# The reproductive biology and early life stages of *Podothecus sachi* (Pisces: Agonidae)*

**Hiroyuki Munehara**

*Usujiri Fisheries Laboratory, Faculty of Fisheries, Hokkaido University*
Minamikayabe-cho Usujiri 152, Hokkaido, 041-16, Japan
E-mail address: hm@f1.hines.hokudai.ac.jp

Within the agonids, 20 genera and 50 species are recognized, with most distributed from the bottom of the north Pacific Ocean to the Bering Sea (Nelson, 1984). The agonid body is covered with bony plates and is unusual among teleost fishes. Several taxonomic studies have been conducted (Jordan and Evermann, 1898; Matsubara, 1955; Kanayama, 1991); however, little ecological information on the agonids exists because of their poor commercial value and small population density. Even for the sail-fin poacher, *Podothecus sachi*, the most common of the Japanese agonids, only larvae and juveniles have been reported from the adjacent waters of northern Japan (Maeda and Amaoka, 1988). Past reports concerning the reproductive ecology of agonids have suggested that they have internal fertilization and that females produce small clutches of eggs almost daily (Iioka and Gunji, 1979; Sugimoto, 1987; Aoyama and Onodera, 1989). Recently, eggs of copulating cottids that were thought to undergo internal fertilization were shown to be fertilized by the received spermatozoa only after eggs were deposited (Munehara et al., 1989, 1991, 1994a, in press; Koya et al., 1993), i.e. there is an internal deposition of sperm that do not penetrate the ova or egg until after the latter are spawned and free in the environment. This spawning mode, named the internal gametic association (Munehara et al., 1989), is characterized by the deposition of unfertilized eggs whose paternity has been fixed before spawning (Munehara et al., 1990; 1994b). This spawning mode is so unique that it is not included in other categories of the parity mode of fishes, as determined on an evolutionary basis (Wourms et al., 1988). A comparative osteological and myological study on Scorpaeniformes indicated that the Agonidae family is most closely related to the Cottidae family (Yabe, 1985). Therefore, it is possible that the internal gametic association mode of spawning that occurs in agonid fishes may provide information concerning the relation of the two families. In this study, I report on the reproductive biology and the early life stages of *P. sachi*, comparing them with those of other agonid fishes.

## Materials and methods

Three adult females of *P. sachi* were collected with gill nets from offshore bottom waters (60–80 m depth) at Usujiri, southern Hokkaido, 7 October 1992. After the live fish had been transported to the laboratory, their ovaries were surgically removed, and ripe eggs and ovarian fluid were extracted. Great care was taken to prevent contamination by seawater, urine, and blood. The ovarian fluid was isolated with a pipette for use in the following test. To determine if egg development began before or after contact with seawater, eggs of each female were placed in separate petri dishes containing either ovarian fluid or seawater at 6°C. After 20 hours, the number of developing eggs were counted on the basis of occurrence of cleavage and formation of the blastodisc, which were regarded as signs of initial fertilization and autoactivation, respectively.

Histological observations were carried out on several eggs before exposure to seawater to determine if internal fertilization occurred. Ovaries were examined to decide their developing mode. The ovaries were fixed in Bouin's fluid. Serial paraffin sections, 5–8 μm, were prepared and stained with Delafield's hematoxylin and eosin. The criteria of the maturing oocytes followed the classification of Yamamoto (1956).

Eggs remaining from the above observations were used for morphological observation of the early life stages of this fish. The eggs not used for artificial insemination were kept in a 1-L glass dish at a mean water temperature of 5°C. No bubbling stone was placed in the dish, but half of the seawater was replaced once a week. Juveniles were fed nauplii of *Artemia salina*. Measurement and observation of embryonic development were conducted once every 1–3 days. Sampling of hatched fish was done at intervals of 1–2 weeks until 93 days after hatching. Specimens were observed under a microscope after fixation in 5% neutral formaldehyde solution. Terminology of the

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bony plates followed Gruchy (1969) and Maeda and Amaoka (1988).

## Results

### General anatomy and histology of the ovary

The paired ovary of *P. sachi* was bilobed anteriorly but fused together from the middle region; its posterior end reached beyond the genital duct, which was located at the middle of the abdominal cavity (Fig 1). The anterior part of the genital duct was retractable and could be everted by pressing the fish's belly. The protruded duct was tapered, about 2 cm length in 27.5–29.1 cm standard-length (SL) specimens (Fig. 1A). Blood vessels in the ovary ran radiately in the tunica of the dorsal side. The ovarian cavity passed through the center of the ovary and then directly faced the ovarian wall lined with epithelia near the genital duct. The genital pore opened just behind the pelvic fins. The cavity and the genital duct contained several hundred ripe eggs (Fig. 1B).

