Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, southern Japan

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Abstract To clarify the feeding habits of fishes in tropical seagrass beds on coral reefs, the gut contents of 53 fish species, collected in an *Enhauls acoroides*-dominated bed at Iriomote Island, southern Japan, were examined. Ontogenetic changes in food preference were recognized in 9 species, including lethrinids, mullids, pomacentrids, labrids, and scarids. Cluster analysis based on dietary overlaps showed that the seagrass fish assemblage comprised seven feeding guilds (small-crustacean, large-crustacean, plant, detritus, hard-shelled mollusc, fish, and planktonic-animal feeders). Of these, small-crustacean feeders were the most abundantly represented. On the other hand, planktonic-animal and hard-shelled mollusc feeders were each represented by only two species. Compared with previous studies on the feeding habits of temperate seagrass fishes, the present fish assemblage was characterized by larger species numbers of detritivores, herbivores, and piscivores and fewer planktonic-animal feeders.

Key words Feeding ecology · Trophic guilds · Ontogenetic diet shift · Tropical seagrass fishes

Studies of resource requirements by various species have been used in attempts to understand factors controlling the distribution and abundance of organisms (Ross, 1986). In addition, studies on food habits of organisms utilizing each habitat help to illustrate the role of the latter in the ecology of several organisms. Therefore, food resources have received by far the most attention (Simberloff and Dayan, 1991); many studies on feeding ecology having been conducted for different fish communities (e.g., Sano et al., 1984; Ross, 1986; Pausey et al., 1995; Piet et al., 1999; Garrison and Link, 2000).

Seagrass beds are a major feature of shallow marine and estuarine areas throughout the world, supporting fish assemblages comprising large numbers of species and individuals, and providing nursery and feeding areas for many species (Pollard, 1984; Gilmore, 1987; Bell and Pollard, 1989; Connolly, 1994; Edgar and Shaw, 1995; Horinouchi and Sano, 1999). Many studies on the feeding habits of each species within such assemblages have been conducted, although most have been made in temperate regions (Kikuchi, 1966; Adams, 1976; Duka, 1978; Livingston, 1982; Bell and Harmelin-Vivien, 1983; Burchmore et al., 1984; Hanekom and Baird, 1984; Robertson, 1984; Whitfield, 1988; Edgar and Shaw, 1995; Horinouchi and Sano, 2000). Studies that have considered the food habits of fishes inhabiting tropical seagrass beds on coral reefs have been conducted infrequently, although some information exists (Ogden and Ehrlich, 1977; Ogden and Zieman, 1977; Ogden, 1980; Robblee and Zieman, 1984; Heck and Weinstein, 1989; Nagelkerken et al., 2000).

In this study, we examined the patterns of food resource utilization within a fish assemblage in a seagrass bed on a fringing coral reef at Iriomote Island, with the specific aims of describing the food habit of each fish species within the assemblage and identifying the feeding guild structures in the assemblage by determining the degree of dietary overlap among various species.

Materials and Methods

This study was conducted in a dense seagrass bed on an inner reef flat of Amitori Bay (24°20′ N, 123°42′ E), situated on the western side of Iriomote Island, one of the Ryukyu Islands, Japan (Fig. 1). The seagrass bed occurred next to a coral-dominated area, forming an extensive belt running parallel to the shore. The vegetation within the bed was dominated by *Enhauls acoroides*; other plants included *Thalassia hemprichii*, *Syringodium isoetifolium*, and *Cymodocea rotundata*. Water depth at the study site was about 2 m at high tide and about 50 cm at low tide.
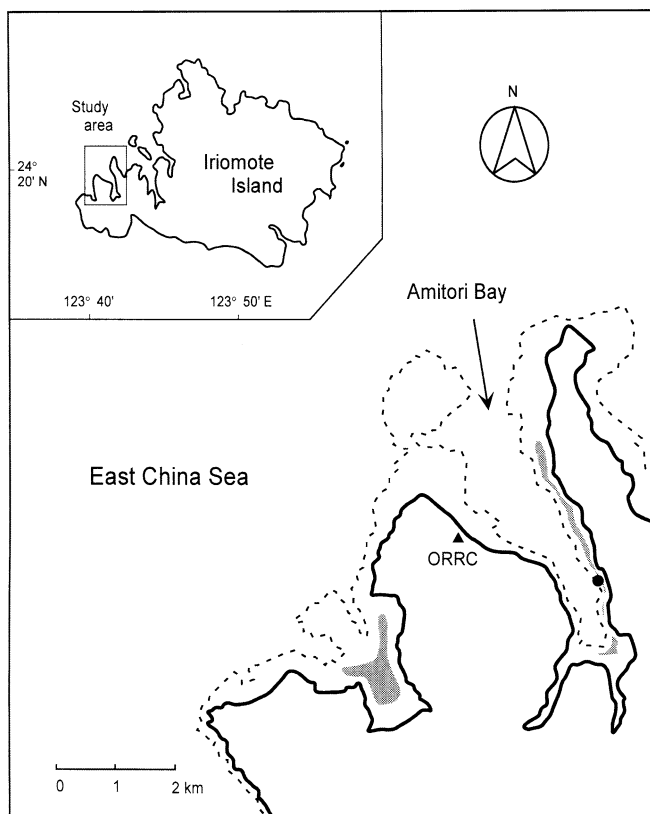
Fig. 1. Map of the study area at Iriomote Island, Ryukyu Islands, Japan. *Dotted line* indicates reef margin. *Shaded areas* show the position of seagrass beds. ●, Sampling site; ▲, Okinawa Regional Research Center, Tokai University (*ORRC*)

