Inter-annual variation in the relationship between early growth rate and potential survival of the western sand lance Ammodytes japonicus in the Seto Inland Sea in western Japan

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Inter-annual variation in the relationship between early growth rate and potential survival of the western sand lance *Ammodytes japonicus* in the Seto Inland Sea in western Japan

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Abstract

This study examined whether the potential early survival of sand lance in the Bisan Strait, central Seto Inland Sea, can be explained by variations in the growth rate and duration in the early life stages. Otolith microstructure analysis was conducted to examine the growth trajectories of specimens collected in six sampling years: 2011–2014, 2019, and 2020. There were significant differences in the growth rates of larvae and juveniles among sampling years, but such differences were likely attributable to variations in temperature in given seasons. Relative growth rates standardized by temperature were negatively correlated with the duration of the larval stage, suggesting that faster-growing individuals at given temperatures had a shorter larval stage. In each sampling year, there was a significant relationship between standardized hatch date and relative growth rate during the larval stage but not the juvenile stage. Within a given season, later-born larvae seemed to grow faster relative to the temperature experienced, and the higher percentages of the faster-growing larvae were likely associated with higher recruitment and recruitment per egg production. These findings suggest that the proportion of faster-growing sand lance larvae in a cohort at given temperatures explains the variation in potential early survival, but the higher temperatures in recent years may not necessarily contribute to improved early survival.

Keywords Early growth rate · Survival · Hatch date · Duration of larval stage · Increased temperature · Recruitment · *Ammodytes japonicus*

Introduction

Understanding the mechanisms driving recruitment variability in fish populations is critical to improving sustainable management schemes. In marine fish species, mass mortality occurs during the early life stages, and slight changes in early survival can lead to large fluctuations in recruitment (Cushing 1990; Houde 2008; Leggett and Frank 2008). Thus, the survival in early life history stages is the primary determinant of year-class strength in fish populations (Hjort 1914). Larger and/or faster-growing individuals (or cohorts) in the early stages of life generally have higher survival and year-class strength (Anderson 1988; Houde 2008). The growth–mortality paradigm, which is observed in various fish species, posits a positive relationship between recruitment abundance and cohort growth rate (Campana 1996; Ottersen and Loeng 2000; Kamimura et al. 2015). Meanwhile, intense selective mortality for slow-growing individuals would result in fast early growth of the cohort, but this may be associated with lower potential survival and recruitment (Robert et al. 2007). Therefore, examination of the growth trajectories of fishes in the early stages of life may be essential for elucidating the potential survival of a cohort and year-class strength.

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Temperature can substantially impact the early-life dynamics of fish species, because their metabolic activity, behavior, and growth during the early life stages are responsive to temperature (Blaxter 1992; Houde 2008). Under favorable thermal conditions, higher temperatures can lead to faster growth, allowing for shorter durations of early life stages when fish are most vulnerable and have the highest mortality. Thus, this may reduce cumulative, stage-specific mortality, thereby increasing the probability of recruitment according to the stage–duration paradigm (Houde 1989). However, this relationship is only apparent when the energetic demand at a given temperature is met. As metabolic and other energy requirements are temperature-dependent, the increase in growth rates relative to temperature in situations of higher temperatures may be attenuated when prey resources are scarce (Buckley et al. 2004; Shelley and Johnson 2022). Temperature can also control prey availability by affecting planktonic production levels and timing (Cushing 1990; Beaugrand et al. 2003). Thus, the key to understanding fluctuations in the early-stage survival of fish depends on identifying a combination of interacting biological and physical factors rather than a single factor (Houde 2008; Peck et al. 2012).

The western sand lance *Ammodytes japonicus* is a cool-water species distributed in the coastal waters off Japan; the Seto Inland Sea is now considered the southern limit of its range (Hashimoto 1984; Takahashi et al. 2021). Landings of sand lance in the Seto Inland Sea have decreased since the 1970s (Takahashi et al. 2021), potentially because of decreased estivation area as a result of sand mining (Tanda and Okamoto 1992) and decreased prey zooplankton abundance (Nishikawa et al. 2020; Hashiguchi et al. 2021). In the Bisan Strait in the central Seto Inland Sea, the egg production of spawning fish significantly impacts recruitment abundance, and the recent decline in stocks may be partly attributable to a decline in the abundance of older, fecund fish (Akai and Yoneda 2021). In addition, a significant relationship between the egg production of spawning fish and annual catch of age-0 fish was recently reported in Harima Nada in the eastern Seto Inland Sea (Uozumi and Nishikawa 2023). Although the egg production of spawning sand lance could be an important predictor of recruitment abundance in the Seto Inland Sea, investigating the relationship between their potential early survival and year-class strength may help elucidate the causes of recruitment variability.

Accordingly, this study aimed to determine whether the potential survival of sand lance linked to year-class strength and recruitment in the central Seto Inland Sea in the Bisan Strait can be explained by variations in growth rate and duration in the early stage of life. Otolith microstructure analysis was conducted to examine the growth trajectories of individuals using specimens collected in six sampling years (i.e., 2011–2014, 2019, and 2020), and the hatch dates and growth rates of larvae and juveniles among sampling years were examined in relation to temperature. The results show that there were inter- and intra-annual fluctuations in temperature during the study period and that the growth rates of sand lance were significantly influenced by temperature. Therefore, to exclude the effect of temperature on growth rate, the relative growth rates standardized by temperature in relation to hatch date were compared across sampling years. In addition, the difference between the actual and expected durations of the larval and juvenile stages (calculated from the growth–temperature relationship) were compared. Finally, the effects of early growth indices on recruitment and recruitment per egg abundance were assessed. This study addressed the following three questions: (1) Do warmer temperatures increase the potential survival of sand lance through faster growth and shorter early life stages? (2) Do the relative growth rates of sand lance vary by hatch date in a given season? (3) Are individual sand lance with higher growth potential more likely to survive until recruitment?

Materials and Methods

Sample collection

A total of 328 specimens collected from commercial catches were obtained in February and March in 2011–2014, 2019, and 2020. Specimens from 2011–2014 were preserved with 80% ethyl alcohol, and those from 2019 and 2020 were frozen at −20 °C. Given that individual juvenile sand lance preserved in 80% alcohol may not shrink (Kusakabe et al. 2007), the standard length (SL) of individuals after preservation was measured and sagittal otoliths were dissected. Otoliths were prepared for observation of daily rings as described previously (Tsukamoto et al. 2002). Given that the increments of the sagittal otoliths of sand lance are very narrow (Tsukamoto et al. 2002), the number and increments of daily rings were observed by both light microscopy and scanning electron microscopy using an otolith measurement system (ARP/W version 4.14, RATOC System Engineering). As the rings on the otolith form daily from hatch day (Omi et al. 2006), the total number of rings from the hatch ring to the margin can be considered as age in days. The hatch date (HD; see Table 1 for a list of abbreviations) was calculated from the date of capture and the age of an individual. Since the relationship between SL and otolith radius (OR) is allometric ($\mathrm{SL} = a\mathrm{OR}^b$) (Kusakabe et al. 2007), an allometric equation, which relates SL to OR, was applied to each individual to estimate body length from otolith measurements using the biological intercept method (Campana 1990). The SL of sand lance at hatching is 4.78 mm (Kusakabe et al. 2007), and the hatching ring radius for each

