Microhabitat selection in the early juvenile mudskipper Boleophthalmus pectinirostris (L.)

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Using laboratory choice experiments, behavioural preferences of the early juvenile mudskipper *Boleophthalmus pectinirostris* for temperature, salinity and sediment were observed. The temperature preference experiments were conducted in an annular chamber with a thermal gradient of 27 to 34° C, and the fish selected a mean \pm s.D. temperature of $31.2 \pm 0.5^{\circ}$ C. The salinity preference experiments were conducted in an aquarium with decreasing salinity from 20 to 15, 10, 5 and 0.5, and significantly more (P < 0.05) fish were found in water with a salinity of 5. The sediment preference experiments were tested in circular tanks which contained four types of sediment (medium sand, fine sand, muddy sand and sandy mud), and the fish showed a clear preference for sandy mud. These results indicated that early juvenile *B. pectinirostris* showed behavioural preference for microhabitats. Temperature and salinity probably set large-scale boundaries on distribution, but sediment should be a critical factor for determining the distribution of the mudskipper.

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Key words: mudskipper; salinity preference; sediment preference; temperature preference.

INTRODUCTION

Animals are dependent on their microhabitat and the diversity of a habitat can often be a function of the heterogeneity of its microhabitats (Sale & Dybdahl, 1975; Leviten & Kohn, 1980; Dean, 1981; Dean & Connell, 1987). Coastal zone systems are highly productive areas that serve as nursery grounds for many marine species of commercial importance (Costanza *et al.*, 1997). There is increasing awareness of the important link between microhabitat and sustainable fisheries for coastal zone species (Langton *et al.*, 1996; Schmitten, 1999). In particular, the mechanisms that make certain coastal zone microhabitats important as nursery grounds need to be understood, and these nurseries need to be identified and protected (Beck *et al.*, 2001). Microhabitat is seldom defined by a single environmental factor (Baltz, 1990) and the distribution of

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coastal-zone fishes is usually affected by salinity, temperature, turbidity, dissolved oxygen, sediment characteristics and macrophyte cover (Blaber & Blaber, 1980; Marchand, 1993; Whitfield, 1996; Marshall & Elliott, 1998).

The mudskipper Boleophthalmus pectinirostris (L. 1758) is distributed throughout the coastal waters of China, Korea and Japan (Murdy, 1989; Clayton, 1993). In China, where this fish is a commercially important species (Hong & Zhang, 2003), it is mainly found in coastal waters to the south-east of the mainland and around Taiwan. Being an amphibious species, the adult fish hides in a mud burrow during flood tide but leaves the tunnel during ebb tide (Zhang et al., 1989). The diets of larval fish include particulate organic detritus, copepod nauplii and copepodites. The larvae reach the early juvenile stage 38-43 days after hatching, depending on water temperature. At this stage, the larvae complete metamorphosis, and the fish begin to settle on the muddy surface, changing their lifestyle from pelagic to benthic and they alter their diets by ingesting benthic diatoms concurrently with copepods, protozoa and organic detritus (Zhang et al., 1989). During ontogeny, the early juvenile fish begin to select a suitable microhabitat in which to settle. If they happen to settle in a less suitable microhabitat, they migrate to a more suitable microhabitat preceding permanent settlement (Wan et al., 2004).

As the fish begin the transition from a planktonic to a demersal habit (settlement), one behavioural process of habitat selection may be influenced strongly by the patterns of the intertidal mudflat habitats. The habitats of early post-settlement fishes have been investigated in some species (Marliave, 1977; Gibson & Robb, 2000; Stoner & Abookire, 2002; Lafrance *et al.*, 2005; Bos & Thiel, 2006). Habitat selection, however, has not been studied in early juvenile amphibious fishes. The habitats of amphibious fishes are structurally complex, including a variety of microhabitats. The present study reports on laboratory-based experimental exploration of microhabitat (temperature, salinity and sediment) preferences of early juvenile *B. pectinirostris*.

