Temporal variations in hatch date and early survival of Japanese anchovy (*Engraulis japonicus*) in response to environmental factors in the central Seto Inland Sea, Japan

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Abstract

Reproductive success can be influenced by the match or mismatch between the spawning season and optimal environmental conditions for larval survival. However, it is challenging to understand how temporal factors affect population dynamics. In the central Seto Inland Sea, Hiuchi-nada, western Japan, the recruitment of Japanese anchovy (*Engraulis japonicus*) has markedly decreased in the last decade. To explore the causes of this decline, egg survey and commercial catch data from 1994 to 2019 (26 years) between April and August were used to examine egg production, hatch date, and early survival in relation to environmental factors. Otolith microstructure analysis indicated that most landed larval and juvenile fish (recruits) hatched in May and June. Egg and recruit abundances were negatively correlated over the study period. The survival indices from hatching to recruitment were higher in waters at 16–24°C in a given season until the mid-2000s. Thereafter, they decreased over the studied temperature range and remained relatively low over the last five years. The copepod nauplii densities from 2015 to 2019 were significantly higher than those from 2002 to 2005 due possibly to the effect of increasing temperature, but the ratio of copepod nauplii density to larval density in May and June from 2015 to 2019 was approximately 34% and 66% of those from 2002 to 2005, respectively. These findings and the hydrodynamic features of these waters suggest that the recent decline in recruit abundance is partly due to a decrease in larval survival in response to increasing intracohort competition for prey in early-life stages.

Keywords

copepod nauplii, early survival, egg production, intracohort competition, Japanese anchovy, recruitment, temperature
1 INTRODUCTION

Long-term changes in marine fish populations have been observed in relation to climate-driven changes in the biological and physical environment (Chavez et al., 2003; Somarakis et al., 2019), but the mechanisms linking environmental factors to population dynamics are unknown. Many small pelagic fishes such as anchovy spawn multiple batches of numerous pelagic eggs over a relatively prolonged spawning season, which may increase offspring survival rates, as the likelihood of encountering favorable environmental conditions is enhanced (Lowerre-Barbierei et al., 2011; Wright & Tripel, 2009). For fishes with indeterminate fecundity, inter- and intra-seasonal variation in egg production can be observed with respect to variations in spawning duration, spawning frequency (i.e., intervals between spawnings), and batch fecundity. Such spawning traits are largely influenced by biological and physical factors (Lowerre-Barbierei et al., 2011; McBride et al., 2015) and in turn impact offspring survival during early-life stages.

According to paradigms on recruitment variability, prey availability is a potential key environmental factor for larval survival. The potential for recruitment success critically depends on the match/mismatch of peak occurrence between prey and larvae (Cushing, 1990). Moreover, larvae must find suitable prey in sufficient quantity before starvation, as starved larvae are unable to recover after subsequent feeding (Hjort, 1914; Kono et al., 2003). Density dependence in early-life stages can result from prey competition affecting growth and survival rates (Cowan et al., 2000; Houde, 2008; Rose et al., 2001). Slower growth leads to prolonged life stage duration and thus potentially greater cumulative mortality over a given period. Density-dependent growth is not simply food limitation of the growth rate but refers to a situation in which the feeding rate of an individual is reduced by the presence of other members of the same population, cohort, or year class (Heath, 1992).

Temperature is another key environmental factor that affects not only larval traits but also prey production phenology. The time required for a first-feeding larvae to feed exogenously before irreversible starvation generally decreases exponentially with temperature (Houde, 2008; Pepin, 1991). Moreover, temperature generally regulates growth rate, development duration, and swimming speed (Green & Fisher, 2004), which largely affect individual survival rate. Temperature can also control prey availability through its effects on planktonic production levels and timing (Beaugrand et al., 2003; Cushing, 1990). Thus, the key to understanding fluctuations in early-stage survival lies in identifying a combination of interacting biological and physical factors rather than a single factor (Houde, 2008; Peck et al., 2012; Somarakis et al., 2019).

Exploitation affects population dynamics of commercially important fish species and regulated exploitation can theoretically stabilize a population and/or maximize production per unit biomass. However, due to susceptibility of small pelagic fishes to environmental cues, natural mortality changes result in increased recruitment variability, making it difficult to conduct their fishery management (Katara, 2014). The central Seto Inland Sea, Hiuchi-nada, western Japan, is a semi-enclosed coastal sea surrounded by the islands of Honshu and Shikoku (Figure 1a). These waters are major fishing and spawning grounds of Japanese anchovy (Engraulis japonicus Temminck & Schlegel). Females spawn mainly from late spring to summer (Suhara et al., 2013) especially in the eastern waters. The western side of Hiuchi-nada experiences a clockwise, circular residual current, whereas a counterclockwise, circular residual current occurs in the eastern waters (Figure 1b; Guo et al., 2004; Sugimatsu et al., 2012). Therefore, anchovy eggs and larvae are maldistributed in eastern Hiuchi-nada (Zenitani, 1998) as they become entrained in the circular residual currents due to the waters’ largely enclosed condition (Zenitani et al., 2009). Small purse seine vessels mainly targeting anchovy larvae (chirimen) and juveniles (kaeri) operate from June to September; the annual catch has largely fluctuated but has decreased since the mid-2000s (Figure 2). The gonadal maturation and condition factor of adult fish and egg abundance have been monitored in these waters since 2010 to ensure enough eggs are left to sustain a certain number of recruit fish during the ongoing season (Fisheries Agency, 2010). However, this approach has not worked well in recent years: 2014 saw the lowest catch on record (almost 0 tons) despite adequate egg production. Therefore, understanding the causes of recruitment failure is of the utmost importance.

