

# Multivariate characterisation of the habitats of seven species of Malayan mudskippers (Gobiidae: Oxudercinae)

Gianluca Polgar (1) Giuseppe Crosa (2)

(1) Dipartimento di Biologia Animale e dell'Uomo, Università degli studi di Roma "La Sapienza", Viale dell'Università, 32, 00185 Rome, Italy e-mail: polgar@alfanet.it; gianluca.polgar@uniroma1.it; gianluca.polgar@gmail.com (2) Dipartimento di Biotecnologie e Scienze Molecolari, Università dell'Insubria, Via Dunant, 3, 21100 Varese, Italy e-mail: Giuseppe.Crosa@uninsubria.it

The original publication (Marine Biology, 2009, 156:1475–1486 - doi:10.1007/s00227-009-1187-0), including the electronic supplementary material (ESM) is available at [springerlink.com](http://www.springerlink.com) (<http://www.springerlink.com/content/n2437r660327505n/>) to authorized users.

## Abstract

Mudskippers (Gobiidae: Oxudercinae) are amphibious gobies. The occurrence and habitats of seven sympatric species of Malayan mudskippers were recorded: *Boleophthalmus boddarti*, *Boleophthalmus pectinirostris*, *Periophthalmodon schlosseri*, *Periophthalmus chrysopilos*, *Periophthalmus gracilis*, *Periophthalmus variabilis* and *Scartelaos histophorus*. A total of 14 surveys were made at six localities along 120 km of the west coast of the Malay Peninsula in August 1996 and September 2006. A multivariate set of ordinal parameters were used to measure the quantity of environmental water in mudskippers' habitats, and three guilds of species were discriminated. The resulting pattern mirrored the adaptive scenario depicted by physiological and anatomical studies of mudskippers' terrestriality, although in one case a terminal taxon was less terrestrial than other more basal ones. Differentiation of trophic niches may also play a role in habitat selection by the herbivorous *Boleophthalmus* spp., which were only found in unvegetated, illuminated areas and on wet mud at low tide. With the more terrestrial guild, a significant negative co-occurrence suggested direct interspecific competition.

## Introduction

With the exception of tetrapods, semi-terrestrial habitats over challenging conditions to vertebrates, and only a small number of species have truly amphibious behaviour. Mudskippers (Teleostei: Gobiidae: Oxudercinae: Periophthalmini) are gobies that are "fully terrestrial for some portion of the daily cycle" (Murdy 1989). They belong to four genera: *Boleophthalmus*, *Periophthalmodon*, *Periophthalmus*, and *Scartelaos*. All 30 mudskipper species (Murdy 1989; Jaafar and Larson 2008) are resident intertidal fishes (Gibson 1982), and are strictly linked to temperate, subtropical and tropical mudflat, mangrove and lower fluvial ecosystems. They are distributed along the Atlantic coasts of Africa and in the entire Indo-West-Pacific region (Murdy 1989).

Although based on a few model species, anatomical and physiological studies show a gradient in adaptation to semi-terrestrial conditions, from species of the genus *Scartelaos* to *Boleophthalmus*, through *Periophthalmodon* and *Periophthalmus* (e.g. Harris 1960; Milward 1974; Low et al. 1990; Kok et al. 1998; Ip et al. 1990; 2001; Aguilar 2000; Zhang et al. 2000, 2003; Chew et al. 2003). When this pattern is compared with the current phylogenetic consensus (Murdy 1989), species found in phylogenetically recent taxa present higher degrees of terrestriality (adaptation to the terrestrial environment), suggesting an increase in adaptation at each cladogenetic event (ESM, S1). In accordance with this scenario, sympatric mudskipper species of different genera are generally found in different habitats in the intertidal zone, with species of more derived genera in more terrestrial habitats (Swennen et al. 1995; Takita et al. 1999). Several accounts also suggest that direct interspecific interactions may influence their habitat distribution (Clayton 1993; Milward 1974; Nursall 1981). Nonetheless, to date quantitative analyses are scarce and a standard measure of "habitat terrestriality" is lacking.

During this study, seven species of mudskippers, belonging to four genera with different degrees of terrestrial adaptation, were recorded in the intertidal zone at six locations in the Malacca Straits, along the west coast of the Malay Peninsula. The species are (Fig. 2): *Boleophthalmus boddarti*; *Boleophthalmus pectinirostris*; *Periophthalmodon schlosseri*; *Periophthalmus chrysopilos*; *Periophthalmus gracilis*; *Periophthalmus variabilis*; and *Scartelaos histophorus*. The oxudercine species recorded from this region are listed in Table 1. The objectives of this study were: (1) to compare the habitat terrestriality of seven sympatric mudskipper species by using a multivariate measure of the quantity of environmental water; and (2) to test for nonrandom species' occurrences amongst locations and sites, so as to detect synecological interactions.

**Table 1.** Recorded mudskipper species in the Malacca Straits

Species	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)	(i)	(j)
<i>B. boddarti</i> (Pallas, 1770)	x	x	x	x	x	x		x	x	x
<i>B. dussumieri</i> Valenciennes, 1837					x <sup>a</sup>			x <sup>a</sup>		
<i>B. pectinirostris</i> (Linnaeus, 1758)	x	x							x <sup>b</sup>	x
<i>Pn. schlosseri</i> (Pallas, 1770)	x	x	x	x	x	x		x	x	x
<i>Pn. septemradiatus</i> (Hamilton, 1822)				x	x		x			x <sup>c</sup>
<i>P. argentilineatus</i> Valenciennes, 1837			x	x				x	x	x <sup>c</sup>
<i>P. chrysospilos</i> Bleeker, 1852		x	x	x	x			x	x	x
<i>P. gracilis</i> Eggert, 1935				x	x	x	x	x	x	x
<i>P. malaccensis</i> Eggert, 1935		x								
<i>P. spilotus</i> Murdy and Takita, 1999					x <sup>d</sup>	x		x	x	x <sup>c</sup>
<i>P. variabilis</i> Eggert, 1935				x <sup>e</sup>	x					
<i>P. walailakae</i> Darumas and Tantichodok, 2002								x	x	x <sup>c</sup>
<i>S. histophorus</i> (Valenciennes, 1837)	x	x	x	x	x					x

(a) Cantor (1849); (b) Koumans, (1953); (c) Berry (1972); (d) Murdy (1989); (e) Takita et al. (1999); (f) Khaironizam and Norma-Rashid (2002); (g) Khaironizam and Norma-Rashid (2003); (h) Polgar and Khaironizam (2008); (i) Polgar (2008); (j) this study. Generic names: *B.* = *Boleophthalmus*; *Pn.* = *Periophthalmodon*; *P.* = *Periophthalmus*; *S.* = *Scartelaos*

<sup>a</sup> *B. dussumieri* Valenciennes = *B. pectinirostris* (Linnaeus) (this study; see also ESM, S4)

<sup>b</sup> *Boleophthalmus* sp. = *B. pectinirostris* (Linnaeus)

<sup>c</sup> In this study, species that were only recorded

<sup>d</sup> *Periophthalmus* sp. = *P. spilotus* Murdy and Takita.

<sup>e</sup> *P. novemradiatus* (Hamilton) from the Malacca Straits = *P. variabilis* Eggert (considered here as a distinct species: Jaafar and Larson, 2008; see also ESM, S4)

## Materials and methods

### Fieldwork and species

Six locations and 26 sites along the whole intertidal zone, including mangrove forests and adjacent peritidal ecosystems, were visited during August 1996 and September 2006 (Fig. 1; ESM, S2, S3). The locations visited and respective sites were: Kuala (estuary) Selangor (03°20.5' N, 101°14.5' E), sites Sel1-Sel10; Sungai (river) Sementa Besar (03°5.0' N, 101°21.5' E), sites Sem1, Sem2; Pulau (island) Kelang (03°3.5' N, 101°19.0' E), sites Kel1-Kel4; Jugra (02°49.0' N, 101°25.0' E), sites Jug1-Jug3; Morib (02°45.5' N, 101°26.3' E), sites Mor1-Mor5; and Tanjung (cape) Tuan (Cape Rachado: 02°24.9' N, 101°51.3' E), sites Tual1-Tua2. These locations span 120 km of the west coast of the Malay Peninsula. The presence of mudskipper species was recorded at each site in areas of 25–50 m<sup>2</sup> where habitats and environmental conditions were essentially the same.

