Spatiotemporal variability in the occurrence of juvenile Japanese jack mackerel *Trachurus japonicus* along coastal areas of the Kuroshio Current

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**Abstract**

To understand the population structure of the Japanese jack mackerel *Trachurus japonicus* in coastal areas adjacent to the Kuroshio Current (referred to as the “CAK”), we analyzed size composition and commercial landing data of juvenile fish in these areas for the period 2005–2015. *Trachurus japonicus* does not undergo population-scale spawning migration, and thus, the connectivity between the spawning and juvenile/adult habitat areas is important. Therefore, our primary aim was to assess the origin of juveniles landed in a number of subareas, including those spawned in local spawning grounds in January–May in the western part of the CAK (w-CAK), those spawned in May–July in the eastern part (e-CAK), and those spawned in February–March in the remote spawning ground in the southern East China Sea (s-ECS). Fishing periods starting in spring (spring onset) were commonly observed in the CAK, which involved relatively small size classes (50–100 mm fork length [FL]). Back estimates based on the growth rate of *T. japonicus* suggested that the contributions from the s-ECS probably dominated most of the spring onsets in April–June because the smallest size class (50–70 mm FL) occurred almost exclusively in April–May. In autumn, onset...
signals were associated with the landing of juveniles from the local spawning ground in an eastern subarea of the e-CAK. Despite the asymmetric transport and migration flows between the habitat areas of *T. japonicus*, its population levels may be sustained because the local and remote spawning grounds are used in different seasons.

**KEYWORDS**
commercial landing data, jack mackerel, population structure, spawning ground, transport

## 1 | INTRODUCTION

Currents and tides transport and widely disperse the eggs, larvae, and juveniles of many marine organisms from the spawning grounds. A proportion of them may reach nursery areas, from where recruitment to the adult habitats occurs. For migratory species, ontogenetic growth is followed by seasonal or spawning migration to spawning grounds. In fisheries science, this life history is called the “migration triangle” (Cadrin & Secor, 2009; Harden-Jones, 1968). Although this concept has been amended numerous times (e.g., the “combined contingent theory”; Secor, 1999), returning to the spawning ground, one of the main components of the triangle, is still widely used to explain the migration patterns of various marine fish species, such as the sardine (*Sardinops melanostictus*: Kuroda, 1991; *S. sagax*: van der Lingen et al., 2010), mackerel (*Scomber scombrus*: Uriarte & Lucio, 2001; *S. japonicus*: Yukami et al., 2018), and herring (*Clupea harengus*: Wheeler & Winters, 1984; *C. pallasii*: Tojo et al., 2007).

However, some fish species do not follow this migration pattern. One species for which no population-scale spawning migration has been observed is the Japanese jack mackerel *Trachurus japonicus*, an ecologically and commercially important species in East Asian waters. *Trachurus japonicus* inhabits the coastal areas of China, Taiwan, Korea, and Japan. The pelagic eggs and hatched larvae of *T. japonicus* are transported passively by surface currents. When the larvae become juveniles exceeding approximately 40 mm in fork length (FL), they move from a surface-layer habitat to a benthic-layer habitat (Sassa et al., 2006, 2009). Because their eggs and larvae are mainly entrained in the Kuroshio Current (Kuroshio) and Tsushima Warm Current (TWC; Kasai et al., 2008), which flow eastward to north-eastward, their distribution tends to shift downstream in these currents as they grow. No spawning migration from the downstream to upstream areas along the Kuroshio or TWC has been observed in *T. japonicus* at the population scale.

A complex population structure has also been suggested for the jack mackerel (genus *Trachurus*) in other regions. In the northeastern Atlantic and the Mediterranean Sea, multiple stocks of *T. trachurus* have been identified by integrating several approaches, including genetic markers, morphometry, parasite analyses, and life history traits (Abauanza et al., 2008; Comesaña et al., 2008). Although the genetic differentiation was low, the morphometrics and parasite-based methods suggested the separation of the Atlantic Ocean and the Mediterranean Sea populations, with a buffer zone in the western-most Mediterranean Sea. In the oceanic northeastern Atlantic Ocean, multiple population units of *T. picturatus* have also been detected with various approaches, including genetic markers, the otolith shape and microchemistry, and parasite associations (Moreira et al., 2020; Vasconcelos et al., 2018). Based on a phenotypic analysis of the otolith of *T. picturatus* off the Canary Islands, Tuset et al., (2019) suggested the contingent theory to explain its population structure. The main spawning the Chilean jack mackerel *T. murphyi* is in the open ocean off the coast of Chile, and its distribution, including its nursery and feeding grounds, includes wide areas extending to the coast of Ecuador to the north and to waters off New Zealand (Acros et al., 2001; Parada et al., 2017; Serra, 1991). Gerlotto et al., (2012) investigated the population structure of these four stocks (Chilean, Peruvian, central South Pacific, and western South Pacific) in a literature review. They noted that the main and permanent spawning ground off Chile suggests the metapopulation structure.

