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Seasonal and spatial variations in prey utilization and condition of a piscivorous flatfish *Paralichthys olivaceus*

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ABSTRACT: We investigated the diet and somatic condition of 5129 individual Japanese flounder *Paralichthys olivaceus*, 20 to 92 cm in total length, in the Joban area along the Pacific coast of Japan (36° 40′ N to 38° 00′ N) from 2001 to 2007. Japanese flounder with food in their stomachs (1668 individuals) consumed chiefly fishes (92% of stomach contents by weight). Predominant prey species were Japanese anchovy *Engraulis japonica* (54% of fishes by weight) and Japanese sandlance *Ammodytes personatus* (22%). Japanese anchovy were consumed by Japanese flounder year round except in March and April, when the anchovy migrate from the Joban area. In March and April, Japanese flounder frequently consumed Japanese sandlance, but only in the northern part of the Joban area (37° 20′ N to 38° 00′ N); Japanese flounder did not feed on this species and had less content in their stomachs in the southern area (36° 40′ N to 37° 20′ N), where the sandlance is absent. Somatic and hepatosomatic conditions of Japanese flounder in the northern area were better than those in the southern area in March and April, suggesting that such spatial and seasonal heterogeneities in prey availability affect the nutritional status of predators.

KEY WORDS: Spatio-temporal variability · Prey availability · Body condition · Piscivory · Flounder · Generalized linear mixed models

INTRODUCTION

Piscivorous animals are generally the top predators in aquatic ecosystems. Predation pressure affects the population dynamics of prey fishes and may have cascading effects on lower trophic niches (Baum & Worm 2009, Eriksson et al. 2009). Additionally, the diet of predators can be an indicator of ecosystem change (Link et al. 2002, Dwyer et al. 2010). Not only the impacts of predation on prey populations but also the responses of predators to changes in prey densities are key subjects for understanding ecosystem functions (Moustahfid et al. 2010).

Japanese flounder *Paralichthys olivaceus* is distributed predominantly at depths <100 m in the coastal waters of Japan, Korea, China, and Russia. This species is the most important flatfish species for coastal fisheries in Japan. Adult Japanese flounder feed mainly on fishes (Sato 1975, Dou 1995, Minami 1997), although larvae feed mainly on copepods and oikopleurids (Ikewaki & Tanaka 1993, Hasegawa et al. 2003) and age-0 juveniles feed on mysids (Yamada et al. 1998, Yamamoto et al. 2004, Tanaka et al. 2006, Tomiyama et al. 2009a). In Japan, juvenile Japanese flounder raised in onshore hatcheries are released into the wild as a part of stock enhancement programs in many local communities because of the high economic value of this species. However, enhancing the stock of this highly piscivorous fish could increase the consumption of prey fishes. To effectively manage the eco-

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system while implementing stock enhancement, the feeding habit of the predator and its relationships with prey, including the sites and seasons of intensive predation, should be understood.

In Sendai Bay, located north of the Joban area along the Pacific coast of northern Japan (Fig. 1), Japanese flounder consume mainly Japanese anchovy *Engraulis japonica* and Japanese sandlance *Ammodytes personatus* (Sato 1975). However, seasonal or spatial patterns in the distributions of these prey fishes could affect the feeding of predators. Japanese anchovy are not available throughout the year; they migrate from southern areas to Sendai Bay and the adjacent northern coasts in the period May to July and migrate southward from Sendai Bay in the period October to December (Nagashima 2007). Japanese sandlance occur in Sendai Bay (Murase et al. 2009) and the adjacent northern Joban area, but their abundance is extremely low in the southern Joban area. Moreover, Japanese sandlance estivate in the substratum to depress their metabolic rate during periods of high water temperature (Tomiyama & Yanagibashi 2004). This estivation, observed in Sendai Bay from August to November (Hashimoto 1991), may also affect the predation success of their predators. Such a temporal pattern should affect the feeding of Japanese flounder.

The aim of the present study was to identify the prey species of Japanese flounder in the Joban area and to reveal their seasonal and spatial patterns of prey utilization. The somatic and hepatosomatic condition of Japanese flounder were investigated to determine whether spatial and temporal variations in their diet affected their nutritional status.

MATERIALS AND METHODS

Study site and sample collection. The Joban area, along the Pacific coast of Japan south of Sendai Bay (36° 40′ N to 38° 00′ N), was chosen as the study site. We divided the area into 2 sections at latitude 37° 20′ N (Fig. 1); the commercial fishery of Japanese sandlance has operated mostly in the area north of this latitude (K. Ebe unpubl. data 1991). We investigated the spatial variation between the areas to the north and south of 37° 20′ N, hereinafter called the 'northern' and 'southern' areas.

From 2001 to 2007, Japanese flounder caught by trawl and gillnet fisheries were sampled from landings at fish markets in Fukushima Prefecture. Because this fishery is managed to restrict the landing of small Japanese flounder (<30 cm total length [TL]; Tomiyama et al. 2008a), the 4640 individual wild and released Japanese flounder sampled at the fish markets were ≥30 cm TL. Location of capture of these samples