Fishes were collected from the seagrass bed at high tide using 32-m and 6-m beach seine nets with 13-mm and 5-mm mesh at the codend, respectively, and small hand nets, between 1000 and 1600 in May, August, and November 1999; February, May, and August 2000; and May 2001. A total of 1233 individuals representing 79 species were collected (Table 1). Immediately after collection, concentrated formalin was injected into the body cavity of each specimen, which was then preserved in 10% formalin. In the laboratory, standard lengths (SL) of all specimens were measured to the nearest 0.1 mm. Food items in the gut contents of each specimen were identified to the lowest possible taxon. The percentage volume of each food item in the diet was visually estimated under a binocular microscope as follows: gut contents were squashed on the 1 × 1 mm grid slide to a uniform depth of 1 mm and the area taken up by each item measured. The latter was then divided by the total area of the gut contents to calculate the percentage volume of that item in the diet. Food resource use was expressed as mean percentage composition of each item by volume, which was calculated by dividing the sum total of the individual volumetric percentage for the item by the number of specimens examined. Specimens with empty stomachs were excluded from the analysis.

Data were pooled for each season and year because the aim of the study was to describe the feeding patterns of the

fish species within the assemblage as a whole. Fifty-three species with five or more individuals containing food were subjected to further analyses, because fewer than five individuals was considered to achieve limited food item representation. Some juveniles of *Lethrinus*, Scarinae, and Sparisomatinae were not identified to species. Such juvenile groups were treated as single taxonomic units (e.g., *Lethrinus* spp.), because the gut contents were similar within each. For some species, individuals with various body size occurred in the present seagrass bed. It was appropriate, therefore, to examine whether differences existed in the feeding habits among different fish size classes. Because the assumption of homogeneity of variances for parametric analysis was not met, even for transformed data, the nonparametric Mann–Whitney U test was employed to test such differences.

To divide the seagrass fishes into groups that took similar food, dietary overlaps were calculated and subjected to a cluster analysis. For the calculation of dietary overlaps, prey items were grouped in mutually exclusive categories (Table 2). Calculation of the dietary overlap between all species pairs was based on mean percentage volume of each prey category. Successive changes in food preference by size class were recognized in nine species. Therefore, each size class of these species was regarded as a separate unit in the cluster analysis. The percentage similarity index (PS) was used to determine the dietary overlap between species (Krebs, 1989):

$$PS = [\Sigma(\text{minimum } P_{ij}, P_{ik})] \times 100$$

where P_{ij} and P_{ik} are proportions by volume of the ith prey category in the diets of species j and k. The index ranges from 0 (no similarity) to 100 (complete similarity). The overlap data were subjected to an average linkage clustering method to generate a diet similarity phenogram for the assemblage. This clustering algorithm was used so as not to unduly distort multivariate space (Jaksic and Medel, 1990). We arbitrarily adopted a level of 40% similarity (intermediate overlap value) as a basis for dividing the fishes into trophic groups.

Results

Feeding groups. The diets of 53 species studied are shown in Fig. 2. Cluster analysis based on the dietary overlap among species showed that the seagrass fish assemblage was divided into seven trophic groups (i.e., guilds) (Fig. 2).

Fish feeders (Group A in Fig. 2).—This group consisted of members that fed on juvenile and/or adult fishes, including labrids, scarids, blenniids, and gobiids. Seven units, representing 11.3% of the total, belonged to this guild. Of these, *Saurida gracilis* and *Fistularia commersonii* preyed predominantly on fishes, whereas other species captured fishes along with invertebrates including shrimps, mysids, and gammaridean amphipods.

Large-crustacean feeders (Group B).—This group included seven units (11.3%). Crabs and shrimps were con-

sumed by all the group members, being the most dominant dietary items.

