Plasticity of Feeding Habits of Two *Plectroglyphidodon* Damselfishes on Coral Reefs in Southern Taiwan: Evidence from Stomach Content and Stable Isotope Analyses

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Cheng-Tze Ho, Yi-Cheng Fu, Chi-Lu Sun, Shuh-Ji Kao, and Rong-Quen Jan (2009) Plasticity of feeding habits of two *Plectroglyphidodon* damselfishes on coral reefs in southern Taiwan: evidence from stomach content and stable isotope analyses. *Zoological Studies* **48**(5): xxx-xxx. On the west bank of the intake bay of a nuclear power plant at Nanwan, southern Taiwan, a recent outbreak of sea anemones has eliminated most branching corals at the site. In this habitat currently dominated by sea anemones, the abundance of Dick's damsel, *Plectroglyphidodon dickii* Lienard 1983, has increased more markedly than the sympatric congener, *P. johnstonianus* Fowler and Ball 1924. To study whether the distribution patterns of the 2 *Plectroglyphidodon* damselfishes were underlain by food availability and feeding habit plasticity, the reef area in the embayment was divided into 2 different zones, zone A dominated by *Acropora* corals and zone B dominated by a sea-anemone, and both stomach content and stable isotope analyses were used to delineate feeding habits of these 2 damselfishes in these 2 zones. Stomach contents showed that the major food items for *P. dickii* in zone A were filamentous algae (33.4%) and coral polyps (22.3%), while in zone B, they were filamentous algae (35.8%) and sea anemones (28.2%). In contrast, coral polyps were the major food item for *P. johnstonianus* in both zones (accounting for 75.5% in zone A and 67.5% in zone B). Analyses of $\delta^{13}C$ and $\delta^{15}N$ values concurred that coral polyps were the major nutrient

source of *P. johnstonianus*.   In addition, the contributions of both coral polyps and sea anemones to *P. dickii* were verified.   Overall, it was postulated that in the sea anemone-dominated habitat, sea anemones were substituted for coral polyps in the diet of *P. dickii*, but similar plasticity did not occur in *P. johnstonianus*.   Thus the higher feeding plasticity of *P. dickii* might have made it possible to more-successfully immigrate to the newly developed habitat.

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Feeding habits of coral reef fish are generally adaptable (Dill 1983).   While most food resources vary both spatially and temporally, fish can shift from feeding on 1 food type to another to take advantage of the most profitable food source at a particular time (Gerking 1994).   For example, at Canos I. near Costa Rica, the puffer *Arothron meleagris* (Tetraodontidae) suffered from loss of its coral food, *Pocillopora*, due to a red tide epidemic.   The puffers first switched to crustose coralline algae, a low-quality food, and then switched to *Porites*, a coral more resistant to red tides (Guzman and Robertson 1989).   In contrast, when crown-of-thorns starfish (*Acanthaster planci* or COTS) decimated hard coral on parts of the Great Barrier Reef in 1983-1984, 2 species of butterflyfish, *Chaetodon rainfordi* and *C. aureofasciatus,* suffered large population losses due to their highly specialized feeding habits (Williams 1986).   Moreover, *C. trifascialis*, a specialist which feeds on plate-forming corals, went locally extinct following a decline in the abundance of plate corals at Lizard I. due to a COTS outbreak (Sale 2002).   These examples indicate that feeding plasticity may also mediate how changes in availability and quality of food sources affect the distribution of fish.

On the west bank of the intake bay of a nuclear power plant in southern Taiwan, the substrate was previously dominated by *Acropora* corals.   A recent outbreak of

sea anemones has eliminated most of the branching corals. Most individuals of territorial *Stegastes* damselfishes have emigrated to other reefs due to substrate changes (Jan et al. 2003, Chen et al. 2008). Among the new inhabitants of the habitat currently dominated by sea anemones, the abundance of Dick's damsel, *Plectroglyphidodon dickii* Lienard 1983, has increased more markedly than its sympatric congener, *P. johnstonianus* Fowler and Ball 1924 (R.Q. Jan, unpubl. data). This difference might be a reflection of differential recruitment limitations, resource availability, competition, plasticity of resource utilization, or a combination of these processes (Begon et al. 1996). Since vast breeding stocks of both damselfishes are available on nearby reefs, differential recruitment limitations can be excluded as a major affecting factor. Knowledge of how each species' diet changed under different food availabilities would be helpful in explaining the difference in the resulting population sizes between these cohabiting fish species.

