at hatching, and although it persists for some days, it is obscured by the dermal sac and spreading pigment.

At hatching the head and trunk are enclosed in an inflated dermal sac containing numerous minute vesicles (Figs. 3A, 4A, 5A). The vesicles extend onto the median fin fold nearly to its margins. The subdermal space decreases and disappears shortly before the scales begin to appear, and the vesicles cease to be visible at about this stage. The highly modified scales which eventually form the carapace-like dermal armour first appear as small, stellate ossifications scattered over head and trunk (Figs. 3C, 4C, 5C). The scales enlarge (Fig. 4D) until, at about 4 mm and prior to notochord flexion, they cover the head and trunk with polygonal plates which are fused into a stiff ossified carapace (Fig. 5D). Shortly after this, some of the carapace plates begin to enlarge to form the characteristic spines of *Lactoria* (Figs. 4E, 5D), although these are not fully formed until well after flexion (Figs. 4F, 5E). Each spine enlarges from a single carapace plate.

We do not know if the larvae pass through a stage where the carapace does not posteriorly encircle the dorsal and anal fin bases (i.e. the condition in aracanids), because we lack specimens of 3–4 mm. However, the distribution of ossifying plates in specimens 2.0–2.7 mm suggests that such a stage does exist. Projections of the carapace dorsally and ventrally over the caudal peduncle, and which provide additional protection for it, are particularly well-developed in *O. meleagris* and *L. fornasini* (Figs. 3D, 4E).

In cross section, the carapace of adult *Ostracion* resembles a trapezoid with rounded corners, and the carapace of adult *Lactoria* resembles a pentangon with curved sides and acute corners (Fujii and Uyeno, 1979). Larvae of all species studied here initially have a cross section resembling a somewhat laterally compressed circle. In *Ostracion*, this shape is maintained until the carapace is fully formed. At this stage, the sides are concave, and the dorsum and ventrum are convex. This shape is maintained as the juvenile grows and its body begins to elongate. In *Lactoria*, the dorsal ridge forms at the time the first dermal plates ossify. However, the young do not attain a cross-sectional shape similar to the adult until the carapace spines begin to elongate. Even at this stage the belly is much more rounded than it is in adults.

At hatching, the pectoral buds and anlagen of dorsal and anal fins are present (except in *O. meleagris* where the dorsal anlage forms a short time following hatching). Incipient (cartilaginous) fin rays appear first in the pectoral fin, next in the anal fin, and then in the dorsal fin. In four-day-old larvae of *L. fornasini*, nine pectoral, five anal, and three dorsal incipient fin rays are present. In eight-day-old larvae one or two more incipient rays are present in each fin. Full complements of fin rays in dorsal (9), anal (9) and pectoral (11) fins are present in all three species at about the time the dermal ossifications first appear. The caudal fin anlage is first visible immediately prior to notochord flexion. Very soon after flexion is completed, all 10 caudal rays are present. The dorsal-most pectoral ray is initially nearly as long as the second, but following flexion, it becomes progressively relatively smaller. In adults, this ray is reduced to a nubbin.

Ostraciid larvae become relatively heavily and uniformly pigmented, particularly compared to other tetraodontiform larvae. The basic pigment pattern is established during the embryonic stage. In the *Lactoria* spp. melanophores on head and trunk are all subdermal (i.e. none on the inflated dermal sac. Figs. 4, 5) while both dermal and sub-

