Acta Oceanologica Sinica 2007, Vol. 26, No. 4, p. 1 ~ 10
http://www.oceanpress.com.cn
E - mail: hyxbe@263.net

Reproductive ecology of the mudskipper *Boleophthalmus pectinirostris*

HONG Wanshu[1,2*], CHEN Shixi[1,2], ZHANG Qiyong[2], WANG Qiong[1,2]

1. State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen 361005, China
2. Department of Oceanography, Xiamen University, Xiamen 361005, China

Received 17 July 2006; accepted 8 January 2007

Abstract

The reproductive ecology of the mudskipper *Boleophthalmus pectinirostris* was investigated during the spawning season in the Funing Bay, Fujian, China. The fish burrows were basically Y-shaped and had two openings onto the mudflats. Part of the intersection at the center of the burrow was dilated to form a "spawning chamber". The dissolved oxygen concentrations (0.40 ~ 0.65 mg/dm^3) of water 15 cm inside the burrows were much lower than those (5.96 ~ 6.19 mg/dm^3) of intertidal pool water. Water temperatures inside the burrows were much lower than those of intertidal pools. Field investigations indicated that eggs were laid on the inner wall and ceiling of the spawning chamber by means of filamentous attachments, and a male stayed inside the burrows to guard it. Field investigations also suggested that fish of both sexes constructed mud burrows by themselves but that the spawning chamber was made only in the male burrow. The male attracted a female to his burrow for mating and spawning. There was no water in the spawning chamber, and thus the eggs were exposed to the air in the chamber. Changes in spawning readiness and GSI indicated that synchronization of spawning was related to the semi-lunar periodicity, and this is the first report of this relationship in the mudskippers.

Key words: *Boleophthalmus pectinirostris*, reproductive ecology

1 Introduction

Mudskippers can be defined as those fishes usually found moving about on the mudflats of estuaries and coastal waters when they are exposed at low tide (Qureshi and Bano, 1971). Mudskippers constitute a group of 25 air-breathing species in four genera (*Periophthalmodon*, *Periophthalmus*, *Boleophthalmus* and *Scartelaos*) which are the most derived and the most amphibious of the ten genera of the teleost subfamily Oxudercinae (Gobiidae) (Aguilar, 2000; Graham, 1997; Clayton, 1993; Murdy, 1989). Mudskippers are exceptional among fishes in their amphibious behavior and have numerous physiological and morphological specializations for amphibious life (Lee and Graham, 2002; Graham, 1997; Clayton, 1993; Gordon et al., 1969).

Intertidal spawning in fishes involves a complex reproductive strategy requiring adaptations in adults, eggs and larvae. The reproductive processes of mudskippers follow a fairly generalized pattern. The burrow, which the mudskipper uses as a refuge, is mod-

* Corresponding author, E - mail: wshong@xmu.edu.cn

ified to form a spawning chamber during the spawning season (Brillet, 1969a, b, 1976; Kobayashi et al., 1971; Mutsaddi and Bal, 1969). Eventually the female spawns and the eggs are laid on the spawning chamber walls (Brillet, 1976; Kobayashi et al., 1971).

Boleophthalmus pectinirostris (Linnaeus 1758) is distributed throughout the intertidal regions of China, Korea and Japan. In China, it is mainly found in coastal waters along the southeast mainland and around Taiwan, China. Being an amphibious species, it hides in a mud burrow during flood tide and leaves the tunnel, and slides on the muddy surface to feed on benthic diatoms, copepods and organic detritus during ebb tide (Zhang et al., 1989). The spawning season is from May to September with a peak spawning period between May and July (Xie and Zhang, 1990). This fish is a commercially important species in China (Hong and Zhang, 2003).

The present study involved a detailed field investigation of the reproductive ecology of *B. pectinirostris*, including spawning habitat characteristics, burrow building and use, and the burrow environment. In addition, whether synchronization of spawning with a lunar or semi-lunar periodicity occurs in *B. pectinirostris* was also investigated.

