Food habits of fishes on unvegetated tidal mudflats in Tokyo Bay, central Japan

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ABSTRACT: To clarify the feeding habits of tidal mudflat fishes, the gut contents of 29 fish species, collected from unvegetated tidal mudflats in Tokyo Bay, central Honshu, Japan, were examined. Ontogenetic changes in food preference were recognized in 21 species, including several of commercial importance (e.g., Acanthogobius flavimanus, Konosirus punctatus, Mugil cephalus cephalus, Plecoglossus altivelis altivelis, and Sardinella zunasi). In general, larvae and/or juveniles of these species fed mainly on small zooplankton or benthic harpacticoid copepods, later switching to other prey items with growth (e.g., gammaridean amphipods, mysids, polychaetes, detritus, bivalves, and juvenile fishes). A cluster analysis based on dietary overlaps showed that the tidal mudflat fish assemblage comprised six feeding guilds (small benthic and epiphytic crustacean, zooplankton, detritus, mollusc, polychaete, and fish feeders). Of these, small benthic and epiphytic crustacean feeders were the most abundantly represented in the number of species.

KEY WORDS: fish assemblage, ontogenetic diet shift, tidal mudflat, trophic guilds.

INTRODUCTION

Unvegetated tidal flats in temperate estuaries and inlets support large numbers of fishes; providing nurseries for a number of species, including some of commercial importance,¹⁻⁷ and the fish assemblage structures differ from those in fringe vegetated habitats.⁶⁻¹⁰ Tidal flats occupy a significant component of the total estuarine habitat available to fishes⁶ and play important roles as foraging grounds.¹¹⁻¹⁴ However, the patterns of food resource utilization within tidal flat fish assemblages have rarely been examined to date, although some information does exist.¹⁵⁻¹⁹

Extensive loss of tidal flats by reclamation has occurred in temperate coastal Japan in the twentieth century, particularly in Tokyo Bay, central Honshu; 93% of the total tidal flat area (136 km²) being lost between 1936 and 1990.²⁰ It is highly likely that the loss of tidal flats in the bay has reduced the habitat available for several fish species and affected their local populations.²¹⁻²⁴ To improve this situation, restorations of some shoreline environments by the construction of artificial tidal flats have been made or are planned.²⁵ The goal of such restorations is to establish stable ecosystems including the species commonly observed on natural tidal flats.²⁶ However, such restorations cannot be realistically achieved without detailed information on the resource utilization patterns of tidal flat fishes, owing to the great influence of predatory fishes on prey population structures.²⁷⁻³⁰

Recently, the structure of a fish assemblage on natural tidal mudflats in Tokyo Bay was reported in detail.¹ In the present study, we investigate the food habit of each fish species within such an assemblage and identify the feeding guild structure in the assemblage by determining the degree of dietary overlap among various species.

MATERIALS AND METHODS

Sampling

The study was carried out on seven estuarine unvegetated mudflats in Tokyo Bay, central Japan (Fig. 1). In general, intertidal flats drain completely at low tide, resulting in most fishes that inhabit such flats at high tide aggregating on subtidal flats as the tide ebbs.⁹ Accordingly, fishes were collected...
Food habits of tidal mudflat fishes

from the subtidal flats (<1 m deep at low tide) using a small seine net (0.8 mm × 0.8 mm square mesh, 10 m wide and 1 m deep with a 3.5-m long purse-bag at its center) at low tide in daytime from April 1997 to March 1998. All samples were fixed in 10% formalin in the field and later preserved in 70% ethanol in the laboratory. Further details of the sampling sites and methods are given in Kanou et al.4

Gut content analysis

In total, 29 fish species with seven or more individuals containing food were subjected to gut content analyses; fewer than seven individuals being considered to achieve limited food item representation.31 The number of specimens and body sizes of each species used for the gut content analyses are given in Table 1. Scientific names of fishes follow Nakabo.32 Food items in the gut contents of each specimen were identified to the lowest possible taxon. The percentage volume of each food item in the diet was visually estimated under a binocular microscope as follows: gut contents were squashed on a 1 × 1 mm grid slide to a uniform depth of 1 mm and the area covered up by each item measured. The latter was then divided by the total area of the gut contents in order to calculate the percentage volume of that item in the diet. Food resource use was expressed as mean percentage composition of each item by volume, which was calculated by dividing the sum total of the individual volumetric percentage for the item by the number of specimens examined.33,34 Specimens with empty stomachs were excluded from the analyses.

