Ichthyol Res (2008) 55:43–52
DOI 10.1007/s10228-007-0009-y

FULL PAPER

Lifestyle of Korean mudskipper *Periophthalmus magnuspinnatus* with reference to a congeneric species *Periophthalmus modestus*

Gun Wook Baeck · Toru Takita · Yang Ho Yoon

Received: 5 January 2007 / Revised: 20 August 2007 / Accepted: 23 August 2007 / Published online: 21 December 2007

Abstract To investigate the life history and ecology of the mudskipper *Periophthalmus magnuspinnatus*, observations and collection were made on coastal mudflats in southern Korea. *Periophthalmus magnuspinnatus* was active from May to September on the mudflats, exclusively occupying rough and elevated or sloped mudflats of the seashore or the stream mouth, usually vegetated with halophilous grasses. The congeneric species, *P. modestus*, mainly occurred on extensive low-elevation and level mudflats with no visible vegetation. An apparent alternation of habitat use by *P. modestus* took place on mudflats at the stream mouth in mid-October, when *P. magnuspinnatus* began wintering in its burrow and *P. modestus* came onto the vacated mudflats to construct burrows for wintering. The active season for *P. magnuspinnatus* at 17°C or higher air temperature was a little shorter than that of *P. modestus*. *Periophthalmus magnuspinnatus* constructed a burrow for the entire season in the highest area of the intertidal mudflat, where they hid themselves during high tide or when frightened, whereas *P. modestus* were likely to use any burrow constructed by other animals or sunken places to hide. The main stomach contents of *P. magnuspinnatus* were crabs and gammarids. During the reproductive season from May to July, *P. magnuspinnatus* performed mating behaviors and constructed a spawning burrow similar to the ones known for *P. modestus*, except their body color turned dark and quivering body movements were observed in the mature male instead of a pink or orange body color and wiggling body movements as in *P. modestus*. Eggs, measuring 1.56–1.69 mm in major axis and 0.94–1.0 mm in minor axis, were laid on the ceiling and the side wall of the "J"-shaped spawning room generally known for *Periophthalmus* species. Young of both species started to occur on the mudflat in June.

Keywords *Periophthalmus magnuspinnatus* · Life style · Mating · Mudflat · Habitat

G. W. Baeck
Korea Inter-University Institute of Ocean Science,
Pukyon National University, Daeyeon-dong,
Nam-gu, Busan 608-737, Korea

T. Takita (✉)
18-8 Hokuei-cho, Nagasaki 852-8063, Japan
e-mail: t-takita@knd.biglobe.ne.jp

Y. H. Yoon
Faculty of Marine Technology,
College of Ocean Science and Technology,
Chonnam National University, Dunduck-dong,
Yeosu, Chonnam 550-749, Korea

Introduction

Mudskippers of the genus *Periophthalmus* are gobiid fishes, comprising 17 species (Larson and Takita 2004), which occur throughout the Indo-Pacific, with a single species in West Africa (Murdy 1989). All these fishes live on tidal flats, exposing almost their whole body to the air at low tide (MacNae 1968; Milward 1974; Takita et al. 1999). The unique lifestyle of this fish group has drawn considerable interest, and many investigations have been conducted (Clayton 1993; Tsuhako 2001). However, probably because of the difficulty in approaching their soft mud habitats, their lifestyle itself has not yet been well elucidated and therefore is not understood.

Periophthalmus magnuspinnatus is a species of mudskipper originally described in Korea by Lee et al. (1995) and recently reported from the Chinese coasts of Bohai, Yellow, East China, and South China Seas (Wang et al.

2006). Lee et al. (1995) gave the morphological description of the species together with notes on their distribution as well as that of a congeneric species, *Periophthalmus modestus*, in the Korean Peninsula. According to these authors, Korean *P. magnuspinnatus* are distributed from Asanman Bay on the northwest coast down to the southwest coasts of the Peninsula, largely overlapping with the distribution of the congeneric species, but less geographically extensive.

As for *P. modestus*, there are many published contributions in various research fields, as this species has been well known on the mudflats of East Asian countries since ancient times and has attracted much biological attention. In contrast, for the taxonomically new *P. magnuspinnatus*, there is only a study on the skin structure (Park 2002), and their lifestyle has not yet been investigated.

The mudflat habitats of mudskippers are a seemingly severe environment for aquatic dwellers, but organisms that dwell there have evolved diverse lifestyles (Reise 1985). There are many contributions on the physiological (e.g., Takeda et al. 1999), morphological (e.g., Schöttle 1931), and behavioral (e.g., Ishimatsu et al. 1998) adaptations of mudskippers, which enable them to live successfully. *Periophthalmus magnuspinnatus* and *P. modestus* have evolved different lifestyles to partition their semiterrestrial habitat, which offers aquatic organisms an environment that is quite different from that of the completely aquatic habitat.

The purpose of this study was to describe in detail the lifestyle of the mudskipper *P. magnuspinnatus* and record how this species partitions resources with the congeneric species, as both species are significant biological components of the tidal flat ecosystem.

Materials and methods

Field surveys to observe the lifestyle and collect specimens were conducted on spring tide days from May to October 2004–2005 and April 2006, once or twice a month each year in the innermost areas of Suncheonman Bay on the southern coast of Korean Peninsula. The main studies were conducted at two sites, Sangnim (34°51′695″ N; 127°29′528″ E) and Sangbong (34°50′437″ N; 127°32′655″ E), both facing Suncheonman Bay. The tidal range of a spring tide is about 3.5 m in the study sites, and enormous mudflats are exposed at every low tide. Because *P. magnuspinnatus* lives on the highest location in the intertidal mudflats, surveys on the mudflats were possible for more than 6 h on every spring tide day.

In Sangnim, the observations and collections were conducted on a sloped mudflat 9 m wide formed at low tide beside a small stream or undulating mudflats formed around the mouth of the stream. On the landward side of the stream, shrimp ponds were located, and the outer artificial walls of the shrimp ponds formed mud levees between the ponds and the stream. The sloped mudflats beside the stream, which were inclined at an angle of about 7° or less to the horizon, were covered by a halophyte, *Suaeda japonica*, on the higher areas (Fig. 1a), and the lower areas close to the tidal channel had no visible vegetation. Outer mud walls of the shrimp ponds were steep with an inclination of 40° or less to the horizon (Fig. 1a), where another halophyte, *Suaeda maritima*, grew at the high water level of spring tides. Around the stream mouth, mudflats were irregularly undulated, and the top of the undulations was vegetated with *S. japonica* (Fig. 1b). Beyond the undulating mudflats, there were extensive level and nonvegetated mudflats.

