

## The mechanisms leading to ontogenetic diet shift in a microcarnivore, *Pterogobius elapoides* (Gobiidae)

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A variety of fish species undergo an ontogenetic change in prey selectivity, and several potentially interacting factors, including nutrient requirement, microhabitat change, and foraging ability, may account for the occurrence of the shift. Here we examine the foraging ecology and ontogenetic diet shift of a micro-carnivorous goby, *Pterogobius elapoides* (serpentine goby), dominant component of fish assemblage in shallow rocky areas off the coast in Korea and Japan. Although most other gobies are primarily benthic carnivores, *P. elapoides* is a semipelagic fish; however, little is known about how those species change their foraging tactics with growth. In our diet analyses, the most common diet was pelagic copepods and benthic amphipods, and diet shift was observed from pelagic to benthic with growth. The ontogenetic diet shift seems to be the result of the preference for energetically more profitable prey in larger-size classes as well as the results of different prey availability due to among-habitat variation in diet. However, differential food preference does not appear to affect individual scope for searching food. Several factors such as predation pressures and interspecific resource partitioning might contribute to the changes in diet observed among size classes, which were included in our ongoing tests.

**Keywords:** ontogenetic diet shift; foraging behavior; serpentine goby; *Pterogobius elapoides*; micro-carnivore; Gobiidae

### Introduction

A variety of fish species undergo an ontogenetic change in prey selectivity, that is, from planktivory to piscivory (Schmitt and Holbrook 1984; Holbrook et al. 1985; Shibuno et al. 1994; Lockett and Suthers 1998; Graham et al. 2007; Schellekens et al. 2010; Baeck et al. 2011). Many potentially interrelating factors may account for the occurrence of these shifts (McCormick 1998). Growth-related morphological differences can lead to differential exploitation of a food resource and, in turn, changes in microhabitat use, being a function of changing in nutrient requirement (MacNeill and Brandt 1990; Luczkovich et al. 1995; Peterson and McIntyre 1998). Likewise, foraging schedule and ability may change with ontogeny, which can be compromised with availability and density of prey organisms (Clements and Choat 1993; Lukoschek and McCormick 2001). A thoughtful consideration of how a species exploits its food resource and how that changes with growth is prerequisite to any examination for the pattern and dynamics of species assemblage on temporal and spatial scales (McCormick 1998).

The Gobiid species (gobies), one of the largest families of fish with more than 200 genera, are commonly distributed in temperate, subtropical, and

tropical regions (Nelson 2006). Gobies are primarily fish of shallow oceanic habitats including tide pools, coral reefs, and sea-grass fields; they are also very abundant in brackish water, and a small number of gobiid species are also entirely adapted to freshwater system (Nelson 2006). Although few are valuable as food for humans, they are generally of great significance as prey and predator species for commercially important organisms. While the occurrence of ontogenetic change in prey selectivity has been reported for gobies in several studies (Gibson 1970; Vass et al. 1975; Grossman 1980; Grossman et al. 1980; Huh and Kwak 1998a, 1998b, 1999), little is known about how those species change their foraging tactics with growth.

In this study, we examine the foraging ecology of a goby, *Pterogobius elapoides* (serpentine goby; Figure 1), a common component of fish assemblage in shallow rocky areas off the coast in Korea and Japan (Masuda et al. 1984; Kim et al. 1986). While most gobies are benthic carnivores, consuming mainly crustaceans and polychaetes (Gibson and Ezzi 1978; Grossman et al. 1980; Behrens 1989; Kikuchi and Yamashita 1992; Aarnio and Bonsdorff 1993; Humphries and Potter 1993; Swenson and McCray 1996), *P. elapoides* is a semipelagic fish, seldom settling on bottom structure (Dōtu and Tsutsumi 1959).

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However, temporal (seasonal) space defense is observed in this species sometimes, but not often, for their benthic feeding territories (personal observation). *P. elapoides* is thus expected to undergo distinct pattern of ontogenetic shifts in foraging ecology from other gobies, even though it has never been thoroughly investigated.