Data analysis

Data were pooled for each season, since the aim of the study was to describe the feeding patterns of fish species within the assemblage as a whole. Such pooling prevent any analysis of temporal changes in diet over the sampling period but is a necessary compromise between a full investigation of seasonal changes in diet and the need to procure samples of adequate size.35

Some tidal mudflat fishes change their diet with body size.17,19 On the present mudflats, individuals of various body size for many species occurred under study. It was appropriate, therefore, to examine whether or not differences existed in the feeding habits among different-size classes. To examine such dietary change with growth, each fish species was subdivided into several size classes. Since the percentage volume of each major food item in the diet of each species changed rather abruptly at a critical size, the length at which this change occurred was taken as the dividing point for the size classes. Because the assumption of homogeneity of variances for parametric analyses was not met, even for transformed data, non-parametric Kruskal–Wallis and Mann–Whitney analyses were employed to test whether or not size class differences in the percentage volume of each major food item existed.

In order to divide the tidal mudflat fishes into groups that took similar food, dietary overlaps were calculated and subjected to a cluster analysis. For the calculation of dietary overlaps, prey items were grouped in mutually exclusive categories (Table 2). Calculation of the dietary overlap between all species pairs was based on mean percentage volume of each prey category. When successive changes in food preference by size class were recognized, each size class of the species was regarded as a separate unit in the cluster analysis. The percentage similarity index (PS) was used to determine the dietary overlap between species.36

Fig. 1 Map of the study sites (●) in Tokyo Bay, central Honshu, Japan.
Table 1  Number of specimens and body size of each species used for gut content analyses

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>No.</th>
<th>Standard length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clupeidae</td>
<td>Konosirus punctatus</td>
<td>32</td>
<td>11–63</td>
</tr>
<tr>
<td></td>
<td>Sardinella zunasi</td>
<td>29</td>
<td>8–53</td>
</tr>
<tr>
<td>Cyprinidae</td>
<td>Tribolodon brandti</td>
<td>31</td>
<td>12–118</td>
</tr>
<tr>
<td>Osmeridae</td>
<td>Plecoglossus altivelis altivelis</td>
<td>40</td>
<td>13–59</td>
</tr>
<tr>
<td>Mugilidae</td>
<td>Chelon affinis</td>
<td>59</td>
<td>15–126</td>
</tr>
<tr>
<td></td>
<td>Moolgara perusii</td>
<td>16</td>
<td>24–36</td>
</tr>
<tr>
<td></td>
<td>Mugil cephalus cephalus</td>
<td>53</td>
<td>21–132</td>
</tr>
<tr>
<td>Atherinidae</td>
<td>Hypothenus valenciennes</td>
<td>10</td>
<td>11–15</td>
</tr>
<tr>
<td>Platycephalidae</td>
<td>Platycephalus sp.</td>
<td>32</td>
<td>10–59</td>
</tr>
<tr>
<td>Percichthyida</td>
<td>Lateolabrax japonicus</td>
<td>131</td>
<td>13–142</td>
</tr>
<tr>
<td>Leiognathidae</td>
<td>Leiognathus nuchalis</td>
<td>32</td>
<td>9–37</td>
</tr>
<tr>
<td>Teraponidae</td>
<td>Rhyncopelates oxyrynchus</td>
<td>47</td>
<td>9–38</td>
</tr>
<tr>
<td></td>
<td>Terapon jarbua</td>
<td>26</td>
<td>10–59</td>
</tr>
<tr>
<td>Pholididae</td>
<td>Pholis nebulosa</td>
<td>44</td>
<td>25–109</td>
</tr>
<tr>
<td>Blenniidae</td>
<td>Omobranchus punctatus</td>
<td>11</td>
<td>61–79</td>
</tr>
<tr>
<td>Gobiidae</td>
<td>Acanthogobius flavidimanus</td>
<td>181</td>
<td>9–114</td>
</tr>
<tr>
<td></td>
<td>Acanthogobius lactipes</td>
<td>72</td>
<td>14–60</td>
</tr>
<tr>
<td></td>
<td>Acentrogobius pflaumii</td>
<td>26</td>
<td>5–35</td>
</tr>
<tr>
<td></td>
<td>Eutaeniichthys gillii</td>
<td>17</td>
<td>15–31</td>
</tr>
<tr>
<td></td>
<td>Favonigobius gymnauchen</td>
<td>72</td>
<td>11–63</td>
</tr>
<tr>
<td></td>
<td>Gymnogobius breunigii</td>
<td>114</td>
<td>10–52</td>
</tr>
<tr>
<td></td>
<td>G. heptacanthus</td>
<td>44</td>
<td>11–46</td>
</tr>
<tr>
<td></td>
<td>G. macrognathos</td>
<td>115</td>
<td>10–42</td>
</tr>
<tr>
<td></td>
<td>G. ichidai</td>
<td>30</td>
<td>15–30</td>
</tr>
<tr>
<td></td>
<td>G. urotaenia</td>
<td>21</td>
<td>12–24</td>
</tr>
<tr>
<td></td>
<td>Pseudogobius masago</td>
<td>10</td>
<td>9–19</td>
</tr>
<tr>
<td></td>
<td>Tridentiger obscurus</td>
<td>31</td>
<td>10–55</td>
</tr>
<tr>
<td>Pleuronectidae</td>
<td>Kareius bicoloratus</td>
<td>47</td>
<td>26–101</td>
</tr>
<tr>
<td>Triacanthidae</td>
<td>Triacanthus biculeatus</td>
<td>13</td>
<td>23–54</td>
</tr>
<tr>
<td>Total no. individuals</td>
<td></td>
<td>1386</td>
<td></td>
</tr>
<tr>
<td>Total no. species</td>
<td></td>
<td>29</td>
<td></td>
</tr>
</tbody>
</table>