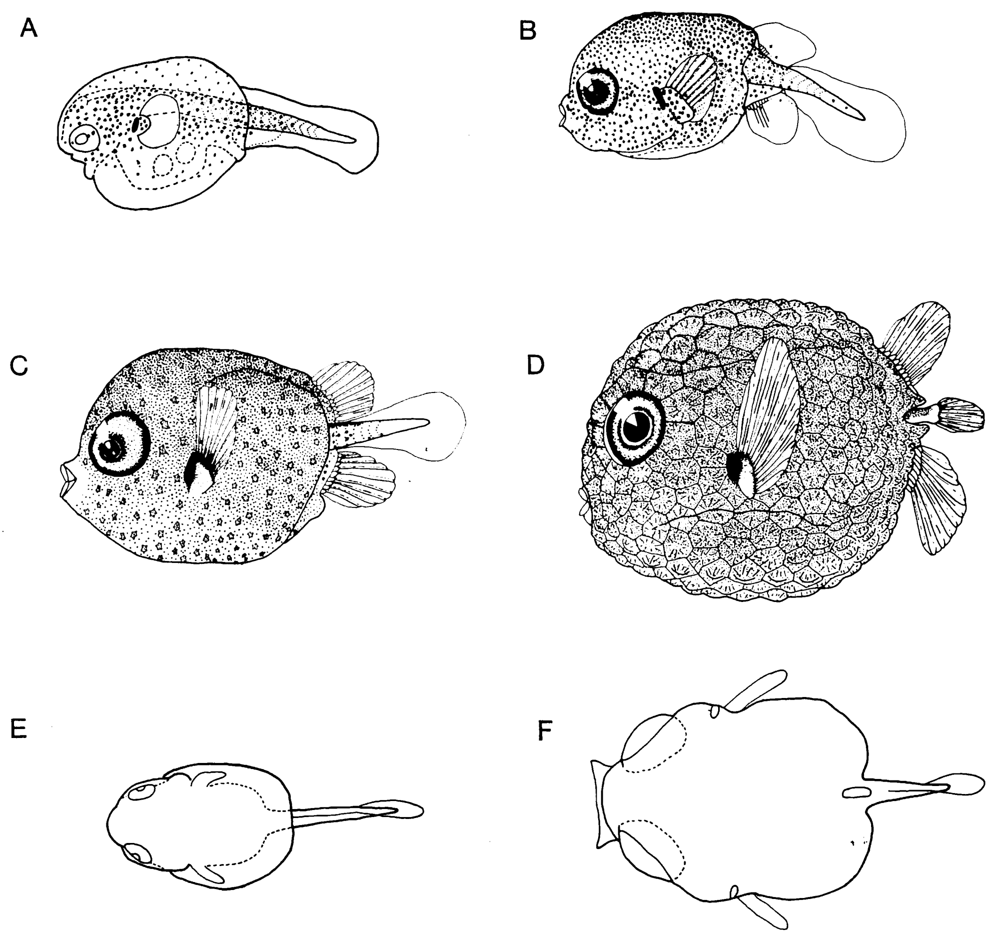

Fig. 3. Larvae and pelagic juvenile of *Ostracion meleagris* from Hawaii. Minute vesicles in dermal sac not shown. A, reared larva on day of hatching, 2.10 mm. (AMS I.23813-037). Note unformed mouth and pigment in dermal sac. B, reared four-day-old larva, 2.30 mm (AMS I.23813-038). Note that subdermal space has disappeared. C, larva from a plankton tow, 2.50 mm (AMS I.24591-002). Note formation of dermal plates. D, pelagic juvenile from a midwater trawl, 5.0 mm (AMS I.24757-001). At this stage the carapace is convex dorsally and ventrally and has concave sides. E, dorsal outline of A to show shape of body. F, dorsal outline of C to show shape of body.

dermal pigment is present in *Ostracion meleagris* (Fig. 3A). The distinction between dermal and subdermal pigment is lost when the subdermal space disappears. Pigment is generally heavier dorsally than ventrally and the intensity and distribution of pigment varies with species. The pigment on the tail varies with species, but the tail is generally more lightly pigmented than the head and trunk. Fins remain unpigmented except at their bases. Nostrils and lips also remain unpigmented. Newly hatched larvae have an overall yellow colour when alive which persists for at least eight days following hatching. In *O. meleagris* the yellow colour combined with the very dark melanistic body colour give the larvae a greenish appearance.

