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FULL PAPER

Seasonal variation of food and feeding in burrowing goby *Parapocryptes serperaster* (Gobiidae) at different body sizes

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Abstract Diet composition and feeding habits of the burrowing fish *Parapocryptes serperaster* were investigated on different fish sizes across dry and wet seasons in the Mekong Delta, Vietnam. The gut length was positively related to fish length; the gut length was 1.57 ± 0.30 times the total length, which is in the range for omnivore (1–3). Detritus, algae and copepods were the main food items in the foregut. The diet composition showed seasonal and intraspecific variations in all fish sizes. The diet diversity varied with fish size and the dry-wet season pattern, and small fish had a higher diet diversity than large fish. The diet evenness index and Costello graphic analysis indicate that this goby is a generalist feeder and feeds mainly on detritus, followed by diatoms, and could obtain food from the bottom and the water column. The feeding intensity of *P. serperaster* was higher in the wet season than in the dry season, but was not significantly affected by fish size. The *P. serperaster* fed on *Navicula* spp. in the wet season, but on *Nitzschia* spp. in the dry season. The understanding of food and feeding habits of *P. serperaster* contributes to our knowledge on feeding adaptation of small-bodied bottom-dwelling gobies to the mud flat habitats in tropical monsoonal regions.

Keywords Trophic guild · Dietary composition · Feeding habit · Omnivore

Introduction

Knowledge on food and feeding is fundamentally important to understand fish biology and trophic interactions between species in a fish community (Brodeur and Pearcy 1992; Wootton 1996; Blaber 2000). Fish stomach contents show diel change and vary with the time of the day. For instance, the round goby *Neogobius melanostomus* mainly feed on chironomid and hydropsychid larvae during the daytime, but on thironomid pupae and heptageniid nymphs at night (Carman et al. 2006). Additionally, seasonal change can also influence the stomach content of some gobiids. For instance, the sand goby *Pomatoschistus minutus* mainly feed on chironomids in spring, amphipods in summer and ostracods in autumn in the northern Baltic Archipelago (Aarnio and Bonsdor 1993), and knout goby *Mesogobius batrachocephalus* mostly feed on bivalves in spring and summer but on isopods in autumn (Roşca and Mânzu 2011). The food composition of the goby *N. melanostomus* is strongly influenced by season, as this species mainly ingests fish eggs in spring but ostracods in autumn in Kingston Basin, Canada (Brush et al. 2012). Moreover, the stomach contents also vary with fish size in some gobiids. For instance, large *N. melanostomus* feed mostly on dreissenids, whereas small gobies consume mainly chironomids (Brush et al. 2012), but copepods are important prey for juvenile *Pomatoschistus marmoratus* (Altin et al. 2015). The discrepancy of food composition is attributable to the foraging behaviour of fish and prey availability in the environment. Thus, the study on the variation of food types of fish at different seasons and sizes

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is critically important to improve our understanding of fish adaptation to the changing environment and habitat.

Stomach contents reflect habitat separation in fish, as the analysis of stomach content can reveal the habitat where fish feed (Gumus et al. 2002). Although the diet composition of fish is species specific, it varies with food availability in the environment. For instance, *Aphia minuta* feed on copepods, cirripede and mysid larvae in the north-eastern Atlantic and the Mediterranean, but mainly feed on copepods in the Black Sea and the north-western Adriatic Sea (Tirelli et al. 2014). When the habitat changes from an artificially made habitat to the natural habitat in the western basin of Lake Erie, the diet of the round goby *N. melanostomus* switches from grain particles to copepods (Thompson and Simon 2014). In the shoreline of Hron River (Slovakia), the monkey goby *Neogobius fluviatilis* mainly feed on chironomids but the diet is mainly composed of crustacean *Corophium curvispinum* in the shoreline Danube River (Slovakia). Likewise, the round goby *N. melanostomus* mainly feed on molluscs and crustaceans in the Danube River (the former Yugoslavia), but ingest a wide range of benthic macroinvertebrates in the St. Clair River (Michigan, USA) (Adámek et al. 2007).

The guild of fish feeding habit is generally classified into herbivore, omnivore and carnivore, and the morphology and function of the alimentary tract vary between fish species of different feeding habits (Geevarghese 1983). However, the feeding habit can be altered by the change of food availability and habitat structure. Several gobiids are considered omnivorous and feed on benthic algae and detritus. For example, *Oxyurichthys tentacularis*, *Oxyurichthys microlepis*, *Stenogobius gymnopomus* and *Oligolepis acutipennis* mainly feed on benthic diatoms and detritus (Geevarghese 1983), but both *Pseudapocryptes elongatus* (Tran 2008) and *Boleophthalmus boddarti* (Ravi 2013; Dinh 2015) mainly ingest diatoms. The coastal areas in tropical Southeast Asia are important nursery grounds for numerous fishes including gobies (Blaber 2000; Hajisamae and Chou 2003; Tue et al. 2012). Oxudercine gobies are typically found on mud flats in creeks, estuaries and coastal waters at low tide (Murdy 1989; Takita et al. 1999; Hajisamae et al. 2006), including the Mekong Delta (Tran et al. 2013). The change of feeding habit and food partitioning among fish species can significantly affect the abundance and community structure of food organisms (Garrison and Link 2000). However, food and feeding habits of gobiid species are poorly understood due to their small size, cryptic behaviour and low economic value.