MATERIALS AND METHODS

EXPERIMENTAL ANIMAL

Early juvenile *B. pectinirostris* for laboratory experiments were collected in Funing Bay, Fujian, China (26°53' N; 120°03' E). The area of mudflats along the coastline of this bay is 23 000 ha. The bay has an extensive, shallow and productive intertidal zone and this, combined with brackish-water spawning and larval *B. pectinirostris* habitats, provides suitable conditions for a substantial *B. pectinirostris* population. The fry fishery in this bay takes c. 100–120 million per year and the early juveniles for this study were collected by professional farmers with a hand-net on 20 August 2006. The captive early juveniles, which had settled onto the mudflat for 1–2 days, were 17–25 mm in total body length (L_T). No fish died during transport to the Xiamen University laboratory and most fed on *Artemia* sp. nauplii within 24 h of arrival. Fish were held indoors, under simulated photoperiod (12L:12D), in a rectangular tank with sea water (mean ± s.D. salinity 10 ± 1 and temperature 29 ± 0·3° C). Fish were fed to satiation with *Artemia* sp. nauplii each day (Zhang *et al.*, 1989). The preference experiments were carried out 2 days after the fish were transported to the laboratory.

TEMPERATURE PREFERENCE EXPERIMENTS

The temperature preference experiments were conducted in an annular chamber of polyvinyl chloride (PVC) (Myrick et al., 2004). The main apparatus consisted of four concentric walls forming four low channels centred on a square base (Fig. 1). The radial flow of water from the exterior towards the interior of the chamber did not provide a single focus point for rheotaxis. In the present experiment, the size of apparatus was modified to match the small size of fish, and water sources of only two temperatures were used in order to operate the apparatus simply. The diameters of the four cylinders measured 80, 120, 180 and 220 mm each from the inner to the outer. To facilitate the establishment of a horizontal gradient, the swimming channel was separated into eight zones using PVC partition walls. Fish were free to move from one zone to another through holes cut in the partition walls. The cold water reservoir received 26° C sea water, and the warm-water reservoir received 35° C sea water. With this experimental set-up, a thermal gradient of c. 8° C was established (27–34° C). Each distinct temperature zone was 1.5-2.0 times as wide as the $L_{\rm T}$ of the early juvenile B. pectinirostris. Water overflowed through V-notch weirs along the inner walls of the mixing, swimming and effluent channels. The V-notches on the top of the swimming channel walls were covered using fine mesh netting in order to prevent the fish from escaping. From each reservoir, two hoses delivered water to a single mixing compartment, and the other two hoses delivered water to two mixing compartments. Delivery rates from each hose were adjusted to $0.12 \ \text{l min}^{-1}$ by making sure that water was always overflowing from the reservoirs, thus ensuring a constant amount of head pressure for the hose outlets.

Twelve similarly-sized early juvenile *B. pectinirostris* were chosen for this experiment and, in order to eliminate the influence between individuals, the fish were tested individually in the experimental chamber. Each fish was transferred into the annular preference chamber at its rearing temperature, and usually took 1 h to recover from handling before exploring the entire tank. The fish was placed in the gradient tank at 1200 hours and observations began 24 h after transfer. Fish locations were monitored at 10 min intervals and the seawater temperatures at the fish's head were measured by thermometer within 10 s. The 12 observations recorded in each experiment were averaged to yield a single value, which was defined as the final thermal preference.

To confirm that the position of the fish in the tank was affected by water temperature rather than by an undesirable tank effect, six controls were conducted in the same experimental tanks, but with the thermal gradient reversed.

SALINITY PREFERENCE EXPERIMENTS

The salinity preference experiments were conducted in a glass aquarium, which consisted of five top-connected U-segments (Bos & Thiel, 2006). The connection to the adjacent U-segment was formed by a water column. The U-segments could be disconnected by placing glass plates into slots. The salinity gradients were created in five steps:



FIG. 1. Diagram of annular chamber for temperature preference experiments.

20, 15, 10, 5 and 0.5. Water with a salinity of 20 (from the estuary) was mixed with water of 0.5 (from the laboratory inlet) to create the different salinities. After removal of the glass plates, haloclines developed except in the 0.5 segment. The stability of the salinity gradient in the aquarium had been tested previously, and the aquarium proved its efficiency since the salinity gradient was stable during the experiment (Bos, 2000). All of the experiments were conducted in a room with light and temperature control. Photoperiod was 12L:12D and temperature was c. 29° C (similar to the holding water).

