The Effect of Feeding Habitats on Dietary Shifts during the Growth in a Benthophagous Suction-Feeding Fish

Authors: Matsumoto, Kazunori, and Kohda, Masanori

Source: Zoological Science, 19(6) : 709-714

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.19.709

ZOOLOGICAL SCIENCE **19**: 709–714 (2002)

The Effect of Feeding Habitats on Dietary Shifts during the Growth in a Benthophagous Suction-Feeding Fish

Kazunori Matsumoto* and Masanori Kohda

Department of Bio- and Geosciences, Graduate School of Science, Osaka City University,
Sumiyoshi-ku, Osaka 558-8585, Japan

ABSTRACT—Several mechanisms of fish ontogenetic dietary shifts, which have important ecological implications, have been proposed. We studied the mechanism of dietary shifts of a benthophagous fish *Goniistius zonatus*, focusing on the effect of foraging on calcareous algal mat, one of its main feeding substrates, through comparison between two local populations (Morode and Arakashi) with different feeding ecology. The studied fish (11–29 cm SL) fed on various kinds of small invertebrates inhabiting the substrates, using a suctorial feeding mode without visual discrimination towards individual prey. At Morode, gut contents of small fish consisted of more epifaunal and less infaunal organisms than those of large fish, that is, mainly small crustaceans in small fish, and many invertebrates other than crustaceans in large fish. By contrast, at Arakashi, gut contents consisted mostly of epifaunal crustaceans regardless of fish size, i.e., fish showing no dietary shifts. At Morode, *G. zonatus* took foods mostly from thick calcareous algal mat, whereas fish foraged mainly on thin algal mat and bare rocks at Arakashi, the difference being due to the local differences in the substrate component. The algal mat of Morode harbored much larger amount of infaunal animals than any substrates of Arakashi. At Morode, large fish more forcefully and deeply thrust the mouth into thick algal mat than small fish, and was likely to suck up more infaunal prey using great suctorial force. The comparison clearly indicates that the dietary shifts of *G. zonatus* at Morode resulted from size-related efficiency in straining foods from heterogeneous micro-topography of thick algal mat.

Key words: benthivore, calcareous algae, feeding habit, feeding habitat

INTRODUCTION

Many fish species experience gradual shifts in diets during ontogeny (Werner and Gilliam, 1984). The shifts occur even after sexual maturation in some fish, which show undetermined growth patterns. Ontogenetic dietary shifts are important for understanding fish ecology, such as life history patterns and niche shifts in terms of intra- and interspecific competition over food resources (Wootton, 1998). Individuals of the same species with dramatic niche shifts involving diet at different or even within the same life stages can be so functionally separated as different species (McCormick, 1998). However, the number of studies on the mechanical process of the dietary shifts has been limited, where evidence is sometimes lacking.

Benthophagous fish predators employ a wide variety of behaviors and mouth structural modification so as to exploit prey organisms, and many benthivores change their diets during the growth (Gerking, 1994). Several mechanisms explaining the dietary shifts have been reported: direct visual prey choice (Dervo *et al*., 1991; Shibuno *et al*., 1994; Keeley and Grant, 1997), morphological constraints (Wainwright, 1988; Gushima *et al*., 1991; Shibuno *et al*., 1993) and/or differences of feeding habitats (Andrew and Hecht, 1992; Wöhler and Sánchez, 1994; McCormick, 1998).

A benthophagous cheilodactylid fish that does not visually choose prey organisms shows ontogenetic dietary shifts, despite the lack of differences in foraging behavior patterns and feeding habitats among various-sized fish (Leum and Choat, 1980). It has been suggested that the dietary shifts of a cheilodactylid fish result from the size-dependent efficiency in straining food items from calcareous algal mat, the most heterogeneous substrate harboring a variety of benthic animals in coastal areas (Leum and Choat, 1980). That is, large fish takes foods mainly from inside algal mat using high suctorial force, while small fish from near the surface due to its low suctorial force (McCormick 1998). However, such effect of feeding habitats on dietary shifts in suction-feeding fishes has not been verified well.