The spawning grounds of *T. japonicus* that contribute to its occurrence in these areas have been classified into the local spawning grounds in the coastal areas along the Kuroshio (collectively referred to as “CAK”) and the remote spawning ground in the southern East China Sea (s-ECS) (Figure 1). The local spawning grounds at the scale of bays and channels along the CAK, identified by sampling mature adults, have been documented since at least the 1950s (Hashida et al., 2019; Hattori, 1964; Sakaji, 2001; Sakamoto et al., 1986; Sawada, 1974; Yakushiji, 2001; Yokota & Mita, 1958). Using maturation indices (mainly the gonadosomatic index) for adult *T. japonicus*, the spawning seasons in each of the areas within the CAK were estimated to be May–July in Sagami Bay (Kobata, 1972; Sawada, 1974), February–June in Kii Channel (Sakamoto et al., 1986), January–June in Sukumo Bay (Sakaji, 2001), and February–June (Yakushiji, 2001) and January–July (Hashida et al., 2019) in Bungo Channel (Figure 1).

Surveys of the ichthyoplankton in the ECS since the 2000s have shown high densities of larvae in the southern ECS (s-ECS) from February to March, and it has been suggested that this is the primary spawning ground for the entire *T. japonicus* population (Sassa et al., 2006, 2009, 2016; Figure 1). However, the paths of the Kuroshio and TWC suggest that not all eggs spawned in the ECS are transported to the CAK, but that some are also transported to coastal areas by the TWC or retained within the ECS. Therefore, the relative contributions of these local and remote spawning areas have yet to be confirmed.

Until the large spawning ground was discovered in the s-ECS (Sassa et al., 2006), studies of the transport of *T. japonicus* to
Japanese waters mainly focused on the eastern ECS near Japan (Kim & Sugimoto, 2002). After the discovery of the spawning ground in the southwest ECS by Sassa et al., (2006), interest shifted to how eggs and larvae are transported from this spawning ground to the fishing grounds in Japanese waters. Kasai et al., (2008) conducted particle-tracking experiments that incorporated fish mortality to investigate the transport of *T. japonicus* larvae from the ECS to the Sea of Japan and the Pacific side of Japan. Their numerical experiments showed that larvae can reach the Sea of Japan or the Pacific side from the ECS and that advection and diffusion transports ~80% of them to the Pacific side (although survival was not considered).

The studies cited above clarified the transport patterns of *T. japonicus* larvae from the s-ECS, but more detailed studies of the distribution of larvae and juveniles after they enter the Pacific side of Japan (i.e., within the CAK) are required to understand the roles of the various spawning grounds. There is some evidence that *T. japonicus* originating in the s-ECS reaches specific areas of the CAK. Xie and Watanabe (2007) used a sagittal otolith analysis to assess the

| Prefecture | Number of fishery unitsa | Temporal coverage (yyyy/mm/dd) | Approximate body length (mm) | Approximate bodyweight (g)  |
|------------|--------------------------|--------------------------------|----------------------------|-----------------------------|
| Kanagawa (KN) | 19 | 2005/01/01-2014/12/31 | <120 |                 |
| Shizuoka (SO) | 7 | 2005/01/01-2015/12/31 | 50–100 |                 |
| Mie (ME) | 9 | 2005/01/01-2014/12/31 | 50–100 |                 |
| Wakayama (WK) | 1 | 2008/04/01-2015/12/31 | 50–100 |                 |
| Kochi (KO) | 2 | 2005/01/01-2015/12/31 | <150 | <50 |
| Ehime (EH) | 1 | 2005/01/01-2015/12/31 | <100 |                 |
| Miyazaki (MZ) | 4 | 2006/01/01-2015/12/31 | 50–100 |                 |
| Kagoshima (KG) | 1 | 2005/01/01-2015/12/31 | <180 | <80 |

aEither the number of set nets or purse seine fisheries (for the EH subarea).
age of juvenile *T. japonicus* collected in Sagami Bay (Figure 1) and found that the hatching period of some individuals was consistent with a spawning season in the s-ECS. More recently, Hashida et al., (2017) suggested that juveniles of *T. japonicus* caught in purse seine nets in Bungo Channel (Figure 1) were spawned in March–April, which overlaps the main spawning season of February–March in the s-ECS. However, these studies alone have been insufficient to generally assess the origins of *T. japonicus* transported to CAK.

