FISHERIES SCIENCE 2004; **70**: 1019–1035

The food habits of four species of triakid sharks, *Triakis scyllium*, *Hemitriakis japanica*, *Mustelus griseus* and *Mustelus manazo*, in the central Seto Inland Sea, Japan

Satoru KAMURA* AND Hiroaki HASHIMOTO

Graduate School of Biosphere Science, Hiroshima University, Higashi-Hiroshima, Hiroshima, 739-8528, Japan

ABSTRACT: The food habits of 595 houndsharks of four species, *Triakis scyllium* ($n = 179$, 42–148 cm total in length), *Hemitriakis japanica* ($n = 57$, 42–102 cm), *Mustelus griseus* ($n = 193$, 39–100 cm), and *Mustelus manazo* ($n = 166$, 43–120 cm), found in the central Seto Inland Sea, Japan, from March 1997 to October 1999 and May 2000 to July 2002, were studied. *T. scyllium* changed their main food items from shrimps to echiuran worms then to cephalopods with their growth. Comparing food habits by the value of similarity (maximum = 1), the small-sized *T. scyllium* had a low value (0.17) compared to larger sharks. *T. scyllium* gradually increased the diversity of food until it reached 700 mm long in total length, however, after that it decreased. *H. japanica* appeared mainly in summer and autumn and ate cephalopods and fishes. *M. griseus* preyed on various crustaceans and decreased the diversity of food with growth. *M. manazo* preferred crustaceans and polychaetes. There was no certain tendency in the diversity of the food habit for *M. manazo*.

KEY WORDS: **diet, food habit, *Hemitriakis japanica*, *Mustelus griseus*, *Mustelus manazo*, prey diversity, Seto Inland Sea, *Triakis scyllium*.**

INTRODUCTION

Houndsharks of the family Triakidae abound on the coast of the subtropical and temperate seas along the coast of Japan,[1] and five species of four genera have been caught by small trawlers, gill-nets or long lines in various regions of the Hokkaido coast and southward. Though these sharks are often regarded as accidental catches with low commercial values, in some regions of Japan they are ordinarily consumed or treated as a ritual food item.[2] In contrast, sharks are one of the important members of the marine ecosystem,[3] so it is indispensable to understand their biological characteristics well for the preservation of ecologic diversity. In previous biological studies of houndshark species in the coastal seas of Japan, some ontogenetic differences have been clarified with detailed investigations of age and growth, reproduction, and food habits for *Mustelus manazo*, Bleeker 1854 at various locations, including Taiwan.[4–13] The growth and reproduction of *M. griseus*, Pietschmann 1908 from Shimonoseki, at the southern point of Honshu Island and Taiwan also have been examined.[6,14,15] There are a few reports about growth and reproduction of *Hemitriakis japanica* Müller et Henle 1839.[16,17] Concerning *Triakis scyllium*, Müller et Henle 1839, only one report has been published at the zostera bed in Mihara in the central Seto Inland Sea.[18] However, it is still insufficient to understand their biological characteristics because most previous studies concentrated on growth or reproduction. Therefore, it is necessary to obtain more biological information on these shark species and to assess their ecologic niche in order to maintain a marine ecosystem compatible with sustainable fishing. The objectives of this study were to investigate the food habits of four species of triakid sharks, *T. scyllium*, *H. japanica*, *M. griseus* and *M. manazo*, being comparatively abundant and caught commercially in the western Hiuchi Nada, the central Seto Inland Sea, almost all year round for human consumption or for fishing bait, and to supply some information to reveal their ecologic role in semi-enclosed shallow sea areas like the Seto Inland Sea.

*Corresponding author: Tel: 81-82-424-7975.
Fax: 81-82-424-7906. Email: kamra@hiroshima-u.ac.jp
Received 10 November 2003. Accepted 21 June 2004.

MATERIALS AND METHODS

Our study site was located in the western Hiuchi Nada Sea, Seto Inland Sea. Most of this area is less than 40 m in depth, with a mainly sandy/muddy bottom. Sand grain size becomes gradually larger toward the Kurushima Channel of the western area of the Hiuchi Nada Sea. Plenty of dissolved oxygen is kept because of the intensity of the tidal current there.[19]

During March 1997 to October 1999 and May 2000 to July 2002, every month we obtained *T. scyllium*, *H. japanica*, *M. griseus* and *M. manazo* sharks for examination from the Imabari Fish Market, Ehime Prefecture, where marine products are mainly caught by shallow-bottom trawlers that operate from 17:00 hours to 03:00 hours. Collected sharks in this period totaled 809 individuals, which consisted of 232 *T. scyllium*, 80 *H. japanica*, 275 *M. griseus* and 222 *M. manazo*, respectively (Table 1). Most *H. japanica* were caught in summer and autumn. However, the other species, *T. scyllium*, *M. griseus* and *M. manazo*, were caught throughout the year with some fluctuation in catches; *M. griseus* was significantly abundant from June to December compared with other months (t-test; $p < 0.01$) and *M. manazo* less in May to October than in other months (t-test; $p < 0.01$).

The sharks were packed in ice immediately and taken to the laboratory where their total length (TL; mm) and body weight (BW; to the nearest 0.1 g) were measured. We computed the weight of stomach contents by extracting the weight of the stomach tube. The individuals with empty stomachs were excluded from the following examinations. The percentage of the stomach contents weight per body weight exclusive of gut, liver and gonad (fullness index; *FI*) in each species was calculated. Except for specimens taken in 1997, which were used for the preliminary examination, the stomach contents were sorted and identified visually and/or microscopically to the species level as possible. Each food of prey was counted and weighed in wet condition to the nearest 0.01 g. Stomach contents were examined in 179 *T. scyllium* (size range, 42–148 cm TL), 57 *H. japanica* (42–102 cm TL), 193 *M. griseus* (39–100 cm TL), and 166 *M. manazo* (43–120 cm TL).

To compare the food habits of shark species quantitatively, we used percentage frequencies of occurrence (%*F*), percentage numbers (%*N*) and percentage weights (%*W*) of their prey items, which were calculated by the following equations.

%*F* = (the number of sharks preying on a particular food item)100/(all)

%*N* = (the number of particular prey in diet)100/(the sum of the number of prey in diet)

%*W* = (the weight of particular prey in diet)100/(the sum of the weight of prey in diet)

We calculated Whittaker's percentage of similarity (*PS*)[20] to compare the changes of food habits by season and size classes in each species. *PS* is expressed between two groups *a* and *b* as follows:

$$PS = 1.0 - 0.5\Sigma(i)(Pai - Pbi)$$
$$= \Sigma(i)\min(Pai - Pbi)$$

Where, *Pai* is %*W* of a certain prey item *i* preyed on by species *a*, and *Pbi* is %*W* of the same prey *i* preyed on by species *b*. The closer *PS* value approaches 1, the more similar the food habits of

Table 1 Monthly number of specimens of houndsharks, family Triakidae, caught off Imabari during March 1997 to October 1999 and May 2000 to July 2002

Species name	Sex	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Sum
Triakis scyllium	M	9	12	12	11	9	4	7	10	2	6	7	24	118
	F	5	20	12	13	9	4	11	8	2	7	9	19	119
	Sum	14	32	24	24	18	8	18	18	4	13	16	43	232
Hemitriakis japanica	M	1				2	8	3	7	2	6	22	2	53
	F						3	6	4	2	7	4	1	27
	Sum	1				2	11	9	11	4	13	26	3	80
Mustelus griseus	M	4	1	3	7	9	17	21	24	13	21	14	10	144
	F	2	1	1	9	4	17	13	18	16	26	17	7	131
	Sum	6	2	4	16	13	34	34	42	29	47	31	17	275
Mustelus manazo	M	5	10	5	22	10	9	5	10	3	3	8	10	100
	F	14	8	14	16	8	3	11	9	3	5	16	15	122
	Sum	19	18	19	38	18	12	16	19	6	8	24	25	222

the two shark groups are. Conversely, the more it approaches 0, the greater the difference between them become. Each food category was classified into high levels of classification such as crabs and shrimps. To analyze the food habits of sharks for body size and season, five size classes were identified: 500 mm TL or below, 501–600 mm TL, 601–700 mm TL, 701–800 mm TL, and 801 mm TL or over, and four seasons were identified: spring (March – May), summer (June – August), autumn (September – November), and winter (December – February). We noticed *%W* because it is considered the most important index for analysis of their energy accounts of the three equations.

To investigate the difference of the diversity of the shark's food habits among size classes, we calculated the evenness (J') using Shannon–Wiener's diversity index (H') shown as the following formula:[12]

$$J' = H' / \log_2 S$$

Where, J' is an index of constancy in their food habits. The closer to 0 the values show, the more unbalanced food habits they have and, oppositely, the closer to 1, the wider the food habits. H' is the relative diversity of their food habits:

$$H' = \Sigma Si \times \log_2 Si$$

Where, Si is the ratio of the number S of their prey category i to the sum of the number of prey.