Goniistius zonatus (Cheilodactylidae) is a benthopha-

---

* Corresponding author: Tel. +81-6-6605-3170;
FAX. +81-6-6605-3172.
E-mail: solokmatsu@hotmail.com

gous fish, occurring over shallow rocky reefs in southern Japan (Masuda and Kobayashi, 1994). This fish takes small benthic animals from the substrate using a suctorial feeding mode without visual discrimination towards individual prey (Matsumoto, 2001). We found many individuals of *G. zonatus* at two locations: plenty of calcareous algal patches, one of the main feeding substrates of this fish, in one site, whereas scanty in the other. If the algal mat greatly affects ontogenetic dietary shifts in *G. zonatus*, the shifts will be expected to be much more apparent at the former site than at the latter. The aim of this study is to compare feeding habitats and diets of *G. zonatus* between the two locations and to examine the effect of calcareous algal mat on dietary shifts during the growth of this fish.

MATERIALS AND METHODS

Field works were conducted at Morode (33°00' N, 132°30' E) and Arakashi (33°02' N, 132°25' E), both locating in Uchiumi Bay in the Uwa Sea, Shikoku Island, Japan. Field observations were from summer to autumn in 1994 at Morode, and in 1993 and 1994 at Arakashi. Underwater observations were conducted with the aid of SCUBA. Study areas (55 m×40 m) were established at both locations (1–10 m deep at Morode, 1–5 m deep at Arakashi), and divided into 5 m×5 m grids. The configuration of substrate (rocks, sand and corals) was recorded for each grid. About 60% of the substrate were rocky at Morode, but only ca. 30% at Arakashi. Calcareous algae (Subfamily: Corallinoideae) formed patches on some rocks, where *Goniistius zonatus* frequently foraged. The thickness of calcareous algal mat was 2–3 cm at Morode, while 1–2 cm at Arakashi. Outline of the calcareous algal mat at each location was sketched once per month during the observation period in 1994. The substrate conditions, especially the thickness and area of algal mat, of each location from summer to autumn were quite similar over the study years.

We identified a total of 16 *G. zonatus* at Morode and 30 at Arakashi individually, depending on the varieties of lateral stripes on the trunk and/or of sites of white spots on the caudal fin. None of them were captured, and their total length (TL) was estimated underwater to the nearest 0.5 cm using a scale placed near the fish, TL ranging from 12.0 cm to 32.0 cm at Morode and from 12.0 cm to 30.0 cm at Arakashi.

Underwater observations were made between 09:00 and 17:00 hr, when *G. zonatus* actively foraged (Sano and Moyer, 1985; Matsumoto, 2001). Each identified individual was focally followed for ca. 20–60 min. Total observation time per individual ranged from 27.3 min to 365.0 min (on average 134.7 min±87.1 SD, n=46). This species forcefully thrusts the mouth against the substrate and takes prey organisms together with sediment using powerful suctorial force produced by the rapid expansion of the buccal cavity, and then filters out the sediment through the gill openings (Matsumoto, 2001). The fish often repeatedly sucks at the same site on calcareous algal mat so as to exploit infaunal organisms inhabiting inside the algal mat, whereas usually takes single sporadic suctions on other substrates (Matsumoto and Kohda, 2001a). Large fish thrust the mouth more deeply into thick algal mat than small fish and dug in the mat. We recorded sucking number with discrimination of substrate types (algal mat, bare rocks, sand and corals). *Goniistius zonatus* maintains a feeding territory against conspecifics of similar size (Matsumoto, 2001). Swimming tracks of the identified individuals were recorded (for ca. 1 hr for each) at the two sites in 1994, and an area enclosed by outermost total swimming tracks was defined as a territory for each fish (Matsumoto, 2001).

