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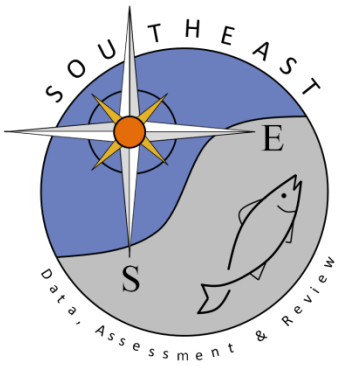

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Simplicity and diversity in the reproductive ecology of triggerfish (Balistidae) and filefish (Monacanthidae)

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SUMMARY: Reproductive ecology of 14 balistoid species (Balistidae and Monacanthidae) was reviewed. There are many common features in the reproductive ecology of the balistid fish: males establish territories; males and females mate in pairs on the sandy bottom; the pairs release gametes in a few seconds; eggs are small in size and a clutch contains large number of eggs; spawning occurs in the morning and embryos hatch after sunset of the day; females tend and guard the eggs at least. Primitive monacanthid species show the same features of the balistids, however, reproductive ecology of the monacanthids is diverse. The evolution of reproductive ecology of the balistoids was discussed referring to the phylogenetic relationships.

KEY WORDS: **spawning behavior, parental egg-care, mating system, territoriality, evolution**

INTRODUCTION

Knowledge of reproductive behavior of reef fish has been accumulated in the past thirty years.[1-3] Many of the studies were focused on the reproductive strategy of fish such as parental egg care, mating system, mate choice and sex change. For example, sex change has been well studied in the labrid and gobiid fishes. Warner[4] theoretically explained the phenomenon with size-advantage model. Kuwamura and Nakashima[5] reported the other two factors, growth-rate advantage and mortality-advantage, to expand the model.

On the other hand, few comparative, evolutionary studies of reproductive behavior of fish have been done. The use of behavioral patterns in resolving phylogenetic relationships between species is increasing in importance, as the phylogenetic methods enable to trace the evolution of behaviors in related taxa.[6, 7] However, data for phylogenetic analysis are not enough in most groups at present.

Balistidae and Monacanthidae are closely related families included in the superfamily Balistoidea in Tetraodontiformes.[8] Approximately 40 species are known in 12 genera in Balistidae and 100 species are known in 21 genera in Monacanthidae.[9] Fricke[10] reported parental care and mating system of the two balistid species, *Pseudobalistes fuscus* and *Odonus niger*, based on field observations. Barlow[11] reported a monogamous filefish, *Oxymonacanthus longirostris*. In the past ten years, studies on both families increased and knowledge on reproductive ecology has accumulated.[12]

In this paper, I review the reproductive ecology of the balistid and monacanthid fish. Spawning behavior, parental egg care and mating system are compared among and between the two families. Furthermore, I discuss the evolution of reproductive ecology of the balistoid fish.

REVIEWED SPECIES

I review reproductive ecology of 8 species in 5 genera in Balistidae, *Odonus niger*,[10] *Pseudobalistes flavimarginatus*,[13] *P. fuscus*,[10] *Xanthichthys mento*,[14] *Sufflamen chrysopterus*,[15, 16] *S. fraenatus*,[12, 17] *S. verres*,[1] *Rhinecanthus aculeatus*,[18] and 6 species in 6 genera in Monacanthidae, *Stephanolepis cirrhifer*,[19] *Paramonacanthus japonicus*,[20] *Cantherhines pardalis*,[21] *Rudarius ercodes*[22-24] *Oxymonacanthus longirostris*,[11,25-27] *Brachaluteres ulvarum*.[28] Most of the studies are based on underwater observations although results of aquarium observations are included. Citation of literature was omitted as a rule in the following descriptions when features of ecology common among the 14 species were described.

