

Feeding relationships among fishes in shallow sandy areas in relation to stocking of Japanese flounder

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ABSTRACT: Juvenile Japanese flounder *Paralichthys olivaceus* inhabit shallow sandy areas and consume chiefly mysids. Hatchery-reared *P. olivaceus* (ca. 100 mm in total length) released in stock enhancement programs also consume mysids. To examine whether stocking is implemented within the available carrying capacity, we assessed the feeding relationships among fishes, based on the stomach contents of fishes collected off the coast of Fukushima, Japan. Similarity in diet suggested that 10 species, particularly the poacher *Ocella iburia* and nibe croaker *Nibea mitsukurii* were potential competitors of *P. olivaceus* juveniles for food. Large inter-annual variability in the abundance of these competitors was observed, suggesting variability in their consumption of mysids. The predominant mysid *Orientomysis mitsukurii* was abundant every year, and growth rates of wild *P. olivaceus*, estimated from otolith microstructure, were mostly high (>1 mm d⁻¹), even in the year when wild *P. olivaceus* were highly abundant. In our statistical model, abundance of mysids and consumption of mysids by fishes significantly affected the growth rates of wild *P. olivaceus* but only accounted for a small proportion (i.e. explained 2.2 and 2.4% of variance, respectively) of the total compared to the body size of juveniles (30.0%) and bottom water temperature (4.5%). These results suggest that the productivity of mysids is usually high enough to support the production of mysid consumers, but exceptionally high abundances of wild *P. olivaceus* or other competitors can reduce the available carrying capacity. In such a situation, stocking should be restricted so as not to reduce productivity of wild fishes.

KEY WORDS: Flatfish · Mysids · Growth rates · Linear models · Stock enhancement · Carrying capacity

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INTRODUCTION

Coastal waters, including estuaries and sandy beaches, are vital nursery grounds for many demersal fishes. These areas are often used for stocking (i.e. releasing hatchery-reared [HR] juveniles) of commercially important organisms. Stocking should be implemented within the 'available' carrying capacity (Støttrup 2004), to allow for a residual production

of prey after consumption by both existing and stocked predators. Some studies suggest methods to determine stocking density within the carrying capacity (Taylor et al. 2005, Yamashita et al. 2006, Taylor & Suthers 2008, Ochwada-Doyle et al. 2012), but current stock enhancement programs have not given this concept much consideration. The number of juveniles released is not determined on an ecological basis, but rather by the ability to produce juve-

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niles (Molony et al. 2003), the demand from stakeholders, or economic and political factors. Ecological problems caused by excess releases of HR juveniles into the field have scarcely been examined or preemptively mitigated. Ecological factors including carrying capacity should be considered in light of responsible stock enhancement (Blankenship & Leber 1995), but the ecological impact of stocking may be masked by natural fluctuations and thus difficult to quantify.

Shallow inshore sandy beaches function as nurseries for many fishes, including Japanese flounder *Paralichthys olivaceus*. This species is the most important flatfish in coastal fisheries and is a major target species for stock enhancement in Japan: >20 million HR juveniles are released per year in coastal waters to increase catches. Wild and HR juveniles primarily utilize mysids as a food source, especially *Orientomysis* (revised from *Acanthomysis*, Fukuoka & Murano 2005) *mitsukurii* off the Pacific coast of northern Japan (Yamada et al. 1998, Tomiyama et al. 2011). Such mysids are the predominant prey for many demersal fishes in shallow coastal waters (Hostens & Mees 1999, Katayama et al. 2008). However, the available productivity of mysids after consumption by wild predators has never been evaluated.

The main objective of this study was to examine the feeding relationships among *Paralichthys olivaceus* and other demersal fishes and to assess whether the carrying capacity in a shallow coastal area is saturated through consumption of mysids by predatory fishes, including wild and HR *P. olivaceus*. We implemented the following 3 steps to accomplish such an assessment. First, we investigated the feeding relationships between fishes in shallow sandy areas through stomach content analysis and identified the fish species that consume mysids. Second, we examined the temporal patterns in the assemblage of both mysids and their predators, and estimated the consumption of mysids by predators. Third, we calculated individual growth rates of wild juvenile *P. olivaceus* and constructed a growth model using measured variables; the individual growth rate can be used as the response to competition (Forrester et al. 2006). The abundance of prey and consumption of prey by predators were considered as potential factors influencing the growth of wild fish. We hypothesized that carrying capacity would not be reached when these factors were eliminated from the model. We also compared mysid consumption by predators to the estimated productivity of mysids to test the validity of our assessment.

MATERIALS AND METHODS

Study site and stocking

The coastal waters off Fukushima (36° 52' to 37° 54' N, 140° 47' to 141° 02' E, ca. 160 km of coastline) in northeastern Japan were selected as the study site. The study area includes 9 sites (Tomiyama et al. 2008a). At each site, 100 000 to 150 000 HR *P. olivaceus* approximately 100 mm in total length (TL) were released annually in areas with depths <10 m during June to September of 2001, 2002, and 2004 to 2006 and during October and November of 2003. Substrata around the release sites primarily consisted of sand (median grain size, mean \pm SD = 163 \pm 35 μ m). We surveyed sites A, B and E (36° 53' to 37° 46' N, see Tomiyama et al. 2009, 2011).

Sample collection

Fishes were collected by towing a 2 m wide, 6 mm mesh beam trawl at a speed of 3.7 km h⁻¹ (2 knots) for 10 min (ca. 0.6 km) during the day. We conducted 3 to 6 hauls per day at depths of 3 to 15 m (1.5 m intervals) with a frequency of ca. 2 days per month from June to October of 2001 to 2006 for a total of 192 hauls. Towing distance was calculated from a differential GPS. The catch efficiency of fishes was consistently assumed to be 0.2, following the efficiency of juvenile *Paralichthys olivaceus* collected by the 2 m beam trawl towed at a speed of 2 knots (Kimoto et al. 2001). Although catch efficiency would vary among fish species and body sizes, such variation was not considered because of the lack of information. During each survey, the water temperature of the bottom layer was measured using a portable salinity and temperature sensor (UC-78, Central Kagaku). This beam trawl survey also aimed to investigate the small-scale bathymetric distribution of fishes (3–15 m).

Due to the low catchability of larger fish in the beam trawl, additional sampling was undertaken using a 360 m gillnet with 108 to 150 mm mesh at depths of 6 to 9 m in July to November 2002 to 2006 (Tomiyama et al. 2009). The gillnet was set before dusk and hauled the next morning. A total of 9 gillnet surveys were carried out.

To investigate the larger-scale bathymetric distribution (10–50 m) of fish species consuming mysids, an otter-trawl (ca. 7.5 m mouth opening, 13 m in length, 10 mm mesh) was towed by the RV 'Takusui' (30 t) at a speed of 4.6 km h⁻¹ (2.5 knots) for 30 min

(ca. 2 km) in the daytime at depths of 10, 20, 30, and 50 m along a latitude 37° 03' N. This survey was conducted monthly from June to October 2006. The number of individuals collected per 30 min of towing was determined for each depth and represented the catch per unit effort (CPUE). All fishes collected by the beam trawl, gillnet, and otter trawl were transported to the laboratory under chilled conditions.