For gut content analyses, 25 *G. zonatus* from Arakashi were collected in or near the study areas in November 1994. There were 26 samples collected just at the study site of Morode in November 1990. These samples made us hesitate to make further sacrifice at Morode because substrate conditions were not different between the two years. Namely, in 1990 as well as in 1994, the rocky surfaces in the study area were broadly covered with calcareous-algae of 2–3 cm thick; foraging behavior of *G. zonatus* which was affected by substrate conditions was similar over a series of years (see Matsumoto *et al*., 1999; Matsumoto and Kohda, 2000, 2001a). Thus, we analyzed gut contents of these Morode samples.

The body cavity of each specimen was injected with a small amount of undiluted formalin within 30 min of capture, and the specimens were subsequently kept in 10% formalin solution. Standard length (SL) ranged from 10.9 cm to 29.2 cm at Morode and from 12.5 cm to 29.0 cm at Arakashi. Gut contents were sorted to phylum or class under a binocular microscope. The volume of each dietary item was estimated from the horizontal area covered on a grid slide.

To examine the benthos fauna, invertebrates inhabiting the substrate were collected in December 1993 at each location. Collection methodology was as follows: the substrate (ca. 15 cm×15 cm area) was scratched with a brush (with 3-cm-long plastic bristles) and the expelled sandy cloud was scooped up in a plankton net of 60 cm diameter and 0.3 mm mesh size. Collections were conducted on calcareous algal mat, bare rocks, sand and corals, five times for each substrate. At Morode, collections on sand and corals were omitted because of rare usage of *G. zonatus*. Within 1 hr of collection, the specimens were placed in 10% formalin solution. The collected animals were analyzed in the same way as gut content analyses.

In statistical analyses, fish SL and TL and food length were transformed logarithmically so that they became approximately normally distributed. Data for substrate compositions, feeding suction and gut contents in the form of proportion were arcsine-square root transformed to meet conditions of normality. Data for feeding suction in 1993 and 1994 at Arakashi were pooled and compared with Morode data, since significant difference was not found between the two years (MANOVA, Pillai's trace=0.211, F=1.68, df=4, 25, P>0.1). In analyses of invertebrate density among substrates, Mann-Whitney U-test was used, since sample size was so small that data could not be normally distributed.

RESULTS

Feeding substrates

The substrate composition in the territory of *G. zonatus* greatly differed between the two locations (MANOVA, Pillai's trace=0.828, F=31.37, df=4, 26, P<0.0001; Table 1). At Morode, rocks predominated in the territories, and calcareous algal mat growing on some rocks was a major substrate. At Arakashi, the substrate was dominated by bare

Table 1. Substrate compositions in the territory of *Goniistius zonatus* at Morode and Arakashi.

Substrate	Morode	Arakashi
Calcareous-algal mat	41.3±28.6	8.7±10.4
Bare rocks	57.2±26.9	48.8±22.0
Sand	1.6±6.3	42.5±28.3
Corals	0.4±1.0	5.4±3.6

Data are mean %±SD (n=16 for Morode; n=15 for Arakashi). Total areas exceed 100% because corals overlapped with rocks.

rocks and sand, and calcareous algal mat was rather minor.

The proportion of sucking number on each substrate greatly differed between the two locations (MANOVA, Pillai's trace=0.686, F=22.35, df=4, 41, P<0.0001; Fig. 1). At Morode,

