Research Article

Food habits of fishes in a subtropical seagrass bed in Nagura Bay, Ishigaki Island, southern Japan

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Abstract

Recent losses of seagrass beds have resulted in a decrease in seagrass-associated fishes, highlighting the need for the improved management of such habitats and resources. Analyses of feeding patterns of fish associated with seagrass habitats are useful for understanding their habitat dependence, which contributes to achieving their effective conservation. The gut contents of 61 fish species were examined to clarify the food habits of subtropical seagrass fishes in Nagura Bay, Ishigaki Island, southern Japan. A cluster analysis based on dietary overlaps showed that the seagrass fish assemblage comprised six trophic groups (small crustacean, large crustacean, detritus, plant, fish and zooplankton feeders). Small and large crustacean feeders were the most abundant, followed by detritus, plant and fish feeders. Zooplankton feeders were represented by only two species. Ontogenetic changes in food preference were recognized in four species, including *Lutjanus fulviflamma*, *Ostorhinchus ishigakiensis*, *Gerres oyena* and *Siganus fuscescens*. Small individuals of the four species generally fed on small crustaceans or detritus, subsequently switching to other larger prey items with growth (e.g. crabs, shrimps and seagrass fronds). The most important food items for the assemblage comprised harpacticoid copepods, shrimps, crabs and detritus, representing high cumulative gut volumes for all fishes. Some species showed diets remarkably different from those determined for fishes in other seagrass beds off a nearby neighbouring island, evidence of the food-use patterns of seagrass fishes varying on a small spatial scale. Such dietary flexibility may increase the adaptability of fishes to seagrass beds characterized by significant variations in available food resources.

Introduction

Seagrass beds are widely distributed in shallow coastal and estuarine areas from tropical to arctic regions (Short *et al.*, 2007), typically supporting large numbers of fish species and individuals compared with adjacent unvegetated areas (Guidetti, 2000; Heck *et al.*, 2003; Tuya *et al.*, 2005). It is generally considered that seagrass beds provide important nursery and feeding grounds for various fishes, including commercially important and endangered species (Gray *et al.*, 1996; Heck *et al.*, 2003; Dorenbosch *et al.*, 2006; Nagelkerken, 2009). For example, in tropical/subtropical regions, juvenile reef fishes, such as from the families Haemulidae, Lethrinidae and Lutjanidae, utilize seagrass beds before moving to nearby coral reefs where they remain as adults, due to seagrass beds functioning as effective juvenile habitats with higher food availability and/or lower predation risks (Grol *et al.*, 2011; Nakamura *et al.*, 2012; Berkström *et al.*, 2013). Therefore, seagrass beds are considered essential for maintaining high levels of biodiversity in coastal ecosystems and supporting local fisheries.

However, seagrass beds have been rapidly lost and degraded around the world due to natural and/or anthropogenic causes, including climate change, overharvesting by mega herbivores, coastal urbanization and vessel grounding (Waycott *et al.*, 2009; Christianen *et al.*, 2014). The loss of such beds results in a decrease in nursery and feeding grounds of seagrass-associated fishes, typically resulting in a significant decrease in numbers of fish species and individuals (Hughes *et al.*, 2002; Nakamura, 2010; Inoue *et al.*, 2021). Accordingly, conservation of seagrass beds and associated fishes is a growing priority. For effective conservation and management of seagrass fishes, a greater understanding of their dependency on seagrass beds is necessary.

Analyses of feeding patterns and trophic guild structures of seagrass fish assemblages are common approaches for understanding habitat use and habitat dependence of fishes. However, most of the many studies on the feeding habits of seagrass fishes have focused on temperate habitats (Kikuchi, 1966; Adams, 1976; Livingston, 1982; Bell & Harmelin-Vivien, 1983; Burchmore *et al.*, 1984; Hanekom & Baird, 1984; Robertson, 1984; Whitfield, 1988;

Edgar & Shaw, 1995; Hindell *et al.*, 2000; Horinouchi & Sano, 2000). Although the diet of a number of fish assemblages in tropical seagrass beds has been reported (e.g. Carr & Adams, 1973; Heck & Weinstein, 1989; Motta *et al.*, 1995; Nagelkerken *et al.*, 2000; Nagelkerken & van der Velde, 2004; Vaslet *et al.*, 2011; Kwak *et al.*, 2015; Dromard *et al.*, 2017), feeding habit analyses targeting entire fish assemblages in tropical and subtropical regions are relatively uncommon (Robblee & Zieman, 1984; Nakamura *et al.*, 2003; Nagelkerken *et al.*, 2006; Horinouchi *et al.*, 2012; Lee *et al.*, 2014).

