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Changes with Growth in Feeding Habits and Gravel Turning Behavior of the Wrasse, *Coris gaimard*

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Abstract Ontogenetic changes in the diet and foraging behavior of the wrasse, *Coris gaimard*, were studied on shallow reefs at Kuchierabu-jima Island, southern Japan. *C. gaimard* selected larger prey with growth, smaller individuals feeding on small crustaceans (e.g., gammarideans) and larger ones feeding on larger molluscs (i.e., pelecypods, gastropods and chitons) and crabs. Although *C. gaimard* usually took prey from the surface of the substrate, individuals of 5 cm TL and over also foraged for prey under gravel by turning over the latter. The relative frequency of gravel turning and size of gravel turned over increased with growth, larger fish being able to take correspondingly larger prey (e.g., molluscs and crabs) hiding under larger gravel. Especially for small individuals, foraging for alternative prey by turning over gravel may reduce the need to extend the foraging range and consequently the risk of predation.

The labrid fish, *Coris gaimard* (Quoy and Gaimard), which attains more than 30 cm TL, is widely distributed in the tropical Indo-Pacific. It is common in the coastal waters of southern Japan (Araga, 1984). The species is solitary, being a bottom-dweller on coral or rocky reefs, and feeds on small benthic invertebrates as well as other labrid fishes (Hiatt and Strasburg, 1960; Hobson, 1974; Gushima, 1981). *C. gaimard* usually takes prey by pecking at the surface of rocks or dead coral, but sometimes searches for prey hiding under gravel by skillfully turning the gravel over (Hobson, 1974; Gushima, 1981). However, ontogenetic changes in its foraging ecology have not been studied until now. In addition, although foraging behavior by turning over gravel has also been reported in the labrids, *Coris aygula* (Gushima, 1981) and *C. dorsomaculata* (Tribble, 1982), the function of such behavior has not been examined in depth.

The gut contents and foraging behavior of *C. gaimard* of various size classes, and the distribution of prey in the foraging area were studied, enabling the ontogenetic changes in feeding habits and foraging behavior to be clarified, and the function of such foraging behavior to be considered.

Materials and Methods

The Island of Kuchierabu-jima (30°28′N, 130°10′E) lies between Kyushu and the Ryukyu Islands (see Gushima et al., 1991). The reef fish fauna of the island shows predominantly tropical characteristics (Gushima and Murakami, 1977). Underwater observations and collections of specimens were made on shallow reefs in Honmura and Nishiura Bays of the island between April and October in 1980-1982.

The substrate of the study area in Honmura Bay consisted of boulders, sand patches and dead coral from the shore to about 100 m offshore, 0-10 m deep, and of sand thereafter to 200 m offshore, 10-20 m deep. The substrate of the study area in Nishiura Bay consisted of dead coral, rocks and sand patches from the shore to about 200 m offshore, 0-20 m deep. There was an accumulation of gravel and dead coral rubble near the shore.

Eighty eight individuals of *Coris gaimard* were collected by spear gun, gill net and hook-and-line in the daytime between 10:00 and 17:00, and fixed immediately in 10% formalin solution. In the laboratory, total lengths (TL) were measured to the nearest mm. The guts were removed and prey items (other than bait) in the gut contents identified under a binocular microscope. The body sizes (length, height and width) of the prey animals were measured, and the percentage of the latter in the diet volume (the total volume of gut contents in all specimens) calculated. Crushed prey animals were restored when possible and measured. The second largest value among dimensions of each prey animal was regarded as its body width.

Foraging behavior was observed by following individuals for about five minutes between 10:00 and 17:00. The total length of each fish observed was estimated visually to the nearest cm. The distance moved between foraging sites was estimated from a map drawn of the fish's path. The stones that were turned over while foraging were collected and their diameters measured.

In addition, prey hiding under the gravel were collected together with the gravel by inserting a square frame (10×10 cm) covered with a plastic bag into the foraging ground to a depth of 2 cm, and closing the frame with a bottom panel slid in from the side. The entire sample was fixed immediately in 10% formalin solution and the animals later sorted, identified and measured. The diameter of the gravel was also measured.