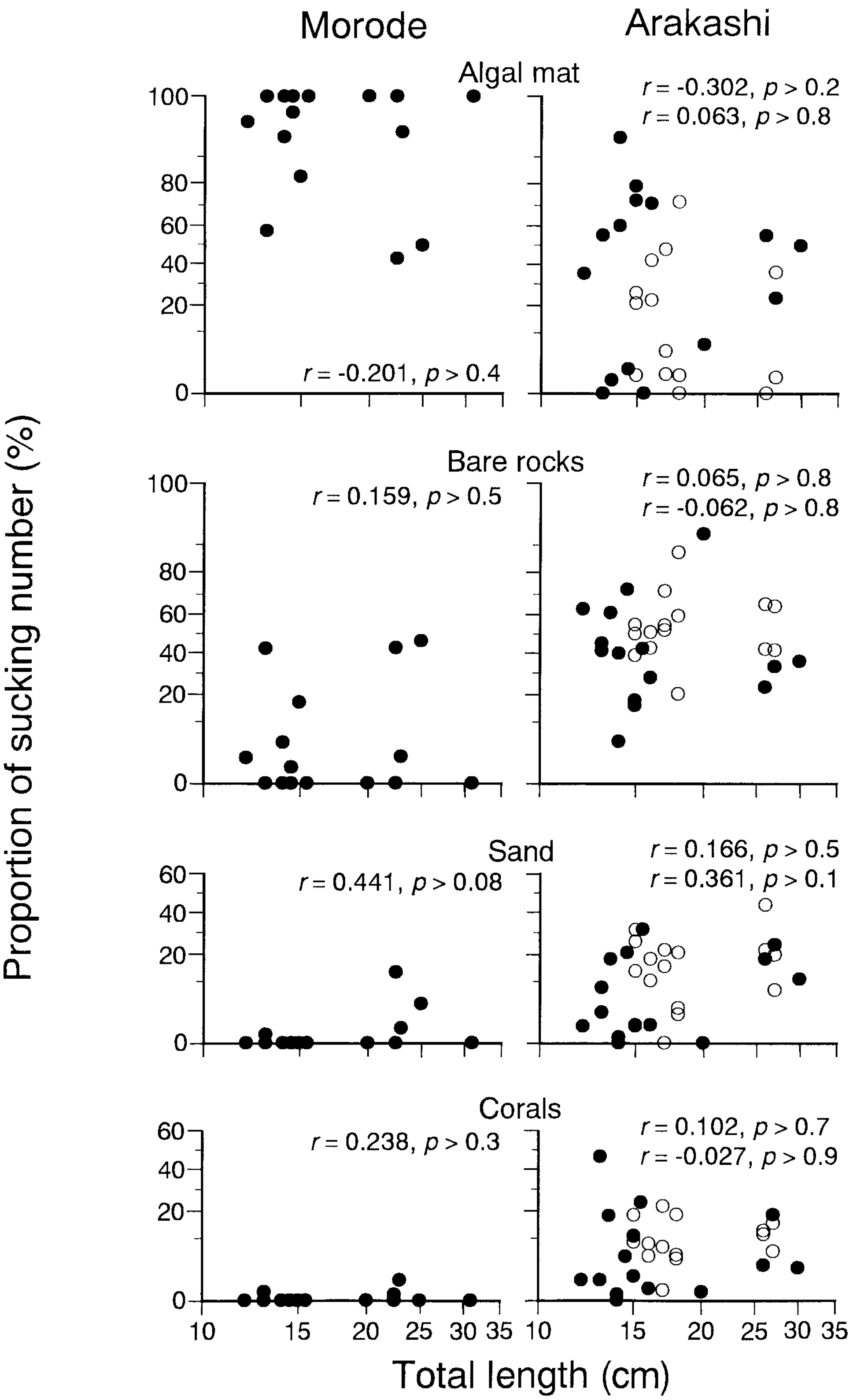

Fig. 1. Proportion of sucking number at each substrate as a function of total length in *Goniistius zonatus* at Morode (n=16 in 1994) and Arakashi (n=15 in both 1993 (open circles) and 1994 (solid circles)). Arakashi regression coefficients in 1993 (top) and 1994 (bottom).

