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# Interannual variations in diet of Japanese jack mackerel (Trachurus japonicus) juveniles in the southwestern Sea of Japan in relation to recent growth rate

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# Interannual variations in distribution and abundance of Japanese jack mackerel *Trachurus japonicus* larvae in the East China Sea

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## Abstract

We examined the interannual variations in distribution and abundance of Japanese jack mackerel *Trachurus japonicus* larvae <5 mm standard length (SL), based on sampling surveys over a broad area of the shelf-break region of the East China Sea (ECS) during late winter and spring for twelve years from 2001 to 2012. Larval abundances in late winter were higher than those in spring. In late winter, ratios (expressed as %) of larval abundance in the southern ECS south of 28°N to the whole study area were highest during the study period, with values ranging from 80.0 to 95.8%. In spring, the ratios in the southern ECS were still high (34.3–88.8%), although the values increased slightly in the northern and central ECS. There was no significant interannual variation in the center of distribution of the larvae, suggesting that the formation of spawning grounds would be related to topographic rather than hydrographic conditions. Habitat temperature of larvae in the central and southern ECS was approximately 3–5°C higher than that in the northern ECS throughout the study period, indicating that larval growth and survival processes may differ between the two areas. In the southern ECS, larval abundances fluctuated largely from year-to-year, and the interannual variations were closely correlated to water temperature and chlorophyll *a* concentration. However, larval abundance did not correlate with an index of recruited juveniles (approximately 50–75 mm SL) in the ECS, suggesting that mortality during the late larval and early juvenile stages is responsible for recruitment success or failure.

**Keywords:** interannual variations, Japanese jack mackerel, larval abundance, larval distribution, southern East China Sea, spawning grounds

## Introduction

Stocks of small pelagic fishes (SPF) fluctuate largely from year-to-year in the world oceans, and these fluctuations are considered to relate to changes in physical oceanographic and biological conditions on regional- and global-scales (Checkley *et al.*, 2009; Kawasaki, 2013). Importance of fisheries production of SPF as a protein supply source is predicted to increase greatly in the near future (Hasan and Halwart, 2009; Laine del Pozo, 2013), thus understanding the recruitment dynamics is a central issue in fisheries science (Checkley *et al.*, 2009). The early life stages have been shown to be the most important stages for determining annual recruitment of fishes (Chambers and Trippel, 1997; Fuiman and Werner, 2002). Recently, numerical models have been developed for the prediction of year-to-year variations in recruitment of the SPF, such as Atlantic mackerel *Scomber scombrus*, Pacific saury *Cololabis saira*, and Japanese sardine *Sardinops melanostictus*, based on information on locations of spawning and nursery grounds and habitat conditions during the early life stages (Suda and Kishida, 2003; Bartsch *et al.*, 2004; Ito *et al.*, 2007; Miller, 2007; Okunishi *et al.*, 2012). The predictive models also contribute to the efficient and sustainable utilization of living marine resources, as well as understanding the mechanisms underlying interannual variations in recruitment of fishes in the oceans.

Species belonging to genus *Trachurus* include many commercially important fisheries resources in the world oceans (FAO, 2013). Of these, Atlantic horse mackerel *T. trachurus*, Chilean jack mackerel *T. murphyi*, Cape horse mackerel *T. capensis*, and Japanese jack mackerel *T. japonicus* are the four species with the highest commercial catch, and the annual catches of each species are in the order of several hundreds of thousands to one million metric tons during 2002 to 2011 (FAO, 2013). In recent years, progress has been made in understanding the biology and ecology of these *Trachurus* species in the world oceans (e.g. Abaunza, 2008; Takahashi *et al.*, 2012; Vásquez *et al.*, 2013; Sassa *et al.*, 2014), although information on the early life history and recruitment processes is markedly less compared to that of other commercial SPF such as sardine, anchovy, and mackerel (Checkley *et al.*, 2009).

*Trachurus japonicus* is widely distributed in East Asian seas and is an important fishery resource in Japan, Korea, China, and Taiwan, forming a shared stock for these countries. Catches of the Japanese fisheries during 1980 to 2013 have fluctuated from 50 to 319 thousand metric tons (Fisheries Agency and Fisheries Research Agency of Japan, 2015). The shelf-break region of the ECS has been considered to be an important spawning and nursery ground for various commercially valuable SPF, including *T. japonicus*, chub mackerel *Scomber japonicus*, spotted mackerel *S. australasicus*, and Japanese amberjack *Seriola quinqueradiata* (Hotta and Nakashima, 1971; Ochiai and Tanaka, 1986; Uehara *et al.*, 1998; Yukami *et al.*, 2009). However, data are limited on the early life stages of all these species. Since 2001, a large scale larval sampling survey over a broad area of the ECS between February and April has been conducted by the Fisheries Research Agency of Japan. Based on the results in 2001, Sassa *et al.* (2006) showed that the primary spawning grounds of *T. japonicus* are formed in the southern part of the ECS south of 28°N during February to March. Subsequently studies have focused on the ecology of *T. japonicus* larvae in the southern ECS, including the fine-scale distribution, feeding, growth, and mortality (Sassa and Konishi, 2006; Sassa *et al.*, 2008a, b, 2014; Sassa and Tsukamoto, 2012). A particle-tracking model was also developed to analyze the transport processes of larvae from the southern ECS (Kasai *et al.*, 2008). However, research on the causes of interannual variations in distribution and abundance of *T. japonicus* larvae, based on yearly ichthyoplankton sampling in the whole ECS, has been limited. This information is fundamental for understanding the fluctuations in recruitment.

In this study, the distribution and abundance of *T. japonicus* larvae are examined in the shelf-break region of the ECS in late winter and spring during twelve consecutive years from 2001 to 2012. The purpose of the present study is twofold. Firstly, we examine the interannual variations in distribution and habitat temperature of *T. japonicus* larvae to investigate the variations in location of the spawning grounds and larval habitat conditions. Secondly, we examine the interannual variations in larval abundance, and the results are investigated in relation to year-to-year variations in the habitat conditions and the subsequent juvenile recruitment.

## Materials and Methods

### Hydrography in the study area

In our study area, the Kuroshio, its branch currents, and the China Coastal Current (CCC) largely influence oceanographic conditions (Figure 1). The main stream of the Kuroshio flows northeastward along the 200 m isobath at the shelf-break, and creates a frontal structure against the shelf waters. In the central part of the ECS, the Kuroshio turns sharply eastward just south of Kyushu, then flows to the northeast along the Pacific coast of Japan. A branch of the Kuroshio intrudes onto the continental shelf (<200 m depth) northeast of Taiwan, i.e. the Kuroshio Branch Current north of Taiwan (KBCNT). Part of the western edge of the Kuroshio separates from its main stream and turns northward along 128–127°E; this branch is called the Kuroshio Branch Current west of Kyushu (KBCWK). In winter, the main origin of the Tsushima Warm Current (TSWC), which flows into the Sea of Japan through the Tsushima Strait, is thought to be the KBCWK. The cold and low-salinity CCC flows southward along the coast of China, and also extends to the central area on the shelf during winter to spring. Ichikawa and Beardsley (2002) and Lie and Cho (2002) provide more detailed information on the physical oceanographic conditions in the ECS.

### Sample collection

Larvae were collected during 38 cruises in the shelf-break region of the ECS from 2001 to 2012 onboard the RV 'Yoko-Maru' (Fisheries Research Agency) for the spring cruises, and the RV 'Yoko-Maru', 'Hokkou-Maru' (Fisheries Research Agency), 'Kaiyo-Maru' (Japanese Fisheries Agency), 'Wakatori-Maru' (Tottori Prefecture), or 'Torishima' (Nippon Kaiyo Co. Ltd.) for the late winter cruises (Table 1). In each year, sampling was conducted during two periods mainly from February to March and in April (hereafter referred to as 'late winter' and 'spring', respectively) (Table 1). The differences of median date among the sampling cruises during the twelve years were up to eleven and six days in late winter and spring, respectively, without any significant interannual trend. Based on gonadal development, the spawning season of *T. japonicus* in the ECS is reported to start in January and cease in May, with a peak during February to April (Hotta and Nakashima, 1971; Yoda *et al*., 2004, 2014). Therefore, our sampling covered the main spawning season. Typical sampling localities are shown in Figure 1. The sampling area was almost the same during the twelve years, and covered a broad area of the shelf-break region from the northern to southern part of the ECS. The number of total sampling stations in a year was in the range of 138–281 in late winter and 69–107 in spring (Table 1). Although the number of sampling stations in spring was fewer than the late winter samplings due to limited ship time, the sampling on all occasions covered similar latitudinal and longitudinal ranges.

A paired bongo net of 60 or 70 cm mouth diameter with 0.32 mm mesh was used for larval sampling. A double-oblique tow was conducted at each station from the surface down to approximately 150 m depth or 10 m above the bottom at shallow stations during the RV 'Yoko-Maru' and 'Kaiyo-Maru' cruises. Although the maximum depth to which the bongo net sampled was 100 m depth during the RV 'Hokkou-Maru', 'Wakatori-Maru', and 'Torishima' cruises, i.e. 50 m shallower than the other cruises, this difference would not have a significant effect on our results, since *T. japonicus* larvae occur in the upper 50 m layer (Sassa and Konishi, 2006; Hirota *et al*., 2009). The towing speed of the net was approximately 1.5 to 2 knots (National Research Institute, Fisheries Agency, 1992). A flow meter (Rigo Co. Ltd., Tokyo, Japan) mounted in the center of the net opening was used for the estimation of volume of seawater filtered. Specimens were first fixed in 10% borax-buffered formalin seawater.