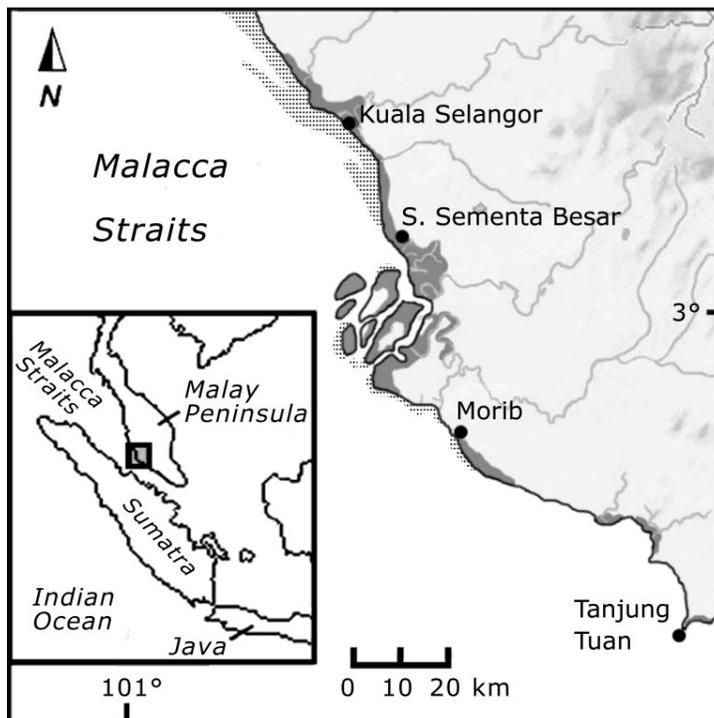
All sites were surveyed ±3 days around spring tides; K. Selangor forests were also surveyed during neap tides. We used tidal data from three reference stations (Hydrographic Directorate RMN 1996): Port Klang (for K. Selangor, P. Kelang and Sg. Sementa Besar); Permatang Sedepa (for Jugra and Morib); and Port Dickson (for Tg. Tuan). The Malacca Straits is a semidiurnal meso-macrotidal system, with tidal ranges of approximately 1–3 m during neap tides and 3–5 m during spring tides. Within the surveyed tract of coast, tidal mudflats have formed from the high sediment loads discharged by fluvial systems (e.g. the Klang-Langat and Selangor rivers), which are transported by currents along the coast, predominantly from the SE to the NW (Coleman et al. 1970). For this reason, mudflats decrease in extension from north to south: the

approximately linear horizontal extension of the intertidal zone in the studied locations was of 30–450 m (Polgar 2008). Salinity in the Malacca Straits varies with rainfall, with average values of 8–32 and two minima in May and November (southern and northern monsoons, respectively: Sasekumar 1980). Within the intertidal zone (creeks, mudflats, mangroves) salinity fluctuations are determined by rainfall, evaporation and tidal action, becoming more extreme towards land (inside higher mangrove forests, 3–50: Sasekumar 1974, 1994).

The presence of mudskippers was recorded during approximately 44 h of direct observation, with or without the aid of binoculars, at distances of 2–10 m between 09:00 and 19:00 hours. A total of 14 surveys (between 2–30 August 1996 and on 28 September 2006) were conducted across the intertidal zone, on foot (forested areas) or by boat (mudflats and creeks). A reference collection was assembled to check *Weld* identifications (Murdy 1989; Murdy and Takita 1999; Takita et al. 1999; Darumas and Tantichodok 2002). Inside mangrove forests, fish were captured by hand net or bait and line, while stake nets and cast nets (Gibson 1999) were used along forest marine fringes, on mud banks and tidal flats. Collected specimens were fixed in 5% formalin, preserved in 70% ethanol and deposited in the Genoa Natural History Museum (MSNG); several museum specimens were also examined (ESM, S4).

We did not include in the analysis records of *Pn. septemradiatus*, *P. argentilineatus*, *P. spilotus*, and *P. walailakae*, for which complete environmental data were lacking, and these were collected by GP and Dr. M.Z. Khaironizam in the same or neighbouring areas (ESM, S4; Polgar and Khaironizam (2008); Khaironizam and Norma-Rashid 2002, 2003; Polgar 2008).

In the laboratory, fish were measured to the nearest millimetre; in the *Weld*, fish size was visually estimated by comparison with objects of known size such as leaves and sticks. To minimise possible size or age-related differences in habitat use (Clayton and Vaughan 1988; Clayton 1993), we analysed only records of individuals that were >50% of the maximum recorded SL (hereafter referred to as “adults”), which also increased the reliability of species’ identifications.



**Fig. 1** Study locations: the west coast of the Malay peninsula; *darker areas*: mangrove forests, *stippled areas*: mudflats exposed during low tide. S. Sungai (river), P. Pulau (island), Tg. Tanjung (cape)

#### *Spatial and temporal distribution*

To compare the terrestriality of different species, we recorded mudskippers and their habitats during both low and high tide. Observations were made  $\pm 2$  h around predicted low tide when waterways and basins were not influenced by rain and the substrate was not influenced by wind (Clayton and Snowden 2000). At this time, the distribution was assumed to be unaffected by water movement. At high tide, we observed

mudskippers when they were reached by the water during the flood tide. At this time, their behaviour was directed at avoiding the advancing water, either by moving away from it or by entering burrows (Sayer 2005; Colombini et al. 1995; Ishimatsu et al. 1998; Lee et al. 2005). Further observations were made during the ebb tide.

*Quantity of environmental water and species occurrence*

We quantified the quantity of environmental water for mudskipper habitats using five ordinal parameters, which were measured in the same sites where mudskippers were recorded: density of vegetation cover (VC); water bodies (WB); tidal influence (TI); structural elements (SE); and external medium (EM). The first four parameters were measured during low tide, whilst the latter was measured when mudskippers were reached by the flood tide. All parameters have higher values in more terrestrial conditions (Table 2; Fig. 2, a–g).

To discriminate between different densities of vegetation cover (VC), we followed a modified version of the Malayan mangrove zonation by Sasekumar (1980). Vegetation cover limits air movement and light penetration, and reduces the evaporation rate at ground level (Macintosh 1977; Clayton and Snowden 2000). Therefore, increasing VCs (Sarpedonti and Sasekumar 1996) reduce evaporation rates on the exposed substrate. We observed six different levels of VC.

Water bodies (WB) are different hydrogeomorphic and bioturbation structures that contain water. Their morphology and persistency depend on the weather, tidal influence, wave action and biological activity. On soft-bottomed accreting shores, they are typically distributed along the intertidal zone during low tide. We observed four different WBs.

**Table 2.** Quantity of environmental water: definitions.

---

VC: density of vegetation coverage

- 1 No vegetation coverage
- 2 Patches of grass and bushes
- 3 Open tree associations: pioneer mangroves (*Avicennia* or *Sonneratia* spp.: Sasekumar, 1980)
- 4 More open and depressed areas in VC5 (bottoms of inlets and gullies: Polgar, 2008)
- 5 *Rhizophora* and *Bruguiera* spp. zone (Sasekumar, 1980)
- 6 *Bruguiera* spp. and halophytic ferns (Sasekumar, 1980)

WB: water bodies

- 1 Flooded, larger waterways/basins, continuously inundated by tides (< 2 m from the edges of rivers, creeks, and seawater)
- 2 Smaller bodies of standing water, intermittently inundated by tides (tide pools >1 m<sup>2</sup>)
- 3 Waterways emptied by ebb tides (bottoms of tidal inlets and gullies)
- 4 Animal burrows (only source of water)

TI: tidal influence

- 1 Partially submerged by MLWN (usually on lower unvegetated mudflats)
- 2 Submerged at least by MHWN (usually along pioneer forest marine fringes)
- 3 Submerged at least by MHWS (usually inside higher mangrove forests)
- 4 Submerged at least by EHWS (usually inside higher mangrove forests)

SE: structural elements

- 1 No structural elements
- 2 Pneumatophores (in front of pioneer forest marine fringes: “pneumatophore zones”)
- 3 Pneumatophores, trees, trunks and branches
- 4 Pneumatophores, aerial, prop and other types of roots, trees and heterogeneous plant debris

EM: external medium during high tide

- 1 Fish took shelter inside burrows when reached by flood tides and remained under water during high tides
- 2 Fish came out of water when reached by flood tides

---

VC, WB, TI and SE were measured during low tide, while EM was measured during flood tide

*MLWN* mean low water neap, *MHWN* mean high water neap; *MHWS* mean high water spring; *EHWS* extreme high water spring (see also Fig. 3).