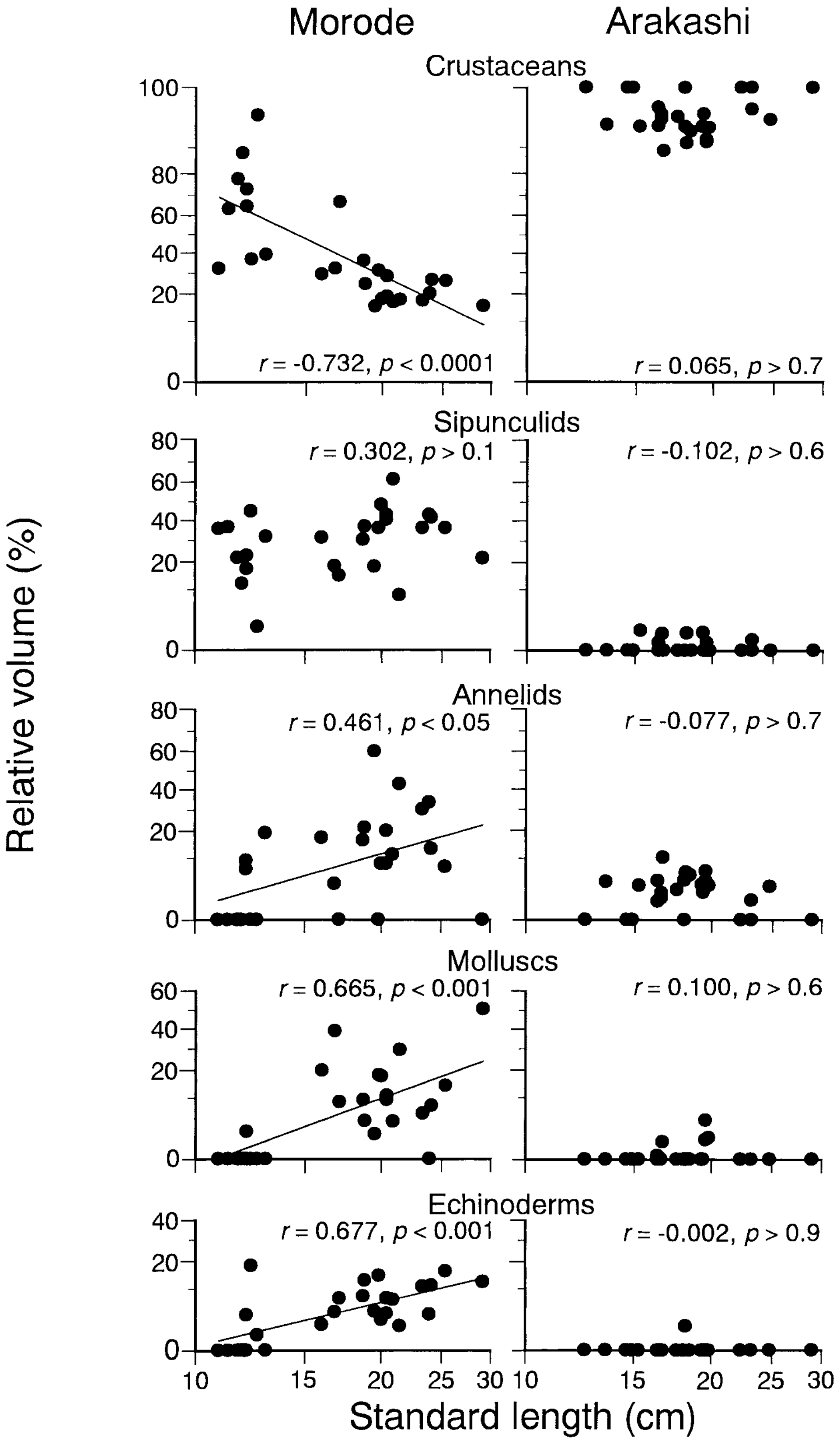

Fig. 2. Relative volume of invertebrates in the diet as a function of standard length in *Goniistius zonatus* at Morode (n=26) and Arakashi (n=25). Regression equations are $\sin^{-1}\sqrt{Y/100} = -0.691 \ln X + 2.638$ (crustaceans), $\sin^{-1}\sqrt{Y/100} = 0.399 \ln X - 0.850$ (annelids), $\sin^{-1}\sqrt{Y/100} = 0.518 \ln X - 1.232$ (molluscs) and $\sin^{-1}\sqrt{Y/100} = 0.332 \ln X - 0.743$ (echinoderms) for Morode. Regression lines with no significance not given.