Mysids and other small crustaceans were collected by towing a sledge net (0.6 m width, 0.4 m height, 0.7 mm mesh) at a speed of 2.8 km h⁻¹ (1.5 knots) for approximately 100 m at depths of 5, 10, and 15 m from June to December 2001. The tows were repeated 4 times at each depth per date. Additional sampling was undertaken at depths from 6 to 10.5 m from 2002 to 2005 without replication. These collections were accompanied by beam-trawl collections for fishes, and the samples were fixed with 10% formalin. The catch efficiency of the sledge net was not considered.

Measurements

TL (mm) and body weight (BW, g) of each fish was measured. *Paralichthys olivaceus* were identified as either wild or HR based on body color anomalies and fin ray counts. HR *P. olivaceus* have hypermelanosis on the blind side or pseudoalbinism on the ocular side, and their fin rays are more numerous than those of wild fish (Tomiyaama et al. 2008b). Stomachs were removed and dissected after being fixed with 10% formalin. Stomach contents were sorted to the species or lowest possible level and then counted and weighed (W , mg in wet weight). Total stomach content weight for each individual fish was used to determine the stomach content index (SCI, %BW). Prey organisms were divided into 10 taxa: mysids, gammarids, cumaceans, shrimps, other crustaceans, fishes, cephalopods, other mollusks, polychaetes, and others. The index of relative importance (%IRI) of each prey taxon was determined as follows: $\%IRI = IRI / \sum IRI \times 100$, $IRI = (\%N + \%W) \times \%F$, where N is number of prey consumed, W is weight of prey consumed, and F is the frequency of fish consuming the prey. The %IRI was determined for each fish species or group. *P. olivaceus* were divided by age, body size, and wild/HR type. Body sizes of age-1 wild *P. olivaceus* largely varied among collection years, and age-1 wild *P. olivaceus* <200 mm often consume mysids, while those ≥ 200 mm chiefly consume fishes (Tomiyaama & Kurita 2011). Hence, the age-1 wild *P. olivaceus* were divided into 2 size classes: ≥ 200 mm and <200 mm. Other fishes in

which ontogenetic diet shifts were observed were also divided into 2 size groups.

Mysids collected by the sledge net were sorted into species. Other prey organisms were identified to the species or lowest possible level. Each species was counted and weighed to determine densities in number (abundance, ind. m⁻²) and weight (biomass, mg m⁻²).

Recent growth rates (RGR, mm d⁻¹) of wild *Paralichthys olivaceus* were investigated by analysis of their otolith microstructure. A total of 197 individuals of wild *P. olivaceus* (15.7 to 146.3 mm TL) collected during 2001 to 2006 were selected for the otolith analysis. Specimens of various sizes were selected from various months each year to consider the growth variability. The lapillus of the ocular side was removed from each individual, air-dried, and mounted onto a glass slide with epoxy resin. The lapilli were polished using a series of 800- to 4000-grit pieces of sandpaper until the nucleus could be observed under a microscope. Daily increment widths over the most recent 6 d were measured on an otolith measurement system (Ratoc System Engineering). The TL of each individual 1 and 6 d before collection was back-calculated using the biological intercept method (Campana & Jones 1992). The smallest individual (10.1 mm TL, collected in 2001) was used as the biological intercept. The average daily growth in TL (mm) from 6 to 1 d prior to collection was used as the RGR.

Analyses

To assess the similarity of feeding habits between fish species, classifications by cluster analysis and non-metric multidimensional scaling (nMDS) were applied based on a Bray-Curtis dissimilarity matrix. Percentage IRI of prey determined for each species/size group was used. Fish species in which <3 stomachs contained food were excluded from the analyses. The cluster analysis was performed by the group average method. Grouping was performed at a dissimilarity of 0.7. Multivariate analyses were conducted using the software R 2.10.1 (www.r-project.org) with version 1.17-2 of the 'vegan' package (Oksanen et al. 2010).

As a potential factor affecting the growth of wild *Paralichthys olivaceus*, daily consumption of mysids by predatory fishes was estimated. The daily ration, namely daily food intake relative to BW, of each fish species (R , %BW) was estimated, modified from Collie (1987):

$$R_i = 24 \times r \times \bar{S}_i \quad (1)$$

$$r = 0.041 \times \exp(0.111 \times WT) \quad (2)$$

where R_i is the daily ration of species i , r is the gastric evacuation rate, \bar{S}_i is the average SCI of species i over 1 d, and WT is water temperature ($^{\circ}C$). The following relationship between \bar{S} and the average SCI in the daytime (S_d) for *P. olivaceus* was obtained from Yamamoto & Tominaga (2007): $\bar{S} = 0.75 \times S_d$. We applied this relationship to all species using their average SCI as S_d . Because HR *P. olivaceus* scarcely eat prey for 6 days after release (DAR; Tomiyama et al. 2011), the R_i was separately determined for those collected before and after 6 DAR. Daily mysid consumption by predators (C_{mys} , $mg\ m^{-2}$) was calculated for each month from June to October in each year as follows:

$$C_{mys} = \sum_i (R_i \times 10^{-2} \times B_i \times P_{mys_i}) \quad (3)$$

where B_i is the biomass ($mg\ m^{-2}$) of predatory fish species i , and P_{mys_i} is the weight proportion of mysids in the diet of species i . P_{mys_i} was determined for each month only when enough samples (≥ 10) were available; otherwise, the value throughout the survey period was used as P_{mys_i} . We excluded the predators who only occasionally consume mysids, because predators with low prey fidelity (i.e. generalists) can switch their prey when competition for food and food limitation increase; 11 fish species were regarded as mysid predators, based on the above cluster analysis (see 'Results').

To explore whether the consumption of mysids exceeded their productivity, we calculated the daily productivity of *Orientomys mitsukurii* for each month from June to October in each year. Although productivity should be estimated with consideration of the size composition of mysids (H. Yamada pers. comm.), we used the daily productivity as follows. Because productivity of *O. mitsukurii* depends on temperature (Yamada & Yamashita 2000), we used the relationship between WT and the production to biomass (P/B) ratio of this species (Yamada 2000): $P/B = 0.005 \times \exp(0.15\ WT)$. The productivity of *O. mitsukurii* was underestimated because the catch efficiency of the sledge net was not considered (Sudo et al. 2011).