Table 2  Gut content components of fishes collected on tidal mudflats in Tokyo Bay and descriptive code used in Fig. 1

<table>
<thead>
<tr>
<th>Category</th>
<th>Food item (code)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zooplankton</td>
<td>Barnacle larvae (Bl), calanoid and cyclopoid copepods (Cc), chaetognaths (Ch), cladocerans (Cl), crab megalops (Cm), crab zoeae (Cz), fish larvae (Fl), mysid larvae (Ml), shrimp larvae (Sl), unidentified crustacean larvae (Ul)</td>
</tr>
<tr>
<td>Small benthic or epiphytic crustaceans</td>
<td>Cumaceans (Cu), harpacticoid copepods (Hc), gammaridean amphipods (Gm), isopods (Is), myodocopid ostracods (Mo), mysids (My), podocopid ostracods (Pd), tanaids</td>
</tr>
<tr>
<td>Large benthic or epiphytic crustaceans</td>
<td>Burrowing shrimps (Bs), crabs (Cr), crustacean fragments, hermit crabs (He), shrimps (Sh), unidentified crustaceans</td>
</tr>
<tr>
<td>Molluscs</td>
<td>Bivalves (Bi), gastropods (Ga)</td>
</tr>
<tr>
<td>Polychaetes</td>
<td>Errant polychaetes (Ep), sedentary polychaetes (Sp)</td>
</tr>
<tr>
<td>Fishes</td>
<td>Juvenile fishes (Jf)</td>
</tr>
<tr>
<td>Detritus</td>
<td>Detritus (De)</td>
</tr>
<tr>
<td>Plants</td>
<td>Diatoms, filamentous algae (Fa), terrestrial plants</td>
</tr>
<tr>
<td>Insects</td>
<td>Aquatic insects (Ai), terrestrial insects (Ti)</td>
</tr>
<tr>
<td>Sand and shell</td>
<td>Sand (Sa), shell fragments (Sf)</td>
</tr>
<tr>
<td>Others (these items were regarded as separate units in the dietary overlap calculations)</td>
<td>Fish eggs (Fe), fish scales (Fs), invertebrate eggs (Ie), nematodes (Ne), oligochaetes, sea anemones, sea squirts (Ss), trematodes (Tr), unidentified sedentary animals, unidentified materials</td>
</tr>
</tbody>
</table>
where $P_i$ and $P_k$ are proportions by volume of the $i$th prey category in the diets of species $j$ and $k$. The index ranges from 0 (no similarity) to 100 (complete similarity). The overlap data were subjected to an average linkage clustering method in order to generate a diet similarity phenogram for the assemblage. This clustering algorithm was used so as not to unduly distort multivariate space. We arbitrarily adopted a level of 50% similarity (intermediate overlap value) as a basis for dividing the fishes into trophic groups.