In this study, both stomach content and stable isotope analyses were used to delineate the diets of the 2 species of *Plectroglyphidodon*. With an understanding of the feeding habits of individuals from different habitats, it is anticipated that the distribution patterns of these 2 species can be explained by differences in food availability and feeding plasticity.

MATERIALS AND METHODS

Fieldwork was carried out on the west bank of an embayment (at 1-7 m in depth) encompassing the water inlet of the Third Nuclear Power Plant at Nanwan, southern Taiwan (21°57'N, 120°45'E; Jan et al. 2007) in Nov. 2006 (for collection I) and Feb. 2007 (for collection II). For sampling design, the reef area was divided into 2 different zones based on substrate differences: zone A which was dominated by *Acropora* branching corals for the past 10 yr, and zone B which was previously

dominated by branching corals but since 2006, has been dominated by the sea anemone *Mesactinia genesis* and coral debris (Fig. 1). Both Dick's damsel, *P. dickii*, and its congener, *P. johnstonianus*, previously occurred in branching corals in both zones. Yearly changes in abundances showed that *P. dickii* substantially increased in zone B in 2006 and 2007 (Fig. 2). In Feb. 2007, there were 65 *P. dickii* in zone A and 55 in zone B, and there were 25 *P. johnstonianus* in zone A and only 6 in zone B. To avoid depleting the stock, for collection I, *P. johnstonianus* was only collected in zone B.
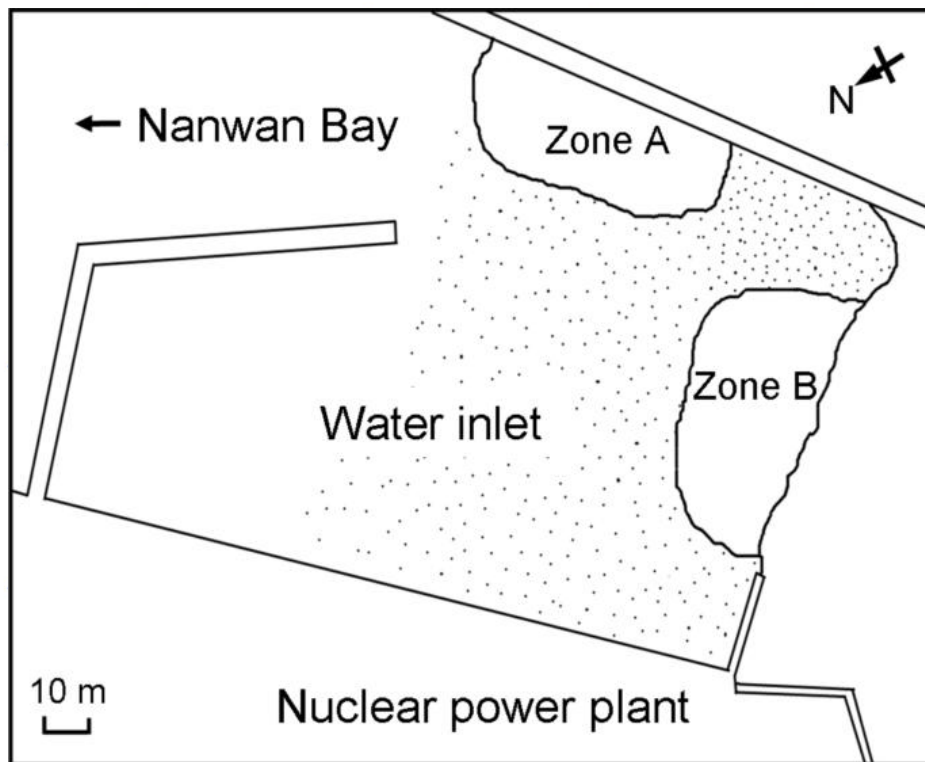