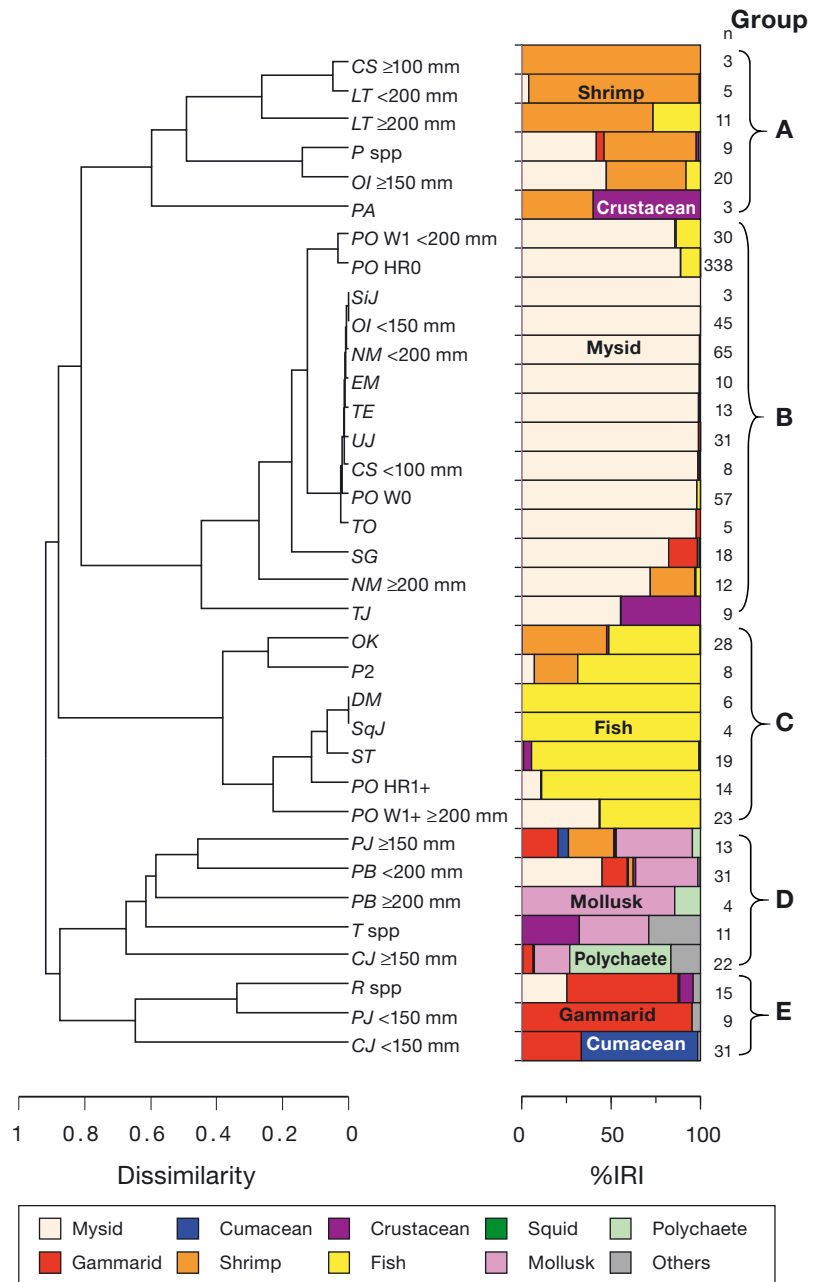


Fig. 1. Hierarchical cluster analysis for dissimilarity of diet among fish species and their prey composition. Full species names are given in Appendix 1. Numerals denote the number of stomachs containing prey. Groups were divided at a dissimilarity = 0.7. IRI: index of relative importance

The relevance of mysid consumption by predatory fishes to the growth rates of wild *Paralichthys olivaceus* was analyzed. A linear model was applied, using the RGR of individual wild *P. olivaceus* as the response variable. WT , TL of *P. olivaceus*, mysid biomass (B_{mys} ; $mg\ m^{-2}$), and C_{mys} were used as initial explanatory variables and were chosen by stepwise backward selection based on the Akaike information

criterion. Preliminarily, TL , B_{mys} , and C_{mys} were natural-logarithm transformed based on the assumption of logarithm-curve fitting to RGR. We assumed that water temperature can be used directly as an explanatory variable for linear models because, under laboratory conditions, the maximum growth rates of juvenile *P. olivaceus* have been shown to increase with water temperatures ranging from 10 to 25°C, peaking at 24°C (Fonds et al. 1995); the observed temperature in our study ranged from 17 to 23.9°C. We used the data from 2001 to 2005 because of the lack of B_{mys} in 2006. Modeling was conducted using the software R.

RESULTS

Fish assemblages

We identified a total of 26 fish species, of which ≥ 5 ind. species⁻¹ were collected by the beam trawl. The dominant fish species (>192 individuals collected by 192 hauls) included the poacher *Ocella iburia*, nibe croaker *Nibe mitsukurii*, the dragonets *Eleutherochir mirabilis* and *Repomucenus* spp. (mostly *R. ornatipinnis*), *Paralichthys olivaceus*, and red tongue sole *Cynoglossus joyneri* (Appendix 1). Age-0 wild *P. olivaceus* were primarily collected in 2005 (308 individuals, 76%). In our gillnet surveys, ≥ 5 ind. species⁻¹ were collected for 8 species.

Mysids were observed in the stomachs of 19 fish species (Appendix 1). Fishes that frequently consumed mysids (>50% occurrence) included *Ocella iburia*, *Nibe mitsukurii*, *Eleutherochir mirabilis*, the red gurnard *Chelidonichthys spinosus*, Japanese whiting *Sillago japonica*, Bensasi goatfish *Upeneus japonicus*, the hairychin goby *Sagamia geneionema*, and 4 Paralichthyidae fishes (*Paralichthys olivaceus*, *Pseudorhombus* spp. [mostly *P. pentopthalmus*], *Tarphops oligolepis*, and *T. elegans*).

Feeding relationships

The cluster analysis assigned 14 fish components (11 species) to the mysid-feeding group (Group B, Fig. 1). Mysids contributed to 55 to 100% of the diet of each component of this group. Other groups chiefly consisted of shrimp-feeding (Group A), piscivorous (Group C), mollusk- and polychaete-feeding (Group D), and gammarid-feeding species (Group E).

Relatively high importances (41 to 47%) were observed in certain species of these groups: *Pseudo-*

rhombus spp., *Ocella iburia* ≥ 150 mm, age-1+ wild *Paralichthys olivaceus* > 200 mm, and stone flounder *Platichthys bicoloratus* < 200 mm.

The ontogenetic dietary shift between the groups was clear in the nMDS biplot (Fig. 2). *Chelidonichthys spinosus*, *Ocella iburia*, and *Paralichthys olivaceus* showed ontogenetic changes from Group B (mysid-feeding) to Groups A or C (shrimp-feeding or piscivorous). The greatest change was observed in *C. spinosus* (i.e. longest distance between the size groups). Ontogenetic dietary shifts were also observed in *Cynoglossus joyneri* and black cow-tongue *Paraplagusia japonica* (Group E to Group D). No shift from Group B to Groups D or E was observed.

Depths of occurrence varied among species. Most mysid feeders were observed at wide ranges of depths, but *Tarphops oligolepis*, *T. elegans*, and *Sagamia geneionema* were observed primarily at > 10 m (Fig. 3a). In contrast, *Eleutherochir mirabilis* were collected primarily at depths < 6 m. In the CPUE survey, most mysid feeders were abundant at 10 to 30 m, except for *T. elegans*.