**RESULTS**

**Ontogenetic diet shift**

The diets of 29 species studied are shown in Fig. 2. Ontogenetic changes in food habits were recognized in 21 species listed below.

**Konosirus punctatus**

Smaller fish (11–25 mm in standard length [SL]) fed mostly on calanoid and cyclopoid copepods, the relative importance of which decreased significantly in the diet of larger fish (32–63 mm SL; Mann–Whitney analysis, $P < 0.001$). The contribution of detritus to the diet increased with body size (Mann–Whitney analysis, $P < 0.001$).

**Sardinella zunasi**

Although the major food items of this species were planktonic copepods, cladocerans, podocopid ostracods, and polychaetes, their relative importance differed between size classes (8–20 and 22–53 mm SL; Mann–Whitney analysis, $P < 0.001$). The contribution of detritus to the diet increased with body size (Mann–Whitney analysis, $P < 0.001$).

**Tribolodon brandti**

Smaller fish (12–21 mm SL) consumed predominantly cladocerans and harpacticoid copepods, although their importance decreased significantly in the diet of larger individuals (23–118 mm SL; Mann–Whitney analysis, $P < 0.01$ for cladocerans and harpacticoid copepods). The latter fed largely on detritus and errant polychaetes (Mann–Whitney analysis, $P < 0.002$ for detritus; $P < 0.002$ for errant polychaetes).

**Plecoglossus altivelis altivelis**

Smaller fish (13–44 mm SL) took predominantly calanoid and cyclopoid copepods, while larger fish (56–59 mm SL) fed mainly on gammaridean amphipods and mysid larvae. Their contributions to the diet differed significantly between the size classes (Mann–Whitney analysis, $P < 0.002$ for calanoid and cyclopoid copepods; $P < 0.02$ for mysid larvae).

**Chelon affinis**

The diet of smaller fish (15–26 mm SL) consisted chiefly of detritus, along with chaetognaths. The contribution of the former to the diet increased in larger individuals (29–126 mm SL), whereas the percentage volume of chaetognaths decreased (Mann–Whitney analysis, $P < 0.001$ for detritus and chaetognaths).

**Mugil cephalus cephalus**

Smaller fish (21–28 mm SL) captured mostly planktonic and harpacticoid copepods, along with detritus. The contribution of the former two items to the diet decreased with body size (Mann–Whitney analysis, $P < 0.001$ for calanoid and cyclopoid copepods; $P = 0.01$ for harpacticoid copepods), whereas detritus played a significant role in the diet of larger individuals (29–132 mm SL; Mann–Whitney analysis, $P < 0.001$).

**Platycephalus sp.**

In the smaller size class (10–19 mm SL), the diet was almost entirely restricted to planktonic animals, including calanoid and cyclopoid copepods. However, their contribution to the diet decreased with body size (Mann–Whitney analysis, $P < 0.001$), the relative importance of mysids increasing in larger individuals (23–59 mm SL; Mann–Whitney analysis, $P < 0.002$).

**Lateolabrax japonicus**

The major food item of smaller fish (13–31 mm SL) was mysids, along with cumaceans and gam-
maridean amphipods. The relative importance of the former, however, decreased with increasing body size (32–111 and 114–142 mm SL; Kruskal–Wallis analysis, $P < 0.001$). Conversely, the percentage volume of juvenile fishes, including *Acanthogobius flavimanus* and *Gymnogobius breunigii*, increased (Kruskal–Wallis analysis, $P < 0.001$).

**Leiognathus nuchalis**

Smaller fish (9–19 mm SL) preyed mainly on calanoid and cyclopoid copepods, and cladocerans. However, the contribution of the latter to the diet decreased in the larger size class (22–37 mm SL; Mann–Whitney analysis, $P < 0.05$), the relative importance of podocopid ostracods increasing with body size (Mann–Whitney analysis, $P < 0.01$).

**Rhyncopelates oxyrhynchus**

Smaller fish (9–18 mm SL) fed largely on calanoid and cyclopoid copepods, along with mysids and gammaridean amphipods. The contribution of the former to the diet, however, decreased in larger individuals (24–38 mm SL; Mann–Whitney analysis, $P < 0.05$). The relative importance of mysids and gammaridean amphipods tended to increase with body size, although the difference was not statistically significant.

