# Ontogenetic and inter-annual variation in the diet of Japanese jack mackerel (*Trachurus japonicus*) juveniles in the East China Sea

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We examined the diet of pelagic juveniles of *Trachurus japonicus* in the surface layer in April, and subsequent demersal juveniles in the near bottom layer during May to June of the East China Sea (ECS) in 2005, 2008 and 2009. Diet composition of the pelagic juveniles showed a significant difference between 2005 and the other two years. That is, they preyed mainly on *Paracalanus parvus* s.l. and occasionally on *Calanus sinicus* in 2008 and 2009, while they fed mainly on *Corycaeus affinis* in 2005, partly corresponding with the between-year difference in prey densities. The demersal juveniles depended heavily on the fifth copepodites and females of *C. sinicus* which store lipids in the body, i.e. high-energy food for the juveniles, without a significant inter-annual difference. The markedly low occurrence of *P. parvus* s.l. and *C. sinicus,* which are considered to be energetically more favourable than *C. affinis,* from the stomach of the pelagic juveniles in 2005 corresponded with the lowest growth rates of the pelagic juveniles in the three years. Potentially, this resulted in the lowest observed recruitment level of the demersal juveniles for the ECS in 2005 over these three years.

## INTRODUCTION

The Japanese jack mackerel (*Trachurus japonicus* (Temminck & Schlegel, 1844)) is a semi-pelagic fish distributed mainly on the continental shelf of the East China Sea (ECS), western Sea of Japan, and Pacific coast of southern and central Japan (Ochiai & Tanaka, 1986). It is commercially fished by the countries adjacent to the ECS, one of the largest marginal seas of the western Pacific (Seikai National Fisheries Research Institute, 2001; FAO, 2013). Catches of the Japanese fisheries during 1980–2015 have fluctuated from 50 to 319 thousand metric tons (Watanabe *et al.*, 2017; Yoda *et al.*, 2017). The catches have reflected the year-to-year variation in recruitment, therefore it is necessary to examine the mechanism underlying the recruitment variability.

The primary spawning ground of *T. japonicus* is found in the shelf-break region of the southern part of the ECS south of 28°N during February to April (Sassa *et al.*, 2016), although they also spawn on a smaller scale in the coastal region off Japan (Ochiai & Tanaka, 1986; Kanaji *et al.*, 2009). The Kuroshio and Kuroshio Branch Current north of Taiwan have been shown to affect transport processes of eggs, larvae and juveniles of *T. japonicus* from the spawning ground of the southern ECS into the nursery grounds in the downstream areas (Figure 1) (Sassa *et al.*, 2006, 2008b; Kasai *et al.*, 2008). During the juvenile stage, the habitat and behaviour of *T. japonicus* change greatly, as well as physiological changes such as rate of digestion and absorption (Ochiai & Tanaka, 1986). The juveniles of ∼10–30 mm standard length (SL) occur in the pelagic layer (hereafter referred to as 'pelagic juveniles'), and associate with gelatinous zooplankters, drift algae and flotsam (Uehara & Mitani, 2002; Sassa *et al.*, 2006; Masuda *et al.*, 2008). Swimming ability of the juveniles markedly increases from ∼30 mm SL (Ochiai *et al.*, 1982). After reaching approximately 30–50 mm SL, *T. japonicus* begin to occur near the bottom layer in the shelf-break region of the southern and central ECS mainly at the depth of 70–140 m between 27° and 31°N (hereinafter referred to as 'demersal juveniles'), which subsequently forms the ECS stock (Sassa *et al.*, 2009; Takahashi *et al.*, 2012).

Recruitment variability of fish is thought to be largely determined during the early life stages, when the larvae and juveniles are vulnerable to a variety of physical and biological factors that can affect their survival (Houde, 1987; Chambers & Trippel, 1997; Fuiman & Werner, 2002). In *T. japonicus*, survival from the larval to demersal juvenile stages is estimated to vary among years in the ECS, which is considered to be a key process for understanding the fluctuations in recruitment (Kasai *et al.*, 2008; Sassa *et al.*, 2014, 2016). Importance of the growth rate during the early life stages for subsequent recruitment has been suggested in various marine fishes (Anderson, 1988; Litvak & Leggett, 1992; Bailey *et al.*, 1996; Meekan & Fortier, 1996; Takahashi *et al.*, 2008). Takahashi *et al.* (2012, 2016) suggested that growth rates during the late larval and pelagic juvenile stages are associated with recruitment success of demersal juveniles and subsequent year-class strength of *T. japonicus* in the ECS. Feeding

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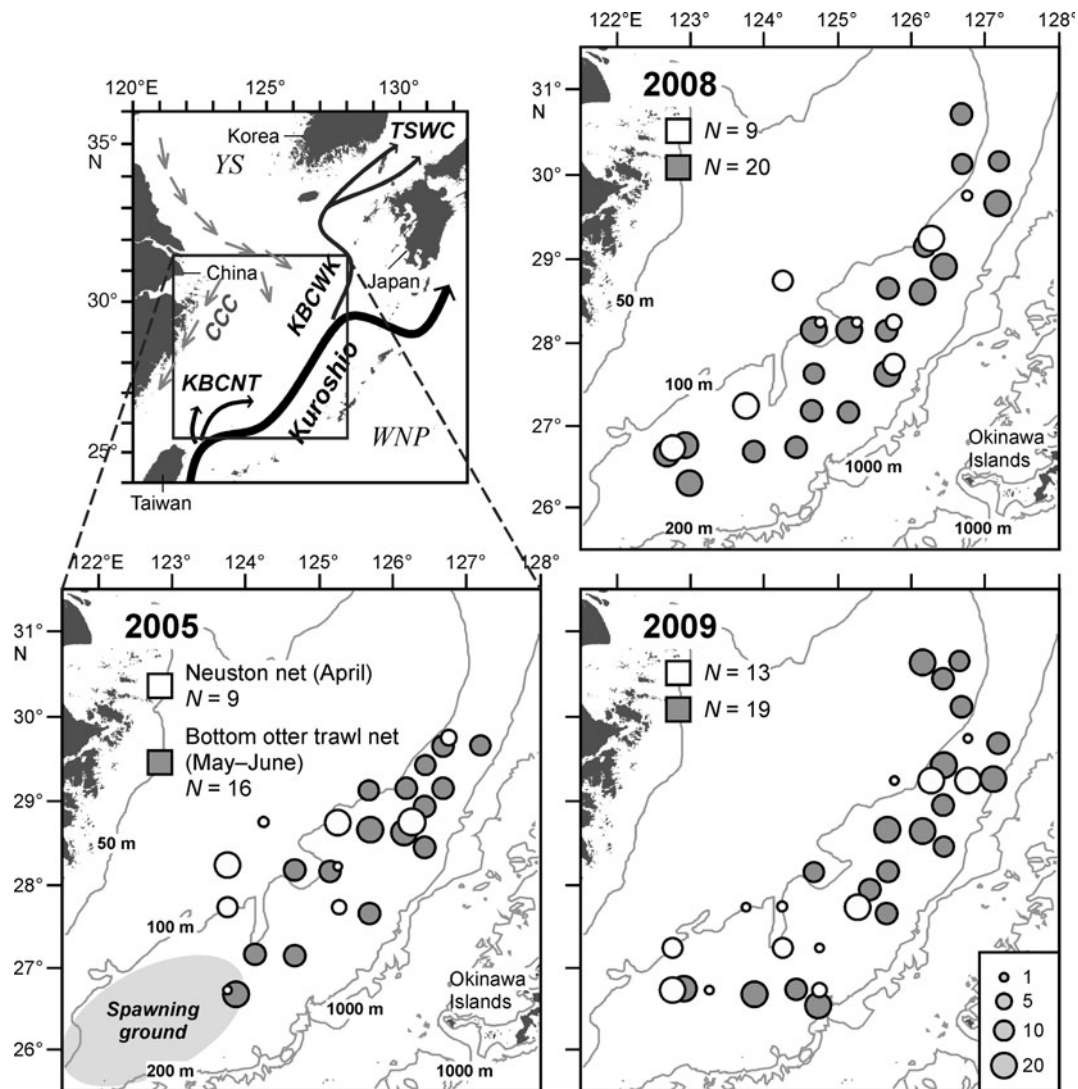C. Sassa
Email: csassa@fra.affrc.go.jp

**Fig. 1.** Sampling locations of Japanese jack mackerel (*Trachurus japonicus*) juveniles during the six cruises in the shelf-break region of the southern and central East China Sea in 2005, 2008 and 2009. The size of circles indicates the number of fish analysed at each site. *N*, total number of sampling stations. KBCNT, Kuroshio Branch Current north of Taiwan; KBCWK, Kuroshio Branch Current west of Kyushu; TSWC, Tsushima Warm Current; CCC, China Coastal Current. YS, Yellow Sea; WNP, western North Pacific.

as well as habitat temperature is directly related to growth of fishes (Takahashi & Watanabe, 2005; Zenitani *et al.*, 2009), thus detailed information on feeding habits during the early life stages is essential for understanding the mechanism of year-to-year variations in recruitment of fishes. Recent papers have detailed the dietary composition, prey size, daily ration and inter-annual variability in diet of *T. japonicus* larvae in the southern ECS during late winter (Sassa *et al.*, 2008a; Sassa & Tsukamoto, 2012; Hirota *et al.*, 2016). However, information on ontogenetic changes and inter-annual variations in feeding habits of *T. japonicus* juveniles is not available in the literature. Any variations in feeding behaviour might have implications for growth and subsequent recruitment to the ECS stock.