Table 2. Volume density of benthic invertebrates (mm^3/ 225 cm^2) inhabiting the substrates at Morode and Arakashi.

	Morode		Arakashi			
	Calcareous-algal mat	Bare rocks	Calcareous-algal mat	Bare rocks	Sand	Corals
Crustaceans	212.1±90.3	228.1±85.5	116.6±47.0	38.6±7.9**	38.6±19.1**	18.0±4.1**
Molluscs	157.9±73.2	25.8±30.3**	55.3±20.2*	1.4±1.8**	49.7±72.0*	9.2±5.6**
Annelids	34.4±6.2	10.2±9.2**	10.8±12.7*	2.1±1.8**	2.9±2.1**	0**
Sipunculids	25.4±11.2	2.4±4.3**	7.4±7.3*	0.6±1.3**	2.1±4.7**	0**
Echinoderms	2.0±2.7	0	0.3±0.7	0.1±0.2	0.8±1.8	0.2±0.4

Data are mean±SD (n = 5). Asterisks show statistical significance (*P<0.05, **P<0.01) against Morode algal mat by Mann-Whitney U-test.

most sucking occurred on calcareous algal mat, and the proportion of sucking at the algal mat was much greater than that at Arakashi ($F_{1,44}$=55.49, P<0.0001). At Arakashi, bare rocks were an important substrate for feeding as well as algal mat, being exploited much more frequently than at Morode ($F_{1,44}$=51.54, P<0.0001). Sand and corals were also sites on which more frequent sucking occurred at Arakashi than at Morode where these were hardly used (sand: $F_{1,44}$=24.82, corals: $F_{1,44}$=36.00, both P<0.0001). The proportion of sucking number on each substrate was not correlated with fish TL at either location (Fig. 1).

Fish diets and potential foods

Goniistius zonatus fed on small benthic invertebrates, such as crustaceans (gammarideans, isopods and decapods), sipunculids, molluscs (gastropods and pelecypods), annelids (polychaetes) and echinoderms (echinoids). The dietary composition greatly differed between two locations (MANOVA, Pillai's trace=0.851, F=51.58, df=5, 45, P< 0.0001; Fig. 2). At Arakashi, crustaceans accounted for nearly 100% by volume in the diet. At Morode, fish consumed less crustaceans and much more the other items than at Arakashi (crustaceans: $F_{1,49}$=157.87, sipunculids: $F_{1,49}$=248.44, annelids: $F_{1,49}$=7.63, molluscs: $F_{1,49}$= 21.47, echinoderms: $F_{1,49}$=44.39, all P<0.0001 except annelids with P<0.01). At Morode, relative volume of crustaceans in the diet was negatively correlated with fish SL (Fig. 2). Conversely, relative volume of annelids, molluscs and echinoderms were all positively correlated with SL. At Arakashi, however, such correlation was not found in any food items.

At both locations, crustaceans were dominant prey animals on each substrate (Table 2). Thick calcareous algal mat at Morode harbored much more molluscs, annelids and sipunculids than any Arakashi substrates including thin algal mat.

DISCUSSION

Food items of *Goniistius zonatus* greatly changed with increase in fish size at Morode, whereas such ontogenetic dietary shifts were not apparent at Arakashi. Fish of all sizes took food from similar substrate at each location, thus posing the question as to how such dietary shifts came about only at Morode.