SIMPLICITY IN BALISTIDAE

Spawning and eggs in Balistidae

Spawning behavior of the balistid fish is simple (Table 1). Spawning always occurs in a pair of male and female. No sneaking or group spawning has been reported. The pair touches abdomens and release gametes in a few seconds. Spawning site is usually sandy bottom or sandy reef. Time of spawning is restricted to early in the morning although that of *X. mento* is not fixed.[14]

The balistid females release 55,500-430,000 eggs in a spawning. Eggs are spherical in shape, measuring 0.47-0.55 mm in diameter. They are demersal and adhesive, released eggs being attached to sand particles. Eggs of *O. niger* and *X. mento* are scattered on the bottom and mixed

Table 1 Comparison of the spawning ecology and eggs in the balistid and monacanthid fish

	Balistidae	Monacanthidae
Spawning style	pair	pair, group
Time to release eggs (sec)	2-3	2-3*1
Time of spawning	early morning*2	not fixed
Time of hatching	after sunset	after sunset
Day of hatching	spawning day*3	1-7 days after
Condition of eggs	scattered, mass	scattered, mass
Nature of eggs	demersal, adhesive	demersal, adhesive
Spawning substratum	sandy bottom	various
Mean egg number	55,500-430,000	160-17,500
Mean egg diameter (mm)	0.47-0.55	0.53-0.82

*1 *Brachaluteres ulvarum* females release eggs in 20 - 30 seconds. *2 Spawning time of *Xanthichthys mento* is not fixed. *3 Eggs of *X. mento* hatch on the next day of spawning.

with sand[10, 14] while those of the others are deposited in a mass. Eggs are cared for by parent(s) and the eggs hatch in the evening on the day although that of *X. mento* hatch on the next day of spawning.[14]

Parental egg-care in Balistidae

Maternal and biparental egg-care is reported in the balistid fish (Fig. 1). Parental egg-care consists of egg-tending and egg-guarding.[22] It is common in all the 8 species that females tend eggs by fanning and blowing water on them and guard the eggs by driving away intruding fish, and that males never tend the eggs. The difference of parental egg-care comes from whether males guard the eggs. Male *O. niger*, *P. flavimarginatus* and *X. mento* guard the eggs, resulting in biparental egg-care.[10, 13, 14] The other males do not guard the eggs, resulting in maternal egg-care.

Territoriality and mating system in Balistidae

It is common in the balistid males to establish a territory (Fig. 1). *P. flavimarginatus* and *X. mento* males temporarily establish a territory for spawning and parental egg-care, but not for feeding.[13, 14] The other balistid males establish a permanent territory for both spawning and feeding. *R. aculeatus* male remained in the same territory for 8 years.[18]

On the other hand, not all females establish a territory (Fig. 1). *P. flavimarginatus* and *X. mento* females visit male's territory to mate[13, 14], *O. niger* females reside in male's territory without establishing territories.[10] The other balistid females reside in male's territory and each of the females establishes smaller exclusive territories to the other resident females.

Mating system is male-territory-visiting (MTV) polygamy[29] in *P. flavimarginatus* and *X. mento*,[13, 14] non-territorial-female (NTF) polygyny[12] in *O. niger*[10] and territorial-female (TF) polygyny[12] in the other balistids (Fig. 1). However, territoriality and mating system may change with some ecological factors and regions as reported in *P. fuscus*.[10, 13]

DIVERCITY IN MONACANTHIDAE

Spawning and eggs in Monacanthidae

Spawning behavior is diverse in the monacanthid fish

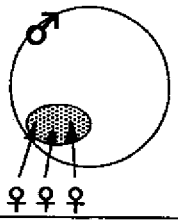
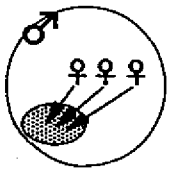
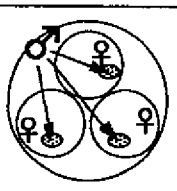
	Territoriality and spawning site	Mating system	Egg tending ♂	Egg tending ♀	Egg guarding ♂	Egg guarding ♀	Parental care
Pseudobalistes flavimarginatus *Xanthichthys mento*		MTV polygamy	no	yes	yes	yes	biparental
Odonus niger		NTF polygyny	no	yes	yes	yes	biparental
Pseudobalistes fuscus *Sufflamen chrysopterus* *S. fraenatus* *S. verres* *Rhinecanthus aculeatus*		TF polygyny	no	yes	no	yes	maternal

Fig. 1 Comparison of territoriality, mating system and parental egg-care in the balistid fish.