Fig. 1. Map showing zones in the study site. Zone A, dominated by branching corals; zone B, dominated by sea anemones. Dotted area, sandy bottom.
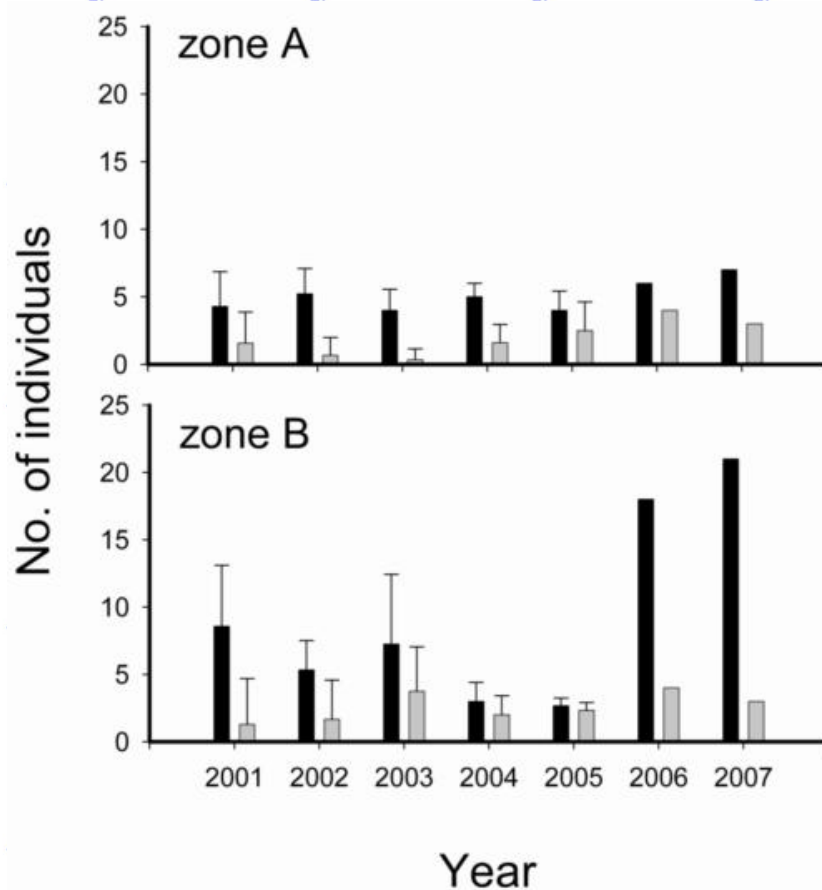
Fig. 2. Yearly changes in the number of individuals (with the standard deviation, where applicable) of *Plectroglyphidodon dickii* (black bars) and *P. johnstonianus* (gray bars) in zones A and B in a fixed quadrat of 50 m^2 (R.Q. Jan, unpubl. data).

Sampling and processing

In total, 22 *P. dickii* and 13 *P. johnstonianus* were collected by hand-netting or angling (Table 1). All collections were conducted by scuba divers. Specimens were kept in an ice-water slurry in sealed plastic bags and immediately transported to the laboratory. For each specimen, standard length was measured (± 1 mm) using calipers; the stomach was removed and preserved in a 10% buffered formalin solution for content analysis; and white dorsal muscle tissue, which tends to be less variable in $\delta^{13}C$ and $\delta^{15}N$ values than other tissues (Pinnegar and Polunin 1999) and is widely

used in food-web studies (Deudero et al. 2004), was taken and frozen for the stable isotope analysis.

Table 1. Sample size (*n*) and range of standard length (SL) of *Plectroglyphidodon dickii* and *P. johnstonianus* collected from 2 zones in 2 collection periods

Species	Collection	Reef zone	*n*	SL range (cm)
P. dickii	I	A	5	7.9-8.5
		B	6	7.6-8.8
	II	A	5	7.7-8.6
		B	6	7.8-8.6
P. johnstonianus	I	A	-[a]	-[a]
		B	5	5.6-6.6
	II	A	4	6.5-7.6
		B	4	5.8-7.2

[a] Specimen collection was not planned.

Potential food items were sampled from the habitats of these 2 damselfishes. Samples were mainly comprised of filamentous algae (including *Gelidium* sp. and *Polysiphonia* sp.), copepods, sea anemones, polychaetes, and coral polyps (including symbiotic algae). Carbonates in the copepods, sea anemones, polychaetes, and coral tissues were removed with 1 N HCl before further treatment.

Stomach contents were spread on slides, and components were identified using a stereomicroscope. Food items were categorized into algae, sea anemones, coral polyps, barnacles, fish scales, oikopleuras, copepods, eggs, crustaceans, detritus, and unidentified fragments. The relative volumetric quantity of each food item was estimated using the point frame method (Hyslop 1980, Jan et al. 1994).

White muscle tissues of fish specimens and food samples were freeze-dried (at -53°C for 48 h) and ground up. Acidified samples (1-2 mg) were combusted in an

elemental analyzer (Flash EA-1100 NC, Thermo-Finnigan) to produce CO_2 and N_2 for separately determining the isotopic compositions (Ho et al. 2007). Isotope ratios were expressed as the difference in parts per thousand (‰) from standard reference material:

$$\delta X \ = \ [(R_{sample} / R_{standard}) - 1] \times 1000;$$

where X is ^{13}C or ^{15}N, R is the corresponding ratio of $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$, and δ is a measure of the heavy to light isotopes in the sample. The reference materials were the international standards, Pee Dee Belemnite (PDB) for carbon and atmospheric N_2 for nitrogen.