In the cited above, Xie and Watanabe (2007) determined fish age from otolith daily rings, whereas Hashida et al., (2017) drew their estimates from the established relationship between fish age and length. Age determination based on the otolith analysis of young-of-year *T. japonicus* is a strong tool for distinguishing spawning seasons (e.g. Klein et al., 2018; Xie & Watanabe, 2007), and therefore, also the origins of individual fish if spawning seasons are different among various spawning grounds. However, simple data on the length composition or catch in weight are generally much readily available than otolith data and have advantages in spatiotemporal resolution and coverage. The otolith data alone cannot trace the spatiotemporal variability in the occurrence of *T. japonicus* in the CAK that can be captured in the landing records.

The commercial landings data for juvenile *T. japonicus* are available over the whole CAK area on a daily time scale. These landing data are stored by local fisheries units operating set nets and purse seine nets, and landing statistics by market size categories have been compiled by local fisheries institutions. A set net is a large-scale fish-trapping system fixed to a shallow seabed. Because the set net passively captures fish in a local area, the fishing effort of a single set net system can be assumed to be constant. Furthermore, long-term data are available because these fisheries have operated for long periods in many parts of Japan. For these reasons, the analysis of landing data based on set net catches can be used to investigate the occurrence of juvenile *T. japonicus* in CAK.

The main aim of this study was to investigate the transport of juvenile *T. japonicus* to the CAK, either from the s-ECS or within the CAK. We assessed whether the patterns of occurrence of juvenile *T. japonicus* differed from west to east in the CAK based on commercial landing data and length measurements. We also compared the patterns of occurrence with several factors that could influence the transport of juvenile *T. japonicus*.

**FIGURE 2** Flowchart of data processing and analysis: (a) catch in weight (landing) data processing, (b) fork length data processing, (c) calculation of weight index, (d) estimation of equivalent number of individuals, (e) definition and detection of the onsets of fishing periods, and (f) correlation analysis of factors potentially influencing the occurrence of juvenile *T. japonicus*.
2 | MATERIALS AND METHODS

2.1 | Study area and spawning period

In the CAK, juvenile *T. japonicus* are mainly caught with set nets in seven subareas corresponding to local prefectures (Kagoshima, KG; Miyazaki, MZ; Kochi, KO; Ehime, EH; Wakayama, WK; Mie, ME; Shizuoka, SO; and Kanagawa, KN). Purse seine netting was used in one subarea (EH) (Figure 1). The daily landing data from 44 fisheries units in these eight subareas were used in this study (Table 1). As mentioned above, the spawning periods in each area partly overlap, but the spawning periods occur later from west to east. In this study, the term “main spawning season” is used to refer to the period in which most adults are mature (after the first maturation).

We assumed in this study that the main spawning season is January–May in the western part of the CAK (corresponding to the waters off the KG–WK subareas; Table 1; referred to as the western CAK or the w-CAK; Figure 1c) and May–July in the eastern part (corresponding to waters off the ME–KN subareas; Table 1; referred to as eastern the CAK or the e-CAK; Figure 1d). These assumptions on the main spawning seasons, based on the surveys of the gonadosomatic index in the previous studies (see Introduction), are consistent with the occurrences of *T. japonicus* eggs and larvae (Sakaji et al., 2013, 2012, 2011, 2010, 2007, 2006, 2004, 2002; Takasuka, Nashida, Udagawa, & Sakaji, 2012, 2013); these reports, covering the period 2006–2016, are hereafter referred to as “FRA_06–16”; egg distribution data have been available since 2013).

2.2 | Commercial landing data

The daily landing data by weights at each fishery unit were first averaged on a weekly basis to reduce the bias caused by occasional no-landing records (Figure 2a). It was often impossible to distinguish between whether a no-landing event occurred despite fishing effort or there was no effort because fishing was suspended for an unspecified reason (e.g., adverse weather conditions). Records of zero catch after the calculation of the weekly means were therefore regarded as missing values.

The weekly landing data at each fishing unit were log-transformed and standardized. The standardized data were then averaged within subareas for each week of the year, to obtain C (Figure 2a). The conversion processes for the weekly landing data for the subareas with single fisheries units altered the amplitude of the data, but not the underlying pattern. Similarly, the weekly long-term mean \( \bar{C} \) was calculated for each subarea by averaging \( C \) over subareas and years. The confidence intervals were calculated with the bootstrap method.