Ostracion meleagris
(Table 2, Fig. 3)

Diagnosis. Larvae heavily and uniformly pigmented, with pigment extending onto tail and caudal peduncle; little or no ventral and no lateral lightening. Snout heavily and uniformly pigmented; dermal sac with scattered melanophores;

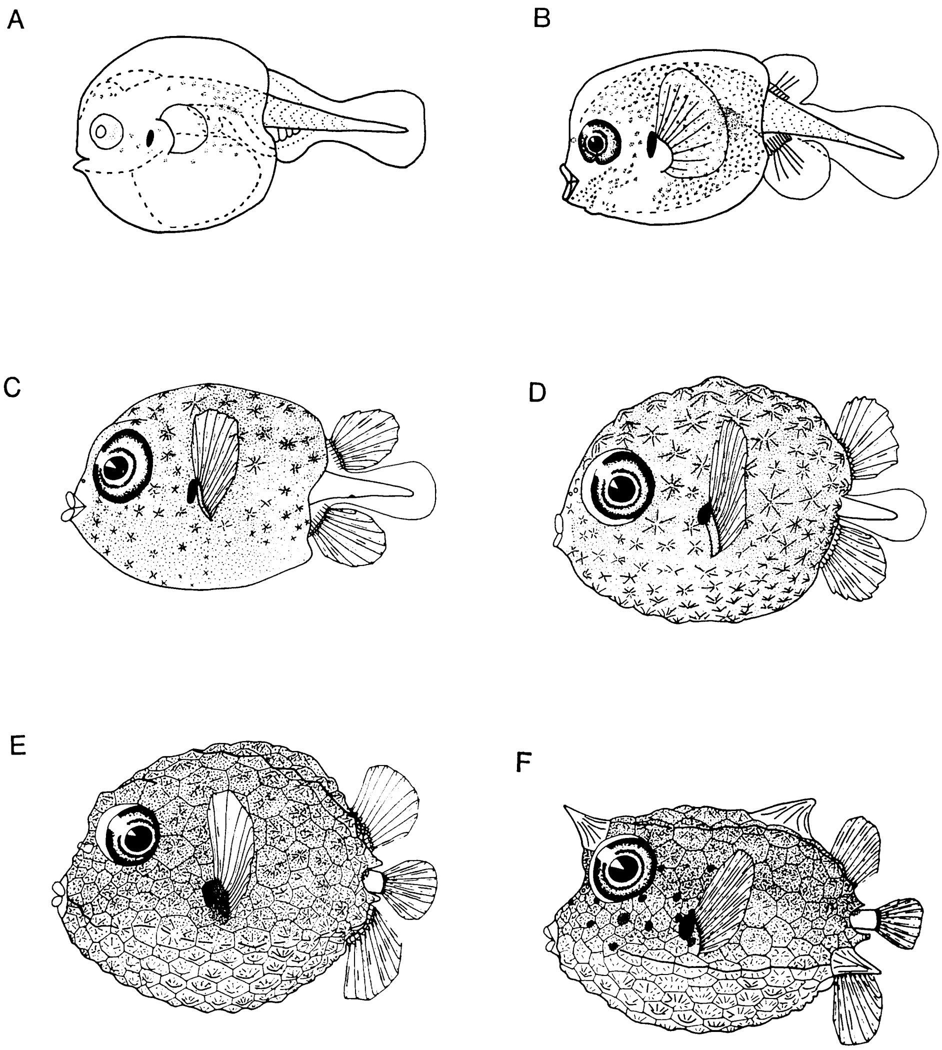

Fig. 4. Larvae and pelagic juveniles of *Lactoria fornasini*. Minute vesicles in dermal sac not shown. A, reared larva from Miyake-jima on day of hatching, 2.20 mm (AMS I.24753-002). B, reared four-day-old larva from Miyake-jima, 2.30 mm (AMS I.24753-004). Note unpigmented snout. C, larva from a plankton tow in Hawaii, 2.15 mm (AMS I.24756-001). Note stellate dermal plates. D, larva from a plankton tow in Hawaii, 2.45 mm (AMS I.24756-001). Dermal plates are now raised in centre and have distinct ridges. E, pelagic juvenile from a mid-water trawl off southeast Australia, 6.25 mm (AMS I.24163-006). At this stage carapace is roundly pentagonal in cross section, but with very rounded corners. F, pelagic juvenile from a mid-water trawl off southeast Australia, 7.8 mm (AMS I.23907-005). Note well developed supraocular, dorsal and postanal carapace spines.

carapace plates relatively uniform in size, particularly on back where none on the mid-line are enlarged; mouth apparently not functional at hatching.