Table 1 List of abbreviations used in this study

Abbreviation	Definition
DJ	Difference between the actual and expected duration of the juvenile stage; calculated by Eq. (6)
DJstd	Standardized DJ; calculated by Eq. (10)
DL	Difference between the actual and expected duration of the larval stage; calculated by Eq. (5)
DLstd	Standardized DL; calculated by Eq. (10)
EPI	Egg production index; calculated by Eqs. (11) and (12)
GJ	Daily growth rate in the juvenile stage; calculated by Eq. (2)
GL	Daily growth rate in the larval stage; calculated by Eq. (1)
GLM	Generalized linear model
HD	Hatch date calculated based on capture date and individual age
HDstd	Standardized HD; calculated by Eq. (9)
GLMM	Generalized linear mixed model
N_{DJ}	Age at which SL reached 30 mm
$N_{\mathrm{DJ}} - N_{\mathrm{DL}}$	Duration of the juvenile stage
N_{DL}	Age at which SL reached 21 mm, indicating the duration of the larval stage
R^2	Pseudo-coefficient of determination from Eq. (13)
rGJ	Relative GJ; calculated by Eq. (4)
rGL	Relative GL; calculated by Eq. (3)
RPE	Recruitment per EPI
WTJ	Water temperature experienced in the juvenile stage
WTL	Water temperature experienced in the larval stage

individual was used as the OR at hatching. Two parameters (a and b) were estimated for each individual from SL and OR at hatching and capture. Water temperature at the estivation sites and fishing areas during the study period was recorded every 30 min by a telemetry buoy installed in Yashima Bay (Fig. 1); this telemetry buoy is set in water at a depth of 1.5 m, where vertical mixing is strong (Hashimoto et al. 1997) and there is almost no thermal vertical stratification throughout the year (Takeoka 1985).

Growth analysis

The SL of sand lance at hatching is 4.78 mm (Kusakabe et al. 2007), while the shift to the juvenile stage occurs at an SL of approximately 21 mm (Tsumoto and Yamada 1997). Thus, the larvae were defined as fish with an SL ≤ 21 mm. The SL at the juvenile stage of the common sand lance is generally considered to be up to about 50 mm SL (Yamada 2011). As the smallest specimen was 30 mm SL in this study, the juveniles were defined as fish between 21 and 30 mm SL.

The water temperature that individuals experienced during the larval stage (WTL) and juvenile stage (WTJ) was estimated based on the mean temperature from the hatch date to the end of the larval stage and from the end of the larval stage to the end of the juvenile stage.

The daily growth rate (mm/day) at the larval stage (GL) was calculated as follows:

$$\mathrm{GL} = (21 - 4.78) / N_{\mathrm{DL}} \tag{1}$$

where N_{DL} is the age at which SL reaches 21 mm, estimated from the age just before reaching an SL of 21 mm and the daily growth rate before and after.

The daily growth rate at the juvenile stage (GJ) was calculated as follows:

$$\mathrm{GJ} = (30 - 21) / \left(N_{\mathrm{DJ}} - N_{\mathrm{DL}}\right) \tag{2}$$

where N_{DJ} is the age at which SL reaches 30 mm, estimated from the age just before reaching an SL of 30 mm and the daily growth rate before and after.

As GL and GJ were significantly correlated with WTL and WTJ (see Results), the relative growth rates—rGL and rGJ, respectively—standardized by temperature were calculated as follows:

$$\mathrm{rGL} = \mathrm{GL} / \mathrm{GL}_{predicted} \tag{3}$$

$$\mathrm{rGJ} = \mathrm{GJ} / \mathrm{GJ}_{predicted} \tag{4}$$

$\mathrm{GL}_{predicted}$ and $\mathrm{GJ}_{predicted}$ were calculated based on the relationships between GL and WTL, and GJ and WTJ, respectively (see Results). There was no significant correlation between rGL and WTL ($R^2 = 0.005$, $p = 0.20$)

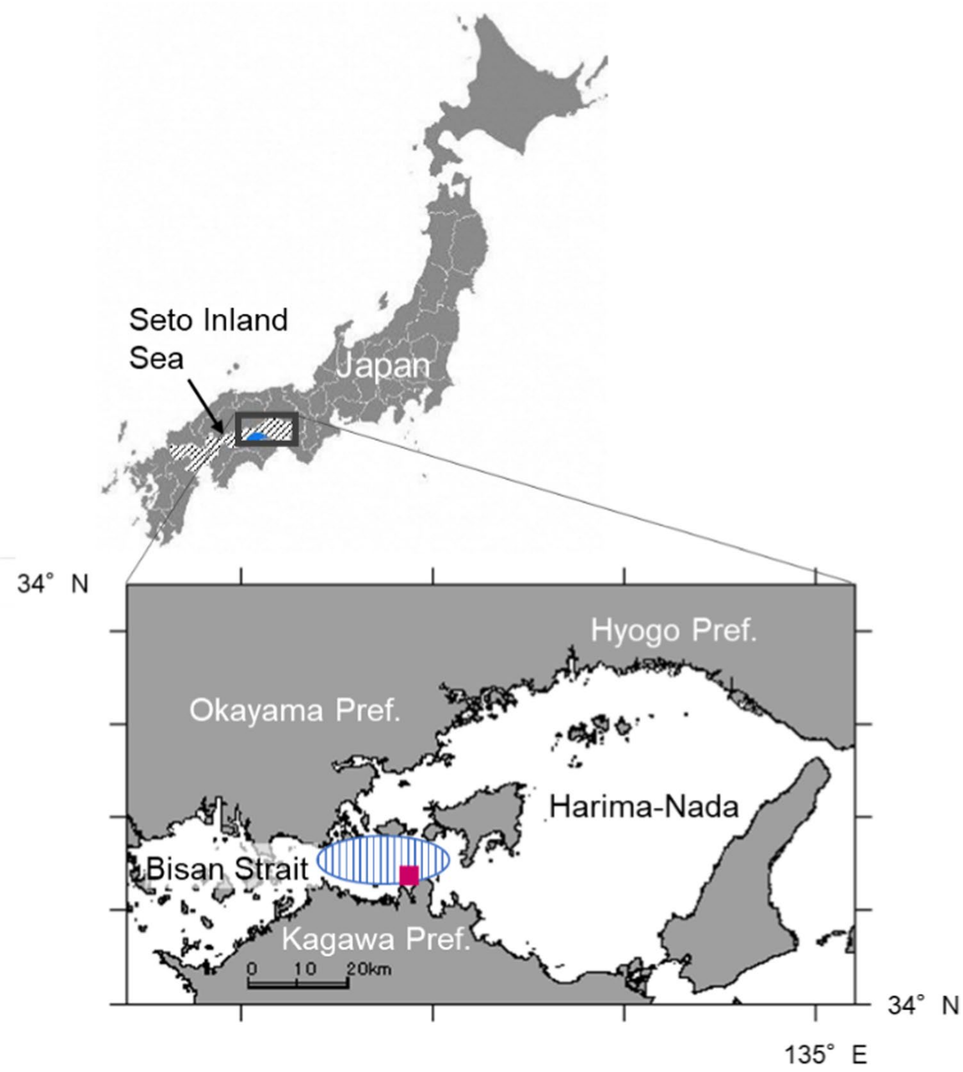


Fig. 1 Sampling and fishing grounds of sand lance (blue-shaded area) and the telemetric monitoring buoy for daily water temperature at a depth of 1.5 m (red square) in the Bisan Straight, central Seto Inland Sea, Japan

or between rGJ and WTJ ($R^2 = 0.007$, $p = 0.13$), indicating that rGL and rGJ are independent of the experienced temperature. The benchmark for the growth of standard fish relative to a given temperature sampled in this study was an rGL or rGJ of 1; values > 1 and < 1 indicate relatively better or worse growth compared to standard fish, respectively.