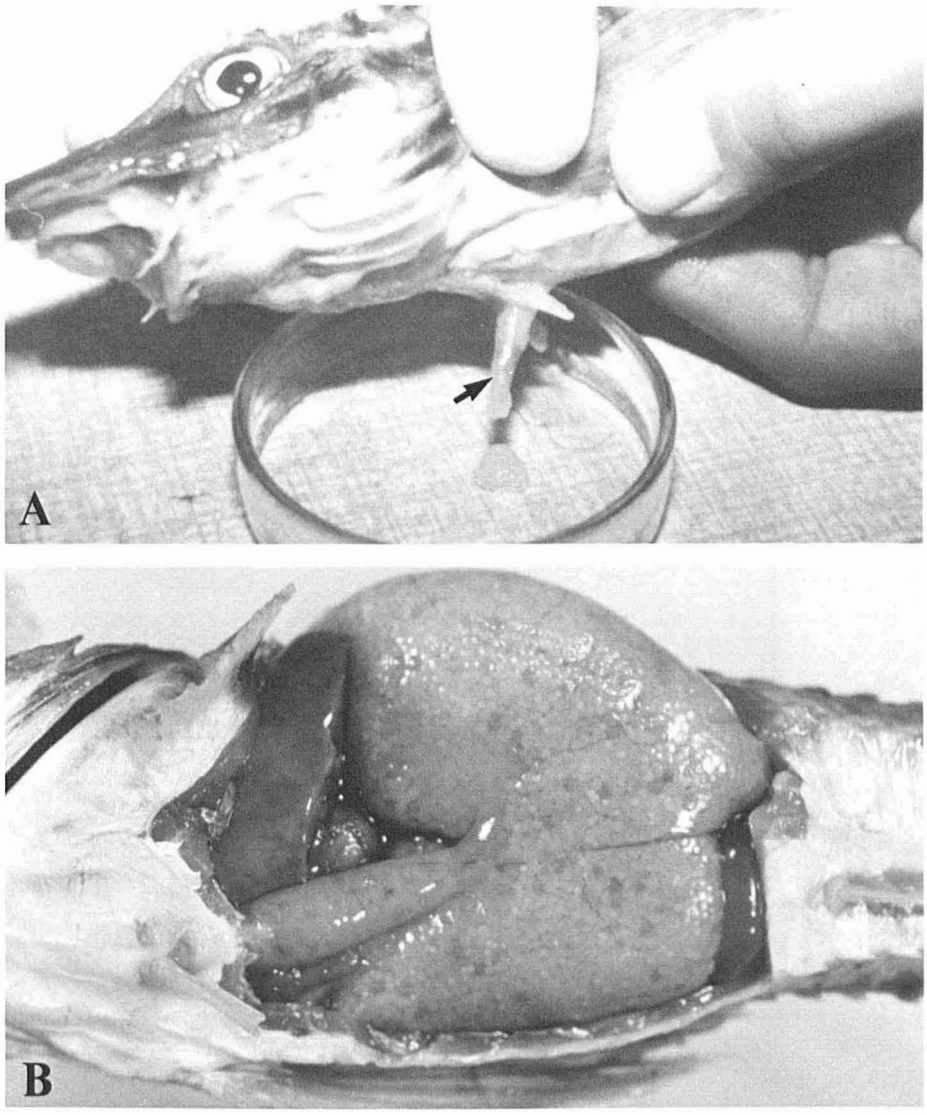


**Figure 1**

Retractable genital duct and mature ovary. (**A**) Genital duct (arrow) and eggs with ovarian fluid extracted from the top of the duct. (**B**) Ovulated eggs in the ovarian cavity and the genital duct.

Sections of the ovary contained oocytes in various developing stages, including the chromatin-nucleolus, perinucleolus, yolk-vesicle, oil-droplet, yolk-globule, migratory-nucleus, premature, and ripe stages (Fig. 2). In addition, postovulatory follicles in the stage just after ovulation or in the stage of regenerating were also found. These observations indicated that female *P. sachi* produce multiple clutches in a breeding season.

### Appearance of eggs

Eggs were demersal, adhesive, and almost spherical in shape. The mean egg size was 1.73 mm in diameter, ranging from 1.70–1.75 mm ($n$=30). The yolk was light pink, and many oil droplets and small, whitish, granular material were observed within the yolk.