In Sangbong, the main study site was the level and extensive mudflats formed on both sides of a tidal channel (Fig. 1c). A part of the area was bordered by 1.5-m-high stone seawalls and another part was bordered by roughly constructed mud levees. Some areas along the shore were vegetated with the reed *Phragmites australis* (Fig. 1d). There was an area of about 30 m^2 about 30 m off the seawall, which was slightly elevated from the surrounding level mudflats and vegetated with *S. japonica* (Fig. 1c).

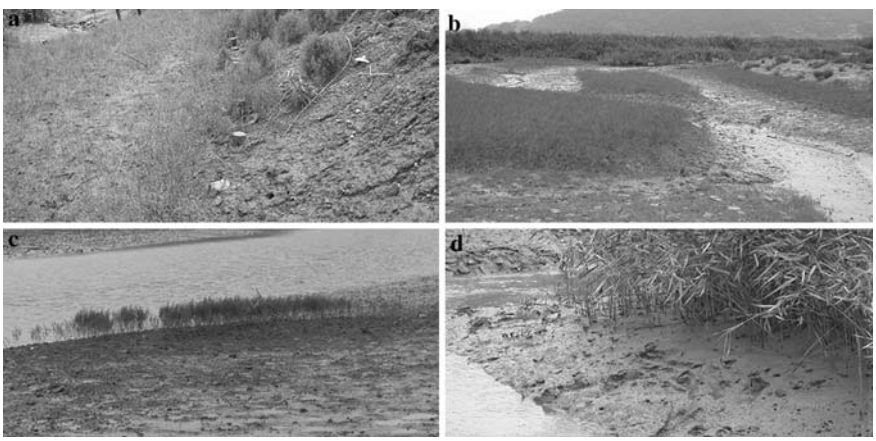

Fig. 1 Muddy study sites in Sangnim and Sangbong. **a** A sloped mudflat beside a stream in Sangnim; **b** undulating mudflats at the stream mouth in Sangnim; **c** mudflats on both sides of a tidal channel in Sangbong with a small elevated area covered by a halophyte, *Suaeda japonica*; **d** a mudflat covered by the reed *Phragmites australis*

The herbivorous mudskipper *Boleophthalmus pectinirostris*, which was distinguishable from *Periophthalmus* species by its larger body size, slender body form, and behavioral characteristics, was common at both study sites.

Observations on *Periophthalmus* mudskippers were made from the top of the seawalls in Sangbong and the top of the shrimp pond levees in Sangnim at a distance of less than 15 m from the fish. For the close observation and collection of specimens, observers approached the object by walking on the soft mud. *Periophthalmus* mudskippers were sensitive to any moving object, especially on the soft mudflat, but if the observer approached slowly and stopped for some time at a point, the observer did not scare them, and close observation of their behavior was possible. Every field survey was conducted from 11 A.M. to 4 P.M. at each location, when the habitats were exposed and *Periophthalmus* mudskippers were active on the mudflat. Eightfold magnification binoculars, cameras, and videos were used to identify the species and record their behaviors. Fish specimens were captured by hand or with a dip net. The salinity of the water left in the burrow at low tide was measured with a field salinometer (S/Mill-E; ATAGO, Japan).

A 36-m^2 area on a mudflat with no covering vegetation was selected about 20 m upstream from the stream mouth in Sangnim, where a shrimp pond facility made approach to the area possible. The number of *P. magnuspinnatus* in the area was counted every month from June to August 2005, when only adult *P. magnuspinnatus* were there, to estimate their density. The number of mudskippers in an area of the mudflat was highly variable, because individuals often moved into and out of the area and often hid in burrows. The count was taken three times for each survey, and the largest count was taken as the rough estimate of the density.

To compare the distribution of the two *Periophthalmus* species in Sangbong, two 85-m-long lines were set on the mudflat parallel to and 5 m and 10 m apart from the shore line. The numbers of both species within the 5-m-wide areas between two lines and between the shore and the line close to the shore were counted on 5 June 2004. The observer walked in the soft mud along the lines to approach, identify, and count the fish. Consequently, the fish counted were the ones that did not hide in the burrow or flee from an approaching observer.

Specimens of *P. magnuspinnatus* and *P. modestus* collected during the study were fixed in 10% formalin solution. Four individuals collected on 4 August 2004 in Sangbong and nine individuals collected on 3 September 2004 in Sangnim were dissected to examine the stomach contents. Samples of both species from these collections are deposited at the National Museum of Nature and Science, Tokyo (NSMT).

Results

Field identification. *Adults*. Living or freshly dead adult *P. magnuspinnatus* and *P. modestus* (Figs. 2, 3a, d) are light brown in body color. Both species ordinarily have irregular lateral dark brown oblique stripes (Fig. 2a), but a temporary color pattern sometimes covers the ordinary stripes in living fish (Fig. 2b). The stripes become obscure or vanish after formalin fixation (Fig. 3a, d). The whole color pattern is a little brighter in *P. magnuspinnatus* than in *P. modestus*, although the brightness is changeable in both species. *P. magnuspinnatus* has many distinctive bright blue dots on the lateral sides of the head and trunk (Figs. 2a, 3a), whereas *P. modestus* has tiny black dots scattered on the lateral side of the trunk (Figs. 2b, 3d). Some *P. magnuspinnatus* have the blue dots only on the lateral surface of the head. Although *P. modestus* also has white dots on the lateral side of the head, those dots are much smaller in size than the blue dots of *P. magnuspinnatus*. The blue dots in *P. magnuspinnatus* and white dots in *P. modestus* vanish immediately after fixation in formalin solution, whereas the black dots in *P. modestus* remain longer.