The goal of this study was to examine the feeding habits of *T. japonicus* juveniles in the surface and near bottom layers of the ECS in the three years of 2005, 2008 and 2009. The results are discussed in relation to reported growth rates and recruitment levels (Takahashi *et al.*, 2012; Yoda *et al.*, 2017).

## MATERIALS AND METHODS

### Sample collection

Specimens were sampled during six cruises in the shelf-break region of the ECS in 2005, 2008 and 2009 (Figure 1). Pelagic juveniles of *T. japonicus* were sampled at 9, 9 and 13 stations during 19–29 April 2005, 18–29 April 2008 and 17–29 April 2009, respectively, from the RV 'Yoko-Maru' (Seikai National Fisheries Research Institute) (Figure 1). A neuston net (mouth size 1.3 × 0.75 m; mesh size 1.0 mm; Oozeki *et al.*, 2001) was towed for 10 min with a vessel speed of 3.5 knots during the daytime. This net is designed to be towed horizontally in the upper 0.75 m layer, with a buoy attached on each side of the frame for keeping it on the surface. Specimens were first fixed in 10% borax-buffered formalin seawater for 6 h, formalin rinsed out with fresh water, and then transferred to 95% ethanol for preservation.

For zooplankton sampling, we used a conical Norpac net with an opening of 45 cm in diameter and with 100 μm

mesh size (Motoda, 1957). The net was towed vertically from 50 m to the surface at each station where the samplings of pelagic juveniles were conducted. The volume of water filtered by the Norpac net was measured with a flowmeter mounted at the net mouth. Plankton samples were fixed with 5% buffered formalin seawater immediately after collection.

Demersal juveniles of *T. japonicus* were sampled at 16, 20 and 19 stations using a bottom otter trawl net from 12 May to 1 June 2005, from 21 May to 20 June 2008, and from 18 May to 15 June 2009, respectively, from the RV 'Kumamoto-Maru' (Kumamoto Prefecture) (Figure 1). The net had a mouth opening of 22 m (width) × 9.4 m (depth) and variable mesh size from 180 mm at the mouth to 66 mm at the cod-end, which was covered with a 18 mm cod-end cover. The net was towed for 30 min at a vessel speed of 3 knots during the daytime. Subsamples of *T. japonicus* were sorted out from the trawl catch and immediately frozen at −10 °C onboard, and fixed in 10% borax-buffered formalin fresh water in laboratory.

During the six cruises, a conductivity-temperature-depth profiler (CTD, Alec Electronics Co., Ltd, Tokyo, Japan) was used at each sampling station from surface to 5 m above the bottom to obtain hydrographic data.

We analysed only specimens sampled between sunrise and sunset, since *T. japonicus* juveniles are daytime visual feeders (Suzuki, 1965; Kozasa, 1970). Number of the pelagic juveniles collected by the neuston net was <10 individuals at 77% of the stations, while >20 demersal juveniles were always sampled by the bottom otter trawl net. To pool a sufficient number of the pelagic juveniles each year for describing the diet composition, we examined all specimens at the stations where <20 individuals occurred, and up to 20 randomly selected specimens at the stations where ≥20 individuals occurred (Figure 1). In the demersal juveniles, we randomly selected from 10 to 15 individuals from each sampling station for the stomach contents analysis. As a whole, a total of 82–100 pelagic juveniles (8.0–29.8 mm SL) and 205–269 demersal juveniles (26.5–105.3 mm SL) were examined during the three years (Figure 2).

## Laboratory analysis

For each specimen, SL was measured to the nearest 0.1 mm. Thereafter, stomachs were dissected and the contents removed. Since the identification of prey items at the species or genus level is fundamental to understand the trophic relationships within a food web, we identified prey items to the lowest possible taxon, based on Chihara & Murano (1997). Copepod species were categorized into the developmental stages of adult female, male and copepodite; euphausiids into calyptopis, furcilia and juvenile; decapods into zoea, mysis, megalopa and juvenile. Body lengths and widths of prey items in good condition were measured to the nearest 0.01 mm for each category under a microscope fitted with an ocular micrometer to estimate mean dimensions. The mean dimensions of each prey category were converted to the approximate dry weight (DW) based on equations from Anraku *et al.* (1986) for copepods, ostracods and decapods; Ikeda (1990) for amphipods; Iguchi & Ikeda (1999) for euphausiids; and Beers (1966), Anraku *et al.* (1986) and Uye *et al.* (1996) for the other taxa.

The results presented below indicated that pelagic juveniles of *T. japonicus* preyed mainly on *Paracalanus parvus* s.l., *Calanus sinicus* and *Corycaeus affinis*. Consequently, we used the densities of these three copepods as indices of the
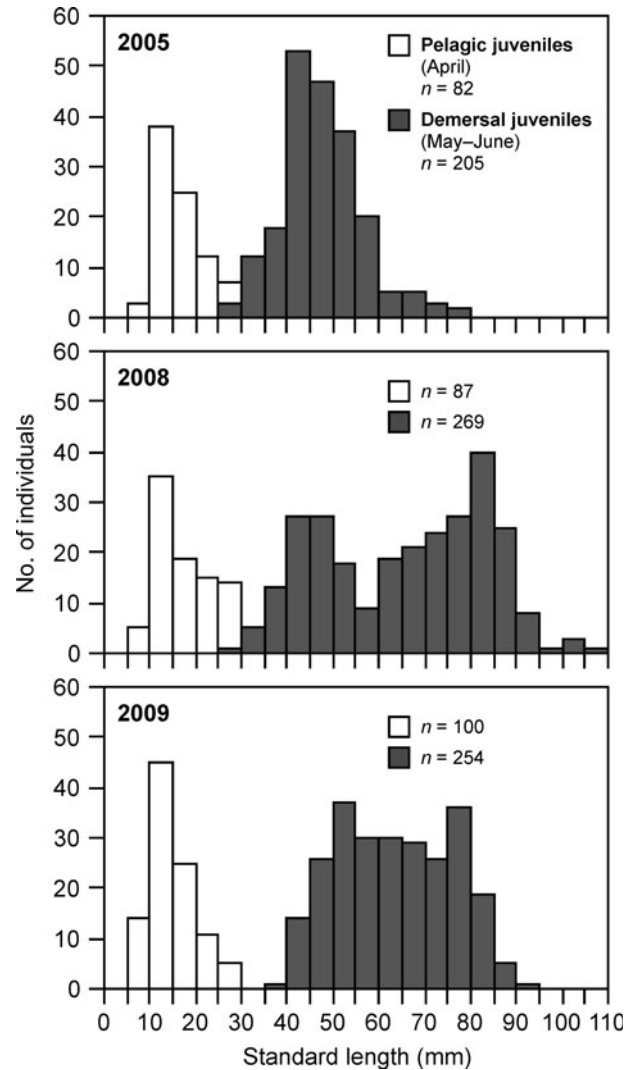


**Fig. 2.** Length-frequency distributions of Japanese jack mackerel (*Trachurus japonicus*) juveniles examined for stomach contents in 2005, 2008 and 2009, where *n* is the total number of juveniles examined.

food availability. To assess inter-annual variations in the food availability for the pelagic juveniles, the three species were identified and counted in the Norpac net samples from each tow in the three years. Since the pelagic juveniles were collected in the top 0.75 m of the water column in this study, the sampling layers of juveniles and zooplankton were largely different. Consequently, applying a selectivity index to the data was not considered adequate. However, in the shelf-break region of the ECS, copepods distribute fairly evenly in the upper 50 m layer during late winter when the mixed layer depth is observed to ~60–100 m (Hirota *et al.*, 2016). In spring, the mixed layer depth becomes shallower, but it is still ~40–60 m in the study area (Sassa *et al.*, 2006). Therefore, we assumed that the densities of the three copepods in the upper 50 m layer would be representative of the food availability for the pelagic juveniles.

## Data analysis

The sampling locations were relatively evenly distributed across the whole area with a similar survey effort in all the

three years (Figure 1). Consequently, the data were pooled for each year to represent the inter-annual variation in the diet composition.

The habitat temperature for the pelagic juveniles in each year was defined as the mean sea surface temperature (SST) across all the stations in April. In the same way, the mean temperature in the near bottom layer in May–June each year represented the habitat for the demersal juveniles. The habitat temperatures for the juveniles were compared among the three years by one-way ANOVA followed by Tukey–Kramer post-hoc test.

The pelagic juveniles were separated into two size classes of <15 and ≥15 mm SL, and the demersal juveniles into <60 and ≥60 mm SL to assess ontogenetic changes in the diet. Stomach data were partitioned into subsets according to these size classes and years. The modified index of relative importance (IRI), i.e. using DW rather than wet weight of prey items (Pinkas *et al.*, 1971; Landingham *et al.*, 1998), was calculated for each data subset to characterize the diet and to rank prey taxa:

$$IRI = (\%N + \%W) \times \%F \qquad (1)$$

where %N is percentage of each prey item to the total number of identifiable prey items, %W is percentage DW of each prey item to the total DW of identifiable prey items, %F is frequency of occurrence of each prey item in the total number of stomachs examined (excluding empty stomachs). The IRI was expressed as the percentage of total IRI (%IRI) for each data subset (Cortés, 1997). The diversity of prey items was analysed using Levins' diet breadth index (B; Levins, 1968):

$$B = \left( \sum_{i=1}^{n} p_i^2 \right)^{-1} \qquad (2)$$

where $p_i$ is the %IRI of each prey category in the diet.