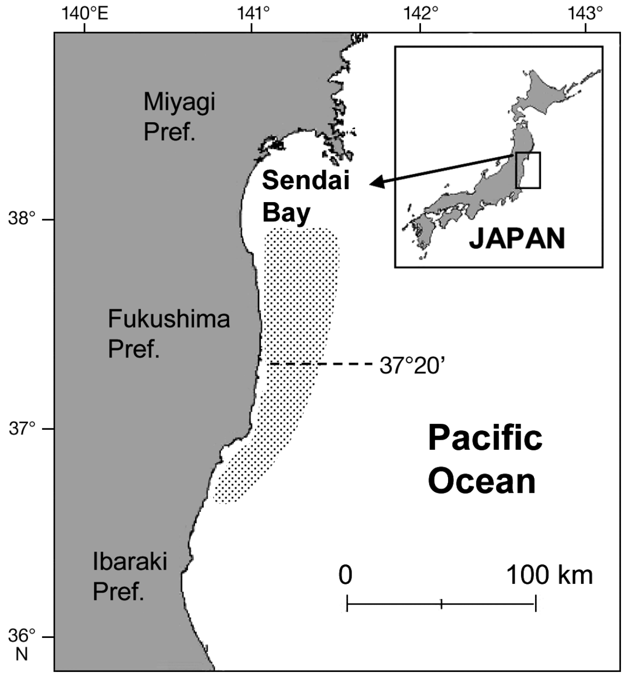

Fig. 1. The Joban area in Japan (36° 40′ N to 38° 00′ N). The dotted area shows the main fishery ground for Japanese flounder (depths ≤100 m). The northern and southern areas were delimited by latitude 37° 20′ N (dashed line). The coast of Fukushima Prefecture extends from 36° 50′ N to 37° 55′ N

was recorded by asking the fishermen who caught the landed samples or by inferring from the operation area of each fishery community. This information enabled us to determine whether the capture area was northern or southern, although the exact location was impossible to determine.

An additional 489 Japanese flounder, including individuals <30 cm TL, were collected through monthly otter-trawl and beam-trawl surveys. An otter trawl with a mouth opening of approximately 7.5 m was towed at depths from 10 to 175 m along latitude 37° 00′ N from April 2001 to March 2007 and at depths from 100 to 200 m along latitude 37° 40′ N from March 2005 to March 2007. A 2 m wide beam trawl was towed at depths of 5 to 15 m at 3 locations in the study area (36° 53′ N, 37° 28′ N, 37° 47′ N) from 2001 to 2007 and at 1 additional location (37° 03′ N) from 2003 to 2007.

The bottom water temperature, as measured monthly by the Fukushima Prefectural Fisheries Experimental Station, was used as a possible factor affecting the feeding of Japanese flounder. Data from 2 sites were used: north (37°50′N, 141°12′E; depth: 37 m) and south (37°00′N, 141°02′E; depth: 55 m).

Laboratory observations. Japanese flounder were first identified as either wild or hatchery-reared on the basis of the hypermelanosis present on the blind side or pseudoalbinism present on the ocular side, and numerous fin-ray counts in the hatchery-reared fish (Tomiyama et al. 2008b). We did not exclude the hatchery-reared fish because they had been released at approximately 10 cm TL and would adapt sufficiently to the natural environment as well as wild fish at least until they grew up to 20 cm TL. The TL (cm) and body wet weight (BW, g) of each Japanese flounder were measured. Sex was determined by gonadal observation. Liver wet weight (LW, g) was measured. Stomachs were removed and the total stomach content wet weight (SCW, g) was determined. Stomach contents were identified to species level or to the level of the lowest possible taxon for each prey item and weighed. As the monogenean parasite *Neoheterobothrium hirame* can affect the feeding of Japanese flounder (Shirakashi et al. 2009), adult *N. hirame* were removed from the buccal cavity wall of the Japanese flounder and counted.

Data analysis. Prey items were separated into 8 categories: Japanese anchovy, Japanese sandlance, other fish species, unidentified fish (mostly digested fish), cephalopods, natantids, mysids, and 'others'. The proportion by weight of each category was used to determine prey importance.

To test whether sizes of captured prey differed between areas, simple linear models were constructed for each season. The seasons were defined as successive 2 mo periods (January–February, March–April, May–June, July–August, September–October, and November–December), based on the similarity in the diet among months. The weight (g) of each prey was used as the response variable after logarithmic transformation. Initial explanatory variables were log(TL of Japanese flounder), area (northern or southern), and their interaction, and then the relevant variables were selected by stepwise backward selection on the basis of the Akaike information criterion (AIC). The model was constructed using the software R, version 2.10.1 (www.r-project.org).

To assess seasonal or spatial variations in the availability of prey fish species, we analyzed the commercial catch of Japanese anchovy and Japanese sandlance. Japanese anchovy is widely distributed inshore and offshore; in Fukushima Prefecture, the commercial purse-seine fishery has operated in offshore areas (mostly around 37° N, >100 m deep) and the commercial 1-boat seine fishery has operated in inshore areas (mostly around 37° N, <50 m deep). Because data for fishing effort were not available, the monthly catch amounts of adult Japanese anchovy for the period 2001 to 2005 were used to examine the seasonal variation in Japanese anchovy occurrence. Additionally, the monthly quantity of Japanese anchovy caught by commercial set-net fishery (operating in the coastal waters between 38° 10′ N and 38° 40′ N, <50 m deep) and landed at Ishinomaki Fish Market in Miyagi Prefecture was used as an index of the anchovy abundance around 38° N.

Commercial fishing for Japanese sandlance in Fukushima Prefecture is performed by 2-boat seine trawl in the area from 37° 10′ N to 38° 00′ N at depths from 36 to 77 m during April and May. For catch information, we used logged data from the sandlance fishery from 2003 to 2006. The catch (t) of adult Japanese sandlance per haul (approx. 1 h tows) was used as the catch per unit effort (CPUE). Annual catch and the CPUE over each 10′ interval of latitude were calculated. Annual catch at these latitudal areas was determined for each fishery community using the ratio of logged catch and statistical catch; the catch of each latitudal area was summed among communities.