The difference between the actual and expected duration of the larval stage (DL) or juvenile stage (DJ) was calculated as follows:

$$\mathrm{DL} = \text{Expected duration of larval stage } \left(\text{expected } N_{\mathrm{DL}}\right) - \text{ duration of larval stage } \left(N_{\mathrm{DL}}\right) \tag{5}$$

$$\mathrm{DJ} = \text{Expected duration of juvenile stage } \left(\text{expected } \left[N_{\mathrm{DJ}} - N_{\mathrm{DL}}\right]\right) - \text{ duration of juvenile stage } \left(N_{\mathrm{DJ}} - N_{\mathrm{DL}}\right) \tag{6}$$

The expected duration was calculated as follows:

$$\text{Expected } N_{\mathrm{DL}} = (21 - 4.78)\,/\mathrm{GL}_{predicted} \tag{7}$$

$$\text{Expected } N_{\mathrm{DJ}} = (30 - 21)\,/\,\mathrm{GJ}_{predicted} \tag{8}$$

For comparison and analysis with the same standard, HD and D (i.e., DL and DJ) were standardized as follows:

$$\mathrm{HDstd} = \left(\mathrm{HD} - \mu_{\mathrm{t}}\right)/\sigma_{\mathrm{t}} \tag{9}$$

$$\mathrm{Dstd} = (\mu - \mathrm{D})\,/\sigma \tag{10}$$

where μ is the mean, σ is the standard deviation, and t is survey year. Dstd employed μ and σ derived from the entire dataset, given that the related $\mathrm{GL}_{predicted}$ and $\mathrm{GJ}_{predicted}$ values were obtained from all specimens. An HDstd or Dstd of 0 was set as the benchmark for the HD and the duration of the early life stages; values < 0 and > 0 indicate relatively earlier or later dates or durations compared to standard, respectively.

Recruitment indices

The estimated egg production index (EPI) and recruitment abundance from 2009 to 2019 have been published previously (Akai and Yoneda 2021). For the year 2020, EPI and recruitment abundance were calculated as described previously (Akai and Yoneda 2021):

$$\mathrm{EPI} = \mathrm{EPI}^{1}_{t-1} + \mathrm{EPI}^{2\&3}_{t-1} \tag{11}$$

$$\mathrm{EPI}^{i}_{t-1} = \mathrm{D}^{i}_{t-1} \times RF_{predicted}{}^{i}_{t-1} \times SW_{predicted}{}^{i}_{t-1} \tag{12}$$

where $t-1$ is the survey year (e.g., for 2019, maturity surveys were conducted in December 2018); i is a specimen aged 1 year, or aged 2 or 3 years at maturity surveys; D^{i}_{t-1} indicates the density of mature females of age i at year $t-1$, which was estimated by multiplying half of the total density of each age class by the maturation rate of each age class (assuming a sex ratio of 0.5); and $RF_{predicted}{}^{i}_{t-1}$ and $SW_{predicted}{}^{i}_{t-1}$ indicate the predicted values of relative fecundity ($RF_{predicted}$) and somatic weight ($SW_{predicted}$) from the mean SL of mature fish of age i at year $t-1$, respectively.

The daily catch records of young-of-the-year sand lance in the eastern Bisan Strait were collected during the 2020 fishing season from January to April. Individual body weight (BW) on the middle day of each 10-day period of a given month was determined on the basis of the growth formula of fish collected in the Bisan Strait in 2020 as well as data on the relationship between SL and BW. Catch numbers were also calculated. Recruitment per EPI (RPE) was used as a proxy of the survival index in each cohort. Recruitment abundance was estimated by virtual population analysis (Hiramatsu 2001) following Pope (1972) on the basis of the catch numbers.

Statistical analysis

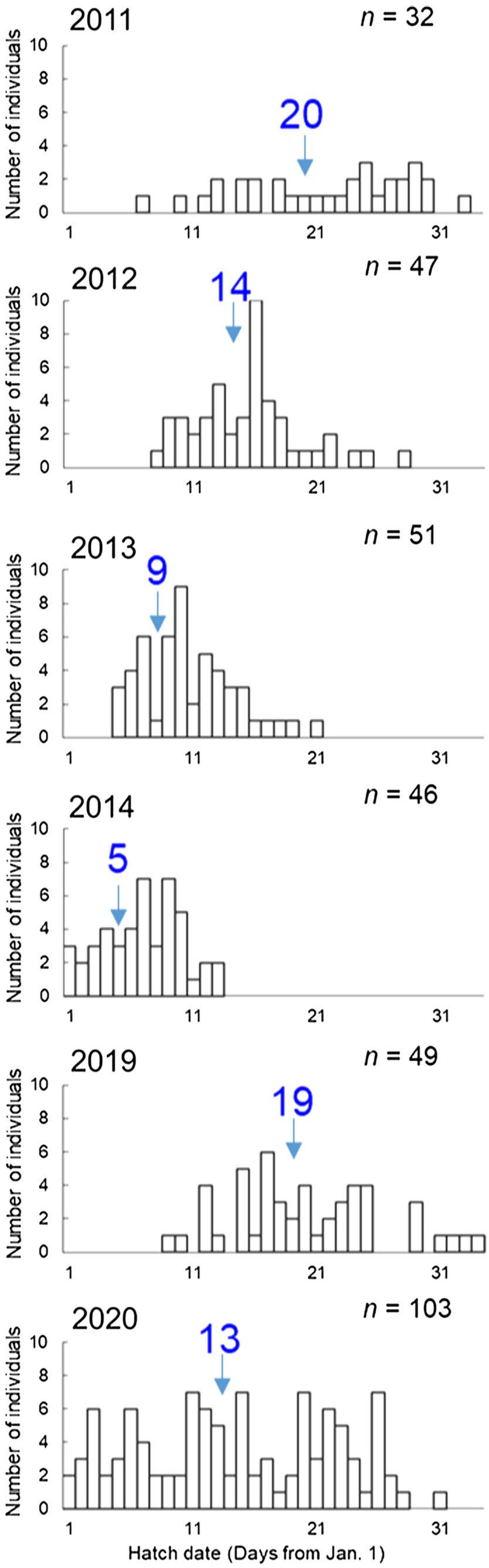
To estimate the day when 50% of the specimens had hatched for each year, a generalized linear model (GLM) was used to adjust a logistic model to the binomial set of data (unhatched = 0, hatched = 1) as follows: $y = [1 + exp(a + b \times x)] - 1$, where y is the hatch rate of individuals, x is the number of days from January 1, and a and b are the model parameters. Using this equation, the date that 50% of the specimens had hatched (i.e., mean hatch date) was calculated as a/b. A generalized linear mixed model (GLMM) was applied to estimate the HDstd, incorporating year as a random effect. Similarly, the days reaching 21 mm and 30 mm were determined. In addition, the standard durations of the larval and juvenile stages were subsequently determined from the HDstd to each transition date.

Differences in GL, GJ, WTL, and WTJ among specimens collected in different sampling years were tested using a GLM incorporating a Gaussian response distribution coupled with an identity link function to connect the mean to the linear predictors. The best model was selected from the 58 groupings of sampling years based on the minimum Akaike information criterion (AIC). As the growth rate varies with respect to water temperature (see Results), a GLMM was applied to evaluate the relationships between GL and WTL, and GJ and WTJ; sampling year was used as a random factor. To determine the effects of estimated GL or GJ on recruitment or RPE (i.e., recruitment/EPI) from 2009 to 2020, a GLM incorporating a Gaussian response into the linear predictors was used. Estimated GL and GJ were determined utilizing the water temperatures for each year during the standard durations of the larval and juvenile stages.