### Initiation of egg development

Although the eggs from the three females were not artificially inseminated, most eggs placed in seawater had developed to the 2-cell stage after 20 hours (Table 1). In contrast, none of the eggs kept in the ovarian fluid showed any sign of development. When

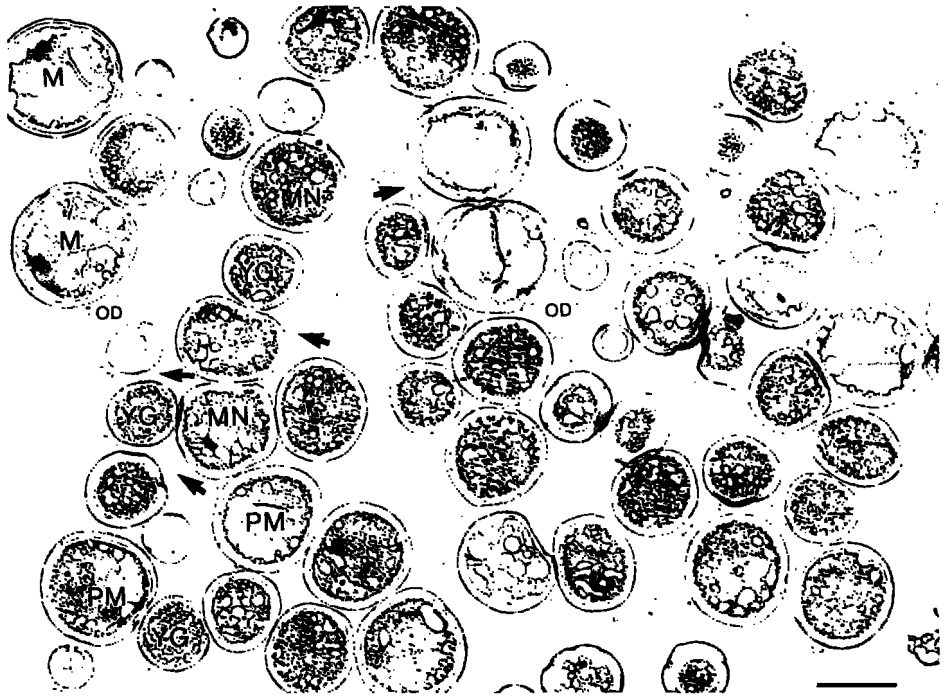


**Figure 2**

A section of mature ovary. M = mature stage oocytes, PM = premature stage oocytes, MN = migratory nucleus stage oocytes, YG = yolk globule stage oocytes, OD = oil droplet stage oocytes. Arrows indicate postovulatory follicles. Bar indicates 1mm.

**Table 1**

Embryonic development of *Podothecus sachi* eggs from 3 specimens 20 hours after immersion in seawater or ovarian fluid at 6°C.

| Rearing medium | Percent (no.) of 2-cell stage eggs | Percent (no.) of undeveloped eggs | Percent (no.) of dead eggs |
|---|---|---|---|
| Seawater | 97.5 (118) | 1.7 (2) | 0.8 (1) |
| Ovarian fluid | 0 (0) | 98.5 (133) | 1.5 (2) |
| 24 h after egg transfer from ovarian fluid to seawater | 96.3 (130) | 1.5 (2) | 2.2 (3) |
| Seawater | 95.5 (106) | 3.6 (4) | 0.9 (1) |
| Ovarian fluid | 0 (0) | 98.3 (117) | 1.7 (2) |
| 24 h after egg transfer from ovarian fluid to seawater | 95.8 (114) | 1.7 (2) | 2.5 (3) |
| Seawater | 97.2 (141) | 1.4 (2) | 1.4 (2) |
| Ovarian fluid | 0 (0) | 98.4 (124) | 1.6 (2) |
| 24 h after egg transfer from ovarian fluid to seawater | 93.7 (118) | 4.8 (6) | 1.6 (2) |

such eggs were transferred into seawater, they developed to the 2-cell stage within 24 hours. This finding indicates that egg development was initiated only after the eggs came in contact with seawater. It appeared that every female used in this study had copulated and that spermatozoa had already been transferred into the ovarian cavity.