To examine seasonal and spatial variations in feeding activity and nutritional status of Japanese flounder, we determined the stomach content index (SCI), hepatosomatic index (H), and relative condition factor (Kr) (Pardoe et al. 2008) in 4 size classes (20.0–29.9, 30.0–39.9, 40.0–49.9, and ≥50.0 cm TL) as follows:

$$SCI = SCW \times (BW - SCW)^{-1} \times 10^2 \quad (1)$$

$$H = LW \times (BW - SCW)^{-1} \times 10^2 \quad (2)$$

$$Kr = (BW - SCW) \times \text{Predicted}(BW - SCW)^{-1} \quad (3)$$

where:

$$\text{Predicted}(BW - SCW) = \exp\,[3.164 \times \log(TL) - 5.142] \quad (4)$$

which was derived from our data set using a generalized linear model (GLM) with a log-link function and gamma distribution. The data were pooled among years and determined for each season. SCI was determined for all individuals, including those with empty stomachs; it should be noted that specimens collected at night by gillnet or trawls usually have no prey or have digested prey in their stomachs and yield lower values for SCI.

To assess possible factors causing variation in the condition of Japanese flounder, generalized linear mixed models (GLMMs) were constructed. First, the condition of fish in all seasons was analyzed. To explain variations in H and Kr, we used LW and (BW – SCW) as response variables, with offset terms of log(BW – SCW) and log[predicted (BW – SCW)], respectively. As initial explanatory variables we used TL, 'wild' or 'released' (W/R), sex, number of attached *Neoheterobothrium hirame*, collection area (northern or southern), and season. Year of collection was included as a random factor. Second, the season with a large difference in diet between areas was chosen; the condition of fish in that season was similarly analyzed. Initial explanatory variables were the same except for 'season'. All response variables were fitted with a GLMM with a Gaussian error structure and log-link function, similar to the GLMs presented by Tomiyama et al. (2010). The GLMMs were constructed and finalized by stepwise backward selection based on the AIC. The modeling was conducted using the software R with the package lme4 (Bates & Maechler 2009).

RESULTS

Diet and ontogenetic shift in feeding

Japanese flounder consumed prey in 18 families and at least 21 genera of Teleostomi (Table 1). The principal prey items were Japanese anchovy (53.6 % of fish by weight) and Japanese sandlance (21.9 %). Japanese anchovy were frequently observed from the stomachs of Japanese flounder in both northern and southern areas, whereas Japanese sandlance were seldom observed in stomachs from southern-area flounder. Japanese anchovy were found in the stomachs of Japanese flounder collected at depths from 3 to 200 m, whereas Japanese sandlance were found in the stomachs of flounder collected at depths from 30 to 77 m.

The ontogenetic change in diet was small for Japanese flounder ≥20 cm TL (Fig. 2). The predominant prey was consistently fish. Mysids were consumed mostly by Japanese flounder <30 cm TL. The proportion of natantids decreased as the body size increased. Cephalopods were consumed by Japanese flounder of all size classes.

Table 1. *Paralichthys olivaceus*. Prey items consumed in the study area. In the northern area (north of 37° 20′ N), 1104 individuals had food in their stomachs, and in the southern area (south of 37° 20′ N), 564 individuals had food in their stomachs. %F: percentage frequency of occurrence; %W: percent by weight. The value '0' indicates not observed

Taxa and prey species (family)	Northern area %F	Northern area %W	Southern area %F	Southern area %W
Teleostomi				
Conger myriaster (Congridae)	1.4	0.4	0.4	1.2
Gnathophis spp. (Congridae)	0.1	0.1	0.5	0.9
Unidentified Congridae	0.5	0.3	0.4	0.4
Sardinops melanostictus (Clupeidae)	0.2	0.6	0	0
Engraulis japonica (Engraulidae)	29.6	44.1	44.7	66.1
Physiculus maximowiczi (Moridae)	0.7	2.4	0.2	0.5
Gadus macrocephalus (Gadidae)	0.3	1.3	0	0
Erisphex pottii (Aploactinidae)	0.5	0.5	0	0
Hexagrammos otakii (Hexagrammidae)	0.2	1.7	0	0
Ricuzenius pinetorum (Cottidae)	0.3	0.0	0.2	0.0
Liparis tanakai (Liparidae)	0	0	0.2	0.0
Trachurus japonicus (Carangidae)	0.4	0.4	1.2	1.1
Evynnis tumifrons (Sparidae)	0.1	0.0	2.5	1.2
Sciaenidae spp. (Sciaenidae)	0	0	0.9	0.3
Ammodytes personatus (Ammodytidae)	21.0	26.4	0.4	0.5
Eleutherochir mirabilis (Callionymidae)	0.1	0.1	0.2	0.0
Repomucenus spp. (Callionymidae)	1.6	0.5	1.1	0.6
Sphyraena sp. (Sphyraenidae)	0	0	0.2	0.4
Scomber sp. (Scombridae)	0.1	0.5	0	0
Paralichthys olivaceus (Paralichthyidae)	0.3	0.3	0.2	0.1
Tarphops spp. (Paralichthyidae)	0.3	0.1	0.4	0.1
Pseudopleuronectes herzensteini (Pleuronectidae)	0.1	0.3	0	0
Unidentified Pleuronectidae	0.4	2.0	0	0
Unidentified	32.2	10.0	29.3	16.2
Cephalopoda				
Loliolus japonica (Loliginidae)	0.4	0.3	0.9	1.8
Loligo bleekeri (Loliginidae)	0.4	2.1	0	0
Todarodes pacificus (Ommastrephidae)	0.2	0.8	0.4	2.6
Unidentified Teuthida	3.8	2.5	6.0	4.5
Unidentified Octopoda	0.1	0.0	0	0
Crustacea				
Metapenaeopsis dalei (Penaeidae)	0.1	0.0	4.6	0.9
Trachysalambria curvirostris (Penaeidae)	0	0	0.2	0.0
Crangon spp. (Crangonidae)	0.3	0.0	4.3	0.4
Unidentified Natantia	8.2	1.1	0.4	0.1
Acanthomysis spp. (Mysidae)	1.0	0.0	5.7	0.3
Other Crustacea	0.4	0.0	0.2	0.0
Others				
Others	1.0	0.0	0.4	0.1