2 Materials and methods

2.1 Study area

The study was carried out in the Funing Bay, Fujian, China (26°53′N; 120°03′E). The area of mudflats along the coastline of this bay is some 23×10^3 hm^2. The Luohan River, the Qidu River and the Beihe River flow to join the mudflats with a total discharge of 7.8×10^9 m^3/a. This bay supports a *B. pectinirostris* fishery that takes about 60 ~ 70 t adult *B. pectinirostris* per year and is believed to be one of the most important populations of *B. pectinirostris* in China. It has an extensive, shallow and productive intertidal zone and this provides suitable habitats for a substantial *B. pectinirostris* population. About $1.0 \times 10^8 \sim 1.2 \times 10^8$ *B. pectinirostris* fry were captured in this area per year.

2.2 Surveys of burrow structure

The *B. pectinirostris* burrows can be identified by means of their pectoral fin traces. To examine if there are differences in the burrow structure between the non-spawning season (October to April) and the spawning season (May to July), the shape of the burrows was established by making casts in the burrows. The casts were made from epoxy resin with hardener at a ratio of 1 to 1. The resin only displaced burrow water lighter than itself, so that those parts of the burrow system, which were filled with liquid mud, were not recorded. Mud was piled around the burrow openings to prevent resin from spilling over onto the mud surface. After 1 or 2 d, the hardened casts were carefully removed from the sediments.

2.3 Surveys of environmental factors in the burrow

To examine the environmental factors in the burrow, fieldwork was carried out at low tide from 28 May to 11 June 2004. A specially constructed apparatus (Fig. 1) was used to measure the concentrations of dissolved oxygen (DO) in the burrow. A sample tube (Telfon: 20 cm long, 0.3 cm outside diameter, 0.2 cm inside diameter) was inserted into the burrow to a depth of 15 cm, and then water was withdrawn from the burrow into the measurement chamber, where the levels of DO were measured using an oxygen meter (model 55, YSI Incorporate, Yellow Springs, OH, USA). Before sampling the water, the apparatus was filled with nitrogen. This pretreatment was performed to obtain proper water samples for determination of DO concentrations in the burrow. Temperatures and salinities of the seawater in the burrows and intertidal pools were measured, as were the temperatures of burrow mud. Salinities were measured using a salinometer. After the environmental factors of each burrow were measured, the burrows were destroyed to examine whether eggs existed inside them. Only the data from burrows with eggs inside were used.

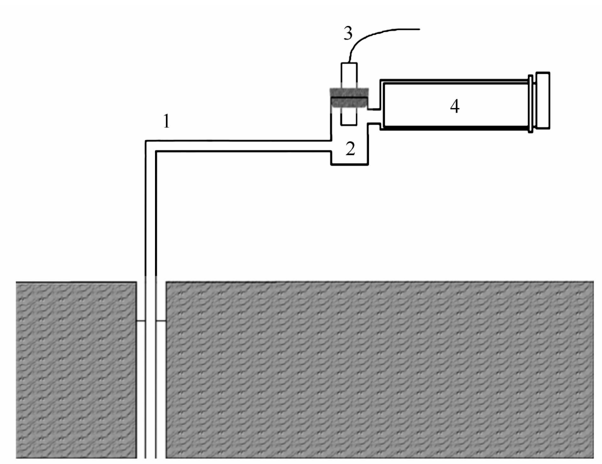

Fig. 1. Apparatus used to measure DO in burrow water. 1. sample tube, 2. measuring chamber, 3. oxygen meter, 4. syringe.

2.4 Reproductive habits

To examine whether fish of both sexes constructed mud burrows by themselves and to check whether the spawning chamber was made in the male burrow or in the female one or both, a mudflat area of 4 m^2 was enclosed with a net, which was embedded 30 cm into the mudflat in order to prevent the fish from escaping. Before the test, all fish in the area were caught and the burrows destroyed. The area was divided into two equal parts with another net embedded into the mudflat, and then six mature female fish were introduced into one part (female area) and six male fish, into the other part (male area). Five days later, six primary openings of the fish burrows were observed in both the female and male areas, indicating that either female or male had built its own burrow. For courtship and mating purposes, the net between the male and female areas was taken away. Seven days later, all burrows in the two areas were destroyed to see if spawning chambers existed inside the male burrows or female ones or both, and if there were eggs in the spawning chambers. All experimental fish were collected from the mudflats, and gender was confirmed based on the shape of the genital papilla (Zhang et al., 1989).