The goby *Parapocryptes serperaster* (Richardson, 1864; Gobiidae) is widely distributed in the Indo-Pacific region including southern China, India, Malaysia, Myanmar, Singapore, Thailand and Indonesia (Murdy 1989; Talwar and Jhingran 1991; Kottelat et al. 1993; Khaironizam and Norma-Rashid 2000), and is common in the estuarine region of the Mekong Delta, Vietnam (Tran et al. 2013). This species has an elongated and round body (Murdy 1989; Rainboth 1996), builds a burrow by twisting its body in coastal and muddy areas to escape from predation (Dinh et al. 2014), exhibits isometric growth (Dinh et al. 2015b) and mainly spawns in the wet season (Dinh et al. 2015a). The *P. serperaster* population in the Mekong Delta has not been subject to overfishing based on the estimate of age structure and fish size (Dinh et al. 2015c). In the riverine areas of Sungai Sembilang, Jeram, Malaysia, where the substrates are very soft and muddy, *P. serperaster* mainly feed on diatoms (Khaironizam and Norma-Rashid (2000). However, it is not clear if the change of food and feeding habit would depend on season and fish size in the field. The understanding of the diet diversity and feeding intensity is important for the management and conservation of aquatic ecosystems. This study aims to understand the variation of food and feeding habit of *P. serperaster* with the season and fish size as measured by diet diversity and feeding intensity. The results of this study will provide an insight into the understanding of diet flexibility and adaptation of gobiids in a changing environment.

Materials and methods

Study site and experimental design. This study was conducted in the Kinh Ba River, Soc Trang Province, Mekong Delta, Vietnam (9°26′3″N, 106°13′28″E) from April 2014 to March 2015. The distance from the river bank to the riverbed of the mudflat was nearly 3 m at the lowest tide. Tides are semi-diurnal with a spring tidal range of ~0.7 m. Soc Trang Province comprises a long coastline connected to mangroves and mudflat habitats. This study covered the span of dry and wet seasons based on monthly precipitation. In the Mekong Delta region, there is almost no rainfall during the dry season from January to May, whereas it heavily rains in the wet season from June to December. This goby reaches first sexual maturation at 15.8 cm total length (TL) (Dinh et al. 2015a). Therefore, we divided the fish size into three groups: small (<16 cm TL), middle (16–18 cm TL) and large groups (>18 cm TL) based on the size at sex maturation and spawning to study the size-dependent diet switch. The average annual temperature is ~27 °C, and Soc Trang is a typical region for the natural environment in the Mekong Delta (Soc Trang Statistical Office 2012).

Fish collection. Fish specimens were collected monthly over a year using three sets of gillnet with a distance of 0.5 km apart. The gill nets had 1.5-cm mesh in the cod end, 2.5-cm mesh in the mouth and were 5.0 m long. These gillnets were set at the highest tide and retrieved after

2–3 h during ebb tide. After separating fish sexes using the feature of the genital papilla, specimens were immediately anesthetised by benzocaine and preserved in 5% formalin before transport to the laboratory.

Feeding habit and intensity determination. After measurement of *TL* (nearest 0.1 cm) and body weight (*W*, nearest 0.01 g), fish specimens were dissected to measure the length of the gastrointestinal tract (nearest 0.1 cm) to calculate the relative gut length (*RGL*) as the ratio of the gut length to the total length. This ratio was used to determine fish feeding habit, e.g., herbivores ($RGL > 3$), carnivores ($RGL < 1$) or omnivores ($RGL = 1$–3) (Al-Hussaini 1947; Nikolsky 1963; Geevarghese 1983).

Alimentary tracts were weighed to the nearest 0.01 mg to determine the gut fullness index (*FI*), which is calculated as $FI = W_i \times 100/W$, where W_i is the weight of the stomach and *W* is the fish body weight, as an index for fish feeding intensity (Watanabe et al. 2004). This index was used to test if fish feeding intensity changes between seasons and fish size classes based on the method of Bakhoum and Fatas (2003).

Diet composition. The stomach contents of each fish were diluted to 1 L with distilled water, and three sub-samples (1 ml/each) were examined in a Sedgewick-Rafter chamber on an inverted microscope connected with a digital camera (Motitc Digital Microscope, Model: DM1802) to count food items. Moreover, the food items in the Sedgewick-Rafter chamber were also photographed for counting and measurement of each food item using Image Pro Plus (software v. 2.0). Diet composition was quantified by prey occurrence in fish stomach ($\%O_i = \frac{O_i}{N} \times 100$), where O_i is the number of fish consuming prey *i* and *N* is the total number of fish examined, excluding individuals with an empty stomach (Hynes 1950; Hyslop 1980; Baeck et al. 2013). For quantification of meal size, the biovolumetric percentage ($\%V_i = \frac{V_i}{V_{total}} \times 100$) was used to determine the diet volume in the fish stomach, where V_i is the biovolume of prey *i* and V_{total} the total biovolume of prey individuals. The biovolume of prey *i* (V_i) was obtained by multiplying the standard biovolume of prey *i* with the number of prey *i* in each stomach. The 30 random photos per sub-sample (90 photos per stomach) were used to measure the area (e.g., biovolume) of each prey (e.g., prey *i*) using Image Pro Plus before obtaining the standard biovolume of prey *i*. The smallest prey item was ascribed one point and was used to calculate the points for the larger food item. This method was modified from the volumetric method of Hynes (1950) and Hyslop (1980), and the biovolumetric method of Vitule et al. (2008) and Alcaraz et al. (2015).