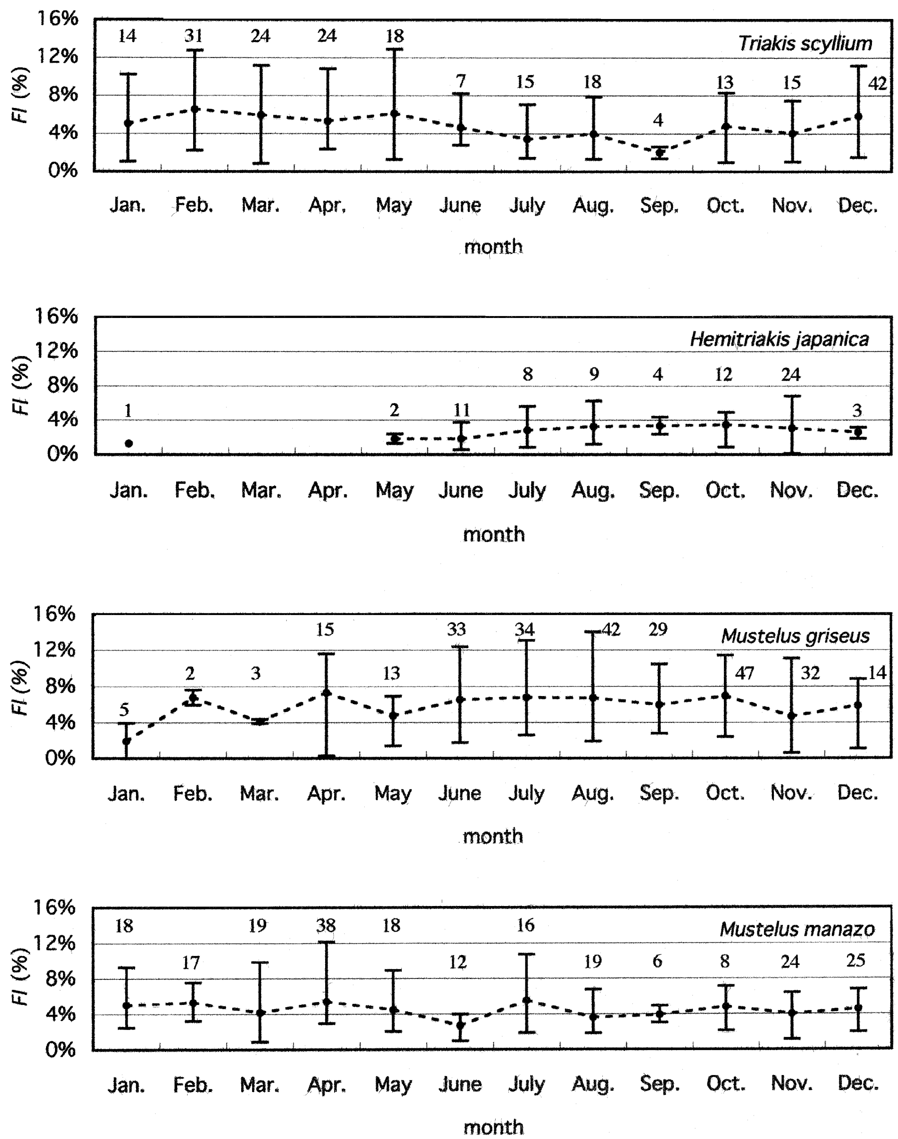

Fig. 1 Monthly changes of fullness index (*FI*) of houndsharks, family Triakidae, caught off Imabari, excepting those with empty stomachs. Closed circles show mean values with the ranges minimum to maximum (vertical bar), and the number of fish examined (figures above circles).

Table 2 Diet composition of *Triakis scyllium* caught off Imabar

Triakis scyllium (*n* = 172)		Empty = 3.91%		
		%*F*	%*N*	%*W*
Crustactions		**90.12**	**48.23**	**21.77**
Crabs		29.65	4.33	1.08
Xanthoidae	spp.	1.16	0.09	0.01
Portunidae	*Portunus hasraroides*	1.16	0.09	0.14
	Chabrybdis bimaculata	1.74	0.22	0.09
	Liocarcinus corragatus	1.74	0.13	0.07
	sp.	0.58	0.04	0.02
Cancridae	*Cancer gibbosurus*	15.12	1.70	0.32
	sp.	0.58	0.04	0.01
Parthenopidae	*Parthenope valida valida*	0.58	0.04	0.02
Majidae	*Hystenus diacanthus*	0.58	0.04	0.00
	Hyastenus elongarus	0.58	0.04	0.01
Leucosiidae	sp.	0.58	0.04	0.01
Drippcidae	*Nobitum japonicum japonicum*	0.58	0.04	0.00
	sp.	0.58	0.04	0.00
Dromiidae	sp.	0.58	0.04	0.00
Unidentified		11.05	1.70	0.38
Shrimps		76.16	37.40	17.31
Scyliaridac	*Scyllarus cultrifer*	1.74	0.13	0.14
Crangonidae	*Crangon affinis*	4.65	0.52	0.20
	spp.	1.74	0.13	0.01
Hippolytidae	*Eualus sinensis*	1.16	0.17	0.06
	Latreates planirostris	1.74	0.17	0.01
	Lysmata vittatu	0.58	0.04	0.00
Ogyrididae	*Ogyrides orientalis*	1.16	0.09	0.00
	Ogyrides striatioauda	0.58	0.04	0.00
Alpheidae	*Alpheus bisincisus*	1.16	0.22	0.12
	Alpheus japonicus	0.58	0.04	0.00
	Alpheus edwardsii	0.58	0.04	0.02
	spp.	15.12	1.97	0.28
Palamonidae	*Palaemon pacificus*	2.91	1.66	0.93
	Palaemon serrifer	13.37	3.98	1.58
	Palaemon gravieri	9.30	1.66	0.64
	Palaemon spp.	8.14	2.01	0.45
Pasiphaeidae	*Leptochela gracilis*	20.35	6.38	0.52
	Pasiphaea sivedo	0.58	0.04	0.03
Penaeidae	*Penaeus japonicus*	0.58	0.04	0.20
	Trachypenaeus lurvirostris	13.37	1.62	3.57
	Trachypenaeus sp.	1.74	0.44	0.18
	Metapenaeopsis lamellata	3.49	0.31	0.25
	Metapenaeopsis barbata	4.07	0.61	0.39
	Metapenaeopsis acclivis	1.74	0.17	0.42
	Metapenaeopsis dalei	2.91	0.31	0.17
	Metapenaeopsis spp.	4.07	0.48	0.12
	spp.	4.07	0.61	0.27
Unidentified		50.58	13.50	6.76
Hermit crabs		20.93	3.23	1.95
Galathoidae	*Galathea pubescens*	0.58	0.04	0.00
Dioganidae	*Diogenes edwardsii*	2.91	0.22	0.20
	Coratopagurus pilosimanus	0.58	0.09	0.11
Unidentified bermit crabs		4.07	0.31	0.10
Upogebiidae	*Upogebia major*	12.79	2.05	1.38
Callianassidae	*Callianassa petalura*	2.91	0.26	0.08
	Callianassa japonica	0.58	0.04	0.01
	Callianassa spp.	2.91	0.22	0.07
Mantis shrimps		4.07	0.52	0.10
Squillidae	*Anchisquilla fasciata*	1.16	0.17	0.06

Table 2 *Continued*

Triakis scyllium (*n* = 172)		Empty = 3.91% %*F*	%*N*	%*W*
	Lophosquilla costaia	0.58	0.04	0.01
	spp.	3.49	0.31	0.02
Isopods	sp.	0.58	0.04	0.00
Mysids	*Gastrosaccus kojimaensis*	1.16	0.13	0.00
Crustaceans fragments		16.86	2.58	1.32
Polychaetes		**58.72**	**12.67**	**7.87**
Echiorans		**47.09**	**16.03**	**18.35**
Urcchidae	*Urechis anicinctus*	32.56	10.31	11.71
Thalassentatidae	*Ikedosoma gogoshimense*	8.14	2.10	2.88
Unidentified		17.44	3.63	3.76
Sipuncalums		29.65	10.53	5.80
Cephaloptods		**41.86**	**8.30**	**38.64**
Sepiidae	sp.	0.58	0.04	0.01
Sepioiidae	*Euprymna morsei*	0.58	0.05	0.09
Unidentified squids		7.56	1.14	2.04
Octopodidae	*Octopus vulgaris*	2.91	0.22	16.08
	Octopus minor	4.07	0.31	4.94
	Octopus murilans	1.74	0.17	2.66
Unidentified octopus		6.98	1.09	6.50
Octopus larvse		0.58	1.14	0.05
Unidentified		25.58	4.11	5.70
Ascidiaceans		12.21	2.75	2.69
Fishes		**10.47**	**1.27**	**5.11**
Eiasmobranohii	*sp.*	0.58	0.04	0.03
Congridae	*Conger myriaster*	0.58	0.04	0.45
Clupeidae	*Sardinopus melanostictus*	0.58	0.04	0.21
	Konosirus punctatus	0.58	0.09	0.09
Engraulidae	*Engraulis japanicus*	0.58	0.17	0.05
Platycephalidae	sp.	0.58	0.04	0.07
Carangidae	*Trachurus japonicus*	1.16	0.09	0.72
Haemulidae	*Hapalogenys mucronutus*	0.58	0.04	0.48
Sciaenidae	*Pennahia argentata*	0.58	0.17	0.53
Pleuronectiformes	sp.	0.58	0.04	0.08
Cynoglossidae	*Cynoglossus robustus*	0.58	0.04	0.32
Unidentified		5.81	0.44	2.07
Unidentified		2.91	0.22	0.36

n, number of stomachs in which at least one prey occurs; %*F*, frequencies of occurrence; %*N*, percentage numbers; %*W*, percentage weights.