Seasonal and spatial variations in diet

Japanese anchovy were consumed mainly from June to February in both areas, making up an especially large proportion (>45 %) in the southern area (Fig. 3a). The size of Japanese anchovy consumed by Japanese flounder ranged from 0.1 to 26 g (average: 9.8 g). They were rarely consumed in either area in March and April, when the water temperature was lowest in both areas (Fig. 3b). During this period, the commercial catch of Japanese anchovy was also scarce in both the inshore and offshore fisheries (Fig. 4). There was a large catch of Japanese anchovy in the period May to November in the inshore set-net fishery in the northern area (average monthly catch: 360 to 2032 t) and in the period August to February in the inshore boat seine fishery in the southern area (15 to 99 t).

Japanese flounder in the northern area primarily consumed Japanese sandlance from March to June (Figs. 2 & 3a). In March and April, Japanese flounder in the northern area chiefly consumed Japanese sandlance of weight 6 to 41 g (average: 14.0 g), whereas in the southern area they consumed unidentified fishes

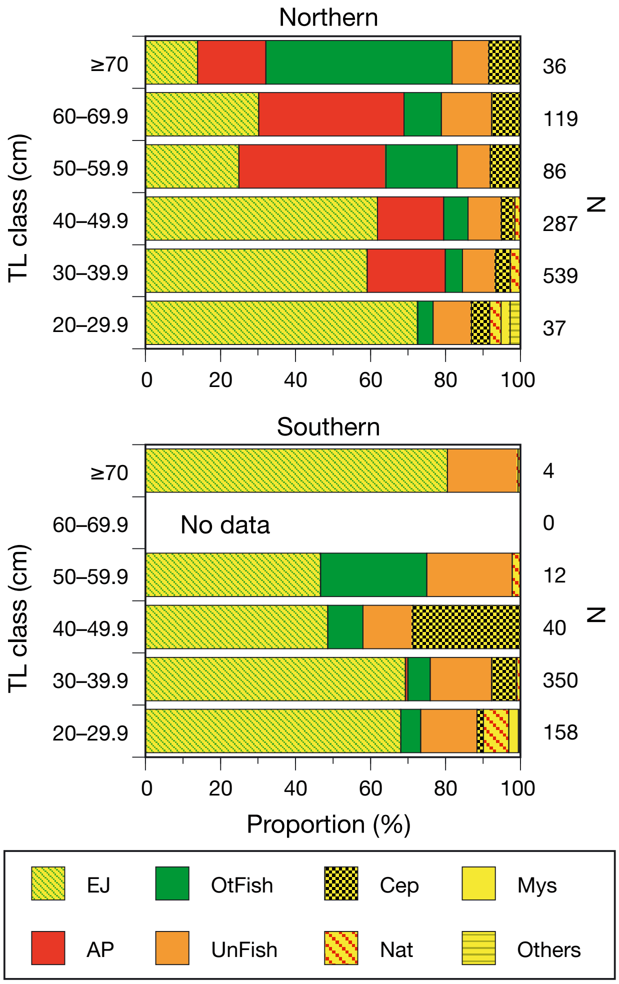

Fig. 2. *Paralichthys olivaceus*. Diet composition (by weight, %) of different total length (TL) classes in northern and southern areas. Data were pooled among years. N: number of examined individuals containing food in their stomach; EJ: *Engraulis japonica*; AP: *Ammodytes personatus*; OtFish: other fish species; UnFish: unidentified fishes; Cep: cephalopods; Nat: natantids; Mys: mysids; Others: prey items other than those listed