Small-crustacean feeders (Group C).—This group consisted of members that fed mainly on small benthic or epiphytic crustaceans, such as amphipods and harpacticoid copepods. Twenty-nine units, representing 46.8% of the total, belonged to this guild. Harpacticoid copepods were consumed by all the group members and were the most dominant dietary item in most cases. Gammaridean amphipods and tanaids were also consumed by most of the group members (27 of 29 units).

Hard-shelled mollusc feeders (Group D).—This group comprised 2 units (3.2%). *Choerodon anchorago* (46–178 mm SL) fed dominantly on gastropods and bivalves, whereas *Lethrinus atkinsoni* (73–162 mm SL) took largely bivalves along with large crustaceans.

Planktonic-animal feeders (Group E).—Only two units (3.2%) belonged to this category. Both species fed predominantly on calanoid and poecilostomatoid copepods.

Detritus feeders (Group F).—This group comprised 9 units (14.5%). Detritus, consumed by all the group members, was the most important food item. Other food items, such as filamentous algae and seagrasses, were also consumed.

Plant feeders (Group G).—This group comprised 6 units (9.7%). Of these, *Leptoscarus vaigiensis* (97–156 mm SL) and *Hyporhamphus quoyi* fed mainly on seagrasses, but *Siganus fuscescens*, *Amblygobius phalaena*, and *Dischistodus prosopotaenia* (32–68 mm SL) took predominantly filamentous algae.

Ontogenetic diet shift. Ontogenetic trophic changes were recognized in nine species described next.

Lethrinus harak.—Juveniles (19–56 mm SL) fed mainly on errant polychaetes and small benthic or epiphytic crustaceans, such as gammaridean amphipods, tanaids, and harpacticoid copepods. The relative importance of these food items tended to decrease in larger individuals (87–200 mm SL) compared to juveniles (19–56 mm SL), although the difference was not statistically significant. Larger individuals preyed largely on crabs, shrimps, and hermit crabs, the relative importance of crabs increasing with increasing fish size ($P = 0.002$).

Lethrinus atkinsoni.—The major food item of juveniles (17–34 mm SL) was errant polychaetes, along with gammaridean amphipods, shrimps, and tanaids. However, larger fish (73–162 mm SL) fed mainly on crabs and bivalves, the contribution of these to the diet increasing with fish body size ($P = 0.03$ for crabs; $P < 0.001$ for bivalves).

Parupeneus ciliatus.—Although smaller fish (30–50 mm SL) fed predominantly on small crustaceans, such as harpacticoid copepods and gammaridean amphipods, larger fish (62–98 mm SL) took mainly larger crustaceans, including crabs and shrimps. Of these, the relative dietary importance of crabs and harpacticoid copepods differed significantly between size classes ($P < 0.001$ for crabs; $P = 0.04$ for harpacticoid copepods).

Parupeneus barberinus.—Smaller fish (28–50 mm SL) consumed mainly small crustaceans, such as gammaridean amphipods and harpacticoid copepods, although their importance decreased significantly in the diet of larger individuals (102–144 mm SL) ($P = 0.008$ for gammaridean amphipods; $P = 0.01$ for harpacticoid copepods). The latter fed mainly on crabs, isopods, shrimps, and bivalves ($P = 0.003$ for crabs; $P = 0.03$ for isopods; $P = 0.007$ for bivalves).

Dischistodus prosopotaenia.—Juveniles (9–13 mm SL) fed mainly on harpacticoid copepods whereas larger fish (32–68 mm SL) took predominantly filamentous algae. The contribution of these to the diet differed significantly between size classes ($P < 0.001$ for harpacticoid copepods; $P < 0.001$ for filamentous algae).

Choerodon anchorago.—Juveniles (17–24 mm SL) fed mainly on small crustaceans, such as gammaridean amphipods and tanaids, and errant polychaetes. Larger individuals (46–178 mm SL), however, preyed on gastropods, bivalves, and crabs, the relative importance of these food items increasing significantly with fish body size ($P < 0.001$ for gastropods; $P = 0.005$ for bivalves; $P = 0.01$ for crabs).

Stethojulis strigiventer.—The major food items of this species were gammaridean amphipods, tanaids, harpacticoid copepods, and detritus, their relative importance differing between size classes (10–25 and 40–74 mm SL) ($P < 0.001$ for gammaridean amphipods; $P < 0.001$ for tanaids; $P < 0.001$ for harpacticoid copepods; $P = 0.05$ for detritus). Juveniles (10–25 mm SL) fed mainly on harpacticoid copepods and detritus, whereas small crustaceans, such as gammaridean amphipods and tanaids, played a significant role in the diet of larger individuals (40–74 mm SL).

Calotomus spinidens.—Smaller fish (25–76 mm SL) consumed mainly detritus, but the contribution of the item to the diet decreased in larger size class (89–136 mm SL) ($P < 0.001$). Conversely, the percentage volume of seagrasses consumed increased significantly ($P < 0.001$).