The Bray–Curtis similarity index (BC; Bray & Curtis, 1957) was used to compare the %IRI of all prey items identified among the three years and between the two size classes of both the pelagic and demersal juveniles. The index comparing the two data sets of stomach contents (A and B) was calculated using the following equation:

$$BC = 100 \times \left( 1 - \frac{\sum_{i=1}^{n} |p_{iA} - p_{iB}|}{\sum_{i=1}^{n} p_{iA} + \sum_{i=1}^{n} p_{iB}} \right) \qquad (3)$$

where $p_{iA}$ and $p_{iB}$ are the %IRI of prey item $i$ in data sets of stomach contents of A and B, respectively. To reduce the influence of dominant prey items, the %IRI values were square root transformed prior to analysis. Clustering by UPGMA (unweighted pair-group method using the arithmetic average) was used to construct similarity matrices. Cluster analysis was performed with PRIMER v6 software package (Clarke & Gorley, 2006).

The number of the three copepods of *P. parvus* s.l., *C. sinicus* and *C. affinis* sampled in the plankton net was standardized to the number per 1 m³ in the upper 50 m layer. Densities of each species were $\log_{10}(x + 1)$ transformed prior to the analyses to normalize the data and decrease the variance. Median prey densities were compared among the three years by the Kruskal–Wallis test followed by the

Steel–Dwass post-hoc test. The significance level for the statistical test was set at α = 0.05.

## RESULTS

## Overall diet composition

Mean habitat temperature for pelagic juveniles ranged from 19.3 to 19.9 °C and for demersal juveniles from 17.6 to 18.2 °C in the three years, without a significant inter-annual difference (ANOVA, $P > 0.05$; Table 1).

The 44 different prey categories detected in the stomachs of pelagic juveniles are listed in Table 2. Copepods were highly abundant and the most diverse prey categories, including four orders, 19 genera and 37 species or species groups, while occurrence of the other taxa was less. The number of taxa that occurred in the stomachs was markedly different among years, and Levins' index B was highest in 2008 (Table 2).

In the stomachs of the demersal juveniles, a total of 82 prey categories were identified (Table 3). Copepods were the most abundant and diverse prey categories, including three orders, 25 genera and 56 species or species groups, although ostracods, amphipods, euphausiids and decapods were also occasionally abundant. The B values of the demersal juveniles were higher than the values of the pelagic juveniles in the three survey years (Table 3).

## Ontogenetic changes and inter-annual variations in diet

In 2005, *Corycaeus affinis* dominated in the stomach contents of pelagic juveniles in both size classes, and the %IRI values were 65.6–85.0% of the total prey identified (Figure 3). *Euphausia* spp. juveniles were also preyed on by juveniles ≥15 mm SL, constituting 20.2% of %IRI. In 2008 and 2009, in contrast, *Paracalanus parvus* s.l. was the most dominant prey item in juveniles <15 mm SL, accounting for %IRI values of 50.9 and 84.9%, respectively, of the total prey identified (Figure 3). In 2008, *P. aculeatus* and *C. affinis* were also preyed on by juveniles <15 mm SL, which constituted 17.5 and 11.8% of %IRI, respectively. In 2008 and 2009, juveniles ≥15 mm SL predated heavily on *P. parvus* s.l., with %IRI values of 35.8–75.6%. In addition, the importance of *Calanus sinicus* was markedly higher in juveniles ≥15 mm SL, which constituted 17.7–55.3% of %IRI values.

In the demersal juveniles, *C. sinicus* was the most important prey item in all survey years in terms of %N, %W, and %F (Table 3), and the %IRI values in juveniles <60 and ≥60 mm SL ranged from 30.8–55.5% and 29.3–62.2%,

**Table 1.** Mean ± standard deviation of the habitat temperature (°C) of Japanese jack mackerel (*Trachurus japonicus*) juveniles, as represented by sea surface temperatures in April, and temperature in the near bottom layer in May–June for pelagic and demersal juveniles, respectively.

| Year | Pelagic juveniles (April) | Demersal juveniles (May–June) |
|------|---------------------------|-------------------------------|
| 2005 | 19.3 ± 2.3 | 17.9 ± 0.6 |
| 2008 | 19.3 ± 2.8 | 18.2 ± 1.5 |
| 2009 | 19.9 ± 1.5 | 17.6 ± 0.8 |

**Table 2.** Summary of prey items in the pelagic juveniles of Japanese jack mackerel (*Trachurus japonicus*) in the epipelagic layer in the southern and central East China Sea in 2005, 2008 and 2009.

| Year | 2005 | | | | 2008 | | | | 2009 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. stomachs examined | 82 | | | | 87 | | | | 100 | | | |
| Total no. prey items identified | 660 | | | | 1642 | | | | 434 | | | |
| Levins' diet breadth index (*B*) | 1.43 | | | | 2.72 | | | | 1.45 | | | |
| Prey taxon | %N | %W | %F | %IRI | %N | %W | %F | %IRI | %N | %W | %F | %IRI |
| Copepoda | | | | | | | | | | | | |
| Nauplius | – | – | – | – | 0.3 | <0.1 | 3.9 | <0.1 | 0.2 | 0.1 | 1.9 | <0.1 |
| Calanoid copepodite | | | | | | | | | | | | |
| *Calanus sinicus* | 1.2 | 14.3 | 7.8 | 1.4 | 21.4 | 75.0 | 30.3 | 37.7 | 5.3 | 44.3 | 16.7 | 9.9 |
| *Canthocalanus pauper* | – | – | – | – | 0.7 | 0.5 | 6.6 | 0.1 | – | – | – | – |
| *Cosmocalanus darwini* | 0.2 | 1.8 | 2.0 | <0.1 | 0.2 | 0.7 | 3.9 | <0.1 | – | – | – | – |
| *Undinula vulgaris* | – | – | – | – | 0.2 | 0.6 | 2.6 | <0.1 | – | – | – | – |
| Calanidae spp. | – | – | – | – | 0.2 | 0.2 | 2.6 | <0.1 | – | – | – | – |
| *Clausocalanus furcatus* | – | – | – | – | 0.1 | <0.1 | 2.6 | <0.1 | 0.9 | 0.7 | 7.4 | 0.1 |
| *Clausocalanus* spp. | – | – | – | – | 0.1 | <0.1 | 1.3 | <0.1 | 0.7 | 0.4 | 5.6 | 0.1 |
| *Ctenocalanus vanus* | – | – | – | – | 0.4 | 0.3 | 3.9 | <0.1 | – | – | – | – |
| *Eucalanus* sp. | – | – | – | – | 0.2 | 0.4 | 3.9 | <0.1 | – | – | – | – |
| *Euchaeta rimana* | – | – | – | – | 0.1 | 0.8 | 1.3 | <0.1 | – | – | – | – |
| *Paraeuchaeta concinna* | – | – | – | – | 0.1 | 0.7 | 1.3 | <0.1 | – | – | – | – |
| *Paraeuchaeta plana* | – | – | – | – | – | – | – | – | 0.2 | 5.7 | 1.9 | 0.1 |
| Euchaetidae spp. | – | – | – | – | 1.8 | 3.0 | 18.4 | 1.2 | 1.6 | 8.5 | 7.4 | 0.9 |
| *Pleuromamma gracilis* | – | – | – | – | – | – | – | – | 0.2 | 0.7 | 1.9 | <0.1 |
| *Acrocalanus gracilis* | – | – | – | – | 0.9 | 0.5 | 10.5 | 0.2 | 2.8 | 4.1 | 3.7 | 0.3 |
| *Paracalanus aculeatus* | – | – | – | – | 3.8 | 1.7 | 27.6 | 2.0 | 2.8 | 2.7 | 14.8 | 1.0 |
| *Paracalanus parvus* s.l. | 1.8 | 0.7 | 17.6 | 0.5 | 43.5 | 8.5 | 69.7 | 46.9 | 64.5 | 26.1 | 75.9 | 82.5 |
| Paracalanidae spp. | – | – | – | – | 2.9 | 0.2 | 25.0 | 1.0 | 7.4 | 1.8 | 25.9 | 2.8 |
| *Temora discaudata* | 0.2 | 0.8 | 2.0 | <0.1 | – | – | – | – | – | – | – | – |
| *Temora turbinata* | 0.2 | 0.4 | 2.0 | <0.1 | 1.0 | 0.5 | 13.2 | 0.3 | – | – | – | – |
| *Temora* sp. | – | – | – | – | – | – | – | – | 0.2 | 0.3 | 1.9 | <0.1 |
| *Tortanus* sp. | – | – | – | – | – | – | – | – | 0.2 | 0.2 | 1.9 | <0.1 |
| Cyclopoid copepodite | | | | | | | | | | | | |
| *Oithona nana* | – | – | – | – | 2.0 | 0.1 | 11.8 | 0.3 | 1.4 | 0.1 | 7.4 | 0.1 |
| *Oithona similis* | – | – | – | – | 1.3 | 0.1 | 10.5 | 0.2 | 3.7 | 0.7 | 13.0 | 0.7 |
| *Oithona* spp. | – | – | – | – | 0.7 | 0.2 | 11.8 | 0.1 | 1.2 | 0.5 | 9.3 | 0.2 |
| Poecilostomatoid copepodite | | | | | | | | | | | | |
| *Corycaeus affinis* | 72.4 | 50.1 | 58.8 | 83.1 | 9.0 | 2.0 | 46.1 | 6.6 | 2.1 | 1.0 | 13.0 | 0.5 |
| *Corycaeus agilis* | – | – | – | – | 0.1 | <0.1 | 2.6 | <0.1 | – | – | – | – |
| *Corycaeus crassiusculus* | 0.5 | 1.2 | 3.9 | 0.1 | 0.1 | 0.1 | 1.3 | <0.1 | – | – | – | – |
| *Corycaeus pacificus* | 0.2 | 0.1 | 2.0 | <0.1 | 0.2 | 0.1 | 3.9 | <0.1 | 0.5 | 0.2 | 3.7 | <0.1 |
| *Farranula concinna* | – | – | – | – | – | – | – | – | 0.2 | 0.1 | 1.9 | <0.1 |
| *Farranula gibbula* | – | – | – | – | 0.4 | 0.1 | 6.6 | <0.1 | – | – | – | – |
| Corycaeidae spp. | 11.5 | 1.9 | 45.1 | 7.0 | 4.3 | 0.4 | 40.8 | 2.5 | 0.5 | <0.1 | 3.7 | <0.1 |
| *Oncaea venusta* f. *typica* | – | – | – | – | 0.2 | 0.1 | 3.9 | <0.1 | 0.2 | 0.1 | 1.9 | <0.1 |
| *Oncaea venusta* f. *venella* | 6.2 | 3.5 | 33.3 | 3.7 | 0.3 | 0.1 | 6.6 | <0.1 | 0.2 | 0.1 | 1.9 | <0.1 |
| *Oncaea* spp. | – | – | – | – | 1.0 | 0.1 | 15.8 | 0.2 | 2.3 | 0.4 | 16.7 | 0.5 |
| Oncaeidae spp. | 1.1 | 0.2 | 7.8 | 0.1 | 0.1 | <0.1 | 2.6 | <0.1 | – | – | – | – |
| Harpacticoid copepodite | | | | | | | | | | | | |
| *Euterpina acutifrons* | – | – | – | – | – | – | – | – | 0.2 | <0.1 | 1.9 | <0.1 |
| Euphausiidae | | | | | | | | | | | | |
| Calyptopis | 0.5 | 0.2 | 5.9 | <0.1 | 1.0 | 0.1 | 11.8 | 0.2 | – | – | – | – |
| Furcilia | 0.6 | 2.2 | 3.9 | 0.1 | 0.9 | 0.6 | 10.5 | 0.2 | 0.5 | 1.1 | 3.7 | 0.1 |
| *Euphausia* spp. juvenile | 1.1 | 18.5 | 11.8 | 2.7 | 0.4 | 2.3 | 3.9 | 0.1 | – | – | – | – |
| Chaetognatha | | | | | | | | | | | | |
| Sagittidae sp. | – | – | – | – | 0.1 | <0.1 | 1.3 | <0.1 | – | – | – | – |
| Gastropoda larva | 0.2 | 0.2 | 2.0 | <0.1 | – | – | – | – | – | – | – | – |
| Bivalvia umbo larva | 2.4 | 3.9 | 15.7 | 1.1 | 0.2 | 0.1 | 2.6 | <0.1 | – | – | – | – |