RESULTS

There were seven, six, six and two individuals with empty stomachs for *T. scyllium* (3.91%), *H. japanica* (10.53%), *M. griseus* (3.11%), and *M. manazo* (1.20%), respectively. The *FI* rarely exceeded 10% in every individual, but that of *M. griseus* showed the highest average (6.19%) and the highest maximum (14.06%) value of all shark species (Fig. 1). *T. scyllium* averaged 5.27% (max. 12.85%), *M. manazo* 4.58% (12.16%) and *H. japanica* 2.84% (6.81%). Monthly changes in *FI* of *T. scyllium* showed a lower tendency in July to November than other months (*t*-test; p <0.001). There was no significant change in *FI* of *H. japanica* by month (ANOVA; $F_{8,64} = 1.768$, $p > 0.1$). While *FI* of *M. griseus* slightly decreased between November and March (*t*-test, p <0.001), that of *M. manazo* showed no certain tendency.

Triakis scyllium

T. scyllium ate various types of food items which were the infaunal benthos such as echiuran worms, epifaunal benthos such as shrimps, and nekton such as cephalopods, dwelling near the sea bottom (Table 2). Of all the prey items, *Urechis unicinctus* was taken in the greatest *%N* as a single prey species (10.31%). Some shrimps, like *Lep-*

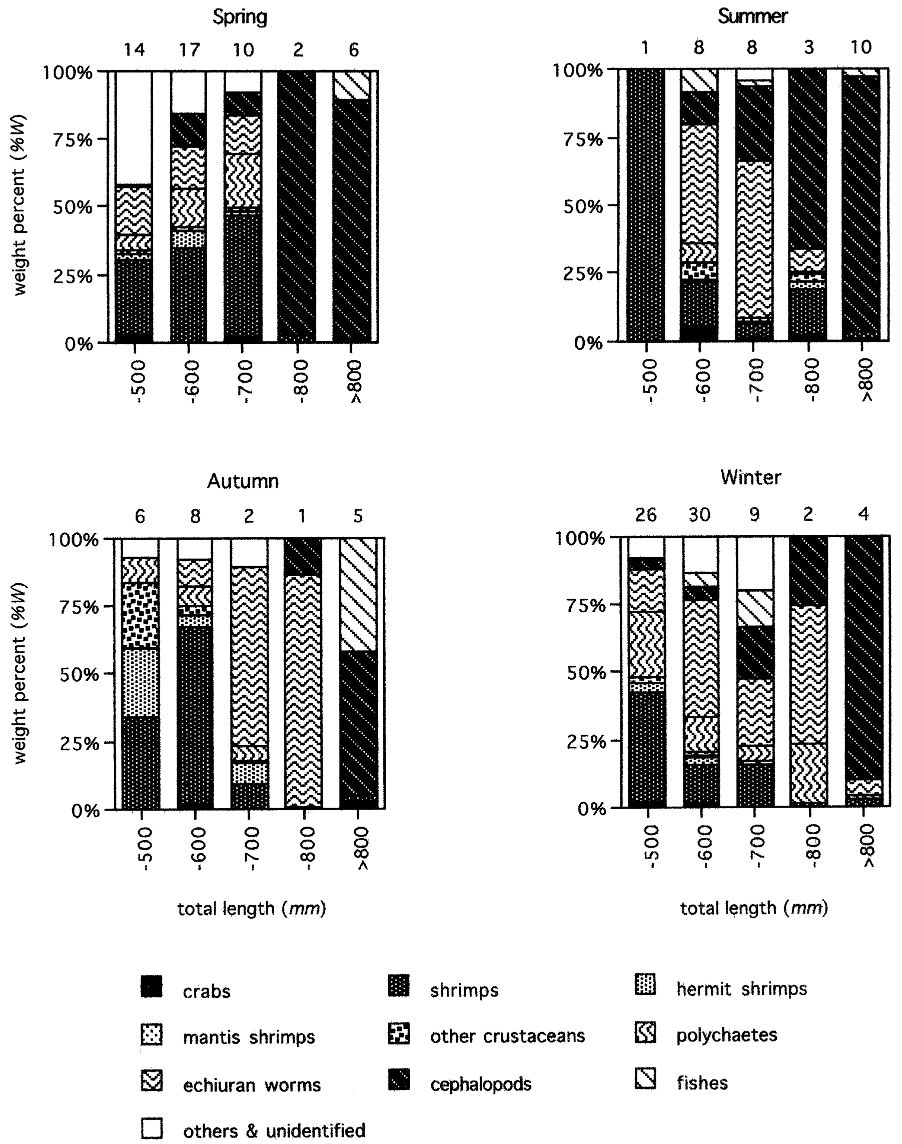

Fig. 2 Seasonal diet change in weight percent (*%W*) by size classes (total length, mm) of *Triakis scyllium* caught off Imabari. The figure above each bar is the number of fish examined.

tochera gracilis (%N = 6.38%, %W = 0.52%), *Palaemon serrifer* (3.98%, 1.58%), and *Trachypenaeus curvirostris* (1.62%, 3.57%) were also important prey items, and shrimps were the most remarkable category with the highest *%N* (37.40%). Cephalopods had the highest *%W* (38.04%) and *Octopus vulgaris* occurred most plentifully as a single prey species (*%W* = 16.08%). Comparing food habits in *%W* by seasons, all *PS* values between each sample, which had at least three specimens, showed over 0.35 (Fig. 2). Establishing 0.33 as a standard, whether a significant difference or not, for the above values would be no serious difference. However, some changes were shown up in TL classes (Fig. 3a). Shrimps were found numerously in the stomachs of sharks 700 mm TL or less, but decreased abruptly from those of 701 mm TL or more. Echiuran worms were taken well by *T. scyllium* of size categories of the 800 mm TL or less, but seldom appeared in the stomachs of individuals over 800 mm TL. In contrast, cephalopods started to appear in the stomachs of 501–600 mm TL sharks in spring and summer, and increased greatly over 700 mm TL in all seasons (Fig. 2). When we divided the smaller individuals (700 mm TL or less) and the larger ones (701 mm TL or more) because of some differences between the *PS* values below 700 mm TL and over 700 mm TL (most of $PS < 0.35$), a great significant difference between both was shown ($PS = 0.17$).