The first dorsal fin is larger in *P. magnuspinnatus* than in *P. modestus* (Fig. 3a, d). In fresh samples, the first dorsal fin has three color zones in *P. magnuspinnatus*: reddish-brown in the narrow outer edge, a black band marginally, and dark reddish brown in the whole area beneath the black band. The reddish-brown color vanishes immediately after fixation, and the whole first dorsal fin turns dark, being

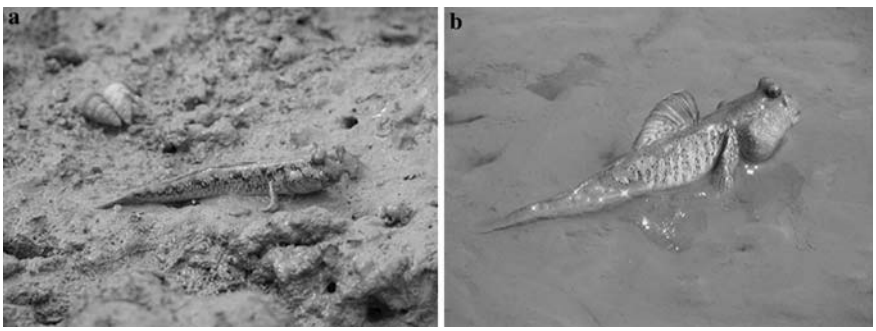

Fig. 2 *Periophthalmus magnuspinnatus* (**a**) and *P. modestus* (**b**) in the habitat. Oblique patterns on the lateral body of both species are changeable

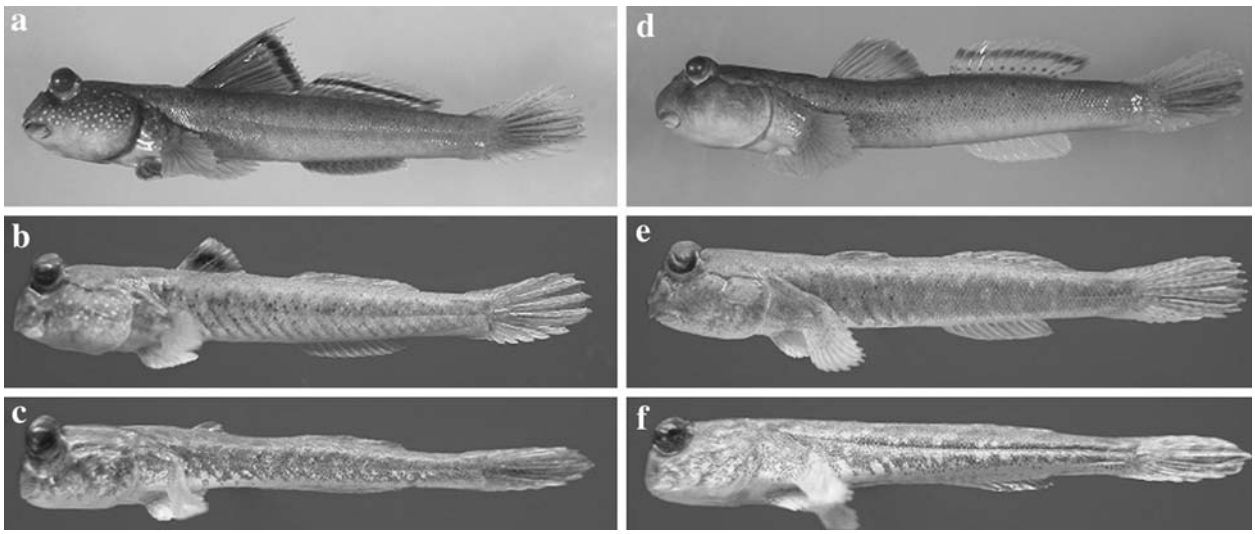

Fig. 3 Fresh *Periophthalmus magnuspinnatus* (*left*) and *P. modestus* (*right*) specimens photographed 30 min after formalin fixation. **a** Adult *P. magnuspinnatus* of 96.6 mm TL; **d** adult *P. modestus* of 84.2 mm TL; **b**, **e** juveniles of about 40 mm TL; **c**, **f** juveniles of about 20 mm TL

darker marginally and pale along the dorsal edge. The first dorsal fin in *P. modestus* is also dark marginally, but the color is much lighter in *P. modestus* than in *P. magnuspinnatus* (Fig. 3a, d). Both species only occasionally spread the dorsal fins in their habitat, and the color pattern on the dorsal fin is not always usable in identifying species, except for the reddish-brown fin edge in *P. magnuspinnatus*, which is visible even if the fin is folded. The elongated fin rays of the first dorsal fin in *P. magnuspinnatus* (Fig. 3a) are also not usable for species identification in the habitat for the same reason as already mentioned.

In *P. magnuspinnatus*, the second dorsal fin has three color bands: in order from its outer margin they are reddish-brown, black, and dark brown. Three bands are divided by thin white lines. *P. modestus* also has three color bands in the second dorsal fin: a marginal zone with a pale color; a midlateral black band; and a line of dark dots basally on each fin ray. The black color of the anal fin in *P. magnuspinnatus* clearly distinguishes it from *P. modestus* when the fin is visible (Fig. 3a). However, the anal fin is usually hidden in the muddy substratum in the habitat (Fig. 2).

The most useful character to distinguish two species in the habitat is the blue dots of *P. magnuspinnatus* on the lateral sides of the head and trunk (Fig. 3a). However, the blue dots are often covered by the mud and difficult to see from a distance, and exact identification is possible with 8× binoculars only when the fish is less than 5 m from the observer unless the fish spread its characteristic vertical fins.

Juveniles. Juvenile *P. magnuspinnatus* of about 40 mm in total length: TL (Fig. 3b) can be discriminated from juvenile *P. modestus* of the same size (Fig. 3e) by the blue dots, which appear on the cheek, and by the first dorsal fin, which has partly become dark in the former species. In *P. modestus*, the first dorsal fin is comparatively small in size and totally gray in color (Fig. 3e). However, the identification requires careful close observation, which is not easy in the muddy habitat. In juvenile *P. magnuspinnatus* of 20 mm or less (Fig. 3c), such characters have not yet appeared, and discrimination from *P. modestus* of the same size (Fig. 3f) cannot be done in the habitat. The melanophores of the anal fin in *P. magnuspinnatus* have started to appear in individuals of 40.7 mm, and the specific color difference in the anal fin can be recognized with the naked eye in a fish of 42 mm or larger.

Habitat. In the Sangnim study site, only *P. magnuspinnatus* was found on mud slopes beside the stream (Fig. 1a) and on undulating mudflats with thick vegetation (Fig. 1b) around the stream mouth from May to September in both 2004 and 2005. Density of the adult *P. magnuspinnatus* taken from June to August, when the young of the year were not included, was 0.3–0.4/m^2 on the mudflat 20 m upstream from the stream mouth. No other area could be approached to ensure the species identification. The fish density obtained in the area was unlikely to be far from the average of the whole habitats beside the stream and around the stream mouth. There were few *P. magnuspinnatus* on the low and level mudflats that extended off the undulating mudflat, but *P. modestus* was abundantly distributed there. The results of October observations, when *P. magnuspinnatus* decreased in number and *P. modestus* appeared on the mudflats beside the stream and around the stream mouth, is shown later.