Field observations of the water's edge were compared with tide tables, and mean elevations (tidal datums) calculated. Then we recorded the tidal datum reached by the water when each site was partially or completely submerged (TI). This parameter is associated with the frequency of submersion and the minimum time interval between wettings (Sasekumar 1974). Lower levels imply higher frequencies, shorter intervals and more aquatic conditions. The study sites were characterised by four TI levels.

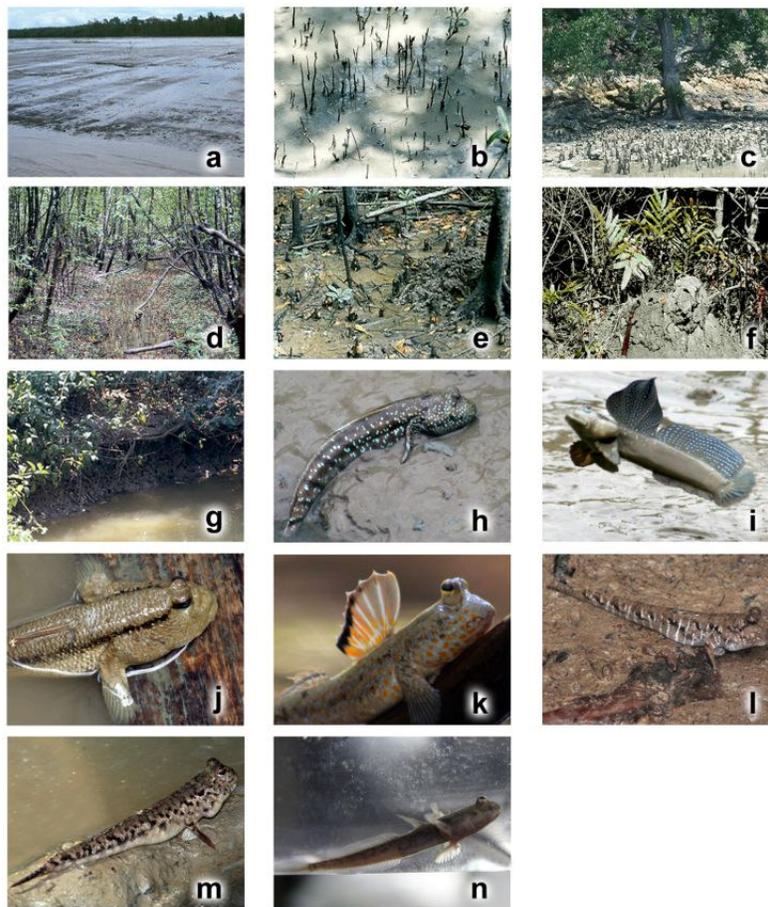
Biotic and abiotic objects or structural elements (SE) whose size is comparable to mudskippers (4–25 cm total length) can greatly increase substrate heterogeneity. More heterogeneous substrates have a greater surface per square meter, thus increasing humidity at ground level and the amount of capillary water. The presence and composition of SE along soft-bottomed tropical intertidal zones depends on plant debris and mangrove diversity (pencil-like pneumatophores, propagules, prop roots, knee-roots, etc.; Tomlinson 1986). We observed a general increase in the diversity and size range of SE from sea to land, and recorded four different combinations of SE.

External medium (EM) during flood and high tide was determined by the different strategies of water column avoidance (Table 2).

To explore the correspondence between sites or environmental variables (observations) relative to the presence of species (modalities), and the degree of association between species, we performed multiple correspondence analysis (MCA: XLSTAT 7.5.3© Addinsoft). MCA, also known as homogeneity analysis, is an exploratory technique analogous to PCA for categorical or ordinal variables (Jobson 1992). To corroborate the species associations in the factorial space, we analysed the same matrix by agglomerative hierarchical clustering (AHC: XLSTAT 7.5.3© Addinsoft), adopting the Jaccard similarity index and the strong linkage aggregation method (Johnson and Wichern 1992). Finally, jackknife protocol was applied to search for influential observations that could bias the analysis (Gotelli and Ellison 2004).

#### *Co-occurrence*

The “co-occurrence” module of ECOSIM (ECOSIM 7.72 © Kesey-Bear and Acquired Intelligence, Inc.; Gotelli and Entsminger 2001) was used to test for non-random patterns of species co-occurrence amongst the different locations (ecosystem level) or sites (habitat level). In the null-model simulation (5,000 reps), the total number of occurrences of each species and the number of species at each site or location were set to be the same as in the original data set. The *C*-score index (Stone and Roberts 1990) was used. These settings were shown to be amongst the least vulnerable to Type I errors (Gotelli and Entsminger 2001).



**Fig. 2 a–g** Selected sites (Table 3; ESM, S2, S3) illustrating the described environmental ordinal variables (Table 2): density of vegetation coverage (VC), water bodies (WB), tidal influence (TI), and structural elements (SE). In each example the values of these four variables are in *parentheses*; **a** site K3, lower mudflat (1, 1, 1, 1, respectively); **b** site S7, pneumatophore zone of an *Avicennia alba* forest (1, 2, 2, 2); **c** site R1, small stand of *Sonneratia alba*: pioneer marine fringe (3, 2, 2, 3); **d** site S5, tidal inlet during neap high tide (4, 3, 2, 4: measured during low tide, when it was empty); **e** site S4, stand of *Bruguiera* spp. (5, 4, 3, 4); **f** site S3, *Acrostichum* sp. halophyte fern on top of a mud mound of *T. anomala* (6, 4, 4, 4); **g** site S2, bank of an artificial brackish creek (2, 1, 1, 1). **h–m** the species studied; **h**: *B. boddarti*; **i** male of *B. pectinirostris* jumping during courtship; **j** *Pn. schlosseri*; **k** *P. chrysopilos*; **l** *P. gracilis*; **m** *P. variabilis*; **n** *S. histophorus*: a young individual in a plastic bag. Photos by G. Polgar; photo f: courtesy of Prof. A. Sasekumar

## Results

### *Mudskipper species*

All the observed and collected species were consistent with the most recent taxonomic keys and Weld identification notes (Murdy 1989; Takita et al. 1999; Larson and Takita 2004; Jaafar et al. 2006; Jaafar and Larson 2008), and with the examination of several museum specimens (ESM, S4, S6). In particular, *S. histophorus* was observed in Morib in September 2006, and was collected at the same site in May 2007; *B. pectinirostris* was only observed at K. Selangor in August 1996 (Table 3; ESM, S2a: 8). This species was subsequently collected in Tg. Piai, Johor (at the southern end of the Malacca Straits, 223 km south of Tg. Tuan), in September 2006.

### *The quantity of environmental water and the habitats of different species*

The environmental conditions found throughout the mudskippers' habitats described an ecological transition from sea to land (Fig. 3; Table 3). With the only exception of P. Kelang (sites *Kel1–Kel4*), in all the surveyed systems the mangrove landward fringe was lost due to land reclamation, and the high intertidal forest ended behind the reclamation bund. If not cultivated, the reclaimed area was rapidly colonised by a freshwater secondary forest. *Avicennia* and *Sonneratia* spp. grew along the pioneer marine fringe of the mangrove forest; these mangroves (e.g. *S. caseolaris*) also followed the bottom of tidal inlets to the middle and high intertidal zone (Tomlinson 1986; personal observation).

Wider and deeper water bodies (WB) within a given site determined both more aquatic conditions, and implied lower energetic costs to find water for mudskippers. Tide pools > 1 m<sup>2</sup> were distributed from the pioneer forest to the lower mudflat (Dyer et al. 2000). At higher levels, the forest floor was crossed by ephemeral tidal inlets flooded only during high tide. Here, some crustaceans (*Thalassina anomala*, *Sesarma* spp.) built large mud mounds, which were rarely submerged by high tides (Sasekumar 1980), creating steep

gradients of humidity on the forest floor. During the flood tide, mudskippers were observed either to enter burrows (aquatic conditions: EM1), or to come out of the water (sub-aerial conditions: EM2; Table 3). During high tide, the EM1 species were never observed out of the water, and thus we assumed that these species remained below water.

Even though it was not observed, it is possible that some individuals of the EM2 species entered burrows during flood tide and remained below water during high tide (e.g. reproductive male egg-guarders like *P. chrysopilos*: Macnae 1968).