Hemitriakis japanica

H. japanica preyed on a large amount of nektons such as cephalopods and fish dwelling near

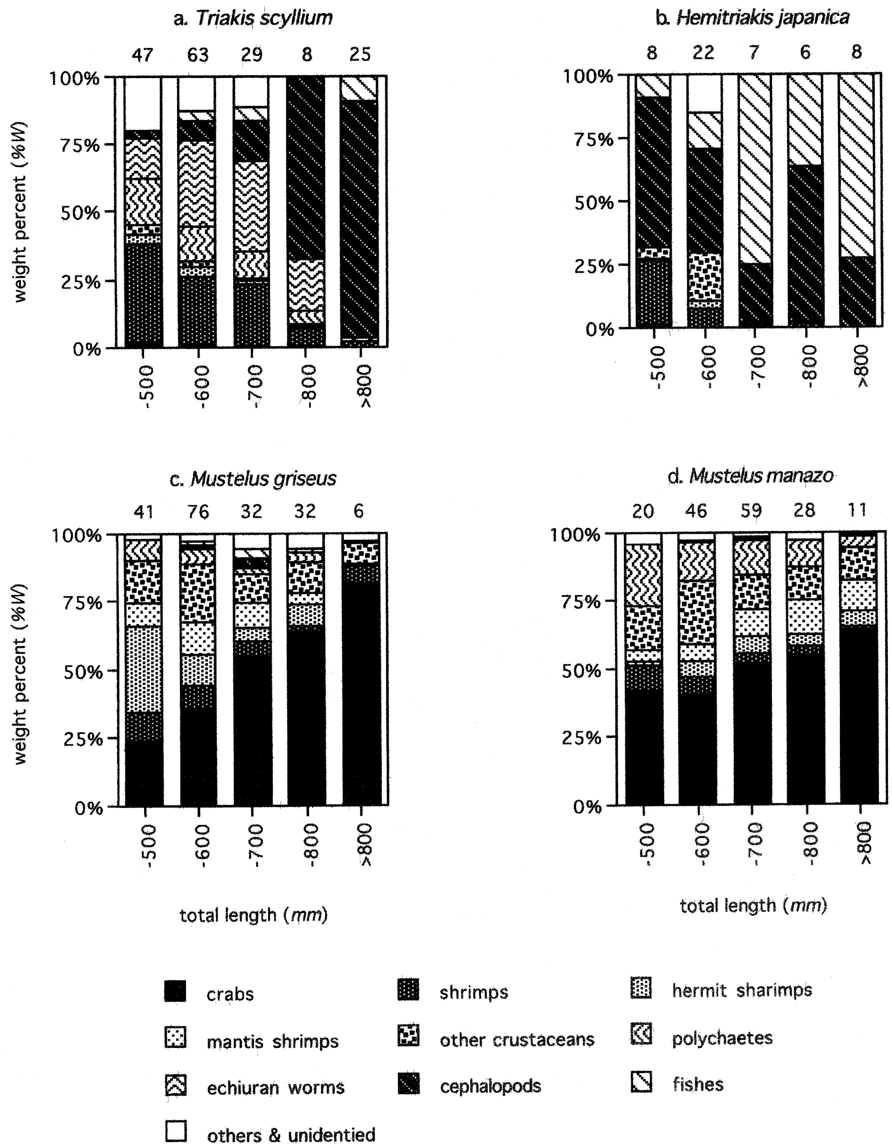

Fig. 3 Diet change by TL class of (a) *Triakis scyllium*; (b) *Hemitriakis japanica*; (c) *Mustelus griseus*; and (d) *M. manazo*, caught off Imabari. The figure above each bar is the number of fish examined.

the bottom (Table 3). Cephalopods were the most important prey category (%N = 39.60%, %W = 52.29%). We could commonly observe fish like *Cryptocentrus filifer*, Gobiidae spp., *Amoglossus tenuis* and so on, but the values in fish as one category, %N = 30.20% and %W= 36.82%, were not greater than cephalopods. Most of crustaceans were as small as *L. gracilis* and they were only important quantitatively (%W = 9.20%). It would be too hasty to conclude whether the food change with growth might occur between the border with 600 mm TL (Fig. 3b) because sample numbers were insufficient to compare in winter and spring. In the same way, there was no clear tendency in *PS* with season (Fig. 4). It could safely be said that cephalopods were considered important regardless of their TL classes based on results in summer and winter.

Mustelus griseus

M. griseus preyed a lot on epifaunal benthos like various crustaceans (%N = 86.29%, %W = 89.04%); *Portunus hastatoides* (3.91%, 8.68%), *L. gracilis* (9.2%, 1.5%), *Diogenes edwardsii* (3.82%, 6.56%), *Cancer gibbosulus* (4.00%, 2.88%), and *Anchisquilla fasciata* (3.82%, 2.78%) as shown in Table 4. In Fig. 5, there was no serious difference of food habits by season (all $PS > 0.40$). Many crabs were found in the stomachs of sharks of all TL classes (Fig. 3c), and crustaceans including crabs amounted to about 70% in %W in all TL classes, so

Table 3 Diet composition of *Hemitriakis japanica* caught off Imabari

Hemitriakis japanica ($n = 51$)		Empty = 10.53%		
		%F	%N	%W
Crastaceaus		**49.02**	**27.52**	**9.20**
Crabs		3.92	1.34	0.49
Unidentified		3.92	1.34	0.49
Shrimps		1.57	13.42	5.57
Hippolytidae	*Latreutes planirosiris*	1.96	0.67	0.03
Ogyrididae	sp.	1.96	1.34	0.02
Alpheidae	sp.	1.96	0.67	0.01
Palamogidae	*Palqemon gravleri*	1.96	0.67	0.41
Pasiphaeidae	*Leptochele gracilis*	5.88	4.03	0.20
Penaeidae	*Trachypenaeus curvirostris*	1.96	0.67	1.62
	Metapenaeopsis acclivis	1.96	0.67	0.44
Unidentified		9.80	4.70	2.85
Hermit crabs		7.84	2.68	0.43
Upogebiidae	*Upogebia major*	3.92	1.34	0.17
Callianassidae	*Callianassa* spp.	3.92	1.34	0.26
Isopods	sp.	1.96	0.67	0.01
Mysids		5.88	2.01	0.02
Mysidae	*Neomysis interrnidia*	1.96	0.67	0.00
	Neomysis japonica	1.96	0.67	0.01
	sp.	1.96	0.67	0.01
Crustaccans fragments		21.57	7.38	2.69
Polychaetes		**3.92**	**1.34**	**0.08**
Cophalopods		**68.63**	**39.60**	**92.29**
Unidentified squids		21.57	10.07	9.35
Unidentified octopus		9.80	3.36	39.23
Unidentified		37.25	26.17	3.71
Fishes		37.25	30.20	36.82
Clupeiformes	sp.	1.96	2.01	0.04
Engraulidae	*Engraulis japonicus*	1.96	0.67	0.96
Sciaenidae	*Atrobucca nibe*	1.96	0.67	1.18
Goblidae	*Cryptacentrus filifer*	3.92	2.01	7.93
	spp.	3.92	2.68	6.33
Pleuronectiformes	spp.	3.92	1.34	0.50
Bothidae	*Amoglossus tenuis*	1.96	0.67	1.78
Unidentified		29.41	20.13	18.11
Unidentified		3.92	1.34	1.63

n, number of stomachs in which at least one prey occurs; %*F*, frequencies of occurrence; %*N*, percentage numbers; %*W*, percentage weights.

that it was expected they were an important shark food item. Despite an increasing tendency on the level of crabs with growth (Fig. 3c), *PS* showed high values between adjacent TL classes (all $PS > 0.70$), so sharks did not generally change food items.

Mustelus manazo

M. manazo took crawling benthos like crustaceans such as *C. gibbosulus* (%N = 6.91%, %W = 5.60%), *P. hastatoides* (3.32%, 12.85%), and *Liocarcinus corrugatus* (2.98%, 7.33%), and also fed on more polychaetes (25.69%, 10.96%; Table 5) than other shark species mentioned previously. Food habits of *M. manazo* seldom changed between each sample, which had at least three specimens, regardless of season (all $PS > 0.40$: Fig. 6). The amount of crabs taken tended to increase with TL (Fig. 3d) but all *PS* values between TL classes were above 0.67, moreover, many values were beyond 0.80, suggesting that their food habit was fixed regardless of TL class.

Table 6 shows the diversity in food habits of the four houndsharks. The most constant average value was in *T. scyllium* (0.72), followed by *H. japanica*, *M. griseus* (0.68, both), and *M. manazo* (0.62). The constancy of *T. scyllium* gradually increased until 700 mm TL, when they