Mysid species in the diet largely included *Orientomysis mitsukurii* (Fig. 3b). The contribution from *O. sagamiensis*, a larger mysid than *O. mitsukurii*, was relatively high (>15% weight) in age-0 wild *Paralichthys olivaceus*, *Tarphops elegans*, *Nibe mitsukurii* ≥ 200 mm, *Ocella iburia* < 150 mm, *Eleutherochir mirabilis*, *Chelidonichthys spinosus* < 100 mm, and *Pseudorhombus* spp., although *Pseudorhombus* belonged to Group A. The proportion of *O. sagamiensis*

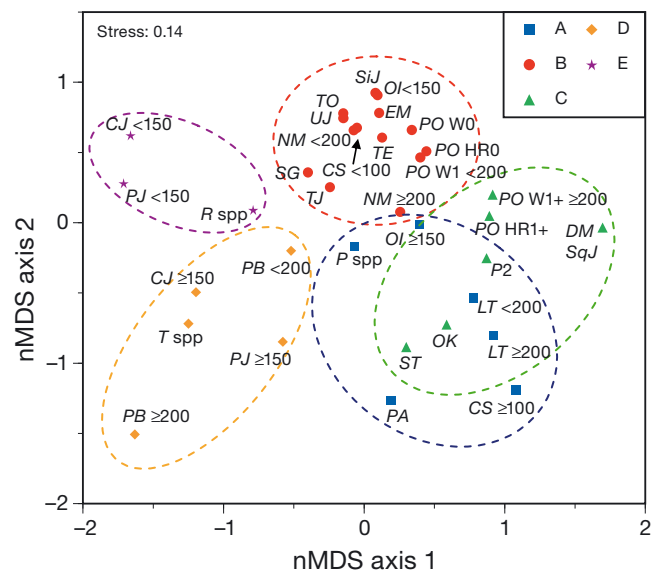


Fig. 2. Non-multidimensional scaling (nMDS) biplot of fish diet. Full species names are given in Appendix 1. Groups were assigned based on the cluster analysis (Fig. 1)

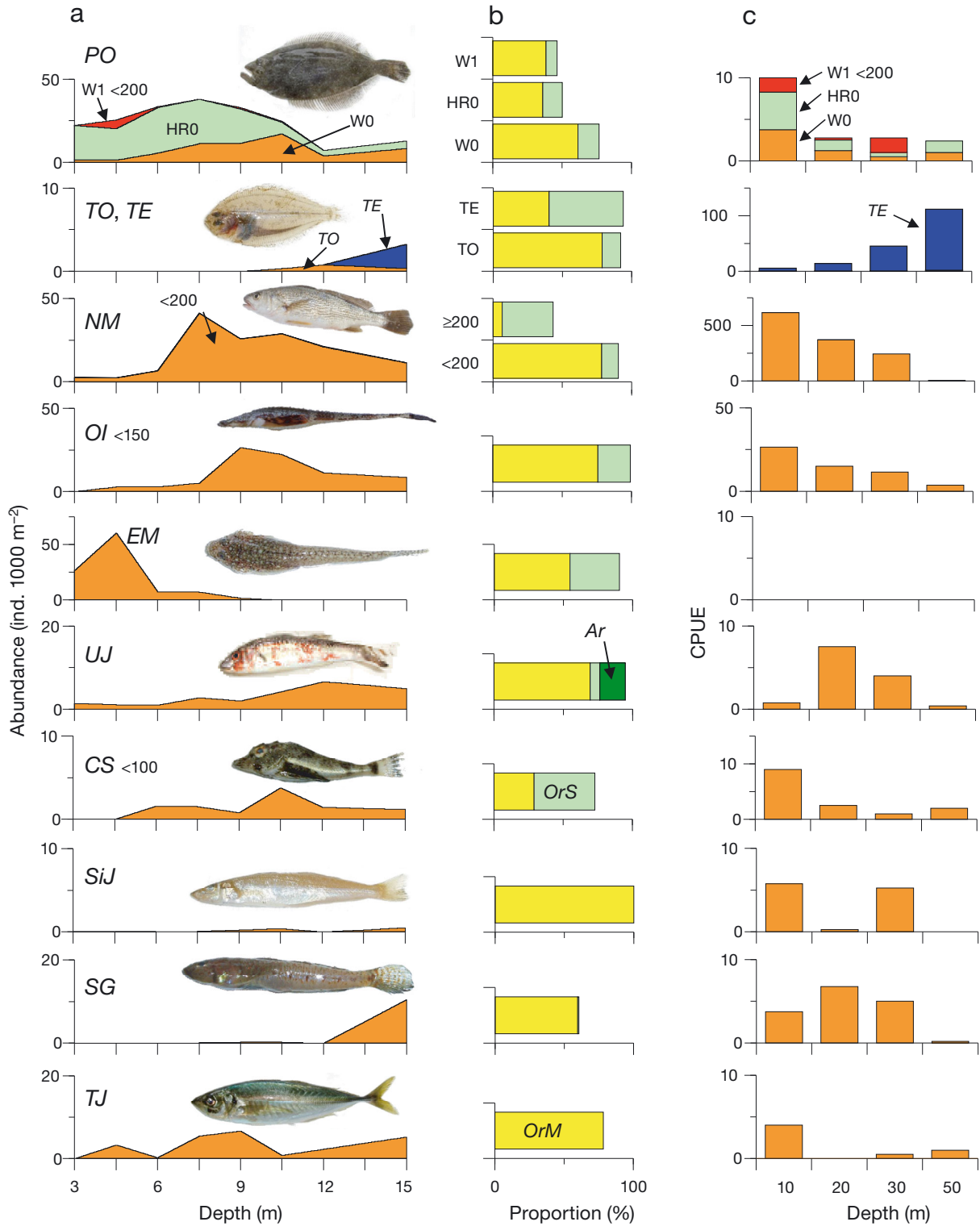


Fig. 3. Bathymetric pattern of the abundance of mysid-feeding fishes and their diet. (a) Average abundance at depths of 3 to 15 m; (b) wet weight proportion of the mysid species to overall diet at depths ≤15 m; and (c) average CPUE (number of collected individuals per 30 min haul of the other trawl) at 10, 20, 30, and 50 m depths in June to October 2006. Full species names of fish are given in Appendix 1. *PO* was divided into age class and origin; *NM* was divided into 2 size classes: ≥200 mm and <200 mm. Mysid species are abbreviated as *OrM*: *Orientomysis mitsukurii*, *OrS*: *O. sagamiensis*, *Ar*: *Archaeomysis* spp. Average abundance (a) was determined for each depth class divided by 1.5 m intervals. The y-axes are different among (a), (b), and (c)

Table 1. Abundance and biomass of small crustaceans collected by a 0.6 m wide sledge net at depths of 5, 10, and 15 m from June to December in 2001. Data are shown as the mean \pm SD from 87 hauls. *O.*: *Orientomysis*