The numbers of both species along the two 85-m lines set parallel to and 5 m and 10 m apart from the shoreline

on the mudflat in Sangbong were counted on 5 June 2004. *P. magnuspinnatus* and *P. modestus* within 5 m from the shore were 7 and 1 in number, respectively, whereas those between the two lines were 1 and 6, respectively. These data are surely an underestimation of fish number on the mudflat, for many fish hid in burrows or fled from the approaching observer. However, it can be assumed from these observations that *P. magnuspinnatus* lives closer to the shore and *P. modestus* lives further offshore. *P. magnuspinnatus* was also dominant in the elevated 30-m^2 area and its periphery in Sangbong (Fig. 1c) from May to September, although a census could not be conducted because of the thick vegetation and rough topography.

It is apparent from these observations and counts in both study sites that there is a segregation of the habitats between the two species. *P. magnuspinnatus* lives on rough and elevated or sloped mudflats, which are usually located close to land and vegetated with some halophilous grasses, while *P. modestus* mainly lives over the extensive level and low mudflats with no visible vegetation.

In October in both 2004 and 2005 on the mudflat in Sangnim, *P. magnuspinnatus*, which had exclusively occupied the areas beside the stream and around the stream mouth until September, was found to have mostly disappeared and the areas were alternatively occupied by *P. modestus*. Of ten *Periophthalmus* adults observed on 14 October 2005 on the mudflat 20 m upstream from the stream mouth, only two *P. magnuspinnatus* were counted and the remainder were all *P. modestus*. This clear alternation in habitat occupation was caused by their wintering behavior, which is shown later.

General lifestyle. *Active season*. We found only a few and inactive *Periophthalmus* mudskippers on mudflats around Suncheonman Bay on 7–8 November 2003 and on 23 March 2004, when excursions were conducted to locate study sites. On 13 April 2006, a few *P. modestus* were found, but these were inactive and stayed almost still in place, and *P. magnuspinnatus* was not found at either study site. From May to early October in both 2004 and 2005, *P. magnuspinnatus* was active on mudflats, and some males had started courtship display by 10 May in 2005. It is assumed from those observations that *P. magnuspinnatus* are active from late April to early October on mudflats of southern Korean coasts. Many *P. modestus* were still active after most *P. magnuspinnatus* had disappeared from the mudflat surface in middle October, so it is likely that the active season of *P. magnuspinnatus* is a little shorter than that of *P. modestus*.

As *Periophthalmus* mudskippers expose most of their body in the air for a long period each day, their activities are not much affected by water temperature, but mainly by air temperature. Air temperatures (in °C) in 2005 at the mouth of Yeoja Bay, which was close to the study sites, rose to 30.8 in August and fell to −1.8 in January (South Sea Fisheries Research Institute, Yeosu, unpublished data). The air temperatures when *P. magnuspinnatus* was active on mudflats from spring to autumn were 17°C or higher. The difference of the temperature in a day as well as the wind might also influence their activities.

Behaviors during high tide. From May to September at high tide in Sangnim, some but not all *P. magnuspinnutus* were moving along the water's edge through sparse halophilous grasses growing on the mudflat. In Sangbong, some *P. magnuspinnutus* were found to stay, exposing their whole or the anterior portion in the air, together with *P. modestus* on the vertical seawall or exposed rocks on the mudflat during high tide in warm seasons. The rest of *P. magnuspinnatus* hid in burrows located just below or less than 1 m from the highest water level on the mudflat. They came out of the burrow and foraged when the burrow opening was exposed by the receding tide. The numbers of *P. magnuspinnatus* present above the water surface and those hiding in the burrows during high tide could not be known, for many of them were hidden under the thick vegetation or in cavities under the seawall.

In Sangbong, from May to September, some *P. modestus* were hanging on the seawall or staying on rocks at high tide. They were few in number compared with the large number distributed over the extensive level mudflats during low tide. It is assumed that many *P. modestus* stay in concave mud structures while the mudflat is covered by water.

Only a few or no individuals of both species were exposed to the air at high tide in September and October, showing that both *Periophthalmus* species are in their burrows during high tide when the temperature is low.

Burrowing. The structure of two *P. magnuspinnatus* burrows for refuge was inspected in Sangnim on 5 August and 3 September 2004, when their spawning season was over. Burrows were located just under the high tide level on sloped mudflats in Sangnim. The mud surrounding the burrow opening was dry and had cracks, showing that the burrows were not inundated by every high tide. The one inspected in August had a vertical shaft 30 cm long and 2–3 cm in diameter. The shaft had an enlarged room 10 cm in diameter and 3 cm in height at 5 cm deep from the burrow opening on the mudflat surface. The burrow was half filled with very muddy water of 25‰ salinity. The one inspected in September was formed obliquely on the steep slope of the mud levee, being 19° to the horizon and 29 cm long from the opening. This burrow was simple in structure, being 2–3 cm in diameter from the opening to the bottom and having no enlarged room. The burrow was half filled with very muddy water of 5‰ salinity. In Sangbong, *P. magnuspinnatus* was often found to hide in burrows formed beneath the seawall, where an inspection could not be done.

Foraging *P. magnuspinnatus* frequently hid themselves in the burrow when frightened by approaching predatory seabirds or human beings. It is likely that *P. magnuspinnatus* generally possesses a burrow all the year round for refuge, although some *P. magnuspinnatus* fled to the tidal channel or into the nearby reedy bushes when frightened.

Most *P. modestus*, when frightened by approaching observers, ran far away on the mudflat, and some individuals hid themselves in burrows or sunken places on the mud. However, *P. modestus*, which hid in burrows, did not stay deep in the burrow, but stayed just under the burrow opening, showing that they transiently hid in any burrow constructed by other animals. It is likely that *P. modestus* does not possess a burrow for refuge except for the season of low temperature.

Periophthalmus magnuspinnatus usually foraged close to the burrow, and threatened approaching conspecifics by erecting its dorsal fins or rushing at them. However, the areas around burrows were not always protected by such aggressive behaviors. *P. magnuspinnatus* does not have a territory, except for the period of spawning, which is described later.