## Histological observation of gametes before exposure to seawater

The micropyle of *P. sachi* eggs consisted of a micropylar vestibule, a funnellike depression about 100 μm across at the level of the egg surface, and a micropylar canal penetrating the approximately 90-μm

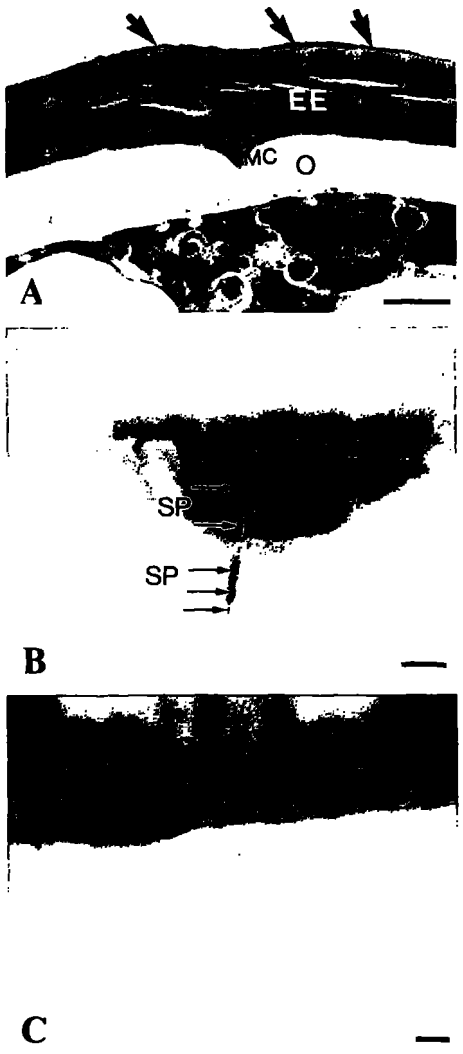


**Figure 3**

Photomicrograph of the eggs internally associated with spermatozoa. (**A**) Irregular particles (arrows) on and near the vestibule, and micropylar canal (MC). EE = egg envelope, O = ooplasm. (**B**) High magnification of micropylar cone in A. Spermatozoa (SP) have entered into micropylar canal. (**C**) Chromosomes and metaphase spindle of second meiotic division. Bars in A and B indicate 50 μm and bar in C indicates 10 μm.

thick egg envelope (Fig. 3A). The external opening of the canal was centrally located at the bottom of the vestibule. The canal was slightly tapered, and its inner opening was situated at the center of the micropylar cone. The external opening of the canal was about 5 μm in diameter. Many irregular particles stained with hematoxylin were deposited on and near the vestibule (Fig. 3A).

In eggs fixed before exposure to seawater, a number of spermatozoa were found to have entered the micropylar cone (Fig. 3B), but membrane fusion had not yet occurred. Furthermore, in the region of the ooplasm near the micropylar cone, chromosomes and a metaphase spindle of the second meiotic division were detected (Fig. 3C).

## Embryonic development

After developing to the 2-cell stage after 20 hours of immersion in seawater, eggs reached the 32-cell, morula, and blastula stages on the 1st, 5th, and 8th days, respectively (Fig. 4A). The embryo became visible on the 13th day. The early embryo was smaller than the egg size, its length approximately 1/5 of the yolk's circumference. A pair of optic vesicles and optic lenses appeared on the 16th and the 21st day, respectively. Myomeres began forming on the 22nd day (Fig. 4B). On the 29th day, the tail of the embryo began to grow free from the yolk. The heart was pulsating and the embryo was moving occasionally on the 31st day. On the 35th day, a pair of otoliths was observed and the eyes began blackening. The embryo elongated to encircle the yolk completely by the 42nd day (Fig. 4C). A pair of pectoral fins began to extend at this time. Melanophores first appeared on the abdominal membrane on the 57th day. They began forming on the side of the trunk on the 62nd day. On the 76th day, the intestine and the liver were differentiated, and blood vessels appeared along the yolk below the thoracic region of the embryo. Just before hatching, the embryo measured 1.5 times the yolk circumference, and some projections of supralateral and infralateral bony plates were observed (Fig. 4D). Hatching began on the 92nd day and ended by the 104th day.

## Larvae and juveniles

Newly hatched larvae were 6.9–7.1 mm in notochord length (NL) (Fig. 4E). Their bodies were slender, white, and pigmented on the head, trunk, and finfold. Yolks had not been completely absorbed yet, and an oil droplet remained in each yolk's anterior part. The larvae were weak swimmers and usually lay on the bottom of the tank. Most hatched 101 days after fertilization. On the 3rd day of hatching, not only supralateral and infralateral bony plates, but dorsal and ventral bony plates began to form. The larvae occasionally fed on *Artemia salina*. The urinary bladders of larvae were always swollen with transparent liquid. On the 14th day, the yolk was completely absorbed; a 7.4-mm-NL specimen had melanophores on the lateral sides of the abdomen and two pairs of fronto-