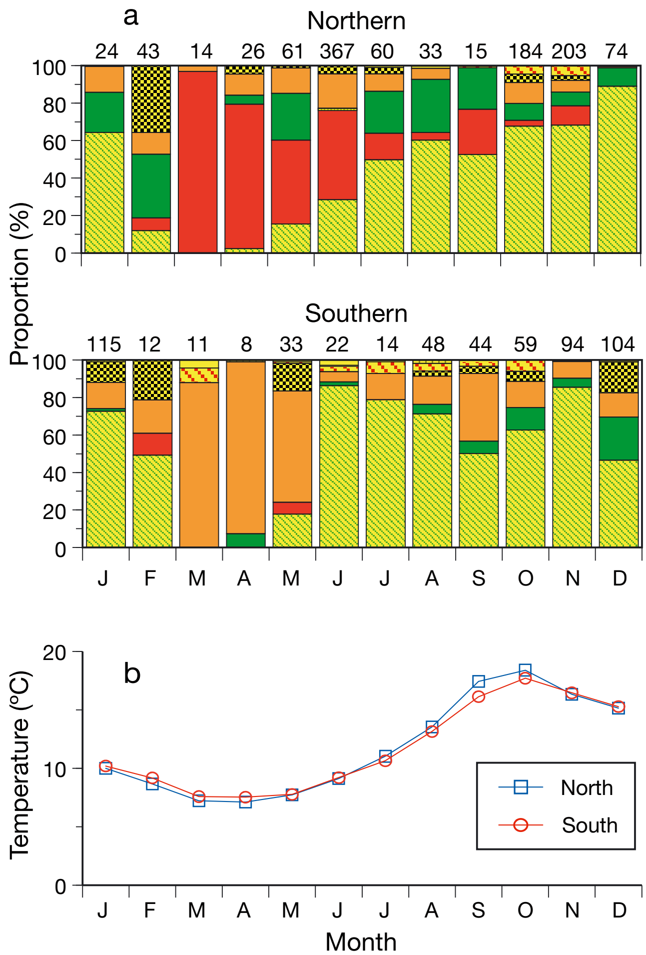

Fig. 3. *Paralichthys olivaceus*. Seasonal changes in (a) diet and (b) bottom water temperature in northern and southern areas. Numerals in (a) denote sample sizes (stomachs with food). Data for diet were pooled among years. See Fig. 2 for prey categories and legend. In (b), water temperatures at 37° 50′ N, 141° 12′ E (37 m deep) and 37° 00′ N, 141° 02′ E (55 m deep) were averaged for the period 2001 to 2005 as representative values for the northern and southern areas, respectively

mostly <6 g (Fig. 5). Prey sizes in March and April were larger in the northern area than in the southern area, without including the interaction term (linear model after stepwise selection; coefficients: intercept = –4.54, log[TL] = 1.73, Area [southern] = –0.97; r^2 = 0.44). A similar tendency was not observed in the other 5 seasons: the interaction term was significant in the period May–June, the effect of area (southern) was positive in January–February and July–August, or area was not adopted as a significant explanatory variable in September–December. On the basis of the catch and CPUE of the commercial sandlance fishery, Japanese sandlance were more abundant in northern latitudes and scarce in the area south of 37° 20′ N (Fig. 6).

Somatic condition

The average SCI of Japanese flounder ≥30 cm was lower (0.0 to 0.2) in the southern area than in the northern area (0.4 to 0.6) in March and April (Fig. 7). Seasonal patterns in SCI were not similar among size classes; a relatively high SCI was observed from May to October in the 20–39.9 cm size classes and from November to February in the ≥40 cm classes.

The average H of Japanese flounder was high from January to August (≥50 cm size class: H was 2.1 to 2.7; 40–49.9 cm: 1.2 to 2.1) and was low from September to December (≥50 cm: 1.3 to 1.4; 40–49.9 cm: 1.1 to 1.3) (Fig. 7). The average Kr of Japanese flounder was

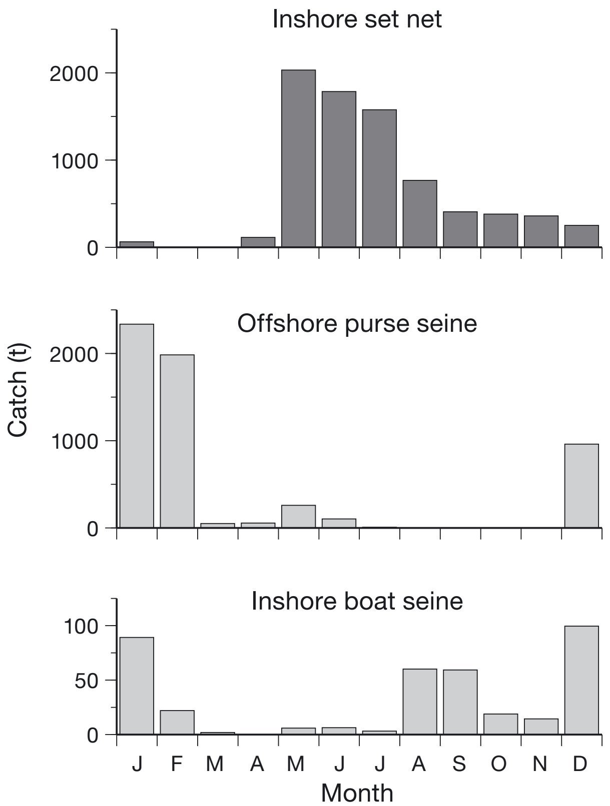

Fig. 4. *Engraulis japonica*. Monthly catches of pre-adult and adult Japanese anchovy by commercial fisheries. Inshore set-net fishery around 38° N; offshore purse-seine fishery around 37° N; and inshore boat seine fishery around 37° N. Data were averaged from 2001 to 2005

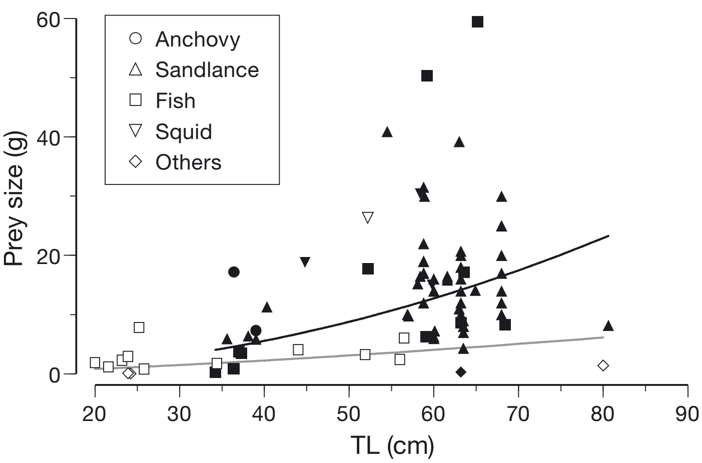

Fig. 5. *Paralichthys olivaceus*. Relationship between total length (TL) of Japanese flounder and prey size in March and April. Prey was divided into Japanese anchovy, Japanese sandlance, other fishes and unidentified fishes ('Fish'), squids, and others. Solid and open symbols indicate northern and southern areas, respectively. Regression curves were fitted: prey size = $0.0030 \times TL^{2.04}$ (north, $r^2 = 0.19$); prey size = $0.011 \times TL^{1.44}$ (south, $r^2 = 0.17$). Data were pooled among years (2001 to 2006)