%N is numerical percentage, %W is dry weight percentage, %F is frequency of occurrence percentage of fish with prey item *i*, and %IRI is per cent of total IRI (index of relative importance) for all prey taxa. IRI = (%N + %W) × %F. –, no occurrence.

respectively (Figure 4). Planktonic halocyprid ostracods were also dominant prey items of demersal juveniles during the three years in terms of %F (Table 3), resulting in %IRI values of 0.9–54.6 and 6.0–26.1% in juveniles <60 and ≥60 mm SL, respectively (Figure 4). In addition, the demersal juveniles preyed considerably on *C. affinis* and *Euphausia nana* in 2005, and on *Paraeuchaeta plana* in 2008 and 2009, all of which accounted for >10% of %IRI values (Figure 4). The %IRI values of hyperiid amphipods in juveniles ≥60 mm SL was higher than those in juveniles <60 mm SL in the three years.

**Table 3.** Summary of prey items in the demersal juveniles of Japanese jack mackerel (*Trachurus japonicus*) in the near bottom layer in the southern and central East China Sea in 2005, 2008 and 2009.

| Year | 2005 | | | | 2008 | | | | 2009 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. stomachs examined | 205 | | | | 269 | | | | 254 | | | |
| Total no. prey items identified | 1619 | | | | 5269 | | | | 3919 | | | |
| Levins' diet breadth index (*B*) | 2.66 | | | | 4.46 | | | | 3.49 | | | |
| Prey taxon | %N | %W | %F | %IRI | %N | %W | %F | %IRI | %N | %W | %F | %IRI |
| Foraminiferida | | | | | | | | | | | | |
|   Globigerinidae sp. | – | – | – | – | – | – | – | – | 0.3 | <0.1 | 1.5 | <0.1 |
| Ostracoda | | | | | | | | | | | | |
|   Halocyprididae spp. | 8.0 | 9.8 | 39.0 | 11.5 | 3.7 | 2.7 | 44.3 | 5.0 | 21.7 | 18.9 | 67.9 | 35.2 |
| Copepoda | | | | | | | | | | | | |
|   Calanoid copepodite | | | | | | | | | | | | |
|     *Aetideus* sp. | – | – | – | – | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Euchirella amoena* | – | – | – | – | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     Aetideidae sp. | – | – | – | – | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Calanoides philippinensis* | 0.2 | 0.1 | 2.9 | <0.1 | 0.1 | <0.1 | 0.6 | <0.1 | 0.1 | 0.1 | 2.2 | <0.1 |
|     *Calanus sinicus* | 40.3 | 28.0 | 51.4 | 58.1 | 28.5 | 10.3 | 46.7 | 32.2 | 37.2 | 20.0 | 53.0 | 38.7 |
|     *Cosmocalanus darwini* | 0.6 | 0.3 | 2.9 | <0.1 | 4.7 | 1.4 | 13.2 | 1.4 | – | – | – | – |
|     *Nannocalanus minor* | 0.1 | <0.1 | 1.0 | <0.1 | 1.0 | 0.2 | 4.2 | 0.1 | – | – | – | – |
|     *Neocalanus gracilis* | – | – | – | – | 0.1 | 0.1 | 1.2 | <0.1 | – | – | – | – |
|     *Undinula vulgaris* | 0.1 | 0.1 | 1.0 | <0.1 | 2.3 | 1.7 | 19.8 | 1.4 | – | – | – | – |
|     Calanidae spp. | – | – | – | – | 0.3 | 0.1 | 2.4 | <0.1 | 0.1 | <0.1 | 2.2 | <0.1 |
|     *Candacia bipinnata* | 0.1 | <0.1 | 1.0 | <0.1 | – | – | – | – | 0.1 | <0.1 | 1.5 | <0.1 |
|     *Candacia catula* | – | – | – | – | <0.1 | <0.1 | 1.2 | <0.1 | – | – | – | – |
|     *Candacia discaudata* | – | – | – | – | 0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Candacia ethiopica* | – | – | – | – | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Candacia pachydactyla* | – | – | – | – | 0.6 | 0.2 | 7.2 | 0.1 | – | – | – | – |
|     Candaciidae spp. | – | – | – | – | 0.6 | 0.1 | 10.2 | 0.1 | – | – | – | – |
|     *Clausocalanus arcuicornis* | 1.2 | 0.1 | 4.8 | 0.1 | 0.1 | <0.1 | 2.4 | <0.1 | – | – | – | – |
|     *Clausocalanus parapergens* | 1.5 | 0.2 | 8.6 | 0.2 | 0.1 | <0.1 | 1.8 | <0.1 | – | – | – | – |
|     *Clausocalanus* spp. | 0.3 | <0.1 | 1.9 | <0.1 | <0.1 | <0.1 | 1.2 | <0.1 | 0.2 | <0.1 | 4.5 | <0.1 |
|     *Rhincalanus cornutus* | 0.1 | 0.3 | 1.9 | <0.1 | <0.1 | <0.1 | 0.6 | <0.1 | <0.1 | <0.1 | 0.7 | <0.1 |
|     *Eucalanus crassus* | – | – | – | – | 0.2 | 0.2 | 4.8 | <0.1 | – | – | – | – |
|     *Eucalanus subtenuis* | – | – | – | – | 0.1 | 0.1 | 1.2 | <0.1 | – | – | – | – |
|     *Eucalanus* spp. | – | – | – | – | 0.2 | 0.1 | 3.0 | <0.1 | 0.1 | 0.1 | 2.2 | <0.1 |
|     *Euchaeta rimana* | 0.4 | 1.1 | 5.7 | 0.1 | 2.0 | 2.6 | 13.8 | 1.1 | 0.2 | 0.4 | 3.0 | <0.1 |
|     *Paraeuchaeta concinna* | 0.4 | 0.6 | 4.8 | 0.1 | 2.0 | 1.8 | 17.4 | 1.2 | 5.0 | 6.6 | 17.9 | 2.6 |
|     *Paraeuchaeta longicornis* | – | – | – | – | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Paraeuchaeta plana* | 0.8 | 1.5 | 3.8 | 0.1 | 18.3 | 19.7 | 49.1 | 33.0 | 6.7 | 11.5 | 29.1 | 6.8 |
|     *Paraeuchaeta russelli* | 0.1 | 0.2 | 1.0 | <0.1 | 0.9 | 1.5 | 6.6 | 0.3 | 4.7 | 12.9 | 11.9 | 2.7 |
|     Euchaetidae spp. | 3.0 | 3.5 | 18.1 | 1.9 | 6.1 | 2.0 | 37.7 | 5.4 | 4.4 | 4.2 | 32.1 | 3.5 |
|     *Lucicutia flavicornis* | 0.2 | <0.1 | 3.8 | <0.1 | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Pleuromamma abdominalis* | 0.1 | 0.1 | 1.0 | <0.1 | 0.1 | 0.2 | 1.2 | <0.1 | – | – | – | – |
|     *Pleuromamma gracilis* | 1.0 | 0.3 | 11.4 | 0.2 | 0.3 | <0.1 | 6.0 | <0.1 | 0.2 | <0.1 | 3.0 | <0.1 |
|     *Pleuromamma indica* | 0.6 | 0.4 | 7.6 | 0.1 | 0.5 | 0.1 | 9.0 | 0.1 | 0.3 | 0.2 | 6.0 | <0.1 |
|     *Pleuromamma* spp. | 0.5 | 0.5 | 4.8 | 0.1 | – | – | – | – | – | – | – | – |
|     *Acrocalanus gibber* | 0.1 | <0.1 | 1.0 | <0.1 | – | – | – | – | – | – | – | – |
|     *Paracalanus aculeatus* | 0.1 | <0.1 | 1.0 | <0.1 | 0.1 | <0.1 | 1.8 | <0.1 | 0.1 | <0.1 | 1.5 | <0.1 |
|     *Paracalanus parvus* s.l. | 8.9 | 0.2 | 26.7 | 4.0 | 0.3 | <0.1 | 3.6 | <0.1 | 6.2 | 0.2 | 23.9 | 1.9 |
|     *Scolecithrix danae* | – | – | – | – | 2.4 | 0.6 | 14.4 | 0.8 | <0.1 | <0.1 | 0.7 | <0.1 |
|     Scolecitrichidae spp. | – | – | – | – | – | – | – | – | <0.1 | <0.1 | 0.7 | <0.1 |
|     *Temora discaudata* | 0.1 | <0.1 | 1.0 | <0.1 | – | – | – | – | – | – | – | – |
|     *Temora turbinata* | – | – | – | – | – | – | – | – | <0.1 | <0.1 | 0.7 | <0.1 |
|     *Temora* sp. | – | – | – | – | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|   Cyclopoid copepodite | | | | | | | | | | | | |
|     *Oithona similis* | 0.1 | <0.1 | 1.0 | <0.1 | – | – | – | – | – | – | – | – |
|   Poecilostomatoid copepodite | | | | | | | | | | | | |
|     *Corycaeus affinis* | 21.5 | 1.0 | 31.4 | 11.7 | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Corycaeus flaccus* | – | – | – | – | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Corycaeus furcifer* | 0.2 | 0.1 | 3.8 | <0.1 | – | – | – | – | – | – | – | – |
|     *Corycaeus limbatus* | – | – | – | – | <0.1 | <0.1 | 0.6 | <0.1 | – | – | – | – |
|     *Corycaeus speciosus* | 0.1 | <0.1 | 1.9 | <0.1 | – | – | – | – | – | – | – | – |
|     *Corycaeus typicus* | 0.1 | <0.1 | 1.9 | <0.1 | – | – | – | – | <0.1 | <0.1 | 0.7 | <0.1 |
|     *Corycaeus* spp. | – | – | – | – | – | – | – | – | 0.2 | <0.1 | 6.0 | <0.1 |
|     *Oncaea media* | – | – | – | – | 0.1 | <0.1 | 2.4 | <0.1 | – | – | – | – |