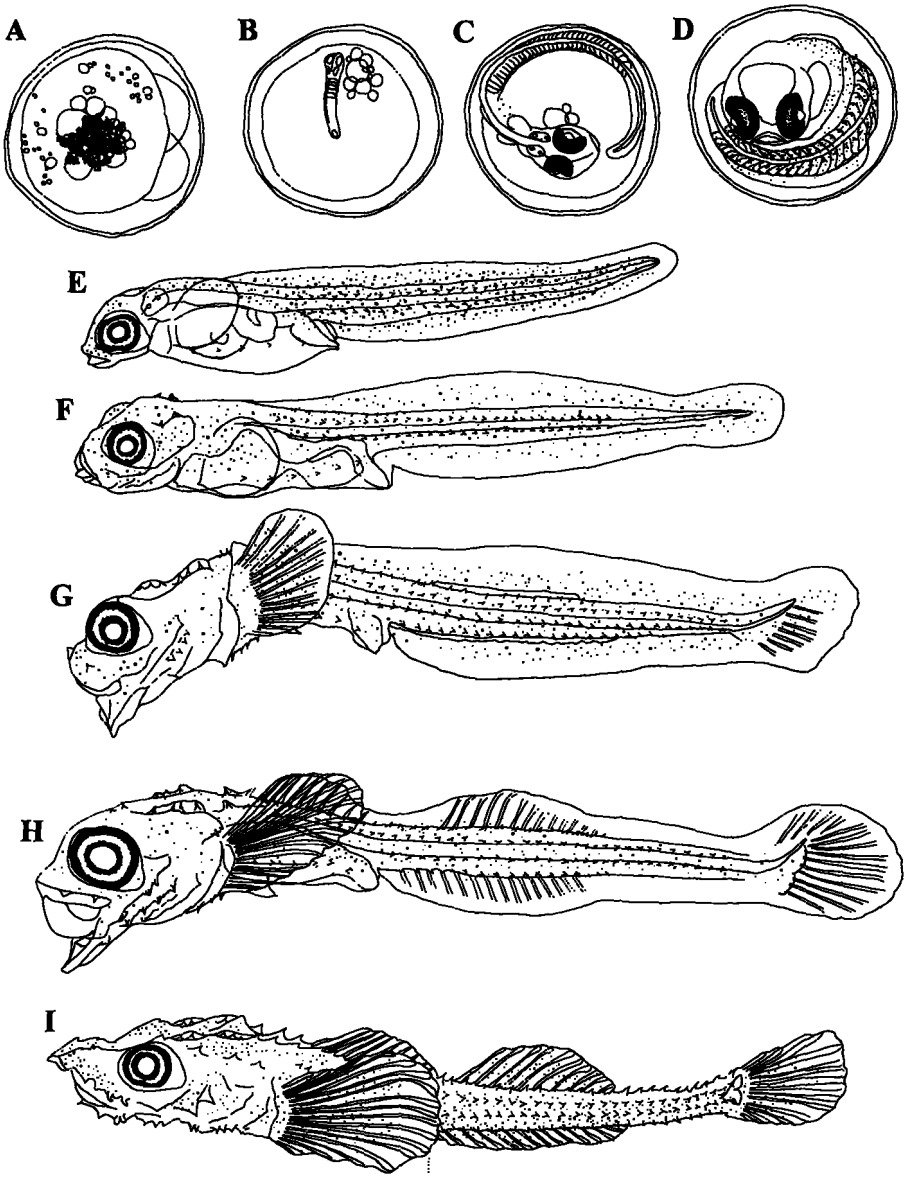


**Figure 4**

Eggs, larvae and juveniles of *Podothecus sachi* kept at 5°C. (**A**) 2-cell stage, 20 hours after immersion in seawater. (**B**) Formation of optic lenses, auditory vesicles, Kupffer's vesicle, and myomeres, 22 days after immersion in seawater. (**C**) Embryo almost in full circle, 42 days after immersion in seawater. (**D**) Just before hatching, 92 days after immersion in seawater. (**E**) Newly hatched larva 7.0 mm in notochord length (NL), 92 days after immersion in seawater. (**F**) 7.4-mm-NL larva, 14 days after hatching. (**G**) 7.7-mm-NL larva, 28 days after hatching. (**H**) Juvenile 8.7 mm in standard length (SL), 42 days after hatching. (**I**) Juvenile 15.6 mm in SL, 60 days after hatching. Dashed vertical line indicates the position of genital duct's opening.