Twenty-five fish were used in the salinity preference experiments. Five fish at a time were carefully released into an outer U-segment of the aquarium for observation. Four glass plates were removed once the fish were released into the aquarium. After 50 h, the numbers of early juvenile *B. pectinirostris* in each segment were recorded at 3 h intervals between 0800 and 2300 hours (six recordings). The fish were not fed during the whole period of observation. Fifteen fish were used in three control groups, and the experiment was carried out in a reverse direction of salinity gradient in order to exclude the influence of the experimental set-up on fish distribution. The ratio of the total number of fish for the six observations in each segment to the total number of fish for the six observations in all five segments was used to calculate the mudskipper preference for each salinity.

SEDIMENT PREFERENCE EXPERIMENTS

Early juvenile B. pectinirostris were tested for sediment preference in three circular tanks. Fine mesh netting was placed around the outside of the tanks and extended inwards over the top of the tanks in order to prevent the fish from escaping. Individual fish were given a choice of four similarly coloured sediments of different grain sizes: fine (<0.125 mm), medium (>0.125 and <0.25 mm), coarse (>0.25 and <0.5 mm) and very coarse (0.5-1 mm). The appropriate range of grain sizes used was determined by the availability of commercial sieves. The fine and medium sediments were made from mud, and the coarse and very coarse sediments, from river sand, respectively. The sediments presented to the fish were elutriated by washing them thoroughly in fresh water and air-dried in order to remove any prey organisms before placing them in the tanks. Each tank was divided into four equal sections with plastic dividers. A different sediment was placed in each of the four 20-30 mm deep sections so that all combinations of habitat placement were investigated. All the tanks were rotated after each run to create different orientations in order to prevent any room or lighting effects. Sea water was provided to a depth of 20 mm above the sediment. The mean temperature was 29° C and the mean salinity was 10. Each of the sediment sections were stirred between runs to keep them loose and aerobic. When the boundaries between sediment types became blurred, the sediments were replaced entirely. All of the experiments were conducted in a light-controlled room and the photoperiod was 12L:12D (as in the holding areas).

One fish was introduced at random to each tank in order to eliminate potential bias of the initial starting position on subsequent sediment preference. Fish were left undisturbed for 24 h for each experimental run, and observation started 24 h after introduction of the fish. Fish can build very shallow burrows, and therefore the sediment, where a burrow was built, was assumed to be the prefered sediment. Each fish was used only once in order to avoid any potential bias from previous experience.

STATISTICAL ANALYSIS

Kruskal–Wallis one-way ANOVA by ranks was used to compare the final thermal preference of fish, conducted according to the type of thermal gradient used. Levene and Kolmogorov–Smirnov tests were used to test for the homogeneity of variance and normality, respectively, and neither of the null hypotheses was assumed. Repeated measurement, using the procedure of general linear models (GLM), was used to compare the final salinity preference of fish according to the type of salinity gradient used.

The distribution of fish on each sediment after 24 h was tested against the null hypothesis of equal distribution using the χ^2 test. The possibility that a fish's final position was related to the combination of sediment placement was also tested using the χ^2 test.

RESULTS

Early juvenile *B. pectinirostris* selected temperatures between 27 and 34° C with a mean \pm s.D. selected temperature of $31.2 \pm 0.5^{\circ}$ C (Fig. 2). Because there was no flow of water around the circumference of the swimming channel, fish exhibited low activity in the annular chamber during the experiment. Experiments comparing the fish positions in the annular chamber with temperature gradients in different directions demonstrated that the fish positions were mainly determined by temperature selection rather than undesirable tank effects, since there was no significant difference in fish thermal preference between reverse thermal gradients (Kruskal–Wallis, P > 0.05).

Significantly more early juvenile *B. pectinirostris* (Kruskal–Wallis ANOVA, P < 0.05) were found in segment U4 (salinity 5) during the observations (Fig. 3), and there was no significant difference in salinity preference with reverse gradients (P > 0.05). This indicated that the fish positions in the salinity gradient aquarium were mainly determined by salinity selection rather than undesirable aquarium effects.