To investigate if there was water inside the spawning chamber, 10 mL of 1% eosin solution was injected using a syringe into each burrow through the primary opening at low tide. After 15 ~ 20 min, the burrows were carefully destroyed to inspect whether the eggs in the spawning chamber were stained by eosin solution or not. Our previous study had shown that mudskipper eggs were stained by eosin solution immediately the dye touched the eggs. Accordingly, if the eggs in the spawning chamber did not turn red, there was no water in the spawning chamber, and vice versa. The average egg number per square centimeter of the chamber wall and ceiling was calculated and the total egg number in a spawning chamber was estimated. The fertilization rate was also calculated.

2.5 Changes in spawning readiness and GSI during the spawning season

To investigate whether synchronization of spawning with lunar or semi-lunar periodicity occurs in *B. pectinirostris*, 20 female fish were sampled at intervals of 3 ~ 4 d with trap nets in May and June 2005, according to the lunar periodicity. Spawning readiness was determined by slightly pressing the fish abdomen from the anterior to the posterior. Ripeness was defined by the release of mature eggs from the genital papilla, and these fish, which were classified as "ripe", frequently released gametes spontaneously when handled. Total body mass (m_t) and ovary mass (m_o) were measured to the nearest 0.01 g and 0.1 mg, respectively. The gonadosomatic index

(i_{gs}) was calculated from $i_{gs} = 100\ m_t\ m_o^{-1}$.

2.6 Statistical analysis

The differences between mean values were compared using student's unpaired t-test. All statistics were performed using the statistical software SPSS for windows (SPSS, Chicago, IL, USA).

3 Results

3.1 Burrow structure

Eight nearly complete burrow casts were recovered (Table 1). The burrow of *B. pectinirostris* was Y-shaped and had two openings onto the mudflats. A tunnel starting from each opening went down obliquely into the mud and joined together with another tunnel and then went down vertically and formed a horizontal tunnel at the bottom of the burrow (see Fig. 2). In addition, there were some gently sloping tunnels and short cul-de-sac side branches. The distance between the two openings was 10 ~ 24 cm. One opening, which had traces of pectoral fins, was called the "primary opening", and the other (without the pectoral fin traces) the "secondary opening". The diameter of the tunnel starting from the primary opening was significantly bigger than that starting from the secondary opening ($P < 0.01$). The vertical tunnel at the center of the burrow was dilated to form an acclivous chamber during the spawning season, but this was not found in the non-spawning season. Field observations showed that the eggs were laid on the inner walls and ceiling of the chamber by means of attaching-filaments. Hence, the chamber was called a "spawning chamber". The diameter of the spawning chamber increased gradually from the entrance to the end (see Fig. 3b).

Table 1. Morphometric data for *Boleophthalmus pectinirostris* burrow casts

Date of observation	h_b/cm	d_{pl}/cm	d_{ps}/cm	d_{sl}/cm	d_{ss}/cm	d/cm	l/cm	h/cm	w/cm
15 Oct. 2003	31.0	3.0	2.0	2.5	1.8	17.0	/	/	/
15 Oct. 2003	21.0	2.5	1.5	2.6	1.4	17.5	/	/	/
15 Oct. 2003	20.0	3.2	1.7	2.5	1.5	14.0	/	/	/
15 Oct. 2003	45.0	3.0	1.6	2.4	1.5	17.0	/	/	/
15 Oct. 2003	20.0	3.5	2.0	2.7	2.2	24.0	/	/	/
12 Jun. 2004	35.5	2.7	1.9	2.5	1.9	20.0	16.0	2.6	3.5
12 Jun. 2004	50.0	3.6	2.4	2.2	1.6	22.0	12.0	2.5	3.2
12 Jun. 2004	13.0	4.2	3.0	2.1	1.9	10.0	15.0	3.6	4.2

Notes: h_b is the burrow depth; d_{pl} and d_{ps} are the primary opening long diameter and the primary opening short diameter; d_{sl} and d_{ss} the secondary opening long diameter and the secondary opening short diameter; d is the distance between the openings; and l, h and w are the spawning chamber length, height and width.