Feeding. *Periophthalmus magnuspinnatus* sometimes dashed against something on the mud and pushed its mouth into the mud. They seemed to catch some prey in or on the mud. The contents of the four stomachs collected on 4 August 2004 in Sangbong contained crabs or crab legs, whereas those of the nine stomachs collected on 3 September 2004 in Sangnim were variable, consisting of gammarids, crabs, other crustaceans, and other benthic animals common on mudflats or tidal channels.

Spawning. *Courtship behavior*. Courtship and egg-caring behaviors typical in mudskippers were performed by *P. magnuspinnatus* from early May to July. Males construct a burrow for spawning by carrying out the mud and spread mud pellets around the burrow opening (Fig. 4a). It is unknown whether males construct a new burrow for spawning or remodel the refuge burrow into a spawning burrow. Then, males darken their body color and move around extensively on the mudflat, occasionally showing jumping and quivering displays. A jump is nearly the body length in distance and half the body length in height. When showing the quivering display (Fig. 4b), males stoop and direct the caudal fin up and quiver their convex body horizontally, which is supported at the bottom of the head and of the caudal peduncle and both pectoral fins. When a female responds, the male decreases the jump frequency and leads her to the burrow, sometimes quivering the body, and occasionally they show each other their lateral body with the dorsal fins spread (Fig. 4c).

Upon arriving at the burrow entrance, the female usually stayed still there for some time, as if hesitating to enter. The male repeatedly moved in and out of the burrow (Fig. 4d) and showed her the quivering movements, until the female went into the burrow (Fig. 4e). Staying only for a short duration in the burrow, the female then moved away from the area, leaving the displaying male there. Sequences of mating by *P. magnuspinnatus* observed during the surveys were all incomplete. The completion of mating and spawning, which usually took several hours in *P. modestus* (Takita et al., unpublished data), has not yet been observed in *P. magnuspinnatus*.

Periophthalmus modestus often performed courtship behavior on the level and wet mudflat in Sangbong at the same season as that of *P. magnuspinnatus*. Courtship behaviors of Korean *P. modestus* were the same as that reported previously (Matoba and Dotsu 1977).

Burrow for spawning. Spawning burrows of *P. magnuspinnatus* were located high in the intertidal zone, where their refuge burrows were located. It is very likely that the spawning burrow is also exposed for a long time in the air and the water inside is not often exchanged.

Male and female couples, who possessed a burrow together, were commonly found during the spawning season (Fig. 4f). They were working together to construct the burrow, repeatedly carrying out the mud from the burrow. The couples were strongly territorial, driving approaching conspecifics and crabs away from the burrow. We removed the mud surrounding two burrows occupied by couples, which revealed that burrows were incomplete in shape, having only a short vertical shaft. It seems that males attract a female before completing the burrow construction and complete it together with the female. However, it was found on 5 June 2004 in Sangbong that a male that had completed a spawning burrow performed the courtship display to females. The burrow had the same structure as the one with a batch of eggs in it. It is still necessary to study the prespawning behavior to know exactly when the spawning burrow is completed.

Four burrows with eggs laid in it were inspected during the surveys in May and June 2005: two in Sangnim and two in Sangbong. The burrows had two or three openings 3–10 cm apart (Fig. 5a, b). Then the shafts went down 3–5 cm from the openings and were united into a main vertical shaft 3–5 cm in diameter (Fig. 5a, c). The shaft went straight down to the bottom, and a short horizontal tunnel connected the shaft bottom to the bottom of the spawning room (Fig. 5a, d). The spawning room was a short column 6–8 cm high, being covered by a dome-like ceiling (Fig. 5a). The horizontal cross section of the spawning room was oval, about 6 cm in major axis and 5 cm in minor axis. Eggs were laid on the ceiling (Fig. 5e) and the upper part of the side wall of the spawning room. Depth from the mudflat surface to the burrow bottom was 21–24 cm (Fig. 5a).

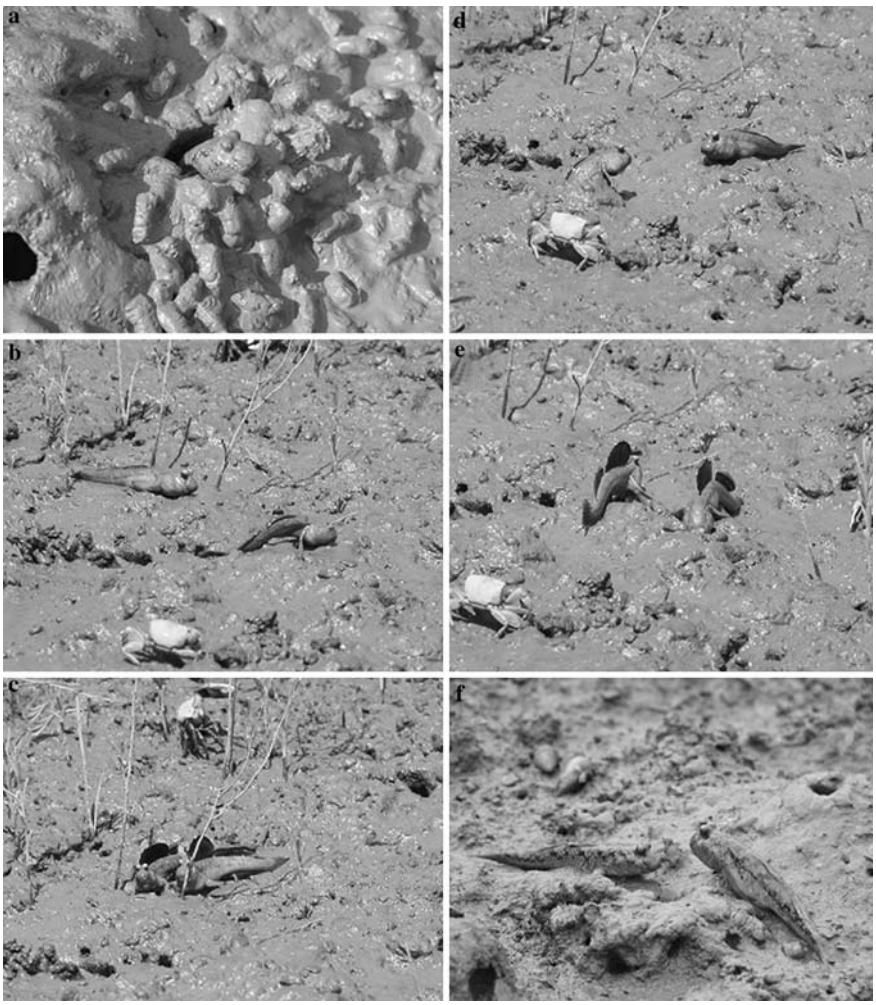

Fig. 4 Prespawning performances in *P. magnuspinnatus*. **a** A male spitting mud pellets around the burrow; **b** a male (*right*) quivering the stooped body in front of a female; **c** a male (*left*) and a female (*right*) showing each other the lateral body with dorsal fins fully spread on the way to the spawning burrow; **d** a male at the opening of the burrow (*left*) attracting a female (*right*) who would not respond to him immediately; **e** a female just entering into the burrow (*right*); **f** a male and a female having established a territory around the burrow