Leptoscarus vaigiensis.—Although smaller fish (19–60 mm SL) fed predominantly on detritus, the most important food of larger individuals (97–156 mm SL) comprised seagrasses ($P < 0.001$ for seagrasses; $P < 0.001$ for detritus).

Important food. Based on the cumulative percentage volume values of all fish units for each food item and the percentage of units consuming each item, harpacticoid copepods were the most important food item for the present seagrass fish assemblage (Table 3). Gammaridean amphipods were also consumed by most of the fish units (70% of total), being the third most important item by cumulative percentage volume. Detritus and filamentous algae were the second and fourth most important items by cumulative percentage volume, respectively, but these items were consumed by about half the fish units.

Discussion

In general, fish species in the seagrass bed studied had similar diets to those determined for other sites. However, there were some exceptions. For example, Sano et al. (1984) reported *Amphiprion clarkii* in coral-dominated areas at Okinawa Island, one of the Ryukyu Islands, as a

Table 1. Number of specimens of each species collected (*n*)

Family	Species	*n*	Standard length range (mm)
Clupeidae	*Spratelloides delicatulus	26	28–41
Synodontidae	*Saurida gracilis	41	35–132
Aulostomidae	Aulostomus chinensis	2	15, 23
Fistulariidae	*Fistularia commersonii	14	111–384
Centriscidae	*Aeoliscus strigatus	55	72–143
Syngnathidae	Corythoichthys haematopterus	4	67–107
	*Syngnathoides biaculeatus	17	61–168
Hemiramphidae	*Hyporhamphus quoyi	5	144–218
Belonidae	Tylosurus crocodilus crocodilus	1	377
Platycephalidae	Cociella crocodila	4	164–218
Centrogenysidae	Cetrogenys vaigiensis	4	96–105
Apogonidae	*Apogon ishigakiensis	37	14–38
	*Cheilodipterus quinquelineatus	25	15–45
	*Sphaeramia nematoptera	16	16–23
Carangidae	Caranx sexfasciatus	1	101
Gerreidae	Gerres erythrourus	1	280
Haemulidae	Plectorhinchus albovittatus	1	31
	Plectorhinchus chaetodonoides	1	27
Nemipteridae	Scolopsis lineata	1	27
Lethrinidae	*Lethrinus atkinsoni	36	17–110
	Lethrinus genivittatus	12	33–145
	*Lethrinus harak	25	19–200
	*Lethrinus obsoletus	14	18–208
	*Lethrinus ornatus	10	17–119
	*Lethrinus spp.	16	15–18
Mullidae	*Parupeneus barberinoides	18	27–58
	*Parupeneus barberinus	20	28–144
	*Parupeneus ciliatus	40	30–98
	*Parupeneus multifasciatus	13	42–86
	Upeneus tragula	5	26–150
Chaetodontidae	Chaetodon argentatus	1	53
	Chaetodon melannotus	4	37–50
	Chaetodon vagabundus	1	96
Pomacentridae	*Amphiprion clarkii	9	21–43
	*Amphiprion ocellaris	10	21–45
	Chrysiptera unimaculata	1	26
	*Dischistodus prosopotaenia	23	9–68
	*Dascyllus trimaculatus	15	17–39
	*Pomacentrus chrysurus	12	11–57
Labridae	*Cheilinus chlorourus	7	70–103
	*Cheilio inermis	44	53–148
	*Choerodon anchorago	16	17–178
	Cymolutes torquatus	4	35–51
	Halichoeres argus	4	37–68
	Halichoeres scapularis	1	41
	*Halichoeres trimaculatus	12	20–127
	*Novaculichthys macrolepidotus	24	47–122
	*Oxycheilinus bimaculatus	11	52–76
	*Stethojulis strigiventer	42	10–70
Scaridae	Calotomus carolinus	1	47
	*Calotomus spinidens	56	25–136
	Hipposcarus longiceps	4	19–25
	*Leptoscarus vaigiensis	25	19–156
	Scarus dimidiatus	1	59
	Scarus schlegeli	4	55–101
	*Scarinae Gen. spp.	22	15–25
	*Sparisomatinae Gen. spp.	12	13–25
Pinguipedidae	*Parapercis cylindrica	19	35–110