Previous studies on the mechanisms of recruitment success of Japanese anchovy in the central Seto Inland Sea focused mainly on prey availability. Field surveys conducted in these waters show that the survival rates of larval anchovy cohorts (standard length [SL]: 3–15 mm) are correlated with the density of small copepod nauplii (Zenitani et al., 2007). Moreover, Zenitani et al., (2009) demonstrate that size-specific growth rates in larvae and juveniles increase with increasing prey availability, while temperature has no significant effect. Consequently, anchovy reproductive success rates are proportional to copepod biomass during the last 10 days of May, which immediately precedes anchovy recruitment (Zenitani et al., 2011). Although potential predators and competitors can affect the early survival of anchovy in these waters (Shoji et al., 1997; Zenitani et al., 2017), prey availability during early-life stages may be one of the most important environmental factors that regulates anchovy population dynamics.

Accordingly, this study explored the causes of the recent decline of anchovy recruitment in the central Seto Inland Sea. Temporal variations in egg abundance, hatch date, and early survival were examined using commercial catch and egg survey data from 1994 to 2019 (26 years) in relation to environmental factors. In these waters, anchovy landings comprise 67%–97% larvae and juvenile fish (Yamamoto et al., 2014). Fishing rates, calculated by dividing total landings until November by initial stock size in June, ranged from 80% to 89% from 1993 to 2011, suggesting that landings of larvae and juveniles might reflect the abundance of recruit fish (Pope, 1972). However, the total landings of larvae and juveniles do not explain the total number of individuals, as the ratio of landings between the two stages differ with respect to month and variations in body weight (Yamamoto et al., 2014). Therefore, to examine annual change in the monthly abundance of recruit fish (i.e., the number
of individuals), the SL, age, and growth rate at each stage were estimated on the basis of the otoliths of landed larvae and juvenile fish. In this study, abundance of recruit fish (RA) was determined as the estimated total number of larvae and juveniles hatched in each month. Next, the temporal variations in the effects of temperature on egg abundance (EA), larval density (LD), and RA were examined by generalized additive models (GAMs) as well as survival indices based on three parameters: (1) LD per EA (LPE), (2) RA per EA (RPE), (3) and RA per LD (RPL) (Table 1). Finally, to determine the effects of prey availability, the densities of copepod nauplii and anchovy larvae were compared between high (2002–2005) and low (2015–2019) landing periods.

2 | MATERIALS AND METHODS

2.1 | Biological data

The summary of biological data used in this study was shown in Table S1. The growth rate and birth date of recruit fish were examined using catch data on anchovy larvae (chirimen; SL < 30 mm) and juveniles (kaeri; 30 ≤ SL < 45 mm) from all fishery cooperatives in Kagawa Prefecture, which account for >50% of the total catch in Hiuchi-nada. Data on fishing date and landing at each developmental stage were available for the June–September fishing season. For daily growth analysis, 826 larval and juvenile specimens collected
from commercial catches were obtained between May and August from 2002 to 2006, 2012, 2013, and from 2015 to 2019. Specimens were first fixed in 5% neutral formalin for 1 h and then transferred to 90% ethyl alcohol after rinsing with freshwater. The SL of each larva or juvenile was measured to within 0.1 mm, and their sagittal otoliths were sampled under a dissecting microscope.

The egg and larval surveys were conducted by the R/V Yakuri of the Kagawa Prefectural Fisheries Experimental Station from April to August from 1994 to 2019 at seven of the 17 stations established in the central Seto Inland Sea, eastern Hiuchi-nada (Figure 1a). The dataset included 3039 net samples (Table S2) obtained by a Marutoku B type net (0.45 m mouth diameter, 0.8 m length, 0.335-mm mesh opening) attached to a 20-m rope towed vertically from around the bottom; the samples were preserved onboard in 5% neutral formalin solution. The volume of filtered water sampled was calculated by a flowmeter (RIGOSHA & Co., Ltd.) attached to the net. In the laboratory, anchovy eggs and larvae were sorted under a stereoscopic microscope and counted at each station. Moreover, eggs of other fishes including Sardinops melanostictus (Japanese sardine) and Konosirus punctatus (gizzard shad) were counted at each station from 1996 to 2019.

Monthly EA estimates in Hiuchi-nada followed Kono and Zenitani (2008) with some modifications. Anchovy eggs were maldistributed in eastern Hiuchi-nada, which accounted for approximately 80% of annual egg production in Hiuchi-nada from 1980 to 2017 (N. Kono, unpublished data). In our study, monthly EA estimates of anchovy were based on egg survey data collected in eastern Hiuchi-nada. The egg density per unit area vertical water column was estimated at the individual tow level according to the number of eggs, which was determined on the basis of the filtering rate. Mean egg density was calculated by arithmetically averaging the egg densities of all tows conducted within the survey areas for each month. Monthly EA was then calculated by multiplying the mean egg density by the sea area. In this process, the egg incubation time (as a function of temperature; Hattori, 1983) and egg survival rate (0.6) were considered to realistically assess the quantitative data (Zenitani et al., 1995).