Data analysis

The food niche breadth (B index) (Zaret and Rand 1971) was used to calculate the niche breadths for the 2 damselfishes by applying the following formula: B = (Σ Pi^2)$^{-1}$, where B is the food niche breadth, and Pi is the relative volume of each prey group, i, in the diet. The range of B is from 1, representing the minimum niche breadth and maximum specialization, to n, representing the maximum niche breadth and maximum generalization (where n is the total number of prey categories). The dietary overlap between the 2 damselfishes was determined using Schoener's index (α), which varies from 0, representing no overlap, to 1, representing complete overlap between species (Schoener 1970). Values of 0.6 or greater are considered to be biologically significant overlap (Martin 1984). Data on the unidentified portion of the stomach contents were excluded from both of the above analyses.

Multivariate analysis of variance (MANOVA) was used to test for dietary differences in the 2 damselfishes between the 2 zones and 2 collection times. The volumetric percentage data of stomach contents were square root-transformed prior to the analysis. Differences in $\delta^{13}C$ and $\delta^{15}N$ values of the damselfish between the 2 zones and 2 collection times were tested by analysis of covariance (two-way

ANCOVA) using fish body length as the covariate.

RESULTS

Stomach content analysis

Plectroglyphidodon dickii

Food composition was affected by zone (MANOVA, Wilks' lambda = 0.086, $F_{10, 9}$ = 9.624, p = 0.001), but not by collection (Wilks' lambda = 0.576, $F_{10, 9}$ = 0.663, p = 0.753).   The interaction between sampling zone and collection was not significant (Wilks' lambda = 0.328, $F_{10, 9}$ = 1.846, p = 0.185).   For each zone, the dietary data from the 2 collections were therefore combined for further analysis (Fig. 3).   In zone A, filamentous algae was the major food item identified (with a mean volumetric percentage of 33.4%), followed by coral polyps (22.3%) and detritus (21.3%).   Other food items included sea anemones (3.0%), oikopleuras (2.5%), and fish scales (0.7%). In zone B, filamentous algae (35.8%) and detritus (19.0%) remained the major food items; however, in contrast to zone A, a large proportion of sea anemones (28.2%) was identified, and no coral polyps (0%) were observed.
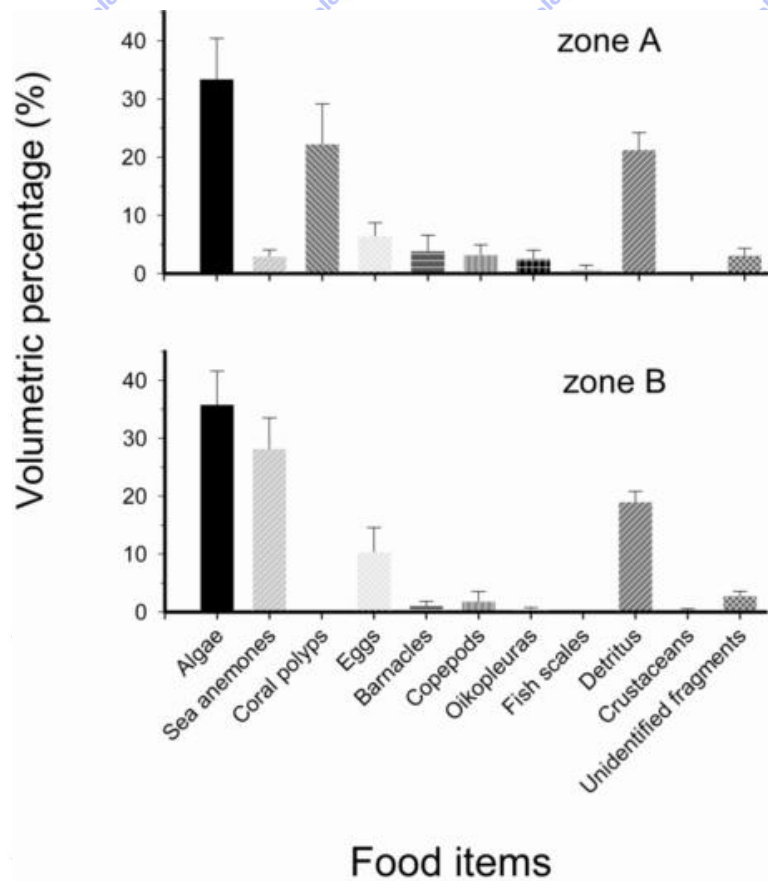
Fig. 3. Stomach content analysis of *Plectroglyphidodon dickii* in zones A and B. Error bars are standard errors.