The trophic guild structures of seagrass fish assemblages vary over broad regional scales. For example, in temperate seagrass beds, small crustacean feeders consuming harpacticoid copepods and gammaridean amphipods, and zooplankton feeders feeding on calanoid copepods, have been considered dominant in the fish assemblages (Burchmore *et al.*, 1984; Hanekom & Baird, 1984; Robertson, 1984; Edgar & Shaw, 1995; Horinouchi & Sano, 2000), whereas in tropical/subtropical seagrass beds, large crustacean feeders preying upon crabs and shrimps were abundant in the assemblage, as well as similarly sized small crustacean feeders (Nakamura *et al.*, 2003; Horinouchi *et al.*, 2012; Kwak *et al.*, 2015). Furthermore, the major food items for each fish species occurring in seagrass beds have often varied among several locations, with variations in ontogenetic trophic shifts (Nakamura *et al.*, 2003; Horinouchi *et al.*, 2012), due to high dietary flexibility in some of the former, suggesting that fish feeding habits may change in different locations, possibly within a single region. Nevertheless, exactly how seagrass fish diets change on a small local scale remains undetermined.

Extensive seagrass beds occurring in Nagura Bay, on the west side of Ishigaki Island, Yaeyama Archipelago, Okinawa Prefecture, Japan (Yamada *et al.*, 2018), support rich seagrass-associated invertebrates (Nakamoto *et al.*, 2018), therefore having potential as fish feeding grounds. However, the feeding patterns of fish assemblages are still unclear in the bay, although the trophic structure of seagrass fish assemblages has already been reported from Amitori Bay, Iriomote Island, adjacent to Ishigaki Island (Nakamura *et al.*, 2003). Accordingly, the seagrass fishes in Nagura Bay present a challenging subject for demonstrating how fish food-use patterns vary in seagrass systems on a small spatial scale (i.e. within an archipelago).

In the present study, the patterns of food resource use within the fish assemblage occupying the subtropical seagrass bed in Nagura Bay were examined, with the specific aims of describing the food habits of each fish species and their ontogenetic trophic shifts, and identifying the trophic guild structures by determining the degree of dietary overlap among species.

Materials and methods

Study area and collection of fish samples

Nagura Bay (24°39′N 124°13′E) is situated on the western side of Ishigaki Island, Yaeyama Archipelago, southern Japan, ~45 km east from Amitori Bay (Iriomote Island; Figure 1), where a previous dietary study of seagrass fish assemblages was conducted (Nakamura *et al.*, 2003). Nagura Bay supports large seagrass beds occupied primarily by *Cymodocea rotundata*, *C. serrulate* and *Thalassia hemprichii*, plus other sandy bottom-dwelling species (Yamada *et al.*, 2018). The beds form an extensive belt (100–500 m width, ~20 km length) along the shoreline of the bay (Tanaka & Kayanne, 2007), being some 300–500 m wide at the study site in the southern part of the bay. Sampling was conducted during spring ebb tides between 1000 and 1700 h in June and September 2018 and 2019, fishes being collected from the seagrass beds at depths between 0.5–1.0 m with a small

seine net (4 m wide, 1.5 m deep, 10 mm mesh size) and two gill nets (15 m wide, 0.9 m deep, 18 mm mesh; 20 m wide, 1.2 m deep, 21 mm mesh, respectively). Immediately after collection, so as to preserve gut contents, specimens were placed into a cooler with ice packs, before being frozen for transport to the laboratory for subsequent identification to species following Nakabo (2013), and measurement of standard length (SL) to the nearest 0.1 mm.

Gut content analysis

In total, 537 individuals representing 61 fish species were collected (Table 1). Food items in the gut contents of each specimen were identified to the lowest possible taxon, the percentage volume of each item in the diet being visually estimated under a binocular microscope as follows. Initially, gut contents were squashed on a Sedgewick–Raffer cell (1 mm × 1 mm grid slide) to a uniform depth of 1 mm and the area taken up by each item measured. The measured area was then divided by the total area of the gut contents to calculate the percentage volume (%V) of that item in the diet (Nakane *et al.*, 2011). 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 (Nanjo *et al.*, 2008). Specimens with empty guts were excluded from the analysis. Although some studies have suggested that analyses of fewer than five individuals are inadequate for realistic food item representation of a species (Nakamura *et al.*, 2003; Inoue *et al.*, 2005), poorly represented species (<5 individuals) were included in the present gut content analyses, because the cumulative prey curves calculated for fish species with a large number of specimens (which represented each trophic group), showed that the dietary composition of each species was represented to some degree, even though in a small number of specimens (Supplementary Figure S1). In fact, such dietary information must also contribute to an understanding of general patterns of food-resource use by the overall seagrass fish assemblage (Horinouchi *et al.*, 2012). The diets of fish species collected in both the present study and previous dietary study in Amitori Bay, on neighbouring Iriomote Island (both islands included within the Yaeyama Archipelago) (Nakamura *et al.*, 2003), were compared. All experimental procedures followed the guidelines for animal welfare of Fisheries Research and Education Agency, Japan (00323005).