To estimate LD, only specimens included larvae at the larval at the early (i.e., nonfeeding) and late (i.e., feeding onset) stages (<about 5 mm in SL), which were assumed to be representative of the larval population (survivors and non-survivors). This was contrary to the assumption of estimate of RA in which the larvae (15.2–30.0 mm in SL, see Results 3.1) and juveniles collected from commercial catches were assumed to be survivors. The LD per unit area vertical water column was estimated at the individual tow level on the basis of the number of larvae. Monthly LD was calculated by averaging arithmetically the larval densities of all tows conducted within the survey areas for each month. Specimens collected by the Marutoku B type net included larvae at the early and late stages; however, larval age component and survival rate were not considered in the analysis. Thus, monthly LD was considered the relative abundance of larvae in a given month.

2.2 | Environmental data

The summary of environmental data used in this study was shown in Table S1. Variations in sea surface temperature (SST) across sampling times and stations, possibly due to weather conditions, were often observed, even within a single sampling day. Therefore, the estimated SST on a given sampling day was calculated from the nonlinear regression (cubic function) of the relationship between SST and Julian days in a given year; SST was derived from data collected by the Kagawa Prefectural Fisheries Experimental Station in eastern Hiuchi-nada (33.6–34.1°N and 133.1–133.4°E). For estimates of copepod nauplii density, 425 water samples were obtained in eastern Hiuchi-nada between April and June from 2002 to 2005 and 2015 to 2019. The former data were obtained from Zenitani et al., (2007), Zenitani et al., (2009): water samples were collected with a 20-L Van Dorn water sampler (RIGOSHA & Co., Ltd.) from 10 m depth (Table S3). Water samples (1 L) were filtered aboard with a cellulose nitrate membrane filter (pore size 5.0 μm; Advantec Toyo Taitoku), and copepod nauplii on the filters were
resuspended and preserved in 5%-10% formalin in a 10 ml test tube. The latter was collected by a 2-L RIGO B Transparent Water Bottle (RIGOSHA & Co., Ltd.) from 10 m depth. Water samples (1 L) were collected with 32-μm openings prescribed in test sieves of metal wire cloth (JIS Z 8801-1) and preserved in 5% neutral formalin. In the laboratory, the water samples were left to stand for >24 h and then supernatant liquid not including copepod nauplii were discarded. Although there were some differences in the sampling device and filtration method between the two sampling periods, water samples collected from 10 m depth for estimate of nauplii concentrations were identical in this study. The body length of the copepod nauplii in sedimentation liquid was measured on the counting plates under an optical microscope. In Hiuchi-nada, the daily survival rate of larval anchovy (3-15 mm SL) was influenced by the density of small nauplii (<100 μm) (Zenitani et al., 2007). Our preliminary observations showed that larvae <5 mm SL could feed on copepod nauplii with prosome length ≤200 μm (T. Fujita, M. Yamamoto, N. Kono, & M. Yoneda, unpublished data). Therefore, the densities of small (i.e., <100 μm; SCD) and all (i.e., <210 μm; CD) copepod nauplii at each station were estimated.

2.3 | Growth and hatch date analysis

Each otolith was mounted on a glass slide with enamel resin. Daily otolith increments were counted using an otolith measurement system (ARP/W version 4.14, RATOC System Engineering). The first daily growth increment is deposited at the onset of exogenous feeding (Tsujii & Aoyama, 1984), but the timing of first feeding can vary depending on temperature (Kono et al., 2003). To estimate the timing and SL at first feeding, laboratory experiments were conducted (Appendix). According to the estimated time (i.e., day) at 50% feeding rates at a given temperature, the regression of the relationship between time at first feeding (TI, day) and temperature (T, °C) was expressed as follows:

\[
TI = -0.33T + 10.22 \quad (R^2 = 0.99)
\]  \hspace{1cm} (1)

Meanwhile, the generalized linear model of SL at first feeding (SLF, mm) was expressed as follows:

\[
SLF = \exp \left[ -0.0197T + 1.74 \right] \quad (R^2 = 0.52, n = 267)
\]  \hspace{1cm} (2)

Thus, the age of an individual was determined by adding TI to the number of otolith daily increments (NDI). Hatch dates were calculated from the date of capture and age of an individual. The SST for the dates was derived from the dataset described above.

The daily growth rate (GR) was calculated using the following equation:

\[
GR = \left( SLC - SLF \right) / NDI
\]  \hspace{1cm} (3)

where SLC is SL at capture.