Table 1. *Continued*

Family	Species	*n*	Standard length range (mm)
Tripterygiidae	*Enneapterygius minutus	20	12–15
Blenniidae	*Meiacanthus grammistes*	2	35, 40
	*Petroscirtes mitratus	11	8–37
	*Petroscirtes variabilis	12	19–81
Callionymidae	*Anaora tentaculata	9	22–47
Gobiidae	*Amblygobius phalaena	12	16–91
	*Asterropteryx semipunctata	12	15–24
	Eviota prasina	2	12, 12
	*Ctenogobiops crocineus	12	17–25
	*Ctenogobiops pomastictus	13	17–31
	*Ctenogobiops sp.	10	14–31
	*Cryptocentrus caeruleomaculatus	17	12–31
	*Fusigobius neophytus	16	11–32
	*Macrodontogobius wilburi	12	18–24
	*Pleurosicya bilobata	11	13–17
	*Vanderhorstia ornatissima	14	19–34
Siganidae	*Siganus fuscescens	11	64–116
	*Siganus sp.	5	60–84
Sphyraenidae	*Sphyraena flavicauda	5	87–133
Monacanthidae	*Acreichthys tomentosus	171	23–83
Tetraodontidae	*Arothron manilensis*	6	81–191

Species marked with an asterisk were subjected to all analyses

planktivore, feeding mostly on planktonic copepods. At Amitori Bay, however, the principal food item of this species was benthic copepods. Furthermore, *Parupeneus barberinus* at Okinawa Island feeds mainly on polychaetes and benthic crustaceans (Sano et al., 1984), although the former prey was hardly consumed by this species at Amitori Bay. Such differences may be partly related to habitat differences or geographic variations, such as differences in food availability at different localities.

Ontogenetic changes in food preference were recognized in nine species. In general, juveniles of these species fed on small crustaceans or detritus, later switching to other prey items with growth. The shift in food preference to large crustacean or hard-shelled animals observed in some fishes may be partly the result of morphological changes, including the development of jaw crushing strength (Wainwright, 1988) or increase in mouth gape size with body size (Lukoschek and McCormick, 2001). Two scarids (*Leptoscarus vaigiensis* and *Calotomus spinidens*) and a pomacentrid (*Dischistodus prosopotaenia*) shifted their food preference from detritus or small crustaceans to plant materials such as seagrasses as they grew. Such a shift in food preference to plant materials may have resulted from factors including development of intestine length (Kramer and Bryant, 1995) and production of digestive enzymes related to changes in the intestinal microbial community (Luczkovich and Stellwag, 1993). Furthermore, the ontogenetic difference in food habits may have resulted from other factors, including differences in catching ability (Juanes, 1994) and niche partitioning, which decreases intraspecific competition (Holbrook and Schmitt, 1992).

In the present seagrass bed, small crustacean feeders were the most abundant by number, the most important food item for the seagrass fish assemblage being benthic or epiphytic small crustaceans, such as harpacticoid copepods and gammaridean amphipods. These findings generally coincided with the food habits of temperate seagrass fishes (Kikuchi, 1966; Livingston, 1982; Bell and Harmelin-Vivien, 1983; Hanekom and Baird, 1984; Edgar and Shaw, 1995; Horinouchi and Sano, 2000).

Planktonic-animal feeders consisted of only two species, *Aeoliscus strigatus* and *Spratelloides delicatulus*, although such feeders are relatively abundant in temperate seagrass beds. For example, they occupied 15.8% and 19.6% of the total species in the seagrass beds at Western Port, southern Australia (Edgar and Shaw, 1995) and at Aburatsubo, central Japan (Horinouchi and Sano, 2000), respectively, although accounting only for 3.2% in the present seagrass bed. In addition, judging from cumulative percentage volume values (see Table 3), planktonic animals were less important as food for the present seagrass fish assemblage, although one of the most important food items of seagrass fishes in temperate regions (Adams, 1976; Livingston, 1982; Horinouchi and Sano, 2000). This difference may be caused by a scarcity of planktonic animals in the present study bed, although supporting data are lacking.

In this study, 28 species (44% of total) were found to have ingested seagrasses, although seagrasses are usually little consumed by fishes (Pollard, 1984; Bell and Pollard, 1989; Klumpp et al., 1989). In most cases, the seagrasses may have been ingested incidentally during the capture of epifaunal prey animals. Several fishes, such as the halfbeak