Burrows in which eggs had been laid were guarded by a male. The male would not venture far away from the burrow unless frightened by approaching observers. Males guarding the burrow repeatedly entered into the burrow, carrying air to the spawning room, a behavior that is known in a tropical mudskipper (Ishimatsu et al. 1998). The air-carrying behavior was observed only when the burrow opening was large enough and the burrow was fully filled with water so that the diving male with air in his inflated mouth could be seen. The air stored by the male was confirmed in all spawning rooms with eggs laid when the burrow was collapsed to observe the burrow structure. Guarding males were territorial, threatening approaching conspecifics and crabs by vertically spreading their dorsal fins or sometimes charging at them.

Eggs. Eggs (Fig. 5f) collected from a spawning room on 4 June 2005 in Sangnim were oval in shape, measuring 1.56–1.69 mm in major axis and 0.94–1.0 mm in minor axis (n = 20). Similar to ordinary gobiid eggs, the egg has numerous chorionic filaments, which are attached at an end of the chorion and form a tuft.

Occurrence of juveniles. Juvenile *P. magnuspinnatus* were first found on mudflats in June. They were from 20 to 40 mm TL in August both in 2004 and 2005, and were abundant on sloped mudflats beside the tidal channel in Sangnim. They were solitary, staying apart from each other, and frequently showed aggressive charges at other conspecific juveniles.

Juvenile *P. modestus* occurred first on the Sangbong mudflat in June both in 2004 and 2005, at the same time as juvenile *P. magnuspinnatus*. They formed loose groups on wet mudflats, without showing serious charges at other conspecific juveniles. However, it is not exactly known whether the aggressive characteristic in juvenile *P. magnuspinnatus* is typical in this species or stage dependent.

Wintering. On 13 October 2004 and 14 October 2005 on the mudflats beside the stream and around the stream mouth in Sangnim, the area in which *P. magnuspinnatus* had been exclusively distributed until September was alternatively occupied by *P. modestus*. No adult *P. magnuspinnatus* were found there, and their young were few in number in the morning. In the afternoon, a few adult

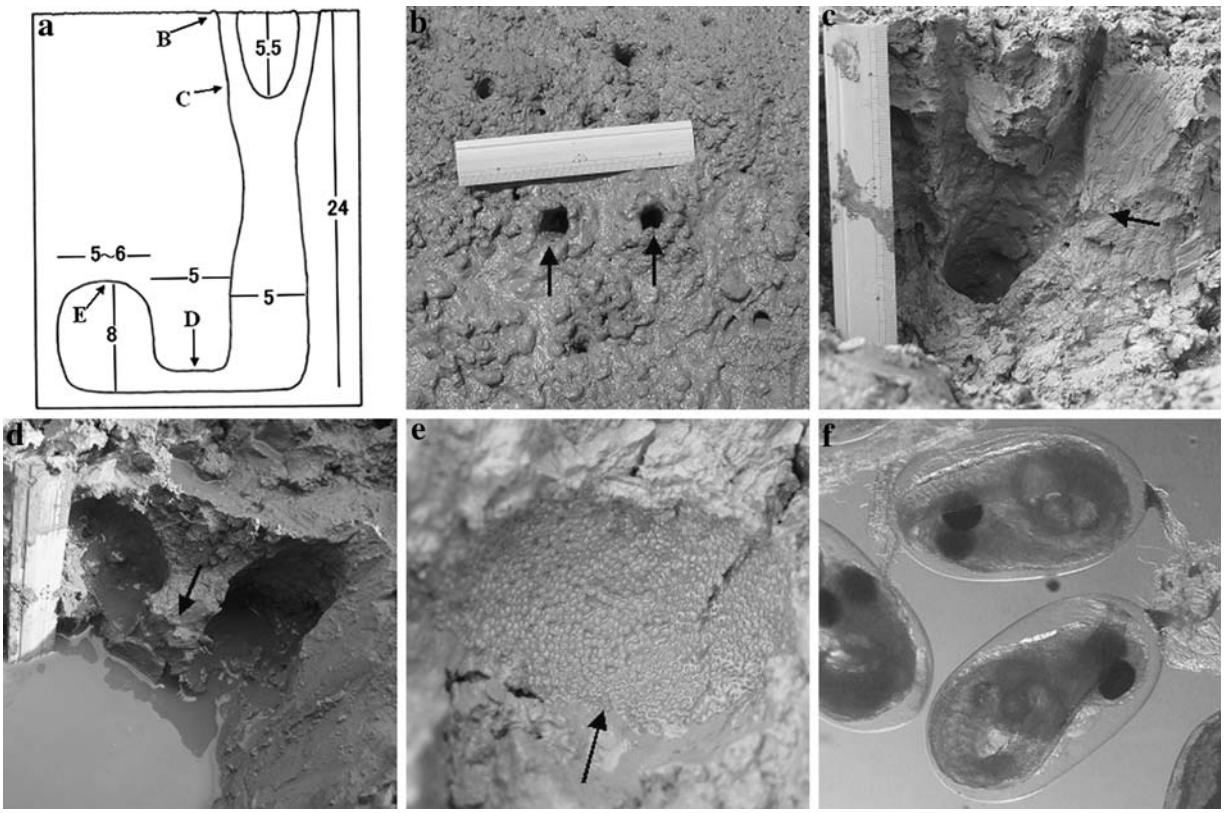

Fig. 5 A spawning burrow of *P. magnuspinnatus* inspected on 4 June 2005 and the eggs laid in it. **a** A drawing of the spawning burrow, with numbers showing the size of each portion in centimeters, *B–E* showing the portions shown in the following photographs. **b** Two openings (*two arrows*) of the spawning burrow; **c** the upper part of the burrow, which takes a "U" shape and is connected to the main shaft; **d** the bottom of the spawning burrow, where the main shaft (*right*) is connected by a narrow tunnel (*arrow*) to the bottom of the spawning room (*left*); **e** eggs laid on the dome-like ceiling of the spawning room; **f** eggs taken from the spawning room