The data for all months were pooled because the environment during the observation periods was stable, and the distribution of prey in the foraging area did not differ from month to month (Gushima, 1981; Gushima et al., 1991).

Results

Gut contents

The collected fish (1.6–30.5 cm TL) were separated into six size classes. Their gut contents are shown in Table 1. In the smallest size class (1.6–4.9 cm), small crustaceans (e.g., gammarideans, copepods, tanaidaceans, ostracods and isopods) comprised the most important group of prey (>80% by volume in the diet). In the 5.0–9.9 cm size class, gammarideans were the dominant prey animals (57%), and pelecypods and gastropods were also eaten (about 8% and 3%, respectively). In the 10.0–14.9 cm size class, while gammarideans remained dominant (42%), molluscs (i.e., pelecypods, gastropods and chitons) had increased greatly to about 39%, and crabs were also eaten (about 9%). In the 15.0–19.9 cm size class, molluscs were the dominant prey group (about 48%). Crabs had increased markedly to about 20%, and gammarideans decreased to about 13%. In the 20.0–24.9 cm size class, molluscs comprised about 42% and crabs about 27%. In the largest size class (25.0–30.5 cm), molluscs and crabs were the dominant prey (about

Table 1. Ontogenetic changes in gut contents (mean percent volume of each prey category) of *Coris gaimard*

Prey	Size class of fish (total length, cm)					
	1.6–4.9	5.0–9.9	10.0–14.9	15.0–19.9	20.0–24.9	25.0–30.5
Gammarideans	38.3	57.0	41.5	13.1	3.6	5.2
Copepods & tanaidaceans	30.8	2.6	0.2		0.1	
Ostracods	12.0	6.9	0.6	0.4		
Isopods				0.1	0.3	
Crabs			8.7	19.7	27.3	31.3
Stomatopods	2.0					1.1
Shrimps			0.1			
Hermit crabs				2.8	3.3	0.7
Pelecypods		7.9	8.2	12.4	12.7	13.0
Gastropods	0.1	2.7	18.4	18.2	19.1	25.3
Chitons			12.2	17.2	10.5	6.6
Polychaetes	0.8		6.4	0.9	5.3	4.0
Sipunculids	0.7	0.4	1.0	3.5	0.8	0.4
Echinoids		0.9	0.4	3.2	2.2	4.0
Asteroids				0.4	1.9	1.4
Others	15.3	21.6	2.3	8.1	12.9	7.0
Number of specimens	19	4	19	11	22	13

45% and 31%, respectively). The crabs included Majidae, Xanthidae, Grapsidae, Leucosiidae and Portunidae. Thus, the rate of small crustaceans, which were the dominant prey of smaller individuals, decreased with growth (Kendall's $\tau=-0.87$, $n=6$, $p<0.05$, two-sided test), while that of molluscs and crabs increased with growth ($\tau=1, p<0.01$), becoming the dominant prey of larger fish.

The size distribution of each major prey item (i.e., gammarideans, crabs and molluscs) for each fish size class is shown in Table 2. Fishes smaller than 10.0 cm took only the smallest gammarideans (0.2–0.9 mm) and molluscs (0.2–0.9 mm or 1.0–2.9 mm). Fishes larger than 10.0 cm also took crabs and molluscs of 3.0 mm or over. Thus, the maximum size of prey increased with growth (Kendall's $\tau=0.97$, $n=6$, $p<0.05$, two-sided test).

Foraging behavior

When *Coris gaimard* found an available habitat while swimming slowly over the bottom, they approached the site and searched for prey visually. Three types of foraging behavior were recognized: 1) finding and consuming exposed prey on the surface of the substrate, 2) turning over gravel, to expose and subsequently comsume previously hidden prey, and 3) accompanying scarid fishes and foraging for prey exposed by the feeding of the former (Gushima, 1981). The second foraging method, turning over gravel, was effected as follows: the fish pushed its snout under the edge of a stone, lifted the latter by bending its body laterally into a "U" shape, and turned it over by rapidly straightening its body. In addition, the fish sometimes flicked away smaller gravel with its snout, moved oblong stones to the side by lifting one end with its snout, or rolled round ones over by pushing with its snout. Immediately after the fish turned over or moved gravel, they searched the newly-exposed sites, catching any prey found by pecking and biting.