Fig. 2. Dendrogram obtained from dietary overlap data and mean percentage volume of food items (%V) of each species. Abbreviations are given in Table 2. *Asterisks*, fish with ontogenetic dietary shift; *M*, items composing less than 3% of the gut content volume of each species; *SL*, standard length; *n*, number of fish examined containing food. At the 40% similarity level, the assemblage was divided into seven trophic groups (coded *A–G*)
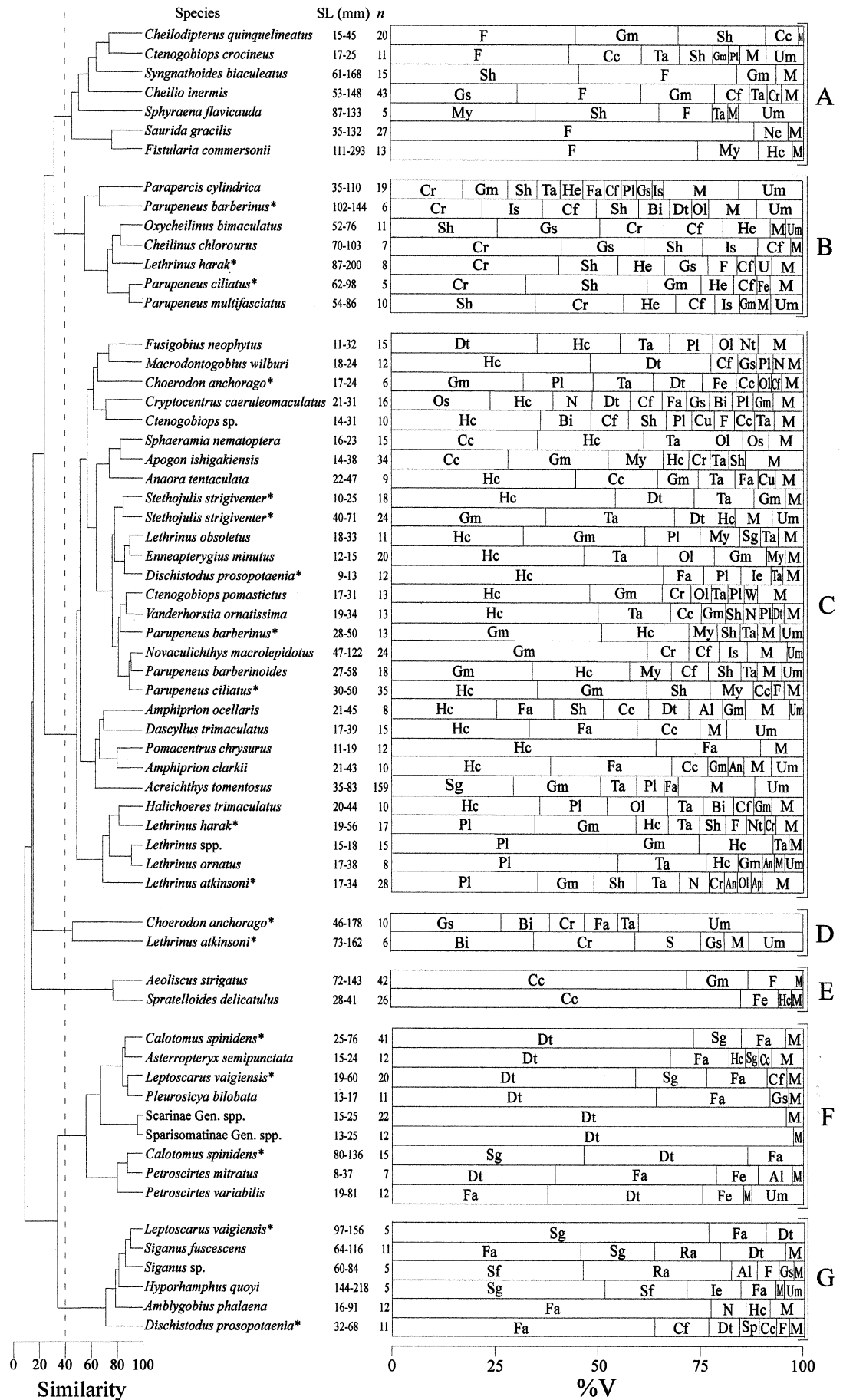
Species	SL (mm)	n	Food items (%V, in order)	Group
Cheilodipterus quinquelineatus	15-45	20	F, Gm, Sh, Cc, M	A
Ctenogobiops crocineus	17-25	11	F, Cc, Ta, Sh, Gm, Pl, M, Um	A
Syngnathoides biaculeatus	61-168	15	Sh, F, Gm, M	A
Cheilio inermis	53-148	43	Gs, F, Gm, Cf, Ta, Cr, M	A
Sphyraena flavicauda	87-133	5	My, Sh, F, Ta, M, Um	A
Saurida gracilis	35-132	27	F, Ne, M	A
Fistularia commersonii	111-293	13	F, My, Hc, M	A
Parapercis cylindrica	35-110	19	Cr, Gm, Sh, Ta, He, Fa, Cf, Pl, Gs, Is, M, Um	B
*Parupeneus barberinus**	102-144	6	Cr, Is, Cf, Sh, Bi, Dt, Ol, M, Um	B
Oxycheilinus bimaculatus	52-76	11	Sh, Gs, Cr, Cf, He, M, Um	B
Cheilinus chlorourus	70-103	7	Cr, Gs, Sh, Is, Cf, M	B
*Lethrinus harak**	87-200	8	Cr, Sh, He, Gs, F, Cf, U, M	B
*Parupeneus ciliatus**	62-98	5	Cr, Sh, Gm, He, Cf, Fe, M	B
Parupeneus multifasciatus	54-86	10	Sh, Cr, He, Cf, Is, Gm, M, Um	B
Fusigobius neophytus	11-32	15	Dt, Hc, Ta, Pl, Ol, Nt, M	C
Macrodontogobius wilburi	18-24	12	Hc, Dt, Cf, Gs, Pl, N, M	C
*Choerodon anchorago**	17-24	6	Gm, Pl, Ta, Dt, Fe, Cc, Ol, Cf, M	C
Cryptocentrus caeruleomaculatus	21-31	16	Os, Hc, N, Dt, Cf, Fa, Gs, Bi, Pl, Gm, M	C
Ctenogobiops sp.	14-31	10	Hc, Bi, Cf, Sh, Pl, Cu, F, Cc, Ta, M	C
Sphaeramia nematoptera	16-23	15	Cc, Hc, Ta, Ol, Os, M	C
Apogon ishigakiensis	14-38	34	Cc, Gm, My, Hc, Cr, Ta, Sh, M	C
Anaora tentaculata	22-47	9	Hc, Cc, Gm, Ta, Fa, Cu, M	C
*Stethojulis strigiventer**	10-25	18	Hc, Dt, Ta, Gm, M	C
*Stethojulis strigiventer**	40-71	24	Gm, Ta, Dt, Hc, M, Um	C
Lethrinus obsoletus	18-33	11	Hc, Gm, Pl, My, Sg, Ta, M	C