Diet diversity and feeding intensity. The dietary diversity of this goby was estimated using the Shannon–Wiener index as $H' = -\sum_{i=1}^{n} p_i \log p_i$, where p_i is the percentage of *i* prey item among the total number of prey (Vitule et al. 2013). The Costello (1990) graphical method modified by Amundsen et al. (1996) was used to plot the percentage of biovolume versus frequency occurrence of food items to determine diet specialization (e.g., feeding strategy) and prey importance. In this graph, the most important prey items are closer to the top right corner and the prey items with low occurrence, but those important by biovolume are closer to the top left corner (Adámek et al. 2007). Moreover, the diet specialization was also determined by the diet evenness index ($\text{Evenness} = H'/H'_{max}$), ranging from a more stenophagous diet (close to zero) to a more euryphagous diet (close to one) based on the method of Oscoz et al. (2005). This evenness index was used together with the Costello (1990) graphical method modified by Amundsen et al. (1996) to estimate the feeding characteristics of this goby.

To obtain the relative abundance and food items available in the field, samples were taken from the river and 100-L water was poured into a tank and concentrated through a ~50 µm mesh to obtain 1 litre of the sample, which was analysed for phytoplankton, zooplankton and detritus. Phytoplankton, zooplankton and detritus in the water were collected at the same site and the same period of fish collection from October 2014 to March 2015 to determine food availability and the overlap of food prey in the fish stomach and the environment (Sabatés and Saiz 2000; Pratchett 2005). After prey identification, the biovolume of food items in the environment was estimated using the same method as in the fish stomach. Thereafter, the biovolume of food items was used to estimate the diet electivity (*E*) using the equation $E = (r_i - p_i)/(r_i + p_i)$, where r_i and p_i are the proportion of each food category in the fish stomach and environment respectively, and *E* ranges from −1 (e.g., strong negative election) through 0 (e.g., random election) to 1 (e.g., strong positive election) (Strauss 1979; Lückstädt and Reiti 2002; Gkenas et al. 2012). When the value of *E* index exceeds 0.6 for a diet item, this index is considered biologically significant for food selection (Wallace 1981; Gkenas et al. 2012).

Data analysis. The influences of two seasons (dry and wet) and three fish size classes ($TL < 16$, 16–18, and > 18 cm) on the variation of diet diversity (*H'*) and feeding intensity (*FI*) were analysed using two-way ANOVA (Alcaraz et al. 2015). As no two-way interaction was detected between fish size and season, one-way ANOVA was used to test the fish size effect and t test to test the season effect. One-way ANOVA was also used to test the effect of fish size on the relative gut length and monthly variation of feeding intensity. The χ^2 test was used to test if the proportion of empty stomachs differs between the wet and dry seasons (SPSS v.21). If the ANOVA assumptions of normality and homogeneity of variance were not met, PERMANOVA was used to examine the influences of season and fish size on the variations of *H'* and *FI*. The biovolume of all food items was analysed using PRIMER v.6.1.11 (Clarke and Gorley 2006) with PERMANOVA+ v.1.0.1 add-on package (Anderson et al. 2008) to compare food composition between season and fish size (Baeck et al. 2013). If food composition was significantly different between season or fish size, Mann–Whitney U tests or Kruskal–Wallis tests were used to examine which prey contributed to the seasonal difference or intraspecific change. The significance level in all tests was set at $p < 0.05$.

Results

Relative gut length and gut fullness. The analysis of feeding habit was based on a total of 240 fish (116 females *TL* = 9–21 cm and 124 males *TL* = 8–24 cm; Table 1). The relative gut length (*RGL*) of *Parapocryptes serperaster* was 1.57 ± 0.30 (mean ± SD, $n = 240$). The number of fish with an empty stomach was not significantly different between the dry and wet seasons (χ^2, $p > 0.05$; Table 1). Similarly, the number of full and moderate full stomachs in the dry season was not significantly different from that in the wet season (χ^2, $p > 0.05$; Table 1). Although the *RGLs* varied significantly with fish size (ANOVA, $p < 0.05$; Fig. 1), the *RGLs* of *P. serperaster* generally fell into the omnivorous feeding category, i.e., *RGL* = 1–3. The length of the gut was positively related to the total body length ($r = 0.644$, $p < 0.001$).

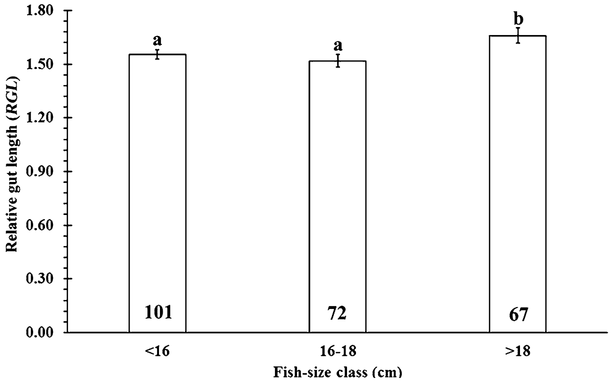

Fig. 1 The variation of the relative gut length between three fish-size groups (group 1: *TL* <16, group 2: *TL* = 16–18 and group 3: *TL* >18 cm). *Different letters* represent significant differences in *RGL* (mean ± SE, $p < 0.05$). *The number of fish in each size group* is given in each column

Table 1 Gut fullness of *P. serperaster* in different months and seasons

Sampling date	Fish (No)		Gut fullness (%)		
	Female	Male	Full	Moderate full	Empty
Apr-14	11	9	10	65	25
May-14	8	12	25	50	25
Jun-14	12	8	25	60	15
Jul-14	9	11	75	25	0
Aug-14	8	12	35	55	10
Sep-14	11	9	15	30	55
Oct-14	11	9	100	0	0
Nov-14	7	13	75	25	0
Dec-14	9	11	90	10	0
Jan-15	9	11	75	15	10
Feb-15	12	8	35	35	30
Mar-15	9	11	70	10	20
Wet season	67	73	59	29	12
Dry season	49	51	43	35	22