2.4 | Data analysis

2.4.1 | Monthly abundance and cohort component

To estimate the monthly abundance and cohort component hatched in commercial catches, the estimated GR, age, and SL of larvae and juveniles were analyzed using linear mixed effects (LME) models with restricted maximum likelihood estimation (Weisberg et al., 2010). Each trait model included developmental stage (two categories) as a fixed effect, and sampling year and month as random effects. The significance of fixed effects was tested by the Satterthwaite’s degrees of freedom method (Kuznetsova et al., 2017). The model of each trait with and without natural logarithmic transformation was selected on the basis of the minimum conditional Aikake information criterion (Vaida & Blanchard, 2005). All models started with a full model and sequentially dropped nonsignificant variables, leaving only significant terms. The estimated body weight (BW) of larvae and juveniles was calculated by the following linear regression model:

\[
BW = 6.00 \times 10^{-7} \times SL^{3.78} \quad (n = 1,291, r^2 = 0.98, 12.8 \leq SL \leq 49.0 mm)
\]  \hspace{1cm} (4)

The estimated number and hatch date of individuals on landing days at each developmental stage were expressed as follows:

\[
\text{Estimated number of individuals} = \text{total landing/BW}
\]  \hspace{1cm} (5)

The hatch date of individuals was estimated by subtracting estimated age from the capture date. Monthly RA was calculated as the sum of the estimated number of larvae and juveniles (survivors) hatched in each month.

2.4.2 | Variations in abundance of eggs and recruits

The relationship between RA and EA during the main hatching season was tested using LME models in which EA was a fixed effect and sampling month was a random effect.

To examine the temporal trend of fish egg occurrence in these waters, the ratio of anchovy eggs to eggs of other fishes was calculated by dividing the total number of fish eggs at each station by the number of anchovy eggs in May and June from 1996 to 2019.

2.4.3 | Effects on sea surface temperature, egg abundance, larval density, and recruit abundance

To examine the effect of sampling year and Julian days on SST, a variable-coefficient GAM with a Tweedie error structure and log-link function was used. The Tweedie distribution model is particularly useful when the data include a large proportion of zeroes, as it avoids separating zero values from positive values in multistage delta models (Shono, 2008). Our data analyses considered Tweedie
distributions for the case in which \( 1 < p < 2 \) (where \( p \) is a power parameter of the Tweedie distribution), which represents the compound Poisson-Gamma distributions. The GAM was formulated as follows, incorporating interactions:

\[
Y = a + s(\text{sampling year}) + s(\text{Julian days}) + s(\text{sampling year, Julian days})
\]

(6)

where \( s \) is smoothing spline. The optimal parameters were estimated by restricted maximum likelihood estimation. To examine the significance of the explanatory variables, a WALD-type test was conducted. All models started with a full model and sequentially dropped nonsignificant variables, leaving only significant terms.

To examine the effects of sampling year and SST on EA, LD, and RA, a variable-coefficient GAM with a Tweedie error structure and log-link function was used, as described above. The GAM was formulated as follows, incorporating interactions:

\[
Y = a + s(\text{sampling year}) + s(\text{SST}) + s(\text{sampling year, SST})
\]

(7)

where \( s \) is smoothing spline.

2.4.4 Variations in early survival at different life stages

To examine the temporal variations in survival at different life stages, three production rates were determined—LPE, RPE, and RPL—whose relationships are assumed to reflect the survival indices mainly from hatching to first feeding, from hatching to recruit, and from first feeding to recruit, respectively. Thus, the RPE relationship includes the LPE and RPL relationships. The effects of sampling year and SST on LPE, RPE, and RPL were analyzed using GAMs as described above.

2.4.5 Relationship between densities of copepod nauplii and larvae

The effects of sampling period and month on LD and copepod nauplii densities were tested using LME models. Copepod nauplii densities were categorized as CD or SCD. The sampling period was categorized as high (2002–2005) or low (2015–2019) based on the landings of larval and juvenile fish (i.e., recruits, Figure 2). Mean annual landings were \( 2.3 \times 10^3 \) ton in 2002–2005 and \( 0.7 \times 10^3 \) ton in 2015–2019. Generalized linear model incorporating a Gaussian response distribution coupled with identity link function to connect the mean to the linear predictors showed that there was a significant difference in annual landing between the two periods \( (t = -3.74, \ p < .01) \). Sampling month was April, May, or June. Sampling year was included as a random variable. Deviance was analyzed by the type III Satterthwaite method (Kuznetsova et al., 2017). Initial explanatory variables included sampling period, month, and their interactions. Because LD, CD, and SCD involved data values of zero, a constant value of 0.5 was added to the three parameters to enable logarithmic transformation (Yamamura, 1999). The model of each trait with and without natural logarithmic transformation was selected on the basis of the minimum conditional Akaike information criterion. All models started with a full model and sequentially dropped nonsignificant variables, leaving only significant terms.

All statistical analyses were performed using R version 3.6.2 (R Core Team, 2019) with the cAIC4, glmmlML, lme4, lmerTest, and mgcv packages.

3 | RESULTS

3.1 Variations in standard length, age, and daily growth rate

The ranges of SL of larvae and juveniles collected from commercial catches were 15.2–30.0 mm, ranges of age were 18–57 and 29–81 days, and ranges of GR were 0.47–1.00 and 0.47–1.06 mm/day, respectively. Variations in SL, age, and GR were observed among larval and juvenile fish across sampling years (Figure 3), but there was no relationship between the temporal trends of those values and the periods of high (i.e., 2002–2005) or low (i.e., 2012–2019) landings (Figure 2). There were significant differences in SL, age, and GR between larval and juvenile fish (SL and age: \( p < .001 \), GR: \( p < .05 \)). LME models showed that for larvae and juveniles, estimated SL was 25.2 and 34.1 mm, estimated age was 35 and 47 days, and estimated GR was 0.68 and 0.70 mm/day, respectively.