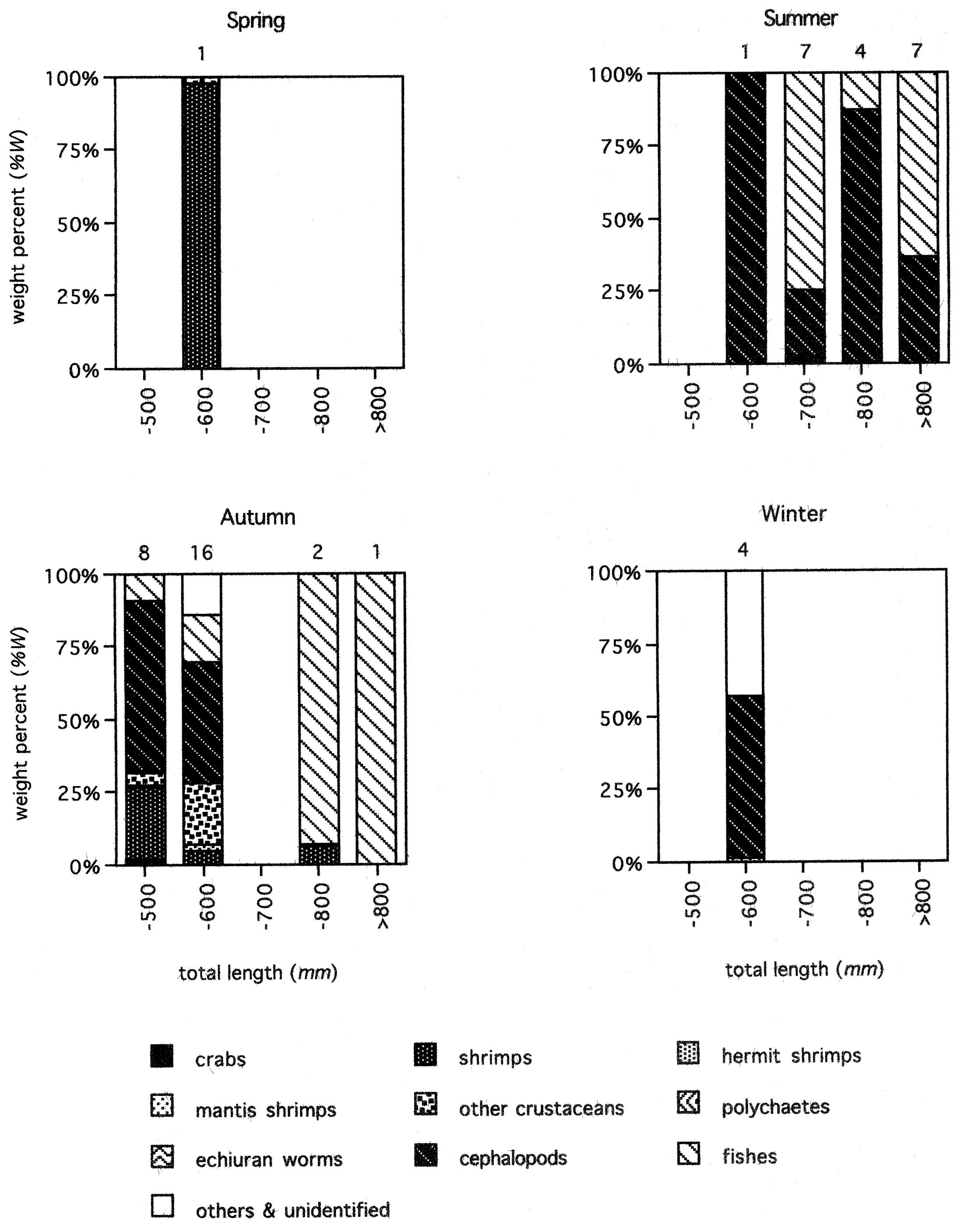

Fig. 4 Seasonal diet change in weight percent (%*W*) by size classes (total length, mm) of *Hemitriakis japanica* caught off Imabari. The figure above each bar is the number of fish examined.

changed prey, and the diversity tended to decrease in 701 mm TL or more. There was no certain tendency in the diversity of *H. japanica* and *M. manazo*, but there was a clear tendency in *M. griseus* to decrease the diversity with the growth.

DISCUSSION

Sharks are generally considered to be nocturnal[21] and if each species in this study preyed actively at night when fishing took effect, it would be pertinent to result in the relative low proportion of indi-

Table 4 Diet composition of *Mustelus griseus* caught off Imabari

Mustelus griseus (*n* = 187)		Empty = 3.11%		
		%*F*	%*N*	%*W*
Crastaceans		**98.93**	**86.29**	**89.04**
Crabs		80.21	36.65	50.82
Pimotheridae	*Pinnotheres pholadis*	0.53	0.04	0.02
	Astenognathus inaequipes	0.53	0.04	0.02
Xanthoidae	*Halomede fragifera*	1.07	0.09	0.39
	Sphaerozius nitidus	0.53	0.04	0.02
	spp.	2.67	0.45	0.32
Hexapodidae	*Hexapinus lanpes*	0.53	0.04	0.01
Goncplacidae	*Eucrate crenata*	1.07	0.18	0.13
Portunidae	*Portunus gladiator*	0.53	0.09	0.40
	Portunus hastatoides	9.25	3.91	8.68
	Chabrybdis variegata	8.56	1.75	5.41
	Chabrybdis bimaculata	1.23	2.29	7.12
	Chabrybdis sp.	0.53	0.04	0.01
	Liocarcinus corrugatus	6.95	1.26	2.10
	Lissocarcinus laevis	0.53	0.13	0.25
	spp.	2.67	031	0.09
Cancridae	*Cancer gibbosulus*	8.72	4.00	2.88
Parthenopidae	*Parthenope valida valida*	4.28	0.94	1.70
	sp.	0.53	0.04	0.01
Majidae	*Hystenus diacanshus*	0.53	0.09	0.44
Leucosjidae	*Narsia japonica*	0.53	0.04	0.01
	spp.	4.81	0.76	0.18
Drippoidae	*Paradrippe granulata*	6.42	0.94	2.73
	spp.	2.67	0.31	0.40
Unidentified		51.34	18.79	17.51
Shrimps		51.87	17.49	5.97
Crangonidae	*Crangon affinis*	5.88	0.58	0.30
	sp.	0.53	0.09	0.00
Hippolytidae	*Latrentes planivastris*	2.14	0.31	0.03
	Lysmata vitrata	0.53	0.04	0.02
Ogyrididae	*Ogyrides orientalis*	2.14	0.18	0.02
	Ogyrides striaticauda	0.53	0.04	0.01
Alpheidae	*Alpheus brevicristatus*	0.53	0.09	0.04
	Alpheus distinguendus	0.53	0.04	0.06
	Alpheus bisincisus	1.07	0.36	0.13
	Alpheus japonicus	1.07	0.13	0.09
	spp.	13.37	1.35	0.38
Palamonidae	*Palaemon serrifer*	2.14	0.27	0.17
	Palaemon spp.	1.60	0.13	0.10
Pasiphaeidae	*Leptochela gracilis*	20.86	9.17	1.50
Penaeidae	*Trachypenacus curvirostris*	3.21	0.27	0.37
	Metapenaeus ensis	0.53	0.04	0.03
	Metapenaeopsis lamellata	0.53	0.04	0.10
	Metapenaeopsis dalei	2.14	0.22	0.49
	Metapenaeopsis sp.	1.07	0.13	0.03
	sp.	0.53	0.04	0.08
Unidentified		25.13	3.91	2.02
Hermit crabs		45.99	8.68	10.57
Galatheidae	*Galathea pubescens*	2.14	0.49	0.03
Diogenidae	*Diogenes edwardsii*	17.11	3.82	6.56
	unidentified hermit crabs	21.39	2.61	1.27
Upogebiidae	*Upogebia major*	8.56	1.08	2.00
Callianassidae	*Callianassa petabura*	2.67	0.40	0.28
	Callianasso japonica	0.53	0.04	0.27
	Callianassa spp.	2.14	0.22	0.15

Table 4 *Continued*

Mustelus griseus (*n* = 187)		Empty = 3.11%		
		%*F*	%*N*	%*W*
Mantis shrimps		41.18	8.86	7.58
Squillidae	*Anchisquilla fasclata*	18.18	3.82	2.78
	Laphosquilla costata	17.65	2.79	3.56
	Oratosquilla oratoria	3.21	0.31	0.51
	spp.	2.83	1.93	0.73
Isopods		2.14	0.36	0.11
Idoteidae	*Cleantoides planicauda*	0.53	0.04	0.00
	spp.	2.14	0.31	0.10
Mysids		1.07	0.13	0.00
Mysidae	*Gastrosaccus kojinaensis*	0.53	0.09	0.00
	sp.	0.53	0.04	0.00
Crastaceans fragments		51.87	14.12	14.00
Polychaetes		**53.48**	**8.77**	**3.75**
Echiurans		**3.74**	**0.31**	**0.57**
Urechidae	*Urechis unicinetus*	2.14	0.18	0.39
Unidentified		1.60	0.13	0.18
Sipunculans		9.63	1.53	2.73
Btyalves		0.53	0.04	0.09
Cephalopods		3.21	0.54	0.91
Sepiidae	sp.	1.07	0.18	0.35
Sepiolidae	*Euprymna morsei*	0.53	0.09	0.19
Ommastrephidae	*Sthenoteuthis oualaniensis*	0.53	0.04	0.10
Unidentified squids		2.14	0.18	0.07
Unidentified		0.53	0.04	0.20
Ophiuroideans		0.53	0.04	0.02
Crinoideans		0.53	0.04	0.00
Ascidiuceans		3.21	0.85	1.28
Fishes		**4.44**	**1.53**	**1.57**
Carangidae	sp.	0.53	0.04	0.01
Callionymidae	sp.	0.53	0.04	0.16
Pleuronectifrmes	sp.	0.53	0.04	0.14
Bothidae	*Amoglossus tenuis*	1.60	0.13	0.32
Unidentified		2.30	1.26	0.93
Unidentified		0.53	0.04	0.02

n, number of stomachs in which at least one prey occurs; %*F*, frequencies of occurrence; %*N*, percentage numbers; %*W*, percentage weights.