The gut fullness index (*FI*) varied significantly between months (ANOVA, $p < 0.001$) and steadily increased from dry season to the pre-spawning period in July before falling to the lowest point during the main spawning period in September (Dinh et al. 2015a) (Fig. 2), coinciding with a high percentage of empty stomachs (55%) in September (Table 1). After post-spawning recovery in October, the *FI* was slightly decreased from the late wet season to the dry season (Fig. 2). The *FI* in the wet season was significantly higher than in the dry season (t test, $p < 0.05$; Fig. 3a), whereas this index did not differ significantly between fish sizes (ANOVA, $p > 0.05$; Fig. 3b). The seasonal change of *FI* of *P. serperaster* did not depend on fish size either ($p > 0.05$).

***General diet composition*.** A total of 202 individuals (102 females with 12.8–21.0 cm in *TL* and 100 males with 9.7–23.5 cm in *TL*) were used to examine diet composition and fish with an empty stomach were excluded (Table 1). Fourteen food items were detected from fish stomachs (Table 2). The biovolume analysis showed that both detritus and Bacillariophyta contributed similarly to the fish stomach content, and this goby also fed on Cyanophyta and copepods (Table 2). The graphic analysis showed that detritus was the most important food followed by *Nitzschia* spp., *Navicula* spp. and *Gyrosigma* sp. (Bacillariophyta). Moreover, detritus was the primarily consumed item, and *Nitzschia* spp., *Navicula* spp. and *Gyrosigma* sp. (Bacillariophyta) were secondarily important, whereas the other food items were rarely consumed.

Seasonal and intraspecific variations in diet composition. The food composition of *P. serperaster* was significantly different between seasons (PERMANOVA, $p < 0.001$) and fish size ($p < 0.001$). The difference in diet composition between the dry and the wet seasons was

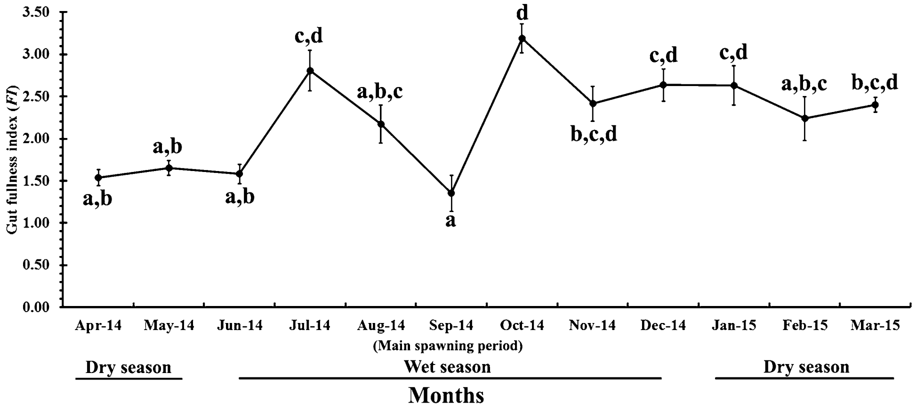

Fig. 2 The monthly variation of the gut fullness index (*FI*) of *P. serperaster*. *Different letters* show the significant differences between months ($n = 202$, $p < 0.05$)

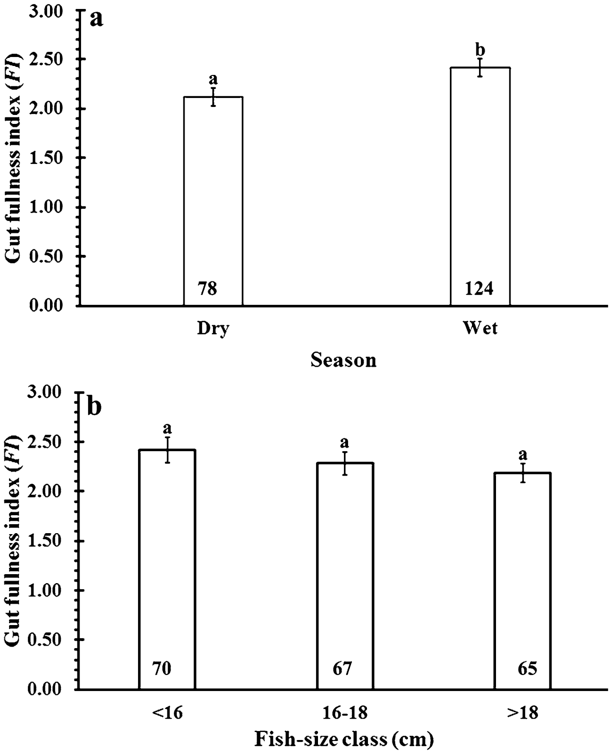

Fig. 3 The variation of the gut fullness index (*FI*) of *P. serperaster* between season (**a**) and fish size (**b**). *Different letters* indicate significant differences (mean ± SE, $p < 0.05$). *The number of fish used for analysis* is given in each column