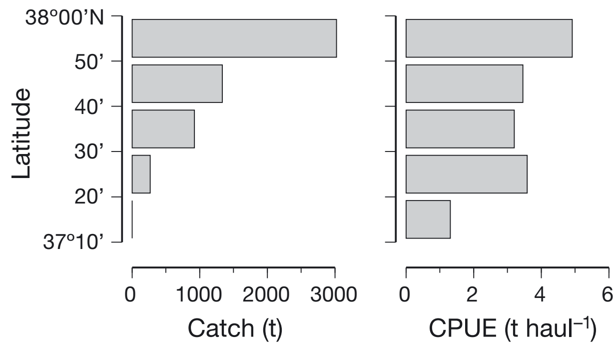

Fig. 6. *Ammodytes personatus*. Annual catch and catch per unit effort (CPUE) of pre-adult and adult Japanese sandlance derived from the logged data of the commercial trawl fishery (2-boat operation) in April and May from 2003 to 2006. Catch per haul (approx. 1 h) was used as CPUE. There is no commercial trawl fishery in the area south of 37° 10′ N because of the scarcity of the sandlance

higher in the period May to August (≥50 cm size class: Kr was 1.02 to 1.09; 40–49.9 cm: 1.00 to 1.04; 30–39.9 cm: 1.00 to 1.07) than in the period September to April (≥50 cm: 0.93 to 0.98; 40–49.9 cm: 0.90 to 0.98; 30–39.9 cm: 0.94 to 1.01). The Kr of Japanese flounder of 20–29.9 cm size class was higher in the period July to October (0.98 to 1.06) than the other periods (0.93 to 0.99). The average H and Kr of Japanese flounder in the northern area were almost always greater than those in the southern area in March and April and were often greater in the period July to October.

In the GLMMs for condition in all seasons, area (northern or southern) was included for explaining Kr but was not included for H (Table 2). The H was greater in larger fish, female fish, released fish, and in the period May to June. The Kr was similarly greater in female fish, larger fish, and in the period May to June.

In the GLMMs in March and April, the variable 'area' was adopted as an explanatory factor for both H and Kr, with the largest absolute *t*-values in the GLMMs (Table 2). Both H and Kr of Japanese flounder were lower in the southern area. Infection by *Neoheterobothrium hirame* had a slightly positive effect in the models for both condition indices.

DISCUSSION

The present study clearly revealed the seasonal and spatial variations in the diet of Japanese flounder over a relatively small area along the Pacific coast of Japan (36° 40′ N to 38° 00′ N), and suggests the effects of spatial differences in prey utilization on the somatic and hepatosomatic condition of the predator. The higher condition indices of Japanese flounder in the northern