A conductivity-temperature-depth (CTD) profiler cast was made at each sampling station to 200 m depth or 5 m above the bottom at shallower stations. Fluorescence was also profiled using a submersible fluorometer mounted on the CTD (Clorotec, ACL220-PDK, JFE Advantech Co. Ltd., Nishinomiya, Japan) during the RV 'Yoko-Maru' and 'Kaiyo-Maru' cruises, except for spring in 2003. The stations where the Clorotec observations were conducted were restricted to the SECS in late winter, while observations covered the whole study area during spring. The chlorophyll *a* fluorescence measured by the Clorotec was calibrated based on standard procedures using extracted chlorophyll *a* from 250 ml water samples at 20 m depth. The chlorophyll *a* data in the eastern half of the southern ECS in late winter in 2009 were not available due to a problem with the CTD.

## Analysis of larval distribution and abundance

In the laboratory, all *T. japonicus* larvae were sorted from the samples and counted. Body lengths (BL) were measured to the nearest 0.1 mm with an ocular micrometer of a stereomicroscope. Notochord length (NL) was measured for preflexion larvae and standard length (SL) for flexion and postflexion larvae. Since transformation from the larval to the juvenile stage begins at approximately 10–12 mm SL (Ochiai *et al*., 1982; Xie *et al*., 2005), we defined individuals <10 mm SL as larvae. Shrinkage due to net-capture damage and effect of preservation is well known in the larval fish of many species (e.g., Theilacker, 1980), and Hewitt *et al*. (1985) reported 4% shrinkage for 10% buffered formalin in congeneric *T. symmetricus* larvae. In this study, there was no significant difference in handling and preservation methods among the samplings, and the shrinkage has not as yet been reported for *T. japonicus* larvae, therefore we present our data here as the unadjusted length. We used data of the small larvae of <5 mm BL, since one of our main purposes is clarifying the spawning grounds and seasons. Notochord flexion begins to occur at approximately 5 mm BL (Ochiai *et al*., 1982; this study), thus the larvae <5 mm BL were at the preflexion stage. In *T. japonicus*, hatching takes place approximately 27–45 h after fertilization at 18–24°C, based on a rearing experiment (Ochiai *et al*., 1983). Larval growth rate is reported to be 0.19–0.30 mm $d^{-1}$ in the ECS with a habitat temperature of 17–21°C, based on otolith increments (Sassa *et al*., 2008b, 2014). Based on the relationship between age and BL (Sassa *et al*., 2014), most of larvae <5 mm BL are estimated to be less than two weeks after hatching. Recently, the morphological characteristics of formalin-preserved eggs of *T. japonicus* were described in detail based on DNA sequencing and a rearing experiment (Nishiyama *et al*., 2014). However, identification of *T. japonicus* eggs at the early embryo stage by morphological characters is still difficult in the ECS, because approximately 20 species of carangid fish are known to occur there (Senou, 2013). Thus, we estimated the spawning ground and season of *T. japonicus* based on the catch of the small larvae.

For analysis of larval habitat conditions, we used data of sea surface temperatures (SST) and salinity (SSS). Since (1) the mixed layer depth is usually observed in approximately 60–100 m during late winter and become shallower depth of approximately 40–60 m in spring in the study area (Ichikawa and Beardsley, 2002; Sassa *et al*., 2006, observations in this study), and (2) *T. japonicus* larvae <5 mm BL occur in the upper 50 m layer with peak densities in the 10–30 m layer (Sassa and Konishi, 2006; Hirota *et al*., 2009), the SST and SSS directly represent the larval habitat conditions. The chlorophyll *a* concentration was integrated for the 0–50 m water column (mg $m^{-2}$).

To describe the geographic distribution of the larvae, the number of larvae collected at each station was standardized to the number under 10 $m^2$ of sea surface using the volume of water filtered by the nets and the maximum depth to which the net sampled (Smith and Richardson, 1977). Catches of *T. japonicus* larvae by the bongo net towing show no significant differences among day, night, and twilight for the body size class <5 mm BL (Sassa *et al*., 2014), which would be mainly due to limited sensory perception of the net and avoidance reactions by the preflexion larvae, thus we pooled these diel periods in this study. To compare the larval distribution and abundance among geographic regions, we categorized our study area into the following three sub areas, which have been used often in the ECS (Figure 1, Table 2) (Sassa *et al*., 2006, 2009): the northern part of the ECS (NECS) between 33°30' and 30°30'N, the central part of the ECS (CECS) between 30°30' and 28°N, and the southern part of the ECS (SECS) between 28° and 25°N. The SECS is located the most upstream of the Kuroshio, and the NECS is the most downstream.

The total abundance of *T. japonicus* larvae in the surveyed area was estimated, based on the procedure of Watanabe *et al*. (1995). The entire survey area was divided into 30'-latitude by 30'-longitude squares and the tow samples for each year were assigned to the square of origin. The total number of squares in the NECS, CECS, and SECS were 32, 29, and 35, respectively, and these had respective areas of approximately 80,160, 80,130 and 96,490 $km^2$. Then, abundance of the larvae in the *i*-th square in each season ($tj_i$) was calculated by averaging the abundances of larvae collected by tows in each square, and expressed as the number of larvae per $m^2$ of sea surface. For both late winter and spring in year *j*, the total abundance ($TJ_j$) in SECS, CECS, and NECS was calculated using the following equations:

$$TJ_j = \sum_{i=1}^{n} \left( tj_i \times a_i \right)$$

where $a_i$ is the area of the *i*-th square in $m^2$ and *n* is the total number of squares. $TJ_j$ was estimated for both larvae <5 and <10 mm BL, and the percentage of larvae <5 mm BL to the total larvae (<10 mm BL) was calculated for each sampling period. The significance of the relationship between the percentage of larvae <5 mm BL and mean SST in the whole study area, and between the percentage of larvae <5 mm BL and $\log_{10}$-transformed total larval abundances during the twelve years was examined.

To describe the center of distribution of the larvae, the weighted mean of catch locations of the larvae in the SECS and NECS for each season was calculated for both latitude and longitude during the twelve years. We did not consider the larvae in the CECS, because most of them would be carried from the SECS by the Kuroshio (see results). In addition, the weighted mean temperature (*WMT*) of the larval habitat for each area and season were calculated. Both weighted mean values (*WM*) were calculated using the following equation:

$$WM = \sum_{i=1}^{N} \left( tj_i \times x_i \right) \bigg/ \sum_{i=1}^{N} tj_i$$

where $tj_i$ is the abundance of *T. japonicus* larvae in the *i*-th sampling station (larvae under 10 $m^2$), $x_i$ is the location (latitude or longitude) or the SST (°C) at the *i*-th sampling station, and *N* is the total number of sampling stations. Before the analysis, the larval abundance was square root-transformed to reduce the bias caused by sampling stations with extremely large catches.

The weighted standard deviation ($sd_w$) of *WMT* was calculated using the following equation:

$$sd_w = \sqrt{\frac{\sum_{i=1}^{N}\left(x_i - \bar{x}_w\right)^2 tj_i}{\frac{\left(N'-1\right)\sum_{i=1}^{N} tj_i}{N'}}}$$

where $x_i$ is the SST at the *i*-th sampling station, $\bar{x}_w$ is the *WMT* of the larvae, and *N'* is the number of non-zero weights. The mean *WMT* of the larval habitat during 2001 to 2012 ($\overline{WMT_{01-12}}$) was calculated in each area and season to describe robust larval habitat temperature.

Comparisons of larval abundance and *WMT* of the larval habitat between the two seasons and among the three sub areas during 2001 to 2012 were evaluated using two-way ANOVA in conjunction with a Tukey HSD post-hoc test. The significance of the relationships between the larval abundance and years and environmental variables (mean SST, SSS, and chlorophyll *a* concentration) during the twelve years was examined in each area. Before this analysis, the larval abundance in each year was $\log_{10}$-transformed to reduce skewness in the data.

### Implications of the larval abundance for recruitment

The Kuroshio and KBCNT have been shown to significantly affect transport processes of eggs, larvae, and early juveniles (10–40 mm SL) of *T. japonicus* from the spawning ground of the SECS into the nursery grounds in the downstream areas (Kasai *et al.*, 2008; Sassa *et al.*, 2006, 2008b). After reaching approximately 40–50 mm SL *T. japonicus* recruits to the benthopelagic habitat in the shelf-break region of the ECS mainly at the depth of 70–140 m between 31° and 27°N (Sassa *et al.*, 2009; Takahashi *et al.*, 2012). Therefore, we examined the relationship between year-to-year variations in the larval abundance in the SECS during late winter to spring and the subsequent recruited juveniles in the ECS. As an index of recruited juveniles in the ECS, we referred to data from daytime research bottom trawl surveys in the shelf-break region of the ECS between 33° and 26°N during May to June (Takahashi *et al.*, 2012; Fisheries Agency and Fisheries Research Agency of Japan, 2015). The recruited age-0 juveniles of *T. japonicus* (mainly 50–75 mm SL) shown as number of individuals in the survey area (138,000 km$^2$) ranged from 2,693 to 70,907 during 2001 to 2012 (Fisheries Agency and Fisheries Research Agency of Japan, 2015), although their sampling would not have covered the whole daytime distribution depth layer of *T. japonicus* juveniles in the bottom layer and the catch efficiency was assumed to be 1, i.e. the abundances would be considerably underestimated. Interannual variations in this value are considered to be indicative of the recruitment abundance of the *T. japonicus* stock in the ECS (Fisheries Agency and Fisheries Research Agency of Japan, 2015). The annual abundance of larvae in the SECS was calculated by summing the abundance of late winter and spring, which covered the main spawning season of *T. japonicus* in the SECS (Hotta and Nakashima, 1971; Yoda *et al.*, 2004; Sassa *et al.*, 2006). Before the analysis, index of recruited juveniles and larval abundance estimated in each year were $\log_{10}$-transformed.