Enneapterygius minutus	12-15	20	Hc, Ta, Ol, Gm, My, M	C
*Dischistodus prosopotaenia**	9-13	12	Hc, Fa, Pl, Ie, Ta, M	C
Ctenogobiops pomastictus	17-31	13	Hc, Gm, Cr, Ol, Ta, Pl, W, M	C
Vanderhorstia ornatissima	19-34	13	Hc, Ta, Cc, Gm, Sh, N, Pl, Dt, M	C
*Parupeneus barberinus**	28-50	13	Gm, Hc, My, Sh, Ta, M, Um	C
Novaculichthys macrolepidotus	47-122	24	Gm, Cr, Cf, Is, M, Um	C
Parupeneus barberinoides	27-58	18	Gm, Hc, My, Cf, Sh, Ta, M, Um	C
*Parupeneus ciliatus**	30-50	35	Hc, Gm, Sh, My, Cc, F, M	C
Amphiprion ocellaris	21-45	8	Hc, Fa, Sh, Cc, Dt, Al, Gm, M, Um	C
Dascyllus trimaculatus	17-39	15	Hc, Fa, Cc, M, Um	C
Pomacentrus chrysurus	11-19	12	Hc, Fa, M	C
Amphiprion clarkii	21-43	10	Hc, Fa, Cc, Gm, An, M, Um	C
Acreichthys tomentosus	35-83	159	Sg, Gm, Ta, Pl, Fa, M, Um	C
Halichoeres trimaculatus	20-44	10	Hc, Pl, Ol, Ta, Bi, Cf, Gm, M	C
*Lethrinus harak**	19-56	17	Pl, Gm, Hc, Ta, Sh, F, Nt, Cr, M	C
Lethrinus spp.	15-18	15	Pl, Gm, Hc, Ta, M	C
Lethrinus ornatus	17-38	8	Pl, Ta, Hc, Gm, An, M, Um	C
*Lethrinus atkinsoni**	17-34	28	Pl, Gm, Sh, Ta, N, Cr, An, Ol, Ap, M	C
*Choerodon anchorago**	46-178	10	Gs, Bi, Cr, Fa, Ta, Um	D
*Lethrinus atkinsoni**	73-162	6	Bi, Cr, S, Gs, M, Um	D
Aeoliscus strigatus	72-143	42	Cc, Gm, F, M	E
Spratelloides delicatulus	28-41	26	Cc, Fe, Hc, M	E
*Calotomus spinidens**	25-76	41	Dt, Sg, Fa, M	F
Asterropteryx semipunctata	15-24	12	Dt, Fa, Hc, Sg, Cc, M	F
*Leptoscarus vaigiensis**	19-60	20	Dt, Sg, Fa, Cf, M	F
Pleurosicya bilobata	13-17	11	Dt, Fa, Gs, M	F
Scarinae Gen. spp.	15-25	22	Dt, M	F
Sparisomatinae Gen. spp.	13-25	12	Dt, M	F
*Calotomus spinidens**	80-136	15	Sg, Dt, Fa	F
Petroscirtes mitratus	8-37	7	Dt, Fa, Fe, Al, M	F
Petroscirtes variabilis	19-81	12	Fa, Dt, Fe, M, Um	F
*Leptoscarus vaigiensis**	97-156	5	Sg, Fa, Dt	G
Siganus fuscescens	64-116	11	Fa, Sg, Ra, Dt, M	G
Siganus sp.	60-84	5	Sf, Ra, Al, F, Gs, M	G
Hyporhamphus quoyi	144-218	5	Sg, Sf, Ie, Fa, M, Um	G
Amblygobius phalaena	16-91	12	Fa, N, Hc, M	G
*Dischistodus prosopotaenia**	32-68	11	Fa, Cf, Dt, Sp, Cc, F, M	G