**Terapon jarbua**

Although the major food items of this species were planktonic copepods, gammaridean amphipods and errant polychaetes, their relative importance differed between the size classes (10–13 and 14–59 mm SL; Mann–Whitney analysis, $P = 0.01$ for calanoid and cyclopoid copepods; $P < 0.02$ for gammaridean amphipods and errant polychaetes). Smaller fish (10–13 mm SL) consumed predominantly planktonic copepods, whereas gammaridean amphipods and errant polychaetes played a significant role in the diet of larger individuals (14–59 mm SL).

**Pholis nebulosa**

Calanoid and cyclopoid copepods, and cladocerans constituted the major food of smaller fish (25–30 mm SL). Their contributions to the diets, however, decreased with body size (31–53 and 74–109 mm SL; Kruskal–Wallis analysis, $P < 0.001$). Conversely, the percentage volume of mysids, gammaridean amphipods and crabs increased (Kruskal–Wallis analysis, $P < 0.001$).

**Acanthogobius flavimanus**

Most of the prey of this species were cladocerans, calanoid and cyclopoid copepods, harpacticoid copepods, gammaridean amphipods and polychaetes, their relative importance differing among four size classes (9–13, 14–20, 21–53 and 54–114 mm SL; Kruskal–Wallis analysis, $P < 0.001$ for cladocerans, planktonic and harpacticoid copepods; $P < 0.01$ for gammaridean amphipods; $P < 0.005$ for errant and sedentary polychaetes). Pelagic larvae and juveniles (9–13 mm SL) took chiefly small planktonic animals, while newly settled and benthic juveniles (14–20 mm SL) consumed predominantly small benthic or epiphytic crustaceans, along with polychaetes. The contribution of polychaetes to the diets increased in larger individuals (21–53 and 54–114 mm SL).

**Acanthogobius lactipes**

Smaller fish (14–33 mm SL) preyed primarily on harpacticoid copepods, along with errant polychaetes and detritus, although the relative importance of the former decreased in the diet of larger individuals (35–60 mm SL; Mann–Whitney analysis, $P < 0.001$). The latter fed mainly on settled juveniles of *Acanthogobius flavimanus*, along with errant polychaetes and mysids (Mann–Whitney analysis, $P < 0.001$ for juvenile fish; $P < 0.002$ for mysids).

**Acentrogobius pflaumii**

The major food items of this species were planktonic and harpacticoid copepods, and gammaridean amphipods, their contribution to the diet differing between the size classes (5–8 and 9–35 mm SL; Mann–Whitney analysis, $P < 0.05$ for...
calanoid and cyclopoid copepods; \(P < 0.001\) for harpacticoid copepods and gammaridean amphipods). Smaller fish (5–8 mm SL) fed mainly on copepods, while larger fish (9–35 mm SL) consumed predominantly amphipods.

**Favonigobius gymnauchen**

Although smaller fish (11–18 mm SL) fed largely on bivalves and, to a lesser extent, harpacticoid copepods, their relative importance decreased with body size (19–25 and 28–63 mm SL; Kruskal–Wallis analysis, \(P < 0.001\) for bivalves and harpacticoid copepods). Conversely, the contribution of mysids and detritus to the diet increased in larger individuals (19–25 and 28–63 mm SL; Kruskal–Wallis analysis, \(P < 0.003\) for detritus).

**Gymnogobius breunigii**

Whereas smaller fish (10–29 mm SL) fed predominantly on cladocerans and planktonic copepods, larger fish (30–52 mm SL) took mainly gammaridean amphipods, errant polychaetes and mysids. The relative dietary importance of cladocerans, planktonic copepods, and errant polychaetes differed significantly between the size classes (Mann–Whitney analysis, \(P < 0.001\)).

**Gymnogobius heptacanthus**

The diet of smaller fish (11–18 mm SL) was almost entirely restricted to planktonic copepods and cladocerans. However, the contribution of the latter to the diet decreased for the larger size class (21–46 mm SL; Mann–Whitney analysis, \(P < 0.001\)), the relative importance of benthic or epiphytic animals increasing significantly with body size (Mann–Whitney analysis, \(P < 0.05\) for errant polychaetes, \(P < 0.001\) for podocopid ostracods and harpacticoid copepods).