## Results

### Percentages of larvae <5 mm BL to the total larvae

The estimated abundance of the total larvae (<10 mm BL) of *T. japonicus* in the whole study area showed significant interannual variations in both seasons (Figure 2). The abundance in late winter and spring ranged from 256 billion to 2700 billion and from 106 billion to 1572 billion, respectively. The percentages of larvae <5 mm BL to the total larval abundances showed extremely high values, with mean ± standard error of 84.8 ± 2.7% (range, 66.9–99.9%) in late winter and 85.7 ± 1.9% (75.5–95.9%) in spring, without a significant seasonal difference (t-test, $p > 0.05$). In both seasons, there was no significant relationship between the percentages of larvae <5 mm BL and mean SST in the whole study area during 2001 to 2012 ($r^2 = 0.002$, $p > 0.05$ in late winter; $r^2 = 0.057$, $p > 0.05$ in spring). In addition, no significant correlation was detected between interannual variations in $\log_{10}$-transformed total larval abundances and the percentages of larvae <5 mm BL in both seasons ($r^2 = 0.245$, $p > 0.05$ in late winter; $r^2 = 0.253$, $p > 0.05$ in spring). Hereafter, we analyzed only data of the larvae <5 mm BL to investigate the spawning grounds, larval habitat conditions, and interannual variations in abundances.

**Comparison of larval abundance among the three sub areas**

During late winter from 2001 to 2012, the estimated abundance of *T. japonicus* larvae <5 mm BL fluctuated largely, ranging from 226 billion to 2541 billion in the whole study area (Figure 2). The percentage of larval abundance in the SECS to the whole study area showed extremely high values of 80.0–95.8% (Figure 2). On the contrary, the percentage in the NECS and CECS were 0.6–7.9% and 1.2–17.7%, respectively, during late winter.

In spring, the estimated larval abundances in the whole study area ranged from 82 billion to 1369 billion, which were significantly lower than in late winter (t-test, $p < 0.05$). Although the percentages in the NECS and CECS increased to 6.6–33.1% and 1.9–36.3%, respectively, the percentage in the SECS were still highest of the three sub areas (34.3–88.8%), except in 2004 when the percentage was highest in the CECS (36.3%) (Figure 2).

**Spatial distribution of larvae**

Horizontal distributions of *T. japonicus* larvae in late winter and spring in the four years of 2004, 2007, 2010, and 2011 are shown in Figure 3, which showed typical distribution patterns. In all four years, extremely high abundances of the larvae were found in the shelf-break region of the SECS in late winter. In spring, high larval abundances in the SECS were also observed in 2007, 2010, and 2011, but were the lowest in 2004. In the CECS, the low abundances of the larvae were observed along the Kuroshio front in both seasons. This pattern indicated a northeastward larval transport by the Kuroshio from the SECS to CECS. In the NECS, the larvae were collected mainly off the southwestern and western coast of Kyushu Island, but the abundances were low. Few larvae were collected in stations near the cold and low-salinity CCC (<16°C SST) in the western part of the study area shallower than 100 m bottom depth throughout the sampling period.

In the SECS, the centers of distribution of the larvae were located in a confined area between 27° and 26°30'N and between 125° and 123°30'E during 2001 to 2012, without significant seasonal and interannual variations (Figure 4). In the NECS, the centers of distribution of the larvae were observed in the area southwest of Koshiki Islands between 32° and 31°N in late winter, and the distribution shifted northward to the area south of Goto Islands mainly between 32°30' and 32°N in spring (Figure 4).

**Habitat temperature**

Comparisons of *WMT* of the larval habitat between the two seasons and among the three sub areas using a two-way ANOVA revealed the presence of main effects of seasons ($F_{1,66} = 21.21$, $p < 0.05$), sub areas ($F_{2,66} = 151.99$, $p < 0.05$), and interaction of these two factors ($F_{2,66} = 8.59$, $p < 0.05$). In the SECS, *WMT* of the larvae in late winter ranged from 19.0 to 22.0°C during 2001 to 2012 (Figure 5). In spring, the values increased to 21.8–23.6°C, which were 0.9–4.2°C higher compared to those in late winter ($p < 0.05$). $\overline{WMT}_{01-12}$ was 21.0°C in late winter and increased to 23.0°C in spring.

In the CECS, *WMT* of the larvae in late winter and spring ranged from 19.6 to 22.0°C and from 20.2 to 24.3°C, respectively (Figure 5), showing significantly higher values in spring ($p < 0.05$). Although there were comparatively large variations in *WMT* of the larvae in the CECS during spring, this was because the number of the larvae collected was small and the larvae occurred along the Kuroshio front where the SST changed largely among the sampling stations. In both seasons, *WMT* of the larvae in the CECS showed similar values to those in the SECS ($p > 0.05$ in both cases).

In the NECS, *WMT* of the larvae was from 17.1 to 19.3°C ($\overline{WMT}_{01-12}$ = 18.0°C) in late winter, and from 16.4 to 19.4°C ($\overline{WMT}_{01-12}$ = 17.8°C) in spring, without a significant seasonal difference ($p > 0.05$). $\overline{WMT}_{01-12}$ in the NECS was approximately 3 to 5°C lower than the values in the SECS and CECS in both seasons ($p < 0.05$ in all cases) (Figure 5).

## Interannual variations in larval abundance

Comparisons of larval abundance between the two seasons and among the three sub areas using a two-way ANOVA revealed the presence of main effects of seasons ($F_{1,66} = 6.99$, $p < 0.05$), sub areas ($F_{2,66} = 23.94$, $p < 0.05$), and interaction of these two factors ($F_{2,66} = 7.34$, $p < 0.05$). In the SECS, the larval abundance showed significant interannual variations in both seasons (Figure 6). The abundance in late winter and spring ranged from 182 billion to 2410 billion and from 49 billion to 1200 billion, respectively. Especially, high abundance was observed in 2004, 2008, and 2011 in late winter, and in 2011 in spring. Coefficient of variation (CV) in larval abundance during the twelve years was 77.9% in late winter and 118.9% in spring, both of which were highest among the three areas. In the SECS, the abundances in late winter were significantly higher than those in spring ($p < 0.05$). Only exception was 2005 when the abundance in spring was slightly higher than that in late winter (292 billion versus 266 billion). In both seasons, the larval abundances in the SECS were significantly higher than those in the CECS and NECS ($p < 0.05$ in all cases).

In the CECS, the larval abundance in late winter and spring ranged from 13 billion to 122 billion and from 2 billion to 82 billion, respectively (Figure 6). In this area, no significant difference in the larval abundance was observed between late winter and spring ($p > 0.05$). Although we analyzed relationship between the larval abundances in the CECS and its upstream SECS in the same year, there was no significant correlation between them in both seasons ($r^2 = 0.046$, $p > 0.05$ in late winter; $r^2 = 0.302$, $p > 0.05$ in spring).

In the NECS, the larval abundance in late winter and spring ranged from 3 billion to 66 billion and from 8 billion to 123 billion, respectively (Figure 6). CV in larval abundance in the NECS was lowest among the three areas in both seasons (70.7% in late winter and 70.4% in spring). In the NECS, the larval abundances in spring were significantly higher than those in late winter ($p < 0.05$), which was the opposite pattern to that in the SECS. In both seasons, there were no significant differences between larval abundances in the CECS and NECS ($p > 0.05$ in all cases).

In the SECS and NECS, there were positive trends in $\log_{10}$-transformed larval abundances over the twelve years in both late winter and spring, while no clear trend was observed in the CECS (Table 3).

## Relationship between larval abundance and oceanographic conditions

The significance of regressions between $\log_{10}$-transformed larval abundance and mean SST, SSS, and chlorophyll *a* concentration was examined for each area in late winter and spring during 2001 to 2012 (Table 4). In the SECS, there was a negative correlation between larval abundance and SST in spring ($p < 0.05$), while there was no correlation in late winter ($p > 0.05$) (Figure 7). In addition, the larval abundances showed significant positive correlations with the chlorophyll *a* concentrations in the SECS during both late winter and spring ($p < 0.05$ in both cases) (Figure 7). The mean chlorophyll *a* concentrations in the SECS explained 56–60% of the interannual variations in larval abundance. On the contrary, in the CECS and NECS, the larval abundances in both seasons did not show significant correlations with both SST and chlorophyll *a* concentrations ($p > 0.05$) (Table 4). No significant correlation was detected between larval abundance and SSS in the all three sub areas ($p > 0.05$ in all cases) (Table 4).

### Relationship between larval abundance and recruited juveniles

An index of recruited *T. japonicus* juveniles in the ECS did not correlate with the larval abundance in the SECS in late winter ($r^2 = 0.003$, $p > 0.05$), spring ($r^2 = 0.042$, $p > 0.05$), and during late winter to spring ($r^2 = 0.011$, $p > 0.05$) (Figure 8). It was notable that recruitment was highest in 2001 when the larval abundance during late winter to spring was lowest, while the recruitment was low in 2011 when the larval abundance was highest.

## Discussion

### Limitations of the samplings and analysis

In this study, there were three major limitations to our samplings and analysis. Firstly, although one of our main purposes was to investigate the spawning of *T. japonicus* in the whole ECS based on ichthyoplankton surveys, we could not analyze egg abundance due to the difficulties of species identification. Instead, we used the abundance data of the larvae <5 mm BL which are mostly post-first feeding larvae. This is because newly hatched yolk-sac larvae were not collected abundantly by the bongo net tows, partly due to net extrusion losses of larvae through the net mesh. To quantitatively analyze the larval distributions and abundances including in the CECS and NECS where the number of larvae collected was much lower compared to that in the SECS, we used the data of larvae <5 mm BL, rather than newly hatched larvae only. In Chilean jack mackerel *T. murphyi* off central Chile, interannual variation in abundance of the eggs have been shown to be similar to that of the larvae (Núñez *et al*., 2008). Similarly, the year-to-year abundances of post-first feeding larvae are positively correlated with egg abundance in chub mackerel *Scomber japonicus* and Japanese sardine *Sardinops melanostictus* in the western North Pacific (Watanabe, 1970; Watanabe *et al*., 1995). Therefore, abundance of small larvae of *T. japonicus* can be considered to be an appropriate proxy for egg production in the spawning grounds however future verification is required.