The foraging behavior pattern exhibited by each size class of fish is shown in Figure 1. In the smallest size class (3–4 cm), only foraging for exposed prey on the surface of the substrate was observed. In the 5–9 cm size class, foraging on hidden prey by turning over gravel was also observed (12%). In the larger size classes, the frequency of foraging directly from the substrate surface tended to decrease, while that of foraging by gravel turning increased to as high as 35%. Thus the relative frequency of foraging by gravel turning increased with growth (Kendall's $\tau=0.87$, $n=6$, $p<0.05$, two-sided test).

The size distribution of the gravel turned over by the fish of each size class is shown in Figure 2. Small fishes of 5–9 cm TL mainly turned over stones smaller than 2.1 cm in diameter. In the 10–14 cm size class, stones of 2.1–5.0 cm were usually turned over, and stones greater than 5.0 cm by fishes larger than 15 cm TL.

The distance moved between foraging sites by each size class is shown in Table 3. In the smallest

Table 2. Size distribution of major prey of each size class of *Coris gaimard*

Prey	Body width (mm)	Size class of fish (total length, cm)					
		1.6–4.9	5.0–9.9	10.0–14.9	15.0–19.9	20.0–24.9	25.0–30.5
Gammarideans	0.2– 0.9	100.0	100.0	63.6	66.7	84.6	50.0
	1.0– 2.9			36.4	33.3	15.4	50.0
Crabs	0.2– 0.9						
	1.0– 2.9			66.7	25.0	38.5	20.0
	3.0– 4.9			33.3	75.0	30.8	30.0
	5.0– 6.9					23.1	20.0
	7.0–10.9					7.7	30.0
Molluscs*	0.2– 0.9	100.0	66.7	12.0			
	1.0– 2.9		33.3	80.0	66.7	43.6	45.8
	3.0– 4.9			8.0	33.3	43.6	45.8
	5.0– 6.9					10.3	8.3
	7.0–10.9					2.6	

Size distribution (%) of maximum prey found in each specimen is given. For number of specimens examined, see Table 1. *Gastropods, pelecypods and chitons.