**Gymnogobius macrognathus**

Calanoid and cyclopoid copepods dominated in the diet of smaller fish (10–21 mm SL), although their importance decreased significantly in the diet of larger individuals (22–42 mm SL; Mann–Whitney analysis, \(P < 0.001\)). The latter fed mainly on benthic or epiphytic crustaceans, including gammaridean amphipods, harpacticoid copepods and mysids (Mann–Whitney analysis, \(P < 0.001\) for gammaridean amphipods).

**Tridentiger obscurus**

Smaller fish (10–20 mm SL) fed mainly on harpacticoid copepods, gammaridean amphipods, and errant polychaetes. Of these, the contribution of harpacticoid copepods to the diet decreased in larger individuals (21–55 mm SL; Mann–Whitney analysis, \(P < 0.001\)). The relative importance of filamentous algae increased with body size (Mann–Whitney analysis, \(P < 0.005\)).

**Kareius bicoloratus**

The major food item of smaller fish (26–56 mm SL) was gammaridean amphipods, along with errant polychaetes and mysids. The relative importance of the former, however, decreased in larger individuals (57–101 mm SL; Mann–Whitney analysis, \(P < 0.001\)). In contrast, the percentage volume of bivalves increased with growth (Mann–Whitney analysis, \(P < 0.001\)).

**Feeding groups**

The cluster analysis based on the dietary overlap among species showed that the tidal mudflat fish assemblage was divided into six trophic groups (i.e. guilds; Fig. 2).

*Fish feeders* (Group A in Fig. 1) included only one unit representing 1.8% of the total units. *Lateolabrax japonicus* (114–142 mm) fed dominantly on juvenile fishes, such as *Acanthogobius flavimanus*, *Gymnogobius breunigii*, and *Mugil cephalus cephalus*.

*Detritus feeders* (Group B) comprised seven units (12.7%). Detritus, consumed by all of the group members, was the most important food item. Other food items, such as zooplankton and polychaetes, were also consumed.

*Zooplankton feeders* (Group C) comprised 16 units (29.1%). Members belonging to this guild took mainly zooplankton, such as calanoid and cyclopoid copepods, and cladocerans.

Small benthic and epiphytic crustacean feeders (Group D) included 25 units (45.5%). Members of this group preyed mostly on small benthic and epiphytic crustaceans, such as harpacticoid copepods, gammaridean amphipods, mysids, and myodocopid ostracods. Errant polychaetes were also consumed by most of the group members.

*Polychaete feeders* (Group E) were made up of three units (5.5%). This group was represented by members that captured mainly errant and sedentary polychaetes.
Mollusc feeders (Group F) included three units (5.5%). Bivalves were consumed by all of the group members, being the most dominant dietary item.

**Important food**

Based on the cumulative percentage volume values of all fish units for each food item and the percentage of units consuming each item, calanoid and cyclopoid copepods were the most important food item for the present tidal mudflat fish assemblage (Table 3). Detritus, gammaridean amphipods, harpacticoid copepods, and errant polychaetes were also consumed by most of the fish units (64–69%), being the second to fifth most important items by cumulative percentage volume.

**DISCUSSION**

In general, fish species on the tidal mudflats studied here had similar diets to those determined for other sites in Japan. However, there were some exceptions. For example, Kikuchi and Yamashita\(^{17}\) reported *Acanthogobius flavimanus* (>50 mm SL) on a tidal mudflat at Amakusa, Kumamoto Prefecture, southern Japan, as a benthic crustacean feeder, taking mostly gammaridean amphipods and crabs. In Tokyo Bay, however, the principal food item of this species was polychaetes. At Mangokuura, Miyagi Prefecture, northern Japan, *Kareius bicoloratus* (50–100 mm in total length) feeds mainly on polychaetes and small benthic crustaceans,\(^{19}\) although bivalves were the most important food item of this species in Tokyo Bay. Such differences may be partly related to habitat differences or geographic variations, such as differences in food availability at different localities.