Organism	Abundance		Biomass	
	(ind. m ⁻²)	(%)	(mg m ⁻²)	(%)
<i>O. mitsukurii</i> (Mysidacea)	406.6 \pm 594.5	91.2	511.3 \pm 828.5	71.2
<i>O. sagamiensis</i> (Mysidacea)	0.8 \pm 1.6	0.2	12.5 \pm 15.8	1.7
<i>Archaeomysis</i> spp. (Mysidacea)	0.1 \pm 0.4	0.0	0.7 \pm 2.1	0.1
Other Mysidacea	0.1 \pm 0.2	0.0	0.2 \pm 0.8	0.0
Gammaridea	11.0 \pm 16.1	2.5	17.8 \pm 38.2	2.5
Cumacea	1.1 \pm 1.5	0.2	10.0 \pm 67.4	1.4
Isopoda	1.3 \pm 4.8	0.3	23.8 \pm 119.8	3.3
Penaeidea	0.6 \pm 1.9	0.1	40.5 \pm 94.6	5.6
<i>Crangon uritai</i> (Caridea)	0.5 \pm 1.5	0.1	54.5 \pm 94.6	7.6
Other Caridea	0.1 \pm 0.6	0.0	6.3 \pm 27.1	0.9
Brachyura	0.3 \pm 0.7	0.1	23.1 \pm 57.2	3.2
Anomura	0.2 \pm 0.6	0.0	4.1 \pm 16.4	0.6
Caridea larvae	10.8 \pm 20.2	2.4	8.4 \pm 15.8	1.2
Brachyura larvae	12.3 \pm 42.9	2.8	3.2 \pm 7.6	0.4
Others	0.1 \pm 0.4	0.0	1.5 \pm 3.8	0.2

was greater than that of *O. mitsukurii* in *T. elegans*, *N. mitsukurii* \geq 200 mm, and *Pseudorhombus*. *Archaeomysis* spp. were often observed only in *Upeneus japonicus*.

Mysid abundance in relation to season and depth

The mysid *Orientomysis mitsukurii* was the predominant small crustacean in numbers and weight (Table 1). Both abundance and biomass were higher at a depth of 5 m than at 10 and 15 m, except in early June (Fig. 4). Abundance at 5 m depth remained high (>900 ind. m⁻²) from late June to mid-September and decreased to <50 ind. m⁻² in mid-November. Biomass decreased dramatically from 2200 to 277 mg m⁻² from mid-July to early August and increased from 319 to 1468 mg m⁻² from late August to mid-September. Seasonal patterns in *O. mitsukurii* abundance were commonly observed in other years where densities were high in August and September (Fig. 5). Biomass of *O. mitsukurii* averaged for each month from June to October were estimated to be 49 to 3020 mg m⁻². The abundance of *O. sagamiensis* was consistently low at <200 ind. m⁻², but the biomass was occasionally high at >1200 mg m⁻² (late August 2005, Fig. 5).

Daily consumption of mysids

The average SCI varied from 0.3 (*Eleutherochir mirabilis* and age-0 HR *Paralichthys olivaceus*) to 3.0 (*Chelidonichthys spinosus* <100 mm; Table 2). The daily ration of mysid feeders at 20°C varied from 1.9% (*E. mirabilis*) to 20.7% (*C. spinosus* <100 mm).

Abundance of mysid predators and C_{mys} largely varied between years (Fig. 6). High abundance (>5 ind. 1000 m⁻²) and biomass (>30 mg m⁻²) were observed in wild and HR *Paralichthys olivaceus*, *Ocella iburia*, and *Nibeia mitsukurii* (Table 2) and these species contributed mostly to C_{mys} . Consumption was highest in October 2005 (50.9 mg m⁻²), mostly due to age-0 wild *P. olivaceus*, and exceed the productivity of *Orientomysis mitsukurii* (4.8 mg m⁻²; Fig. 7). In other months, C_{mys} did not exceed the productivity of *O. mitsukurii*, except in October 2001.

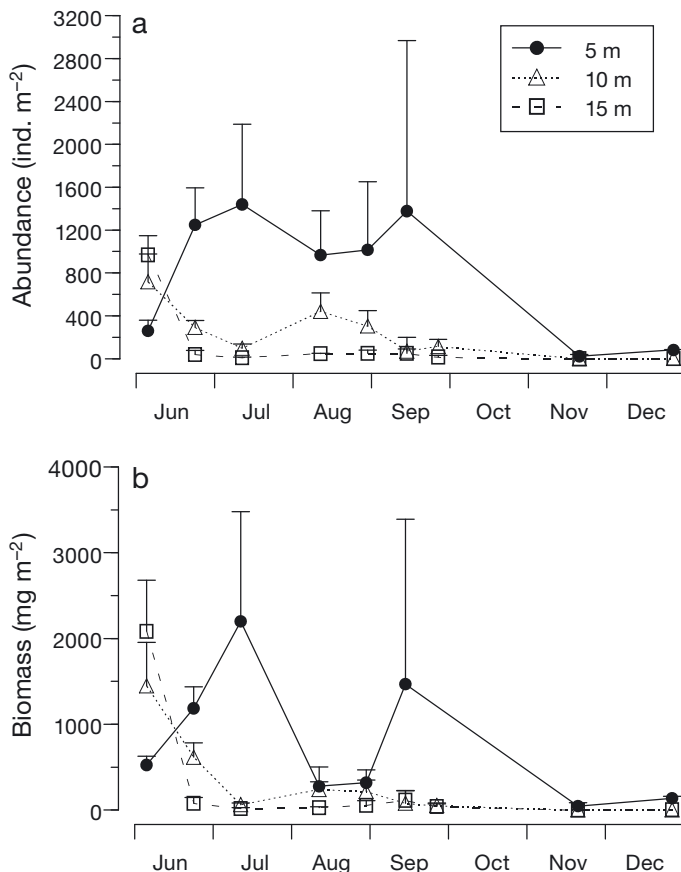


Fig. 4. *Orientomysis mitsukurii*. Seasonal changes (mean \pm SD) in (a) abundance and (b) biomass at 3 depths along the latitude 37° 28' N in 2001

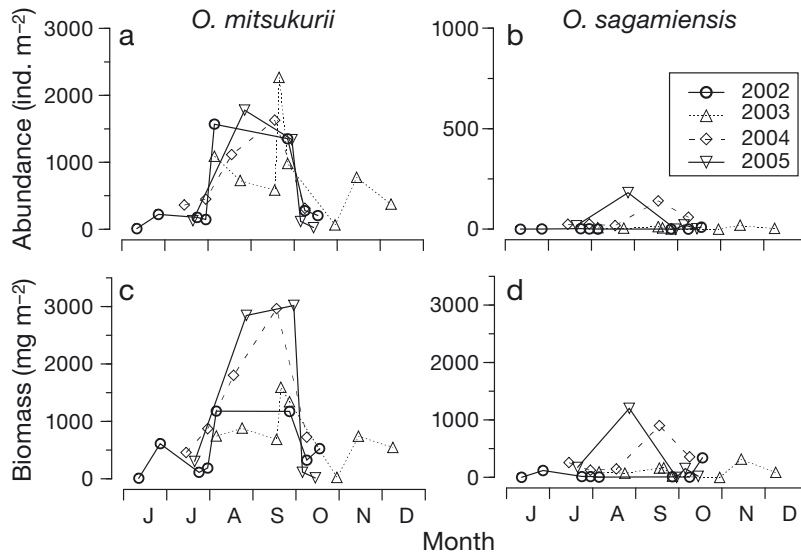


Fig. 5. *Orientomysis mitsukurii* and *O. sagamiensis*. Seasonal changes in (a,b) abundance and (c,d) biomass in 2002 to 2005. Samples were collected at depths <10 m