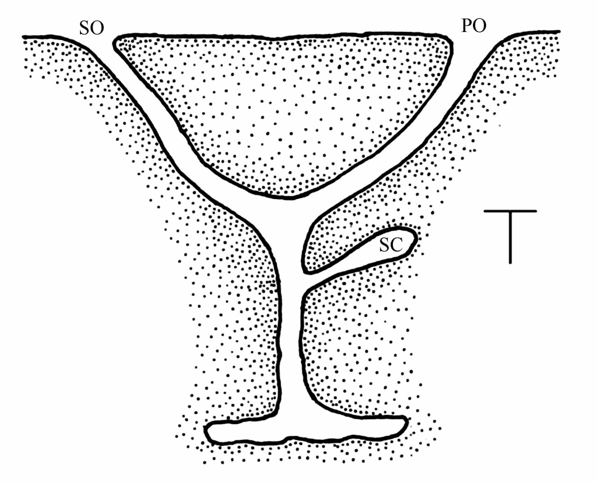

Fig. 2. Diagrammatic vertical section through a basic *Boleophthalmus pectinirostris* burrow in the intertidal mudflat. PO is abbreviaed from primary opening, SO secondary opening, and SC spawning chamber. Scale bar length represents 3 cm.

3.2 Burrow environment

The mudflat inhabited by *B. pectinirostris* is fine grained and dense (hence it is not very porous or permeable), and it is also highly organic (hence it probably has high chemical and biological oxygen demands). These burrows were always filled to their openings with water.

Levels of the burrow environmental factors are shown in Table 2. In the spawning season, the DO concentration in the water taken 15 cm inside six different burrows ranged from 0.40 to 0.65 mg/dm^3. These values were much lower than those in intertidal pool waters (5.96 ~ 6.19 mg/dm^3). Burrow water temperatures (26.0 ~ 26.4 ℃) were higher than burrow mud temperatures (25.0 ~ 25.2 ℃), but

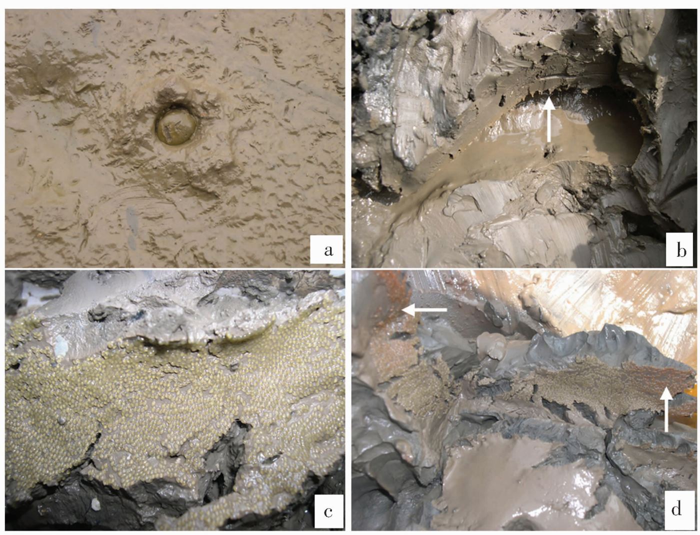

Fig. 3. Reproductive habits of *Boleophthalmus pectinirostris*. a. The burrow opening is blocked with a mud ball. b. Vertical section of a spawning chamber. The arrow indicates the eggs adhering to the ceiling of a spawning chamber. c. One layer of dense eggs adhering to the inner walls and ceiling of a spawning chamber with attaching-filaments. d. After eosin solution injection, a few eggs near the entrance of a spawning chamber turn red (arrows), while most eggs on the inner walls and ceiling of the spawning chamber were not stained red.

much lower than intertidal pool water temperatures (34.8 ~ 35.0 ℃). Salinities (27.6 ~ 28.9) inside the burrows were similar to those (28.3 ~ 28.7) in the intertidal pools.

3.3 Reproductive habits

Field observations showed that if both the primary and secondary openings of a *B. pectinirostris* burrow were blocked with mud balls (see Fig. 3a), there was always a spawning chamber together with fertilized eggs inside the burrow. One layer of dense eggs adhered onto the inner walls and ceiling of the spawning chamber by means of attaching-filaments (see Figs 3b, c), and a male stayed in the burrow to guard it. The densities of eggs in the chambers varied from 58 to 114 cm^{-2}, with an average of 87 cm^{-2}. The total egg number in the chambers ranged from 3 595 to 4 314, with an average of 3 957. Average fertilization rate of eggs reached 99.67%.