Plectroglyphidodon johnstonianus

In collection I, specimens were not collected from zone A; thus the comparison between collections was only available for zone B, and the comparison between zones was only available for collection II.

In zone B, diet was not affected by collection (Wilks' lambda = 0.094, $F_{6, 2}$ = 3.216, $p = 0.256$), while for collection II, diet was not affected by zone (Wilks' lambda = 0.184, $F_{4, 3} = 3.326$, $p = 0.176$). Data were accordingly combined and are presented in fig. 4. Overall, for both zones A and B, coral polyps were the major food item identified (75.5% and 67.5%, respectively), followed by detritus (17.7% and 19.7%, respectively). Small amounts of algae, copepods, eggs, and barnacles
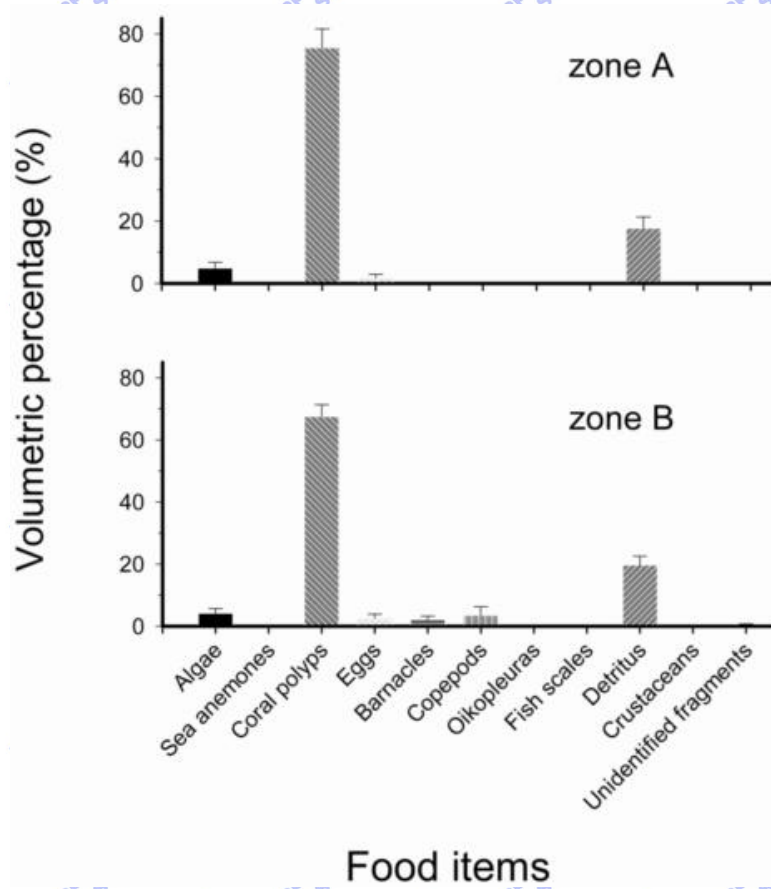
were also identified.

Fig. 4. Stomach content analysis of *Plectroglyphidodon johostonianus* in zones A and B. Error bars are standard errors.

Food niche breadth and dietary overlap

The food niche breadth indices (B) of *P. dickii* were 4.65 in zone A and 3.92 in zone B, and those of *P. johnstonianus* were 2.07 in zone A and 2.00 in zone B, indicating that the feeding habit of *P. dickii* was less specialized than that of *P. johnstonianus* in both zones.

Dietary overlap indices between these 2 damselfishes were < 0.6 in both zones (α

= 0.50 for zone A and 0.39 for zone B). Individual *P. johnstonianus* in both zones ingested almost identical foods (α = 0.92), while foods consumed by *P. dickii* were partially similar (α = 0.62) between zones.

Stable isotope analysis

Fishes

For both fish, the $\delta^{13}C$ signature was affected by zone, but not by collection (Table 2a). It was not linked to the covariate of body length. In addition, for *P. dickii*, the interaction between sampling zone and collection was not significant. By contrast, the $\delta^{15}N$ value was affected by neither zone nor collection (Table 2b). It was not linked to the covariate of body length. For *P. dickii*, the interaction between sampling zone and collection was not significant.