During the entire experimental series, all early juvenile *B. pectinirostris* tested were able to build a shallow burrow within 24 h after being introduced to the circular tanks. The fish used the burrow as a refuge when they were disturbed. It was found that the fish only built burrows in sandy mud, indicating that the fish had a clear preference for the sandy mud sediment. The sediment placement combinations did not influence this preference.

DISCUSSION

The range of temperature to which intertidal amphibious fishes are exposed is among the greatest met by any fish. Within wide tolerance limits, mudskippers are extremely eurythermal using body colour changes (Stebbins & Kalk, 1961), evaporative cooling and behavioural thermoregulation (Tytler &



FIG. 2. Histogram showing the distribution of temperatures selected by early juvenile *Boleophthalmus pectinirostris* in the annular preference chamber.



FIG. 3. Histogram of early juvenile *Boleophthalmus pectinirostris* presence in five U-segments with different salinities. Data presented as mean + s.p. of five replicated experiments.

Vaughan, 1983). In general, the body temperatures are the same as the mud and surface water where they are captured. Stebbins & Kalk (1961) found that the body temperatures of *Periophthalmus argentilineatus* (Valenciennes) in Mozambique range from 28.7 to 34.4° C with a mean of 31.5° C during late summer. Body temperatures of Periophthalmus kalolo (Lesson) and P. argentilineatus in Java have a mean value of 32.6° C in tide pools and 30.6° C in reef flats (Burhanuddin & Martosewojo, 1979). The normal activity range of body temperatures of Periophthalmus waltoni (Koumans) is 26-34.5° C in summer (Tytler & Vaughan, 1983). In Periophthalmus modestus (Cantor), the fish display a strong preference for higher temperatures (30–35° C), even though these temperatures are close to those known to cause distress or death (Gordon et al., 1985). Suitable temperatures for B. pectinirostris prelarval development range from 22 to 32° C, and the optimum temperature is 26° C (Pan, 1988). The preferred temperature of early juvenile B. pectinirostris in this study was c. 31° C. This result indicated underlying thermal behavioural tendencies actually present in the early juvenile stage, and the early juvenile fish preferred warmer temperatures than did the prelarvae. The preference for high water temperature shown by the early juvenile fish appeared to be ecologically reasonable, since shallow-water temperatures of intertidal mudflats are usually higher than deep-water temperatures in the subtidal area during the migration period of B. pectinirostris. Like adult mudskippers, early juvenile B. pectinirostris prefer a warmer thermal environment, up to temperatures which are actually hazardous (Ye et al., 2006).

The salinity preferences of adult *P. argentilineatus* (Gordon *et al.*, 1968) and *P. waltoni* (Ai-Naqi, 1977) were assessed by choice trials in groups of fish preadapted to different levels of salinity. Both studies showed that seawateradapted fish preferred the terrestrial habitat to any dilution of sea water and that 100% sea water was generally the least preferred salinity. In a groupchoice experiment without pre-adaption, *P. modestus* also preferred land to water of any salinity (Gordon *et al.*, 1985). Pan (1988) reported that the suitable salinity for prelarval development of *B. pectinirostris* ranged from 10 to 40, and the optimum salinity was 25. Early juvenile *B. pectinirostris* showed a significant preference for lower salinity sea water. The results suggest that salinity is a major factor affecting the behaviour of early juvenile mudskippers during the settlement period. Early juvenile mudskippers are more mobile and can easily migrate and have been found to inhabit tidal flats and estuaries at a low salinity. Many tidal flats inhabited by the mudskipper have freshwater inlets and the volume of the fry fishery has been positively related to the amount of rainfall around the mudflat (Wan *et al.*, 2004).

In the present laboratory study, early juvenile B. pectinirostris showed a clear preference for the finest sediments. There is a growing body of evidence suggesting that sediment structure is important in determining the distribution patterns of juvenile fishes (Gibson, 1994; Moles & Norcross, 1995). Laboratory experiments demonstrated that several species have an ability to distinguish between and select sediments based on grain size (Marliave, 1977; Tanda, 1990; Gibson & Robb, 1992). These examples suggest that the selection of habitat by larval and juvenile fishes may have important impacts on their subsequent growth and survival. Two major biotic factors that determine the suitability of a habitat are the preference of organisms as suitable prey and the ability to bury or burrow, which may reduce predation and conserve energy (Gibson & Robb, 2000). Juvenile mudskippers graze on the surface sediment with distinctive side-to-side movements of the anterior body and skim off the diatoms and other algae that are their predominant food items. The finest sediment can both promote the growth of diatoms and reduce the harm when the fish slide on the sediment surface (Watermann et al., 1999). The finest sediment is also most suitable for the juvenile mudskipper to form a burrow. The burrow functions as a refuge, observation post and nest. The ability of mudskipper to burrow in sediments is considered to be important in reducing predation risk.