viduals with empty stomachs. *T. scyllium* caught around the zostera bed at the Mihara Channel were approximately 200 mm in body length and preyed on polychaetes amounting to 60% of diet in quantity.[18] During our investigation, polychaetes amounted to merely 16.67%*W* of the diet in individuals below 500 mm TL (Fig. 3a). Further study will be required to explain what caused this difference, for the detailed fishing location in this study was indistinct. The studies on *T. megalopterus*[22] and *T. semifasciata*,[23–25] genus *Triakis*, showed a tendency to prey on crustaceans dwelling near the bottom, echiuran worm, *Urechis caupo*, and cephalopods. Both *T. megalopterus* and *T. semifasciata* species changed prey with their growth; crustaceans to cephalopods and then to fish in the diet of *T. megalopterus*,[22] and crabs to echiuran worms and fish in the diet of *T. semifasciata*,[24,25] which coincide with our results (Fig. 3a). It is assumed that the genus *Triakis* improves, with body growth, the ability to chase and seize larger and more mobile prey such as cephalopods or fish. Diversity of diet (Table 6) suggests that *T. scyllium* can utilize more variety of prey such as shrimps and echiuran worms, extending their prowling range as they grow, and then tending to specialize in cephalopods when over 700 mm TL. Also, they preyed on *Palaemon serrifer* and *P. gravieri* inhabiting estuaries,[26,27] so it seemed that the smaller *T. scyllium* prowls around estuaries to forage shrimps as well as *T. semifasciata* that commonly live in inland seas influenced by rivers.[28]

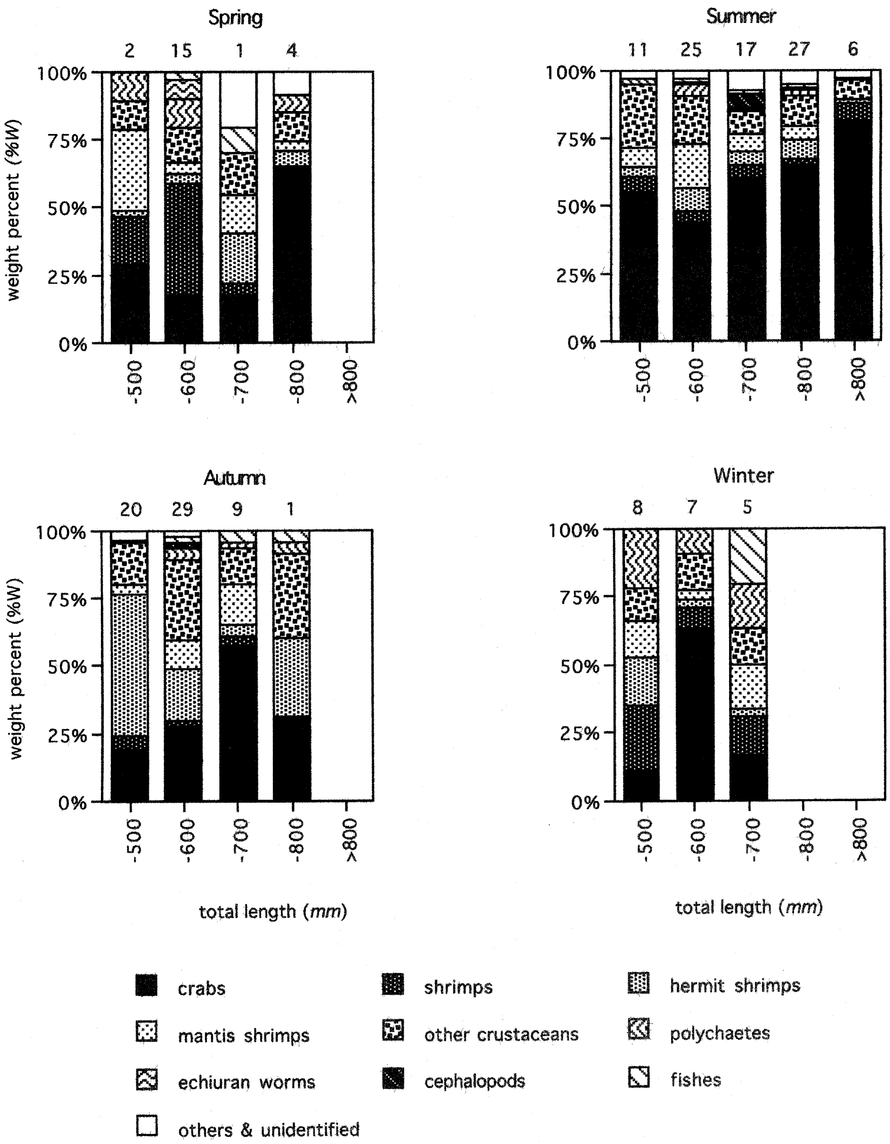

Fig. 5 Seasonal diet change in weight percent (*%W*) by size classes (total length, mm) of *Mustelus griseus* caught off Imabari. The figure above each bar is the number of fish examined.

H. japanica ate squids and other cephalopods exclusively, but we could not clarify any tendency of their food habit because of a small number of samples on the whole. *H. japanica* originally distributes on the coasts of Southern Japan, the East China Sea, and around Taiwan, deeper than 100 m around the continental shelf of the East China Sea.[29] Also, the 70–80 cm TL sharks are frequently fished at Tachibana Bay in Nagasaki.[29] In the present study, most sharks were below 600 mm TL, which were smaller than those in Tachibana Bay.[29] Yokogawa and Yamaguchi first recorded this size 108 cm TL in the Seto Inland Sea,[30] however, judging from the other records or reports,[29,31] small-sized *H. japanica* might migrate into the shallow water of the inland sea to forage in summer.

It is supposed that *M. griseus* prowls around the sandy/muddy bottom at Hiuchi Nada Sea to forage for prey items all year round. They ate less polychaetes and more greatly depended on crustaceans than *M. manazo*. The decline in their food diversity choices with size increasing (Table 6) suggests that their food habit is to gradually specialize in crabs with growth without the changing in main food items (Fig. 3c).

The primary food category of *M. manazo* (Table 5) was crustaceans dwelling commonly around the sandy/muddy bottom. The whole foraging tendency of this species resembles that of *M. griseus*, but *M. manazo* does not show food diversity with growth, which is different from *M. griseus* (Table 6). There are several previous

Table 5 Diet composition of *Mustelus manazo* caught off Imabari

Mustelus manazo (n = 164)		Empty = 1.20%		
		%*F*	%*N*	%*W*
Crastaceans		**99.39**	**71.89**	**86.42**
Crabs		88.41	36.27	52.86
Grapsidae	*Hemigrapsus sanguineus*	1.22	0.08	0.06
Xanthoidae	*Halomede fragifera*	1.83	0.26	0.66
	Sphaerozius nitidus	0.61	0.04	0.01
	spp.	3.05	0.26	0.15
Hexapodidae	*Hexapinus latipes*	0.61	0.04	0.03
Goneplacidae	*Carcinoplas vestira*	0.61	0.04	0.66
	Heteroplux nitida	0.61	0.04	0.01
	Eucrate crenata	8.54	1.02	1.22
	Goneplas renoculis	1.22	0.08	0.03
Poriunidae	*Portunus hastatoides*	5.24	3.32	12.85
	Chabrybdis variegata	3.66	0.42	0.91
	Chabrybdis bimaculata	7.32	1.10	3.79
	Liocarcinus corrugatus	0.12	2.98	7.33
	Lissocarcinus larvis	1.83	0.11	033
	spp.	2.44	0.19	0.47
Cancridae	*Cancer gibbosuius*	7.80	6.91	5.60
	sp.	1.22	0.15	0.07
Parthenopidae	*Parthenope valida valida*	1.83	019	0.14
Majidae	*Hyastenus elongatus*	0.61	0.04	0.04
Leucosiidae	spp.	1.22	0.08	0.03
Calappidae	*Calappa calappa*	0.61	0.04	0.04
Drippoidae	*Nobilum japonicum japonicum*	1.83	0.15	0.33
	Paradrippe granulata	3.05	0.42	0.78
	spp.	1.22	0.08	0.04
Unidentified		64.02	18.25	17.25
Shrimps		49.39	10.35	3.79
Soyllaridae	*Scyllarus cultrifer*	1.22	0.08	0.10
Crangonidae	*Crangon affinis*	6.10	0.60	0.25
	Scierocrangen angusticauda	1.83	0.11	0.07
	spp.	1.83	0.23	0.07
Hippolytidae	*Latreutes planirostris*	6.10	0.87	0.08
	Lysmata kukonthali	0.61	0.04	0.01
	spp.	1.83	0.19	0.01
Ogyrididae	*Ogyrides striaticauda*	1.22	0.08	0.01
Alpheidae	*Alpheus distinguendus*	0.61	0.04	0.04
	Alpheus bisincisus	2.44	0.15	0.18
	Alpheus lobidens lobidens	1.22	0.08	0.38
	Alpheus japonicus	0.61	0.04	0.04
	spp.	8.90	1.74	0.63
Palamonidae	*Conchodytes nipponensis*	0.61	0.04	0.03
	Palaemon serrifer	1.22	0.08	0.14
	Palaemon sp.	0.61	0.15	0.03
Pasiphaeidae	*Leptochela gracilis*	10.37	2.68	0.41
Penaeidae	*Metapenaeopsis occlivis*	0.61	0.04	0.00
	sp.	0.61	0.04	0.05
Unidentified		25.00	3.10	1.26
Hermit crabs		36.59	4.23	5.90
Porcellanidae	*Porcellana pulchra*	0.61	0.11	0.01
Galatheldae	*Galathea orientalis*	0.61	0.04	0.02
	Galathea pubescens	3.05	0.72	0.07
Diogenidae	*Diogenes edwardsii*	7.93	0.91	2.61
	unidentified hermit crabs	15.85	1.21	1.02
Upogetiidae	*Upogebia major*	9.76	0.83	1.57
Callianassidae	*Callianassa petatura*	2.44	0.15	0.38
	spp.	2.44	0.26	0.23