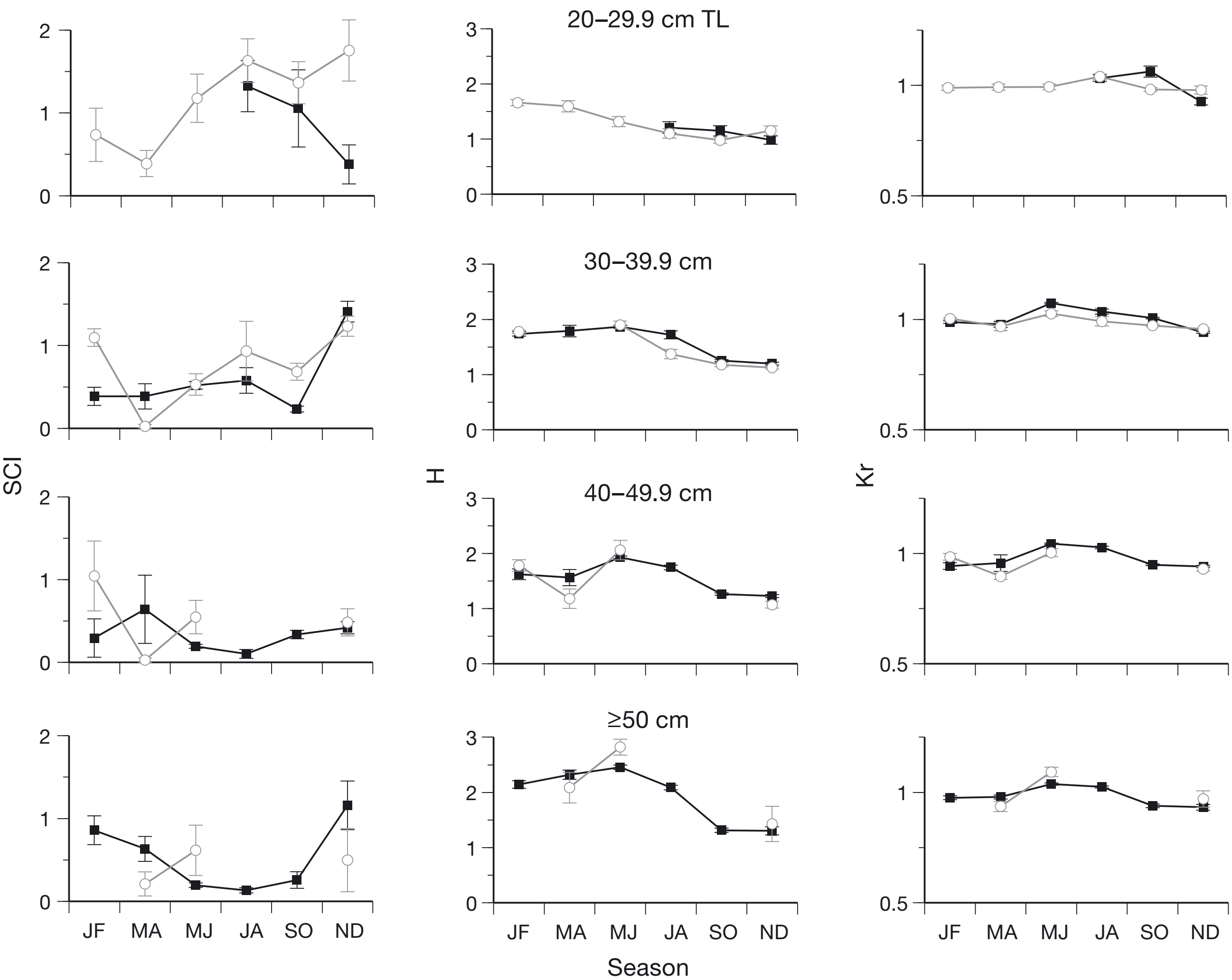

Fig. 7. *Paralichthys olivaceus*. Seasonal changes in average stomach content index (SCI), average hepatosomatic index (H), and average relative condition factor (Kr) in 4 total length (TL) classes. Data from 2001 to 2007 were pooled and are shown as mean ± SE. Seasons were defined as successive 2 mo periods (e.g. JF: Jan–Feb). Solid and open symbols denote northern and southern areas, respectively. Data with small sample sizes (<5) were excluded

area, especially in March and April (Table 2), are thought to reflect the difference in prey utilization: Japanese flounder in the northern area consumed many Japanese sandlance (Figs. 2 & 3a) whereas simultaneously those in the southern area had less content in their stomachs (Fig. 7). Most prey fish from stomachs of Japanese flounder in the southern area in March and April were unidentified, but they seemed to be small demersal fishes (e.g. sculpin, dragonet, goby, or flatfish). The size of prey was larger in the northern area only in that season (Fig. 5). The higher H and Kr of Japanese flounder in the northern area from July to October in many cases (Fig. 7) might also reflect the difference in prey availability, although no evidence for this was observed; SCI during this period was lower in the northern area. The importance of prey utilization for the condition of predatory fishes has also been suggested for other demersal fishes such as Greenland halibut *Reinhardtius hippoglossoides* (Román et al. 2007), Atlantic cod *Gadus morhua* (Pardoe et al. 2008), bighand thornyhead *Sebastolobus macrochir* (Hattori et al. 2009), and grey gurnard *Eutrigla gurnardus* (Weinert et al. 2010).

The most outstanding variation in the diet of Japanese flounder was the spatio-temporally limited utilization of Japanese sandlance, observed in the northern area especially from March to June (Fig. 3a). Absence of sandlance in the southern area (Fig. 6) is probably related to the substratum, which is mostly very fine sand in that area (Aoyagi & Igarashi 1999); sandlance prefer the area with medium to coarse sand for their estivation (Kobayashi et al. 1995). The utilization of Japanese

Table 2. *Paralichthys olivaceus*. Generalized linear mixed models (GLMMs) for hepatosomatic condition (H) and somatic condition (Kr) in the study area. Shown are the final models selected on the basis of the Akaike information criterion. Response variables were liver wet weight and body weight, expressed as BW–SCW. Initial explanatory variables were total length (TL), sex, wild or released (W/R), area, number of attached *Neoheterobothrium hirame*, and season. Seasons were defined as consecutive 2 mo periods. GLMMs were conducted with offset terms of log(BW – SCW) and log(GLM-predicted BW – SCW) for H and Kr, respectively, and with Gaussian family and log-link function. Year was included as a random factor. The influences of W/R, sex, area, and season were assessed on the basis of released fish, female, northern area, and July–August, respectively. GLM: generalized linear model; BW: body wet weight; SCW: stomach content wet weight

	Hepatosomatic index			Relative condition factor		
	Estimate	SE	*t*	Estimate	SE	*t*
All seasons						
Intercept	−3.94	0.22	−18.19	0.071	1.053	0.068
TL	0.002	0.0004	3.90	−0.001	0.0001	−8.79
Sex (male)	−0.30	0.017	−17.77	−0.032	0.004	−8.36
W/R (wild)	−0.072	0.014	−5.07	Excluded		
Area (south)	Excluded			−0.006	0.006	−0.91
N. hirame	0.008	0.004	1.91	0.00005	0.001	0.050
Season (Jan–Feb)	0.011	0.018	0.63	−0.028	0.005	−5.61
Season (Mar–Apr)	0.066	0.015	4.30	−0.054	0.005	−11.84
Season (May–Jun)	0.17	0.010	17.10	0.025	0.003	8.41
Season (Sep–Oct)	−0.47	0.019	−23.94	−0.097	0.004	−24.56
Season (Nov–Dec)	−0.42	0.036	−11.61	−0.080	0.006	−12.38
March–April						
Intercept	−3.66	1.77	−2.06	−0.068	21.11	−0.003
TL	0.0007	0.003	0.20	0.0002	0.0008	−0.21
Sex (male)	0.024	0.14	0.18	−0.014	0.030	−0.45
W/R (wild)	−0.10	0.089	−1.08	0.071	0.023	3.06
Area (south)	−0.42	0.16	−2.71	−0.11	0.027	−4.06
N. hirame	0.005	0.024	0.21	0.007	0.005	1.52