To determine the effects of N_{DL} or $(N_{\mathrm{DJ}} - N_{\mathrm{DL}})$ and sampling year on rGL or rGJ, a GLM incorporating a Gaussian response into the linear predictors was used. A GLMM with sampling year as a random effect was applied to evaluate the relationships of WTL or WTJ with HDstd. The relationships of HDstd with rGL, rGJ, DLstd, and DJstd were analyzed using a GLM incorporating a Gaussian response coupled with the linear or quadratic function. When the quadratic function was used, the D'Agostino–Pearson normality test was performed to determine whether the dataset followed a Gaussian distribution. If no effect of HDstd was observed, differences in the dependent variable among specimens collected in different sampling years were tested using a GLM incorporating a Gaussian response distribution coupled with an identity link function to connect the mean to the linear predictors. To assess the combined effects of the proportion of individuals with rGL $\geq$ 1 and DLstd $\leq$ 0 on recruitment abundance and RPE for the years 2011–2014, 2019, and 2020, a GLM incorporating a Gaussian response into the linear predictors was used. Due to the limited sample size, these proportions were analyzed together in a single model for a more comprehensive evaluation of their impact.

Models for each factor were assessed in both their ln transformed and untransformed states. The optimal models were selected on the basis of the minimum conditional AIC. Statistical analyses were performed using R version 4.3.1 (R Core Team 2023). Models were selected through stepwise selection based on the AIC. An additional measure of model fit was based on a pseudo-coefficient of determination (R^2), which was the fraction of the total variation explained by the following:

Fig. 2 Distribution of the hatch dates of sand lance collected in the Bisan Strait, central Seto Inland Sea. Sample size and the mean hatch date of the specimens are indicated in each histogram



$$R^2 = 1 - \left(\text{residual deviance} \times \text{null deviance}^{-1}\right) \tag{13}$$

where deviance is analogous to the residual sum of squares. The level of statistical significance was set at $p < 0.05$.

Results

Hatch date and the effect of temperature on early growth

The ages of specimens ranged from 32 to 84 days during the study period. HD ranged from January 1 to February 3, with a peak in January (Fig. 2). The shortest duration of hatching (13 days) occurred in 2014, while the longest (31 days) occurred in 2020. Sampling year was significantly affected by HD: mean HD (from January 1) in 2011, 2012, 2013, 2014, 2019, and 2020 was 20, 14, 9, 5, 19, and 13 days, respectively (Fig. 2, Online Resource, Table S1).

The durations of the larval and juvenile stages during the study period were 24–48 and 5–15 days, respectively. GL and GJ ranged from 0.34 to 0.67 mm/day and 0.61 to 1.84 mm/day, respectively. WTL and WTJ ranged from 7.89 to 11.70 °C and 7.65 to 10.66 °C, respectively. GL, GJ, WTL, and WTJ differed significantly among sampling years (Fig. 3a, b). The GLMM showed that there was a significant effect of experienced water temperature on growth rate in the relationships between GL and WTL and between GJ and WTJ. Therefore, the predicted values of GL and GJ obtained from WTL and WTJ are designated as $\mathrm{GL}_{predicted}$ and $\mathrm{GJ}_{predicted}$. Specifically:

$$\mathrm{GL}_{predicted} = 0.128 + 0.035 \times \mathrm{WTL}\ (\mathrm{WTL} : p < 0.001) \tag{14}$$

$$\mathrm{GJ}_{predicted} = \exp(-0.904 + 0.109 \times \mathrm{WTJ})\ (\mathrm{WTJ} : p < 0.01) \tag{15}$$

Relative growth rate and early-stage duration in relation to hatch date

The standard durations of the larval and juvenile stages were January 13 to February 18 and February 19 to February 27, respectively. The only significant relationship was between the natural log (ln)-transformed recruitment and EPI of mature females in all age classes ($n = 12$, $R^2 = 0.48$, EPI: $p < 0.05$); there was no significant relationship between

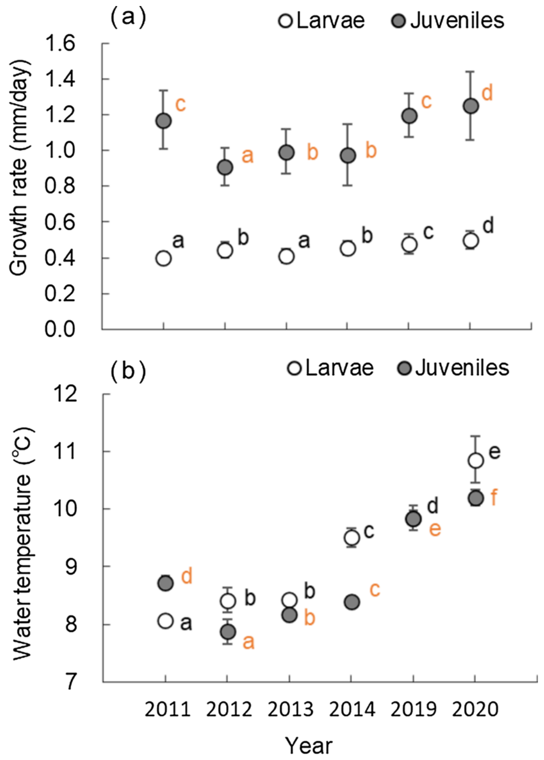


Fig. 3 Daily growth rates of larval and juvenile sand lance (**a**), and water temperatures during the larval and juvenile stages (**b**) from 2011 to 2014, 2019, and 2020. Data are mean ± SE. Letters indicate different sampling year groups in the best generalized linear model ($a < b < c < d < e < f$; $p < 0.001$), with the colors corresponding to life stage (black for larval and orange for juvenile)

ln-transformed recruitment or RPE and ln-transformed estimated GL or estimated GJ (Table 2).

There were significant negative correlations between rGL and N_{DL} and between rGJ and ($N_{DJ} - N_{DL}$) (Fig. 4a, b). The sampling year also significantly affected these relationships ($p < 0.001$). WTL and WTJ differed significantly with HDstd (Fig. 5, $p < 0.001$). WTL appeared to decrease as HDstd progressed, whereas during the juvenile stage, later-born individuals appeared to experience warmer temperatures. There were significant linear or nonlinear relationships between rGL and HDstd during the larval stage throughout the study period, except in 2020 (Fig. 6). Similarly, DLstd was significantly correlated with HDstd throughout the study period, except in 2020 (Fig. 7). During the juvenile stage, there was no significant relationship between rGJ and HDstd (Fig. 8), although rGJ differed significantly among sampling years ($p < 0.001$). Similarly, DJstd was not significantly correlated with HDstd but did differ significantly among sampling years ($p < 0.001$; Fig. 9).

Relationship between relative growth rate and potential survival

Significant relationships were found between rGL or DLstd and HDstd in 2011, 2012, 2013, 2014, and 2019 (Figs. 6 and 7). However, in 2020, the HDstd relative to rGL and DLstd was constant (Figs. 6 and 7, Table 3). During the juvenile stage, the HDstd relative to rGJ and DJstd was constant in each sampling year (Figs. 8 and 9, Table 3).