In the present study, we investigated for the first time whether diet changes with ontogeny and explored the mechanisms by which partitioning of the food resource occurs among different size classes in *P. elapoides*. First, the stomach of individuals from different size classes was dissected open, and the contents inside were examined to find differences, if any, in diet taxa. Second, information on prey species availability, size-related feeding mechanics, and microhabitat selectivity was used to find the potential factors accounting for the occurrence of the shift.

## Materials and methods

### *Locations and study species*

Collections for estimation and observation were carried out on shallow rocky areas off the coast of Kurahashi Island (Honmura Bay, the Seto Inland Sea; 34°5'14''N, 132°30'0''E) in Japan. *P. elapoides* is one of the dominant inhabitants in our study sites. Many individuals cruise around boulders and conceal themselves in cracks beneath boulders or inside of brown algae patches to avoid predation (S.-H. Choi, personal observation). *P. elapoides* is relatively smaller in size than that of other *Pterogobius* species. This species exhibit pale brown with six or seven transverse black bands on their body side continuing behind the dorsal and anal fins, which make each individual visually conspicuous (Figure 1). This species reaches sexual maturity at



Figure 1. The serpentine goby, *Pterogobius elapoides*, hovering to search prey on the bottom in the ocean around Kurahashi Island, Japan.

around 70–80 mm in standard length (hereafter SL; Dōtu and Tsutsumi 1959). The breeding season of the studied population starts in November and continues well into December. The male builds a nest underneath a boulder and provides exclusive paternal care for eggs, which includes fanning and defending the brood until hatching (Dōtu and Tsutsumi 1959). Adult individuals generally die at the completion of the breeding season.

### *Diet analysis*

A total of 34 individuals were collected in the study site using a gill net during the daytime (dates were chosen based on the weather condition; 16–17 May, 22–23 June, 17 July, and 6 August in 2000). The captured fishes were preserved in 10% buffered formalin solution and were measured to the nearest 0.01 mm by digital calipers. Each individual was allocated into three different size classes: small (50–60 mm SL), medium (61–70 mm SL), and large (> 70 mm SL). The stomach of each individual was dissected open, and the contents inside were examined under a binocular dissecting microscope. Prey were removed from the stomach and identified to the lowest taxon feasible. The greatest length or carapace length of all of the individuals was measured to the nearest 0.01 mm using an ocular micrometer. Prey volume was estimated by measuring the length and width of each item and calculating its cylindrical or spherical volume, depending on its shape. For each sample, the percent composition was calculated in number and in volume.

### *Invertebrate fauna*

To obtain fauna information of planktonic, algal and benthic invertebrates in the study site, different methods were used for sampling from May to July 2000. Planktonic invertebrates were sampled by quickly sweeping a portable handle-fitted plankton net (0.1 mm mesh) in the upper 30–50 cm of the sediment. Algal invertebrates were collected (eight replicates) by taking (into the 0.1 mm mesh bag) parts of algae where fish were feeding. Benthic invertebrates were sampled from substrates taken in the sandy and muddy bottom between boulders (eight replicates) using a metal core (100 × 100 mm). All the samples collected were preserved in 5% formalin solution prior to examination. Each invertebrate were identified and counted, and 50 intact individuals randomly chosen per taxon were measured for their maximum length in the laboratory. The total counts were adjusted to the number per cubic meter for planktonic invertebrates or per square meter for algal and benthic invertebrates.

### Foraging behaviors and microhabitat preferences

Foraging behaviors and microhabitat preference (including home ranges) for each of the three size classes were examined using scan field observations with scuba diving and snorkeling at a chosen time depending on the weather condition between 08:00 and 17:00 for 30–60 min per dive from May to August in 2000. The observation was made in depth ranging from 1 to 6 m on rocky terrain with cracks and crevices irregularly formed and overgrown brown algae. A total of 17 individuals (53–78 mm SL) were captured from the study site using encircling monofilament nylon net (15 × 1 m; 5 mm square mesh). The collected individuals were marked by color paint injection (blue acrylic paint) over the skin (see Thresher and Gronell 1978 for the method). After measuring their SL using a scale bar to the nearest 1 mm, each individual was allocated into three size classes (see Diet analysis section) and was released. Seventeen individuals were tracked down for observation; small- ( $N=6$ ), medium- ( $N=6$ ), and large-size class individuals ( $N=5$ ) were observed for 21, 17, and 27 h, respectively.