Data analysis

Data were pooled for each year and month, because the aim of the study was to clarify overall food habits of fishes within the assemblage, rather than seasonal fluctuations. For some species, which included various size classes, ontogenetic trophic shifts were assessed between different size classes. Because the assumption of homogeneity of variances was not met, the non-parametric Mann–Whitney U test was employed to test whether or not size class differences existed in the percentage volume of each major food item.

To evaluate the overall relative importance of each food item for the entire fish assemblage, we calculated the cumulative percentage volume of each food item (%V total) by summing the total of all-species individual volumetric percentages for the item, as well as calculating the percentage of fish units consuming each item (%U). Four of the 61 species were analysed in two length classes, resulting in 65 fish units being considered.

To separate the seagrass bed fishes into groups that feed upon similar food, dietary overlaps were calculated, and a cluster analysis applied. For the calculation of dietary overlaps, food items were grouped in mutually exclusive categories (Table 2).
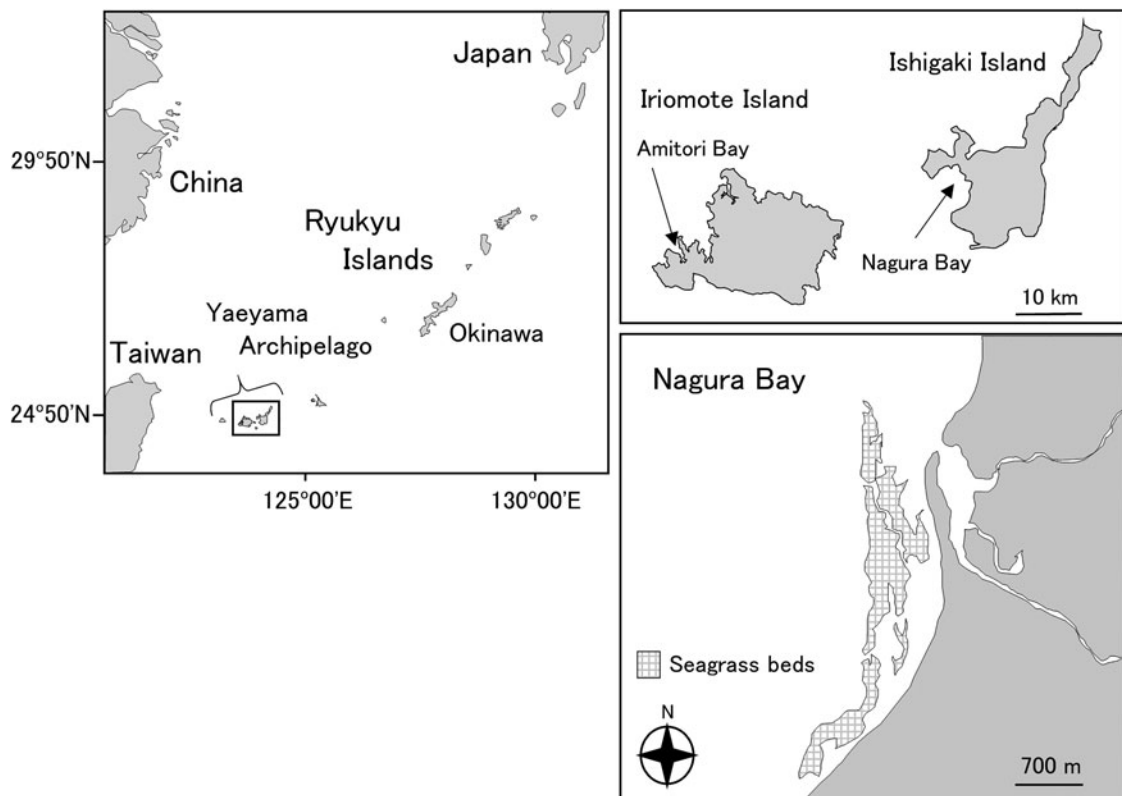
Fig. 1. Map of Nagura Bay, Ishigaki Island (present study site) and Amitori Bay, Iriomote Island (previous study site, Nakamura *et al.*, 2003), Yaeyama Archipelago, Okinawa Prefecture, Japan.

Calculations of the dietary overlaps between all species pairs were based on mean percentage volumes of each prey category. For species in which food habits differed by size class, each size class 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 ranging from 0 (no similarity) to 100 (complete similarity). Overlap data were subjected to an average linkage clustering method to generate a diet similarity phenogram for the assemblage. A level of 43 similarity (intermediate overlap value) was arbitrarily adopted as the basis for dividing the fishes into feeding groups. Kruskal–Wallis tests were used to examine differences in the percentage volume of each major food category among trophic groups. When significant effects were indicated, subsequent multiple comparison tests using the Holm method were applied.