*Continued*

**Table 3.** Continued

| Year | 2005 | | | | 2008 | | | | 2009 | | | |
| No. stomachs examined | 205 | | | | 269 | | | | 254 | | | |
| Total no. prey items identified | 1619 | | | | 5269 | | | | 3919 | | | |
| Levins' diet breadth index ($B$) | 2.66 | | | | 4.46 | | | | 3.49 | | | |
| Prey taxon | %N | %W | %F | %IRI | %N | %W | %F | %IRI | %N | %W | %F | %IRI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Oncaea mediterranea* | 0.1 | <0.1 | 1.9 | <0.1 | 0.3 | <0.1 | 6.6 | <0.1 | 0.3 | <0.1 | 3.7 | <0.1 |
| *Oncaea venusta* f. *venella* | 0.1 | <0.1 | 1.0 | <0.1 | 0.2 | <0.1 | 3.6 | <0.1 | 0.2 | <0.1 | 3.7 | <0.1 |
| *Oncaea venusta* f. *typica* | 0.7 | <0.1 | 4.8 | 0.1 | 0.1 | <0.1 | 2.4 | <0.1 | <0.1 | <0.1 | 0.7 | <0.1 |
| *Triconia conifera* | 0.2 | <0.1 | 3.8 | <0.1 | 0.1 | <0.1 | 2.4 | <0.1 | 0.1 | <0.1 | 1.5 | <0.1 |
| *Sapphirina darwinii* | – | – | – | – | – | – | – | – | 0.1 | 0.1 | 3.0 | <0.1 |
| Cirripedia | | | | | | | | | | | | |
| Cypris | 0.1 | <0.1 | 1.9 | <0.1 | – | – | – | – | – | – | – | – |
| Mysidae | | | | | | | | | | | | |
| Mysidae spp. | 0.1 | 0.1 | 1.9 | <0.1 | – | – | – | – | – | – | – | – |
| Amphipoda | | | | | | | | | | | | |
| Hyperiidae spp. | 1.5 | 2.0 | 5.7 | 0.3 | 2.1 | 0.9 | 22.8 | 1.2 | 7.8 | 9.1 | 35.1 | 7.6 |
| *Anchylomera blossevillei* | – | – | – | – | 0.6 | 0.4 | 7.8 | 0.1 | – | – | – | – |
| Phrosinidae spp. | – | – | – | – | 1.1 | 3.1 | 10.8 | 0.8 | – | – | – | – |
| Pronoidae spp. | – | – | – | – | 0.6 | 1.2 | 10.8 | 0.4 | – | – | – | – |
| Platyscelidae spp. | – | – | – | – | 1.9 | 1.6 | 13.8 | 0.9 | – | – | – | – |
| Euphausiidae | | | | | | | | | | | | |
| Calyptopis | 0.2 | <0.1 | 1.9 | <0.1 | – | – | – | – | – | – | – | – |
| Furcilia | – | – | – | – | – | – | – | – | <0.1 | <0.1 | 0.7 | <0.1 |
| *Euphausia* spp. juvenile | 1.4 | 5.8 | 7.6 | 0.9 | 2.8 | 5.5 | 31.7 | 4.7 | 0.3 | 0.9 | 3.7 | 0.1 |
| *Euphausia nana* | 4.0 | 38.6 | 14.3 | 10.0 | 8.6 | 19.0 | 10.2 | 5.0 | 0.6 | 4.7 | 2.2 | 0.2 |
| *Nematoscelis* sp. juvenile | – | – | – | – | 0.8 | 7.5 | 5.4 | 0.8 | – | – | – | – |
| Decapoda | | | | | | | | | | | | |
| Sergestidae juvenile | – | – | – | – | 0.2 | 2.3 | 2.4 | 0.1 | – | – | – | – |
| *Leptochela* sp. zoea | – | – | – | – | 0.9 | 0.2 | 13.2 | 0.2 | 0.1 | <0.1 | 2.2 | <0.1 |
| *Leptochela* sp. mysis | 0.4 | 0.6 | 4.8 | 0.1 | 0.4 | 1.7 | 9.6 | 0.4 | 1.6 | 4.6 | 5.2 | 0.4 |
| *Leptochela* sp. | – | – | – | – | – | – | – | – | 0.2 | 4.7 | 1.5 | 0.1 |
| Anomura zoea | 0.1 | 0.5 | 1.0 | <0.1 | 0.5 | 2.9 | 9.0 | 0.5 | – | – | – | – |
| Brachyura megalopa | 0.1 | 0.3 | 1.0 | <0.1 | 1.0 | 6.7 | 16.2 | 2.2 | 0.1 | 0.5 | 1.5 | <0.1 |
| Chaetognatha | | | | | | | | | | | | |
| Sagittidae spp. | – | – | – | – | 0.2 | 0.3 | 2.4 | <0.1 | – | – | – | – |
| Pteropoda | | | | | | | | | | | | |
| *Creseis acicula* | – | – | – | – | 0.2 | <0.1 | 2.4 | <0.1 | 0.2 | <0.1 | 3.7 | <0.1 |
| Gastropoda larva | 0.1 | <0.1 | 1.9 | <0.1 | 1.1 | 0.4 | 7.2 | 0.2 | 0.3 | 0.1 | 5.2 | <0.1 |
| Bivalvia umbo larva | – | – | – | – | – | – | – | – | 0.4 | <0.1 | 7.5 | <0.1 |
| Cephalopoda larva | 0.1 | 3.0 | 1.0 | <0.1 | 0.4 | 0.1 | 4.8 | <0.1 | – | – | – | – |
| Osteichthyes larva | 0.1 | 0.4 | 1.0 | <0.1 | 0.2 | 0.4 | 1.8 | <0.1 | – | – | – | – |

%N is numerical percentage, %W is dry weight percentage, %F is frequency of occurrence percentage of fish with prey item $i$, and %IRI is per cent of total IRI (index of relative importance) for all prey taxa. IRI = (%N + %W) × %F. –, no occurrence.