Remarks. *O. meleagris* larvae are readily distinguished by their heavier pigment, and particularly by the pigment on the tail and dermal sac. The heavy, uniform pigment of head and trunk extends onto the tail with little dimunition, and extends posterior to the base of the dorsal and anal fins. Light spots begin to form from about 12.5 mm.

A B C D E

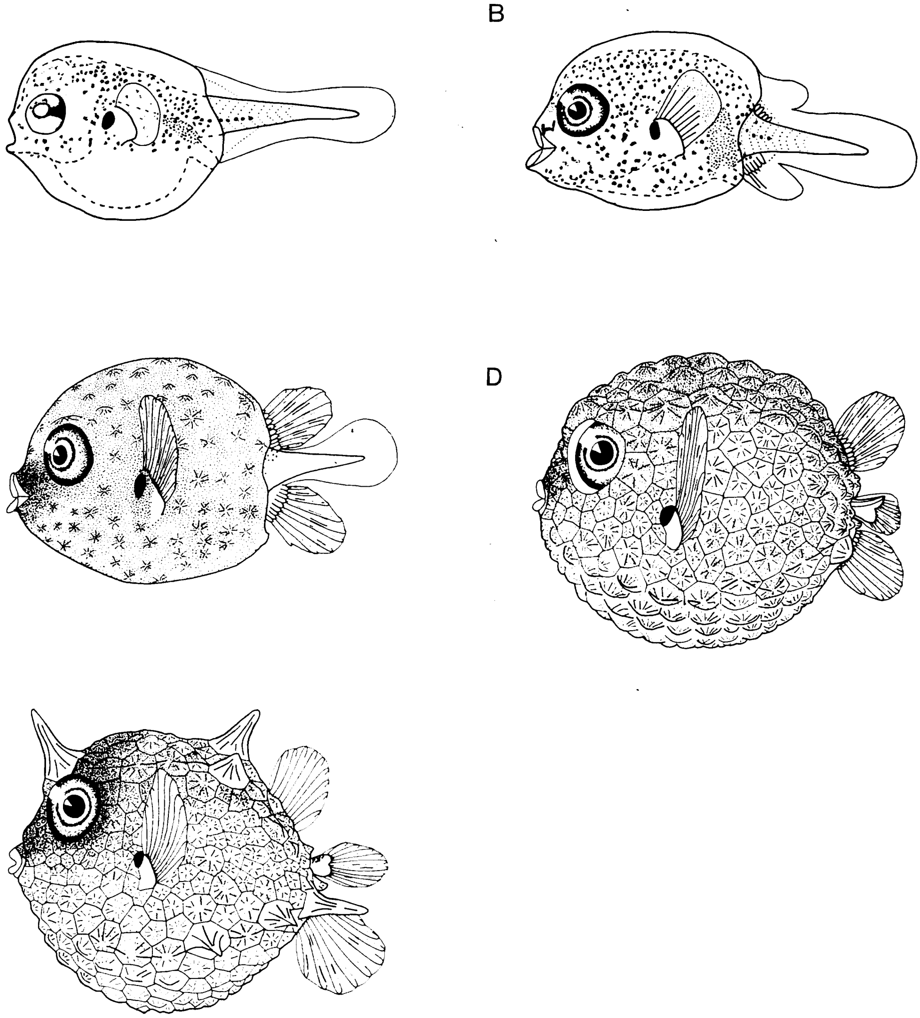

Fig. 5. Larvae and pelagic juveniles of *Lactoria diaphana*. Minute vesicles in dermal sac not shown. A, recently hatched larva from a neuston tow in the eastern Pacific, 1.85 mm (AMS I.24762-001). Note unpigmented dermal sac and partially pigmented eye. B, larva from a neuston tow in the eastern Pacific, 2.00 mm (AMS I.24763-001). Note melanophores on snout. C, larva from a plankton tow in Hawaii, 2.65 mm (AMS I.24755-004). Note stellate dermal plates and pigmented snout. D, very late flexion-stage larva from a plankton tow in the eastern Pacific, 5.30 mm (NMFSLJ-ETP 60.159). At this stage carapace is nearly round in cross section, but with a mid-dorsal ridge. E, pelagic juvenile from a plankton tow in the southwest Pacific, 6.8 mm (ZUMC CF3587-7). Note well developed carapace spines. At this stage, carapace is pentagonal, but much more inflated and wider ventrally than dorsally.

The carapace plates of *O. meleagris* are relatively uniform in size and shape, particularly those on the dorsum. None along the dorsal midline are enlarged.

The eggs of *O. meleagris* hatch at a slightly less well developed stage than do those of *Lactoria* spp. Eye pigment is limited to a few small melanophores, the jaws are open, but apparently not functional and no dorsal fin anlage is present.

The maximum size attained by pelagic juveniles of *O. meleagris* is unknown. The largest of 46 *O. meleagris* from Hawaiian midwater trawls was 30 mm, and settled juveniles as small as 28 mm are known (Randall, 1972).

Lactoria fornasini
(Table 2, Fig. 4)