Results

Relative importance of each food item

A wide variety of food items were consumed by the seagrass fishes examined (Figure 2, Table 2). According to the cumulative percentage volume values of all fish units for each food item, and the percentage of fish units consuming each item, harpacticoid copepods were the most important food item for the present seagrass fish assemblage (Table 2). Shrimps were consumed by about half of the fish units (49% of total), being the second most important food item by cumulative percentage volume and percentage of units. Detritus was the third most important food

item with a high cumulative percentage volume, since some species (such as *Siganus argenteus* and *Petroscirtes mitratus*) fed almost exclusively on detritus, although the percentage of units consuming this item was only 26% of the total. Crabs and fishes were next, consumed by 25% and 12% of the total units, respectively.

Feeding groups

A cluster analysis based on the dietary overlap among species (units) showed that the present seagrass fish assemblage was divided into six trophic groups at a similarity index level of 43 (Figure 2).

Fish feeders (FI in Figure 2) comprised six units, representing 9.2% of the total (65 units). Most members predated on juvenile and/or adult fishes, such as gobiids and siganids, whereas some members, such as *Lutjanus fulviflamma*, also fed on large crustaceans, including shrimps and crabs.

Large crustacean feeders (LC) included 12 units (18.4%). Shrimps and crabs were predominant food items for all members of this group. Some fishes, such as *Choerodon schoenleinii*, *Chelonodon patoca*, *Lethrinus lentjan* and *Lethrinus nebulosus*, also took gastropods.

Small crustacean feeders (SC) comprised 34 units (52.3%). Members fed primarily on small crustaceans, such as harpacticoid copepods, gammaridean amphipods, tanaids and isopods. Harpacticoid copepods were consumed by most of the group members (32 of 34 units).

Zooplankton feeders (ZP) included only two units (3%), *Spratelloides delicatulus* and *Aeoliscus strigatus*. These species fed mainly on calanoid copepods.

Plant feeders (PL) comprised five units (7.6%). Members of this group fed primarily on plant materials, such as seagrass

Table 1. Number of specimens (N) and standard length (SL) of each species used for gut content analyses

Family	Species	N	SL (mm)
Clupeidae	*Spratelloides delicatulus*	18	25.5–41.5
Synodontidae	*Saurida gracilis*	3	37.1–63.0
	Saurida nebulosa	4	47.0–85.2
Fistulariidae	*Fistularia commersonii*	3	117.4–153.2
Centriscidae	*Aeoliscus strigatus*	15	37.9–78.3
Syngnathidae	*Hippichthys (Hippichthys) cyanospilos*	9	87.7–127.2
	Hippocampus kelloggi	5	65.3–97.1
	Syngnathoides biaculeatus	6	125.1–207.3
Hemiramphidae	*Hyporhamphus quoyi*	3	180.0–212.0
Pseudochromidae	*Congrogadus subducens*	2	52.2, 59.4
Apogonidae	*Ostorhinchus ishigakiensis*	29	14.2–44.9
	Apognidae sp.	16	16.6–24.4
	Foa sp.	4	17.4–38.1
Lutjanidae	*Lutjanus fulviflamma*	18	17.0–138.3
	Lutjanus gibbus	1	30.3
	Lutjanus kasmira	1	95.0
Caesionidae	*Caesio caerulaurea*	3	31.3–34.3
Gerreidae	*Gerres oyena*	11	19.1–147.2
	Gerres shima	1	159.6
	Gerreidae sp.	11	14.7–29.0
Lethrinidae	*Lethrinus harak*	3	128.8–176.6
	Lethrinus lentjan	2	80.1, 128.1
	Lethrinus nebulosus	1	116.1
	Lethrinus obsoletus	3	71.9–126.0
	Lethrinidae spp.	24	15.8–67.4
Mullidae	*Parupeneus barberinoides*	10	34.5–60.2
	Parupeneus barberinus	2	64.2–69.2
	Parupeneus ciliatus	6	32.7–42.4
	Parupeneus indicus	9	31.8–130.0
	Parupeneus multifasciatus	1	50.7
	Upeneus tragula	5	29.5–63.4
Pomacentridae	*Abudefduf sexfasciatus*	2	4.8–22.9
	Dascyllus aruanus	1	14.0
	Dischistodus prosopotaenia	11	16.2–25.4
Labridae	*Cheilio inermis*	5	44.6–101.6
	Choerodon anchorago	17	14.2–25.7
	Choerodon schoenlenii	11	27.1–62.1
	Stethojulis strigiventer	39	10.8–62.4
Scaridae	*Calotomus spinidens*	4	48.5–85.1
	Leptoscarus vaigiensis	3	26.3–38.6
	Scaridae spp.	14	18.4–53.1
Blenniidae	*Petroscirtes mitratus*	22	14.4–40.9
	Petroscirtes variabilis	1	60.6
Callionymidae	*Anaora tentaculata*	3	29.7–39.5
	Paradiplogrammus enneactis	12	24.4–47.9
Gobiidae	*Acentrogobius multifasciatus*	6	21.7–43.2
	Amblygobius phalaena	17	20.0–53.5

(*Continued*)

Table 1. (Continued.)