Secondly, our results were snapshot data of the distribution and abundance of the larvae during each sampling period. *Trachurus japonicus* is a multiple spawner with an asynchronous oocyte development that carries out multiple spawning events during the reproductive season, and spawning frequency is estimated to maintain a relatively high value of >0.3 in the ECS (Hotta and Nakashima, 1971). This indicates that spawning takes place at least every 3–4 days, i.e., active spawning by each individual during the spawning season and a relatively continuous supply of eggs and larvae into the water column, thus our results can be considered to be appropriate proxies of abundance of small larvae.

Finally, in this study, the abundance of *T. japonicus* larvae should be considered as an underestimate in the SECS where the largest spawning ground was usually formed as detailed later. High larval abundances often occurred at the westernmost stations where a weak northeastward flow of the KBCNT originating from the west of our study area prevails (Tang *et al*., 2000; Kasai *et al*., 2008). This indicates that the distribution of small larvae extends to Taiwanese territorial waters to the west of our study area where Japanese research vessels are unable to conduct larval sampling. Recent ichthyoplankton sampling surveys in the inshore and offshore waters around Taiwan in late winter shows that *T. japonicus* larvae occur off northeastern Taiwan, i.e. just west of our study area, but the abundances are markedly lower than that in this study (Hsieh FJ *et al*., 2007; Hsieh HY *et al*., 2007; Lo *et al*., 2010). Therefore, our study area can be considered to include the main distributional area of small larvae of *T. japonicus*.

### Spawning ground and its regional and interannual variations

The percent composition of larval abundance of *T. japonicus* in the SECS to the whole study area was highest among the three sub areas during 2001 to 2012, thus we confirmed that the SECS is the primary spawning ground. Since the SECS is located in the upstream region of the Kuroshio and its branch currents, the prevailing currents greatly contribute to the dispersal of *T. japonicus* eggs and larvae (Kasai *et al*., 2008). Both during the early 1960s when the stock of *T. japonicus* in the ECS was high with annual catches of approximately 200 to 300 thousand tons and during the late 1960s to early 1970s when the stock decreased to <100 thousand tons (Yamada *et al*., 2007), dense larval distributions are reported to have been formed in the SECS, especially in the waters northeast of Taiwan, based on the results of ichthyoplankton surveys (Shojima, 1963; Shojima *et al*., 1966; Asami, 1974). This was also recognized during our study period (2001–2012) when the stock was at a moderate level with annual catches of 109 to 192 thousand tons in the ECS and southwestern Sea of Japan (Fisheries Agency and Fisheries Research Agency of Japan, 2015).

The seasonal difference of the centers of distribution of the larvae in the NECS indicates a northward shift of the spawning ground that is possibly related to the rise in water temperature from winter to spring. In the SECS, on the contrary, the centers of distribution of the larvae were located in a rather confined area, without significant seasonal and interannual variations, although this area has extremely complex hydrographic conditions (Kasai *et al*., 2008; Sassa *et al*., 2008b). Topographically induced upwelling, relating to the intrusion of the Kuroshio across the continental shelf, is found year-round at the shelf-break northeast of Taiwan, centered at approximately 25°15’–25°45’N and 121°45’–122°45’E, i.e. just west of our study area (Gong *et al*., 1997; Hsu *et al*., 2000; Wong *et al*., 2000). This permanent upwelling is a major source of nutrients that support primary production in the SECS (Wong *et al*., 2000), which would provide good feeding conditions for both adult and larval *T. japonicus*. Although there is no detailed information on spawning behaviors, including spawning depth, timing, and schooling behaviors within spawning aggregations, adult *T. japonicus* aggregate in this upwelling region during the spawning seasons to form a large spawning ground without a large interannual variation in its geographical position. In addition, the spawning of *T. japonicus* is related to the bottom features such as shoals (Ochiai and Tanaka, 1986; Nishiyama *et al*., 2014), however the location of shoals in the SECS is restricted to a small area, compared to the NECS off western Kyushu Island. These would be the main reason why the centers of distribution of the larvae did not differ interannually in the SECS.

A large spawning ground of *T. japonicus* had previously been suspected to occur in the shoal area in the CESC (approximately 29°30’–29°N and 127°–126°30’E) based on the catch statistics (Research Division, Fisheries Agency of Japan, 1973), however we could not find any evidence supporting this hypothesis during the twelve years. Instead, low abundance of the larvae usually occurred along the Kuroshio front in the CECS, suggesting that they are larvae transported by the Kuroshio from its upstream region of the SECS where markedly higher abundances of larvae were always observed. Although we could not detect a significant relationship between the year-to-year larval abundances in the CECS and SECS, this would be because (1) there is a large interannual variation in the ratio of larvae transported by the Kuroshio from the SECS (Kasai *et al*., 2008), and/or (2) the appropriate estimation of larval abundance is difficult in the CECS where the Kuroshio transports the larvae rapidly out of the area, i.e. possibly masking the relationship. Since a particle-tracking model shows that most of the larvae occurring along the Kuroshio front in the CECS are transported to the Pacific coast of Japan (Kasai *et al*., 2008), interannual variations in the ratio of the larvae entrained by the Kuroshio in the SECS would affect the recruitment of *T. japonicus* in the ECS each year.

Spawning habits of two commercially valuable *Trachurus* species appear to differ considerably between the western and eastern Pacific. *Trachurus murphyi* population has a widespread oceanic spawning habitat off central Chile, extending more than one thousand nautical miles offshore, associating with the southern boundary of the Subtropical Convergence Zone (Cubillos *et al*., 2008; Núñez *et al*., 2008; Vásquez *et al*., 2013). On the contrary, the spawning ground of *T. japonicus* was formed in rather confined area in the shelf-break region of the SECS during late winter, suggesting that mature adults aggregate in compact schools there. During winter, large fishing grounds of SPF by purse seine fisheries have not been formed in the SECS due to the rough sea conditions caused by the strong northwest monsoon, which would have partly contributed to protect the spawning population of *T. japonicus* from high fishing pressure.

## Habitat temperature and possibility of two subpopulations

Under laboratory conditions, egg development and hatching of *T. japonicus* occurs normally at incubation temperature of 18–24°C, while eggs do not hatch in water temperatures of ≤15°C (Ochiai *et al*., 1983; T. Sakai, unpublished data). In this study, $\overline{WMT}_{01-12}$ of the larvae <5 mm BL ranged from 17.8 to 23.0°C in the three sub areas, falling within the range of the hatching temperate under laboratory conditions.

There was no significant interannual variation in habitat temperature of *T. japonicus* larvae in each sub area. In the SECS, $\overline{WMT}_{01-12}$ was 21°C in late winter and increased to 23°C in spring. $\overline{WMT}_{01-12}$ in the CECS was similar to these values. Generally, growth rate of larval fish is closely related to habitat temperature, since temperature greatly affects the larval metabolic rate (Houde, 1989a; Houde and Zastrow, 1993; Shoji *et al*., 2006; Sassa *et al*., 2014). Watanabe and Xie (2007) conducted a rearing experiment of *T. japonicus* large-sized larvae and juveniles (approximately 17–45 days after hatching) at incubation temperatures of 16, 19, 22, and 25°C. They found that (1) the growth rate in 16–22°C increases linearly, and (2) the growth rate at 25°C was similar to that at 22°C, but occurrence of malformation of otolith is markedly higher, i.e. 25°C would be physiologically too high as a suitable habitat temperature. Therefore, growth of *T. japonicus* during the early life stages is considered to be highest at 22°C (Watanabe and Xie, 2007), overlapping with the habitat temperature in the SECS. In many marine fish species, higher growth rate is related to higher survival rate during early life stages, including *T. japonicus* in the ECS (Takahashi and Watanabe, 2005; Shoji *et al*., 2006; Castonguay *et al*., 2008; Robert *et al*., 2009; Zenitani *et al*., 2009; Takahashi *et al*., 2012), although there is information showing that the impact of growth rates on larval survival may be less important in *T. japonicus* in the southwestern Sea of Japan (Kanaji *et al*., 2009). The temperature condition in the SECS can be considered to be advantageous for larval survival in this area.

On the other hand, $\overline{WMT}_{01-12}$ in the NECS was 18°C in late winter and 17.8°C in spring, and approximately 3 to 5°C lower than the $\overline{WMT}_{01-12}$ in the SECS in both seasons. There is a negative relationship between hatching time of *T. japonicus* eggs and temperature in the range of 18–24°C, and hatching takes place approximately 45 h after fertilization at 18°C, and 27 h at 24°C (Ochiai *et al*., 1983). In addition, according to a rearing experiment, when prey densities were the same, a 5°C increase in habitat temperature leads to a doubling of the larval daily growth (Ochiai *et al*., 1983, 1984). This indicates that hatching time and larval growth are slower in the NECS compared to the SECS, and the larval survival processes are different between the two sub areas.