2.3 | Length compositions and equivalent numbers of individuals

The landings of these units are dominated by 0- and 1-year-old fish (Watanabe et al., 2018). The smallest length in the market size categories is about 50–150 mm FL (Table 1; hereinafter called “juveniles”). Subsamples were taken for scientific analysis from these commercially based landings almost monthly, and their length compositions were recorded.

The FL composition data were used to assess the size of *T. japonicus* corresponding to the landing data (Figure 2b). The length composition data covered 11 years, from 2005 to 2015, in the KN, ME, KO, and MZ subareas, for which sufficient data were available to represent the seasonal variability. The dataset comprised the FL data for *T. japonicus* obtained from markets, typically sampled 1–3 times per month during the main fishing period (but sometimes not in other periods). The FL measurements were made at the National Research Institute of Fisheries Science and prefectural fisheries research institutes and were compiled across intervals of 10 mm FL from 50 to 380 mm FL. From the length composition data, we found that the smallest frequency mode within the FL range was 50–150 mm, which we assumed represented the presence of juveniles. The mid-values of the bin at the smallest frequency mode (e.g., 55, 65, and 75 mm FL), L, were then regarded as the FL of the juveniles in that week (Figure 2b).

Although the approximate FL range for the commercial landing data was assumed based on interviews with local fishermen (Table 1), the FL of the fish sold in the market varied. Because we were more interested in the pattern of transport of juveniles than in the somatic growth of individuals, reference data that included both numbers and biomasses were required to interpret the landing time series. The length–weight relationship was determined from the length and weight measurements of samples in four subareas (MZ, EH, WK, ME, and KN) during 2010–2017. The allometric relationship between FL (x in mm) and weight (y in g) is then estimated as \( y = 1.033 \times 10^{-5} x^{3.046} \), based on the least-square log-linear fitting (\( R^2 = 0.99, p = 0.00 \)). Therefore, we estimated the weight index W as:

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W = L^{3.046} \tag{1}
\]

where \( W \) and \( L \) are the weight index and FL, respectively (Figure 2c).

The linear coefficient of \( 1.033 \times 10^{-5} \) for the length–weight relationship is not included in Equation (1), because \( L \) in Equation (1) is standardized and does not have a unit, unlike the original formulation, and the elimination of this constant does not affect the fluctuation pattern. An index of the catch in numbers, called the “equivalent numbers of individuals,” was then estimated by dividing the landing of the smallest market categories by \( W \). For the weekly data, this was denoted as \( N_W \) and the weekly long-term mean, calculated from the weekly long-term mean landing and the weight index, was denoted as \( \bar{N}_W \) (Figure 2d).

2.4 | Onset of the fishing period: A weight-based index to detect increases in numbers

Although the average seasonal fluctuation pattern can be examined with \( \bar{N}_E \) calculated from the long-term mean data (Figure 2d), the patterns in single years cannot be similarly examined with \( N_E \). This
is because of the sparseness of L (0–3 times per month), which was used to calculate $N_L$. However, the weekly mean catch in weight $C$ is dense, although its seasonal peak is probably influenced by the increase in the weight of individuals. Therefore, considering the relationship between $\bar{N}_L$ and $\bar{C}$, we introduced another index, the onset of the fishing period from $C$, which is less affected by the weight increase (Figure 2e).

The definition of "onset" is based on the relationship between $\bar{N}_L$ and $\bar{C}$ (Figure 2e). We defined the fishing periods as those in which the standardized weekly year-to-year landing data continuously exceeded the 25th percentile of the log-normal distribution (0.5094) for periods of ≥5 weeks. The onset and termination weeks were then specified for each fishing period. The criterion of the 25th percentile was selected because it properly detected major onsets of the weekly long-term mean equivalent number of individuals, and the 5-week criterion was selected to detect monthly scale signals. The detections of onsets based on $\bar{N}_L$ and $\bar{C}$ are actually consistent over the percentile range of 20–35%. Nevertheless, the sensitivity test showed that adopting a different percentile criterion within this range does not change the seasonal onset pattern when applied to the weekly data (Figure S1).

### 2.5 Coastal temperature, Kuroshio axis, and population level

The coastal water temperature and the stream of the Kuroshio are major environmental factors affecting the $T. japonicus$ transported to the CAK. Interannual fluctuations in population size should also directly cause fluctuations in the total number. Therefore, we undertook a correlation analysis of $N_L$ and these three factors (Figure 2f).