parietal ridges with one spinule (Fig. 4F). The pectoral fins began to enlarge, and the larvae spent more time swimming near the surface than lying on the bottom. A 7.7-mm-NL specimen observed on the 28th day had 14 rays in its pectoral fins, melanophores on the ventral sides of the abdomen, and both jaws protruded slightly (Fig. 4G); four spines on preopercular and 2–4 spinules on each frontoparietal ridge were found. Another specimen measuring 8.3 mm NL on the 28th day was found to be in flexion; the larva

had 13, 16, and 15 rays in its dorsal, anal, and pectoral fins, respectively. On the 42nd day, a specimen measuring 8.7 mm SL had 10 spines and 13 rays on its dorsal fin and 15 and 16 rays on its anal and pectoral fins, respectively, forming a full complement (Fig. 4H). The pelvic fins were still buds. The opening position of the anal and the genital pore began moving from just anterior to the anal fin toward the base of the pelvic fins. Whiskers, a mustache, and pelvic fins first appeared in a 15.6-mm-SL specimen on the 60th day (Fig. 4I) and were completely formed in a 24.6-mm-SL specimen on the 93rd day. Juvenile *P. sachi* almost corresponded to adults in morphological features, but movement of the anal and genital pore openings were only half finished. The 24.6-mm specimen swam, using its elongated pectoral fins, but never used its posterior trunk for propulsion owing to hardened bony plates.

## Discussion

### Internal gametic association and external fertilization

As noted, *P. sachi* eggs placed in seawater and without artificial insemination began to develop and grow to juveniles, whereas eggs maintained in ovarian fluid showed no signs of development. In addition, histological observations of eggs directly obtained from the ovary showed that spermatozoa had entered the micropyle before contact with seawater, indicating that fertilization was not initiated in the ovarian fluid. This observation demonstrates that the spawning mode of *P. sachi* is of the internal gametic association type, reported in previous studies of copulating cottids (Munehara et al., 1989, 1991, 1994a; Koya et al., 1993). Atlantic wolffish, *Anarichas lupus* (Perciformes, Anarhichadidae), is also known to undergo copulation before egg laying, but the spawning mode of this fish is not comparable to that of *P. sachi* because inseminated eggs of Atlantic wolffish develop internally (Pavlov, 1994). This information seems to support Yabe's hypothesis (1985), based on comparative osteological and myological observations, that the family Agonidae may be the most closely related family to the Cottidae.

### Early life history

Many larvae and juveniles, 8.3–25.1 mm SL, have been collected by plankton nets (Maeda and Amaoka, 1988). In the present study, the largest specimen took 93 days to grow to 24.6 mm SL after hatching. Thus, *P. sachi* probably inhabits the pelagic ocean during its first three months. It seems reasonable that whiskers and mustache, which function as sensory organs for detection of benthic prey (Sato, 1977), are completed before juveniles become benthic.

### Reproductive style of agonid species

Information on the reproduction of agonids is available for only 6 of 50 species (Table 2). Many common characteristics are recognized among these species.

First, the reproductive behavior of the Agonidae involves copulation. All the agonid species whose reproductive styles are known (*Agonomalus proboscidalis*, *Occella iburia*, and *Bracdyopsis rostratus*) have been described as internally fertilizing species on the basis of the development of eggs deposited without male involvement (Iioka and Gunji, 1979; Sugimoto, 1987; Aoyama and Onodera, 1989). These agonids probably exhibit external fertilization with internal insemination, as does *P. sachi*, because *B. rostratus* has been determined to be of the internal gametic association type from the same investigations done for *P. sachi*, and information on internal fertilization of the agonids was proposed prior to the first recognition of the internal gametic association in teleost fishes (Munehara et al., 1989).

A second characteristic of the reproductive style is that agonids have a long embryonic period, ranging from 100 days to 1 year. In addition to the Agonidae, such extraordinarily long embryonic periods in teleost fishes are known for only a few trichodontids and cottid species (Okiyama, 1990; Munehara and Shimazaki, 1991).

The third and fourth characteristics are egg deposition in concealed sites and lack of parental care. Naturally deposited egg masses of *Agonus cataphractus* were collected from the roots of kelp (Breder and Rosen, 1966). Spawning of captive *Agonomalus mozinoi* and *A. proboscidalis* was performed by concealing eggs in the exoskeletons of invertebrates or between rocks (Marliave, 1978; Aoyama and Onodera, 1989). Egg masses of *B. rostratus* were found deposited on the bottom of a tank, but the spawner was kept in a bare tank with no suitable substrate (Sugimoto, 1987). It is still unknown where *P. sachi* spawns its eggs. However, it is probable that the spawning of this fish involves brood hiding and lack of parental care because this species has a retractable genital duct and a long incubating period, similar to other copulating cottids that deposit their eggs into sponges, polychaete tube colonies, and narrow fissures (Gomelyuk and Markevich, 1986; Munehara, 1991, 1992, 1996). Deposition of egg masses on such spawning substrates limits predation on the eggs. In addition, flagellar movements of