Between *T. japonicus* in the SECS and NECS, there were clear differences in both the spawning location and the spawning temperature. This suggests that they might be two subpopulations, that is, different stocks. A large proportion of *T. japonicus* larvae hatched in the NECS in April are hypothesized to be transported to the southwestern Sea of Japan by the TSWC, bringing recruits into the fishing ground (Fukataki, 1960; Kidokoro *et al*., 2005; Xie and Watanabe, 2005; Shimura *et al*., 2009; Kanaji *et al*., 2009). On the other hand, most of the eggs and larvae in the SECS are considered to recruit into the ECS (Kasai *et al*., 2008; Sassa *et al*., 2008b; Takahashi *et al*., 2012). Therefore, *T. japonicus* larvae in the SECS and NECS can be considered to recruit into different areas and possibly completing the life cycle in each area, although there must be some exchange between them, mainly due to larval transport by the Kuroshio and its branch currents. In this sense, the populations in the ECS and Sea of Japan can be considered to be a metapopulation. In the Northeast Atlantic and Mediterranean Sea, *Trachurus trachurus* showed low levels of genetic differentiation, but morphometric and parasite approaches support the separation between the populations in the Atlantic Ocean and the Mediterranean Sea (Abaunza *et al*., 2008; Comesaña *et al*., 2008). Because stocks are the basic units of fisheries management and for the study and modeling of the population dynamics (Begg *et al*., 1999; Abaunza *et al*., 2008), further research on the population structure of *T. japonicus* is needed using a holistic approach such as genetic and morphometric techniques and further assessment of life history characteristics (Abaunza *et al*., 2008) to clarify this.

## Interannual variations in larval abundance in relation to oceanographic conditions

The larval abundance of *T. japonicus* fluctuated largely in the SECS in both seasons. In late winter, there was no correlation between larval abundance and habitat temperature in the SECS. This would be because water temperature in late winter was within the range of the optimum habitat temperature of larvae (20–22°C) during the study periods, except for 2005 when the mean temperature showed the lowest value of approximately 19°C and larval abundance tended to be low. On the other hand, in spring, there was a significant negative correlation between larval abundance and temperature. Generally, the water temperature condition is a main factor that causes initiation and termination of the spawning period of fishes (Lam, 1983; Bye, 1984; Shimizu, 2010), thus spawning ends after the water temperature exceeds the optimum range for spawning. The negative correlation observed in this study shows that in years when the rate of water temperature increases during winter to spring was low, the spawning of *T. japonicus* extended to spring. On the other hand, in years when the rate of temperature increase was high, the spawning mostly ended before spring.

A positive correlation was detected between the larval abundance and the chlorophyll *a* concentration in the SECS during both late winter and spring. The chlorophyll *a* concentrations explained approximately 60% of the interannual variations in larval abundances. In *S. melanostictus* and neon flying squid *Ommastrephes bartramii* in the western North Pacific, positive correlations have been reported between interannual variations in the chlorophyll *a* concentration and early survival rate in the nursery grounds (Nishikawa *et al*., 2013, 2014). Larvae of *T. japonicus* feed mainly on copepod nauplii and calanoid copepodites (Sassa *et al*., 2008a; Sassa and Tsukamoto, 2012). In the SECS, densities of these prey items have been found to show positive correlations with chlorophyll *a* concentrations both spatially and interannually (Okazaki *et al*., 2008; Sassa and Tsukamoto 2010; Sassa *et al*., 2014). In *T. japonicus*, *Scomber japonicus*, and spotted mackerel *S. australasicus* in the SECS, during years of higher chlorophyll *a* concentrations and subsequent high prey availability, larval growth tends to be higher than years of low prey availability, possibly resulting in higher larval survival (Sassa and Tsukamoto, 2010; Sassa *et al*., 2014). Therefore, food availability for the larvae might be one of the possible factors affecting the interannual variations in larval abundances, although further study on relationship among physical oceanography, chlorophyll *a* concentration, larval prey production, and larval survival is needed for a better understanding of mechanism of interannual variation in larval abundance in the SECS.

## Implications of larval abundance for recruitment

In this study, the larval abundances in the SECS did not correlate with an index of recruited juveniles in the ECS that is considered to be a reliable indicator of year-class strength (Takahashi *et al*., 2012; Fisheries Agency and Fisheries Research Agency of Japan, 2015). This indicates that the recruitment was not fixed by the abundance of small larvae <5 mm BL. Sassa *et al*. (2014) reported that the larval survival rate of *T. japonicus* did not clearly correspond with recruitment levels in the ECS and suggested that a high survival rate of the larvae is necessary but may not be a sufficient criterion of a strong year-class, supporting the present results. A similar phenomenon showing that recruitments was not correlated with the abundance of eggs and larvae has been observed in several other SPF belonging to Clupeidae, Engraulidae, and Scombridae (Watanabe, 1970; Peterman *et al*., 1988; Butler, 1991; Watanabe *et al*., 1995).

Our results suggest that mortality during the large larval (>5 mm BL) and juvenile stages is responsible for recruitment success or failure of *T. japonicus*. Studies over the last three decades have indicated that cumulative mortality through the larval and juvenile stages during the first several months post hatch, rather than instantaneous mortality at any specific early life stage, is critical in establishing recruitment success or failure and eventual population fluctuations of SPF (Houde, 1989b; Watanabe *et al*., 1995). As a next step, we need to focus on the ecology of the larger larvae (5–10 mm BL) and juveniles in the pelagic layer.

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**Figure captions**

**Figure 1.** Sampling localities of Japanese jack mackerel *Trachurus japonicus* larvae in the East China Sea during late winter and spring in 2002. SECS, southern East China Sea; CECS, central East China Sea; NECS, northern East China Sea; *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.

**Figure 2.** Interannual variations in abundance of Japanese jack mackerel *Trachurus japonicus* larvae <10 mm body length (BL) and percentages of larvae <5 mm BL to the total larvae in the shelf-break region of the East China Sea during later winter and spring (upper) and the percent composition of abundance of larvae <5 mm BL among the three sub areas (lower). SECS, southern East China Sea; CECS, central East China Sea; NECS, northern East China Sea.

**Figure 3.** Horizontal distributions of Japanese jack mackerel *Trachurus japonicus* larvae <5 mm BL and sea surface temperature (SST, °C) in the East China Sea during late winter and spring in 2004, 2007, 2010, and 2011. Circles represent the abundance as a continuous range of values. Crosses indicate no catch. *N*, total number of sampling stations. The 50, 100, and 200 m isobaths are shown with the fine lines.

**Figure 4.** Centers of distribution of Japanese jack mackerel *Trachurus japonicus* larvae <5 mm BL in the southern East China Sea (SECS) and northern East China Sea (NECS) during late winter and spring during 2001 to 2012. Circles and squares represent locations of annual weighted mean catch of the larvae in the SECS and NECS, respectively.

**Figure 5.** Weighted mean temperature (*WMT*) of Japanese jack mackerel *Trachurus japonicus* larval habitat in the three sub areas of the East China Sea during later winter and spring. Black and gray lines are the weighted mean and weighted standard deviation, respectively. $\overline{WMT}_{01-12}$ is the mean value of *WMT* of the larval habitat during the twelve years, with a standard deviation. SECS, southern East China Sea; CECS, central East China Sea; NECS, northern East China Sea.

**Figure 6.** Interannual variations in abundance of Japanese jack mackerel *Trachurus japonicus* larvae <5 mm BL in the three sub areas of the East China Sea during later winter and spring. SECS, southern East China Sea; CECS, central East China Sea; NECS, northern East China Sea. CV, coefficient of variation.

**Figure 7.** Relationships between $\log_{10}$-transformed abundance of Japanese jack mackerel *Trachurus japonicus* larvae <5 mm BL and oceanographic conditions (mean sea surface temperature and chlorophyll *a* concentration in the upper 50 m of the water column) in the southern East China Sea during later winter and spring. $r^2$, coefficient of determination. Sampling year is indicated for each plot.

**Figure 8.** Relationship between $\log_{10}$-transformed index of recruited juveniles in the East China Sea (ECS) and $\log_{10}$-transformed abundance of Japanese jack mackerel *Trachurus japonicus* larvae <5 mm BL in late winter, spring, and during late winter to spring in the southern East China Sea (SECS) in the twelve years from 2001 to 2012. As an index of recruited juveniles, we referred to data from research bottom trawl surveys in the shelf-break

region of the ECS between 32° and 26°N during May to June (Fisheries Agency and Fisheries Research Agency of Japan, 2015). Sampling year is indicated for each plot. The plots for 2004 and 2010 overlap with each other on the graph during late winter to spring. Maps at the upper left and right represent sampling areas of the larvae and recruited juveniles, respectively. $r^2$, coefficient of determination.