The temperature in the CAK is monitored by a moored buoy array of the real-time marine information acquisition and analysis system operated by the Japan Fisheries Research and Education Agency (Table 2; http://buoy.nrifs.aaffrc.go.jp/top.php). Although the data are recorded at several depths, those from the deepest layer (10–30 m; Table 2) were used to investigate the influence of physical oceanographic conditions on juvenile $T. japonicus$, which usually inhabit near-bottom waters. The data for the MZ, KO, and KN subareas were selected, based on their proximity to the set nets (Figure 1). The daily mean temperatures were calculated from hourly records using a 6th-order Butterworth low-pass filter with a half-attenuation period of 50 h. The weekly means were then calculated as for the landing data.

The location of the Kuroshio axis (the center of the mainstream) of the current during the period 2006–2015 was also investigated. The dataset comprised the latitude at intervals of 1° longitude (Japan Coast Guard: https://www1.kaiho.mlit.go.jp/KANKYO/KAIYO/qboc/kurosio-num.html). Because we focused on the MZ, KO, ME, and KN sites in the analysis of temperature, longitudes of 132°E (MZ), 134°E (KO), 137°E (ME), and 139°E (KN) were selected. The weekly means were calculated in the same manner as for the landing data.

The relationship between $N_L$ and the recruitment of $T. japonicus$ in 2005–2015 (KN, KO, and ME) and 2006–2015 (MZ) was investigated using recruitment data derived from a virtual population analysis (VPA; Watanabe et al., 2018).

## 3 RESULTS

### 3.1 Seasonal size fluctuations

Juvenile $T. japonicus$ were predominantly landed in March–June in the four subareas for which size data were available (Figures 3 and 4). Although few data were available until March, especially in January and February, the presence of 50–70 mm FL size classes was frequently observed from March to May. The observed sizes usually exceeded 100 mm FL by the end of June, and after July, the mean size gradually increased, exceeding 120 mm in August. Size classes > 130 mm FL were typically observed in September–December in the MZ, KO, and ME subareas. However, in the KN subarea, there was a second occurrence of smaller sizes from the end of September to the end of October, with a size range of 80–120 mm FL. Although less clear, slight shifts from >140 to <140 mm FL were occasionally detected in the ME and MZ subareas, mainly in November–December (Figure 3).

### 3.2 Seasonal landing fluctuations

The patterns of the seasonal fluctuations in landing in the eight subareas along CAK were estimated from the weekly long-term means of the standardized landing data (Figure 5). At the seasonal scale, there

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**TABLE 2** Summary of temperature data from buoys of the National Research Institute of Fisheries Science

| Site    | Latitude (°N) | Longitude (°E) | Temporal coverage (yyyy/mm/dd) | Bottom depth (m) | Sensor depth (m) |
|---------|---------------|----------------|---------------------------------|------------------|-----------------|
| Nagai   | 35°12.06’     | 139°35.80’     | 2008/01–2014/12/31              | 10               | 5               |
| Katada  | 34°14.16’     | 136°52.14’     | 2005/01–2015/12/31              | 60               | 10              |
| Cape Muroto | 33°19.56’   | 134°11.95’     | 2009/01–2015/12/31              | 50               | 30              |
| Kushima | 31°28.59’     | 131°23.24’     | 2006/01–2015/12/31              | 50               | 10              |

*The deepest layer was selected if thermistors were moored in multiple layers.
was one peak in the standardized landing data in July–September in the KN, SZ, ME, and KG subareas, and in June in the EH subarea, in the middle of the short fishing season that exclusively targeted very small FL (≤100 mm). Although less clear than in these subareas, increases were observed in August–September in the WK subarea, in September–October in the KO subarea, and in June–August in the MZ subarea.

Because the seasonal fluctuations were gradual, the onsets defined by the 25th percentile were detected well before the peak, except in the EH subarea, whereas second onsets were observed during autumn in the ME and KG subareas. The first onsets appeared from mid-March to May in the KN, SZ, ME, WK, EH, and KG subareas, and during February in the KO and MZ subareas.

Fluctuations in the long-term mean weekly equivalent number of individuals ($N_E^{*}$) showed a markedly different pattern (Figure 6) from that of the weight-based landing data (Figure 5). Although $N_E^{*}$ was generally low from late autumn to early winter, marked increases were observed from late winter to spring. Peaks in $N_E^{*}$ on the seasonal scale were then observed from late March to May in the four subareas, whereas in MZ, a second peak appeared at the end of May.