P. magnuspinnatus appeared from burrows and the number of young increased gradually as it became a little warmer, but they were still few in number. *P. magnuspinnatus* were all inactive with some adults remaining at the burrow opening (Fig. 6a). It was assumed that most *P. magnuspinnatus* had started wintering and were hidden in their burrow, closing the opening with mud. Some *P. modestus* had constructed a burrow and stayed at its opening (Fig. 6b), indicating that the time to winter was also nearing for *P. modestus*. Burrows of *P. modestus* were located about 1 m below the area where burrows of *P. magnuspinnatus* were located.

No *P. magnuspinnatus* was found on 12 October 2004 and 14 October 2005 in Sangbong, suggesting that they had already hidden deep in the burrow or in cavities under the seawall. Many *P. modestus* were still foraging on the mudflat, and some were staying at their burrow opening.

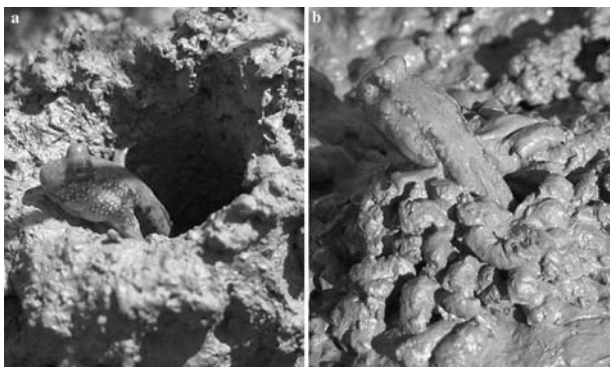

Fig. 6 *Periophthalmus magnuspinnatus* (**a**) and *P. modestus* (**b**) at the opening of the burrows for wintering in middle October

Discussion

Periophthalmus magnuspinnatus stayed on some exposed substratum during high tide in warm seasons on southern coast of Korea, whereas only a few or no individuals exposed their body to the air in September and October, when the temperature was lower. The behavior of staying out of water during high tide is temperature dependent, as reported in *P. modestus* (Ikebe and Oishi 1996). In October, when the habitats were quite cool, *P. magnuspinnatus* was found to stay in the burrow or at its opening until the air temperature became high enough for them to move onto

the mudflat surface, as reported in a species (*Periophthalmus koelreuteri*) of Kuwait (Tytler and Vaughan 1983). Burrowing of Korean *Periophthalmus* species in fall and winter is the mechanism for protection from low temperatures. The severe climate of Korea limits *P. magnuspinnatus* activity on mudflats to only half the year, from April to October.

It appears that many *P. magnuspinnatus* possess burrows all the year round to hide in emergencies during low tide and stay inside during high tide, not venturing far away from the burrow. In contrast, *P. modestus* does not possess its own burrow for refuge in warm seasons, roving agilely and extensively during low tide periods. It was often observed that *P. modestus* in an emergency used burrows or concave mud structures that seemed to have been excavated by other animals. The use of crab burrows by *P. modestus* for refuge has been reported in Okinawa (Oshiro et al. 2005).

Wading birds, which are also abundant in Korean mudskipper habitat, are thought to be the main predator of Indian *Periophthalmus* mudskippers (Mukherjee, 1971a, b). The main function of the *Periophthalmus* burrow is assumed to be the concealment of eggs or the fish themselves from predators (Atkinson and Taylor 1991). The specific difference in burrowing between *P. magnuspinnatus* and *P. modestus* is likely to be their reaction to avian predators. *P. magnuspinnatus* has obtained safety by keeping a refuge nearby, consequently limiting their home range for foraging. *P. modestus*, which has the ability of swift movement to escape from predators, has obtained a broader home range to seek for suitable foods.

Individual *P. magnuspinnatus* always maintain a space around themselves in or out of the breeding season, but aggressive behavior to defend a territory was exerted only after pairing. Nursall (1981) observed in Australian species of *Periophthalmus* that there was aggressively forced spacing of individuals, but no defense of territory, unless it was during breeding season. MacNae (1968) reported in male *Periophthalmus chrysospilos* a territorial behavior with vigorous display in defense of an area with a female in it. It is unknown whether the territoriality reported in *P. modestus* (as *Periophthalmus cantonensis*) (see Matoba and Dotsu 1977) and *Periophthalmus sobrinus* (see Stebbins and Kalk 1961) is present throughout the year or only during the breeding season.

Periophthalmus magnuspinnatus live high in the intertidal mudflat and construct a burrow for refuge in or near their home range all the year round. While hiding in the burrows, *P. magnuspinnatus* are unlikely to have to stay long in the hypoxic water in the burrow. Their burrows, which are located high in the intertidal zone, are immersed only for a short duration or remain out of water during the high tide period, providing fish with a hiding space containing adequate air.

Periophthalmus modestus (as *P. cantonensis*) construct a "J"-shaped spawning burrow with a depth of ca. 25 cm from the mudflat surface (Kobayashi et al. 1971; Matoba and Dotsu 1977). This study revealed that the burrow of *P. magnuspinnatus* was similar in shape to that of *P. modestus*. *Periophthalmus modestus* also performed courtship displays concurrently near the *P. magnuspinnatus* habitat. During courtship, male *P. modestus* (as *P. cantonensis*) change their brown body color to pink or orange (Matoba and Dotsu 1977), and jumps are much higher and wiggles are much slower than those in the *P. magnuspinnatus* display. Because of the differences in coloration and style of courtship behavior, hybridization is likely to be avoided.

The mystery of embryo incubation in the extreme hypoxic condition in the mud mentioned in some papers (Atkinson and Taylor 1991; Graham 1997) was solved as Ishimatsu et al. (1998) confirmed brooding behavior by *Periophthalmodon schlosseri*, which consists of storage of air in the nest. Eggs of *P. modestus* (see Kobayashi et al. 1971) and *Periophthalmus sobrinus* (see Brillet 1976) were reported to be laid at the end of the burrow, which goes upward from the bottom of the shaft in the mud so that air can be stored and the eggs will be exposed in the moist air.