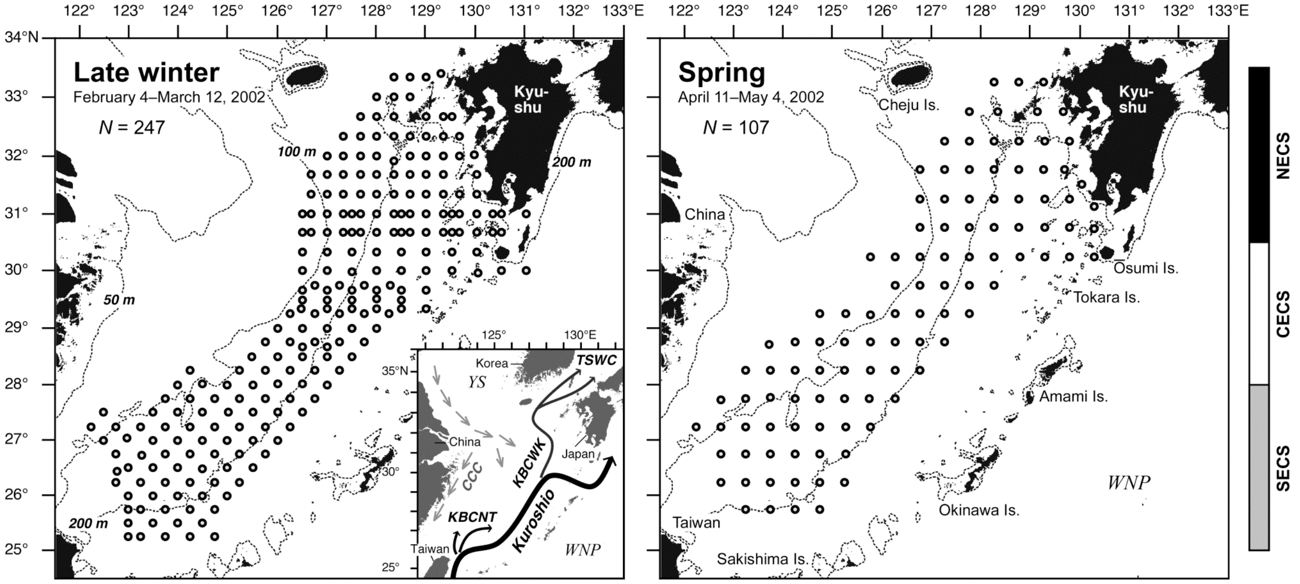
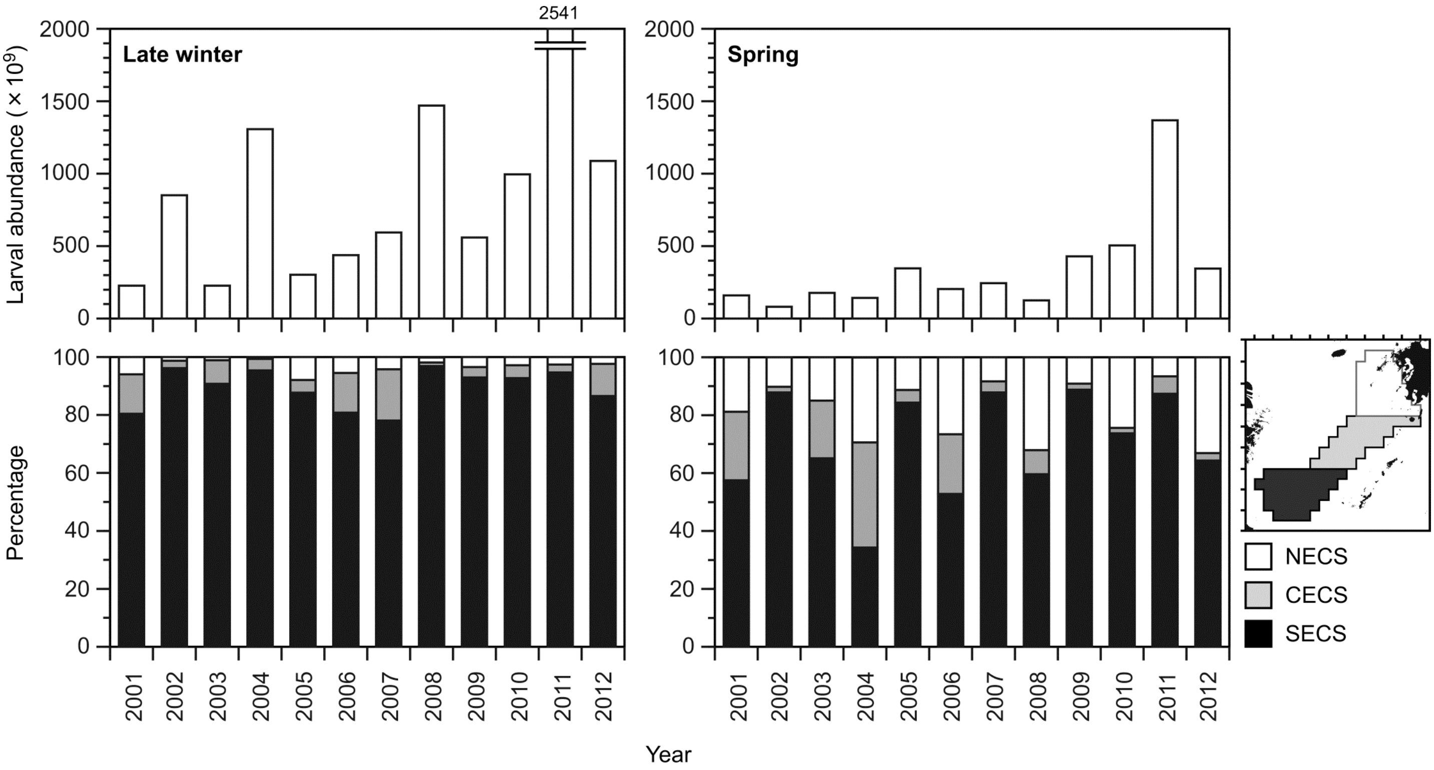


Fig. 1-Sassa et al.



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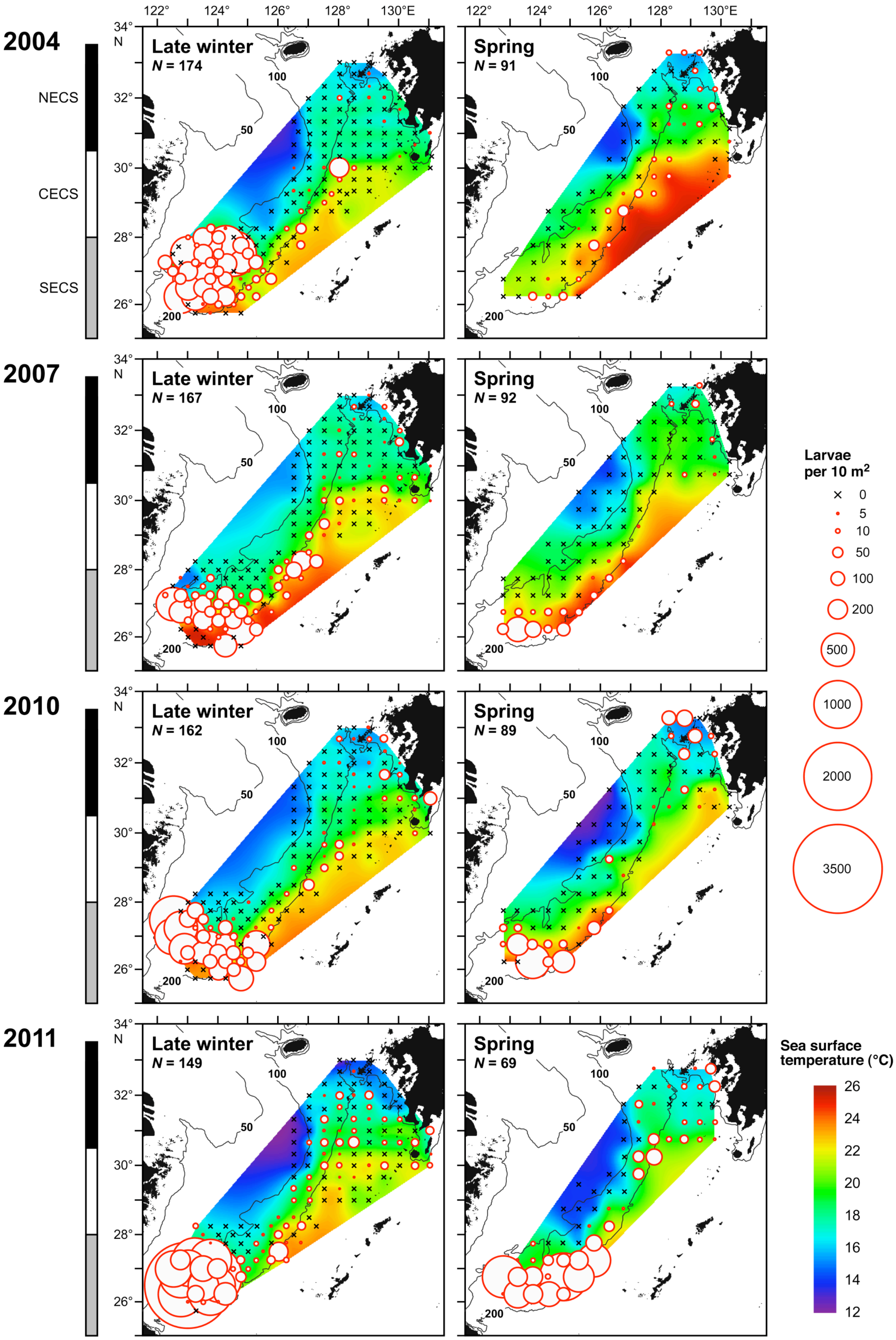

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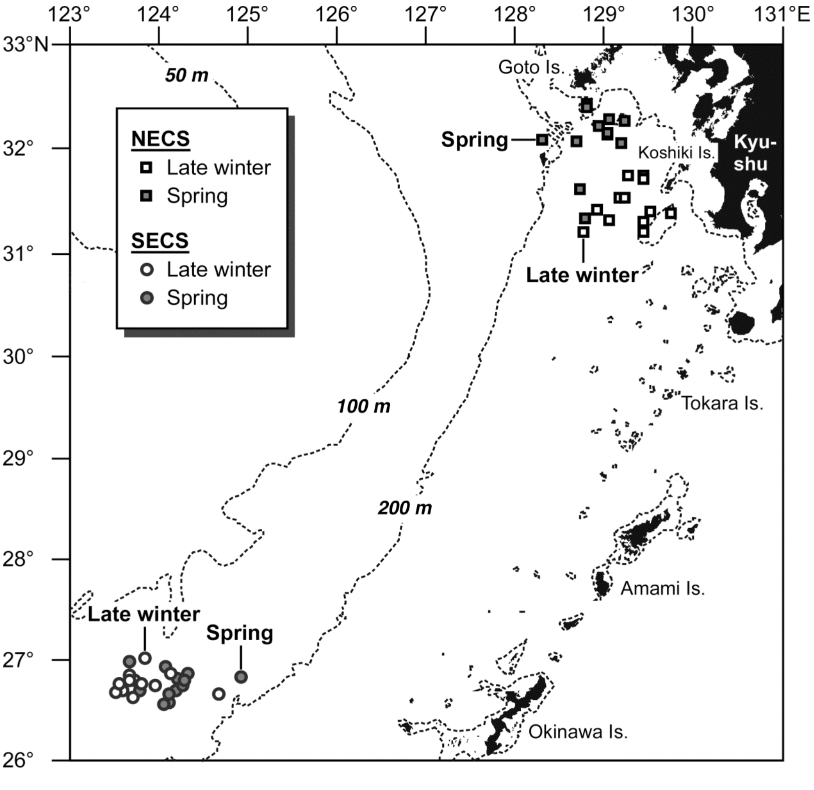