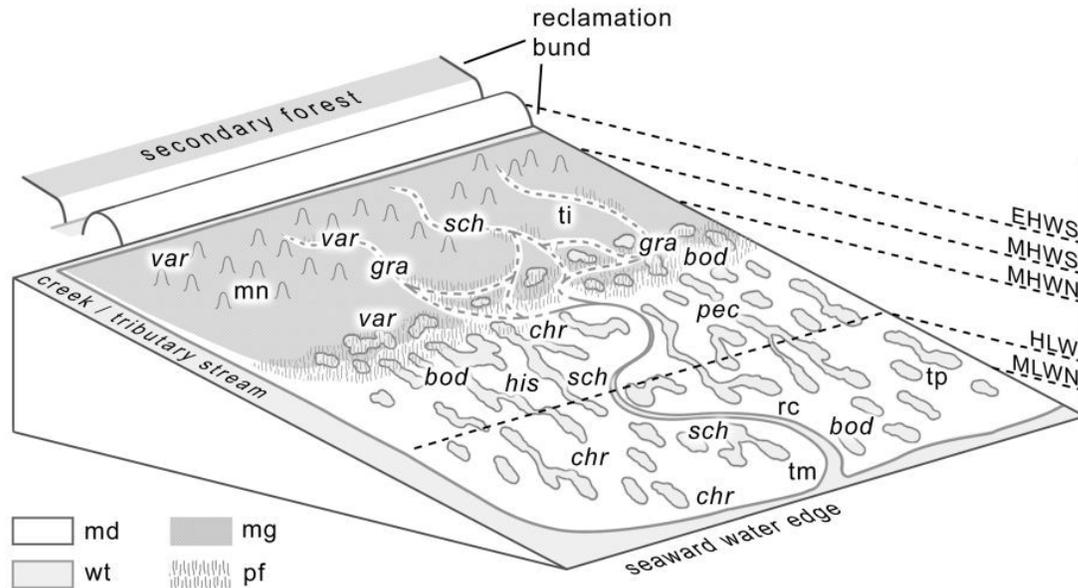
**Table 3.** Species distribution and level of environmental water

	Species distribution							Environmental parameters				
	bod	pec	sch	chr	gra	var	his	VC	WB	TI	SE	
chr, var, gra, and sch were always observed to avoid water when reached by the flood tide (EM1), while bod, pec and his always entered burrows (EM2).	Sel1 (1)	1	0	1	0	0	0	0	1	2	1	1
Other abbreviations and definitions as in Tab. 2 and Fig. 3.	Sel2 (3)	0	0	1	0	0	0	0	2	1	1	1
In parentheses, number of replicate observations per site.	Sel3 (2)	0	0	0	0	0	1	0	6	4	4	4
	Sel4 (3)	0	0	0	0	0	1	0	5	4	3	4
	Sel5 (5)	0	0	1	0	1	1	0	4	3	2	4
Study sites and their respective locations: Sel1-Sel10: Kuala Selangor; Sem1-Sem2: Sg. Sementa Besar; Kel1-Kel4: P. Kelang; Jug1-Jug3: Jugra; Mor1-Mor7: Morib; Tua1-Tua2: Tg. Tuan.; nobs: total number of observations per species	Sel6 (1)	0	0	0	0	0	1	0	5	4	3	4
	Sel7 (1)	1	0	0	0	0	0	0	1	2	2	2
	Sel8 (2)	0	1	0	0	0	0	0	1	2	2	1
	Sel9 (1)	1	0	1	0	0	0	0	1	1	2	1
	Sel10 (1)	1	0	0	1	0	0	0	1	1	1	1
	Sem1 (1)	1	0	1	1	0	0	0	1	1	1	1
	Sem2 (1)	0	0	0	0	1	1	0	5	4	3	4
	Kel1 (1)	1	0	1	0	0	0	0	1	1	1	1
	Kel2 (1)	0	0	0	0	1	1	0	5	4	3	4
	Kel3 (1)	0	0	0	1	0	0	0	1	1	1	1
	Kel4 (1)	1	0	1	0	0	0	0	1	1	1	1
	Jug1 (1)	1	0	1	0	0	0	0	1	1	1	1
	Jug2 (1)	0	0	1	0	0	0	0	1	1	1	1
	Jug3 (1)	0	0	0	0	0	1	0	5	4	4	4
	Mor1 (2)	0	0	0	0	1	0	0	3	2	2	3
	Mor2 (2)	0	0	0	0	1	0	0	5	2	2	4
	Mor3 (2)	0	0	0	0	1	0	0	3	4	3	4
	Mor4 (1)	1	0	1	1	0	0	0	1	1	1	1
	Mor5 (2)	0	0	0	1	0	0	1	1	2	2	1
	Tua1 (1)	0	0	0	0	1	1	0	3	2	2	3
	Tua2 (1)	0	0	0	0	1	0	0	5	4	3	4
	nobs:	9	2	16	6	15	15	2	-	-	-	-

In a preliminary MCA (Fig. 4), we set sites as observations, species as active modalities, and environmental categories as supplementary variables; replicate observations were also considered (Table 3; Fig. 4). We assumed that species were equiprobably distributed according to the overall conditions present at each site (habitat level). In this way, we explored whether different classes of sites were associated with different species and the environmental conditions described by our variables. The distribution of sites and supplementary environmental variables in the F1, F2 factorial space defined by the species' composition, suggest that sites with similar species' composition also corresponded to similar environmental conditions.

A second MCA (Fig. 5) was made with environmental variables as observations, and species as modalities. To do so, we recorded the occurrences of each species in the conditions described by environmental variables (ESM, S5), assuming an equiprobable distribution among different environmental

conditions. This allowed exploration of both the association between the studied parameters and the species, and between different species. This latter MCA confirmed that groups of species were associated with habitats with different quantities of environmental water. The first two factorial axes of this MCA (F1, F2) accounted for 73.9% of total variance (Fig. 5a). All species were significantly associated with environmental variables in the factorial space (significant test values at the level  $\alpha = 0.05$ ). Three groups of species were supported both by the MCA and the AHC (cutoff similarity value = 0.6: Fig. 5b).



**Fig. 3** Block diagram of a typical Malayan mangrove and mudflat intertidal system during low tide. The drawing is not to scale; the distribution of the species (adults) and the relative position of tidal datums are also illustrated. Species are abbreviated with the first three letters of their specific name; *md* (white) unvegetated mud, *mg* (dark grey) mangrove area, *mn* mud mounds of *Sesarma* spp. and *Thalassina anomala*, *pf* pneumatophores of *Avicennia* and *Sonneratia* spp., *rc* run-off channels, *ti* (dashed lines) ephemeral tidal inlets, *tm* tidal mouths, *tp* tide pools > 1 m<sup>2</sup>, *wt* (pale grey) water contained in creeks, rivers and run-off channels during low tide. *HLW* highest low water. The mudflat can be divided into different zones relative to tidal datums: from *MHWS* to *MHWN* upper mudflat, from *MHWN* to *MLWN* middle mud-flat, below *MLWN* lower mudflat. See Table 2 for other abbreviations and definitions