The timing of the onset was nearly concurrent with that of the landings. This indicates that it is possible to detect the mass emergence of small juveniles through onset signals.
3.3 | Year-to-year variations in weekly landings

The weekly landing time series for individual years indicated intermittent fishing periods, the timing, duration, and magnitude of which differed among years (Figures 7–9). As shown in Figures 5 and 6, the peaks in the landing time series lagged behind those for $N_E$, but the onsets of the fishing periods almost coincided with these peaks. Therefore, we focused mainly on the onsets of the fishing periods.

Apart from the EH subarea, where the fishing season was concentrated in the April–June period, weekly landings occurred almost throughout the year and most frequently in April–October. There were 1–4 onsets detected each year (Figures 7–9), except for some specific years or subareas in which all the fishing periods were <5 weeks (mainly in the EH subarea). The frequencies of onsets with respect to the weeks of the year in the eight subareas are shown in Figure 10. Purse seine fishing in the EH subarea selectively targeted the very small size class, and thus, the short fishing season in April–May probably corresponded to the period of the peak in the number of individuals. In almost every year and subarea, early-onset signals occurred from February to June (hereafter called the “spring onset”; Figure 10), corresponding to the increase in landings in summer (Figures 7–9).

The fishing periods that started at the spring onsets typically ended in late summer, and autumn onsets occurred in the KN, WK, KO, MZ, and KG subareas, as detected in probability modes (Figure 10a, d–e, and g–h). Although autumn onsets did not occur every year, substantially increased landings were often observed in the KN (Figure 7a; 2007, 2008, and 2012) and KO subareas (Figure 8b; 2011 and 2015). Relatively small size classes (<120 mm FL) were detected in autumn in 2007 and 2008 in the KN subarea (Figure 4a).

3.4 | Environmental conditions and relationship with population level

The weekly equivalent numbers of individuals ($N_E$) were compared within the corresponding weeks (Figure 11). Although the temperature ranges differed among subareas and seasons, the range in which substantial numbers of individuals were found was 15–25°C (Figure 11a, c, e, g). High $N_E$ values were mainly detected during January–March, but the temperature range in this period differed among subareas. The linear correlation between temperature and $N_E$ was not significant, except for the MZ subarea during October–December ($r = -0.64, p < 0.05$). The effects of abrupt intrusions of the Kuroshio into coastal areas, which typically cause rapid temperature rises over 1–2 days (e.g., Akiyama & Saitoh, 1993), were not evident in the data.

The latitude of the Kuroshio axis generally indicated the distance of the mainstream from the coast, and this distance is smaller at higher latitudes (Figure 11b, d, f, h). Although there was substantial
variability in the latitude of the axis during the study period, it had no significant relationship with $N_E$, except in the MZ subarea during the period July–September ($r = -0.69, p < 0.05$).

To investigate the heterogeneity in the population distribution, the average $N_E$ over the period April–June (when data coverage was relatively good) was compared with the data on recruitment (estimated number of age 0 fish) derived with VPA (Figure 12). Although the $N_E$ value was highest when the population level was relatively high in the KN (Figure 12b), ME (Figure 12c), and MZ subareas (Figure 12e), the relationship was not significant.

### 4. DISCUSSION AND CONCLUSIONS

#### 4.1 Spring onsets

The fishing periods for juvenile *T. japonicus* on seasonal and subseasonal timescales were detected in the weekly landing time series for the eight subareas. A comparison of the data on the long-term mean landings and the equivalent numbers of individuals ($N_E$) indicated that the timing of onset almost coincided in these time series, whereas the peaks in landings lagged substantially behind those in $N_E$, probably because the sizes of individual fish had increased. Assuming that the cohorts causing onsets and peaks were the same, we can infer the spawning season corresponding to each onset from the length obtained for the season of the peak in $N_E$. In this context, the growth rate of *T. japonicus* recorded by Ochiai et al., (1983) in rearing tanks probably represents the upper bound of the growth rate in the natural environment. Their study showed that it takes 60, 105, and 230 days from hatching to reach FLs of 48, 101, and 152 mm, respectively. The growth from 48 to 101 mm FL is mostly linear (Ochiai et al., 1983), and based on this, the growth periods for the other sizes can be estimated. Although there is great variability in growth rates, especially in the larval stage, those individuals with a very low growth rate are less likely to survive (Takahashi et al.,...
We assumed that the growth rate of survivors was substantially lower than the reference values cited above in winter in CAK and the northern ECS, where the surface temperature is typically <20°C (Sassa et al., 2016; Xie & Watanabe, 2007). The main spawning seasons differed among the s-ECS (February–March), w-CAK (January–May), and e-CAK (May–July); although there was substantial overlap in the spawning months for s-ECS and e-CAK, the duration of the spawning periods differed. Therefore, assessments of the spawning periods based on the onset signals can be used to infer the origins of the fish landed in each season in each subarea.