Family	Species	N	SL (mm)
	Asterropteryx semipunctata	2	23.2, 29.9
	Yongeichthys criniger	4	20.9–35.0
	Valenciennea longipinnis	6	22.8–58.3
	Favonigobius reichei	2	20.7, 39.0
	Favonigobius sp.	11	17.5–23.1
Siganidae	*Siganus argenteus*	18	31.2–46.0
	Siganus fuscescens	47	21.0–141.9
	Siganus punctatus	4	34.4–53.6
	Siganus virgatus	20	20.0–28.9
Sphyraenidae	*Sphyraena barracuda*	11	39.2–153.2
Bothidae	*Bothus pantherinus*	1	52.4
Balistidae	*Balistoides viridescens*	2	59.5, 60.1
Monacanthidae	*Acreichthys tomentosus*	11	13.3–41.9
Tetraodontidae	*Chelonodon patoca*	1	102.3

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

Category	Food item (code)	%V total	%U
Small crustaceans	Harpacticoid copepods (Hc)	1571	63
	Gammaridean amphipods (Gm)	273	25
	Tanaids (Ta)	118	15
	Isopods (Is), ostracods (Os), mysids (My), small crustacean fragments (Sc)	148	34
Large crustaceans	Shrimps (Sh)	992	55
	Crabs (Cr)	604	25
	Crustacean fragments (Cf)	52	6
	Squillas (Sq), hermit crabs (He), crustacean fragments (Cf)	34	3
Zooplankton	Calanoid and poecilostomatoid copepods (Cc)	375	38
	Shrimp larvae (Sl)	13	3
Molluscs	Gastropods (Gs)	214	32
	Bivalves	8	5
Polychaetes	Polychaetes (Po)	67	18
Fishes	Juvenile and adult fishes (F)	444	12
Detritus	Detritus (Dt)	813	26
Plants	Seagrass fronds (Sg)	316	31
	Filamentous algae (Fa)	167	15
	Brown algae fronds (Bf)	114	17
Others	Gastropod eggs (Ge), fish eggs (Fe), fish scales (Fs), nematodes (Ne), unidentified material (Um)	154	40

Cumulative percentage volume (%V total) for each important food item (top three items ranked in decreasing order) and percentage of fish units consuming each item (%U). Others – items regarded as separate units for dietary overlap calculations.

fronds, filamentous algae and brown algae fronds. Most units (excluding *Hyporhamphus quoyi*) also consumed detritus.

Detritus feeders (DT) included six units (9.2%), which fed mainly on detritus.

The percentage volume of major food categories differed significantly among trophic groups (Table 3), each group feeding exclusively on food items which characterized that group (Figure 2).

Ontogenetic trophic shift

Ontogenetic trophic shifts were recognized in four species: *Lutjanus fulviflamma*, *Ostorhinchus ishigakiensis*, *Siganus fuscescens* and *Gerres oyena* (Figure 2).

Lutjanus fulviflamma
Smaller fish (17.0–22.4 mm SL) fed mainly on harpacticoid copepods, but less so in larger size classes (26.2–138.3 mm SL) (Mann–Whitney U test, $P = 0.01$). In contrast, larger individuals consumed predominantly shrimps, the relative importance of shrimps increasing with growth (Mann–Whitney U test, $P = 0.004$).

Ostorhinchus ishigakiensis
Harpacticoid copepods dominated the diet of the smaller size class (14.2–19.9 mm SL), whereas shrimps and crabs were significant prey of the larger size class (22.9–44.9 mm SL). The importance of these items in the diet differed significantly between the size classes (Mann–Whitney U test, $P < 0.001$ for harpacticoid copepods, $P = 0.006$ for shrimps).