Table 2. Abundance and biomass, the daily ration of mysid-feeding fishes, and the weight proportion of mysids in their diet for the estimation of mysid consumption by predatory fishes. Data are shown as the mean \pm SD from all months. Catch efficiency was consistently assigned as 0.2. See Appendix 1 for species names. Hatchery-reared Japanese flounder (age 0) were divided into 2 groups: juveniles collected within 5 d after release (DAR) and those collected from 6 DAR. SCI: stomach content index; BW: body weight

Species	Abundance (ind. 1000 m ⁻²)	Biomass (mg m ⁻²)	SCI (%BW)	Daily ration at 20°C (%BW)	Weight proportion of mysids (%)
CS <100 mm	1.5 \pm 2.2	5.7 \pm 12.3	3.0 \pm 2.0	20.7	81.4
OI <150 mm	11.7 \pm 17.0	49.1 \pm 69.0	0.8 \pm 0.6	5.2	99.2
TJ	2.6 \pm 4.5	3.1 \pm 5.2	1.4 \pm 1.7	9.6	78.3
NM <200 mm	25.2 \pm 40.8	66.4 \pm 114.6	0.5 \pm 0.5	3.1	90.4
NM \geq 200 mm	0.1 \pm 0.3	8.7 \pm 30.3	0.5 \pm 0.9	3.1	43.4
SiJ	0.3 \pm 0.5	0.7 \pm 0.8	0.8 \pm 0.9	5.3	100
UJ	2.6 \pm 5.9	3.4 \pm 8.8	2.3 \pm 2.2	15.3	94.8
EM	4.6 \pm 6.3	5.2 \pm 9.9	0.3 \pm 0.5	1.9	90.5
SG	2.1 \pm 3.9	2.0 \pm 3.8	0.7 \pm 0.4	4.5	60.6
PO W0	5.6 \pm 14.8	35.1 \pm 113.8	2.9 \pm 1.3	19.6	76.8
PO HR0 (\leq 5 DAR)	1.7 \pm 7.4	11.4 \pm 42.9	0.3 \pm 0.6	2.0	59.0
PO HR0 (\geq 6 DAR)	5.5 \pm 7.8	74.4 \pm 89.6	1.2 \pm 1.3	7.8	49.9
PO W1 <200 mm	0.6 \pm 2.1	32.8 \pm 103.8	1.2 \pm 1.3	8.3	46.4
TO	0.9 \pm 1.5	3.9 \pm 7.8	0.6 \pm 0.3	4.2	92.1
TE	0.9 \pm 2.3	4.8 \pm 11.5	0.6 \pm 0.7	4.3	93.9

Growth rate of wild Japanese flounder

The RGR of wild *Paralichthys olivaceus* ranged from 0.6 to 2.9 mm d⁻¹ and increased with increases in TL (Fig. 8). No clear difference in RGR between years was observed, except for the relatively low RGR in 2006. Inter-annual differences were not tested because a significant interaction between

years and ln(TL) was observed (1-way analysis of covariance, $F_{5,185} = 3.23$, $p < 0.01$).

Our final linear model for the RGR explained 39% of the variance (Table 3). All initial explanatory variables were selected in the model; neither B_{mys} nor C_{mys} were eliminated from the model. *Paralichthys olivaceus* TL accounted for most of the variance (30.0%). WT, B_{mys} and C_{mys} accounted for 4.5, 2.2, and 2.4% of the variance, respectively. TL, WT, and B_{mys} were positively correlated with the growth of *P. olivaceus*, whereas C_{mys} was negatively correlated. The model for the RGR in 2001 to 2006, in which B_{mys} was not included as the initial explanatory variable because of lack of data in 2006, also showed a similar tendency: TL and WT showed positive relationships with RGR while C_{mys} showed a negative relationship.

DISCUSSION

Feeding relationships

The mysid-feeding group (Group B) was the largest of the 5 clusters, supporting the importance of mysids in the production of fishes in shallow sandy areas. Predators with similar trophic preferences often segregate spatially (e.g. Darnaude et al. 2001, Rooper et al. 2006, Yamada et al. 2010). However, it has been hypothesized that specialists concentrate in the most suitable areas to exploit their primary prey (Colloca et al. 2010), as prey distribution affects the predator assemblages (Nemerson & Able 2004). In the present study, spatial and seasonal overlap between the dominant mysid *Orientomysis mitsukurii* and many mysid feeders, abundant at depths ≤ 10.5 m from July to September, may indicate the high abundance and productivity of mysids that can support the coexistence of the mysid feeders. High productivity of the congener *O. robusta* has also been reported, with an annual P/B ratio estimated to be 21 (Sudo et al. 2011).