Males owning a spawning burrow maintain the narrow size of the opening in *P. modestus* before spawning, and females struggle when getting through (Matoba and Dotsu 1977). They speculate the function of the narrow size is that mature females have their inflated belly pressed so hard by the narrow opening when getting through that the females might be stimulated to accelerate maturation. The opening of the burrow is not very small in *P. magnuspinnatus*, and the behavior of females struggling to get through the burrow opening has not been observed.

In Queensland (Australia), four *Periophthalmus* and one *Periophthalmodon* species, which live sympatrically by partitioning the habitat, interact with a hierarchical response (Nursall 1981). *Periophthalmus magnuspinnatus* appears to be dominant and control the distribution of *P. modestus*, as *P. modestus* enters *P. magnuspinnatus* habitat after the congeneric species has disappeared or ceased its activity on the mudflat. However, no aggressive interaction has been found between these two species. It is assumed that their habitat segregation is not a result of their specific interaction, but results from the difference between species in ways of escaping from predators and foraging for food. *P. modestus* is likely to move onto elevated areas to winter, when *P. magnuspinnatus*, which are not adapted to low temperatures, have retreated to their burrow and the mudflat is thus empty.

Acknowledgments This study was supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science, Sport, and Culture, Japan to Dr. A. Ishimatsu of ECSER, Nagasaki University (No. 15405028). Dr. J.M. Dean (the University of South Carolina) kindly commented on the manuscript. We thank Dr. Zhang,

Jie (the Institute of Zoology, Chinese Academy of Sciences) who provided information on fish distribution in China. Mr. J.M. Park and Mr. H.W. Kim of Pukyong University helped us in our field surveys.

References

Atkinson RJA, Taylor AC (1991) Burrows and burrowing behaviour of fish. Symp Zool Soc Lond 63:133–155

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

Clayton DA (1993) Mudskippers. Oceanogr Mar Biol Annu Rev 31:507–577

Graham JB (1997) Air-breathing fishes. Academic Press, San Diego

Ikebe Y, Oishi T (1996) Correlation between environmental parameters and behaviour during high tides in *Periophthalmus modestus*. J Fish Biol 49:139–147

Ishimatsu A, Hishida Y, Takita T, Kanda T, Oikawa S, Takeda T, Khoo KH (1998) Mudskippers store air in their burrows. Nature (Lond) 391:237–238

Kobayashi T, Dotsu Y, Takita T (1971) Nest and nesting behavior of the mud skipper, *Periophthalmus cantonensis* in Ariake Sound. Bull Fac Fish Nagasaki Univ 32:27–40

Larson HK, Takita T (2004) Two new species of *Periophthalmus* (Teleostei: Gobiidae: Oxudercinae) from northern Australia, and a re-diagnosis of *Periophthalmus novaeguineaensis*. Beagle 20:175–185

Lee YJ, Choi Y, Ryu BS (1995) A taxonomic revision of the genus *Periophthalmus* (Pisces: Gobiidae) from Korea with description of a new species. Korean J Ichthyol 7:120–127

MacNae W (1968) A general account of the fauna and flora of mangrove swamps and forests in the Indo-west-Pacific region. In: Russell FS, Yonge M (eds) Advances in marine biology, vol 6. Academic Press, London, pp 73–270

Matoba M, Dotsu Y (1977) Prespawning behavior of the mud skipper *Periophthalmus cantonensis* in Ariake Sound. Bull Fac Fish Nagasaki Univ 43:23–33

Milward NE (1974) Studies of the taxonomy, ecology, and physiology of Queensland mudskippers. PhD thesis, University of Queensland, Brisbane

Mukherjee AK (1971a) Food-habits of water-birds of the Sundarban, 24-Parganas District, West Bengal, India. II. Herons and bitterns. J Bombay Nat Hist Soc 68:37–64

Mukherjee AK (1971b) Food-habits of water-birds of the Sundarban, 24-Parganas District, West Bengal, India. III. Egrets. J Bombay Nat Hist Soc 68:691–716

Murdy EO (1989) A taxonomic revision and cladistic analysis of the oxudercine gobies (Gobiidae: Oxudercinae). Rec Aust Mus Suppl 11:1–93

Nursall JR (1981) Behavior and habitat affecting the distribution of five species of sympatric mudskippers in Queensland. Bull Mar Sci 31:730–735

Oshiro M, Tsuhako Y, Tachihara K (2005) Habitat selection for burrow making by two species of mudskippers, *Periophthalmus argentilineatus* and *P. modestus* on the Okinawa Island, Japan. Okinawa J Biol Educ 37:9–18

Park JY (2002) Structure of the skin of an air-breathing mudskipper, *Periophthalmus magnuspinnatus*. J Fish Biol 60:1543–1550

Reise K (1985) Tidal flat ecology. An experimental approach to species interaction. Springer-Verlag, Berlin

Schöttle E (1931) Morphologie und Physiologie der Atmung bei wasser-, schlamm-, und landlebenden Gobiiformes. Z Wiss Zool 140:1–114

Stebbins RC, Kalk M (1961) Observations on the natural history of the mud-skipper, *Periophthalmus sobrinus*. Copeia 1961:18–27

Takeda T, Ishimatsu A, Oikawa S, Kanda T, Hishida Y, Khoo KH (1999) Mudskipper *Periophthalmodon schlosseri* can repay oxygen debts in air but not in water. J Exp Zool 284:265–270

Takita T, Agusnimar, Ali AB (1999) Distribution and habitat requirements of oxudercine gobies (Gobiidae: Oxudercinae) along the Straits of Malacca. Ichthyol Res 46:131–138

Tsuhako Y (2001) List of the studies on the oxudercine gobies (Gobiidae: Oxudercinae). Biol Mag Okinawa 39:103–139

Tytler P, Vaughan T (1983) Thermal ecology of the mudskipper *Periophthalmus koelreuteri* (Pallas) and *Boleophthalmus boddarti* (Pallas) of Kuwait Bay. J Fish Biol 23:327–337

Wang Z-Q, Yang J-Q, Tang W-Q (2006) A long-term misidentified new record species of Gobiidae from China—*Periophthalmus magnuspinnatus*. Acta Zootaxon Sin 31:906–910