## Results

### Ontogenetic shift in diet composition

The stomach of small-size class *P. elapoides* contained pelagic copepods, amphipods, and branchiopods. More than 90% of the stomach contents (in volume) were pelagic copepods, including *Palacalanus* spp. (Calanoida), *Euterpina* spp. (Harpacticoda), *Oithona* spp. (Cyclopoida), and *Calanus* spp. (Calanoida; Figure 2a). Among them, *Palacalanus* species were exclusively predominant, covering 76.5% in the total volume (Figure 2a), as expected from the fact that genus *Palacalanus* is the most abundant species found in the water column (Table 1). Although other copepods, including *Oithona* spp. and *Nauplius* spp., were also abundant in water column (Table 1), they were rarely found in the stomach contents of this size class.

Individuals of medium-size class are likely to consume more diverse items of prey than do smaller ones (Figure 2b). Copepods, including Harpacticoda, Mysidacea, and Calanoida, were no more exclusively dominant food items for medium-size class (44.68% in number, 23.66% in volume), while various amphipod species (algal amphipods such as *Pontogeneia* spp. and *Caprella* spp., and benthic amphipods such as *Melita* spp., *Corphium* sp., and Cumacea) were more frequently found (47.68% in number, 54.11% in volume; Figure 2b). Big organisms, such as benthic annelid worms (Polychaeta), were also included in the items. In the medium-size fishes, Harpacticoid is one of the predominant item in number ( $26.38 \pm 4.68\%$ ) but was

Table 1. Individual numbers, numeric occurrence (%; in bracket), and mean sizes (mm ± standard deviation) of the taxa collected from water column, alga, and substratum in the study site.

	Prey available from the environments	
	Individual number (%)	Mean body size ± SD
<i>Water column</i>		
Copepoda		
Calanoida		
<i>Palacalanus</i> spp.	1487 (56.6)	0.6 ± 0.17
Copepodid stages	289 (11.4)	0.6 ± 0.19
Nauplii	286 (10.9)	0.4 ± 0.22
<i>Calanus</i> spp.	43 (1.6)	1.8 ± 1.22
Poecilostomatoida		
<i>Corycaeus</i> sp.	85 (3.2)	0.7 ± 0.08
Cyclopoida		
<i>Oithona</i> spp.	128 (4.9)	0.5 ± 0.08
Harpacticoda		
<i>Euterpina</i> sp.	45 (1.7)	0.6 ± 0.06
Others (Copepoda)	85 (3.2)	0.7 ± 0.34
Cladocera		
<i>Evadne</i> sp.	25 (1.0)	0.7 ± 0.10
Appendicularia		
<i>Oikopleura</i> ssp.	98 (3.7)	5.7 ± 1.67
Others	42 (1.6)	1.1 ± 0.73
<i>Algal collections</i>		
Amphipoda		
<i>Pontogeneia</i> ssp.	1571 (52.7)	1.8 ± 0.64
<i>Caprella</i> ssp.	234 (7.9)	16.4 ± 17.63
Mysidacea	28 (0.9)	4.5 ± 1.63
Copepoda		
Harpacticoda	1016 (34.1)	0.7 ± 0.07
Crustacea		
Tanaidecia	85 (2.9)	2.2 ± 1.08
Others	48 (1.6)	2.7 ± 1.55
<i>Benthic substratum</i>		
Amphipoda		
<i>Melita</i> spp.	6196 (10.7)	2.0 ± 1.11
<i>Corphium</i> sp.	2327 (4.0)	3.1 ± 1.56
<i>Maera</i> sp.	1004 (1.7)	3.8 ± 1.23
<i>Grandidierella</i> sp.	976 (1.7)	2.4 ± 0.54
Other (Amphipoda)	429 (0.7)	2.7 ± 1.81
Copepoda		
Harpacticoida	42878 (74.1)	0.7 ± 0.05
Cumacea	447 (0.8)	3.1 ± 0.71
Polychaeta	2893 (5.0)	22.7 ± 16.40
Ostracoda	684 (1.2)	1.0 ± 0.11