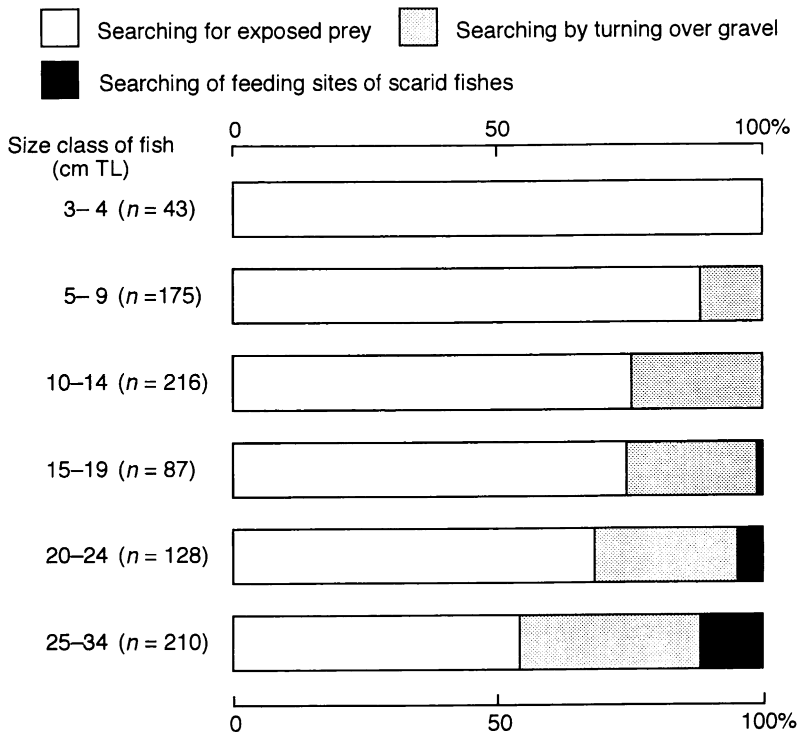

Fig. 1. Foraging methods of each size class of *Coris gaimard*. Number of foraging events observed given in parentheses.

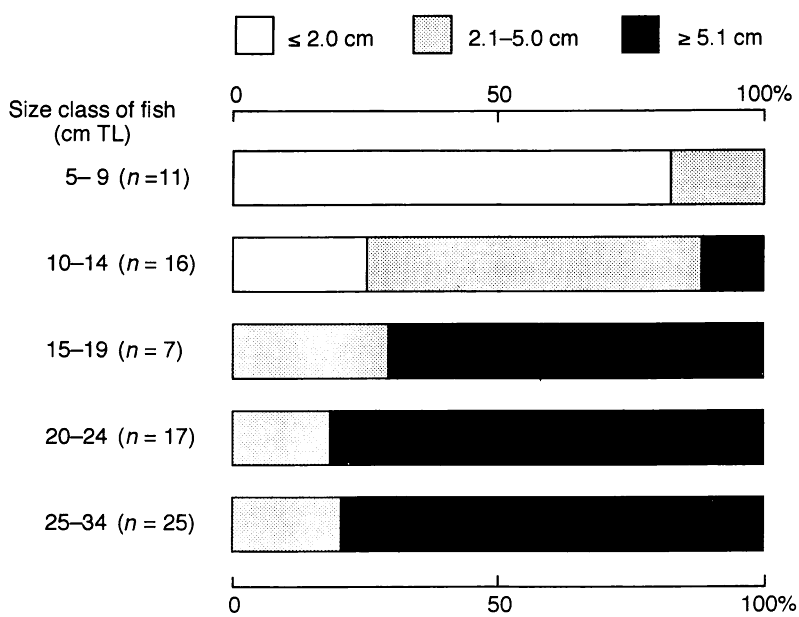

Fig. 2. Size distribution of gravel turned over by each size class of *Coris gaimard*. Number of stones given in parentheses.

size class (3–4 cm), each fish foraged within a limited area (mean 0.28 m^2 ±0.03 SD, $n=8$) during the five minute observation period. Small fishes of 5–9 cm TL moved only 2.3 m. In the 10–14 cm and 15–20 cm size class, the distance of movements increased to about 10 m. Fishes larger than 20 cm, progressively increased the distance moved.

Prey under gravel

The size distribution of the major prey items (i.e., gammarideans, crabs and molluscs) under the gravel of each size class is shown in Table 4. Under the smallest gravel (≦2.0 cm) only small prey items (0.2–0.9 mm or 1.0–2.9 mm) were found, whereas larger prey (3.0–4.9 mm or 5.0–6.9 mm) were found only under larger gravel (2.1–5.0 cm or ≧5.1 cm). Crabs which lived under the gravel included Majidae, Xanthidae, Grapsidae and Portunidae.

Table 3. Distance moved between foraging sites for each size class of *Coris gaimard*

Size class of fish (total length, cm)	Distance of movements (m)*	*n*
3– 4	—**	8
5– 9	2.3± 1.5	5
10–14	10.2± 5.8	11
15–19	9.8± 5.2	7
20–24	16.3± 7.5	22
25–34	24.6±10.1	31

* Mean±SD per 5 minutes is given; ** not measured.