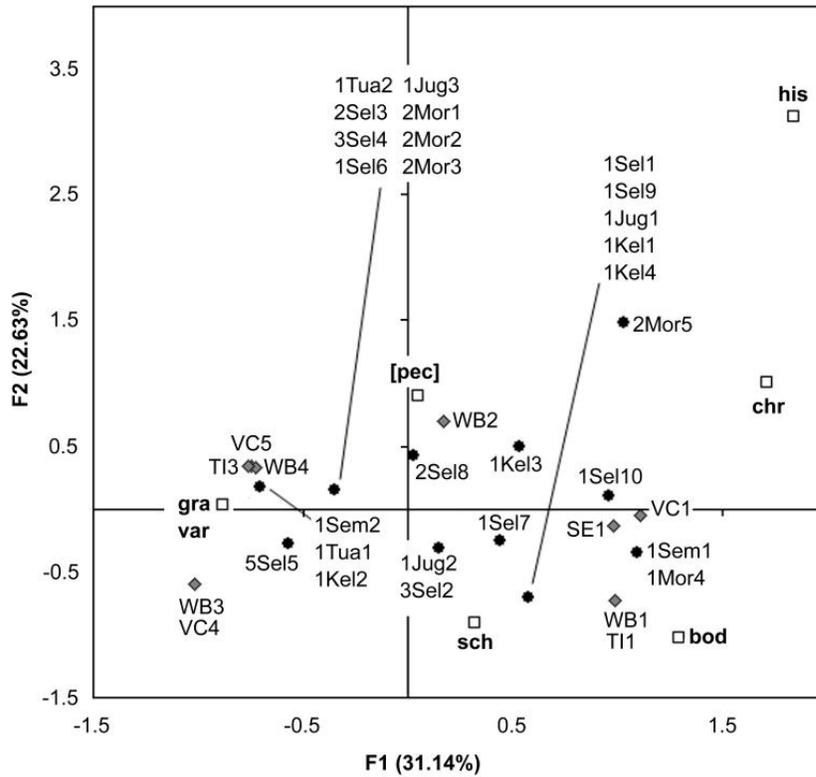
Group A included *P. variabilis* and *P. gracilis* (node's similarity = 0.85); this group was associated with denser vegetation coverage (VC3-5), higher spatial heterogeneity (SE3,4), areas flooded at least by the mean high water spring (TI3), bottoms of ephemeral waterways or areas with animal burrows as the only source of water (WB3,4), and with sub-aerial conditions during high tide (EM2). *P. gracilis* (SLmax = 45 mm: Murdy, 1989) was found in lower, relatively open pioneer mangrove forests, and, at higher levels, on the bottom of ephemeral inlets. In this latter habitat, it was often found densely aggregated around the large burrow openings of *Pn. schlosseri*, filled with water. By contrast, *P. variabilis* (SLmax = 65 mm: Takita et al. 1999; Table 1; ESM, S4) was found everywhere inside mangrove forests, up to the supratidal zone (VC6, TI4) (Table 3; Fig. 3; ESM, S2, S3).

Group B included only *Pn. schlosseri* (SLmax = 240 mm: Swennen et al. 1995), which was weakly related to group C (node's similarity = 0.52, Fig. 5b). This species plotted in an intermediate position in the factorial space and was not specifically associated with any environmental condition (Fig. 5a). It was found on the banks of creeks and run-off channels, on open mudflats and inside mangrove forests (Table 3; Fig. 3; ESM, S2, S3). In this latter case, adults were always found near the large openings of their burrows (approximately 30–60 cm in diameter), typically dispersed along the bottom of ephemeral inlets, where very young individuals were also found (20–30 mm SL). This species was also the only one that was observed along the banks of flooded artificial channels (ESM, S2a: 2) and followed the water's edge when reached by the flood tide (EM2).

Group C included *S. histophorus*, *B. boddarti*, *B. pectinirostris*, and *P. chrysopilos* (node's similarity = 0.59). This group was associated with the absence of vegetation coverage (VC1) and absence of structural elements (SE1). During low tide, adults of *S. histophorus* (SLmax = 140 mm: Rainboth 1996), *B. boddarti*

(SLmax = 128 mm: Murdy 1989), and *B. pectinirostris* (SLmax = 175 mm: Takita et al. 1999, this study) were always found in the lower intertidal zone, near the water's edge (tidal creeks, tide pools, seaward edge: Table 3, ESM, S2, S3). *B. boddarti* was observed to follow the ebb tide, to feed near the water's edge. During low tide, this species also reached areas with a higher tidal influence and in the proximity of larger water bodies than *B. pectinirostris* and *S. histophorus* (WB1, TI1 vs. WB2, TI2, respectively: Fig. 5a; ESM, S5). Within C, *P. chrysopilos* (SLmax = 88 mm: Murdy 1989; ESM, S4) was the only species, which remained out of water during the high tide (EM2); in the AHC, it was the sister group of all the other species (Fig. 5b). During high tide, *P. chrysopilos* perched on pneumatophores, trunks and prop roots of the pioneer forest marine fringe. When the tide ebbed, it gathered in small shoals of 20–30 individuals, which oriented and migrated towards the sea, eventually dispersing on the middle and lower mudflat. During flood tide, these fishes followed the water's edge without forming shoals and entered the forest marine fringe, climbing on emerged roots and trunks. As was the case with *B. boddarti*, *P. chrysopilos* also reached areas with a higher tidal influence and in proximity of larger water bodies than *B. pectinirostris* and *S. histophorus* (Fig. 5a; ESM, S5).

Jackknifing changed only the AHC topology of *P. chrysopilos* and *Pn. schlosseri*. These species always remained in intermediate positions.



*Co-occurrence and possible synecological effects*

Species composition significantly differed only amongst sites. Observed *C*-scores between locations were lower than expected by chance (positive co-occurrence), but not significantly so ( $P > 0.05$ ). Instead, observed *C*-scores between sites were significantly higher than expected by chance (negative co-occurrence:  $P = 0.0004$ ). This would suggest the presence of competitive interactions between species amongst sites. Nonetheless, our previous results (Fig. 5) suggest that this pattern could simply reflect a habitat checkerboard (Gotelli and Entsminger 2001) with respect to the quantity of environmental water; that is, different species may occur together less frequently than expected by chance, simply because they live in different habitats. Therefore, we analysed two separate matrices containing either the species of groups A + B, or C + B (Fig. 5a). The observed *C*-scores were significantly higher than expected by chance only in the first case (negative co-occurrence:  $P = 0.002$  vs.  $P = 0.098$ , respectively).

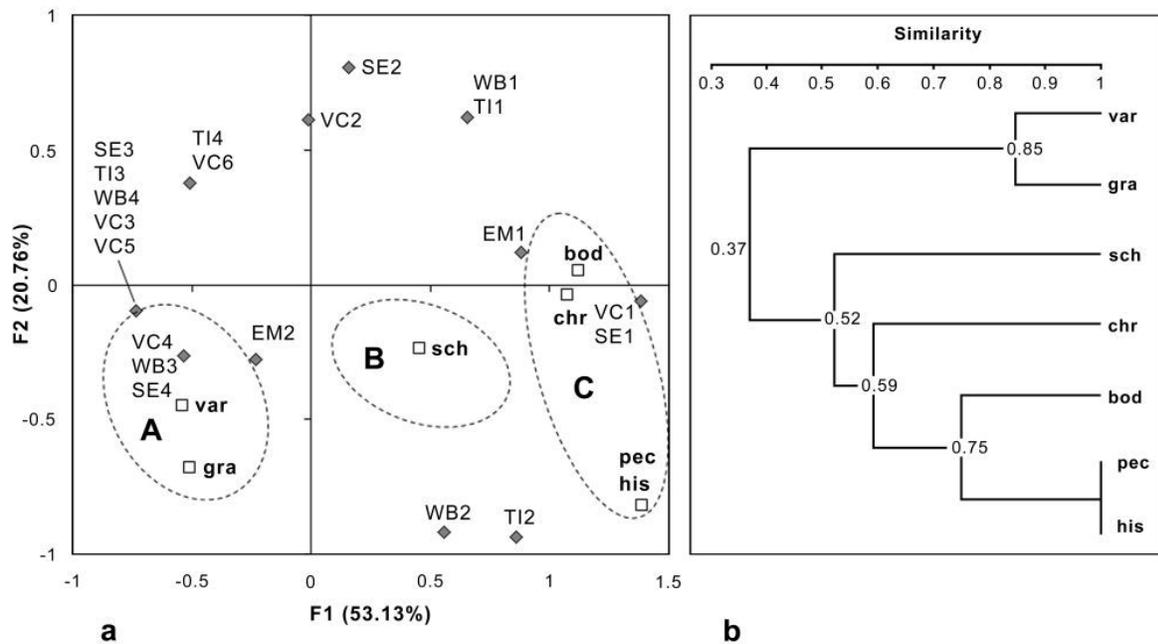
**Discussion and conclusions**

Previous descriptive accounts of mudskippers' habitat terrestriality are generally consistent with our analysis. Takita et al. (1999), Khaironizam and Norma-Rashid (2005) and Swennen et al. (1995) also found *B. boddarti* in intertidal areas vegetated by mangrove forests. During this study, adults were only observed on unvegetated substrates. Nonetheless, during low tide, young individuals were frequently found well inside forests, at the bottom of ephemeral tidal inlets.

*Pn. schlosseri* was associated with an intermediate quantity of environmental water (group B). During low tide, adults of *Pn. schlosseri* were found along the whole intertidal zone, but it was frequently found immersed and always at less than 1 m from the water's edge, suggesting a limited adaptation to terrestrial locomotion relative to *Periophthalmus* spp. (Harris 1960 [= *P. schlosseri*]).