only a minor component volumetrically ( $4.33 \pm 0.74\%$ ), probably due to its relatively small sizes (Figure 2b). On the contrary, *Caprella* spp., Mysidacea and Polychaeta showed low proportions in numbers but not volumetrically (Figure 2b).



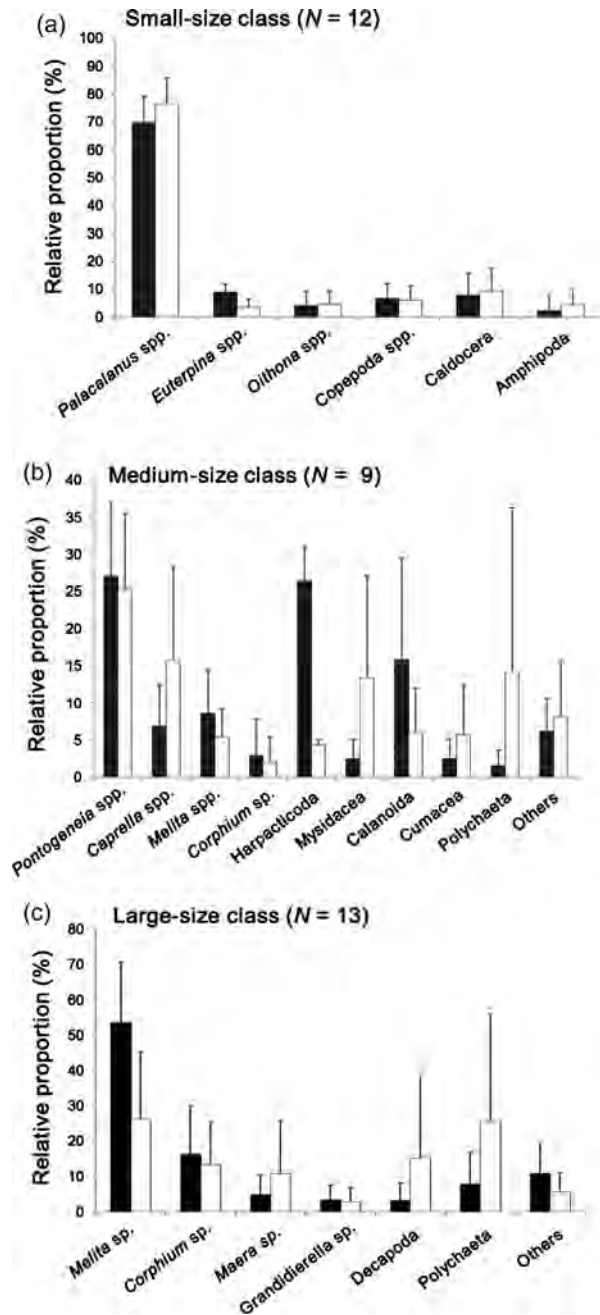


Figure 2. Comparison of numeric (shaded bar) and volumetric (empty bar) occurrence (presented as relative frequencies;  $\% \pm$  standard deviation) of major dietary items found in the stomach contents among three size classes investigated.