found in half of the prey items consumed (Mann–Whitney U, $p < 0.05$), except for detritus, *Thalassiosira* sp., *Biddulphia* spp., *Pleurosigma* sp., *Oscillatoria* sp., *Acartia* sp. and *Calanus* sp. ($p > 0.05$, Table 2). The food items contributing most to the difference of diet composition between fish sizes were detritus, *Nitzschia* spp., *Oscillatoria* sp., *Spirulina* sp., *Anabaena* spp. and *Canalus* sp. (Kruskal–Wallis, $p < 0.05$; Table 3). The PERMANOVA analysis of four major food categories showed that the diet composition significantly differed between the dry and wet seasons ($p = 0.004$) and between three fish size groups ($p < 0.001$). The Cyanophyta species contributed most to the difference between seasons (Mann–Whitney U, $p < 0.05$), while both detritus and Cyanophyta contributed to the diet differences between three fish sizes (Kruskal–Wallis, $p < 0.05$; Table 4). The amount of detritus in the wet season (51%) was not different from that in the dry season (50%, Mann–Whitney U, $p > 0.05$; Table 4). The diet of larger *P. serperaster* was predominantly composed of detritus compared to the smallest fish (Kruskal–Wallis, $p < 0.05$; Table 4), whereas the reverse was the case for Cyanophyta ($p < 0.05$; Table 4) based on the biovolume data.

Diet diversity, feeding strategy and prey election. This goby showed a high diet diversity as the value of *H'* index was high ($n = 202$, $H' = 1.37 \pm 0.02$ SE). The food item diversity of *P. serperaster* was not significantly different between the dry and wet seasons (PERMANOVA, $p = 0.30$; Fig. 4a), whereas the smallest fish group had a higher diet diversity compared to size groups 2 and 3 ($p = 0.04$; Fig. 4b). The variation in the diet diversity of this goby species was not significantly different for the interaction of season and fish size ($p = 0.88$).

The Costello graphic analysis on the relationship between biovolume and occurrence of four major food categories showed that *P. serperaster* was a generalist feeder and fed mainly on detritus and Bacillariophyta (Fig. 5a). Similarly, the graphic analyses on the frequency of occurrence and biovolume for 14 food items also revealed that the feeding strategy of this goby species was that of a generalist feeder as no food items fell into the scenario of low occurrence but high in prey biovolume (Fig. 5b). This result was confirmed by the high value of the evenness index (0.64 ± 0.01). The Costello graphic analysis for three fish sizes in both dry and wet seasons showed that *P. serperaster* was also a generalist feeder and fed mainly on detritus and Bacillariophyta. Similarly, the value of the evenness index was high across all fish sizes (0.68 ± 0.01 for small size, 0.63 ± 0.01 for middle size, and 0.61 ± 0.01 for large size) and seasons (0.61 ± 0.01 in dry and 0.63 ± 0.01 in wet seasons).

Table 2 Frequency of occurrence and biovolume of food items of *P. serperaster* in the dry and wet seasons (%)

Food	Occurrence		Biovolume (Mean±SE)	
	Dry	Wet	Dry	Wet
Detritus	100	100	50.25 ± 1.51^{a}	51.23 ± 0.69^{a}
Bacillariophyta				
Coscinodiscus spp.	87.18	91.13	1.02 ± 0.14^{a}	0.42 ± 0.04^{b}
Thalassiosira sp.	71.79	85.48	0.66 ± 0.08^{a}	0.70 ± 0.07^{a}
Navicula spp.	100	100	5.49 ± 0.41^{a}	7.27 ± 0.29^{b}
Gyrosigma sp.	98.72	100	13.83 ± 1.18^{a}	4.87 ± 0.32^{b}
Biddulphia spp.	97.44	98.39	5.20 ± 0.60^{a}	4.20 ± 0.27^{a}
Pleurosigma sp.	80.77	97.58	2.65 ± 0.31^{a}	2.67 ± 0.21^{a}
Nitzschia spp.	100	100	12.07 ± 0.79^{a}	18.91 ± 0.69^{b}
Cyanophyta				
Oscillatoria sp.	64.1	95.97	2.07 ± 0.24^{a}	2.49 ± 0.19^{a}
Spirulina sp.	5.13	24.19	0.05 ± 0.03^{a}	0.16 ± 0.03^{b}
Anabaena spp.	71.79	97.58	1.40 ± 0.17^{a}	1.80 ± 0.12^{b}
Copepods				
Acartia sp.	44.87	59.68	1.34 ± 0.23^{a}	1.53 ± 0.16^{a}
Calanus sp.	66.67	84.68	2.96 ± 0.39^{a}	2.55 ± 0.22^{a}
Paracalanus sp.	35.9	54.84	0.96 ± 0.18^{a}	1.19 ± 0.13^{b}

Different letters in each category show significant differences ($p < 0.05$) between seasons

Table 3 Percentage of the prey frequency of occurrence and biovolume in *P. serperaster* of three size groups (1: TL <16, 2: 16–18, 3: >18 cm)