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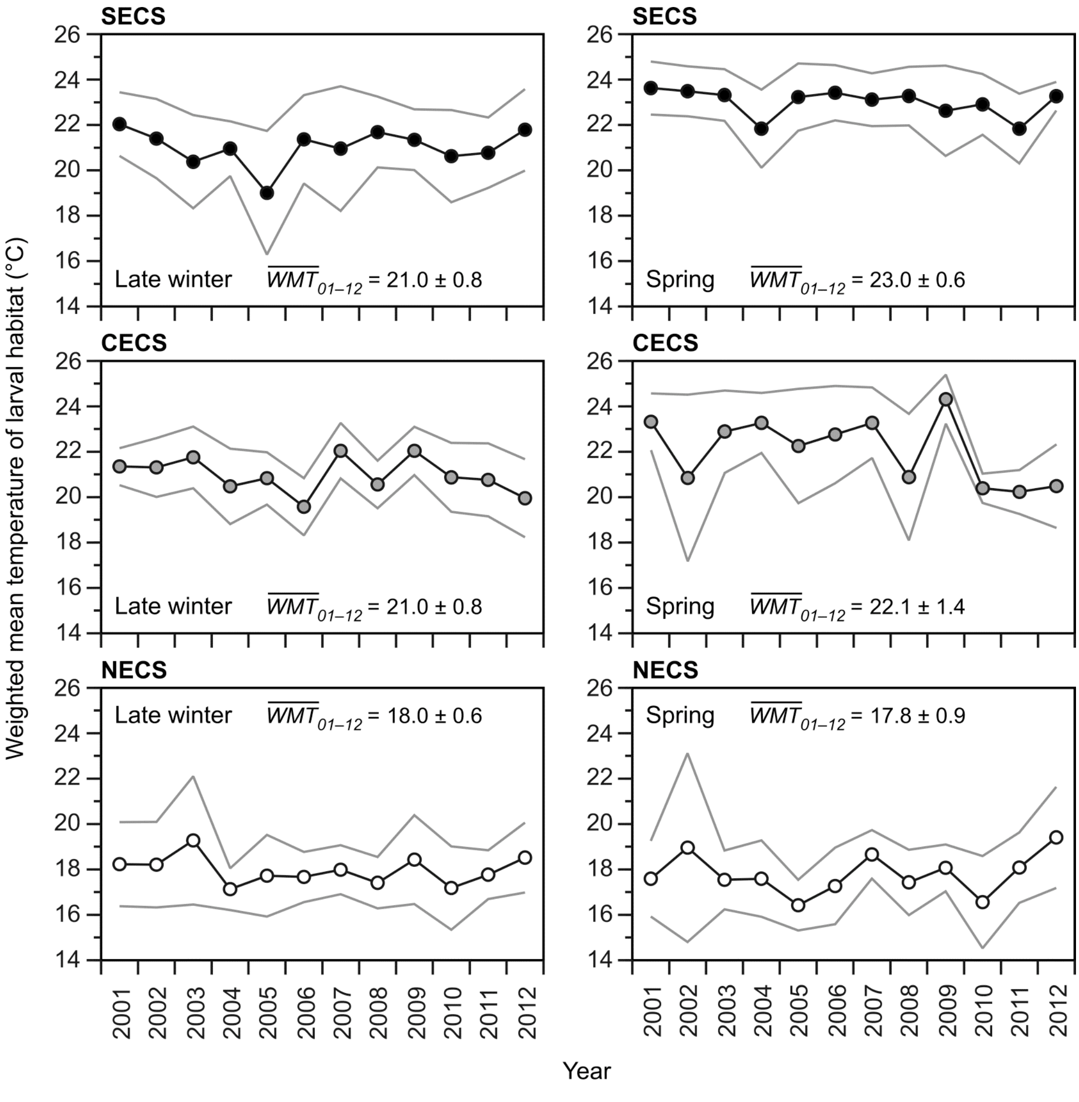

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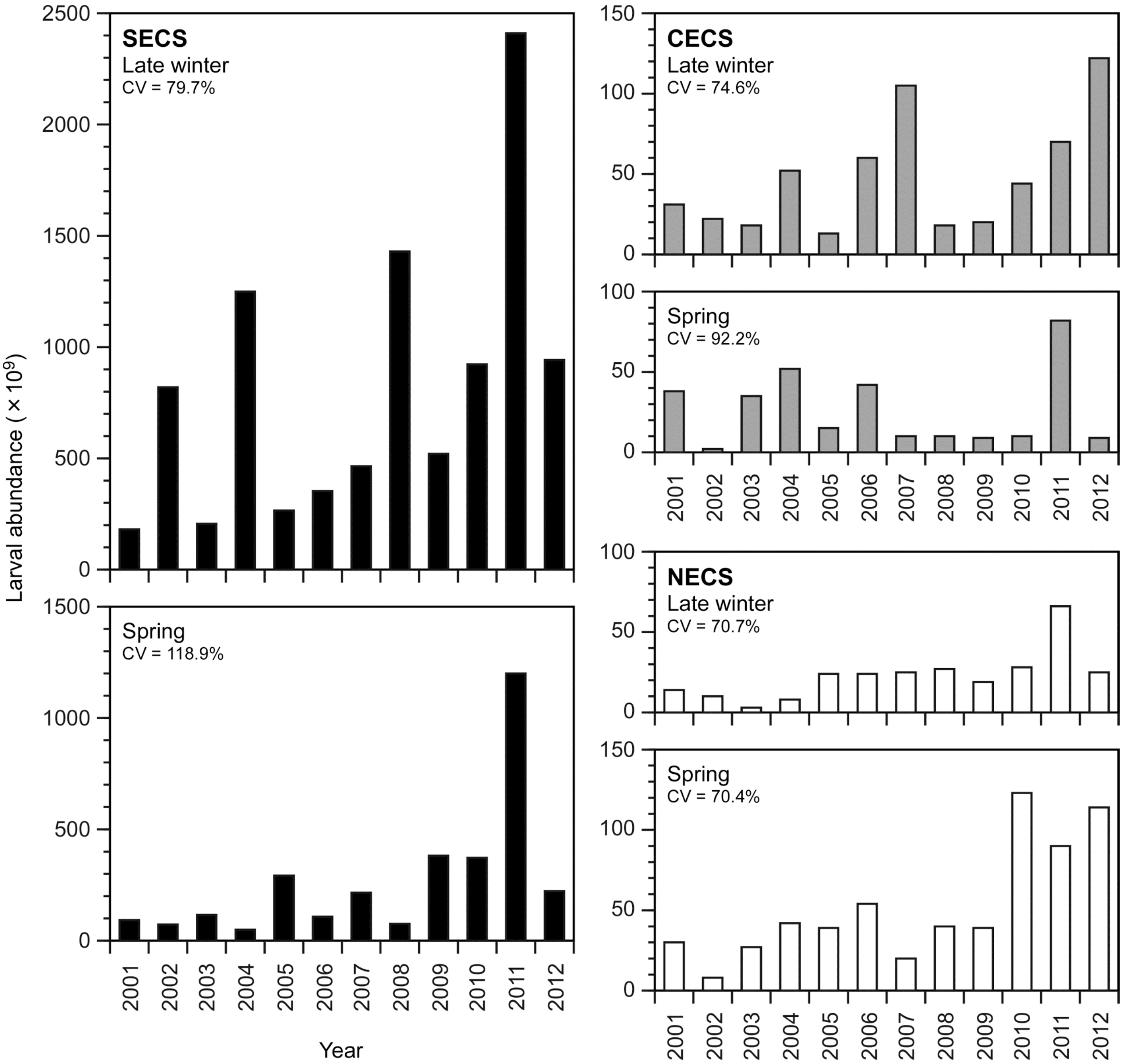