The cluster analysis of the compiled data of diet composition (%IRI) showed the level of similarities among years and juvenile types (Figure 5). Three clusters were delineated at a similarity level of 40%. Cluster I included only the pelagic juveniles in 2005, cluster II included the pelagic juveniles in 2008 and 2009, while cluster III included the demersal juveniles from all three surveys.

## Sex and developmental stages of prey items

In the stomach contents of the pelagic juveniles, percentages of adult females of *P. parvus* s.l. were higher than percentages of males and earlier copepodite stages (Table 4). On the contrary, a preponderance of adult males over females was significant in *C. affinis* found in the stomachs of pelagic juveniles. In the stomachs of both pelagic and demersal juveniles, percentages of adult females and the fifth copepodite stage (CVs) of *C. sinicus* were markedly higher than percentages of

males and fourth copepodite stage (CIVs), constituting >80% of the total (Table 4).

Based on the mean body size and the reported body size–carbon relationship, carbon content of *P. parvus* s.l. females was approximately twice as high as that of *C. affinis* males (Table 5). Carbon contents of adult females and CVs of *C. sinicus* were ~23 and 13 times higher than the value of *P. parvus* s.l. females.

## Zooplankton in the water column

The density of zooplankton in April showed both inter-annual and spatial variations (Figure 6). Median density of *P. parvus* s.l. in 2005 was significantly lower than in 2008 and 2009 (Kruskal–Wallis test and Steel–Dwass test, $P < 0.05$). The interquartile range of density of *C. sinicus* in 2005 was lower than in the other two years, while median density of *C. affinis* was markedly higher in 2005 (Figure 6). However, the densities of *C. sinicus* and *C. affinis* were not significantly
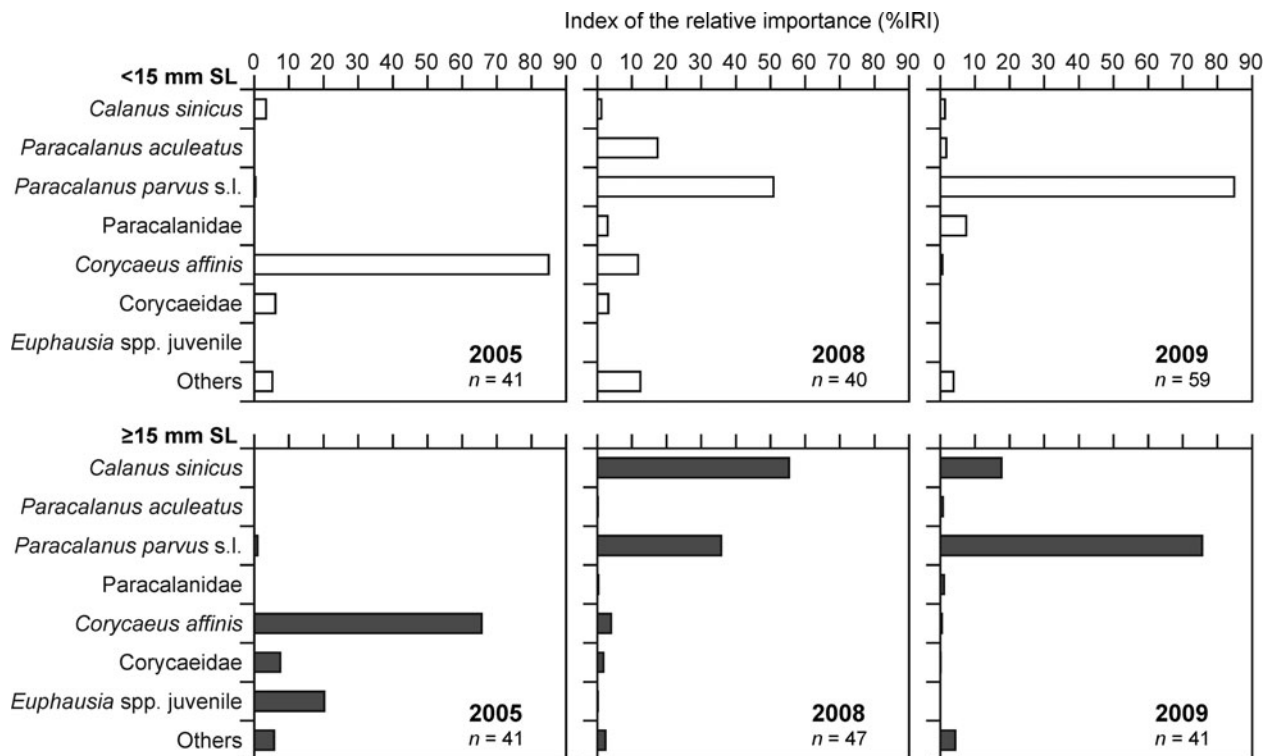
Index of the relative importance (%IRI)



**Fig. 3.** Dietary composition of pelagic juveniles of Japanese jack mackerel (*Trachurus japonicus*) in the surface layer in April from the East China Sea in 2005, 2008 and 2009, expressed as per cent of an index of the relative importance (%IRI) of each prey category in relation to two size classes of juveniles, where *n* represents the total number of juveniles examined. Only prey categories that accounted for more than 5% of %IRI values of the total prey categories identified in at least one of the years are shown.

Index of the relative importance (%IRI)
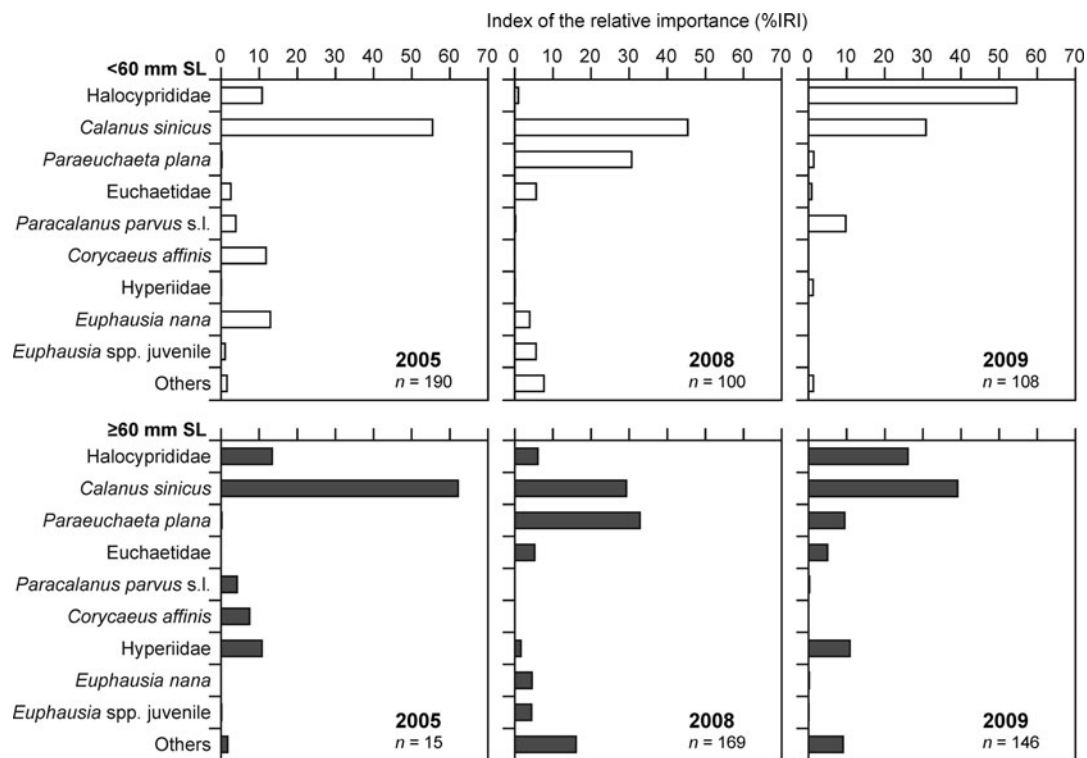


**Fig. 4.** Dietary composition of demersal juveniles of Japanese jack mackerel (*Trachurus japonicus*) in the near bottom layer during May to June from the East China Sea in 2005, 2008 and 2009, expressed as per cent of an index of the relative importance (%IRI) of each prey category in relation to two size classes of juveniles, where *n* represents the total number of juveniles examined. Only prey categories that accounted for more than 5% of %IRI values of the total prey categories identified in at least one of the years are shown.