Observations further showed that spawning chambers were only present inside the male burrows, where the male and female mated and spawned. This phenomenon suggests that in the spawning season the male attracts a female to his burrow. Eosin solution staining experiments showed that burrow water and a few of the eggs (10% ~ 15%) near the entrance of the spawning chamber turned red (see Fig. 3d). On the contrary, most eggs on the inner walls and ceiling of the spawning chamber were not stained red. This suggests that no water exists inside the spawning chamber and that most eggs are therefore exposed to the chamber air.

3.4 Changes in spawning readiness and GSI during the spawning season

Spawning readiness values (percentage of ripe fish) for females reflected the semi-lunar synchronization of spawning (Fig. 4). Trends of spawning readiness values were consistent with GSI values. Spawning readiness values were above 80% at GSI peaks and less than 50% between peaks. GSI values also reflected a semi-lunar synchronization of spawning (Fig. 4). The first peak (10.54 ± 2.56) was observed on 26 May between full moon and waning moon. Compared with that peak, the GSI decreased significantly (4.73 ± 2.67) (P < 0.01) on 1 June, between waning moon and new moon. However, it increased again (8.10 ± 1.85) on 5 June, reached a second peak (8.18 ± 2.70) on 9 June between new moon and young moon, and decreased significantly (3.45 ± 1.687) (P < 0.01) back to the basal level with the young moon.

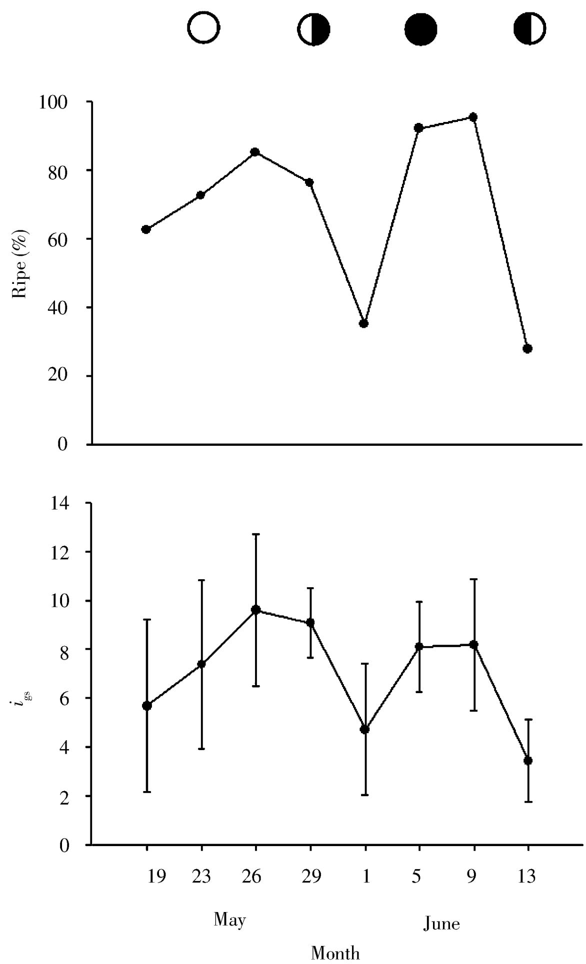

Fig. 4. Changes in spawning readiness (ripe, %) and GSI values in the female *Boleophthalmus pectinirostris* in the 2005 spawning season. Data presented as means plus or minus SD of 20 replicate samples. Lunar phases are indicated as: ○ full moon; ◑ waning moon; ● new moon; and ◐ young moon.