The stable isotope data from the 2 collections were therefore combined for each zone (Fig. 5). $\delta^{13}C$ values of *P. dickii* ranged -14.7‰ to -12.1‰ in zone A, and -15.3‰ to -14.6‰ in zone B. In *P. johnstonianus*, they ranged -11.5‰ to -12.3‰ in zone A, and -14.5‰ to -13.1‰ in zone B. The difference in $\delta^{13}C$ between the 2 damselfishes was not significant in zone A (F = 0.38, *d.f.* = 1 and 13, p = 0.55), but was significant in zone B (F = 4.92, *d.f.* = 1 and 20, p = 0.04).
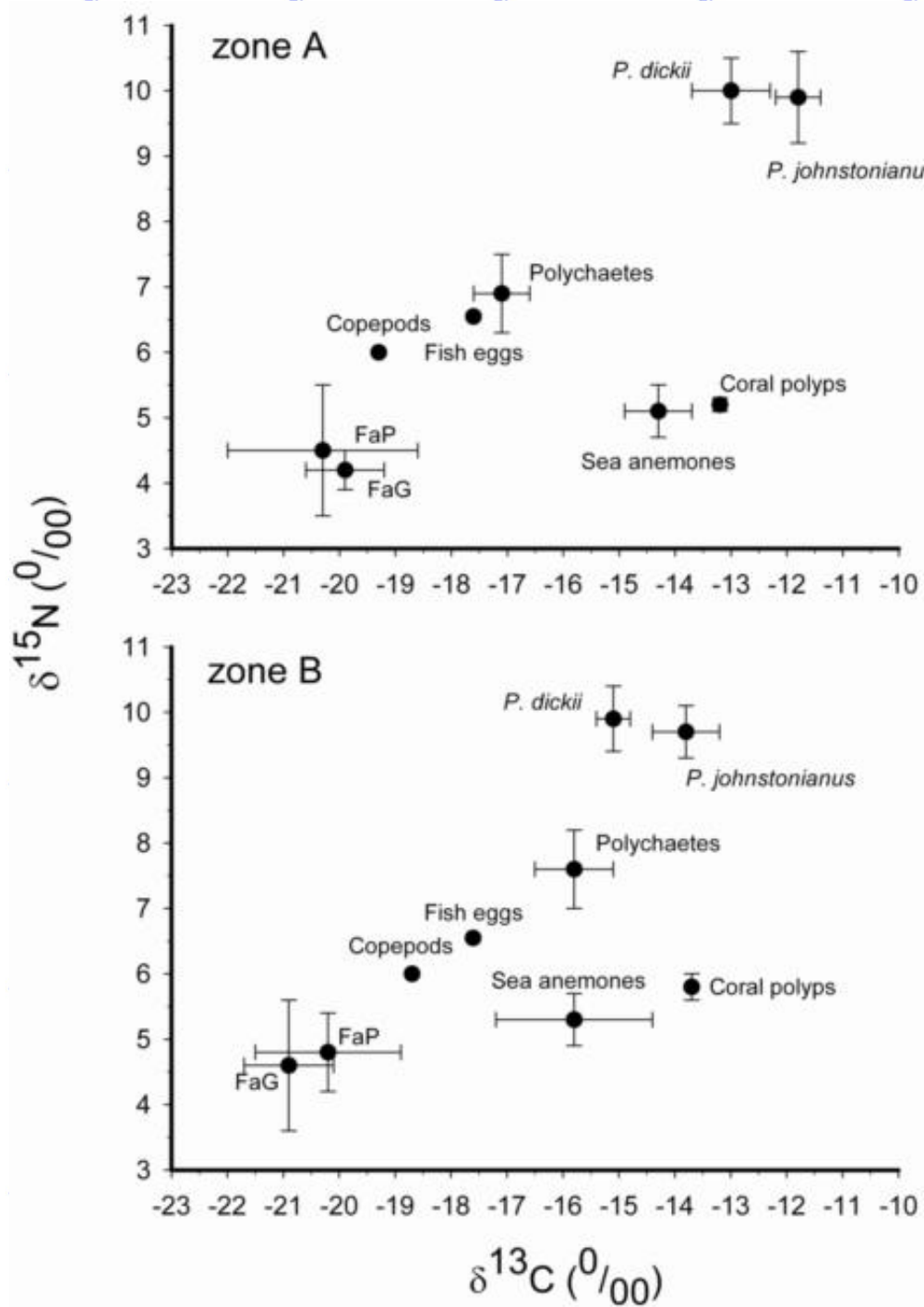
Fig. 5. Mean (± SD) carbon and nitrogen isotope values of *Plectroglyphidodon dickii, P. johnstonianus,* and potential food items in zones A and B. FaP, filamentous alga *Polysiphonia* sp.; FaG, *Gelidium* sp.