Siganus fuscescens
The major food item of smaller fish (21.0–51.8 mm SL) was detritus, but this was consumed less by the larger size class (57.6–141.9 mm SL) (Mann–Whitney U test, $P < 0.001$), for which seagrass fronds became the major food item (Mann–Whitney U test, $P < 0.001$).
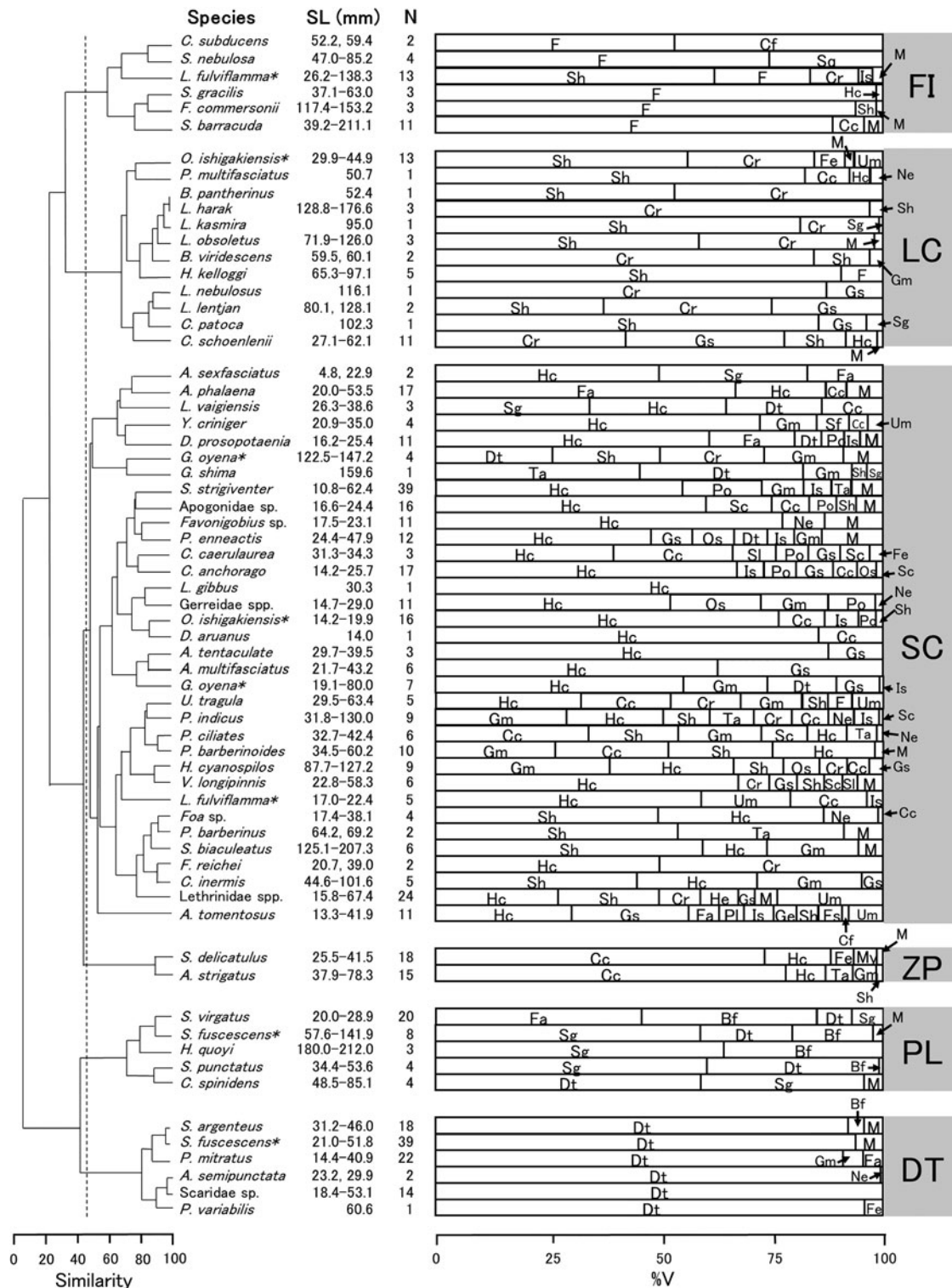
Fig. 2. Dendrogram obtained from dietary overlap data and mean percentage volume of food items (%V) of each fish species. Abbreviations of each food item given in Table 2. M, food items comprising less than 3% of gut content volume of each species. *, fish species showing ontogenetic trophic shifts; N, number of fish examined containing food; SL, standard length. At a similarity index level of 43, the fish assemblage was divided into six trophic groups. FI, fish feeders; LC, large crustacean feeders; SC, small crustacean feeders; ZP, zooplankton feeders; PL, plant feeders; DT, detritus feeders.

Gerres oyena

The diet of smaller fish (19.1–80.0 mm SL) consisted mainly of small crustaceans, such as harpacticoid copepods and gammaridean amphipods. However, harpacticoid copepods decreased with increasing fish body size (Mann–Whitney U test, $P < 0.001$). Shrimps, crabs and detritus were significant dietary components of the larger size class (122.5–147.2 mm SL) (Mann–Whitney U test, $P = 0.042$).