3.2 Temporal variations in recruit fish and egg abundance

Although the hatch date of RA ranged from April to August, approximately 93% of RA were born in May or June over the 26-year study period (Figure 4a). Most RA hatched in May or June until the mid-2000s. Thereafter, hatch estimates for May gradually decreased and remained low after 2010. Hatch estimates for June also gradually decreased from the mid-2000s and accounted for the largest proportion of RA over the last five years, when historically low recruitment was recorded.

Anchovy spawning in the central Seto Inland Sea was observed from April to August (Figure 4b), corresponding to the hatch period of RA. EA in August varied largely across the study sampling years, whereas EA in June and May has increased since 2011 and 2015, respectively, apparently resulting in an increase in total EA in that season over the last five years. In May and June, RA was negatively correlated with EA over the 26-year study period \( (r^2 = .24, \ p < .01, \ Figure 5) \).
The ratio of anchovy egg occurrence in May versus June varied until the late 2000s (Figure 6); thereafter, it increased and remained relatively high (approximately 88%) over the last decade.

3.3 Effects of sampling year and sea surface temperature on egg abundance, larval density, and recruit fish hatched

Sampling year, Julian day, and their interactions had significant effects on SST ($p < .001$, Table 2). SST in the beginning of May (Julian day = about 120) increased gradually over the study period (Figure 7); the observed temperatures were 14.5°C in 1995 and 18.1°C in 2018. SST from the middle of May to the beginning of June (Julian day = 140–160) also increased rapidly after 2015.

Temperature and interactions between sampling year and SST had significant effects on EA ($p = .001$, Table 3). EA appeared to increase as SST increased over the study period (Figure 8a). Since around 2000, the range of higher EA has gradually expanded from warmer waters ($≥25°C$); over the last 5 years, it has been found in waters $≥18°C$. Sampling year and SST also had significant effects on LD (both $p < .001$). LD increased as SST increased in waters $≤20°C$ (Figure 8b). LD gradually increased over the study period, showing two peaks around $20°C$ and $≥27°C$. Interactions between sampling year and SST had a significant effect on RA ($p < .001$). Higher RA was observed in waters from 16–23°C until the 2000s (Figure 8c). Thereafter, the range of higher RA declined, especially in cooler waters ($≤18°C$) over the last decade.

3.4 Effects of sampling year and sea surface temperature on LPE, RPE, and RPL

Sea surface temperature had a significant effect on LPE ($p < .05$, Table 4) with a peak in waters around $20°C$ (Figure S1). Interactions between sampling year and SST had a significant effect on RPE ($p < .001$). RPE was higher in waters from 16 to 24°C from the 1990s to mid-2000s (Figure 9a), peaking in the early 2000s; it decreased thereafter, especially in cooler waters ($≤20°C$), and remained relatively low over the examined SST range. Interactions between sampling year and SST also had a significant effect on RPL ($p < .001$). RPL was higher in waters from 16 to 24°C from the 1990s to late 2000s, peaking in the mid-1990s (Figure 9b). After 2005, relatively higher RPL appeared to expand to cooler and
warmer waters until the early 2010s, but RPL rapidly decreased in cooler waters and remained relatively low over the examined SST range.

3.5 | Relationship between larvae and nauplius densities

Sampling period, month, and their interactions had a significant effect on LD (period: \( p < .01 \); month: \( p < .001 \); period, month: \( p < .001 \); Table 2).

| Parameter | EDF | \( F \) | \( p \) | Deviance explained (%) |
|-----------|-----|--------|-------|-----------------------|
| SST       |     |        |       | 94.0                  |
| \( s(Y) \) | 8.17 | 12.02  | <.001 |                       |
| \( s(JD) \) | 1.00 | 136.03 | <.001 |                       |
| \( s(Y, JD) \) | 22.94 | 22.59  | <.001 |                       |

Abbreviations: EDF, estimated degrees of freedom; \( s() \), smoothing spline function; SST, sea surface temperature; Y, sampling year. EDF, \( F \)-values, and \( p \)-values are shown for each term for each final model with deviance explained.
LD in April, May, and June from 2015 to 2019 was higher than that in the corresponding months from 2002 to 2005 (Figure 10a). Sampling period had significant effects on CD and SCD (CD: \( p < .001 \), SCD: \( p < .01 \); Figure 10b,c). CD and SCD from April to June from 2015 to 2019 were approximately 2.4 and 4.4 times larger than their respective values 2002–2005.

The estimated CD/LD ratios in April, May, and June from 2015 to 2019 were approximately 4%, 34%, and 66%, respectively, of those from 2002 to 2005 (Table 5). The estimated SCD/LD ratios in April and May from 2015 to 2019 were lower than those from 2002 to 2005, while estimates in June from 2015 to 2019 were higher than those from 2002 to 2005.