Table 5 *Continued*

Mustelus manazo (n = 164)		Empty = 1.20%		
		%F	%N	%W
Mantis shrimps		37.80	6.99	9.49
Squillidae	*Anchisquilla fasciaia*	10.37	1.21	1.56
	Lophosquilla costata	17.68	2.87	5.32
	Oratosquilla oratoria	6.10	0.57	2.31
Mantis shrimp larvae		3.05	1.93	0.14
	spp.	6.10	0.42	0.16
Isopods		6.71	0.57	0.17
Idoteidae	*Cleantoides planicauda*	0.61	0.08	0.02
Cirolanidae	*Excirolana chiitoni*	0.61	0.04	0.00
	spp.	6.10	0.45	0.15
Mysids		3.05	0.19	0.01
Mysidae	*Gastrosaccus kojimaensis*	2.44	0.15	0.01
	sp.	0.61	0.04	0.00
Amphipods	spp.	1.22	0.08	0.01
Crustaceans fragments		18.17	13.22	14.18
Polychaetes		**89.63**	**25.69**	**10.96**
Echiurans	*Urechis unicinctus*	**1.22**	**0.11**	**0.31**
Sipenculous		5.24	2.08	2.07
Blvalves		1.22	0.08	0.03
Cephalopods	sp.	**0.61**	**0.04**	**0.01**
Ophioroldeans	sp.	0.61	0.04	0.00
Fishes		**1.22**	**0.08**	**0.29**
Ammodytidae	*Ammodytes personatus*	0.61	0.04	0.12
Unidentified		0.61	0.04	0.17

n, number of stomachs in which at least one prey occurs; %*F*, frequencies of occurrence; %*N*, percentage numbers; %*W*, percentage weights.

Table 6 Diet diversities of four houndsharks, family Triakidae, caught off Imabari according Shannon-Wiener's diversity indices

Size class (*mm* total length)	Shark species			
	Triakis scyllium	*Hemitriakis japanica*	*Mustelus griseus*	*Mustelus manazo*
–500	0.66 (47)	0.85 (8)	0.77 (41)	0.73 (20)
–600	0.72 (63)	0.76 (22)	0.78 (76)	0.78 (46)
–700	0.77 (29)	0.81 (7)	0.70 (32)	0.60 (59)
–800	0.69 (8)	0.73 (6)	0.60 (32)	0.78 (28)
>800	0.61 (25)	0.97 (8)	0.36 (6)	0.62 (11)
ave.	**0.72 (172)**	**0.68 (51)**	**0.68 (187)**	**0.62 (164)**

Figure in parenthesis; the number of sharks examined.

reports about the food habit of *M. manazo*, in which they took mainly crustaceans and depended on live communities in each habitat.[4,7,13] Polychaetes were also commonly found in the shark diet in any area,[4,7,13] so it is definite that they are regular prey items. In contrast, they have different selectivity on fish species as a food by areas, showing relatively higher values at Aomori,[4,13] Choshi,[7] Maizuru,[13] Simonoseki,[13] and Taiwan,[13] but yet a relatively lower value in Tokyo Bay.[13] These results might support that *M. manazo* in the inland seas prefer crustaceans which are more plentiful and easily available prey items than fishes.

Some studies about food habits have been carried out on genus *Mustelus*; *M. antarcticus*,[32] *M. asterias*,[3] *M. californicus*,[33] *M. canis*,[34,35] *M. henlei*,[23,33,36] *M. lenticulatus*,[37] *M. mustelus*,[38,39] *M. palumbes*[39] and *M. schmitti*,[40] and each of them indicated that crustaceans dwelling near the sea bottom were their important prey items. Some of them revealed that some species change their food habits with growth[32,33,38–40] or differ between the sexes,[32,37] which was different from this study. But it

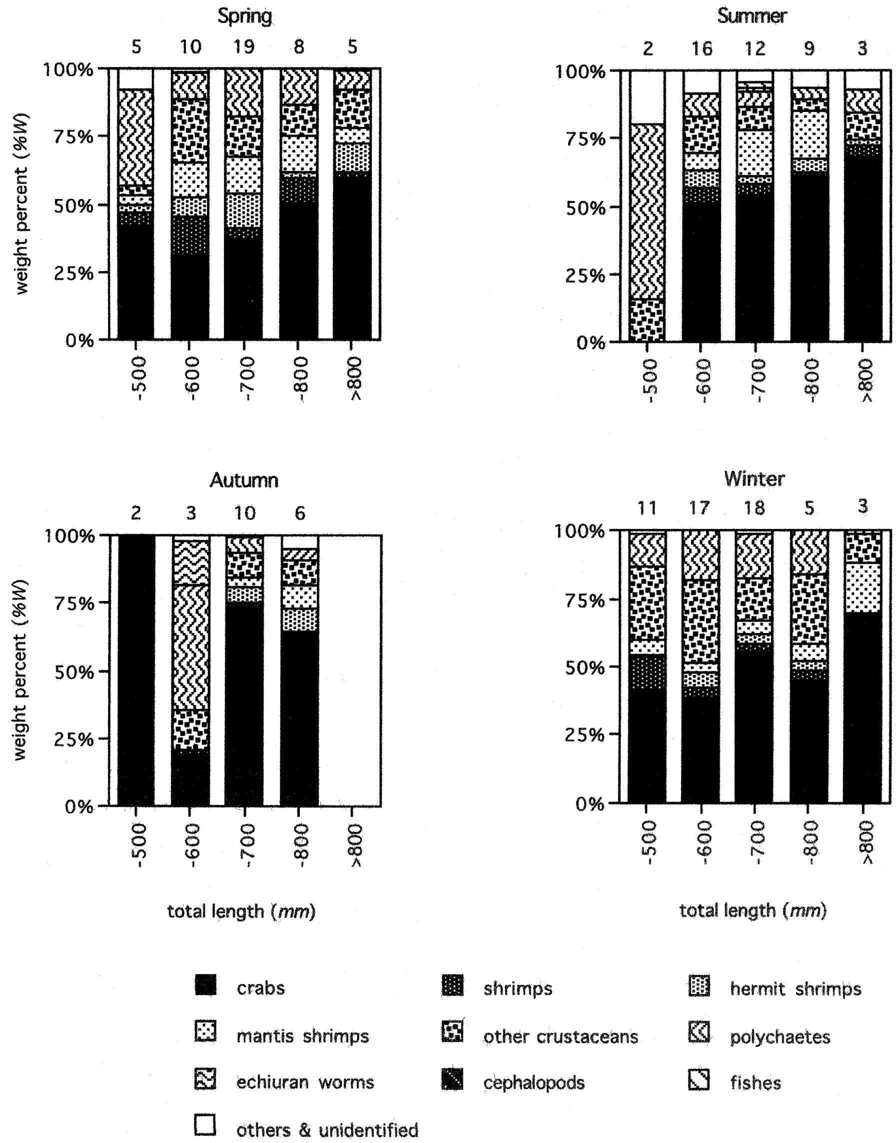

Fig. 6 Seasonal diet change in weight percent (%*W*) by size classes (total length, mm) of *Mustelus manazo* caught off Imabari. The figure above each bar is the number of fish examined.

still remains unknown what caused the differences between each result, so further study will be required.

Summarizing food habits of four houndshark species: the small sized *T. scyllium* has a unique food habit of mainly shrimps and echiuran worms at inshore and estuary waters,[26,27] but the large sized *T. scyllium* and *H. japanica* seize cephalopods. In contrast, both *M. griseus* and *M. manazo* prefer crustaceans dwelling near the sandy/muddy bottom. In this way, each houndshark species must hold a high ecologic niche as the top predator in this inland sea. But it is obscure how these plural species establish interspecific relationships because each detailed habitat or living environment of their prey remains unidentified, therefore, further investigation will be vital to reveal their role in the marine ecosystem.