*P. gracilis* and *P. variabilis* were included in group A. Milward (1974); Swennen et al. (1955); and Takita et al. (1999) found these species (*P. novemradiatus* (Hamilton) = *P. variabilis* Eggert: see Table 1) in relatively aquatic conditions compared to those observed during low tide in this study. Nonetheless, during flood tide, these species aggregated along the vegetated banks of flooded creeks and ephemeral inlets.

*P. chrysopilos* was included in group C; the perching behaviour during high tide was also observed by Polunin (1972) in Singapore, while Murdy (1986) has apparently made the only other report of the observed shoaling and orientation behaviours of *P. chrysopilos* during ebb tide.



**Fig. 5** **a** MCA made with environmental parameters as observations and species as modalities; the two factorial axes *F1* and *F2* explain the highest percentage of variance (*in parentheses*); the arbitrary *dashed ellipses* outline species' associations corresponding to AHC clusters (cutoff similarity value: 0.6). Other abbreviations as in **Fig. 4**. **b** AHC, applied to the same data matrix. Both analyses support three mudskipper associations: group A was found in more terrestrial conditions and group C in more aquatic conditions; group B was intermediate

Within group C, the relatively closer proximity of adult *P. chrysoopilos* and *B. boddarti* to larger bodies of water and the higher tidal influence in the factorial space are probably related to the movement of these species to the water's edge during ebb tide.

For the remainder, our results are consistent with previous reports of the species studied from the Malacca Straits, the Gulf of Thailand, China and Australia (Macnae 1968 [*B. boddaerti* (Pallas), emend. incorr.; *S. viridis* (Hamilton), auctt. = *S. histophorus*]; Berry 1972; Milward 1974; Sasekumar 1974; Frith et al. 1976; Nateewathana and Tantichodok 1984; Murdy 1986 [*S. pectinirostris* (Linnaeus) sensu Murdy 1986 = *S. histophorus*: ESM, S4]; Swennen et al. 1995; Townsend and Tibbetts 1995, 2005; Yang 1996; Takita et al. 1999; Polgar and Khaironizam 2008 [*B. dussumieri* Valenciennes, sensu Takita et al. 1999; Polgar and Khaironizam 2008 = *B. pectinirostris*: ESM, S4]; Aguilar 2000; Khaironizam and Norma-Rashid 2005; Hong et al. 2007).

It is worth noting that the occurrence of *Boleophthalmus* spp. at lower intertidal levels, on wet substrates where vegetation was sparse or absent, may not indicate a relatively lower degree of adaptation to terrestriality, but their highly specialised feeding preferences. Adults of *Boleophthalmus* spp. are benthic diatom-feeders, which are particularly abundant on well-illuminated intertidal mud deposits (e.g. Yang 1996; Yang et al. 2003; Norma-Rashid and Khaironizam 2005). During low tide, the adults of these species were invariably found in well-illuminated areas with no vegetation coverage and on wet mud substrates near the water's edge. The Malayan *Boleophthalmus* species exhibit notched teeth in the lower mandible (Murdy 1989). We interpret this character as an adaptation to efficiently skim the biofilm made by diatoms on the mud surface (Bellinger et al. 2005). Nonetheless, the Australian *B. birdsongi*, which also lives on exposed mudflats and creek mud banks, does not exhibit notched teeth (Murdy 1989). If this latter condition is assumed to be plesiomorphic, this would suggest that specialisation towards herbivory occurred when these species were already living in similar habitats. In this case, it appears that during their evolutionary adaptation to sub-aerial conditions, specialisation towards herbivory constrained *Boleophthalmus* species to more aquatic habitats.

The trophic niches of the other species studied are not so highly specialised, being either omnivores (*S. histophorus*), or opportunistic carnivores (*Periophthalmus*, *Periophthalmodon* spp.; Clayton 1993). In these latter cases, no possible connections between feeding niches and the selection of habitats with different quantity of environmental water were found.

Synecological interactions may also influence mudskippers' habitat distribution. Nonetheless, the analysis of co-occurrence between different locations, i.e. at ecosystem level, was not statistically significant. In fact, the different number of species in different locations probably reflects a lack of suitable habitats, determined by differences in the horizontal extension of intertidal gradients (Polgar 2008).

Rather, the significantly negative species co-occurrence between sites and among species of groups A and B suggests the presence of strong interspecific interactions. In particular, both pairs composed of *P. variabilis* or *P. gracilis* and the much larger *Pn. schlosseri* exhibited greater numbers of checkerboard units, accounting for significantly higher *C*-scores (Gotelli and Entsminger 2001), consistent with observations by Swennen et al. (1995) in the Weld. *Pn. schlosseri* is a known predator of mudskippers (Clayton 1993; personal observation). A similar account of habitat segregation probably mediated by predator-prey interactions was reported by Nursall (1981) between the Australian *Pn. schlosseri* [misidentif. = *Pn. freycineti* (Quoy and Gaimard, 1824)] and *P. expeditionum* (syn. *P. novaeguineensis* Eggert, 1935; Jaafar and Larson 2008; identification could not be confirmed). Since water availability is relatively limited inside forests during low tide, the large, flooded burrows of *Pn. schlosseri* may act as decoys, attracting other mudskippers searching for water (e.g. the observed aggregations of *P. gracilis* around these pools). As also noted by Swennen et al. (1995), we observed that these peculiar, funnel-shaped burrows also act as efficient traps for small marine visitors.

The lack of significantly negative co-occurrence among species living in more aquatic habitats may simply reflect a sample bias. In fact, we observed both prey-predator interactions (*Pn. schlosseri* predating *B. boddarti*), and aggressive interspecific interactions (between *P. chrysoopilos* and *B. pectinirostris*).

Predation probably has a higher impact on mudskippers in more aquatic conditions and at lower intertidal levels, due both to the lower substrate heterogeneity (Wilson 1989; this study) and the higher abundance and diversity of both marine and terrestrial visitors. In fact, during low tide mudskippers' predators are typically abundant on tidal flats, or along creek banks, near the water's edge: birds (Clayton 1993; Sasekumar and Chong 1986; Sasekumar 1980); monitor lizards (Clayton 1993; Sasekumar 1980); crocodiles (Clayton 1993); and colubrid snakes (Jayne et al. 1988; personal observation). All these predators are only rarely found inside mangrove forests (Sasekumar 1980; Noske 1995; personal observation), where

the other potential predators are only the larger mudskippers (*Pn. schlosseri*: Clayton 1993), mangrove skinks (Clayton 1993) and arboreal snakes (although in this latter case, there are no records of predation on mudskippers). During high tide, marine visitors enter the mudflat and the creek network (Sasekumar 1980), but their size, diversity and abundance generally decreases along the intertidal gradient, from the mudflat to the inlets' upper tracts (Sasekumar et al. 1994; Blaber and Brewer 1989).

Mudskippers living in unvegetated areas, at lower levels, remain below water and can avoid marine visitors only by burrowing. Instead, mudskippers that live at higher levels and in forested areas can more efficiently avoid them by climbing onto emerged objects or by moving away from the water's edge. Therefore, both predation and competition avoidance were apparently important selective factors for the origin and evolution of terrestriality in mudskippers.

The MCA and the AHC generally mirrored the systematic/ adaptive pattern described by the morphology and physiology of the species studied (Murdy 1989). Species of the most derived genera *Periophthalmus* and *Periophthalmodon* occurred in habitats with smaller to intermediate quantities of environmental water (*P. gracilis*, *P. variabilis*, *Pn. schlosseri*: groups A, B). The less derived *Boleophthalmus* spp. were found in more aquatic habitats (group C).

Nonetheless (1) the basal *S. histophorus* was found in the same environmental conditions of *B. pectinirostris*; and (2) the derived *P. chrysospilos* was included in group C. In the first case, it is possible that our indirect multivariate measure could not detect more subtle differences among different microhabitats at lower intertidal levels; alternatively, the different degrees of terrestriality of *S. histophorus* and *Boleophthalmus* spp. are reflected by behavioural traits (habitat use) that we did not consider. Instead, the relatively aquatic habitat of *P. chrysospilos* may either be the result of an evolutionary reversal of habitat selection, or a less derived condition within the genus *Periophthalmus*. More probably, the adaptive significance of the EM2 condition in *P. chrysospilos* is actually higher than the adaptive significance of the quantity of environmental water in the habitat during low tide.