Similarity scale: 0 20 40 60 80 100

%V scale: 0 25 50 75 100

Table 2. Gut content components of seagrass fishes collected in Amitori Bay and descriptive codes used in Fig. 2

Category	Food item (code)
Small benthic or ephiphytic crustaceans	Harpacticoid copepods (Hc), gammaridean amphipods (Gm), isopods (Is), ostracods (Os), cumaceans (Cu), mysids (My), tanaids (Ta), anthurids (An)
Large benthic or ephiphytic crustaceans	Shrimps (Sh), crabs (Cr), crustacean fragments (Cf), hermit crabs (He)
Planktonic animals	Calanoid and poecilostomatoid copepods (Cc), shrimp larvae
Molluscs	Gastropods (Gs), bivalves (Bi)
Polychaetes	Errant polychaetes (Pl), sedentary polychaetes, Oligochaetes (Ol)
Fishes	Juvenile and adult fishes (F)
Detritus	Detritus (Dt)
Plants	Seagrass fronds (Sg), filamentous algae (Fa), *Sargassum* fronds (Sf), red algal fronds (Ra), unidentified algal fronds (Al)
Others (these items were regarded as separate units in the dietary overlap calculation)	Invertebrate eggs (Ie), fish eggs (Fe), nematodes (N), sponges (Sp), sea urchins (U), sea cucumbers (C), water mites (W), sipunculoids (S), nemerteans (Nt), ophiuroids, bryozoans, sea anemones, foraminiferans, aplysiids (Ap), unidentified materials (Um)

Hyporhamphus quoyi and the parrotfish *Leptoscarus vaigiensis* (97–156 mm SL), however, fed mostly on seagrasses. Several scarid and halfbeak species in other seagrass beds have also been reported as consuming mainly seagrasses (Randall, 1965; Klumpp and Nichols, 1983; Robertson and Klumpp, 1983). Clearly, therefore, seagrasses are an important food item to such species inhabiting seagrass beds.

Although detritivores are not usually common in temperate seagrass beds (in most cases, less than 2% of the total species) (Livingston, 1982; Bell and Harmelin-Vivien, 1983; Burchmore et al., 1984; Hanekom and Baird, 1984; Robertson, 1984; Edgar and Shaw, 1995; Horinouchi and Sano, 2000), nine species (14.5%) fed largely on detritus in the present study area. In four species, such as juvenile parrotfishes, detritus comprised more than about 60% of total food volume. The cumulative percentage volume value of detritus and high proportion of units consuming this food source showed detritus to be one of the most important food items for the present seagrass fish assemblage, contrary to the usual situation for temperate seagrass fishes (Bell and Harmelin-Vivien, 1983; Burchmore et al., 1984; Robertson, 1984; Edgar and Shaw, 1995; Horinouchi and Sano, 2000).

At the seagrass bed in Amitori Bay, seven species (11.3%) were piscivorous, hunting a variety of juvenile fishes including labrids and gobiids. The proportion (11.3%) of piscivorous species collected in this study was relatively high, compared with those (<7% in most cases) obtained during other studies in temperate seagrass beds (Livingston, 1982; Bell and Harmelin-Vivien, 1983; Hanekom and Baird, 1984; Robertson, 1984; Horinouchi and Sano, 2000).

Few species fed predominantly on molluscs in the present seagrass bed. Furthermore, the cluster analysis based on dietary overlap among species failed to identify a group of polychaete feeders. These findings coincided with those of many previous studies, which have shown little importance of infaunal animals to seagrass fish diets (Livingston, 1982; Edgar and Shaw, 1995; Horinouchi and Sano, 2000).

Table 3. Cumulative percentage volume (%V) values for each important food item (listed in decreasing order) and the percentage of fish units consuming each item (%U)

Food items	%V total	%U
Harpacticoid copepods	853	73
Detritus	751	48
Gammaridean amphipods	580	70
Filamentous algae	509	46
Fishes	379	32
Shrimps	334	44
Calanoid copepods	328	54
Errant polychaetes	316	62
Seagrasses	278	44
Tanaids	262	68

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