The cumulative frequency distribution of HDstd for each sampling year was fitted to a logistic model (Online Resource, Table S2). The percentages of fish with an

Table 2 Generalized linear models of ln(recruitment abundance) and ln(RPE) of western sand lance *Ammodytes japonicus*

Model	Explanatory variable	Coefficient Estimate	SE	*t* values	*p*	AIC
For ln(recruitment abundance)						
1	Intercept	0.144	3.33	0.043	0.967	34.95
	ln(EPI)	1.035	0.47	2.210	0.055	
	ln(estimated GL)	−0.802	4.78	−0.168	0.870	
2	Intercept	0.958	1.12	0.853	0.416	34.76
	ln(EPI)	1.001	0.42	2.389	0.041	
	ln(estimated GJ)	−1.402	3.38	−0.415	0.688	
3	Intercept	0.682	0.87	0.786	0.450	32.99
	ln(EPI)	1.082	0.35	3.053	0.012	
For ln(RPE)						
1	Intercept	0.052	2.94	0.018	0.986	32.96
	ln(estimated GL)	−1.017	3.61	−0.281	0.784	
2	Intercept	0.960	0.29	3.325	0.008	32.76
	ln(estimated GJ)	−1.405	2.83	−0.497	0.630	

AIC: Akaike information criterion, EPI: egg production index; GJ: daily growth rate in the juvenile stage, GL: daily growth rate in the larval stage, RPE: recruitment per EPI, SE: standard error

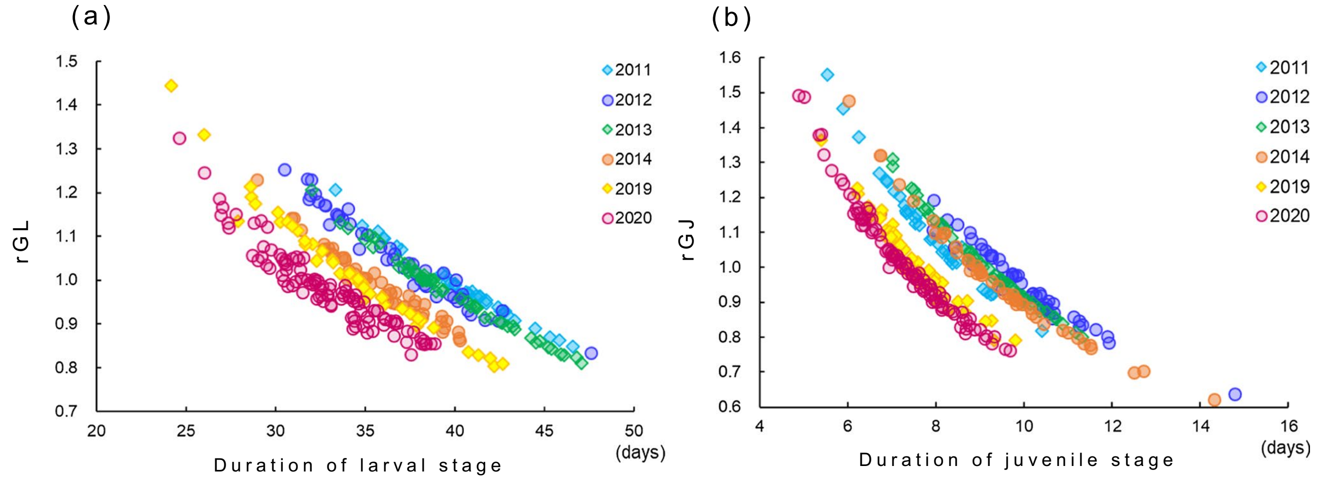


Fig. 4 Relationships of the relative growth rates standardized by temperature (rGL, rGJ, respectively) during the larval stage (**a**) and juvenile stage (**b**) with the duration of the larval stage (N_{DL}) and the juvenile stage (N_{DJ}–N_{DL}) from 2011 to 2014, 2019, and 2020

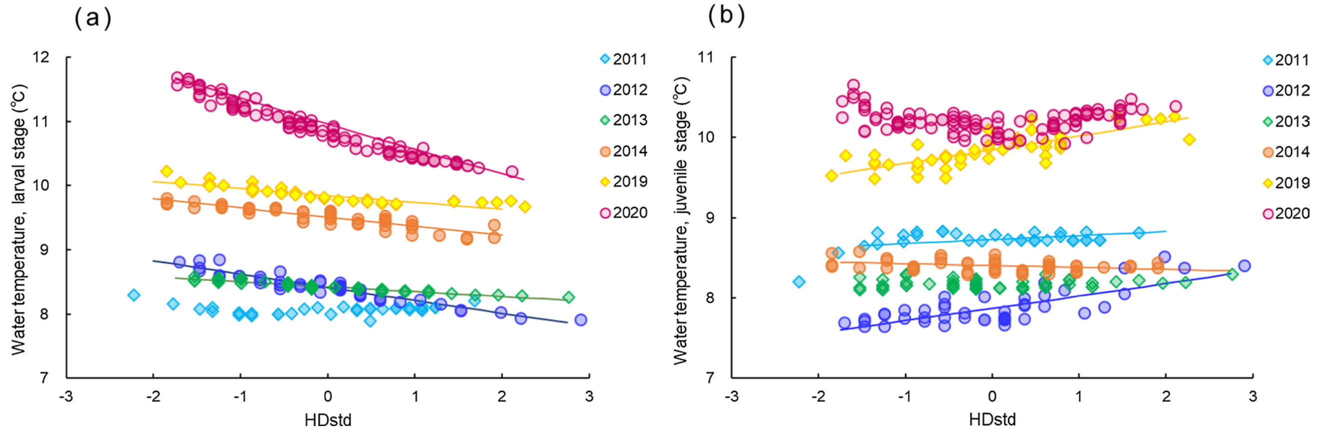


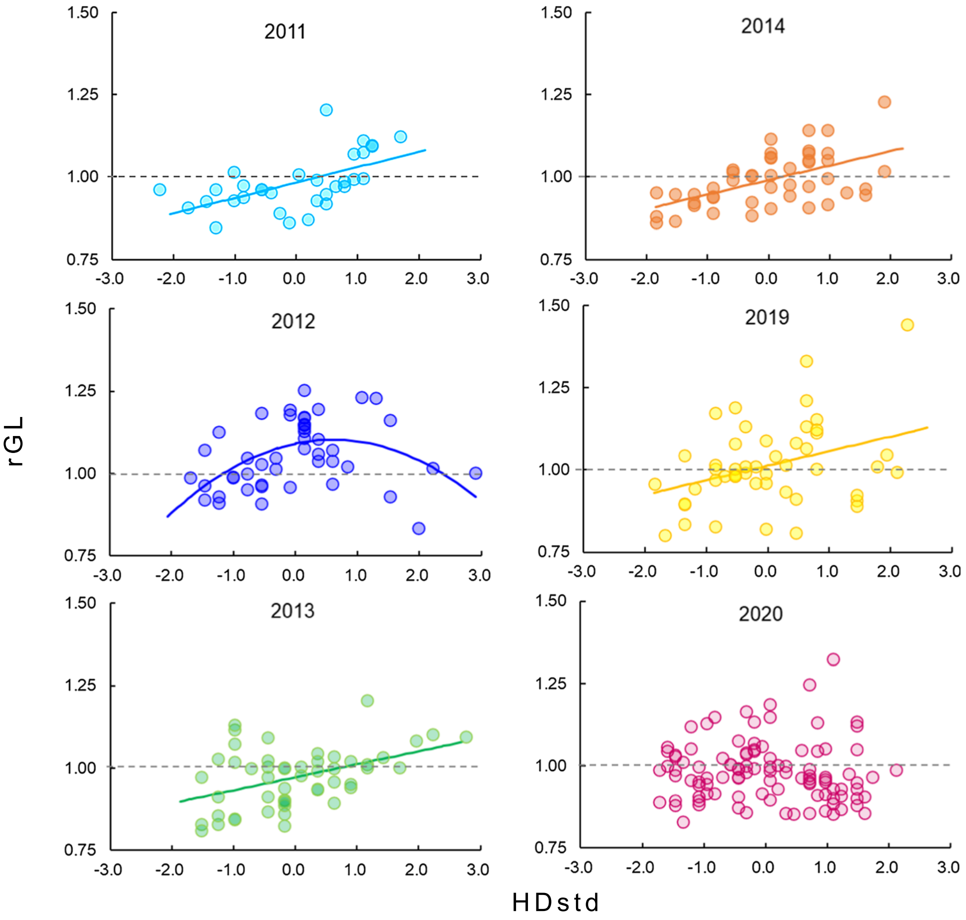
Fig. 5 Relationships of water temperature during the larval stage (**a**) and juvenile stage (**b**) with standardized hatch date (HDstd) from 2011 to 2014, 2019, and 2020