Table 2. *Boleophthalmus pectinirostris* burrow environments

Date of observation	DO/mg · dm^{-3}		Temperature/℃			Salinity	
	burrow water	intertidal pool water	burrow water	intertidal pool water	burrow mud	burrow water	intertidal pool water
28 May 2004	0.40	6.02	26.2	35.0	25.1	28.5	28.7
28 May 2004	0.44	5.96	26.1	34.8	25.2	27.6	28.5
28 May 2004	0.45	6.19	26.0	34.9	25.0	28.9	28.6
11 Jun. 2004	0.63	5.98	26.2	34.9	25.1	27.9	28.3
11 Jun. 2004	0.65	6.05	26.4	34.8	25.0	28.1	28.6

4 Discussion

Burrow structure of several fish species has been studied in order to investigate the general ecology of animals. The burrows are structurally diverse, but may be divided into those in which the main development is horizontal and those in which it is vertical (Atkinson and Taylor, 1991). The present study showed that the main development of *B. pectinirostris* burrows is vertical and Y-shaped. The structure of *B. pectinirostris* is similar to other mudskipper burrows investigated (Clayton and Vaughan, 1988, 1986; Brillet, 1984, 1969a; El-Ziady et al., 1979; Kobayashi et al., 1971; Macnae, 1968). In the spawning season, a spawning chamber was also found in the burrows in *Periophthalmus cantonensis* (Matoba and Dotsu, 1977; Kobayashi et al., 1971) and *P. sobrinus* (Brillet, 1976). However, the position of the spawning chamber in the burrows differed between different species. In *B. pectinirostris*, it is located at the centre of the burrow; while in *P. cantonensis* and *P. sobrinus*, it is located at the bottom of the burrow (Brillet, 1976; Kobayashi et al., 1971).

Fishes which form burrows in intertidal sediments will experience more extreme conditions of hypoxia at low tide, when irrigation of the burrow is impossible (Atkinson and Taylor, 1991). Our field observations indicated that the DO concentration levels in the water of *B. pectinirostris* burrows ranged from 0.40 ~ 0.65 mg/dm^3, which were as low as those in the water of *P. cantonensis* (Gordon et al., 1978) and *P. koelreuteri* burrows (El-Ziady et al., 1979). Our previous studies indicated that the oxygen consumption rate of *B. pectinirostris* eggs was similar to that of pelagic fish eggs, which developed in normoxic conditions (Chen et al., 2006). These results, together with the fact that eggs were laid in the spawning chamber, brought up an additional question. How can *B. pectinirostris* eggs survive under such hypoxic conditions? In fact the eosin staining experiment indicated that there was no water in the spawning chamber, and that the eggs were exposed to the air in the chamber. Ishimatsu et al. (1998) reported that *P. schlosseri* stores air in its burrow. In *P. sobrinus* the eggs required a moist atmosphere, but not total immersion in water, in order to achieve complete development (Brillet, 1976). Hence, the results of the present study suggest that because the spawning chamber has an acclivous portion that is not connected to the mudflat surface, *B. pectinirostris* can deposit air in the spawning chamber, and this can serve as a significant oxygen reservoir for developing embryos.

Our previous laboratory study showed that in *B. pectinirostris* the fertilization rate reached 90% at water temperatures of 25 ~ 28 ℃ and salinities of 25

~ 27 (Zhang et al., 1989). Our field study indicated that, in the spawning season, temperatures of burrow water (26.0 ~ 26.4 ℃) and burrow mud (25.0 ~ 25.2 ℃), and water salinities (27.6 ~ 28.9) inside the burrows were optimum for *B. pectinirostris* embryonic development.

Synchronization of spawning with lunar or semi-lunar periodicity is a common phenomenon in many marine teleost species, especially within or near the tropics (Taylor, 1984; Johannes, 1978; Schwassman, 1971;). Our data on spawning readiness and GSI of the female *B. pectinirostris* demonstrated that synchronization of spawning with semi-lunar periodicity exists in *B. pectinirostris*. There are at least two aspects to be considered with respect to the importance of a semi-lunar cycle. One aspect is related to the fact that synchronization of the males and females during some phase of their reproductive behavior can increase the rate of fertilization (Neumann, 1975) and the rate of mating (Korringa, 1947). Because *B. pectinirostris* eggs develop in the spawning chamber and are exposed to air, the other aspect concerns whether the variable tidal movement can be the means of triggering the hatching and transportation of free-living larvae (Taylor, 1999). To our knowledge, this is the first report of synchronization of spawning with semi-lunar periodicity in the mudskipper.