Diagnosis. Larvae moderately and nonuniformly pigmented, at most a single ventral melanophore on tail; distinct ventral countershading present; snout very lightly pigmented if at all; dermal sac unpigmented; carapace plates of the dorsal midline longer and higher than other dorsal plates, forming a ridge; mouth functional at hatching.

Remarks. *L. fornasini* larvae are most easily distinguished by the virtual lack of tail pigment and lightly pigmented snout. Pigment spreads onto the tail of postflexion juveniles. Dark head and trunk are present from about 8 mm.

From their earliest formation, the carapace plates of the dorsal midline are elongate and higher than surrounding plates. These plates form a ridge, and from one of them, the mid-dorsal spine arises. The preorbital spines and the postanal spines develop from plates which are little if any enlarged prior to the elongation of the spines (Fig. 4E).

Eggs of *L. fornasini* hatch with the mouth apparently functional and eyes wholly, if lightly, pigmented.

We examined fewer pelagic juveniles of *L. fornasini* than the other two species, and the largest was 15.8 mm. We have examined ripe female *L. fornasini* as small as 63 mm from bottom trawls at a depth of 100 m in Hawaii. At Miyake-jima, the smallest individuals in the shallow habitats studied by Moyer (1979) were 70–90 mm long. It is possible, therefore, that *L. fornasini* settles in deeper environments before moving into shallow water. Juveniles of this species are commonly eaten by pelagic predatory fishes such as tunas (Moyer, 1979).

The egg and larva described by Mito (1962, 1966) as Ostraciontina 2 are probably *Lactoria fornasini*. The larvae illustrated by Mito are very similar to our specimens of *L. fornasini* in development at hatching, morphology and pigment, with the exception that Mito's larvae had a pigmented snout. Mito's (1962) Ostraciontina 1 more closely resembles *Lactoria* than *Ostracion*, but does not seem to be one of the species described here.

Sanzo (1930) reared the egg of an ostraciid from the mouth of the Red Sea, but misidentified it as a tetraodontid (only his figs. 68–72 are ostraciids). Sanzo's illustrations also more closely resemble *Lactoria* than *Ostracion*.