rGL ≥ 1 and a DLstd ≤ 0 by the HDstd were determined from the logistic model (Table 3, Online Resource, Tables S2 and S3). The combined proportion of individuals with rGL ≥ 1 and DLstd ≤ 0 was positively correlated with ln-transformed recruitment abundance ($n = 12$, $R^2 = 0.48$, recruitment abundance: $p < 0.01$). The combined proportion of individuals with rGL ≥ 1 and DLstd ≤ 0 by HDstd was also positively correlated with ln-transformed recruitment abundance ($n = 10$, $R^2 = 0.53$, recruitment abundance: $p < 0.01$). While ln-transformed RPE was not significantly correlated with the ln-transformed combined proportion of individuals with rGL ≥ 1and DLstd ≤ 0 ($n = 12$, $R^2 = 0.21$, RPE: $p = 0.11$), it was relatively strongly correlated with the ln-transformed combined proportion of individuals with rGL ≥ 1and DLstd ≤ 0 by HDstd ($n = 10$, $R^2 = 0.61$, RPE: $p < 0.001$). As such, higher percentages of HDstd of rGL ≥ 1 and duration ≤ 0 were likely to be associated with higher recruitment abundance and RPE (Table 3).

Discussion

Our findings revealed inter-annual variations in the growth trajectories of sand lance in the early stages of life during the study period. This is primarily attributable to temperature fluctuations in given seasons, as there were significant relationships between growth rates and temperatures experienced: warmer temperatures resulted in faster early

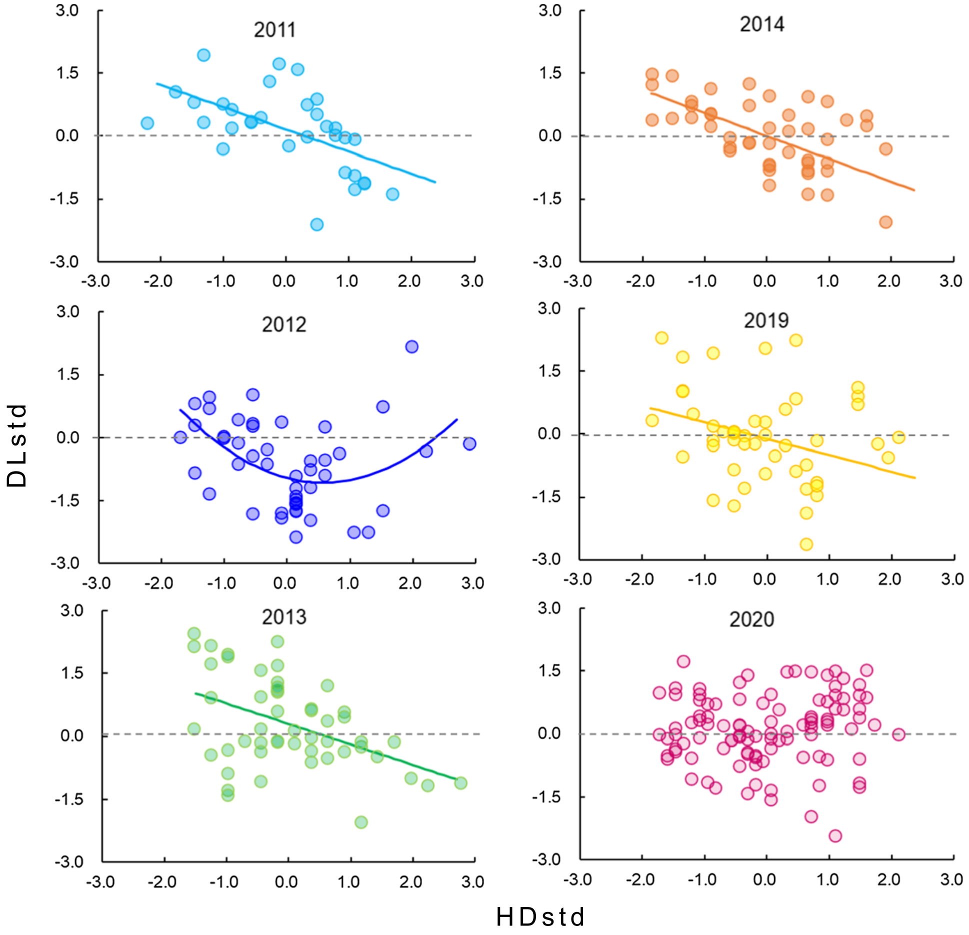
Fig. 6 Relationship between the relative growth rate of larvae (rGL) and the standardized hatch date (HDstd) from 2011 to 2014, 2019, and 2020. The solid lines indicate the generalized linear models fitted to the observed data



growth. This is consistent with previous findings on sand lance showing that individuals in the early stages grow faster in warmer sampling years in Ise Bay in Central Japan and Osaka Bay in the eastern Seto Inland Sea (Tomiyama and Komatsu 2006; Kusakabe et al. 2007). As a result, individuals hatched in warmer winter years experienced a shorter transition from the larval to the juvenile stage. This is likely concordant with the stage duration hypothesis, wherein a shorter transition between the two early stages results in higher individual survival (Houde 2008; Leggett and Frank 2008). However, the growth rates (GL and GJ) during the larval stage did not significantly affect recruitment abundance or early survival, indicating that neither individual growth rates nor the duration of the larval stage appear to explain the variations in recruitment or RPE in these waters. For example, the highest GL occurred in the warmest year—2020—when recruitment and RPE were lower than in other sampling years (Fig. 3, Table 3). This appears to be concordant with findings for *Ammodytes* spp. In the North Sea, warmer temperatures during the egg and larval periods of *Ammodytes marinus* are correlated with below-average recruitment (Arnott and Ruxton 2002). In *A. japonicus* in Ise Bay, the average temperature in January is negatively correlated with the number of recruited sand lance; the most recruited sand lance occurred in 1996, which was the coldest year with the slowest growth in the study period (Tomiyama and Komatsu 2006). There are two possible reasons for this relationship in sand lance in Ise Bay: the influence of prey availability, and the density-dependent effect. Regarding the former, the biomass of some copepods, which are the prey items of larval and juvenile sand lance, increased in cooler winter years in this bay (Nakata 2001). Regarding the latter, the growth rates of the age-0 group are negatively correlated with their population density (Nagoshi and Sano 1979).

Although the WTL gradually decreased as HDstd progressed (Fig. 5a), the rGL appeared to increase with later HDstd except in 2020 (Fig. 6). Similarly, DLstd showed that later-born individuals appeared to have a shorter larval stage (Fig. 7). This indicates that faster-growing individuals at a given temperature had a shorter larval stage. Accordingly, these results suggest that temperature may not be the only

Fig. 7 Relationship of the standardized difference between the actual and expected durations of the larval stage (DLstd) with the standardized hatch date (HDstd) from 2011 to 2014, 2019, and 2020. The solid lines indicate the generalized linear models fitted to the observed data



factor that influences individual growth rates and potential survival. A previous study attributes the significant relationship between hatch date and larval growth rate of *A. marinus* from Shetland waters to varying food intake, as the density of prey microzooplankton increased from the middle of the hatch date (Wright and Bailey 1996).