In the field observations, the spawning chamber of *B. pectinirostris* only appeared in the male burrow. This phenomenon indicated that, in the spawning season the male attracts a female to his burrow and then the burrow is modified to form a spawning chamber. Further work is needed to determine whether the spawning chamber is constructed by the male or female alone, or by both.

The egg care provided by the male seems to have three basic functions. It protects the eggs from predators, keeps the eggs clean and free from detritus, and provides an adequate supply of oxygen for embryonic development. Egg predation is prevented by the aggressive behavior of the male toward intruders (De Martini, 1978; Wirtz, 1978; Marliave and De Martini, 1977). Removal of the guardian male results in the eggs being eaten by conspecifics (Wirtz, 1978) or by other predators (De Martini, 1978; Wirtz, 1978).

In conclusion, in the spawning season the male attracts a female to his burrow and then the burrow is modified to form a spawning chamber. The eggs are deposited in one rather dense layer on the inner walls and ceiling of the spawning chamber by means of attaching – filaments. After spawning, the female leaves the burrow, each opening is blocked with a mud ball, and then the male stays in the burrow to guard it. During egg development, air exists in the spawning chamber, and provides a significant oxygen reservoir for the developing embryos. The microclimate in the burrow is suitable for embryonic development. Synchronization of spawning with semi – lunar periodicity in *B. pectinirostris* can increase the rates of mating and fertilization. Tidal movement, which is synchronized with semi – lunar periodicity, could trigger hatching and the transport of free – living larvae from inside the burrow onto the intertidal mudflats.

Acknowledgements

We thank Lin L J for help in collection of fish, and Yang L Q for his assistance in field observations. Professor John Hodgkiss is thanked for his help with English. This work was supported by the National Natural Science Foundation of China under contract No. 40476056 and the Key Projects of Science and Technology of Fujian Province in China under contract Nos 2003NO26 and 2004SZ01 – 02.

References

Aguilar N M. 2000. Comparative physiology of air-breathing gobies: [dissertation]. San Diego: University of California

Atkinson R J A, Taylor A C. 1991. Burrows and burrowing behaviour of fish. Symposium of Zoological Society of London, 63: 133 ~ 155

Brillet C. 1969a. Etude du comportement constructeur des poisons amphibies Periophtalmidae. Terre et Vie, 23: 496 ~ 520

Brillet C. 1969b. Premiere description de la parade nuptiale des poisons amphibies Periopthalmidae. Comptes Rendus Hebdomadaires des Seances de L Academie des Sciences, 269: 1 889 ~ 1 892

Brillet C. 1976. Structure du terrier, reproduction et comportement des jeunes chez le poisson amphibie *Periophthalmus sobrinus* Eggert. Terre et Vie, 30: 465 ~ 483

Brillet C. 1984. The habitat and behavior of the amphibious fish *Periophtalmus koelreuteri africanus* at tulear—comparison with the sympatric *Periophthalmus sobrinus*. Terre et Vie, 39: 337 ~ 345

Chen S X, Hong W S, Zhang QY, et al. 2006. Rate of oxygen consumption and tolerance of hypoxia and desiccation in mudskipper (*Boleophthalmus pectinirostris*) and Chinese black sleeper (*Bostrichthys sinensis*) embryos. Acta Oceanologica Sinica, 25: 91 ~ 98

Clayton D A. 1993. Muskipper. Oceanography and Marine Biology, an Annual Review, 31: 507 ~ 577

Clayton D A, Vaughan T C. 1986. Territorial acquisition in the mudskipper *Boleophthalmus boddarti* (Teleostei, Gobiidae) on the mudflats of Kuwait. Journal of Zoology, London (A), 209: 501 ~ 519

Clayton D A, Vaughan T C. 1988. Ethogram of *Boleophthalmus boddarti* (pallas) (teleostei, gobiidae), a mudskipper found on the mudflats of Kuwait. Journal of the University of Kuwait, 15: 115 ~ 139

De Martini E E. 1978. Spatial aspects of reproduction in buffalo sculpin, *Enophrys. Bison*. Environmental Biology of Fishes, 3: 331 ~ 336