**Table 2**

Comparison of reproductive characteristics in some agonid fishes.

| Species name | Spawning mode | Embryonic period and egg diameter | Spawning substrate | Parental care | Spawning system | References |
|---|---|---|---|---|---|---|
| *Agonomalus mozinoi* | unknown | unknown<br>1 mm | barnacle, tube worm[2] | without | remarkable iteroparity of small clutches | Marliave, 1978 |
| *A. probosciadalis* | internal fertlization[1] | 110–114 days<br>2.05–2.30 mm | between rocks and sand on bottom | without | remarkable iteroparity of small clutches | Iioka and Gunji, 1979<br>Aoyama and Onodera, 1989 |
| *Agonus cataphractus* | unknown | 1 year<br>1.76–2.23 mm | on roots of kelp | unknown | remarkable iteroparity of small clutches | Eherenbaum, 1936 in Breder and Rosen, 1966 |
| *Bracdyopsis rostaratus* | internal gametic association[1] | 287–324 days<br>2.1 mm | on bottom[2] | without | remarkable iteroparity of small clutches | Sugimoto, 1987; this study |
| *Ocella iburia* | internal fertilization[1] | unknown<br>unknown | unknown | unknown | unknown | Sugimoto, 1987 |
| *Podothecus sachi*[1] | internal gametic association[1] | 92–104 days<br>1.70–1.75 mm | unknown | unknown | remarkable iteroparity of small clutches | this study |

[1] The studies had been reported before publication of internal gametic association (Munehara et al., 1989).
[2] The findings were observed in aquaria.

host invertebrates, for aspiration and filtration, incidentally supply oxygen to eggs deposited inside or on the invertebrates (Munehara, 1991). The protracted period of incubation may have promoted egg deposition in any safe cradle for embryos rather than parental care.

Multiple clutches are produced by agonid species during a breeding season, as demonstrated by histological observation of the ovary of *P. sachi*; moreover, observations of *A. mozinoi*, *A. proboscidalis*, and *B. ostratus* indicate that females spawn small clutches almost daily in aquaria (Marliave, 1978; Iioka and Gunji, 1979; Sugimoto, 1987; Aoyama and Onodera, 1989). The fifth characteristic is the remarkable iteroparity of small clutches, which may have evolved in association with the laying of eggs, both into narrow spaces and without male involvement.

In summary, it is suggested that five common characteristics, i.e. copulation, a protracted period of incubation, concealment of deposited eggs, lack of parental care, and remarkable iteroparity of the reproductive ecology of agonids have been closely correlated with each other through evolutionary construction of their distinctive reproductive style. Copulation enabling impregnated females to spawn eggs without subsequent involvement of male fish seems to be a principal element of these characteristics.

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## Literature cited

**Aoyama, S., and H. Onodera.**
**1989.** Breeding habits, larvae, and juveniles of the agonid fish, *Agonomalus proboscidalis* in captivity. J. Jpn. Assoc. of Zoological garden and Aquarium 31:14–20. [In Japanese.]

**Breder, C. M., and C. E. Rosen.**
**1966.** Modes of reproduction in fishes. The American Museum of Natural History, New York, NY, 941 p.

**Gomelyuk, V. E., and A. I. Markevich.**
**1986.** On the strength of the egg case of the sea raven, *Hemitripterus villosus* (Cottidae). J. Ichthyol. 26:148–150.

**Gruchy, C. G.**
**1969.** Canadian records of the warty poacher *Occa verrucosa*, with notes on the standardization of plate terminology in Agonidae. J. Fish. Res. Board Can. 26:1467–1472.

**Iioka, M., and Y. Gunji.**
**1979.** Breeding of *Agonomalus proboscidalis* in the aquarium. J. Japan. Assoc. of Zoological Garden and Aquarium 21:21–25. [In Japanese.]

**Jordan, D. S., and B. W. Evermann.**
**1898.** The fishes of North and Middle America: a descriptive catalogue of the species of fishlike vertebrates found in the waters of North America, north of the Isthmus of Panama. Part II. Bull. U.S. Nat. Mus. 47:1241–2183.

**Kanayama, T.**
**1991.** Taxonomy and phylogeny of the family Agonidae (Pisces: Scorpaeniformes). Mem. Fac. Fish. Hokkaido Univ. 38:1–199.