(Table 1). Spawning occurs in a heterosexual pair though group spawning with one female and multiple males is also observed.[22, 23, 30] Gametes are released in a few seconds although it takes 20-30 seconds in female *B. ulvarum*.[28] Spawning substratum is sandy bottom in *S. cirrhifer* and *P. japonicus*,[19, 20] algae in *C. pardalis*, *R. ercodes* and *O. longirostris*,[11, 21-25] and calcareous sponges in *B. ulvarum*.[28] Time of spawning is restricted in the morning in *S. cirrhifer* and *R. ercodes*[19, 22, 23] while this changes according to the water temperatures in *O. longirostris*.[27]

The monacanthid females release 160-17,500 eggs in a spawning. Eggs are demersal and adhesive, measuring 0.53-0.82 mm in diameter. Eggs are deposited in a mass or scattered on the substrata.

Parental egg-care in Monacanthidae

Parental egg-care is diverse in the monacanthid fish. *S. cirrhifer* female exhibits egg-care, however, it is restricted to a few minutes after spawning and no further parental care is observed.[19] Both male and female *P. japonicus* show egg guarding and tending until hatching for 2-3 days. They care for multiple clutches on separate sites when spawning occurs over successive days.[20] Maternal egg-care is common in *R. ercodes*.[20] Biparental egg-care is also observed when a parental male also guards the eggs around the clutch. Rarely, paternal egg-care is observed when the male takes the female's position.[22] No parental egg-care is observed in the other three monacanthids.

Territoriality and mating system in Monacanthidae

Territoriality and mating systems of the monacanthids differ among species. An *S. cirrhifer* male establishes a territory, in which 1-4 resident females establish smaller territories. Furthermore, non-resident females visit male's territory for spawning. Thus, the territorial male mates with both types of females, mating system being TF polygyny and MTV polygamy in a single population.[19] On the other hand, there is one resident female in *P. japonicus* and *O. longirostris* male territory; the mating system is monogamy.[20] *R. ercodes* males establish no territories. Dominant males pair with specific females, but mating does not always occur between the pair; the mating system is promiscuity.[22]

EVOLUTION OF REPRODUCTIVE BEHAVIOR

Phylogenetically, Tetraodontiformes is divided into three sub-order of Triacanthoidei, Tetraodontoidei and Balistoidei. Triacanthoidei is the most primitive, and Tetraodontoidei and Balistoidei have derived from the common ancestor of Triacanthoidei. Balistoidei consists of super-family Ostracioidea (Aracanidae and Ostraciidae) and Balistoidea (Balistidae and Monacanthidae).[31, 32] Phylogenetic analysis of the Balistoidea based on anatomical characters clearly revealed that the characters are various in the Monacanthidae while they are very simple in the Balistidae. Furthermore, the monacanthids are more specialized than the balistids and the monacanthids were derived from the balistids or, at least a balistid-like ancestor.[8] Here, I refer to the phylogenetic relationship and discuss the behavioral evolution of the balistoid fish.

Evolution of spawning

Eggs of the balistid fish are deposited on the sandy bottom and attached to sand particles. This is also common to the phylogenetically primitive species of *S. cirrhifer* and *P. japonicus*, while derived species utilize various objects as spawning substrata (Table 1). It seems that the primitive spawning substratum of the balistoid fish is sandy bottom. Substratum requirments have broadened in derived balistids while various additional substrata are used by monacanthids.

Spawning patterns and features of eggs of balistids have some common aspects with those of pelagic-egg spawning fish: gamates are released in a few seconds; eggs are small in diameters; embryonic development goes fast and eggs hatch within a day (Table 1). Furthermore, pelagic-egg spawning species are reported in Triacanthidae which is included in the most primitive group in Tetraodontiformes and Ostraciidae which is a family related to the Balistidae.[33, 34] The phylogenetic relationship and spawning patterns suggest that the balistids may be derived from the ancestor of pelagic-egg spawning fish.