Bray–Curtis similarity (%)
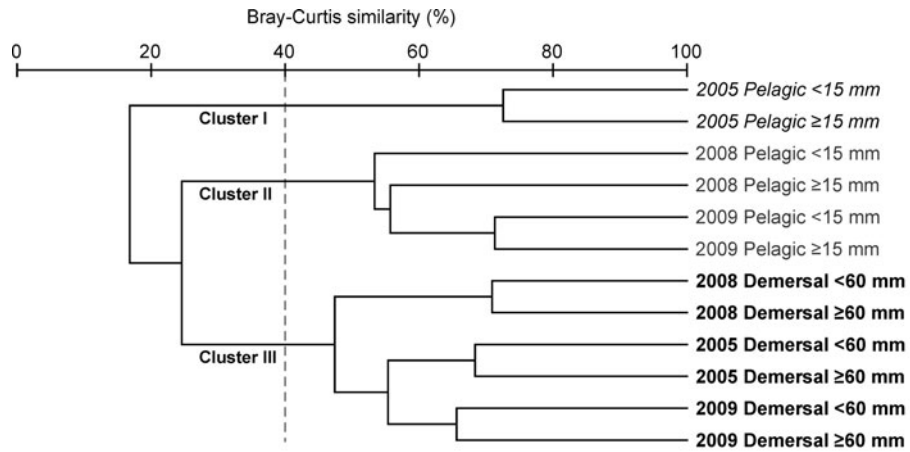
**Fig. 5.** Dendrogram by cluster analysis based on the Bray–Curtis similarity index on square root-transformed %IRI of prey items in the stomach contents of Japanese jack mackerel (*Trachurus japonicus*) juveniles in the East China Sea in 2005, 2008 and 2009.

different among the years (Kruskal–Wallis test, $P > 0.05$ in both species), which is probably driven by the variations among locations within each year.

In *P. parvus* s.l., females were more abundant than males in the water column, while in *C. affinis* males were more abundant than females (Table 6). In *C. sinicus*, percentage of CVs was highest (61.9%). Although the percentage of adults was low in *C. sinicus*, females were more abundant than males (Table 6).

## DISCUSSION

### Diet composition of pelagic juveniles and its inter-annual variations

Diet composition of the pelagic juveniles showed a significant difference between 2005 and the other two years. That

is, in 2008 and 2009, the pelagic juveniles <15 mm SL ate mainly *P. parvus* s.l., and started to prey on *C. sinicus* when they reached ≥15 mm SL. In 2005, on the other hand, the pelagic juveniles predated heavily on *C. affinis* in both size classes. The observed difference in diet partly corresponded with the between-year difference in the prey densities in the field. That is, in 2005, the median density of *P. parvus* s.l. was significantly lower than in 2008 and 2009. Also, the density of *C. sinicus* in the water column was lowest in 2005, although the difference between the other two years was much smaller compared with *P. parvus* s.l. In contrast to these two species, *C. affinis* density in 2005 was highest among the three years. Therefore, the difference in the prey densities in the field could be one of the main factors influencing the between-year difference in the diet. However, it must be noted that the prey density in the upper 50 m layer, although well mixed, may be different from the food availability for the pelagic juveniles occurring in the surface layer (upper 0.75 m).

**Table 4.** Composition (%) of developmental stages of the dominant copepod species in the stomachs of pelagic juveniles of Japanese jack mackerel (*Trachurus japonicus*) in the epipelagic layer in April and demersal juveniles in the near bottom layer during May to June in the shelf-break region of the East China Sea.

| *Trachurus japonicus* | Prey items | 2005 | 2008 | 2009 |
|---|---|---|---|---|
| Pelagic juveniles | *Paracalanus parvus* s.l. | | | |
| | F | – | 92.8 | 90.3 |
| | M | – | 0.4 | 3.8 |
| | CIV–V | – | 6.8 | 5.9 |
| | *Corycaeus affinis* | | | |
| | F | 28.7 | 6.9 | 10.8 |
| | M | 71.3 | 93.1 | 89.2 |
| | *Calanus sinicus* | | | |
| | F | – | 12.1 | 52.0 |
| | M | – | 1.1 | 0.0 |
| | CV | – | 86.0 | 38.7 |
| | CIV | – | 0.9 | 9.3 |
| Demersal juveniles | *Calanus sinicus* | | | |
| | F | 37.5 | 53.8 | 15.1 |
| | M | 5.1 | 18.6 | 2.7 |
| | CV | 50.7 | 26.7 | 69.2 |
| | CIV | 6.7 | 0.0 | 12.7 |

F, adult female; M, adult male; CIV, the fourth copepodite stage; CV, the fifth copepodite stage. –, total number of individuals sampled from the stomachs was <65.

**Table 5.** Dimensions and carbon contents of the four major prey items taken by Japanese jack mackerel (*Trachurus japonicus*) juveniles.

| Taxon | Total length (mm) | | Prosome length (mm) | | Body width (mm) | | Carbon (μg) |
|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD | |
| *Paracalanus parvus* s.l. (F) | 0.90 | 0.06 | 0.69 | 0.05 | 0.29 | 0.03 | 2.70 |
| *Corycaeus affinis* (M) | 0.91 | 0.05 | 0.54 | 0.04 | 0.25 | 0.02 | 1.43 |
| *Calanus sinicus* (CV) | 2.19 | 0.14 | 1.75 | 0.10 | 0.61 | 0.09 | 34.60 |
| *C. sinicus* (F) | 2.63 | 0.12 | 2.07 | 0.12 | 0.75 | 0.06 | 61.00 |

The mean prosome length was converted to the approximate carbon contents based on equations from Liang and Uye (1996) for *P. parvus* s.l., Satapoomin (1999) for *C. affinis*, and Uye (1988) for *C. sinicus*. F, adult female; M, adult male; CV, the fifth copepodite stage. SD, standard deviation.

*Paracalanus parvus* s.l. is numerically the most dominant small-sized copepod in the epipelagic layer of the ECS shelf and its adjacent waters (Liang & Uye, 1996; Lan et al., 2008; Chou et al., 2012). Except for 2005, pelagic juveniles of *T. japonicus* depended on *P. parvus* s.l. adult females, while



**Fig. 6.** Box plots of $\log_{10} (x + 1)$ transformed densities (individuals per m³, 0–50 m depth) of *Paracalanus parvus* s.l., *Calanus sinicus* and *Corycaeus affinis* collected by Norpac net (0.1 mm mesh) in the shelf-break region of the southern and central East China Sea in April 2005, 2008 and 2009. The total number of stations in 2005, 2008 and 2009 were 9, 9 and 13, respectively. The box plots denote median values and 25% and 75% interquartiles (IQ25 and IQ75 respectively); the lower and upper whiskers represent IQ25 − 1.5 × (IQ75 − IQ25) and IQ75 + 1.5 × (IQ75 − IQ25) respectively; dots represent outliers. Different letters beside plots indicate statistical difference ($P < 0.05$) among the three years.

larvae of *T. japonicus* preyed mainly on early developmental stages of *Paracalanus* spp. copepodites (mainly *P. parvus* s.l.) in the southern ECS (Sassa et al., 2008a; Sassa & Tsukamoto, 2012). This indicated that various developmental stages of *P. parvus* s.l. provide a wide size spectrum of prey items, being a key species for the early survival of *T. japonicus*. The density of *P. parvus* s.l. shows a peak from spring to early summer on the ECS shelf (Chihara & Murano, 1997; Chou et al., 2012; Kitajima, unpublished data), corresponding to the seasonal peak abundance of the pelagic juveniles (Sassa et al., 2006; Takahashi et al., 2016). This seasonal overlap with *P. parvus* s.l. is most likely advantageous for the survival of *T. japonicus* during the pelagic juvenile stage.

*Corycaeus affinis* is a neritic corycaeid copepod and commonly distributed in the epipelagic layer of the ECS shelf (Chihara & Murano, 1997; Lan et al., 2008). In 2005 when low densities of *P. parvus* s.l. were observed, pelagic juveniles of both size classes ate mainly *C. affinis*. This indicated that pelagic juveniles adapted their diet to the available prey having a similar body size to *P. parvus* s.l. This also suggests that they are opportunistic predators. However, based on the carbon content, *C. affinis* would be energetically less favourable prey than *P. parvus* s.l. and the pelagic juveniles in 2005 had trophically poorer conditions than in 2008 and 2009. In addition, no ontogenetic variation in diet of the pelagic juveniles in 2005 should have resulted in increased intraspecific competition among the different size classes.