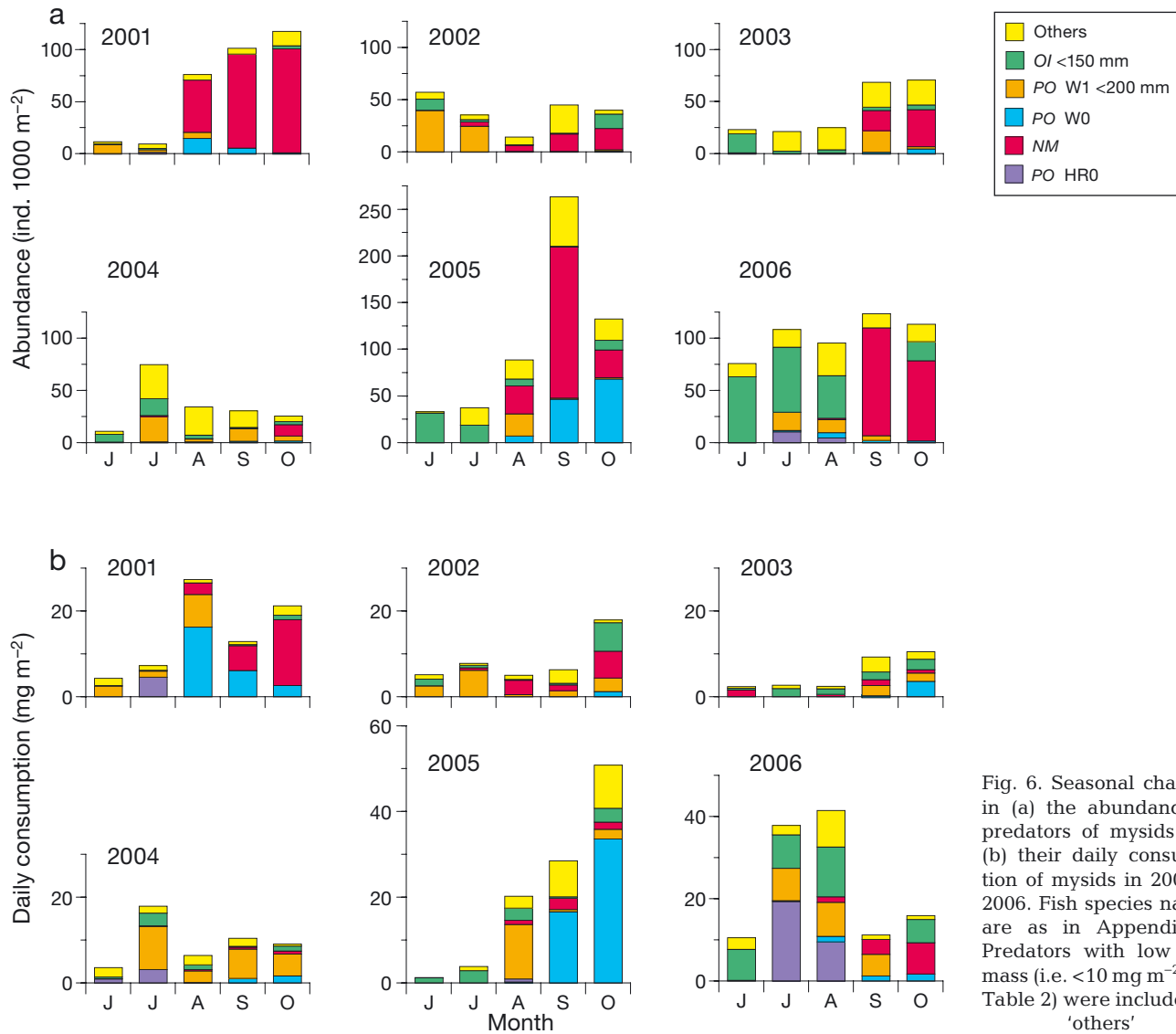


Fig. 6. Seasonal changes in (a) the abundance of predators of mysids and (b) their daily consumption of mysids in 2001 to 2006. Fish species names are as in Appendix 1. Predators with low biomass (i.e. $<10 \text{ mg m}^{-2}$, see Table 2) were included in 'others'

In the study area, there was no interaction through ontogeny between epifaunal feeders (Groups A, B, and C) and infaunal feeders (Groups D and E), as revealed by the nMDS. Morphological or behavioral differences may be related to these independent groups.

Competition for mysids

Dietary overlap, as observed in many environments (Sá et al. 2006, Castellanos-Galindo & Giraldo 2008, Dolgov 2009, Velasco et al. 2010), does not necessarily imply competition unless utilization of the same resources causes harmful results to the individuals (Underwood 1997, Link et al. 2005). In this study,

the selected model for growth of wild *Paralichthys olivaceus* included the biomass of mysids and consumption of mysids by predators as explanatory variables, suggesting the possibility of competition for mysids among predators. Additional experiments with appropriate designs are necessary to provide evidence of competition (Connell 1983, Underwood 1986, 1997).

Competition for mysids would be weak, if it was indeed occurring in the study area, for the following 3 reasons. First, mysids were abundant in the study area, and their coexistence with many mysid feeders was observed, as previously mentioned. Second, the contribution of both mysid biomass and consumption of mysids in the model for the growth of wild *Paralichthys olivaceus* was small. Third, for the most part,

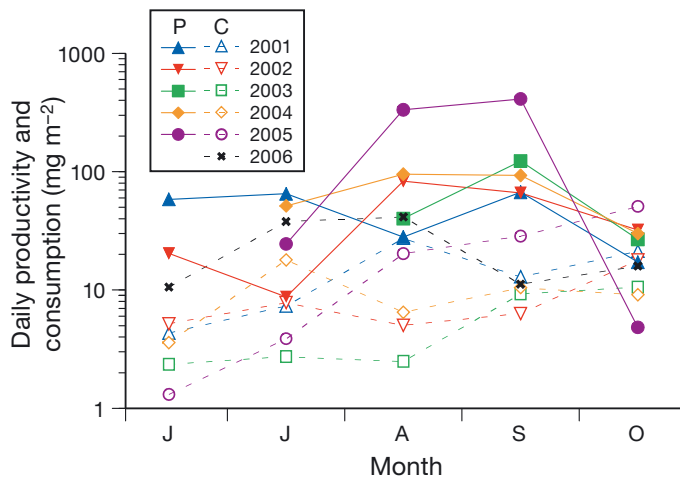


Fig. 7. Seasonal changes in the daily productivity and consumption by predators of *Orientomysis mitsukurii*. Productivity was not determined for 2006 due to lack of the mysid biomass data in that year. P: productivity; C: consumption

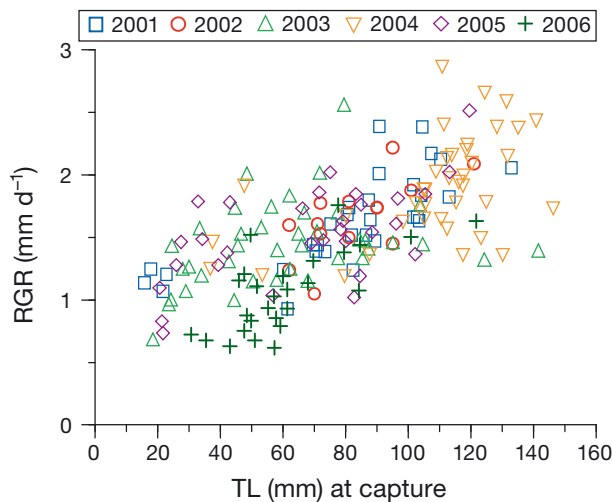


Fig. 8. *Paralichthys olivaceus*. Total length (TL) at capture and recent growth rates (RGR) of age-0 wild juveniles, collected from July to August 2001, September to October 2002 and 2003, August to October 2004 and 2005, and July to September 2006

Table 3. *Paralichthys olivaceus*. Results of the linear model for recent growth rates of wild juveniles. Multiple R-squared of the model was 0.39. TL: total length; WT: bottom water temperature; B_{mys} : biomass of mysids; C_{mys} : daily consumption of mysids by predators

Source	ANOVA				Model summary			
	df	SS	F	p	Parameter	Estimate	SE	p
Error	165	17.1			Intercept	-2.01	0.46	<0.001
ln TL	1	8.4	81.2	<0.001	ln TL	0.56	0.055	<0.001
WT	1	1.3	12.3	<0.001	WT	0.049	0.012	<0.001
ln B_{mys}	1	0.6	5.9	0.017	ln B_{mys}	0.074	0.031	0.017
ln C_{mys}	1	0.7	6.5	0.012	ln C_{mys}	-0.091	0.048	0.060

consumption of mysids by predators was lower than the productivity of *Orientomysis mitsukurii*, with 1 exception. Consumption was much greater than productivity only in October 2005, largely due to the occurrence of an exceptionally large year class of *P. olivaceus* (Tomiyama et al. 2008a). Wild *P. olivaceus* chiefly consumed larval *Engraulis japonica* and juvenile *Nibea mitsukurii* around that month, while *N. mitsukurii* and *Occella iburia* still consumed mysids (T. Tomiyama unpubl. data). Such a dietary change in *P. olivaceus* may mitigate competition. Nonetheless, it is unrealistic to assume that the daily consumption of mysids was ca. 11 times the daily production of *O. mitsukurii* in October 2005. The consumption of mysids might be overestimated, or mysid production might be underestimated due to the sampling bias of mysids. The estimation of consumption can be modified, although the daily ration of *P. olivaceus* was similar to that reported in another study (18.1%, Yamamoto & Tominaga 2007).