At Morode, *G. zonatus* took foods mostly from thick calcareous algal mat which harbored much more molluscs, annelids and sipunculids than any Arakashi substrates, and large fish consumed plenty of annelids, molluscs and echinoderms which rarely occurred in the diets of small fish. Small annelids and molluscs are infaunal organisms usually inhabiting inner side of the substrate covered with algae (Gushima, 1981; McCormick, 1998), and were not many on bare rocks at Morode. In suction feeding fishes, the success of a suction attack depends on the feeder's ability to create a jet of water to drag the prey into its mouth (Norton, 1995), and is related to fish size (Liem, 1990). Large *G. zonatus* dug deeply in thick algal mat while foraging, whereas small fish did not. Ontogenetic dietary shifts of *G. zonatus* at Morode will largely reflect the predator's size-dependent ability to exploit infaunal organisms from the inside of thick algal mat, as has been suggested in another cheilodactylid fish (Leum and Choat, 1980; McCormick, 1998). No dietary shifts at Arakashi with lack of thick algal mat, where all individuals sucked up similar epifaunal crustaceans, support the hypothesis of the importance of thick algal mat to ontogenetic dietary shifts in this fish.

At Arakashi, molluscs were rarely exploited by *G. zonatus*, although they were abundant in algal mat and sand. The gill rakers of *G. zonatus* were spaced more widely at Arakashi than at Morode, and retention efficiency for small-sized prey by inter-raker spacing is suggested to be poorer at Arakashi (Matsumoto and Kohda, 2001b). Molluscs were the smallest animals among benthic invertebrates (Matsumoto, 1999), and will not be retained efficiently by the inter-raker gaps at Arakashi. Other infaunal invertebrates were usually larger than crustaceans (Matsumoto, 1999), and therefore should be retained, suggesting that inter-raker spacing is unlikely to cause the dietary differences between the two study sites except for molluscs.

Most examples of ontogenetic dietary shifts in fishes have hitherto been due to the changes of feeding habitats, feeding behaviors and morphs according to body size (Magurran, 1993; Gerking, 1994). Feeding habitats were not different among various-sized fish at Morode, and fish morphs including gill raker spacing will not play a major role. The comparison of trophic biology of the fish between the two locations confirms that the ability for exploiting foods in calcareous algal mat of complex micro-topography greatly affects the dietary shifts of *G. zonatus*. Generally, the structure of micro-habitat has a marked effect on dietary breadth (e.g., Werner and Hall, 1974; Whitfield, 1990). Micro-topographic complexity such as calcareous algal cover should play one of major roles on ontogenetic dietary shifts of suction-feeding fishes.

ACKNOWLEDGMENTS

We are grateful to Y. Yanagisawa, Ehime University, for his generous help. N. Ohnishi, Kyoto University, supported our field research. This work was partly supported by a Grand-in-Aid for Scientific Research (No. 08640811) from the Japan Ministry of Education, Science, Sports and Culture, and an Osaka City University Grant for Graduate Course Students.

REFERENCES

Andrew TG, Hecht T (1992) Feeding biology of *Acantholatris monodactylus* (Pisces: Cheilodactylidae) at Tristan da Cunha and Gough Island, South Atlantic. S Afr J Antarct Res 22: 41–49

Dervo BK, Hegge O, Hessen DO, Skurdal J (1991) Diel food selection of pelagic Arctic charr, *Salvelinus alpinus* (L.), and brown trout, *Salmo trutta* L., in Lake Atnsjo, southeast Norway. J Fish Biol 38: 199–210

Gerking DS (1994) Feeding Ecology of Fish. Academic Press, San Diego

Gushima K (1981) Study on the feeding ecology of reef fishes in Kuchierabu Island. J Fac Appl Biol Sci, Hiroshima Univ 20: 35–63 (In Japanese with English summary)