sandlance in this season can be explained by its life cycle, i.e. feeding from February to July, estivating from August to November, and spawning in December and January (Hashimoto 1991). Japanese sandlance actively feed on copepods from February to April and on krill *Euphausia pacifica* in May and June before estivation, with increasing SCI as the season progresses (Kobayashi et al. 1995). Highly active sandlance in the period March to June are probably easy prey for Japanese flounder to catch. Additionally, bathymetric correspondence in the distributions of Japanese flounder and Japanese sandlance could account for the consumption of sandlance: Japanese sandlance were abundant at depths from 50 to 70 m, where Japanese flounder were frequently caught by fisheries.

Japanese anchovy was the primary food consumed by Japanese flounder (Table 1, Fig. 3a). Utilization of such pelagic fish reflects the off-bottom feeding behavior of Japanese flounder. Although the importance of Japanese anchovy to Japanese flounder's diet has already been reported (Sato 1975, Yamada et al. 1998), the relationship between the anchovy's seasonal occurrence and feeding by the flounder has not been considered. The disappearance of the anchovy from the diet of Japanese flounder in both northern and southern areas in March and April (Fig. 3a) probably reflects the migration of the anchovy away from the study site. Indeed, the biomass of small pelagic fish (mainly Japanese anchovy) was extremely small off Fukushima in March and April compared with that in other seasons, as revealed by acoustic surveys using a 38 kHz Simrad EK500 scientific echo-sounder (T. Mizuno & K. Yamaki unpubl. data 2006). The low catches of anchovy in March and April (Fig. 4) also provide evidence of this migration. The departure of anchovy from the study area might be related to the low water temperature (<10°C in the bottom layer) in the inshore area from February to May (Fig. 3b). The disappearance of anchovy in March and April would be disadvantageous for Japanese flounder in the southern area, although those in the northern area could utilize Japanese sandlance during that period and hence minimize the negative impact.

The results of the present study agree with those of other studies in terms of the importance of pelagic fishes as prey for piscivorous demersal fishes (Overholtz et al. 2000). Other prey fishes were of relatively low importance, with most accounting for <1% by weight (Table 1). Most prey fishes other than sandlance and anchovy do not form dense groups but instead have a scattered distribution, possibly indicative of a low encounter frequency with Japanese flounder. Additionally, the present study results were consistent with other studies of Japanese flounder diets, in terms of the importance of piscivory (Dou 1995) and identification of ontogenetic shifts in prey consumption from mysids to fishes (Minami 1997, Yamada et al. 1998).

The Sendai Bay–Joban area is highly productive for Japanese flounder, possibly resulting in high stocking effectiveness (Fujita et al. 1993, Tomiyama et al. 2008a), with an annual commercial catch of this species of >1000 t in Miyagi, Fukushima, and Ibaraki Prefectures from 2006 to 2008 (Kurita et al. 2010). The present study demonstrated the 2 predominant food items (anchovy and sandlance) for Japanese flounder in this area. Both anchovy and sandlance are important prey for many piscivorous animals in the study area, such as other fishes (Kosaka 1969), seabirds (Takahashi et al. 2001, Watanuki et al. 2004, Ito et al. 2009), and cetaceans (Kasamatsu & Tanaka 1992, Tamura & Fujise 2002, Murase et al. 2007), suggesting the general importance of these prey fishes for top predators. Additionally, the impact of *Neoheterobothrium hirame* infection on Japanese flounder has been small in this area (Tomiyama et al. 2009b) and no negative effects on hepatosomatic or somatic condition were detected in the present study (Table 2). This parasite has serious impacts (anemia and reduction in somatic condition) on Japanese flounder populations in other localities (Shirakashi et al. 2006). Japanese flounder can resist *N. hirame* infection by feeding sufficiently (Nakayasu et al. 2005), and our results reflect the high food availability in the study area.

The presence of anchovy and sandlance strongly support the production of piscivorous fishes. Utilization of sandlance has been observed in Japanese temperate bass *Lateolabrax japonicus* (Kosaka 1969) and the snailfish *Liparis tanakai* (Kawasaki et al. 1983) in Sendai Bay. Japanese anchovy is consumed by many piscivorous fishes, such as white-spotted conger *Conger myriaster* (K. Goto unpubl. data 2004), amberfish *Seriola quinqueradiata* (Okata 1975), and the flathead *Platycephalus* sp. 2 (T. Tomiyama unpubl. data 2009). The anchovy has flourished in recent decades (1990 to 2010) and is the most important food source for top predators in some areas (Zhang et al. 2007). Japanese sandlance population in the study area drastically declined in the period 1988 to 1990 because of high fishing pressure (Kobayashi et al. 1995). Such fluctuation in stocks might affect predator feeding. Further studies are necessary to clarify the long-term changes in predator–prey relationships and subsequent effects on the condition of predators.

The spatial differences in prey utilization and somatic condition were especially observed in March and April, before the spawning season of Japanese flounder in the study area (May to September; Kurita et al. 2010). The greater body weight of females than males in March and April (Table 2) and high body weight from May to August (Fig. 7) are probably related to gonad development. Prey consumption can affect spawning (Tsuruta 1992, Kurita et al. 2003) and subsequent egg and larval survival in some fishes (Marteinsdottir & Begg 2002). Future studies will assess the impact of spatial variation in fish condition on reproductive success.

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