Table 2. The results of two-way ANCOVA comparing (a) $\delta^{13}C$ and (b) $\delta^{15}N$ of *Plectroglyphidodon dickii* and *P. johnstonianus* between zones and collections using body length as the covariate

(a) $\delta^{13}C$

Species	Effects	d.f.	F	p
P. dickii	zone	1, 21	87.01	< 0.001
	collection	1, 21	4.27	0.054
	body length	1, 21	0.67	0.424
	zone x collection	1, 21	2.38	0.142
P. johnstonianus	zone	1, 12	22.97	0.001
	collection	1, 12	2.89	0.123
	body length	1, 12	1.89	0.202

(b) $\delta^{15}N$

Species	Effects	d.f.	F	p
P. dickii	zone	1, 21	0.13	0.723
	collection	1, 21	0.26	0.614
	body length	1, 21	0.35	0.570
	zone x collection	1, 21	0.19	0.670
P. johnstonianus	zone	1, 12	0.01	0.946
	collection	1, 12	1.32	0.280
	body length	1, 12	2.09	0.182

In contrast, δ^{15}N values of *P. dickii* ranged 9.1‰ to 10.3‰ in zone A, and 9.3‰ to 11.0‰ in zone B.   In *P. johnstonianus*, they ranged 9.1‰ to 10.9‰ in zone A, and 9.1‰ to 10.4‰ in zone B.   The difference in δ^{15}N values between the 2 damselfishes was not significant for either zone A ($F = 0.34$, *d.f.* = 1 and 13, $p = 0.57$) or zone B ($F = 0.49$, *d.f.* = 1 and 20, $p = 0.49$).

Potential food items

The stable isotopic signatures of potential food items in both zones are presented in fig. 5. δ^{13}C values of the filamentous algae, *Polysiphonia* sp., ranged -22.8‰ to -19.6‰ in zone A and -20.9‰ to -18.8‰ in zone B; those of *Gelidium* sp. ranged -20.9‰ to -18.9‰ in zone A and -20.8‰ to -20.5‰ in zone B. δ^{13}C values of polychaetes ranged -18.1‰ to -14.6‰ in zone A and -17.1‰ to -14.1‰ in zone B. δ^{13}C values of coral polyps ranged -13.3‰ to -13.1‰ in zone A, and were -13.7‰ in zone B. δ^{13}C values of sea anemones ranged -15.0‰ to -13.7‰ in zone A and -17.9‰ to -15.4‰ in zone B. δ^{13}C values of copepods were -19.9‰ in zone A and -18.7‰ in zone B. δ^{13}C values of fish eggs were -17.6‰ in both zones A and B.

δ^{15}N values of filamentous algae ranged 3.8‰ (*Gelidium* sp.) to 5.5‰ (*Polysiphonia* sp.) in zone A and 4.1‰ (*Polysiphonia* sp.) to 5.6‰ (*Gelidium* sp.) in zone B.   In polychaetes, values ranged 5.6‰ to 9.6‰ in zone A and 6.7‰ to 8.1‰ in zone B. For coral polyps, values ranged 5.2‰ to 5.3‰ in zone A and 5.7‰ to 6.0‰ in zone B. In sea anemones, values ranged 4.7‰ to 5.0‰ in zone A and 4.8‰ to 5.9‰ in zone B. δ^{15}N values of copepods were 6.0‰ in both zones A and B. δ^{15}N values of fish eggs were 6.5‰ in both zones A and B.

DISCUSSION

To respond to the heterogeneity of the environment in both space and time, a large number of fish species possess broad trophic adaptabilities (Gerking 1994). In the present study, temporal food availability was one of the unpredictable factors delineating environmental heterogeneity. However, an explanation for the ecological outcome seemed to stem mostly from the differential feeding plasticity of the different fish species.

Feeding habits of *Plectroglyphidodon dickii*

Different food combinations were found for *P. dickii* in different geographic areas. Algae were reported to be its major food item in the Marshall Is. (Hiatt and Strasburg 1960). However, at Okinawa I., Japan, it mainly fed on coral polyps (37%) and sea anemones (36%) (Sano et al. 1984). In the South Sea, it fed on filamentous algae and small benthic invertebrates (Lieske et al. 1994). In the present study, its major food items were filamentous algae (33.4%) and coral polyps (22.3%) in zone A (dominated by branching corals), in contrast to the dominance of filamentous algae (35.8%) and sea anemones (28.2%) in zone B (which was, itself, dominated by sea anemones). The above zonal differences in food combinations reveal that feeding habits of *P. dickii* are flexible, and tend to be affected by the differential availability of cnidarian food items in its habitat.