In summary, the present study indicates that early juvenile *B. pectinirostris* showed behavioural preference for microhabitats. Temperature and salinity probably set large-scale boundaries on distribution, but sediment should be a critical factor for determining the distribution of mudskippers because they live in direct association with the sediment and because the sediment provides both food, and shelter from predation. Field studies are necessary in the future to determine the combined effects of such environmental factors.

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References

- Ai-Naqi, Z. A. (1977). Ecological and physiological studies on the mud-skipper fish, *Periophthalmus chrysospilos*, inhabiting the muddy shores of Kuwait. MSc Thesis, Kuwait University, Kuwait.
- Baltz, B. M. (1990). Autoecology. In *Methods for Fish Biology* (Schreck, C. B. & Moyle, P. B., eds), pp. 585–608. Bethesda, MD: American Fisheries Society.
- Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders,
 B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J.,
 Sheridan, P. F. & Weinstein, M. R. (2001). The identification, conservation, and

management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* **51**, 633–641.

- Blaber, S. J. M. & Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology* **17**, 143–162.
- Bos, A. R. (2000). Aspects of the life history of the European flounder (*Pleuronectes flesus* L. 1758) in the tidal River Elbe. PhD Thesis, University of Hamburg, Berlin.
- Bos, A. R. & Thiel, R. (2006). Influence of salinity on the migration of postlarval and juvenile flounder *Pleuronectes flesus* L. in a gradient experiment. *Journal of Fish Biology* 68, 1411–1420.
- Burhanuddin & Martosewojo, S. (1979). Observations on the natural history of ikan gelodok *Periophthalmus koelreuteri* in Par Island. In *Proceedings of the Seminar on Mangrove Forest Ecosystems, Jakarta* (Soemodihardjo, S., ed.), pp. 86–92. Jakarta: LIPI Press (in Malay with English abstract).
- Clayton, D. A. (1993). Mudskippers. Oceanography and Marine Biology, An Annual Review **31**, 507–577.
- Costanza, R., Darge, R., Degroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., Oneill, R. V., Paruelo, J., Raskin, R. G., Sutton, P. & Vandenbelt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- Dean, T. A. (1981). Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology* 53, 163–180.
- Dean, R. L. & Connell, J. H. (1987). Marine organisms in an algal succession. III. Mechanisms linking habitat complexity with diversity. *Journal of Experimental Marine Biology and Ecology* 109, 249–273.
- Gibson, R. N. (1994). Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32**, 191–206.
- Gibson, R. N. & Robb, L. (1992). The relationship between body size, sediment grain size and the burying ability of juvenile plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* 40, 771–778.
- Gibson, R. N. & Robb, L. (2000). Sediment selection in juvenile place and its behavioural basis. *Journal of Fish Biology* **56**, 1258–1275.
- Gordon, M. S., Boetius, L., Evans, D. H. & Oglesby, L. C. (1968). Additional observations on the natural history of the mudskipper, *Periophthalmus sobrinus*. *Copeia* 1968, 853–857.
- Gordon, M. S., Gabaldon, D. J. & Yip, A. Y.-W. (1985). Exploratory observations on microhabitat selection within the intertidal zone by the Chinese mudskipper fish *Periophthalmus cantonensis. Marine Biology* 85, 209–215.
- Hong, W. S. & Zhang, Q. Y. (2003). Review of captive bred species and fry production of marine fish in China. Aquaculture 227, 305–318.
- Lafrance, P., Castonguay, M., Chabot, D. & Audet, C. (2005). Ontogenetic changes in temperature preference of Atlantic cod. *Journal of Fish Biology* **66**, 553–567.
- Langton, R. W., Steneck, R. S., Gotceitas, V., Juanes, F. & Lawton, P. (1996). The interface between fisheries research and habitat management. North American Journal of Fisheries Management 16, 1–7.
- Leviten, P. J. & Kohn, A. J. (1980). Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. *Ecological Monographs* **50**, 55–75.
- Marchand, J. (1993). The influence of seasonal salinity and turbidity maximum variations on the nursery function of the Loire estuary (France). *Netherlands Journal of Aquatic Ecology* **27**, 427–436.
- Marliave, J. B. (1977). Substratum preferences of settling larvae of marine fishes reared in the laboratory. *Journal of Experimental Marine Biology and Ecology* **27**, 47–60.
- Marshall, S. & Elliott, M. (1998). Environmental influences on the fish assemblage of the Humber estuary, U.K. *Estuarine, Coastal and Shelf Science* 46, 175–184.
- Moles, A. & Norcross, B. L. (1995). Sediment preference in juvenile Pacific flatfish. Netherlands Journal of Sea Research 34, 177–182.