The predation by pelagic juveniles on *C. sinicus* in 2008 and 2009 was largely limited to the larger juveniles (≥15 mm SL). Since a bimodal vertical distribution of *C. sinicus* is observed on the ECS shelf, with the maximum abundance near the bottom layer and another peak in the epipelagic layer (Wang et al., 2003; Kitajima, unpublished data), not only the demersal juveniles but also pelagic juveniles can encounter *C. sinicus*. The occurrence of *C. sinicus* in stomachs of pelagic juveniles ≥15 mm SL can most likely be linked to larger mouth size and increased swimming availability of *T. japonicus*. The total length and width of *C. sinicus* found in stomachs ranged from 2.2–2.6 mm and 0.6–0.8 mm, respectively, with dimensions which were ~2–3 times larger than those of *P. parvus* s.l. The upper jaw length and mouth width, a proxy of mouth size (Shirota, 1970), of *T. japonicus* at 15 mm SL were 2.4 and 1.3 mm, respectively (Sassa, unpublished data), which is considered to be large enough to begin eating *C. sinicus*. Carbon contents of *C. sinicus* were 13–23 times higher than that of *P. parvus* s.l., implying a higher energetic gain for the pelagic juveniles. Accordingly, the occurrence of *C. sinicus* in the stomachs of pelagic juveniles in 2008 and 2009 indicates that the food availability for the juveniles was markedly higher than in 2005.
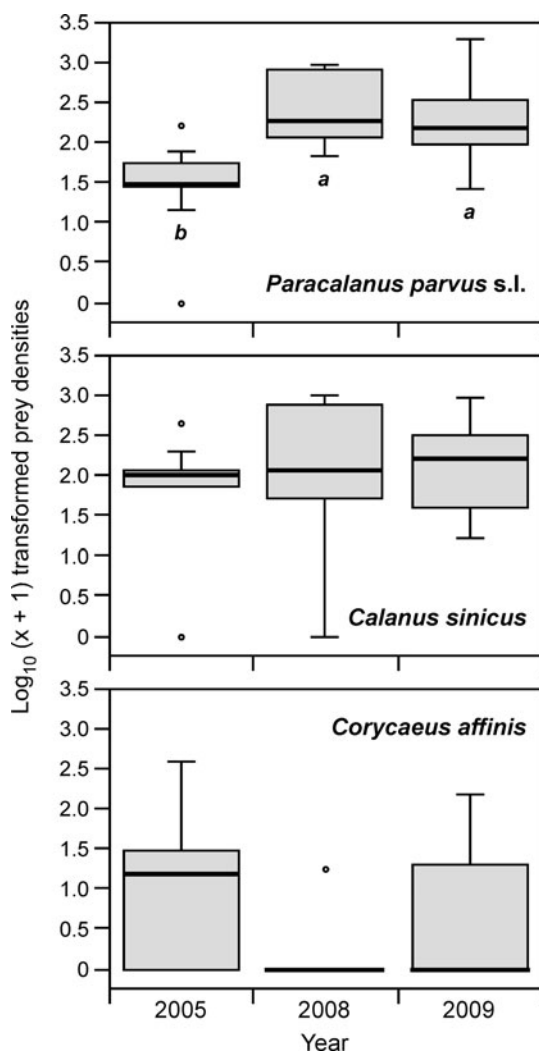
**Table 6.** Composition (%) of developmental stages of the three copepod species collected by Norpac net (0.1 mm mesh) in the shelf-break region of the East China Sea in April.

| Prey items | % | Prey items | % |
|---|---|---|---|
| *Paracalanus parvus* s.l. | | *Calanus sinicus* | |
| F | 90.5 | F | 8.2 |
| M | 9.5 | M | 2.8 |
| | | CV | 61.9 |
| *Corycaeus affinis* | | CIV | 22.1 |
| F | 28.4 | CIII | 1.8 |
| M | 71.6 | CII | 1.4 |
| | | CI | 1.8 |

F, adult female; M, adult male; CI–V, copepodite stages I–V. Data in 2005, 2008 and 2009 was pooled for *C. affinis*, while data in 2008 and 2009 for *P. parvus* s.l. and *C. sinicus*.

In this study, *P. parvus* s.l. and *C. sinicus* found in the stomach of the pelagic juveniles were mostly females, while *C. affinis* were mostly males in all the three years. Extremely female-skewed sex ratios in the water column have been observed in various copepods including *P. parvus* s.l. and *C. sinicus* (Chen, 1964; Hirst et al., 2010; Gusmão et al., 2013; this study). In *C. affinis*, on the contrary, males were more abundant than females in the water column of the ECS shelf, corresponding with the previous study of Böttger-Schnack et al. (1989) in the Red Sea that showed a high percentage of *Corycaeus* spp. males. For the three copepod species, the prosome length of the females is slightly larger than of the males (~1.1 fold difference; Kitajima, unpublished data). Thus, potential selection of larger prey by the juveniles should hardly impact the sex ratios observed in the stomachs. Consequently, the skewed sex ratios of prey items in the stomachs of the pelagic juveniles are considered to reflect the sex ratios of the prey in the field.

## Importance of *C. sinicus* as prey for demersal juveniles

After the habitat transition from the surface to the near bottom layer, the index of importance of *P. parvus* s.l. and *C. affinis* as prey items for *T. japonicus* juveniles decreased greatly. Instead, *C. sinicus* became the dominant prey item for the demersal juveniles in the three survey years. Also, the demersal juveniles occasionally fed on halocyprid ostracods and *Paraeuchaeta plana* as numerically dominant prey items. No difference in the diet composition was observed between the two size classes of the demersal juveniles, although the juveniles ≥60 mm SL would have sufficient swimming ability and a large mouth to feed on larger prey items. Jiang et al. (2013) also found *C. sinicus* in the stomach of *T. japonicus* juveniles (mostly 65–85 mm SL) in the ECS during spring. In addition, stomach contents of the age-0 *T. japonicus* (80–140 mm SL) mainly consisted of calanoid copepods (probably *C. sinicus* based on the body width) in the northern ECS in summer (Tanaka et al., 2006). This suggests that *T. japonicus* prefers *C. sinicus* for at least three months after the habitat transition to the near bottom layer. *Calanus sinicus* is one of the key components of the ecosystem on the ECS shelf and adjacent waters, supporting the production of commercially important fishes including both pelagic and demersal species (Chen, 1994; Uye, 2000; Wang et al., 2003; Hwang & Wong, 2005; Xu & Chen, 2007). Density of *C. sinicus* shows a strong monthly variation, with a single peak season from May to June on the ECS shelf (Chen, 1994; Wang et al., 2003; Xu & Chen, 2007). This corresponds to the seasonal peak abundance of the demersal juveniles (Sassa et al., 2009), and is likely advantageous for survival of *T. japonicus* during the demersal juvenile stage.

In the stomachs of the demersal juveniles, percentages of CVs and adult females of *C. sinicus* were markedly higher than of the other developmental stages. This corresponds to the composition of *C. sinicus* in the southern Yellow Sea and the ECS during spring to summer (Wang et al., 2003; Pu et al., 2004; Hwang & Wong, 2005; Wang et al., 2014). The CVs and females of *C. sinicus* store lipids in the body, and the total lipid content in CVs and females are 22.4–40.1% and 5.4–17.2% of their body DW, respectively, in the ECS and Yellow Sea (Wang et al., 2014), i.e. they are high-calorie prey items.

## Implications of diet for growth and recruitment

Growth during the larval and juvenile stages has been suggested to be an important factor determining survival and recruitment success of fishes including both pelagic and demersal species, even if competing alternative hypotheses for recruitment variation exist as well (Anderson, 1988; Chambers & Trippel, 1997; Fuiman & Werner, 2002; Robert et al., 2007). Early growth is directly related to feeding and habitat temperature (Takahashi & Watanabe, 2005; Zenitani et al., 2009). In this study, diet composition of the pelagic juveniles showed a significant difference between 2005 and the other two years, although no difference was observed in the habitat temperature. Takahashi et al. (2012, 2016) reported that growth rates of *T. japonicus* during the late larval and pelagic juvenile stages in 2005 were lower than in 2008 and 2009 in our study area. Also, they discussed that this lower growth rate potentially resulted in the lowest observed recruitment level of the demersal juveniles for the ECS in 2005 over these three years (Yoda et al., 2017). The diet composition of the pelagic juveniles in the three years studied, likely impacted the growth and recruitment of the stock for these years. That is, the markedly low occurrence of *P. parvus* s.l. and *C. sinicus*, which are considered to be energetically more favourable than *C. affinis*, from the stomach of the pelagic juveniles in 2005 potentially relates to the lower growth rate that year and consequently poor recruitment.

In the upper 50 m water column, the density of *P. parvus* s.l. in 2005 was significantly lower than in 2008 and 2009. Also, the density of *C. sinicus* tended to be low in 2005,

although a significant difference was not detected between the other two years. This suggests that the availability of the two prey items in 2005 may have been lower compared with the other two years. However, our results of stomach contents are just a snapshot picture of the three years. We need to analyse the relationships among the diet, growth, and recruitment levels for other years that show significantly different levels of recruitment.

In contrast to the pelagic juveniles, there was no difference in the diet of the demersal juveniles among the three years. This indicates that food availability did not differ greatly during the study period and/or the prey items were abundant enough for their feeding, although we have no data on prey density in the near bottom layer in May–June to confirm this conclusion. This would also be related to the active feeding behaviour of demersal juveniles that have enough swimming ability to search for their favourable prey items. Our results suggest that if *T. japonicus* successfully survive the pelagic juvenile stage, they can reach a habitat with favourable food conditions in the near bottom layer of the southern and central ECS where *C. sinicus* densities are consistently high (Chen, 1994; Wang *et al.*, 2003; Xu & Chen, 2007). Thus, we conclude that the survival rate during the demersal juvenile stage is relatively stable among years. Inter-annual variations in abundance of demersal juveniles in May–June have been shown to correlate with the recruitment of the *T. japonicus* stock in the ECS (Yoda *et al.*, 2017), which supports our conclusion.

Our results suggested that inter-annual fluctuations in food availability, especially *P. parvus* s.l. and *C. sinicus*, during spring is one of the key factors determining the growth and survival of the pelagic juveniles, and possibly subsequent year-class strength in the ECS. As a next step, we need to analyse the mechanism of fluctuations in densities of *P. parvus* s.l. and *C. sinicus* during spring in the nursery ground of *T. japonicus* in detail. In addition, factors other than food availability, such as transport processes of larvae and pelagic juveniles and abundances of predators and competitors for prey may also affect fluctuations in early survival of *T. japonicus*. Comprehensive information on factors potentially affecting early survival is needed for understanding of the mechanism of inter-annual variations in recruitment of *T. japonicus* to allow forecasts of annual recruitment levels.

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