Despite the high volumetric percentage in the stomach contents, filamentous algae might not be the major nutrient source for *P. dickii*, as indicated by the signature of stable isotopes obtained from the 2 zones. The least differences in $\delta^{13}C$ between *P. dickii* and algae (6.9‰ for zone A and 5.1‰ for zone B) were much higher than the expected 1‰ (± 1‰, SD) between consumers and their food resources (Minagawa and Wada 1984, Post 2002); the concurrent differences in $\delta^{15}N$ (5.5‰ for zone A and 5.1‰ for zone B) were also higher than the expected 3.4‰ (± 1‰, SD) for

per-trophic level increases (Wada et al. 1991).

As the next most important food items for *P. dickii*, coral polyps and sea anemones bore similar $\delta^{15}N$ signatures in both zones (Fig. 5). The enrichment in $\delta^{13}C$ of 0.2‰-1.3‰ and in $\delta^{15}N$ of 4.8‰-4.9‰ between *P. dickii* and these cnidarians in zone A, and in $\delta^{13}C$ of 0.7‰ and in $\delta^{15}N$ of 4.9‰ between *P. dickii* and sea anemones in zone B did not deviate from the stomach content analysis.

Some cryptic dietary components might be expected for *P. dickii*. In coral reef systems, the epilithic algal community consists of a mixture of filamentous algae, sediment, detritus, and invertebrates (Wilson and Bellwood 1997). When *P. dickii* feeds on filamentous algae, it may also ingest hidden benthic invertebrates. Attention is particularly drawn to polychaetes because the 3.5‰ depletion in $\delta^{13}C$ values and 3.0‰ in $\delta^{15}N$ in zone A, and 0.2‰ in $\delta^{13}C$ and 2.2‰ in $\delta^{15}N$ in zone B suggest that polychaetes may be an important nutrient contributor to *P. dickii*. Since polychaetes are rapidly digested, and the undigested chaetae are too minute to be observed with dissecting microscopes due to resolution limits (Hyslop 1980), they could have occurred as unidentified digested animal fragments (3.15% for zone A and 2.93% for zone B) or detritus (21.3% for zone A and 19.1% for zone B) in the stomach contents. This may also explain why *P. dickii* and the specialized coral-polyp feeder, *P. johnstonianus*, were at the same trophic level (as indicated by similar $\delta^{15}N$ signatures they bore, Fig. 5).

Feeding habits of *Plectroglyphidodon johnstonianus*

Stomach content analyses showed that *P. johnstonianus* preferred coral polyps in a wide geographic range. The proportion of coral polyps in diets of *P. johnstonianus* was 94.3% in Hawaii, USA (Hobson 1974) and 96% at Okinawa I., Japan (Sano et al. 1984). In the present study, coral polyps also dominated other food items (at 75.5% in zone A and 67.5% in zone B). The 1.4‰ depletion of $\delta^{13}C$ values in zone A and

-0.1‰ in zone B, and 4.6‰ depletion of $\delta^{15}N$ in zone A and 3.9‰ in zone B of coral polyps are within per-trophic level differences, thereby indicating that coral polyps were the major organic source for *P. johnstonianus*.

Effects of feeding plasticity on fish distribution

Fish distributions can be affected by their use of different food resources. With a preference for coral polyps, *P. johnstonianus* exhibited a narrower food niche breadth (B = 2.00-2.07) than did the cohabiting *P. dickii* (B = 3.92-4.65). With a diet restricted to coral polyps, *P. johnstonianus* could avoid competition with other fish species by reducing the overlap in resources (Ebersole 1985; Gerking 1994). However, because *P. johnstonianus* uses few food types, its distribution is more likely to be limited by the availability of coral (Brown 1984). Thus it is not surprising that *P. johnstonianus* was less abundant in the sea anemone-dominated zone B than in the coral-dominated zone A.

Plectroglyphidodon dickii is a generalist which feeds on a broad spectrum of foods. Filamentous algae are a common dietary item for *P. dickii*. Other than that, conspecifics that would otherwise eat coral polyps in zone A might switch to eating sea anemones to respond to low coral availability in zone B. When their outbreak in zone B changed the substrate types, eliminating some fish species (Chen et al. 2008), sea anemones could also have become a food source for other organisms including fish. Since *P. dickii* was able to switch to feeding on sea anemones, those on nearby reefs (i.e., zone A) might have taken this opportunity to immigrate into zone B. Thus the higher feeding plasticity may help explain the recent dramatic increase of *P. dickii* in the newly developed sea anemone-dominated habitat.

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