The selected environmental parameters increased in value from sea to land; therefore, when the intertidal zone was sufficiently wide (in this study: K. Selangor, Sg. Sementa Besar, P. Kelang), this differentiation also corresponded with a spatial partition along the intertidal zone.

In fact, probably only adult *Pn. schlosseri* are able to use creeks and inlets to move between zones at higher and lower levels during the tidal cycle, as is also suggested by the unique presence of this species along the banks of flooded artificial channels.

These results are a first attempt to describe the ecology of the mudskippers' adaptive radiation in semi-terrestrial habitats in a more objective way. Nonetheless, quantitative data concerning mudskipper distribution and abundance remain comparatively scarce. Mangrove and adjacent peritidal systems also exhibit a wide range of structures (Robertson and Alongi 1992). Therefore, different ecosystems should be systematically surveyed to gradually build a general model for the habitat distribution and differentiation of mudskipper species within a particular biogeographic region.

**Acknowledgments** Thanks to Dr. A. Sasekumar (University of Malaya, Kuala Lumpur), who greatly helped with the field collection and granted access to the zoological collection of the museum of the University of Malaya. Thanks also to Mr. M. Rasainthiran (Park Manager of the Kuala Selangor Marine Nature Park in 1996), Dr. H. K. Larson (Museum and Art Gallery, Darwin, Australia) and Dr. T. Takita (University of Nagasaki, Japan) for their help and support. Many thanks also to the staff of all the museums and institutions that loaned fish specimens or sent photos. The survey made in 2006 was the result of a scientific collaboration between GP and Prof. J. Pignatti (University of Rome "La Sapienza", Italy), Dr. A. Sasekumar and Prof. V. C. Chong (University of Malaya, Kuala Lumpur), Mr. H. Singh and Mrs. L. Tokiman (Kukup and Tanjung Piai Taman Negara, Johor National Parks Corporation). Part of this survey was funded by a doctoral grant by the University of Rome "La Sapienza". Thanks to Prof. M. Rosenzweig (University of Arizona, USA); Prof. J. Clack (University of Cambridge, UK); Prof. S. Milli and Dr. F. Colloca (University of Rome "La Sapienza"), and to the three anonymous reviewers for a revision of the manuscript. GP also wishes to thank the Yoon family in Petaling Jaya for facilities during the stay in 1996.

## References

- Aguilar NM (2000) Comparative physiology of air-breathing gobies. PhD dissertation in Marine Biology, University of California, San Diego
- Bellinger BJ, Abdullahi AS, Gretz MR, Underwood GJC (2005) Bio-film polymers: relationship between carbohydrate biopolymers from estuarine mudflats and unialgal cultures of benthic diatoms. *Aquat Microb Ecol* 38:169–180. doi:10.3354/ame038169
- Berry AJ (1972) The natural history of west Malaysian mangrove faunas. *Malay Nat J* 25:135–162
- Blaber SM, Brewer DT (1989) Species composition and biomasses of fishes in different habitats of a tropical northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. *Estuar Coast Shelf Sci* 29:509–531. doi:10.1016/0272-7714(89)90008-5
- Cantor T (1849) Catalog of Malayan Wshes. *J Asiat Soc Bengal* 18:983–1443
- Chew SF, Hong LN, Wilson JM et al (2003) Alkaline environmental pH has no effect on ammonia excretion in the mudskipper *Periophthalmodon schlosseri* but inhibits ammonia excretion in the related species *Boleophthalmus boddarti*. *Physiol Biochem Zool* 76:204–214. doi:10.1086/374281
- Clayton DA (1993) Mudskippers. *Oceanogr Mar Biol Annu Rev* 31:507–577
- Clayton DA, Snowden R (2000) Surface activity in the mudskipper, *Periophthalmus waltoni* in relation to prey activity and environmental factors. *Trop Zool* 13:239–249
- Clayton DA, Vaughan TC (1988) Ethogram of *Boleophthalmus boddarti* (Pallas), a mudskipper found on the mudflats of Kuwait. *J Univ Kuwait Sci* 15:115–138
- Coleman JM, Gagliano SM, Smith WG (1970) Sedimentation in a Malaysian high tide tropical delta. In: Morgan JP (ed) *Deltaic sedimentation, modern and ancient*. Special Publ. No 15, S.E.P.M., pp 185–197
- Colombini I, Berti R, Ercolini A et al (1995) Environmental factors influencing the zonation and activity patterns of a population of *Periophthalmus sobrinus* Eggert in a Kenyan mangrove. *J Exp Mar Biol Ecol* 190:135–149. doi:10.1016/0022-0981(95)00020-R
- Darumas U, Tantichodok P (2002) A new species of mudskipper (Gobiidae: Oxudercinae) from southern Thailand. *Phuket Mar Biol Cent Res Bull* 64:101–107
- Dyer KR, Christie MC, Wright EW (2000) The classification of intertidal mudflats. *Cont Shelf Res* 20:1039–1060. doi:10.1016/S0278-4343(00)00011-X
- Frith DW, Tantanasiwong R, Bathia O (1976) Zonation and abundance of macrofauna on a mangrove shore, Phuket Island. *Phuket Mar Biol Cent Res Bull* 10:1–37
- Gibson RN (1982) Recent studies on the biology of intertidal fishes. *Oceanogr Mar Biol Annu Rev* 20:363–414
- Gibson RN (1999) Methods for studying intertidal fishes. In: Horn MH, Martin KLM, Chotkowski MA (eds) *Intertidal Wshes: life in two worlds*. Academic Press, San Diego, pp 7–25
- Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer Associates Inc, Sunderland
- Gotelli NJ, Entsminger GL (2001) EcoSim: null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. Available via DIALOG. <http://homepages.together.net/~gentsmin/ecosim.htm>. Accessed 20 Nov 2009
- Harris VA (1960) On the locomotion of the mud-skipper *Periophthalmus koelreuteri* (Pallas): (Gobiidae). *Proc Zool Soc Lond* 134:107–135
- Hong W, Chen S, Zhang Q, Wang Q (2007) Reproductive ecology of the mudskipper *Boleophthalmus pectinirostris*. *Acta Oceanol Sin* 26:72–81
- Hydrographic Directorate (1996) Tide tables. RMN, Ministry of Defence, Kuala Lumpur, Malaysia
- Ip YK, Low WP, Lim ALL, Chew SF (1990) Changes in lactate content in the gills of the mudskipper *Periophthalmus chrysopilus* and *Boleophthalmus boddarti* in response to environmental hypoxia. *J Fish Biol* 36:481–487. doi:10.1111/j.1095-8649.1990.tb03550.x
- Ip YK, Lim CB, Chew SF et al (2001) Partial amino acid catabolism leading to the formation of alanine in *Periophthalmodon schlosseri* (mudskipper): a strategy that facilitates the use of amino acids as an energy resource during locomotory activity on land. *J Exp Biol* 204:1615–1624
- Ishimatsu A, Hishida Y, Takita T et al (1998) Mudskipper store air in their burrows. *Nature* 391:237–238. doi:10.1038/34560
- Jaafar Z, Larson HK (2008) A new species of mudskipper, *Periophthalmus takita* (Teleostei: Gobiidae: Oxudercinae), from Australia, with a key to the genus. *Zool Sci* 25:946–952. doi:10.2108/zsj.25.946
- Jaafar Z, Lim KKP, Chou LM (2006) Taxonomical and morphological notes on two species of mudskippers, *Periophthalmus walailakae* and *Periophthalmodon schlosseri* (Teleostei: Gobiidae) from Singapore. *Zool Sci* 23:1043–1047. doi:10.2108/zsj.23.1043
- Jayne BC, Voris HK, Heang KB (1988) Diet, feeding behaviour, growth and numbers of a population of *Cerebrus rynchops* (Serpentes: Homalopsinae) in Malaysia. *Fieldiana Zool* 50:1–15
- Jobson JD (1992) Applied multivariate data analysis. Volume II: Categorical and multivariate methods. Springer, New York, pp 462–465
- Johnson RA, Wichern DW (1992) Applied multivariate statistical analysis. Prentice-Hall, Englewood Cliffs, pp 584–602
- Khaironizam MZ, Norma-Rashid Y (2002) A new record of mudskipper *Periophthalmus spiloptus* (Gobiidae: Oxudercinae) from Selangor coast, Peninsular Malaysia. *Nat Hist Bull Siam Soc* 50:245–250