In the Seto Inland Sea, sand lance larvae can utilize a relatively wide variety of copepod eggs, nauplii, and copepodids (Mitsuzawa et al. 2017), suggesting that the timing of prey production is important for individual growth. If this is the case in the present study, the prey utilization of larvae may increase in the latter half of the HDstd; this may occur even when prey availability remains constant, because energetic demands decrease at lower temperatures (Buckley et al. 2004; Shelley and Johnson 2022).

On the other hand, rGJ did not vary significantly with HDstd in the present study but did differ significantly among sampling years (Fig. 8). This implies that the growth potential during the juvenile stage relative to the temperatures may reflect inter-annual variation in prey availability rather than the intra-annual variation. Compared to sand lance larvae, juveniles exhibit prey selectivity for *Calanus sinicus* and *Paracalanus* sp. in the Seto Inland Sea (Hashiguchi et al. 2021)—the biomass of which is higher in winter and spring (Uye et al. 1987; Nishikawa et al. 2023). The present results show that the growth rates of individuals were much faster in the juvenile stage (GJ) than in the larval stage (GL), even at similar temperatures. In *Ammodytes* spp., the size-related differences in vertical distribution and migration patterns are likely due to changes in anatomical structures and swimming abilities; moreover, such patterns in the post-larval and juvenile stages appear to be related to the corresponding patterns in their preferred copepod prey (Richards and Kendall 1973; Yamashita et al. 1985; Potter and Lough 1987; Jensen et al. 2003).

In 2012, the proportions of faster-growing (i.e., rGL $\geq$ 1) and shorter-duration (i.e., DLstd $\leq$ 0) larvae were particularly high, with 93.0% and 93.9%, respectively, observed throughout HDstd (Fig. 6, Fig. 7). This corresponds to the highest recruitment value and relatively higher RPE (Table 3). On the other hand, 2020 did not exhibit a significant relationship between rGL or DLstd and HDstd, and was marked by the lowest recruitment abundance and

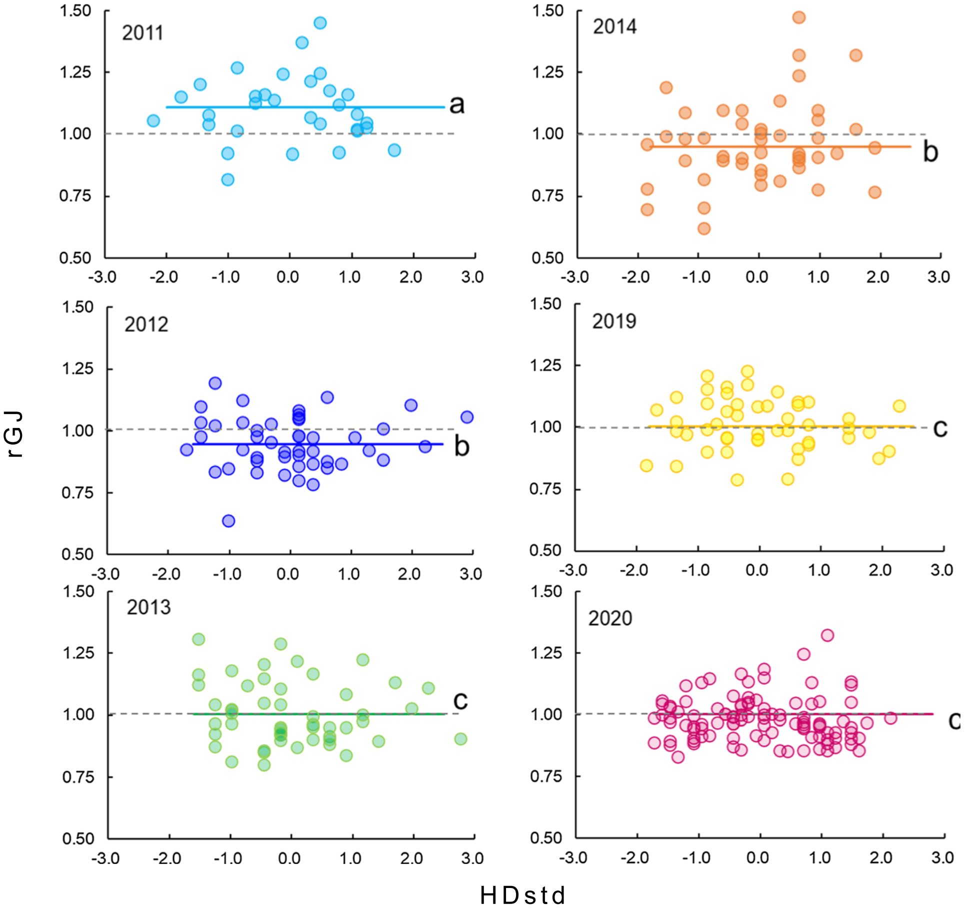


Fig. 8 Relationship between the relative growth rate in the juvenile stage (rGJ) and the standardized hatch date (HDstd) from 2011 to 2014, 2019, and 2020. The solid lines indicate the generalized linear models fitted to the observed data. Matching letters indicate a combination with significant differences ($p < 0.001$)

relatively lower RPE (Table 3). There appear to be positive relationships between recruitment abundance or RPE and the proportion of the occurrence of faster-growing (i.e., $rGL \geq 1$) and shorter-duration (i.e., $DLstd \leq 0$) larvae (Table 3). This relationship is notably reinforced when HDstd is factored into the analysis, underscoring the significance of hatch timing in understanding recruitment success. These findings suggest that the growth potential of individuals during the larval stage at a given temperature may be a significant determinant of survival until recruitment. This likely also corroborates the finding that rGJ and duration of the juvenile stage are independent of the variations in recruitment abundance or RPE (Figs. 8 and 9, Table 3).

Selection pressure from predators in the early life stages may be an important component influencing the survival rate and year-class strength of sand lance (Houde 2008; Leggett and Frank 2008). In Atlantic mackerel, the fast growth during the larval stage in surviving individuals reflects strong growth mortality that eliminates average individuals, which resulted in the lowest recruitment during the study period (Robert et al. 2007). Conversely, fast growth reflects favorable environmental conditions for growth and relaxed selective mortality—a combination that leads to the survival of average individuals and outstanding recruitment. As only commercially caught specimens (i.e., recruited fish) were used in the present study, it is unclear to what extent sand lance were subjected to selective pressure during the larval stage. However, if strong growth-selective mortality occurs in a given year, recruitment abundance or RPE may be negatively correlated with the proportion of individuals with higher growth rates relative to temperature. It is likely that the effect of selection pressure on recruitment abundance or RPE in this study is negligible. On the other hand, the positive correlation between recruitment and the proportion of faster-growing larvae found in this study also implies the possibility of density-independent growth, which may be inconsistent with the abovementioned findings in sand lance in Ise Bay (Nagoshi and Sano 1979).