ACKNOWLEDGMENTS

We wish to thank Dr Kenji Gushima and Dr Yoichi Sakai, Hiroshima University, for giving helpful comments on the manuscript. Dr Hiromichi Imabayashi and Dr Susumu Otsuka, Hiroshima University, Dr Seung-Ho Choi, Chonbuk National University, Dr Gun-Wook Baeck, Pukyong National University, and Mr Yoshifumi Kawamura helped with the identification of prey items. We also thank Bronwyn Bennett and Kerry Greer of Edanz Editing for copyediting the manuscript.

REFERENCES

1. Compagno LJV. FAO Species Catalogue, Vol 4, Part 1; Sharks of the World. *FAO Fish Synop.* 1984; **125**: 381–434.
2. Yamaguchi A. On the sharks as fishery resources and aspects of their life histories. *Aquabiology* 2002; **24**: 401–408.
3. Ellis JR, Pawson MG, Shackley SE. The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the North-east Atlantic. *J. Mar. Biol. Ass. UK* 1996; **76**: 89–106.
4. Mikawa M. On the feeding habits of some demersal sharks. *Report Tohoku Reg. Fish. Res. Laboratory* 1971; **31**: 109–124.
5. Tanaka S, Mizue K. Studies on Sharks –XV, Age and Growth of Japanese Dogfish *Mustelus manazo* Bleeker in the East China Sea. *Bull. Jap. Soc. Sci. Fis.* 1979; **45**: 43–50.
6. Teshima K. Studies on the reproduction of Japanese smooth dogfish, *Mustelus manazo and M. Griseus*. *J. Shimonoseki University Fish.* 1981; **29**: 133–199.
7. Taniuchi T, Kuroda N, Nose Y. Age, growth, reproduction and food habits of the Star-spotted Dogfish *Mustelus manazo* collected from Choshi. *Bull. Jap. Soc. Sci. Fis.* 1983; **49**: 1325–1334.
8. Yamaguchi A, Taniuchi T, Shimizu M. Age and growth of the starspotted dogfish *Mustelus manazo* from Tokyo Bay, Japan. *Fish. Sci.* 1996; **62**: 919–922.
9. Yamaguchi A. *Studies on stock identification of the starspotted dogfish Mustelus manazo.* PhD Thesis. University of Tokyo, Tokyo, 1997.
10. Yamaguchi A, Taniuchi T, Shimizu M. Reproductive biology of the starspotted dogfish *Mustelus manazo* from Tokyo Bay, Japan. *Fish. Sci.* 1997; **63**: 918–922.
11. Yamaguchi A, Taniuchi T, Shimizu M. Geographic variations in growth of the starspotted dogfish *Mustelus manazo* from five localities in Japan and Taiwan. *Fish. Sci.* 1998; **64**: 732–739.
12. Yamaguchi A, Taniuchi T, Shimizu M. Geographic variations in reproductive parameters of the starspotted dogfish *Mustelus manazo* from five localities in Japan and Taiwan. *Environ. Biol. Fish.* 2000; **57**: 221–233.
13. Yamaguchi A & Taniuchi T. Food variations and ontogenetic dietary shift of the starspotted dogfish *Mustelus manazo* at five locations in Japan and Taiwan. *Fish. Sci.* 2000; **66**: 1039–1048.
14. Wang TM, Chen CT. Reproduction of Smooth Dogfish, *Mustelus griseus* in Northwestern Taiwan Waters. *J. Fish. Soc. Taiwan* 1981; **8**: 25–37.
15. Wang TM & Chen CT. Age and Growth of Smooth Dogfish, *Mustelus griseus* in Northwestern Taiwan Waters. *J. Fish. Soc. Taiwan* 1982; **9**: 1–12.
16. Chen CT, Mizue K. Reproduction of *Galeorhinus japonicus*. *Bull. Fac. Fish. Nagasaki University* 1973; **36**: 37–51.
17. Tanaka S, Chen CT, Mizue K. Studies on Sharks –XVI, Age and Growth of Eiraku Shark *Galeorhinus japonicus* (Müller et Henle). *Bull. Fac. Fish. Nagasaki University* 1978; **45**: 19–28.
18. Imabayashi H, Hanaoka T, Takamori S. Feeding activities of juvenile and young Red Sea Bream, *Chysophrys major* Temminck et Schlegel, in the biotic community-I. Relation to the other species. *Bull. Nansei. Reg. Fish. Res. Laboratory* 1975; **8**: 101–111.
19. Iuchi Y, Takeoka H. Seto Inland Sea I and II. In: Coastal Oceanography Research Committee, The Oceanographical Society of Japan (eds). *Coastal Oceanography of Japanese Inlands*. Tokai University Press, Tokyo, 1985; 607–624, 694–698.
20. Kimoto S. *Study Methods of Animal Communities I –the Diversity and Composition*. Kyoritsu Shuppan, Tokyo, 1976; 135–136.
21. Randall JE. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 1967; **5**: 665–847.
22. Smale MJ, Goosen AJJ. Reproduction and feeding of gully shark, *Triakis megalopterus,* off the Eastern Cape, South Africa. *Fish. Bull.* 1999; **97**: 987–998.
23. Russo RA. Observations on the food habits of Leopard Sharks (*Triakis semifasciata*) and Brown Smoothhounds (*Mustelus henlei*). *Calif. Fish Game* 1975; **61**: 95–103.
24. Talent LG. Food habits of the leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. *Calif. Fish Game* 1976; **62**: 286–298.
25. Webber JD, Cech JJ Jr Nondestructive diet analysis of the leopard shark from two sites in Tomales Bay, California. *Calif. Fish Game* 1998; **84**: 18–24.
26. Inaba A (ed). *Fauna and Flora of the Seto Inland Sea*, 2nd edn. *II.* Marine Biological Laboratory, Graduate School of Science, Hiroshima University, Hiroshima, 1988; 101–205.
27. Ogawa Y, Kakuda S, Takahashi M. On the Shrimp Fauna of Kojima Bay in the Seto Inland Sea. *J. Fac. Appl. Biol. Sci. Hiroshima University* 1983; **22**: 235–240.
28. Hopkins TE, Cech JJ Jr. The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. *Env. Biol. Fish.* 2003; **66**: 279–291.
29. Yamada U, Kishida S. In: Seikai Regional Fisheries Research Laboratory (eds). *Fishes of the East China Sea and the Yellow Sea*. Regional Fisheries Research Laboratory, Nagasaki, 1986; 12–14, 16.
30. Yokokawa H, Yamaguchi A. First Record of two shark species from Seto Inland Sea. *I.O.P Diving News* 1997; **8**: 2–7.
31. Kamura S, Hashimoto H, Gushima K. The second record, tendency of occurrence and food habit of Eiraku Shark *Hemitriakis japanica* in the Seto Inlands Sea. *J. Fac. Appl. Biol. Sci. Hiroshima University* 2000; **39**: 1–7.
32. Simpfendorfer CA, Goodreid A, McAuley RB. Diet of three commercially important shark species from Western Australian waters. *Mar. Freshwater Res.* 2001; **52**: 975–985.
33. Talent LG. Food habits of the Gray Smoothhound, *Mustelus californicus*, the Brown smoothhound, *Mustelus henlei*, the Shovelnose Guitarfish, *Rhinobatos productus*, and the Bat Ray, *Myliobatis californica*, in Elkhorn Slough, California. *Calif. Fish Game* 1982; **68**: 224–234.
34. Rountree RA, Able KW. Seasonal abundance, growth, and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey estuary. *Fish. Bull.* 1996; **94**: 522–534.
35. Gelsleichter J, Musick JA, Nichols S. Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. *Env. Biol. of Fish* 1999; **54**: 205–217.
36. Haeseker SL, Cech JJ Jr. Food habits of the brown smoothhound shark (*Mustelus henlei*) from two sites in Tomales Bay. *Calif. Fish Game* 1993; **79**: 89–95.

37. King KJ, Clark MR. The food of rig (*Mustelus lenticulatus*) and the relationship of feeding to reproduction and condition in Golden Bay. *NZ J. Of Mar. Freshwater Res.* 1984; **18**: 29–42.
38. Morte S, Redon MJ, Sanz-Brau A. Feeding habits of juvenile *Mustelus mustelus* (Carcharhiniformes, Triakidae) in the western Mediterranean. *Cah. Biol.* March 1997; **38**: 103–107.
39. Smale MJ, Compagno LJV. Life history and diet of two southern African smoothhound sharks, *Mustelus mustelus* and *Mustelus palumbes*. *SA J. Mar. Sci.* 1997; **18**: 229–248.
40. Chiaramonte GE, Pettovello AD. The biology of *Mustelus schmitti* in southern Patagonia, Argentina. *J. Fish Biol.* 2000; **57**: 930–942.