Food	Occurrence			Biovolume (Mean±SE)		
	Size group			Size group		
	1	2	3	1	2	3
Detritus	100	100	100	47.75 ± 1.48^{a}	53.09 ± 1.02^{b}	51.88 ± 1.07^{b}
Bacillariophyta						
Coscinodiscus spp.	88.57	86.57	93.85	0.81 ± 0.13^{a}	0.71 ± 0.10^{a}	0.43 ± 0.06^{a}
Thalassiosira sp.	78.57	76.12	86.15	0.88 ± 0.12^{a}	0.56 ± 0.07^{a}	0.61 ± 0.06^{a}
Navicula spp.	100	100	100	5.87 ± 0.45^{a}	7.01 ± 0.42^{a}	6.92 ± 0.39^{a}
Gyrosigma sp.	100	98.51	100	9.48 ± 1.02^{a}	8.51 ± 1.09^{a}	6.96 ± 0.90^{a}
Biddulphia spp.	100	94.03	100	5.31 ± 0.62^{a}	4.32 ± 1.09^{a}	4.07 ± 0.34^{a}
Pleurosigma sp.	87.14	89.55	96.92	3.42 ± 0.38^{a}	2.07 ± 0.21^{a}	2.44 ± 0.28^{a}
Nitzschia spp.	100	100	100	14.94 ± 0.89^{a}	14.98 ± 0.99^{a}	19.02 ± 1.02^{b}
Cyanophyta						
Oscillatoria sp.	84.29	77.61	89.23	3.01 ± 0.28^{a}	2.2 ± 0.27^{b}	1.73 ± 0.17^{b}
Spirulina sp.	10	11.94	29.23	0.09 ± 0.04^{a}	0.08 ± 0.03^{a}	0.20 ± 0.04^{b}
Anabaena spp.	90	83.58	89.23	2.23 ± 0.22^{a}	1.46 ± 0.14^{b}	1.22 ± 0.11^{b}
Copepods						
Acartia sp.	55.71	52.24	53.85	1.79 ± 0.24^{a}	1.36 ± 0.25^{a}	1.22 ± 0.18^{a}
Calanus sp.	80	76.12	76.92	3.47 ± 0.40^{a}	$2.42 \pm 0.30^{a,b}$	2.19 ± 0.32^{b}
Paracalanus sp.	38.57	50.75	53.85	0.98 ± 0.18^{a}	1.23 ± 0.19^{a}	1.10 ± 0.18^{a}

Different letters in each category show significant differences of each prey between fish sizes ($p < 0.05$)

The *P. serperaster* fed on *Navicula* spp. ($E = 0.69$) in the wet season, but on *Nitzschia* spp. ($E = 0.76$) in the dry season (Table 5). *Navicula* spp. were mostly fed by the goby in all size groups with an increasing tendency as fish size increased. In the wet season, *Spirulina* sp. were rarely ingested, followed by *Paracalanus* sp. and *Acartia* sp., but in the dry season, *Anabaena* spp. were rarely consumed followed by *Spirulina* sp., *Paracalanus* sp. and *Acartia* sp. (Table 5). Cyanophyta and copepods were rarely fed by the fish at all sizes, followed by *Thalassiosira* sp. and

Table 4 Percentage of frequency of occurrence and biovolume of four major categories of food items between three fish-size groups (group 1: *TL* <16 cm, group 2: *TL* 16–18 and group 3: *TL* >18 cm) during the dry and wet seasons

Food			Detritus	Bacillariophyta	Cyanophyta	Copepods
Occurrence	Size group	1	100	100	92.86	82.86
		2	100	100	88.06	88.06
		3	100	100	93.85	83.08
	Season	Dry	100	100	98.39	87.9
		Wet	100	100	80.77	79.49
Biovolume (Mean ± SE)	Size group	1	47.75 ± 1.48^{a}	40.70 ± 1.39^{a}	5.32 ± 0.38^{a}	6.23 ± 0.59^{a}
		2	53.09 ± 1.02^{b}	38.16 ± 1.13^{a}	3.74 ± 0.34^{b}	5.00 ± 0.44^{a}
		3	51.88 ± 1.07^{b}	40.46 ± 1.11^{a}	3.14 ± 0.24^{b}	4.51 ± 0.49^{a}
	Season	Dry	50.25 ± 1.51^{a}	40.97 ± 1.42^{a}	3.52 ± 0.35^{a}	5.27 ± 0.55^{a}
		Wet	51.23 ± 0.69^{a}	39.03 ± 0.73^{a}	4.46 ± 0.24^{b}	5.28 ± 0.35^{a}

Different letters in each category (fish size and season) show significant differences ($p < 0.05$) between fish sizes and seasons

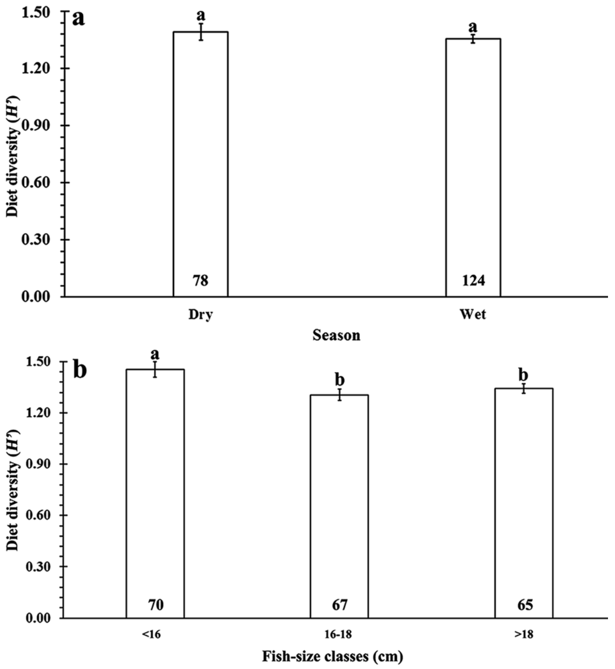

Fig. 4 Variations of diet diversity (*H*) of *P. serperaster* between season (**a**) and fish size (**b**). *Different letters* show significant differences (mean ± SE, $p < 0.05$). *The number of fish used for analysis* is given in each column