El – Zaidy S, Eissa S M, Al – Naqi Z. 1979. Ecological studies on the mudskipper fish, *Periophthalmus chrysospilos* (Bleeker) in Kuwait. Bulletin of the Faculty of Science, Cario University, 48: 113 ~ 133

Gordon M S, Boetius L, Evans D H, et al. 1969. Aspects of the physiology of terrestrial life in amphibious fishes: Ⅰ. The mudskipper, *Periophthalmus sobrinus*. Journal of Experimental Biology, 50: 141 ~ 149

Gordon M S, Ng W W – S, Yip A Y – W. 1978. Aspects of the physiology of terrestrial life in amphibious fishes: Ⅰ. The Chinese mudskipper, *Periohthalmus cantonensis*. Journal of Experimental Biology, 72: 57 ~ 75

Graham J B. 1997. Air-Breathing fishes. San Diego: Academic Press

Hong W S, Wang Y L. 1989. Induction of ovulation in female mud skipper (*Boleophthalmus pectinirestris*) by HCG, analogue of LHRH and pimozide. Chinese Journal of Oceanology and Limnology, 7: 283 ~ 287

Hong W S, Zhang Q Y. 2003. Review of captive bred species and fry production of marine fish in China. Aquaculture, 227: 305 ~ 318

Ishimatsu A, Hishida Y, Takita T, et al. 1998. Mudskippers store air in their burrows. Nature, 391: 237 ~ 238

Johannes R E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Environmental Biology of Fishes, 3: 65 ~ 84

Kobayashi T, Dotsu Y, Takita T. 1971. Nest and nesting behaviour of the mudskipper *Periophthalmus cantonensis*, in Ariake Sound. Bulletin of the Faculty of Fisheries, Nagasaki University, 32: 27 ~ 39

Korringa P. 1947. Relations between the moon and periodicity in the breeding of marine animals. Ecological Monographs, 17: 347 ~ 381

Lee H J, Graham J B. 2002. Their game is mud. Nature History, 9/02: 42 ~ 47

Macnae W. 1968. A general account of the fauna and flora of mangrove swamp and forests in the Indo – West-Pacific region. Advances in Marine Biology, 6: 73 ~ 270

Marliave J B, De Martini E E. 1977. Parental behavior of intertidal fishes of stichaeid genus *Xiphister*. Canadian Journal of Zoology, 55: 60 ~ 63

Murdy E O. 1989. A taxonomic revision and cladistic analysis of the oxudercine gobies (Gobiidae: Oxudercinae). Records of Australian Museum Supp, 11: 1 ~ 93

Mutsaddi K B, Bal D V. 1969. Some observations on habits and habitat of *Boleophthalmus dussumierei* (Cuv. and Val.). Journal of the University of Bombay, 39: 33 ~ 41

Neumann D. 1975. Lunar and tidal rhythms in development and reproduction of an intertidal organisms. In: Vernberg F J, ed. Physiological Adaptation to the Environment. New York: Intext Educational Publishers, 451 ~ 463

Qureshi M R, Bano A. 1971. Common gobioid fishes of subfamilies Periophthalminae and Apocrypteinae. Pakistan Journal of Science, 23: 143 ~ 146

Schwassmann H O. 1971. Biological rhythms. In: Hoar W S, Randall D J, eds. Fish Physiology, v6. New York: Academic Press, 371 ~ 428

Taylor M H. 1984. Lunar synchronization of fish reproduction. Transactions of the American Fisheries Society, 113: 484 ~ 493

Taylor M H. 1999. A suite of adaptations for intertidal spawning. American Zoologist, 39: 313 ~ 320

Wirtz P. 1978. The behaviour of the Mediterranean *Tripterygion* species (Pisces, Blennioidei). Zeitschrift Fur Tierpsychologie, 48: 142 ~ 174

Xie X G, Zhang Q Y. 1990. Studies on the gondal development in female mudskipper, *Boleophthalmus pectinirostris*. Journal of Oceanography in Taiwan Strait (in Chinese), 9: 217 ~ 221

Zhang Q Y, Hong W S, Dai Q N, et al. 1989. Studies on induced ovulation, embryonic development and larval rearing of the mudskipper (*Boleophthalmus pectinirostris*). Aquaculture, 83: 375 ~ 385