- Khaironizam MZ, Norma-Rashid Y (2003) First record of the mudskipper, *Periophthalmodon septemradiatus* (Hamilton) (Teleostei: Gobiidae) from Peninsular Malaysia. *Raffles Bull Zool* 51:97–100
- Khaironizam MZ, Norma-Rashid Y (2005) Distribution of mudskippers (Gobiidae: Oxudercinae) on the Selangor coast. In: Sasekumar A, Chong VC (eds) *Ecology of the Klang Strait*. Faculty of Science, University of Malaya, Kuala Lumpur, pp 101–114
- Kok WK, Lim CB, Lam TJ, Ip YK (1998) The mudskipper *Periophthalmodon schlosseri* respire more efficiently on land than in water and vice versa for *Boleophthalmus boddarti*. *J Exp Zool* 280:86–90. doi:10.1002/(SICI)1097-010X(19980101)280:1<86::AID-JEZ10>3.0.CO;2-U
- Koumans FP (1953) Gobioidae. In: Weber M, de Beaufort LF (eds) *Fishes of the Indo–Australian archipelago*, 10. EJ Brill, Leiden, pp 1–423
- Larson HK, Takita T (2004) Two new species of *Periophthalmus* (Teleostei: Gobiidae: Oxudercinae) from northern Australia, and a re-diagnosis of *Periophthalmus novaeguineensis*. *The Beagle. Rec Mus Art Galleries N Territ* 20:175–185
- Lee HJ, Martinez CA, Hertzberg KJ et al (2005) Burrow air phase maintenance and respiration by the mudskipper *Scartelaos histophorus* (Gobiidae: Oxudercinae). *J Exp Biol* 208:169–177. doi:10.1242/jeb.01361
- Low WP, Ip YK, Lane DJW (1990) A comparative study of the gill and skin morphometries of three mudskippers: *Periophthalmus chrysopilus*, *Boleophthalmus boddarti* and *Periophthalmodon schlosseri*: correlations and interpretations. *Zool Sci* 7:29–38
- Macintosh DJ (1977) Some responses of tropical mangrove fiddler crabs (*Uca* spp.) to high environmental temperatures: physiology and behaviour of marine organisms. In: McLusky DS, Berry AJ (eds) *Proceedings of the 12th European symposium on marine biology*. Pergamon Press, Stirling, pp 49–56
- Macnae W (1968) A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Adv Mar Biol* 6:73–270. doi:10.1016/S0065-2881(08)60438-1
- Milward NE (1974) Studies on the taxonomy, ecology and physiology of Queensland mudskippers. PhD dissertation. University of Queensland, Brisbane
- Murdy EO (1986) Mudskippers of Malaysia: the lords of the mudflat. *Freshw Mar Aquar* 9:20–23
- Murdy EO (1989) A taxonomic revision and cladistic analysis of the oxudercine gobies (Gobiidae: Oxudercinae). *Rec Aust Mus Suppl No.* 11:1–93
- Murdy EO, Takita T (1999) *Periophthalmus spilotos*, a new species of mudskipper from Sumatra (Gobiidae: Oxudercinae). *Ichthyol Res* 46:367–370. doi:10.1007/BF02673979
- Nateewathana A, Tantichodok P (1984) Species composition, density and biomass of macrofauna of a mangrove. In: Soepadmo E et al (eds) *Proceedings of the Asean symposium on the mangrove and management: research and management*. University of Malaya and UNESCO, Kuala Lumpur, pp 258–285
- Norma-Rashid Y, Khaironizam MZ (2005) Some biological aspects of mudskippers (Gobiidae: Oxudercinae) from Langkawi Island. *Malays J Sci* 24:139–144
- Noske RA (1995) The ecology of mangrove forest birds in Peninsular Malaysia. *Ibis* 137:250–263. doi:10.1111/j.1474-919X.1995.tb03247.x
- Nursall JR (1981) Behaviour and habitat affecting the distribution of five species of sympatric mudskippers in Queensland. *Bull Mar Sci* 31:730–735
- Polgar G (2008) Species–area relationship and potential role as a biomonitor of mangrove communities of Malayan mudskippers. *Wetland Ecol Manage* 17:157–164. doi:10.1007/s11273008-9090-x
- Polgar G, Khaironizam MZ (2008) First record of *Periophthalmus walailakae* (Gobiidae: Oxudercinae) from Peninsular Malaysia. *Cybium* 32:349–351
- Polunin I (1972) Who says fish can't climb trees? *Natl Geogr Mag* 141:84–92
- Rainboth WJ (1996) *Fishes of the Cambodian Mekong: FAO Species identification field guide for fishery purposes*. FAO, Rome
- Robertson AI, Alongi DM (1992) *Tropical mangrove ecosystems: coastal estuarine studies 41*. American Geophysical Union, Washington DC
- Sarpedonti V, Sasekumar A (1996) The abundance of diatom species on a low-shore mangrove forest, Sementa, Malaysia. *Wallaceana* 77:21–26
- Sasekumar A (1974) Distribution of macrofauna on a Malayan mangrove shore. *J Anim Ecol* 43:51–69. doi:10.2307/3157
- Sasekumar A (1980) The present state of mangrove ecosystems in southeast Asia and the impact of pollution. FAO/UNEP project: impact of pollution on the mangrove ecosystem and its productivity in Southeast Asia; (SCS/80/WP/94b). Publication of the South China Sea Fisheries Development and Coordinating Programme, 4–8 February 1980, Manila
- Sasekumar A (1994) Meiofauna of a mangrove shore on the west coast of peninsular Malaysia. *Raffles Bull Zool* 42:901–915
- Sasekumar A, Chong EL (1986) The macrobenthos at feeding sites of shorebirds in Pulau Tengah. *Wallaceana* 45:6–7
- Sasekumar A, Chong VC, Lim KH, Singh HR (1994) The fish community of Matang mangrove waters, Malaysia. In: Sudara S, Wilkinson CR, Chou LM (eds) *Proceedings of the third ASEAN: Australia symposium on living coastal resources*. Research papers, vol 2. Chulalonghorm University, Bangkok, pp 457–464

- Sayer MDJ (2005) Adaptations of amphibious fish for surviving life out of water. *Fish Fish* 6:186–211. doi:10.1111/j.1467-2979.2005.00193.x
- Stone L, Roberts A (1990) The checkerboard score and species distributions. *Oecologia* 85:74–79. doi:10.1007/BF00317345
- Swennen C, Ruttanadakul N, Haver M et al (1995) The five sympatric mudskippers (Teleostei: Gobioidae) of Pattani area, Southern Thailand. *Nat Hist Bull Siam Soc* 42:109–129
- 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. doi:10.1007/BF02675431
- Tomlinson PB (1986) *The botany of mangroves*. Cambridge University Press, London
- Townsend KA, Tibbetts IR (1995) Re-appearance of the blue mudhopper, *Scartelaos histophorus* in the Greater Brisbane area. *Mem Qld Mus* 38:671–676
- Townsend KA, Tibbetts IR (2005) Behaviour and sexual dimorphism of the blue mudskipper, *Scartelaos histophorus* (Pisces: Gobiidae). *Proc R Soc Qld* 112:53–62
- Wilson KA (1989) Ecology of mangrove crabs. predation, physical factors and refuges. *Bull Mar Sci* 44:263–273
- Yang KYJ (1996) The feeding ecology of the mudskipper *Boleophthalmus pectinirostris* (Pisces: Periophthalmidae) at the Mai Po marshes nature reserve, Hong Kong. MP dissertation, Faculty of Science, Hong Kong University, Hong Kong
- Yang KY, Lee SY, Williams GA (2003) Selective feeding by the mudskipper (*Boleophthalmus pectinirostris*) on the microalgal assemblage of a tropical mudflat. *Mar Biol (Berl)* 143:245–256. doi:10.1007/s00227-003-1067-y
- Zhang J, Taniguchi T, Takita T, Ali AB (2000) On the epidermal structure of *Boleophthalmus* and *Scartelaos* mudskippers with reference to their adaptation to terrestrial life. *Ichthyol Res* 47:359–366. doi:10.1007/BF02674263
- Zhang J, Taniguchi T, Takita T, Ali AB (2003) A study on the epidermal structure of *Periophthalmodon* and *Periophthalmus* mudskippers with reference to their terrestrial adaptation. *Ichthyol Res* 50:310–317. doi:10.1007/s10228-003-0173-7