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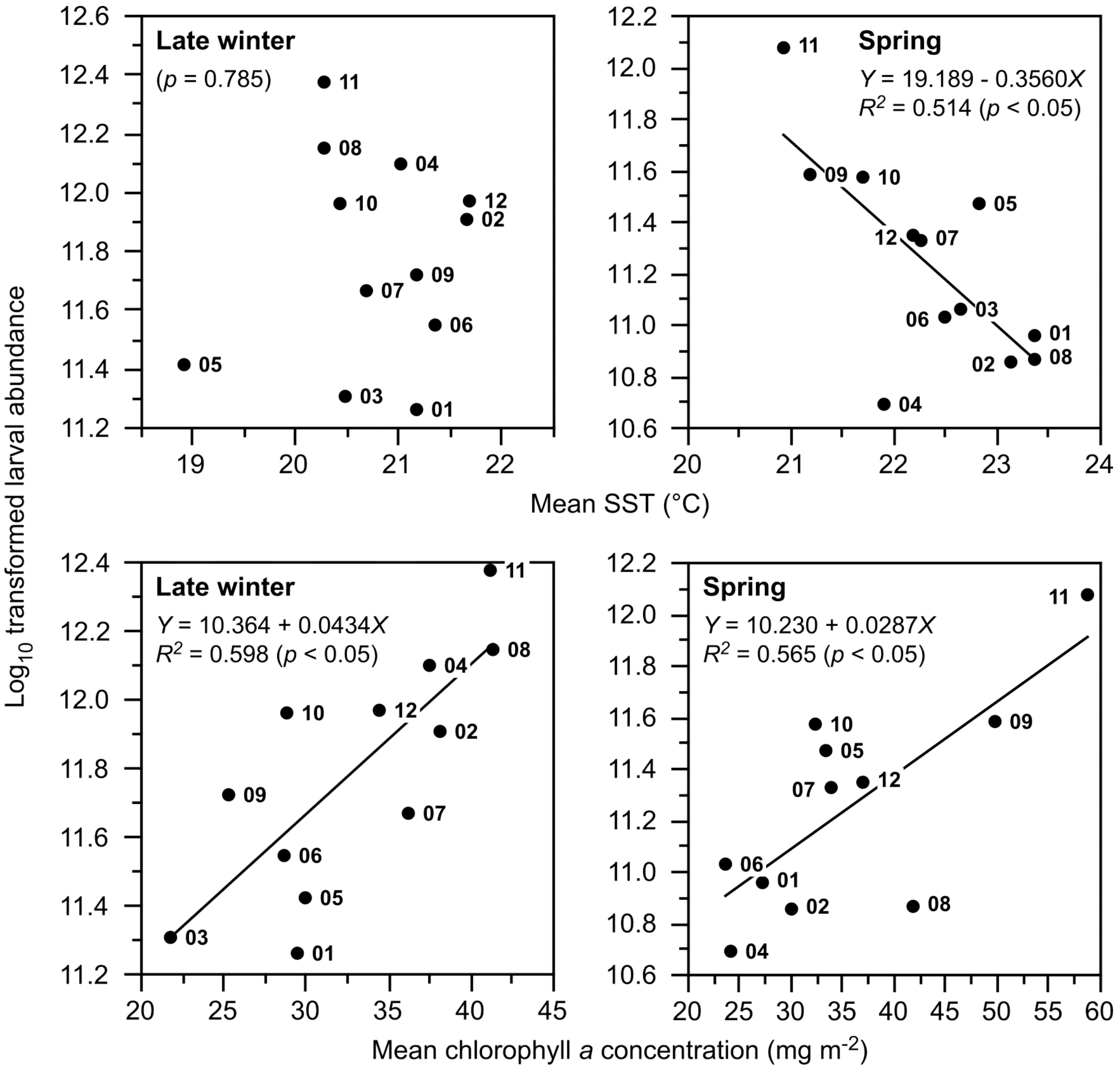

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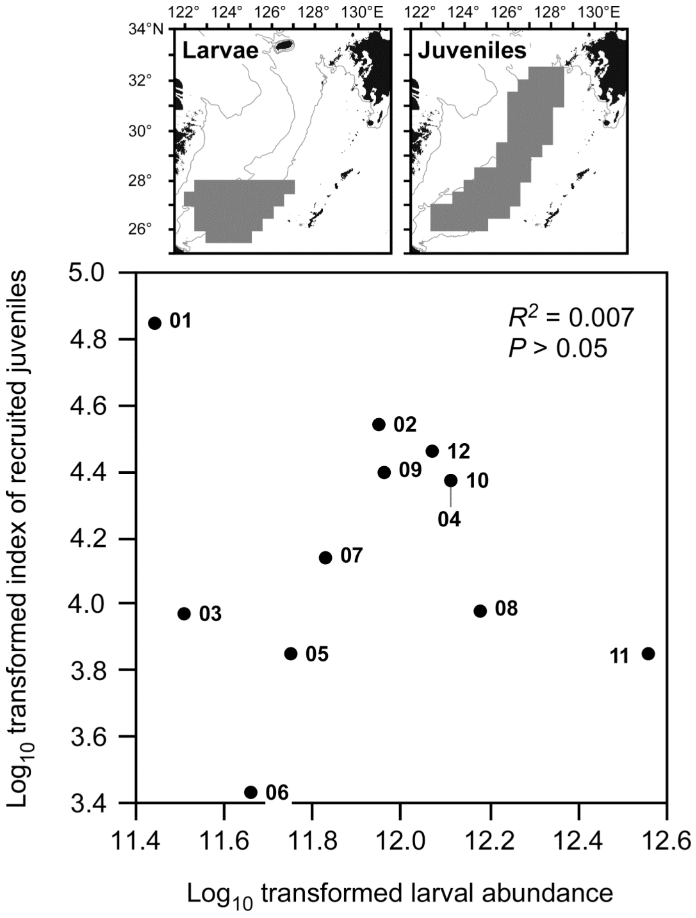

Fig. 8-Sassa et al.

Table 1. The number of sampling stations in the shelf-break region of the East China Sea in late winter and spring during 2001 to 2012. YK, Yoko-Maru; KY, Kaiyo-Maru; HK, Hokkou-Maru; WT, Wakatori-Maru; TR, Torishima. *N*, total number of sampling station. *, Chlorophyll *a* fluorescence was measured using a submersible fluorometer mounted on the CTD.

| | Late winter | | | Spring | | |
|---|---|---|---|---|---|---|
| Year | *N* | Period | Research ship | *N* | Period | Research ship |
| 2001 | 260 | February 4–March 10 | KY*, HK, WT | 89 | April 11–30 | YK* |
| 2002 | 247 | February 4–March 12 | YK*, HK, WT | 107 | April 11–May 4 | YK* |
| 2003 | 281 | February 1–March 13 | KY*, TR | 95 | April 11–30 | YK |
| 2004 | 174 | February 1–March 10 | YK*, WT | 91 | April 9–28 | YK* |
| 2005 | 167 | February 4–March 11 | YK*, WT | 93 | April 11–30 | YK* |
| 2006 | 167 | February 2–March 8 | YK*, WT | 95 | April 11–30 | YK* |
| 2007 | 167 | January 31–February 25 | YK*, WT | 92 | April 11–30 | YK* |
| 2008 | 159 | January 30–February 25 | YK*, WT | 84 | April 13–May 1 | YK* |
| 2009 | 161 | February 1–March 2 | YK*, WT | 90 | April 10–29 | YK* |
| 2010 | 162 | January 28–February 27 | YK*, WT | 89 | April 9–28 | YK* |
| 2011 | 149 | January 28–March 7 | YK*, WT | 69 | April 8–27 | YK* |
| 2012 | 138 | January 27–March 14 | YK*, WT | 73 | April 11–26 | YK* |

Table 2. The number of sampling stations in the three sub areas defined. SECS, southern East China Sea between 28°N and 25°N; CECS, central East China Sea between 30°30’N and 28° N; NECS, northern East China Sea between 33°30’N and 30°30’N.

| Year | SECS | | CECS | | NECS | |
|---|---|---|---|---|---|---|
| | Late winter | Spring | Late winter | Spring | Late winter | Spring |
| 2001 | 49 | 23 | 89 | 29 | 122 | 37 |
| 2002 | 78 | 32 | 74 | 38 | 95 | 37 |
| 2003 | 107 | 27 | 121 | 31 | 53 | 37 |
| 2004 | 67 | 22 | 54 | 32 | 53 | 37 |
| 2005 | 67 | 26 | 49 | 30 | 51 | 37 |
| 2006 | 67 | 28 | 47 | 30 | 53 | 37 |
| 2007 | 67 | 26 | 47 | 28 | 53 | 38 |
| 2008 | 63 | 24 | 45 | 27 | 51 | 33 |
| 2009 | 66 | 26 | 42 | 27 | 53 | 37 |
| 2010 | 64 | 26 | 45 | 25 | 53 | 38 |
| 2011 | 43 | 22 | 53 | 18 | 53 | 29 |
| 2012 | 35 | 23 | 47 | 19 | 56 | 31 |

Table 3. Regression analysis of the relationships between $\log_{10}$-trasnformed mean abundances of *Trachurus japonicus* larvae and mean sea surface temperature (°C), sea surface salinity (PSU), and chlorophyll *a* concentration in the upper 50 m of the water column (mg $m^{-2}$) in each area during later winter (during February and March) and spring (in April) during 2001 to 2012.

| Area | Season | Temperature | | | Salinity | | | Chlorophyll *a* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *n* | $R^2$ | Significance test (*P*-value) | *n* | $R^2$ | Significance test (*P*-value) | *n* | $R^2$ | Significance test (*P*-value) |
| SECS | Late winter | 12 | 0.008 | NS (0.779) | 12 | 0.007 | NS (0.793) | 12 | 0.598 | S (0.003) |
| | Spring | 12 | 0.514 | S (0.009) | 12 | 0.007 | NS (0.791) | 11 | 0.565 | S (0.008) |
| CECS | Late winter | 12 | 0.026 | NS (0.619) | 12 | 0.078 | NS (0.379) | – | – | – |
| | Spring | 12 | 0.005 | NS (0.822) | 12 | 0.034 | NS (0.565) | 11 | 0.005 | NS (0.831) |
| NECS | Late winter | 12 | 0.056 | NS (0.461) | 12 | 0.045 | NS (0.510) | – | – | – |
| | Spring | 12 | 0.195 | NS (0.151) | 12 | 0.023 | NS (0.640) | 11 | 0.314 | NS (0.073) |

$R^2$, coefficient of determination; S, significant at the 5% level; NS, insignificant. *n*, total number of years analyzed; –, no data. SECS, southern East China Sea; CECS, central East China Sea; NECS, northern East China Sea.