- Murdy, E. O. (1989). A taxonomic revision and cladistic analysis of the oxudurcine gobies (Gobiidae: Oxudercinae). *Records of the Australian Museum* 11 (Suppl.), 1–93.
- Myrick, C. A., Folgner, D. K. & Cech, J. J. (2004). An annular chamber for aquatic animal preference studies. *Transactions of the American Fisheries Society* **133**, 427–433.
- Pan, K. H. (1988). Effects of temperature and salinity on the development of eggs and larvae of mudskipper (*Boleophthalmus pectinirostris* L.). MA Thesis, Xiamen University, Fujian, P.R. China (in Chinese with English abstract).
- Sale, P. F. & Dybdahl, R. (1975). Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology* 56, 1343–1355.
- Schmitten, R. A. (1999). Essential fish habitat: opportunities and challenges for the next millennium. In *Fish Habitat: Essential Fish Habitat and Rehabilitation* (Benaka, L., ed.), pp. 3–10. Bethesda, MD: American Fisheries Society.
- Stebbins, R. C. & Kalk, M. (1961). Observations on the natural history of the mudskipper *Periophthalmus sobrinus*. *Copeia* **1961**, 18–27.
- Stoner, A. W. & Abookire, A. A. (2002). Sediment preferences and size-specific distribution of young-of-the-year Pacific halibut in an Alaska nursery. *Journal of Fish Biology* 61, 540–559.
- Tanda, M. (1990). Studies on burying ability in sand and selection to the grain size for hatchery-reared marbled sole and Japanese flounder. *Nippon Suisan Gakkaishi* 56, 1543–1548.
- Tytler, P. & Vaughan, T. (1983). Thermal ecology of the mudskippers *Periophthalmus koelreuteri* (Pallas) and *Boleophthalmus boddarti* (Pallas) of Kuwait Bay. *Journal of Fish Biology* 23, 327–337.
- Wan, C. G., Hong, W. S., Zhang, Q. Y., Cai, Z. J. & Ye, Q. W. (2004). Sustainable development strategies for mudskipper aquaculture in Xiapu County of Fujian Province. *Journal of Fujian Fisheries* 3, 64–67 (in Chinese with English abstract).
- Watermann, F., Hillebrand, H., Gerdes, G., Krumbein, W. E. & Sommer, U. (1999). Competition between benthic cyanobacteria and diatoms as influenced by different grain sizes and temperatures. *Marine Ecology Progress Series* 187, 77–87.
- Whitfield, A. K. (1996). A review of factors influencing fish utilization of South African estuaries. *Transactions of the Royal Society of South Africa* **51**, 115–138.
- Ye, Q. W., Hong, W. S., Zhang, Q. Y., Jiang, G. Q., Cai, Z. J. & Wan, C. G. (2006). Larval rearing of the mudskipper in the earth ponds. *Marine Sciences* 4, 1–4 (in Chinese with English abstract).
- Zhang, Q. Y., Hong, W. S., Dai, Q. N., Zhang, J. & Cai, Y. Y. (1989). Studies on induced ovulation, embryonic development and larval rearing of the mudskipper (*Boleoph-thalmus pectinirostris*). Aquaculture 83, 375–385.