Lactoria diaphana
(Table 2, Fig. 5)

Diagnosis. Larvae moderately and nonuniformly pigmented, but more uniformly pigmented than *L. fornasini*; in young larvae a series of 0–5 melanophores midlaterally on tail, but no pigment extending posterior to anal fin base; snout with a distinct cluster of melanophores laterally; dermal sac unpigmented; carapace plates of dorsal midline longer and higher than other dorsal plates, forming a ridge; mouth functional at hatching.

Remarks. *L. diaphana* larvae are most readily distinguished by their limited tail pigment and heavily pigmented snout. The midlateral melanophores on the tail of most very young *L. diaphana* larvae are replaced in older larvae by scattered melanophores which do not extend posterior to the dorsal fin base. In postflexion larvae, melanophores extend onto the caudal peduncle. With growth, the cluster of melanophores on the snout becomes increasingly difficult to distinguish from the overall pigment, but *L. fornasini* larvae of similar size have very sparsely pigmented snouts.

The carapace plates of *L. diaphana* are similar to those of *L. fornasini*. However, the spines seem to begin to elongate while the notochord is flexing in *L. diaphana* (5.3 mm) and not until after flexion is complete in *L. fornasini* (>6.3 mm). In contrast, the spines of *L. cornuta* do not begin to elongate until well into the juvenile stage (>14 mm, Günther, 1910).

Lactoria diaphana attains a large size and may even reach sexual maturity and spawn prior to settlement. The presence of newly-spawned eggs and larvae of *L. diaphana* in oceanic areas of the eastern Pacific indicates the species can complete its life cycle while pelagic. In addition, we have examined a specimen of about 100 mm taken by midwater trawl in the upper 1,000 m in an area about 4,500 m deep and more than 1,200 km from shallow water in the Eastern Tropical Pacific. At Miyake-jima six newly settled individuals of this species measured 102 to 130.9 mm in length.

Discussion

The early life history characteristics of ostraciids were used by Leis (1984b) in a phylogenetic analysis of tetraodontiform fishes. A complete discussion is found in that paper, and because the characters of the eggs and larvae of the three species described here were used in the analysis, there is little to add. However, Leis (1984b) concluded that further research on tetraodontiform fishes was required, and specifically mentioned the ostraciids in this regard. The lack of any information on larvae of aracanids represents a particular gap, and until it is filled, full assessment of the relationships of the ostraciids to other tetraodontiform families will be difficult.

The great similarity of the eggs and larvae of the ostraciid species described to date (this paper and Aboussouan and Leis, 1984) indicates that early life history characters will probably shed little light on relationships within the family. However, it is possible this assessment is premature, as eggs and larvae of a number of ostraciid genera have not been described.

Information on the eggs and larvae of other tetraodontiform fishes is contained in Leis and Rennis (1983), Aboussouan and Leis (1984) and Leis (1984a).

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インド・太平洋産ハコフグ科3種 (*Ostracion meleagris*, *Lactoria fornasini* 及び *L. diaphana*) の卵，仔魚，浮遊稚魚

J. M. Leis・J. T. Moyer

ハワイ，日本，オーストラリア及び東太平洋から得られたクロハコフグ *O. meleagris*, シマウミスズメ *L. fornasini*, 及びウミスズメ *L. diaphana* の卵，仔魚，浮遊稚魚を記載する．記載は野外採集標本と飼育標本に基づくものである．卵は大型の分離浮性卵で卵膜表面一部に小突起群がある．多数の小油球が密集する．孵化時の仔魚は発育が進み，丸く肥大して被膜に包まれる．この被膜は尾部上屈開始に先立って消失し甲板が形成される．3種の仔魚は色素胞の配列や甲板の形成経過によって相互に識別し得るが，卵期には種相互の識別はできない．仔魚期終了時の体長は小さく 6 mm 以下であるが，稚魚は浮遊生活をつづけ浮遊期中に著しく成長する．ウミスズメは東太平洋では沖合で成熟し産卵する．

(Leis: オーストラリア博物館; Moyer: 100–12 東京都三宅村阿古　田中達男記念生物実験所)