If both inter- and intraspecific competition are negligible, flatfish can achieve maximum growth under conditions of ample food (Amara et al. 2001, Reichert 2003, Tomiyama et al. 2007). Here, maximum growth is controlled primarily by water temperature (van der Veer & Witte 1993). However, such cases are rare because the growth of juvenile flatfish is usually limited by their food supply (Poxton et al. 1983, Karakiri et al. 1989, Jenkins et al. 1993, Furuta 1999).

Stocking of Japanese flounder

This study illustrated the large interannual variability in the consumption of mysids by predators, due to large fluctuations in the abundance of mysid consumers. This result indicates that optimal stocking density, i.e. the maximal number of releases within the available carrying capacity, can vary among years. The optimal stocking density is regulated mostly by the abundances of predators and prey (Yamashita et al. 2006) or the area of key habitat (Taylor et al. 2006). In Ohno Bay, a semi-closed area in Japan, the carrying capacity is sometimes reached, and stocking of *Paralichthys olivaceus* causes growth reductions of their wild counterparts, as simulated by an ecophysiology model (Yamashita et al. 2001, 2006). Although the mysid abundance appeared to be greater in our study area compared to Ohno Bay

(e.g. average biomass of mysids in late August to early September; 1606 mg m⁻² in our study area versus 324 mg m⁻² in Ohno Bay), the variation in the available carrying capacity should be considered to avoid overstocking (i.e. excess release of HR juveniles reducing the growth of the wild counterparts). Determining the optimal stocking density is a difficult issue because the abundances of predator and prey and their seasonal changes are currently unpredictable before the release of HR fish. It may be realistic to determine the stocking density empirically from the average available carrying capacity based on a long-term monitoring of abundances of predator and prey as well as consumption of prey. Predictive models using the preliminarily obtained parameters (Yamashita et al. 2006, Taylor & Suthers 2008) may also be useful to determine the stocking density.

The impact of stocking on the production of wild counterparts should also be examined. Overstocking is a concern (Yamashita et al. 2006), but it has never been demonstrated that stocking actually affects the productivity of wild fish: mass release of HR *Paralichthys olivaceus* juveniles does not reduce the growth of wild juveniles and only temporarily reduces the consumption of prey mysids by wild juveniles (Tanaka et al. 2005). Rapid post-release mortality of HR fish (Sparrevohn & Støttrup 2007, Sudo et al. 2008) and their low feeding rates during a short period after release (Tomiyaama et al. 2011) may also indicate a low impact of stocking. Further studies are required.

In conclusion, predation pressure determined by both availability of prey and predator abundance largely varies among seasons and years, leading to a variation in the optimal stocking density. The level of stocking should be carefully determined, especially in highly competitive environments, so as not to reduce the productivity of wild animals.

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Appendix 1. Fishes collected by 192 hauls of a 2 m wide beam trawl and 9 gillnet surveys. Fish species for which <5 individuals were caught were excluded. The numbers of collected individuals, ranges of total lengths (TL), and occurrences of mysids in the stomachs are shown. Abbreviated names were assigned to species for which ≥ 3 stomachs with food were observed. Mysid occurrence is shown as the number of individuals consuming mysids/number of observed stomachs with food (number of empty stomachs); nd: no data

Family	Species	Abbreviation	N	TL (mm)	Mysid occurrence
Beam trawl surveys					
Rajidae	<i>Okamejei kenojei</i>	OK	19	nd ^a	nd
Dasyatidae	<i>Dasyatis akajei</i>		9	nd ^a	nd
Engraulidae	<i>Engraulis japonica</i>		32	60–146	nd
Syngnathidae	<i>Syngnathus schlegeli</i>		16	117–213	0 (1)
Triglidae	<i>Chelidonichthys spinosus</i>	CS	68	37–166	8/11 (0)
Platycephalidae	<i>Platycephalus</i> sp.2	P2	9	237–452	1/7 (1)
Agonidae	<i>Ocella iburia</i>	OI	467	73–231	47/47 (4)
Liparidae	<i>Liparis tanakae</i>	LT	13	141–284	2/11 (2)
Carangidae	<i>Trachurus japonicus</i>	TJ	161	35–90	5/11 (4)
Sciaenidae	<i>Nibea mitsukurii</i>	NM	769	23–230	66/66 (6)
	<i>Pennahia argentata</i>	PA	16	92–135	0/3 (3)
Sillaginidae	<i>Sillago japonica</i>	SiJ	7	44–66	3/3 (1)
Mullidae	<i>Upeneus japonicus</i>	UJ	152	38–76	30/31 (4)
Pholidae	<i>Pholis nebulosa</i>		6	104–262	1/2 (0)
Ammodytidae	<i>Ammodytes personatus</i>		11	86–124	0 (1)
Callionymidae	<i>Eleutherochir mirabilis</i>	EM	317	47–65	9/10 (10)
	<i>Repomucenus</i> spp.	R spp	295	59–157	2/15 (3)
Gobiidae	<i>Sagamia geneionema</i>	SG	34	46–78	11/18 (0)
Paralichthyidae	Age-0 wild <i>Paralichthys olivaceus</i>	PO W0	407	13–151	54/57 (1)
	Age-0 HR <i>P. olivaceus</i>	PO HR0	780	52–191	299/338 (49)
	Age-1+ wild <i>P. olivaceus</i>	PO W1+	66	135–335	32/53 (13)
	Age-1+ HR <i>P. olivaceus</i>	PO HR1+	20	187–353	2/14 (6)
	<i>Pseudorhombus</i> spp.	P spp	9	107–146	6/9 (0)
	<i>Tarphops oligolepis</i>	TO	9	57–71	5/5 (2)
	<i>Tarphops elegans</i>	TE	15	64–117	12/13 (2)
Pleuronectidae	<i>Platichthys bicoloratus</i>	PB	55	51–443	13/31 (9)
Cynoglossidae	<i>Cynoglossus joyneri</i>	CJ	587	52–276	2/53 (53)
	<i>Paraplagusia japonica</i>	PJ	74	38–317	0/22 (16)
Tetraodontidae	<i>Takifugu</i> spp.	T spp	35	57–71	0/11 (9)
Gillnet surveys					
Scyliorhinidae	<i>Scyliorhinus torazame</i>	ST	20	374–470	0/19 (1)
Squatinae	<i>Squatina japonica</i>	SqJ	5	254–811	0/4 (1)
Rajidae	<i>Okamejei kenojei</i>	OK	29	273–554	2/28 (1)
Dasyatidae	<i>Dasyatis matsubarae</i>	DM	6	580–715	0/6 (0)
Liparidae	<i>Liparis tanakae</i>	LT	5	315–387	0/5 (0)
Sciaenidae	<i>Nibea mitsukurii</i>	NM	22	208–319	7/11 (8)
Pleuronectidae	<i>Platichthys bicoloratus</i>	PB	5	216–274	0/4 (1)
Cynoglossidae	<i>Paraplagusia japonica</i>	PJ	7	296–325	(7)

^aTotal lengths of *O. kenojei* and *D. akajei* were both >200 mm