The stomach contents of the large-size class comprised only of benthic invertebrates, including benthic amphipods, decapods, and Polychaetes (Figure 2c). Benthic amphipods, including *Melita* spp., *Corphium* sp., *Maera* sp., and *Grandidierella* sp., were the dominant ones in numbers, while pelagic copepods and algal amphipods were not found in the stomach items of this size class (Figure 2c). Decapoda

and Polychaeta showed high values in volume but not in number (Figure 2c). Although Harpacticoids were the most abundant invertebrate in the substratum (Table 1), they were rarely found in the stomach of large-size fishes. The large fish consumed proportionally more benthic amphipods in their diet than did the medium-sized fish (Mann–Whitney  $U$ -test,  $U = 108.0$ ,  $p < 0.001$ ).

#### Ontogenetic shift in foraging behaviors

*Pterogobius elapoides* show three distinct foraging behaviors to catch prey in three types of environments: capturing in mid-water (CM), sucking algal invertebrates (SA), and picking benthic invertebrates (PB). The three size classes significantly differ in occurrence of three different foraging behaviors ( $\chi^2 = 61.51$ ,  $df = 1$ ,  $p < 0.001$ ; Table 2). CM and SA were observed in small-size fishes (Table 2). For CM, small-size fishes generally hover in water column around rocks where they rapidly feed on pelagic prey. When potential prey available for SA are found on the surface of brown algae, individuals halt around the algae for 3–4 seconds and feed on the prey with powerful suction. In this size class, CM was more frequently observed than SA (Wilcoxon signed rank test,  $z = -4.15$ ,  $p < 0.001$ ; Table 2).

All types of foraging behaviors were observed in the fishes of medium-size class (Table 2). The frequency of the CM was significantly decreased compared to small-size class ( $z = -4.97$ ,  $p < 0.001$ ), while the frequency of SA was increased relative to the small fish ( $z = -4.36$ ,  $p < 0.001$ ). For PB, individuals search for prey on the substrate surface, and they always stop hovering for a few seconds when they found prey on the substrate. After taking the prey, the fish generally churn the prey with sediment and expel inedible materials out of opercula and mouth. SA seems to be the dominant foraging pattern in medium-size class (Kruskal–Wallis  $H = 262.10$ ,  $df = 2$ ,  $p < 0.001$ ).

Capturing in mid-water (CM) and SA were not observed at all among the fishes of large-size class (Table 2). The frequencies of feeding were the lowest ( $9.64 \pm 7.77$ ) when compared with small-size class ( $27.88 \pm 21.05$ ) and medium-size class ( $16.88 \pm 8.53$ ; Kruskal–Wallis test  $H = 104.15$ ,  $df = 2$ ,  $p < 0.001$ ).

#### Microhabitat preferences

Home ranges did not appear to change with growth as this species primarily prefer to stay in areas with boulders and sand bottoms around the reefs. However, individuals in different size classes showed clear difference in space use, suggesting that *P. elapoides* undergo vertical microhabitat shifts from water

Table 2. Ontogenetic changes in using different types of foraging behavior by serpentine gobies, that is, capturing in mid-water (CM), sucking algal invertebrate (SA), and picking benthic invertebrates (PB).

Size class	CM	SA	PB
Small	25.38 ± 21.95 (80.08%)	2.59 ± 2.10 (19.92%)	0 (0%)
Medium	3.46 ± 2.30 (25.37%)	11.47 ± 8.98 (59.94%)	1.96 ± 1.29 (14.69%)
Large	0 (0%)	0 (0%)	9.64 ± 7.77 (100.00%)

Note: Values indicate frequency of the behavior per 10 min (mean ± standard deviation) and are also presented on percentage basis (%).

columns to the bottom with growth. The individuals in small-size class were usually found around reefs in the middle water column. The individuals in medium-size class always swam around reefs with patches of brown algae. The individuals in large-size class generally hovered around reefs in 5–10 cm upper from the bottom.

### Discussion

The most common prey, by number and volumetrically, in *P. elapoides*' diet were pelagic copepods and benthic amphipods. There was an ontogenetic diet shift from pelagic to benthic prey, as well as among-habitat variation in diet as a result of different prey availability. *P. elapoides* has been known as omnivorous fish because copepod, organic deposit, and algae particles were found from the stomach contents in a previous study (Dötu and Tsutsumi 1959), which did not consider the feeding microhabitats and prey availability. Algae particles were not found as stomach contents in our study. Our diet analyses consequently show that *P. elapoides* is microcarnivore, as is the case for many other gobies (Blaber and Whitfield 1977; Gibson and Ezzi 1978; Grossman et al. 1980; Kikuchi and Yamashita 1992; Onadoko 1992; Aarnio and Bonsdorff 1993; Humphries and Potter 1993; Swenson and McCray 1996).