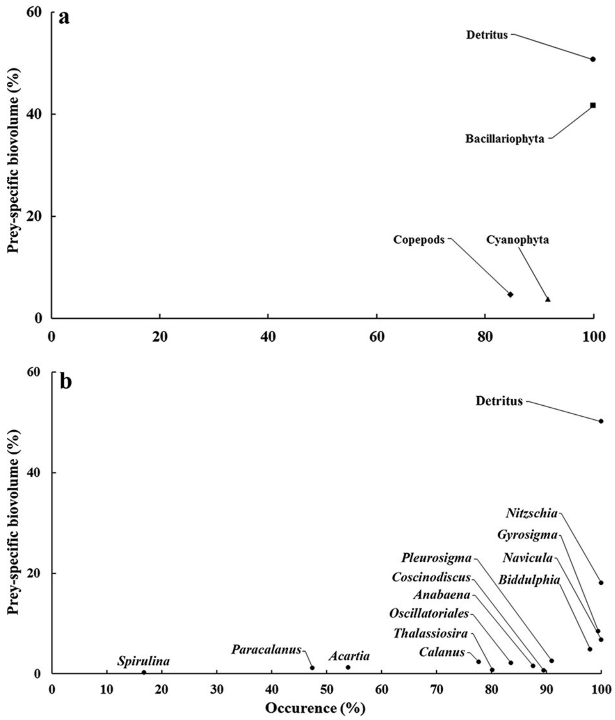

Fig. 5 The modified Costello graphics represents feeding strategy based on plotting the relationship between percentage of biovolume and frequency of occurrence in four major taxonomic categories (**a**) and in 14 prey items (**b**) for *P. serperaster*

Pleurosigma sp. (Table 5), suggesting the possibility of feeding in the water column as pelagic copepods were found in fish stomach.

Discussion

As the gut length is proportional to the fish body length, the relative gut length index (*RGI*) has been used as an indicator to classify feeding habits (Xie et al. 2001; Pouilly et al. 2003; Hernaman et al. 2009; Berumen et al. 2011). In the present study, the *RGL* showed that *P. serperaster* is omnivorous according to the scale described by Geevarghese (1983), coinciding with a previous study on this goby in Malaysian water (Khaironizam and Norma-Rashid 2000). The omnivorous category is found in the goby *Pseudapocryptes elongatus* (Tran 2008). Although the *RGL* of *Parapocryptes serperaster* varied with fish size, the

Table 5 Diet electivity (*E*) of *P. serperaster* between dry and wet seasons and among fish size groups (size 1 <16 cm, size 2 16–18 cm and size 3 >18 cm TL)

Food items	Diet electivity (*E*)				
	Wet	Dry	Size 1	Size 2	Size 3
Detritus	0.21	0.33	0.43	0.45	0.45
Bacillariophyta					
Rhizosolenia sp.	−1	−1	−1	−1	−1
Navicula spp.	0.69	0.54	0.67	0.72	0.73
Nitzschia spp.	0.60	0.76	0.39	0.22	0.45
Thalassiosira sp.	−0.58	−0.78	−0.72	−0.8	−0.79
Pleurosigma sp.	−0.27	−0.34	−0.49	−0.65	−0.62
Biddulphia spp.	0.32	0.34	0.04	−0.13	−0.16
Coscinodiscus spp.	−0.15	−0.55	−0.28	−0.45	−0.58
Ditylum spp.	−1	−1	−1	−1	−1
Gyrosigma sp.	0.62	0.26	0.36	0.28	0.02
Cyanophyta					
Oscillatoria sp.	−0.24	−0.35	−0.81	−0.85	−0.89
Spirulina sp.	−0.85	−0.75	−0.97	−0.99	−0.97
Anabaena spp.	−0.31	−0.88	−0.96	−0.97	−0.98
Chlorophyta					
Cosmarium spp.	−1	−1	−1	−1	−1
Euglenozoa					
Phacus sp.	−1	−1	−1	−1	−1
Copepods					
Acartia sp.	−0.73	−0.75	−0.97	−0.98	−0.98
Calanus sp.	−0.44	−0.53	−0.92	−0.95	−0.95
Paracalanus sp.	−0.79	−0.63	−0.98	−0.98	−0.98
Larva	−1	−1	−1	−1	−1

feeding habits of this goby species did not change as fish grew and the values of *RGLs* were 1–3, an indicator of omnivorous feeding. In contrast, the monkeyface prickleback *Cebidichthys violaceus* change their food from small invertebrates (carnivores) to algae (herbivores) as fish grow (German and Horn 2006). The *RGL* has been successfully used to classify the trophic guild in most fish species (Geevarghese 1983; Elliott and Bellwood 2003; Karachle and Stergiou 2010), though it did not reliably reflect the trophic level of some gobiid species in a tropical Indo-Pacific seagrass bed (Pogoreutz and Ahnelt 2014). In the present study, the *RGL* was successfully applied to *P. serperaster* as supported by the proportion of relative values between the fish total length and gut length. The analysis of stomach contents also revealed omnivorous feeding of this fish as its stomach mainly contained detritus, phytoplankton and zooplankton.

Feeding intensity of *P. serperaster* varied with month as demonstrated by monthly variation in the gut fullness index (*FI*). This goby species actively fed during the pre- and post-spawning periods to gain the energy needed for gonad development and compensate energy loss due to spawning (Dinh et al. 2015a). In comparison to the dry season, this goby species showed intensive feeding in the wet season, but low feeding in the dry season possibly due to seasonal variation in food availability (Nedeco 1993). A seasonal change in feeding intensity is also found in the Bayad fish *Bagrus bajad* in Egypt (Bakhoum and Fatas 2003) and the naked goby *Gobiosoma bosc* (see D'Aguillo et al. 2014) in western Atlantic estuaries. However, the feeding intensity did not vary with fish size in the present study, suggesting that food competition is not severe between small and large fish.