Table 4. Size distribution of major prey categories under gravel

Prey	Body width (mm)	Diameter of gravel (cm)		
		≦2.0	2.1–5.0	≧5.1
Gammarideans	0.2–0.9	26.1	22.7	26.1
	1.0–2.9			0.1
Crabs	0.2–0.9			1.3
	1.0–2.9	0.7	0.7	0.7
	3.0–4.9		0.1	0.2
	5.0–6.9			0.1
Molluscs*	0.2–0.9	0.2	0.3	1.1
	1.0–2.9		0.1	0.5
	3.0–4.9		0.1	0.2
	5.0–6.9		0.1	
Number of samples		6	22	20

Mean number of individuals per 100 cm^2 is given.
* Gastropods, pelecypods and chitons.

Discussion

The type of prey taken by *Coris gaimard* changed with fish growth, from small, soft-bodied crustaceans (e.g., gammarideans and copepods) to larger hard-bodied molluscs and crabs. Similar ontogenetic changes in labrid feeding habits have been reported in *Thalassoma lutescens* (Gushima et al., 1991) and *T. cupido* (Shibuno et al., 1993). The change in feeding habits of labrid fishes is strongly related to the development of a prey-crushing, pharyngeal jaw (Yamaoka, 1978; Wainwright, 1988; Gushima et al., 1991). Because small fish have a weakly developed pharyngeal jaw, the food items of *Coris gaimard* smaller than 10 cm TL seem to be limited to small, soft-bodied crustaceans and smaller molluscs, which can be swallowed whole.

Foraging behavior by turning over gravel has to date simply been considered as an effective way of taking prey otherwise hidden (Hobson, 1974; Gushima, 1981; Tribble, 1982). In *C. gaimard*, foraging by turning over gravel seems to be strongly related to ontogenetic changes in prey size selection. Fish of less than 5 cm TL did not turn over gravel probably because of the abundance of small crustaceans (e.g., gammarideans and copepods), their most important prey, on the surface of the substrate overgrown with small algae, as Gushima et al. (1991) and Shibuno et al. (1993) reported. As the fish grew larger, however, they selected larger prey, necessitating the turning over of larger gravel to take the larger molluscs and crabs living underneath. The relative caloric content of larger molluscs and crabs is higher than that of small crustaceans (Ellison et al., 1979).

Thalassoma lutescens and *T. cupido* take larger prey, which are difficult to find because of their low density, by foraging over increasingly larger areas as they grow (Gushima et al., 1991; Shibuno et al., 1993). However, the foraging areas of *C. gaimard* were smaller than those of *Thalassoma lutescens* and *T. cupido* of the same size classes. By turning over gravel, *Coris gaimard* can probably take correspondingly larger prey as it grows, while still making use of a limited foraging area. The foraging area of small reef fishes is limited by high predation pressure (Hobson, 1974; Helfman, 1978; Jones, 1984). Therefore, when small individuals (5.0–9.0 cm TL) change their preference from small crustaceans to molluscs, foraging by turning over gravel seems to be an effective way of taking prey without expanding the foraging area and increasing the predation risk.

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ツユベラ *Coris gaimard* の成長に伴う食性変化と小石を裏返す採餌行動

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ツユベラ *Coris gaimard* の成長に伴う食性と採餌行動の変化を，南西諸島の口永良部島の磯水域で調査した．ツユベラは成長に伴いヨコエビを主体とする小型甲殻類から大型の貝類，カニ類へと食性を移行させた．採餌方法は基本的には基質表面の餌を捕る方法であったが，全長 5 cm を越えると小石を裏返してその下の餌を捕る方法が認められるようになった．そして，この小石を裏返して採餌する割合と裏返す小石の大きさは成長に伴い増加した．大きな小石には，より大きなカニ類が隠れている．つまり，小石を裏返すというツユベラの特徴的な採餌方法は成長に伴う餌サイズの選択と密接に関係しており，ツユベラは成長に伴いより大きな小石を裏返すことで，その下に隠れているより大きな餌（貝類，カニ類）を獲得しようとしていた．同時に，小石を裏返す採餌行動によって，小型個体は小型甲殻類から他の餌へ選択性を移行させる時に行動圏の拡大を押さえることができ，その結果，捕食リスクを下げることができると思われる．

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