Although we did not have the size composition data at weekly intervals (unlike the landing data), increases in size from 50 mm FL in the four available subareas in CAK typically commenced no earlier than March and predominantly ended in June (Figures 3 and 4). Some exceptions were several anomalous occurrences of the small size classes (<100 mm FL) in summer in the ME subarea. If an onset was observed in a month when the expected size was 65 mm FL, spawning was calculated to have occurred 74 days earlier. For an onset in June, when the expected size was 90–100 mm FL, spawning was calculated to have occurred 100 days earlier, in early March.

To establish the origins of T. japonicus juveniles forming the spring onsets, onset signals were detected in February–March in the KO subarea, but the corresponding length composition data were only available for 2013–2014. The back-estimated spawning period for the size range >80 mm FL in 2013–2014 was at the beginning of January, at the latest. This is clearly earlier than the main spawning period in the s-ECS but near the beginning of the spawning period in w-CAK. However, an ichthyoplankton survey indicated the presence of eggs in January, especially in the western part of the w-CAK, from south of Kyushu Island to Shikoku Island (FRA_06–16), suggesting possible contributions to the early onset in the KO subarea. Contributions from the w-CAK were also possible for some onsets in late March in the ME and KN subareas (Figure 10a, c). Although the 60–70 mm FL size class was frequently observed during March in the ME subarea (Figure 4b), the spring onsets generally commenced in April in this area (Figure 10g).

From April to at least early summer, when spring onsets were detected in subareas other than KO, back-estimation suggested contributions from both the s-ECS and w-CAK. However, in the weekly size data available for April to summer (Figure 4), the smallest size range (50–70 mm FL) was found almost exclusively from April–May, corresponding to an estimated spawning period of February–March. This fact strongly supports the previous hypothesis that the s-ECS is the primary spawning ground for the entire T. japonicus population, including in the CAK (e.g., Sassa et al., 2006). The abundance of larvae at the preflexion stage was markedly higher in the s-ECS (100–1000 × 10^12; Sassa et al., 2016) than in w-CAK (10–1000 × 10^5; FRA_06–16). Although the proportions of eggs/larvae from the s-ECS either transported to CAK or the Sea of Japan or retained within the ECS still remain unknown, the present study indicates that the s-ECS exerts the major influence, based on actual landing data.

Although T. japonicus in the size class 50–70 mm FL originating in w-CAK should be present even in June and July, their abundance may have been substantially smaller than that from the s-ECS, and therefore, they may not have been an obvious class in the size distribution. However, some exceptions were observed, including in 2012 in the ME subarea (Figure 4b). As discussed below, landings from set nets depend on small-scale currents and the migration of schools, and juveniles from w-CAK could occasionally dominate at the local scale, even if the abundance at the area scale (e.g., w-CAK and e-CAK) was lower than that from the s-ECS. A similar inference was also made for the EH subarea by Hashida et al., (2017), Hashida et al., (2019), who reported a difference between the main hatching period for juveniles (March–April) and the local spawning period (late April–early July). Because spawning in the e-CAK occurs considerably later (May–July), no contribution to the spring onset was expected.

In summary, early landings during March mainly originated from w-CAK (local and neighboring spawning grounds for the w-CAK and e-CAK fishing grounds, respectively), whereas landings from April
until mid-autumn largely originated from the s-ECS (remote spawning ground).

4.2 Autumn onsets

Unlike the spring onsets, those in autumn were not necessarily composed of size classes ≤100 mm FL (Figures 3, 4 and 10). Among the four subareas in which the size data included multiple seasons, contributions of relatively small size classes (80–120 mm FL) were only evident in the KN subarea for several weeks from late September to late October (Figure 4a). Back-estimation of the spawning period for the 100 mm FL juveniles in September–October suggested that they originated in July–August. Spawning in July suggested that the origin was the e-CAK. However, the main spawning period there was assumed to be May–July, and August is one month beyond the main spawning season. A possible explanation is the interannual variation in the spawning period in subarea KN. Recent surveys have shown that in some years, eggs appear in the KN subarea around August (FRA_06–16). Another possibility is that spawning occurred in Chiba Prefecture, the area neighboring KN but at the exterior of the CAK. High densities of eggs are often observed in August there (Figure 1; not included in e-CAK in the present study) just east of the KN subarea (FRA_06–16), which may also have contributed to the autumn onset in the KN subarea.