The goby *P. serperaster* primarily ingested detritus, coinciding with a high proportion of this item in the environment. This goby also fed on Bacillariophyta, which is similar to the mudskipper *Boleophthalmus pectinirostris* that feeds mainly on diatoms (Yang et al. 2003). A small percentage of Cyanophyta and copepods was found in the stomach of *P. serperaster*, suggesting that these prey items were randomly fed, which is supported by the low occurrence of these items in the environment. This finding is similar to a related goby *Pseudapocryptes elongatus* that also feeds on detritus and Bacillariophyta (Tran 2008). In contrast, Khaironizam and Norma-Rashid (2000) reported that *P. serperaster* mainly ingested Bacillariophyta and suggested that the food availability in the environment is the main factor involved in food selection, which is similar to the round goby *Neogobius melanostomus*, a non-random or nonopportunistic feeder that can adapt to different environments (Thompson and Simon 2014). The common goby *Pomatoschistus microps* is an opportunistic carnivore feeding on prey according to its availability; the fish stomach comprises Mysidacea in the upper Tagus estuary (Salgado et al. 2004), but not in fish found in the Mondego estuary due to low prey abundance in the environment (Leitão et al. 2006).

The high rainfall in the wet season leads to the change of nutrient input (Nedeco 1993), resulting in the variation of food composition of *P. serperaster* between the dry and the wet seasons. The seasonal change in diet composition may also be caused by the large size of gonad that occupied the major space in the body cavity prior to spawning. Seasonal variation was also found in the diet of the sand goby *Pomatoschistus minutus* feeding mainly on foraminifers in the autumn and mysids in the summer, and the common goby *Pomatoschistus microps* mostly ingesting copepods in the winter and polychaetes in the spring and summer in the upper Tagus estuary, Portugal (Salgado et al. 2004). Likewise, the diet of the round goby *N. melanostomus* is varied with season, feeding mainly on fish eggs in the spring and ostracods in the autumn in the Kingston Basin, Lake Ontario (Brush et al. 2012). The differences in diet composition of *P. serperaster* between the wet and dry seasons suggest that the diet composition is reflected by prey availability in the environment. The increasing body size or increasing feeding activity as fish grow may result in the difference in diet composition of *P. serperaster* in three size groups. A variation of diet with fish size is also found in the sand goby *Pomatoschistus minutus* feeding mainly on copepods in small fish but on oligochaetes, fish, bivalve and shrimp in large fish, whereas the common goby *Pomatoschistus microps* shows no clear trend of diet preference between fish sizes (Salgado et al. 2004).

Based on the estimate of food biovolume, *P. serperaster* mainly fed on detritus and some Bacillariophyta (*Navicula* spp., *Nitzschia* spp. and *Gyrosigma* sp.), but this fish rarely consumed Cyanophyta and copepods. The possible reason is that the Cyanophyta such as *Oscillatoria* sp. and *Spirulina* sp. are not easy to digest compared to other algae (Vu and Duong 2013), and *Acartia* sp., *Calanus* sp. and *Paracalanus* sp. (copepods) rarely appeared in the environment. The biovolume method is concomitant with the result of other methods for food item determination and can be used to determine the seasonal and intraspecific variations in small fish that feed on small-sized prey. The contribution of four major food categories to the *P. serperaster* diet varied with food analysis methods, especially for the diet occurrence frequency, suggesting that prey size eventually influenced its determination for the trophic guild. This situation was found in round goby *N. melanostomus* (Thompson and Simon 2014) and in the mudskipper *B. pectinirostris* (Yang et al. 2003), suggesting that the biovolumetric method is useful to study the dietary composition of small fishes such as gobiids.

Like most other goby species (Thiel et al. 1996; D'Aguillo et al. 2014), *P. serperaster* is considered a generalist feeder as various food types (14 type of preys) were found in its stomach, enabling *P. serperaster* to adapt to a variety of environmental conditions. The matching result between the modified Costello graphical method and the evenness index shows that the graphical analysis is applicable to quantify fish feeding on small prey items. The high diet diversity was also found in other gobiids such as *P. minutus* and *P. microps* (Salgado et al. 2004; Leitão et al. 2006), *Achondrostoma arcasii, Pseudochondrostoma duriense*, *Salmo trutta* and *Gasterosteus gymnurus* (Sánchez-Hernández et al. 2011). By contrast, the goby *Economidichthys pygmaeus* has a narrow diet breadth and is a specialist feeder, feeding mainly on copepods and chironomids (Gkenas et al. 2012). Although only 19 food items belonging to six main categories such as detritus, Bacillariophyta, Cyanophyta, Chlorophyta, Euglenozoa and copepods were found in the environment, more microalgae might have been found if more samples had been collected. In the wet season, *Navicula* spp. were mostly ingested whereas *Spirulina* sp. was rarely fed. In the dry season, *Nitzschia* spp. were mostly fed, while *Anabaena* spp. were rarely consumed. *Navicula* spp. were mainly ingested, whereas Cyanophyta and copepods were rarely fed by fish at all sizes. The diet overlap of food preys between the fish stomach and the water column suggests that *P. serperaster* may feed in the water column. Likewise, the co-occurring *Pseudapocryptes elongatus* in the same site also feed in the water column (Tran 2008).

In conclusion, *P. serperaster* was an omnivorous fish, consumed mainly detritus and some Bacillariophyta, and its feeding habits varied with the availability of food items in the environment. The food composition of this goby varied with fish size and season, and this fish showed a high diet diversity and was a generalist feeder. Its feeding intensity peaked before and after spawning and varied with season but did not vary with fish size. The present study provides a basis for further research on the feeding biology of this goby species.

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