### Table 3: Results of generalized additive models of effects on egg abundance, larval density, and the number of recruits \( (10^9) \) of *Engraulis japonicus* in the central Seto Inland Sea

| Parameter \( (10^{12}) \) | EDF | \( F \) | \( p \) | Deviance explained (%) |
|---------------------------|-----|-------|------|------------------------|
| EA \( (10^{12}) \)        |     |       |      |                        |
| \( s(STT) \)              | 8.42| 6.00  | <.001| 54.6                   |
| \( s(Y, STT) \)           | 3.96| 5.82  | <.001|                        |
| LD                        |     |       |      |                        |
| \( s(Y) \)                | 1.95| 5.88  | <.01 |                        |
| \( s(STT) \)              | 4.36| 11.68 | <.001|                        |
| RA \( (10^9) \)           |     |       |      |                        |
| \( s(Y, STT) \)           | 22.83| 11.03 | <.001| 73.6                   |

Abbreviations: EA, egg abundance; EDF, estimated degrees of freedom; LD, larval density; RA, number of recruits; \( s() \), smoothing spline function; SST, sea surface temperature; \( Y \), sampling year. EDF, \( F \)-values, and \( p \)-values are shown for each term for each final model with deviance explained.

### Figure 7: Effect of sampling year and Julian days on sea surface temperature (SST) in the eastern Hiuchinada. SST was derived from fitted generalized additive models. Red–yellow, green, and blue indicate high, moderate, and low temperatures, respectively; solid lines are contour lines.

### Figure 8: Effects of sampling year and sea surface temperature (SST) on egg abundance (EA, \( \times 10^{12} \)), larval density (LD), and abundance of recruit fish (RA, \( \times 10^9 \)) of *Engraulis japonicus*. EA, LD, and RA were derived from fitted generalized additive models. Red–yellow, green, and blue indicate high, moderate, and low abundance, respectively; solid lines are contour lines.
4 | DISCUSSION

Our findings showed that inter- and intra-annual variations in SST affect recruitment fluctuation of Japanese anchovy in the central Seto Inland Sea. SST in the beginning of May has increased gradually over the 26-year study period; SST from the middle of May to the beginning of June increased rapidly after 2015 (Figure 7). Such rising SST could be one of the factors for increasing EA (Figure 4b) and LD (Figure 10a) in recent years. Temperature rising above about 15°C is the trigger for spawning onset of Japanese anchovy (Tsuruta & Hirose, 1989); spawning fractions of female are temperature dependent, whereby intervals between batch spawnings shorten as temperature increases (Takasuka et al., 2005; Yoneda et al., 2014). Higher CD and SCD in 2015–2019, compared with those in 2002–2005 (Figure 10b,c), may also be caused by rising SST as temperature affects the production rate of copepod nauplii (Uye et al., 1996). However, the abundance of phytoplankton, as prey items for copepods, might be more influential for the production rate under oligotrophic conditions recently observed in the Seto Inland Sea (Abo & Yamamoto, 2019). The information on temporal variation in production rate of copepod nauplii and larval daily ration remain unclear.

TABLE 4  Results of generalized additive models of effects on larval density per egg abundance, the number of recruits per egg abundance, and the number of recruits per larval density of *Engraulis japonicus* in the central Seto Inland Sea

| Parameter                  | EDF | F   | p    | Deviance explained (%) |
|----------------------------|-----|-----|------|------------------------|
| LPE (10^{−12})             |     |     |      | 10.8                   |
| s(STT)                     | 3.70| 3.00| <.05 |                        |
| RPE (10^{−3})              |     |     |      | 75.9                   |
| s(Y, STT)                  | 21.36|17.69| <.001|                        |
| RPL (10^{−9})              |     |     |      | 68.4                   |
| s(Y, STT)                  | 22.34|26.56| <.001|                        |

LPE, larval density per egg abundance; RPE, number of recruits per egg abundance; RPL, number of recruits per larval density; s(), smoothing spline function; STT, sea surface temperature; Y, sampling year. EDF, F-values, and p-values are shown for each term for each final model with deviance explained.

However, marked differences in the CD/LD and SCD/LD ratios between the periods of 2002–2005 and 2015–2019 (Table 5) imply that the relationship between food requirement and food availability in early stage of life has likely been mismatched, leading to decreasing survival indices (RPE, RPL) in recent years (Figure 9).