In *Ammodytes* spp., prey availability during the larval stage could be a key for determining survival in the early stages of life and year-class strength in accordance with

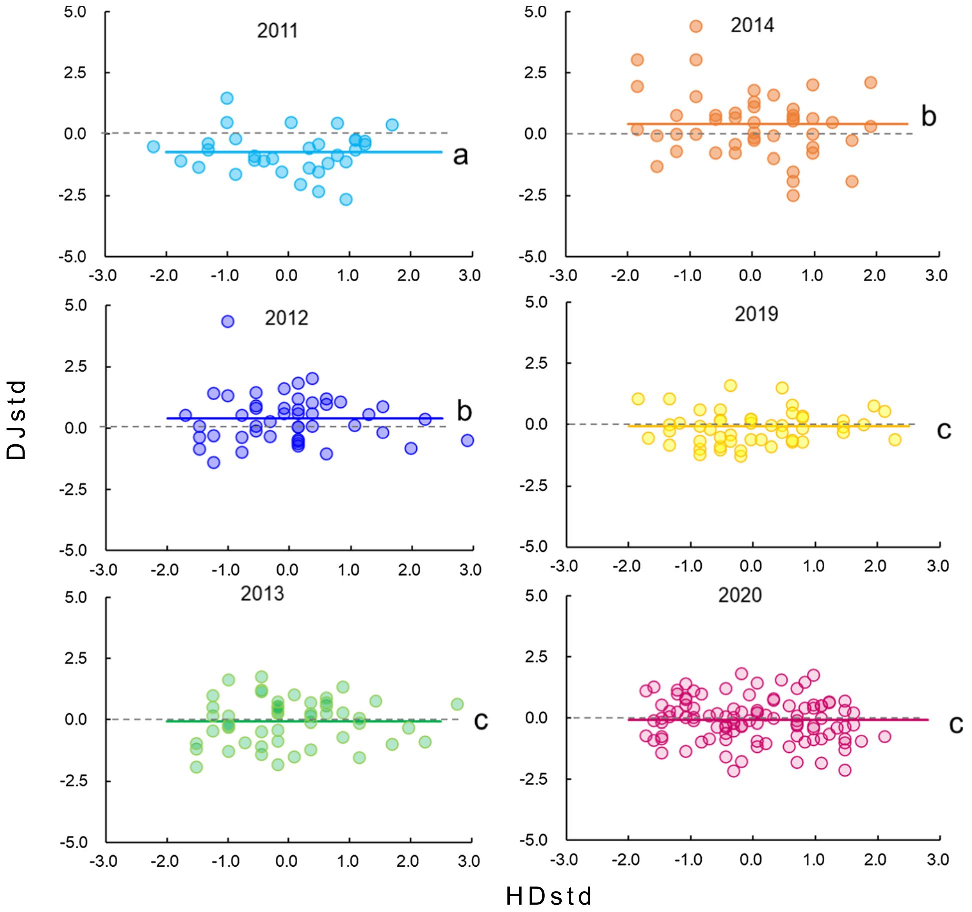


Fig. 9 Relationship of the standardized difference between the actual and expected duration of the juvenile stage (DJstd) with the standardized hatch date (HDstd) from 2011 to 2014, 2019, and 2020. The solid lines indicate the generalized linear models fitted to the observed data. Matching letters indicate a combination with significant differences ($p < 0.001$)

the match–mismatch hypothesis (Fortier et al. 1995; Arnott and Ruxton 2002; van Deurs et al. 2009; Gurkan et al. 2013; Régnier et al. 2017). For example, in *A. marinus* in the North Sea, year-class strength depends on the degree of synchrony between the hatching and egg production of *Calanus helgolandicus*, the most abundant copepod species (Régnier et al. 2017). In the eastern Seto Inland Sea, the biomass of prey zooplankton (i.e., copepods) for sand lance has decreased in the last several decades, likely because of decreased nutrient levels (Hashiguchi et al. 2021; Nishikawa et al. 2022). Similarly, the recent decline in the biomass of cool-water copepods in the central Seto Inland Sea, including *Calanus sinicus*, may be due to the influences of elevated temperature and decreasing levels of chlorophyll *a* (Yoneda et al. 2022). Thus, physical and biological environmental changes in the habitat of sand lance in the Seto Inland Sea would substantially impact their early survival and recruitment processes.

In conclusion, this study shows for the first time (to our knowledge) that later-born larvae seem to grow faster relative to the temperature experienced within a given season, and a larger percentage of faster-growing sand lance larvae (i.e., rGL $\geq$ 1) in a cohort at a given temperature is likely associated with higher recruitment abundance and RPE, although increased temperature leads to faster GL and shorter larval stage duration. Temperature had significant effects on growth rate and larval stage duration of individual fish, but these traits did not appear to be related to recruitment abundance and early survival in a given year. Additional research on the interaction between temperature and prey availability during the early stage of life of sand lance may assist in answering this question. In the Bisan Strait, the egg production of sand lance has decreased in recent years as a result of fewer older and more fecund individuals (Akai and Yoneda 2021). The estimated EPI was similar in 2019 and 2020, and lower than in previous years. However, there were marked differences in recruitment abundance and RPE in these years. In 2019 and 2020, temperatures during the early life stages of sand lance were higher than in other sampling years, whereas the percentage of faster-growing larvae differed among sampling years. This implies that the recent increase in temperature does not necessarily favor initial survival and that environmental changes in the early stages

Table 3 Proportions of larval stages with faster relative growth rates (rGL $\geq$ 1), shorter standardized difference between the actual and expected durations (DLstd $\leq$ 0), and proportions determined by HDstd for stages with rGL $\geq$ 1 and DLstd $\leq$ 0, the standardized hatch date (HDstd) to relative growth rates (rGJ), and the standardized difference between the actual and expected duration of the juvenile stage (DJstd), egg production index (EPI), recruitment abundance, and recruitment per EPI (RPE)

Year	Larval stages				Juvenile stages[III]				EPI $(-10)^3$	Recruitment abundance $(-10)^8$	RPE $(-10)^5$
	rGL $\geq$ 1		DLstd $\leq$ 0		rGJ		DJstd				
	(%)[I]	HDstd (%)[II]	(%)[I]	HDstd (%)[II]	Median estimate		Estimated mean				
2011	28.1	34.3	37.5	36.6	1.11	a	−0.74	a	14.0	29.2	2.1
2012	68.1	93.0	68.1	93.9	0.95	b	0.40	b	20.3	88.3	4.3
2013	43.1	24.9	51.0	27.2	1.00	c	−0.07	c	33.6	38.1	1.1
2014	43.5	41.4	47.8	50.3	0.95	b	0.40	b	13.2	69.9	5.3
2019	51.0	64.2	57.1	65.4	1.00	c	−0.07	c	5.6	42.8	7.7
2020	34.0	–	42.7	–	1.00	c	−0.07	c	5.3	12.4	2.3

For larvae: [I] rGL $\geq$ 1 and DLstd $\leq$ 0 (%) indicate the overall percentage of individuals with rGL $\geq$ 1 and DLstd $\leq$ 0, respectively. [II]The percentages of fish with rGL $\geq$ 1 and DLstd $\leq$ 0 by the HDstd (%) were calculated using a logistic model fitted to the cumulative frequency distribution of HDstd for each sampling year (Online Resource, Tables S2 and S3)

[III]For juveniles: As the relationships of HDstd with rGJ and DJstd were constant in each sampling year, a generalized linear model incorporating a Gaussian response distribution coupled with an identity link function linking means to the linear predictors was used to determine the differences in the dependent variables among samples collected in different sampling years. Models for rGJ were assessed in both their ln-transformed and untransformed state; the ln-transformed model was selected on the minimum conditional AIC. As a result, the model estimates represent values on a logarithmic scale. Applying an exponential function to these estimates converts them back to the original scale, yielding values that are closer to the median rather than the mean of the original data. Therefore, the term "estimated median" is used in the table to reflect this methodology. Due to the presence of negative values in DJstd, which cannot be ln-transformed, the untransformed model was used for DJstd. Matching letters indicate a combination with significant differences ($p < 0.001$)

of life may result in uncertainty when predicting recruitment against a background of declining egg production. Continued monitoring of the reproductive capacity (i.e., egg production) of spawning fish and the environmental conditions in early stages of life is essential to improving the accuracy of recruitment prediction and proper stock management of sand lance.

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Data Availability The data supporting the findings of this study are available from the corresponding author, NA, upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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