Evolution of parental egg-care and mating system

The different mating systems and patterns of parental care among the balistids appear to be related to the distribution of food and breeding sites: those two are available in TF polygyny mating system with maternal care although the former is limited or separated from the latter in the other two systems with biparental care.[18] If egg-tending (fanning) is essential for egg development and survival in the balistids, evolutionary transitions have been from no care to maternal care instead of paternal care because one parent alone may not be able to allocate enough time to fanning each of the multiple clutches.[18] However, egg-tending dose not seem to be essential for species such as *X. mento* because most of the eggs hatch normally with much less frequent female tending.[14] In this case, there is another possibility in the evolution of parental care: paternal care with egg-guarding has evolved first and then biparental care with additional egg-guarding and tending by females has evolved.

Features of the mating system and parental care are common across balistid fish: males establish territories and mate with female(s) there; at least, female(s) care for the eggs. This pattern is also common in the primitive monacanthid species however, mating systems and parental care are much more diverse in this family and the evolutionary pathways are unknown. Further knowledge is needed to discuss the evolution of mating systems and parental care of the balistoid fish.

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REFERENCES

1. Thresher RE. Reproduction in reef fishes. T. F. H. Publications, New Jersey. 1984.
2. Kuwamura T, Nakashima Y. Reproductive strategies in fishes vol. 1. Kaiyusha Publishers Co. Ltd. Tokyo, 1996 (in Japanese).
3. Kuwamura T, Nakashima Y. Reproductive strategies in fishes vol. 2. Kaiyusha Publishers Co. Ltd. Tokyo, 1997 (in Japanese).
4. Warner RR, Robertson DR, Leigh EG. Sex change and sexual selection. *Science* 1975; **190**: 633-638.
5. Kuwamura T, Nakashima Y, Yogo Y. Sex change in either direction by growth-rate advantage in the monogamous coral goby, *Paragobiodon echinocephalus*. *Behav. Ecol.* 1994; **5**: 434-438.
6. Brooks DR, McLennan DA. Phylogeny, ecology, and behavior. The University of Chicago Press, Chicago, 1991.
7. Donaldson TJ. Courtship and spawning behavior of the pygmy grouper, *Cephalopholis spiloparaea* (Serranidae: Epinephelinae), with notes on *C. argus* and *C. urodeta*. *Env. Biol. Fish.* 1995; **43**: 363-370.
8. Matsuura K. Phylogeny of the superfamily Balistoidea (Pisces: Tetraodontiformes). *Mem. Fac. Fish. Hokkaido Univ.* 1979; **26**: 49-169.
9. Nelson JS. Fishes of the world. John Wiley & Sons Inc, New York. 1994.
10. Fricke HW. Mating systems, maternal and biparental care in triggerfish (Balistidae). *Z. Tierpsychol.* 1980; **53**: 105-122.
11. Barlow GW. Spawning, eggs and larvae of the longnose filefish *Oxymonacanthus longirostris*, a monogamous coralivore. *Env. Biol. Fish.* 1987; **20**: 183-194.
12. Kawase H. Reproductive behavior and evolution of triggerfish (Balistidae) and filefish (Monacanthidae). *Japan. J. Ichthyol.* 1998; **45**: 1-19 (in Japanese).
13. Gladstone W. Lek-like spawning, parental care and mating periodicity of the triggerfish *Pseudobalistes flavimarginatus* (Balistidae). *Env. Biol. Fish.* 1994; **39**: 249-257.
14. Kawase H. Spawning behavior and biparental egg care of the crosshatch triggerfish, *Xanthichthys mento* (Balistidae). (in prep.)