In this study, there were intra-annual variations of the EA, LD, and RA of Japanese anchovy in the central Seto Inland Sea from 1994 to 2019. EA appeared to increase as SST increased over spawning seasons when higher LD was observed in waters ≥20°C due to temperature-dependent spawning fractions (Takasuka et al., 2005; Yoneda et al., 2014). The onset of harvesting adult fish from June may lead to density dependence in egg production, because Japanese anchovy are income breeders that exhibit continuous spawning with better ongoing resource conditions (Tanaka et al., 2016; Tsuruta & Hirose, 1989; Yoneda et al., 2014). Meanwhile, the estimated batch fecundity of anchovy in the central Seto Inland Sea gradually decreased from May to September (Suhara et al., 2013). However, the frequency distribution of the SL of adult females (Suhara et al., 2013) suggests that spawning fish cohorts renewed from July, as anchovy in these waters may have a one-year lifespan (Fujita, T. & Yamamoto, M., personal observation). Thus, the observed intra-seasonal changes in EA could be due to such combined effects on this population's egg production process. Most RA were hatched in May or June at least until the late 2000s, corresponding to the higher RA observed in the mid-temperature range (i.e., 17–23°C) during spawning season. Marine fish species frequently exhibit ontogenetic shifts in thermal habitats or tolerance, specifically narrower ranges in the larval stage and broader ranges in the juvenile and adult stages (Pörtner & Peck, 2010). The egg size of Japanese anchovy is temperature dependent, whereby size decreases with increasing temperature (Tsuruta & Hirose, 1989; Yoneda et al., 2014). Smaller larvae hatched from smaller eggs in warmer temperatures might have an increased risk of mortality due to lower tolerance to starvation and higher predation opportunities (Houde, 2008). Meanwhile, cooler waters might be outside the optimal temperature for larval growth as observed in Japanese anchovy around the Seto Inland Sea (Yamamoto et al., 2018; Yasue & Takasuka, 2009).

Regarding the inter-annual scales, EA and RA in May and June were negatively correlated over the study period. RA in May has
decreased dramatically since the late 2000s and remained at historic lows since the early 2010s. Moreover, RA in June has gradually decreased since the mid-2000s and remained relatively low. Consequently, RA in June constituted the bulk of recruits in recent years. Such trends agree with our preliminary observation that RA per fishing effort in these waters has decreased dramatically in the last decade (T. Fujita, unpublished data). These observations are reflective of the SST range of greater RA narrowing especially in cooler waters, thereby limiting the temperature window for viable larval hatching (20–22°C) in recent years despite increased EA over the SST range examined. Moreover, the ratio of the occurrence of anchovy eggs between May and June has increased since the late 2000s and achieved predominance in the last decade. Increasing SST in April–June appeared to be one reason why EA has increased over the last decade despite decreased RA, which are considered adult fish in the following season. Another possibility is that fish hatched in autumn (outside the study period) might account for the increase in EA, as Japanese anchovy in the Seto Inland Sea mature within approximately 6 months after hatching (Kono & Takahashi, 2019) and can spawn under temperatures below 15°C and photoperiods shorter than 12 h (Tsuruta & Hirose, 1989).

The EA-based indices, LPE and RPE, can be used to understand environmental effects on recruitment dynamics by elucidating early-life survival processes (Takasuka et al., 2019). While the effect of temperature on LPE was significant, sampling year had no significant effect on the relationship between LPE and SST. This suggests that survival mainly from hatching to first feeding at a given temperature likely remained constant throughout the study period. Meanwhile, the interactions between sampling year and SST had significant effects on RPE and RPL, suggesting that survival after first feeding could significantly affect recruitment variability in these waters. The temporal variations in RPE and RPL indicated that the optimal temperature window for successful recruitment of hatched larvae was 16–24°C until the late 2000s. Thereafter, RPE and RPL decreased over the SST range examined, especially in cooler waters. As such, the optimal temperature window in the past has disappeared in the last decade, suggesting that massive mortality of larval anchovy could occur after first feeding during the spawning season, especially until the SST reached approximately 20°C in recent years.

Larval density, CD, and SCD were compared between the periods of high (i.e., 2002–2005) and low (i.e., 2015–2019) landings; all three indices were significantly higher in the latter period. The interaction between sampling period and months had no significant effect on CD or SCD. Meanwhile, CD and SCD numbers increased in recent years due possibly to the effect of rising SST.

### TABLE 5 Estimated copepod nauplii density per larval density and small copepod nauplii density per larval density in April, May, and June from 2002–2005 and 2015–2019.

| Month | CD/LD 2002–2005 | CD/LD 2015–2019 | Ratio | SCD/LD 2002–2005 | SCD/LD 2015–2019 | Ratio |
|-------|-----------------|-----------------|-------|-----------------|-----------------|-------|
| April | 2,272.0         | 96.0            | 0.04  | 73.91           | 5.63            | 0.08  |
| May   | 17.4            | 6.0             | 0.34  | 0.57            | 0.35            | 0.62  |
| June  | 19.7            | 13.0            | 0.66  | 0.64            | 0.76            | 1.19  |

Abbreviations: CD, copepod nauplii density; LD, larval density; SCD, small copepod nauplii density. LD, CD, and SCD estimates were calculated using linear mixed effect models. The ratios of differences in CD/LD and SCD/LD between the two periods are also shown.
The ratios of CD to LD from 2015 to 2019 were much lower than those from 2002 to 2005. In addition, the SCD/LD ratio exhibited similar trends in April and May but not June. As described earlier, anchovy larvae <5 mm SL were able to feed on copepod nauplii with prosome length ≤200 µm (Fujita et al., unpublished data). These findings suggest that the lower RPE and RPL in recent years may reflect increasing intracohort competition for prey in early-life stages, potentially explaining the ratio of the occurrence of anchovy eggs achieving predominance in the last decade. Anchovy larvae appear more susceptible to mortality from starvation, as the point of no return occurs within 1–2 days after first feeding (Kono et al., 2003). Meanwhile, lower feeding rates likely lead to slower growth, which increases cumulative mortality in early-life stages, which is termed "negative density-dependent population regulation" (Cowan et al., 2000; Houde, 2008; Rose et al., 2001). To explore this possibility, it would be beneficial to compare growth rate at age between a reference larval population (e.g., all larvae within 10 days after first feeding) and survivors (e.g., larvae and juveniles landed at age >30 days) during the periods of high and low landings (Robert et al., 2007).