The ontogenetic diet shift was the result of the preference for energetically more profitable prey in *P. elapoides* in larger-size classes, as shown in many other microcarnivores (Grossman 1980; Schmitt and Holbrook 1984; MacNeill and Brandt 1990; Gill and Hart 1994; Luczkovich et al. 1995; Peterson and McIntyre 1998). Pelagic copepods, in particular Calanoida, are generally much smaller than amphipods and polychaetes that are consumed by the individuals from medium- and large-size classes. Pelagic copepods may energetically be less profitable, but are valuable for the individuals in the small-size class with reduced handling and foraging efforts and with relatively high abundance. By contrast, the increased searching and capturing efforts for larger individuals can be compensated by exploitation of differing prey sources and the increased caloric profitability (Ellison et al. 1979). This

is in perfect agreement with optimal foraging theory of Estabrook and Dunham (1976) predicting that ontogenetic diet shift of an individual is a stepwise development to maximize its net energy gain.

Foraging techniques is an essential determinant of ontogenetic difference in the diets of *P. elapoides*. CM is the foraging pattern appropriate for taking small copepods and most frequently observed in small-size class, while large-size individuals generally pick up relatively large benthic invertebrates. The exploitation of differing prey sources is directly constrained by morphological capacity of feeding apparatus (Schmitt and Holbrook 1984; Stoner and Livingston 1984; MacNeill and Brandt 1990; Peterson and McIntyre 1998). In the study of a microcarnivorous fish, *Cheilodactylus spectabilis*, the increase in size of the buccal cavity, hyoid complex, and associated musculature lead directly to an increase in the suction primarily used to capture prey (McCormick 1998). In *P. elapoides*, the increasing size of the feeding apparatus with growth (Kendall's rank correlation test; gape width,  $\tau = 0.874$ ,  $p < 0.001$ ; snout length,  $\tau = 0.890$ ,  $p < 0.001$ ; S.-H. Choi and H.Y. Suk, unpublished data) may contribute to a feeding on larger prey. However, the present data do not provide any direct evidence for increasing efficiency of handling procedure with the growth in feeding apparatus.

Growth-related preference for different food resources might require individuals to change their microhabitats, as also shown in many other studies (Werner and Hall 1988; Clements and Coat 1993; Lukoschek and McCormick 2001). Vertical up-shifting in microhabitat was observed in the present study. Water column is the perfect place for small individuals to feed pelagic organisms with occupying exposed perches within rocky reef habitats. Although the medium-sized fish consume prey in the water column, they seem to prefer to find algal invertebrates, as they spend much time for foraging and searching around algae patches on the reefs. The large-sized fish only feeds on prey found on sediments in the sand bottom. However, ontogenetic shift in food preferences does not appear to affect individual scope for searching food, as the home ranges of individuals from different size classes (collected in the same site) were totally

overlapped, and the sizes of the home ranges were not different from the individuals in different size classes (actually decreased with growth).

In conclusion, ontogenetic diet shift in *P. elapoides* is influenced by several factors, including body size and the availability of prey, and results in differential microhabitat utilization. A number of factors have not been assessed, and they might contribute to the changes in diet observed among size classes, even though several more factors are included in our ongoing tests and upcoming publications. For instances, exposure of individuals to predation has been shown to be an important determinant of microhabitat utilization in many fish species (e.g., Schmitt and Holbrook 1984; Werner and Hall 1988) and may influence the patterns documented in our study. Intraspecific territorial interaction and the resultant resource partitioning may also be a factor determining the home range size and evolutionary processes related to feeding strategies.

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