Discussion

Sixty-one fish species occurring in the seagrass bed in Nagura Bay were classified into six trophic groups by the cluster analysis. Of these, ontogenetic trophic shifts were observed in four species (*Lutjanus fulviflamma*, *Ostorhinchus ishigakiensis*, *Gerres oyena* and *Siganus fuscescens*), with smaller individuals feeding on small crustaceans or detritus, and subsequently switching to larger

Table 3. Results of Kruskal–Wallis tests and Holm tests examining differences in the percentage volume value of each major food category among trophic groups

Food categories	df	χ^2	P	Holm test
Fishes	5	366.0	<0.001	Other groups < FI
Large crustaceans	5	212.2	<0.001	Other groups < LC
Small crustaceans	5	318.9	<0.001	Other groups < SC
Zooplankton	5	206.7	<0.001	Other groups < ZP
Detritus	5	440.1	<0.001	Other groups < DT
Plants	5	228.8	<0.001	Other groups < PL

FI, fish feeders; LC, large crustacean feeders; SC, small crustacean feeders; ZP, zooplankton feeders; PL, plant feeders; DT, detritus feeders.

prey items (e.g. crabs, shrimps and seagrass fronds) when attaining larger sizes. Such shifts in food preference in some fishes may result partly from an increase in jaw crushing strength (Wainwright, 1988) or mouth gape size with body growth (Lukoschek & McCormick, 2001).

The most important food items of the seagrass fishes in Nagura Bay comprised harpacticoid copepods, detritus, shrimps and crabs, comprising high cumulative gut volumes in all fishes and high numbers of fish units consuming them. The trophic guilds which mainly consumed the above items also included a large number of units. Previous studies in other tropical/

subtropical and temperate seagrass beds have also shown that a wide variety of fish species feed on small crustaceans (Burchmore et al., 1984; Hanekom & Baird, 1984; Edgar & Shaw, 1995; Horinouchi & Sano, 2000; Kwak et al., 2015). Hence, small crustaceans such as harpacticoid copepods and gammaridean amphipods, are important epiphytic/benthic prey for seagrass fishes. The degree of dependence on larger crustaceans (e.g. shrimps and crabs) as food resources for seagrass fishes differs among regions. For example, Horinouchi et al. (2012), who studied the feeding habits of seagrass fishes in Trang, west coast of Thailand, reported that shrimps were one of the most important food items for the overall fish assemblage, which supports the results of the present study. However, in other studies, there has not been a significant number of seagrass fish species found to feed mostly on large crustaceans, whether in subtropical (Nakamura et al., 2003) or temperate regions (Adams, 1976; Hanekom & Baird, 1984; Horinouchi & Sano, 2000). Although the contribution of detritus to seagrass fish diets has been reported as relatively small in temperate seagrass beds, due to low numbers of detritus-feeding fishes (Livingston, 1982; Burchmore et al., 1984; Hanekom & Baird, 1984; Edgar & Shaw, 1995; Horinouchi & Sano, 2000), detritus was one of the most consumed food items by seagrass fishes in the present study. Similar results have been reported for other tropical/subtropical seagrass beds, including Crystal River, Florida (Carr & Adams, 1973), Trang, west coast of Thailand (Horinouchi et al., 2012), and Amitori Bay, Iriomote Island (Nakamura et al.,

Table 4. Fish species showing diets different from those determined for fishes in other seagrass beds off a nearby neighbouring island (Iriomote Island) (Nakamura et al., 2003) (food items comprising more than 40% of gut content volume of each species in bold)

Species	Nagura Bay in Ishigaki Island			Amitori Bay in Iriomote Island		
	Cymodocea rotundata and *C. serrulate* beds			*Enhaulus acoroides* beds		
	SL	N	Main food items	SL	N	Main food items
Syngnathoides biaculeatus	125.1–207.3	11	**Shrimps**	61–168	15	**Shrimps**, **fishes**
Ostorhinchus ishigakiensis	14.2–19.9	16	**Harpacticoid copepods**	14–38	34	Calanoid copepods, gammaridean amphipods
	29.9–44.9	13	**Shrimps**			
Lethrinus harak	128.8–176.6	3	**Crabs**	87–200	8	**Crabs**, shrimps, hermit crabs, gastropods
Parupeneus barberinus	64.2–69.2	2	**Shrimps**	28–50	13	**Gammaridean amphipods**
				102–144	6	Crabs, isopods, crustacean fragments
Parupeneus ciliatus	32.7–42.4	6	Calanoid copepods, shrimps	30–50	35	Harpacticoid copepods, gammaridean amphipods
				62–98	5	Crabs, shrimps
Cheilio inermis	44.6–101.6	5	**Shrimps**	53–148	43	Gastropods, fishes
Choerodon anchorago	14.2–25.7	17	**Harpacticoid copepods**	17–24	6	Gammaridean amphipods, errant polychaetes
Stethojulis strigiventer	10.8–62.4	39	**Harpacticoid copepods**	10–25	18	**Harpacticoid copepods**
				40–71	24	Gammaridean amphipods, tanaids
Leptoscarus vaigiensis	26.3–38.6	3	Seagrass fronds, harpacticoid copepods	19–60	20	**Detritus**
				97–156	5	**Seagrass fronds**
Petroscirtes mitratus	14.4–40.9	22	**Detritus**	8–37	7	Detritus, filamentous algae
Petroscirtes variabilis	60.6	1	**Detritus**	19–81	12	Detritus, filamentous algae
Siganus fuscescens	21.0–51.8	39	**Detritus**	64–115	11	**Filamentous algae**
	57.6–141.9	8	**Seagrass fronds**			

SL, standard length; N, number of specimens.