Density-dependent growth and/or survival affecting population dynamics can generally be observed in the juvenile stage in nursery or feeding grounds, as pelagic eggs and/or larvae are quickly dispersed by ocean currents, with their spatial distribution increasing or feeding grounds, as pelagic eggs and/or larvae are quickly dispersed by ocean currents, with their spatial distribution increasing. The particle tracking mode also indicated that the patterns of transportation of anchovy eggs and larvae (at least until around the day of first feeding) in the eastern waters in 2005 and 2015 were almost identical (K. Sugimatsu, unpublished data). This egg distribution pattern together with hydrodynamic conditions may affect the varying levels of competition for prey in early-life stages.

Cannibalism potentially impacts the density-dependent regulation of fish populations through variation in early survival rates (Cushing, 1990). While anchovy egg cannibalism may regulate population size, cannibalism of anchovy larvae is infrequently observed possibly due to the short digestion time of larvae (Hunter & Kimbrell, 1980). In *Engraulis anchoita* (Argentine anchovy), anchovy egg cannibalism increases as copepod density decreases, suggesting that such cannibalism could be an extra source of energy needed for reproduction (Pájarol et al., 2007). Although adult Japanese anchovy can eat their own eggs and larvae (Hayashi, 1967), active cannibalism appears unrealistic (Baba et al., 2018; Yamamoto & Katayama, 2012). In the central Seto Inland Sea, the feeding habits of Japanese anchovy and Japanese sardine are similar, with both eating mainly zooplankton prey items (Yamamoto & Katayama, 2012). Japanese sardine also feed on fish eggs including those of anchovy, whereas no fish eggs were found in anchovy stomachs during the period of intraspecific competition for prey in 1995. There have been almost no Japanese sardine landings in the central Seto Inland Sea since the early 2000s due to decreased resources of North Pacific stock sardine (Furuichi et al., 2019). Hence, the effect of cannibalism on anchovy eggs and larvae is unlikely to explain the variation in RA in these waters.

In the central Seto Inland Sea, jellyfish potentially compete with anchovy larvae for prey (Zenitani et al., 2017). Zenitani et al., (2017) showed that anchovy larvae cannot survive a shortage of food items at first feeding when the abundance of jellyfish with a 100-mm bell diameter exceeds 10 individuals per 100 m². This suggests that the declining anchovy fishery stock during the late 2000s may be partly due to a higher abundance of jellyfish. However, visual investigation shows that the abundance of jellyfish was relatively lower in May and June in recent years (Kagawa Fisheries Stations, 2020). Thus, the presence of jellyfish as a competitor for prey items might have a negligible effect on the early survival of anchovy.

Predation is one of the main factors that affects the early survival rates of fish (Houde, 2008; Somarakis et al., 2019). In the central Seto Inland Sea, *Scomberomorus niphonius* (Japanese Spanish mackerel) spawned from May to June at 16–23°C (Kishida, 1988). Their larvae are almost exclusively piscivorous, and their most important prey is Clupeiformes larvae with slender body forms, which includes anchovy larvae (Shoji et al., 1997). The concentration of Clupeid larvae significantly affects the growth and mortality of *S. niphonius* larvae, which might have caused recruitment fluctuations (Shoji et al., 1997; Shoji & Tanaka, 2005). The stock abundance of *S. niphonius* in the Seto Inland Sea has gradually increased since the late 1990s, increasing further since the late 2000s (Ishida & Katamachi, 2019). Hence, the inconsistency between increases in EA and LD and decreases in RPE and RPL over the last decade might be partly due to increased predation opportunities of *S. niphonius* larvae; however, further research on the two species’ prey–predator relationship is needed.

In conclusion, our findings show that temporal variations in egg production, hatch date, and early survival of Japanese anchovy are related to environmental factors. As such, the recent decline in recruit abundance is partly due to a decrease in larval survival in response to increasing intracohort competition for prey in early-life stages. The hydrodynamic features of the central Seto Inland Sea and the resultant maldistribution of anchovy eggs and larvae may affect the levels of such competition. These factors must be examined in order to understand the mechanisms of population dynamics in Japanese anchovy in the central Seto Inland Sea, although clarifying such mechanisms is beyond the scope of a single study. Further research on potential factors impacting larval survival, including...
maternal factors, and environmental effects on growth and survival in early-life stages should also be considered.

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CONFLICT OF INTERESTS
The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS
T. Fujita, M. Yamamoto, and M. Yoneda designed the study. T. Fujita and M. Yamamoto implemented field survey, and M. Yoneda conducted rearing experiment. T. Fujita and M. Yoneda analyzed the data. M. Yoneda interpreted the data and wrote the original manuscript. T. Fujita, M. Yamamoto, N. Kono, T. Tomyiama, and K. Sugimatsu gave beneficial advice and edited the manuscript. All authors have given approval to the final version of the manuscript.

DATA AVAILABILITY STATEMENT
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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