Gushima K, Hazumi Y, Kakuta S (1991) Growth-related changes in diet and foraging behavior of the yellow wrasse *Thalassoma lutescens* at Kuchierabu Island. Japan J Ichthyol 38: 307–313 (In Japanese with English abstract)

Keeley ER, Grant JWA (1997) Allometry of diet selectivity in juvenile Atlantic salmon (*Salmon salar*). Can J Fish Aquat Sci 54: 1894–1902

Leum LL, Choat JH (1980) Density and distribution patterns of the temperate marine fish *Cheilodactylus spectabilis* (Cheilodactylidae) in a reef environment. Mar Biol 57: 327–337

Liem K (1990) Aquatic versus terrestrial feeding modes: possible impacts on the trophic ecology of vertebrates. Am Zool 30: 209–221

Magurran AE (1993) Individual differences and alternative behaviours. In "Behaviour of Teleost Fishes 2nd ed" Ed by TJ Pitcher, Chapman and Hall, London, pp 441–477

Masuda H, Kobayashi Y (1994) Grand Atlas of Fish Life Modes. Tokai University Press, Tokyo

Matsumoto K (1999) Intra- and interspecific relationships of benthophagous fishes (*Goniistius zonatus* and two species of *Pseudolabrus*) in reference to their feeding ecology. Sci D dissert, Osaka City University, Osaka

Matsumoto K (2001) Overlapping territory of a benthophagous fish, *Goniistius zonatus* (Teleostei: Cheilodactylidae). Ecol Res 16: 715–726

Matsumoto K, Kohda M (2000) Energy allocation and foraging activities in the morwong, Goniistius zonatus (Cheilodactylidae). Ichthyol Res 47: 416–419

Matsumoto K, Kohda M (2001a) Differences in feeding associations of benthophagous fishes in two locations. Env Biol Fish 61: 111–115

Matsumoto K, Kohda M (2001b) Differences in gill-raker morphology between two local populations of a benthophagous filter-feeding fish, *Goniistius zonatus* (Cheilodactylidae). Ichthyol Res 48: 269–273

Matsumoto K, Kohda M, Yanagisawa Y (1999) Size-dependent feeding association of two wrasses (genus *Pseudolabrus*) with the morwong, *Goniistius zonatus*. Ichthyol Res 46: 57–65

McCormick MI (1998) Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: relationship between feeding mechanics, microhabitat selection and growth. Mar Biol 132: 9–20

Norton SF (1995) A functional approach to ecomorphological patterns of feeding in cottid fishes. Env Biol Fish 44: 61–78

Sano M, Moyer JT (1985) Bathymetric distribution and feeding habits of two sympatric Cheilodactylid fishes at Miyake-jima, Japan. Jpn J Ichthyol 32: 239–247

Shibuno T, Murakami H, Hashimoto H, Gushima K (1993) Growth-related changes in diet and foraging behavior of the wrasse *Thalassoma cupido* at Kuchierabu-jima. J Fac Appl Biol Sci, Hiroshima Univ 32: 93–100 (In Japanese with English abstract)

Shibuno T, Hashimoto H, Gushima K (1994) Changes with growth in feeding habits and gravel turning behavior of the wrasse, *Coris gaimard*. Jpn J Ichthyol 41: 301–306

Wainwright PC (1988) Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. Ecology 69: 635–645

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15: 393–425

Werner EE, Hall D (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55: 1042–1052

Whitfield DP (1990) Individual feeding spcializations of wintering turnstones *Arenaria interpres*. J Anim Ecol 59: 193–211

Wöhler OC, Sánchez F (1994) Feeding ecology of Castañeta (*Cheilodactylus bergi*; Pisces: Cheilodactylidae) in the southwestern Atlantic (34–47°S). Aust J Mar Freshwater Res 45: 507–520

Wootton RJ (1998) Ecology of Teleost Fishes. 2nd ed, Kluwer Academic Publishers, Dordrecht

(Received February 26, 2002 / Accepted April 5, 2002)