Ontogenetic changes in food habits were recognized in 21 species (over 70% of total species examined), indicating that the tidal mudflats would function as their diet-shift area. In general, larvae and/or juveniles of these species fed on zooplankton or harpacticoid copepods, later switching to other prey items with growth (e.g. gammaridean amphipods, mysids, polychaetes, detritus, bivalves and fishes). The major food of some gobids (e.g. *Acanthogobius flavimanus, Gymnogobius breunigii*, and *G. macrognathos*) changed from zooplankton to benthic or epiphytic crustaceans at their settlement sizes.\(^{30}\) Such changes in food habits may reflect differences in food availability between pelagic and benthic habitats. The shift in food preference to fishes in *Lateolabrax japonicus* may be due to acquiring the ability to catch highly mobile animals with growth, similar to fish feeders in seagrass beds.\(^{31}\) In addition, ontogenetic differences in feeding habits may have resulted from other factors, including increasing mouth gape size with growth,\(^{39–41}\) changing numbers of gill rakers\(^{42,43}\) or jaw and pharyngeal teeth\(^{44}\) and development of the alimentary system.\(^{35,46}\)

On the tidal mudflats in Tokyo Bay, benthic or epiphytic crustacean feeders were the most abundant category by number; the major food items for the tidal mudflat fish assemblage being gammaridean amphipods, harpacticoid copepods and mysids. These findings generally coincided not only with those from other temperate tidal flats,\(^{17–19}\) but also with those from fringe vegetated habitats, such as salt marshes and seagrass beds, in temperate regions.\(^{15,16,31,47–49}\)

Zooplankton feeders were the second most abundant by number, with planktonic copepods being one of the most important food items for the fishes examined here. Almost all of the units belonging to this trophic category were pelagic larval and juvenile fishes, except for a nektonic gobiid, *Gymnogobius heptacanthus*. The phenomenon of adult stage planktivorous fishes being relatively scarce at the present site has also been reported from other tidal flats.\(^{17–19}\)

In this study, only a few fish species fed predominantly on infaunal animals, such as molluscs and polychaetes, as has been found by many previous studies.\(^{15,44}\) However, polychaete feeders (trophic group E) were a relatively abundant component of the fish sampled in the present area; Kanou *et al.*\(^{3}\) having reported *Acanthogobius flavimanus*, a polychaete feeder, as the most abundant species of those sampled. Furthermore, polychaetes were consumed in varying quantities by many units (67% of the total). These findings indicate that polychaetes comprised one of the major food items in the overall diet of the present fish assemblage.

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

<table>
<thead>
<tr>
<th>Food items</th>
<th>%V total</th>
<th>%U</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calanoid and cyclopoid copepods</td>
<td>1096</td>
<td>69</td>
</tr>
<tr>
<td>Detritus</td>
<td>748</td>
<td>64</td>
</tr>
<tr>
<td>Gammaridean amphipods</td>
<td>680</td>
<td>64</td>
</tr>
<tr>
<td>Harpacticoid copepods</td>
<td>439</td>
<td>67</td>
</tr>
<tr>
<td>Errant polychaetes</td>
<td>426</td>
<td>67</td>
</tr>
<tr>
<td>Mysids</td>
<td>402</td>
<td>33</td>
</tr>
<tr>
<td>Cladocerans</td>
<td>306</td>
<td>36</td>
</tr>
<tr>
<td>Bivalves</td>
<td>201</td>
<td>22</td>
</tr>
<tr>
<td>Juvenile fishes</td>
<td>179</td>
<td>16</td>
</tr>
</tbody>
</table>
Detritus is generally considered to be one of the most abundant food resources in tidal flat sediments, being utilized by most small invertebrates (such as copepods, ostracods, amphipods, annelids and snails) commonly consumed by tidal flat fishes.\textsuperscript{11} In the present study area, seven units, including mugilids, blenniids, clupeids, and cypriinids, fed largely on detritus. In fact, detritus was consumed by most of the fish units (64%), being the second most important item by cumulative percentage volume. The high cumulative percentage value of detritus and high proportion of units consuming this food source (Table 3) showed detritus to be a significant food resource for Tokyo Bay’s tidal mudflat fishes.

Although juvenile fishes were consumed in varying quantities by nine units, specialist fish feeders comprised only one unit, that is \textit{Lateolabrax japonicus} (114–142 mm SL). This species occurred abundantly on the tidal flats of Tokyo Bay\textsuperscript{4} and has often been recognized as a piscivore at other sites,\textsuperscript{19,50,51} indicating that it may be one of the most critical predators of juvenile fishes on tidal flats.

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