No reductions in size were observed in the autumn onsets in subareas other than the KN subarea (Figure 4). Although the possibility that small size classes were present cannot be completely excluded because the data available for autumn are limited (no data for the WK and KG subareas), the origin of the juveniles in these subareas in the w-CAK was expected to differ from those in the KN subarea (e-CAK), where the local spawning period was May–July. We assume that these signals were caused by juveniles spawned locally within the w-CAK in April–May. Those from the s-ECS are likely to dominate during summer in the w-CAK and reach the upper bound of the market size range (~150 mm FL) in October (7.5 months after February–March). Therefore, the movement of schools originating from the w-CAK, either via currents or the local-scale migration of juveniles, might be responsible for the autumn onsets in these subareas.

4.3 Transport and population structure

The temperature at 10–30 m recorded by monitoring buoys near the set nets showed that juvenile T. japonicus were mainly landed at the
temperature range of 15–25°C in the CAK (Figure 11). This is consistent with the previous finding of bottom water temperature of >15°C in the East China and Yellow Seas during all seasons (Sassa et al., 2009), and 20–50 m layer (where acoustic signals were detected) temperature of 19–21°C in the Sea of Japan during June–July (Nakamura & Hamano, 2009). It is thus reasonable to assume that the habitat temperature alone does not determine the abundance of *T. japonicus*. However, the habitat temperature alone does not determine the abundance of *T. japonicus*. Given the source-sink network caused by the unidirectional transport of the Kuroshio, sustainability of the adult stock in the s-ECS and the Sea of Japan form a metapopulation (Sassa et al., 2016). Although *T. japonicus* share its metapopulation structure with other *Trachurus* species (e.g., *T. picturatus*: Moreira et al., 2020; *T. murphyi*: Gerlotto et al., 2012), one way in which it differs from those inhabiting in the northeastern Atlantic and the southeastern Pacific Oceans is in its apparent unidirectional dispersal, which may be caused by the strong streams of the Kuroshio and the TWC. Rules of disturbances diverged from the mainstream in retention and dispersal of larvae and juveniles may be important for *T. japonicus* in forming the population structure.

Because the population of *T. japonicus* is probably highest in the ECS, allochthonous larval supplies from the s-ECS may be important for subpopulations in the CAK, as well as for the autochthonous reproduction within the local areas. If the recruitment estimated with the VPA accurately reflects the population in the entire CAK, then the total number of individuals within the CAK increases as the population increases. Although we did not compare the VPA-based recruitment with the total number of individuals, but with the sum of *N*<sub>e</sub> in each subarea in April–June, a positive relationship was expected for any subarea in which the connectivity to a major subpopulation (e.g., those transported from s-ECS) was sufficient. However, the relationship was not statistically significant, possibly because of the highly stochastic variability in landings. More detailed data are required to more fully explore this statistical relationship.

![Figure 12](image-url) (a) Population of *T. japonicus* at age 0, estimated with a virtual population analysis, and its relationship to the average *N*<sub>e</sub> value for the period January–March in subareas (b) KN, (c) ME, (d) KO, and (e) MZ.

![Figure 12](image-url) (a) Population of *T. japonicus* at age 0, estimated with a virtual population analysis, and its relationship to the average *N*<sub>e</sub> value for the period January–March in subareas (b) KN, (c) ME, (d) KO, and (e) MZ.
adult T. japonicus likely aggregate in the s-ECS during late winter but they are almost free from fishing pressure because of adverse weather condition caused by the East Asian winter monsoon. The self-recruitment and the low adult mortality may thus contribute to sustain the source area of T. japonicus.

Migratory and resident forms of T. japonicus with slightly differing morphologies are known to occur in various coastal areas of Japan, including the CAK (e.g. Azeta & Ochiai, 1962; Kanaji et al., 2010). Both forms occur in the same fishing grounds, but although the migratory form originates in the remote s-ECS, the differences between them are phenotypic and not genetically determined. The effects of their differing life histories may be critical in sustaining the population of T. japonicus, despite the asymmetric transportation and migration flows between distant habitat areas.

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CONFLICT OF INTEREST
The authors have no conflict of interest to declare.

AUTHORS CONTRIBUTIONS
KI and SI conceived and designed the study; TT, HH, DH, TO, TT, MK, YS, ST, and RF provided the commercial landings data; CW provided the length composition data; TK provided the coastal water temperature data; KI compiled and analyzed the data and drafted the manuscript; CW, TK, and SI contributed to revise the manuscript; All authors participated in discussion and approved the final version of the manuscript.

DATA AVAILABILITY
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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