2003). In contrast, zooplanktonic prey have been considered a less important food item for seagrass fishes in subtropical regions (Nakamura et al., 2003), again coinciding with the results of the present study, whilst zooplankton have been found to be relatively more important in temperate seagrass beds (Adams, 1976; Livingston, 1982; Horinouchi & Sano, 2000). Hence, greater dietary importance of detritus and lesser importance of zooplankton may be one of the characteristics of seagrass fish diets in tropical/subtropical regions. The mechanisms underlying such food preferences of tropical/subtropical seagrass fishes are unclear, requiring further study.

Twenty-two species collected in Nagura Bay, Ishigaki Island overlapped the seagrass fish assemblages in Amitori Bay, Iriomote Island, a neighbouring island within the Yaeyama Archipelago, with the trophic structure of the former being similar to that in Amitori Bay (Nakamura et al., 2003). However, 12 overlapping species exhibited different diets to those determined in Amitori Bay, most in Nagura Bay feeding mainly on harpacticoid copepods, shrimps or crabs (Table 4). For example, Nakamura et al. (2003) reported that Cheilio inermis (53–148 mm SL) in Amitori Bay fed mostly on gastropods and fishes, whereas similarly sized individuals (44.6–101.6 mm SL) in Nagura Bay consumed mainly shrimps. Similarly sized Choerodon anchorago (17–24 mm SL and 14.2–25.7 mm SL, respectively) fed on gammaridean amphipods in Amitori Bay (Nakamura et al., 2003), and harpacticoid copepods in Nagura Bay, supporting food habits of the species previously determined in Nagura Bay (Fukuoka & Yamada, 2015). The most consumed food items of Leptoscarus vaigiensis (19–60 mm SL and 26.3–38.6 mm SL, respectively) were detritus in Amitori Bay (Nakamura et al., 2003), and seagrass fronds and harpacticoid copepods in Nagura Bay, resulting in the species being allocated to different feeding groups; detritus feeders in Amitori Bay and small crustacean feeders in Nagura Bay. Some species exhibited different patterns in ontogenetic trophic shifts at the above two locations. Stethojulis strigiventer underwent an ontogenetic trophic shift in Amitori Bay, important prey shifting from harpacticoid copepods to gammaridean amphipods and tanaids with fish growth (small size class, 10–25 mm SL; large size class, 40–71 mm SL) (Nakamura et al., 2003). However, a similar shift was not apparent during the present study, both small and large fish (10.8–62.4 mm SL) feeding mostly on harpacticoid copepods. On the contrary, Ostorhinchus ishigakiensis (14–38 mm SL) fed mostly on calanoid copepods and gammaridean amphipods in Amitori Bay (Nakamura et al., 2003), whereas in the present study, the species exhibited a trophic shift; smaller individuals (14.2–19.9 mm SL) consuming mostly harpacticoid copepods, and larger individuals (29.9–44.9 mm SL) feeding on shrimps and crabs. Such differences in overlapping fish species diets suggest that harpacticoid copepods, crabs and shrimps were more readily available food resources for fishes in the present seagrass beds, compared with Amitori Bay.

The differences in food availability at different locations, responsible for the variations in fish feeding habits, may have been determined by differences in habitat complexity and seagrass species. For example, seagrasses with long leaves, such as Enhaulus acoroides (which is dominant in Amitori Bay), often support a large number of small epiphytic crustaceans, including gammaridean amphipods (Nakamura & Sano, 2005). However, epifaunal amphipods may not always be abundant in seagrasses with short leaves (including Cymodocea rotundata in Nagura Bay), because the former often preferentially select seagrasses with high surface area (Stoner, 1980). Subsequently, small infaunal crustaceans, such as harpacticoid copepods, are more likely to be dominant in short-leafed seagrass beds (see Fukuoka & Yamada, 2015). Furthermore, food sources supporting

amphipods have sometimes differed from those for harpacticoids in seagrass systems (Hyndes & Lavery, 2005), indicating different trophic pathways to fish feeding on them. The impacts of seagrass bed characteristics (e.g. habitat complexity and seagrass species) and prey abundance on fish food-use patterns should be considered in future studies.

The present study revealed that feeding habits of seagrass fishes can vary on a small local scale, even between adjacent islands within the Yaeyama Archipelago. The food habits of some species were restricted, whilst the diets of other species were more varied, which may be related to habitat dependence of each species. More varied diets may increase the adaptability of some species to seagrass beds characterized by significant variations in available food resources. In fact, differences in major fish food resources imply differences in the food web structure supporting fish production. The analyses of fish food use patterns, therefore, should contribute to our understanding of the mechanisms underlying fish production and diversity supported by seagrass beds.

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