15. Kawase H, Nakazono A. Reproductive behavior of the flagtail triggerfish, *Sufflamen chrysopterus*. *Proc. 7th Int. Coral Reef Symp., Guam* 1994: 905-907.
16. Ishihara M, Kuwamura T. Bigamy or monogamy with maternal egg care in the triggerfish, *Sufflamen chrysopterus*. *Ichthyol. Res.* 1996; **43**: 307-313.
17. Kawabe R. Spawning behavior of the bridled triggerfish, *Sufflamen fraenatus*, in the aquarium. *Japan. J. Ichthyol.* 1984; **31**: 193-197 (in Japanese with English abstract).
18. Kuwamura T. Evolution of female egg care in haremic triggerfish, *Rhinecanthus aculeatus*. *Ethology* 1997; **103**: 1015-1023.
19. Kawase H, Nakazono A. Two alternative female tactics in the polygynous mating system of the threadsail filefish, *Stephanolepis cirrhifer* (Monacanthidae). *Ichthyol. Res.* 1996; **43**: 315-323.
20. Nakazono A, Kawase H. Spawning and biparental egg-care in a temperate filefish, *Paramonacanthus japonicus* (Monacanthidae). *Env. Biol. Fish.* 1993; **37**: 245-256.
21. Kawase H, Nakazono A. Reproductive behavior of the honeycomb leatherjacket, *Cantherhines pardalis* (Monacanthidae), at Kashiwajima, Japan. *Japan. J. Ichthyol.* 1994; **41**: 80-83.
22. Kawase H, Nakazono A. Predominant maternal egg care and promiscuous mating system in the Japanese filefish, *Rudarius ercodes* (Monacanthidae). *Env. Biol. Fish.* 1995; **43**: 241-254.
23. Akagawa I, Okiyama M. Reproductive behavior of the filefish *Rudarius ercodes*: male spawning parades and female choice. *Env. Biol. Fish.* 1995; **43**: 51-62.
24. Akagawa I, Okiyama M. Reproductive and feeding ecology of *Rudarius ercodes* in different environments. *Ichthyol. Res.* 1997; **44**: 82-88.
25. Kokita T, Nakazono A. Plasticity in the mating system of the longnose filefish, *Oxymonacanthus longirostris*, in retation to male availability. *J. Ethol.* 1998; **16**: 81-89.
26. Kokita T, Nakazono A. Pair territoriality in the longnose filefish, *Oxymonacanthus longirostris*. *Ichthyol. Res.* 1999; **46**: 297-302.
27. Kokita T, Nakazono A. Seasonal variation in the diel spawning time of the coral reef fish *Oxymonacanthus longirostris* (Monacanthidae): parental control of progeny development. *Mar. Ecol. Prog. Ser.* 2000; **199**: 263-270.
28. Akagawa I, Tsukamoto Y, Okiyama M. Sexual dimorphism and pair spawning into a sponge by the filefish, *Brachaluteres ulvarum*, with a description of the eggs and larvae. *Japan. J. Ichthyol.* 1995; **41**: 397-497.
29. Kuwamura T. An introduction to reproductive strategies of fishes. In: Kuwamura T, Nakashima Y (eds), *Reproductive strategies in fishes vol 1*. Kaiyusha Publishers Co. Ltd., Tokyo. 1996; 1-41 (in Japanese).
30. Kitada T, Yoshida N, Imura N, Yoshida M. Spawning behavior of Unicorn Filefish, *Aluterus monoceros* (Linnaeus) in rearing tank. *Bull. Nagasaki Pref. Inst. Fish.* 1985; **11**: 25-27 (in Japanese).
31. Tyler JC, Sorbini L. New superfamily and three new families of tetraodontiform fishes from the Upper Cretaceous: The earliest and most morphologically primitive plectognaths. *Smithsonian Contr. Paleobiol.* 1996; **82**: 1-59.
32. Winterbottom R. The familial phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as evidenced by their comparative myology. *Smithsonian Contr. Zool.* 1974; **155**: 1-201.
33. Moyer JT. Mating strategies and reproductive behavior of Ostraciid fishes at Miyake-jima, Japan. *Japan. J. Ichthyol.* 1979; **26**: 148-160.
34. Suzuki K, Hioki S, Kitazawa H. Spawning behabior and life history of *Triacanthus brevirostris* (Tetraodontiformes). *J. Fac. Mar. Sci. Technol. Tokai Univ.* 1983; **17**: 131-138 (in Japanese with English abstract).