**Koya, Y., K. Takano, and H. Takahashi.**
**1993.** Ultrastructural observations on sperm penetration in the egg of elkhorn sculpin, *Alcichthys alcicornis*, showing internal gametic association. Zool. Sci. (Tokyo) 10:93–101.

**Maeda, K., and K. Amaoka.**
**1988.** Taxoo+mic study on larvae and juveniles of agonid fishes in Japan. Mem. Fac. Fish. Hokkaido Univ. 35:47–124.

**Marliave, J. B.**
**1978.** Spawning and yolk-sac larvae of the agonid fish species, *Agonomalus mozinoi* Wilimovsky and Wilson. Syesis 11:285–286.

**Matsubara, K.**
**1955.** Fish morphology and hierarchy. Part II. Ishizaki-shoten, Tokyo, 1605 p. [In Japanese.]

**Munehara, H.**
**1991.** Utilization and ecological benefits of a sponge as a spawning bed by the little dragon sculpin *Blepsias cirrhosus*. Jpn. J. Ichthyol. 38:179–184.
**1992.** Utilization of polychaete tubes as spawning substrate by the sea raven *Hemitripterus villosus* (Scorpaeniformes). Environ. Biol. Fish. 33:395–398.
**1996.** Sperm transfer during copulation in the marine sculpin *Hemitripterus villosus* (Pisces: Scorpaeniformes) by means of a retractable genital duct and ovarian secretion in females. Copeia 1996:452–454.

**Munehara, H., and K. Shimazaki.**
**1991.** Embryonic development and newly hatched larvae of the little dragon sculpin *Blepsias cirrhosus*. Jpn. J. Ichthyol. 38:31–34.

**Munehara, H., Y. Koya, and K. Takano.**
**1991.** The little dragon sculpin *Blepsias cirrhosus*, another case of internal gametic association and external fertilization. Jpn. J. Ichthyol. 37:391–394.
**1994a.** Conditions for initiation of fertilization of eggs in the copulating elkhorn sculpin. J. Fish Biol. 45:1105–1111.

**Munehara, H., A. Takenaka, and O. Takenaka.**
**1994b.** Alloparental care in the marine sculpin *Alcichthys alcicornis* (Pisces: Cottidae): copulating in conjunction with paternal care. J. Ethol. 12:115–120.

**Munehara, H., H. Okamoto, and K. Shimazaki.**
**1990.** Paternity estimated by isozyme variation in the marine sculpin *Alcichthys alcicornis* (Pisces: Cottidae) exhibiting copulation and paternal care. J. Ethol. 8(1):21–24.

**Munehara, H., K. Takano, and Y. Koya.**
**1989.** Internal gametic association and external fertilization in the elkhorn sculpin, *Alcichthys alcicornis*. Copeia 1989:673–678.

**Munehara, H., Y. Koya, Y. Hayakawa, and K. Takano.**
**In press.** Extracellular environments for the initiation of external fertilization and micropylar plug formation in a cottid species, *Hemitripterus villosus* (Pallas) (Scorpaeniformes) with internal insemination. J. Exp. Mar. Biol. Ecol.

**Nelson, J. S.**
**1984.** Fishes of the world, 2nd ed. John Wiley and Sons, Inc., New York, NY, 475 p.

**Okiyama, M.**
**1990.** Contrast in reproductive style between two species of sandfishes (family Trichodontidae). Fish. Bull. 88:543–549.

**Pavlov, D. A.**
**1994.** Fertilization in the wolffish, *Anarhichas lupus*: external or internal? J. Ichthyol. 34:140–151.

**Sato, M.**
**1977.** Histology of barbels of *Blepsias cirrhosus draciscus* (Cottidae). Jpn. J. Ichthyol. 23:220–224.

**Sugimoto, T.**
**1987.** Embryonic development, larvae and juveniles of the longsnout poacher *Bracdyopsis rostratus*. Marine Snow 6:1–2. [In Japanese.]

**Wourms, J. P., B. D. Grove, and J. Lombaridi.**
**1988.** The maternal-embryonic relationship in viviparous fishes. *In* B. W. S. Hoar and D. J. Randall (eds.), Fish physiology XI, p.1–134. Academic Press, Inc., London.

**Yabe, M.**
**1985.** Comparative osteology and myology of the superfamily cottoidea (Pisces: Scorpaeniformes), and its phylogenetic classification. Mem. Fac. Fish. Hokkaido Univ. 32:1–130.

**Yamamoto, K.**
**1956.** Studies on the formation of fish eggs. I, annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. J. Fac. Sci. Hokkaido Univ. Ser. VI Zool. 12:362–373.