

Determinants of mean length at age of spring spawning herring off the coast of Hokkaido, Japan

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ABSTRACT: The stock of Hokkaido spring spawning herring *Clupea pallasii* collapsed in the middle of the 20th century. In the first half of the 20th century, large amounts of spawning herring were caught by set nets at coastal spawning grounds off the coast of Hokkaido, Japan. Using the catch data, we analyzed the mean length at age with respect to sea-surface temperature and density-dependent growth during the years 1910 to 1954 by generalized additive modeling (GAM). This stock is distributed at the southern boundary of the distribution range of Pacific herring, and we thus hypothesized that high temperatures have a negative effect on growth. Our study shows that length of Hokkaido spring spawning herring is highly dependent on growth during the first years of life and on temperatures preceding and during the feeding season. Higher temperatures during winter have a negative effect on growth. We found only weak indications of density-dependent growth in the stock of Hokkaido spring spawning herring.

KEY WORDS: *Clupea pallasii* · Hokkaido herring · Growth · GAM · Generalized additive modeling

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INTRODUCTION

The Hokkaido spring spawning (HSS) herring *Clupea pallasii* was a commercially important herring stock for Japan in the 19th and the first half of the 20th century. The catch by coastal set nets during the 3 mo spawning season was as high as 970 000 t at the end of the 19th century, but declined steadily in the first half of the 20th century, and the catch virtually disappeared in the mid-1950s (Hanamura 1963). A virtual population analysis (VPA) estimated that stock size fluctuated profoundly (Fig. 1a). The stock experienced the first remarkable decline in the early 1930s, but resurged after the end of the 1930s and reached another peak in the early 1940s. The stock again

declined precipitously in the second half of the 1940s, and the spawning run of adult herrings finally disappeared in the mid-1950s (Morita 1985). The stock collapsed and has not been able to rebuild to its previous strength.

Nagasawa (2001) and Tanaka (2002) showed that recruitment of this stock is negatively affected by increasing temperatures in coastal waters. Several studies from other herring stocks have shown a close link between growth and temperature (Heath et al. 1997, Ottersen et al. 2004, Rose et al. 2007). Since HSS herring are distributed at the southern boundary of the Pacific herring distribution range (Whitehead 1985, Froese & Pauly 2007), it seems likely that high temperatures can have a negative effect on growth. An

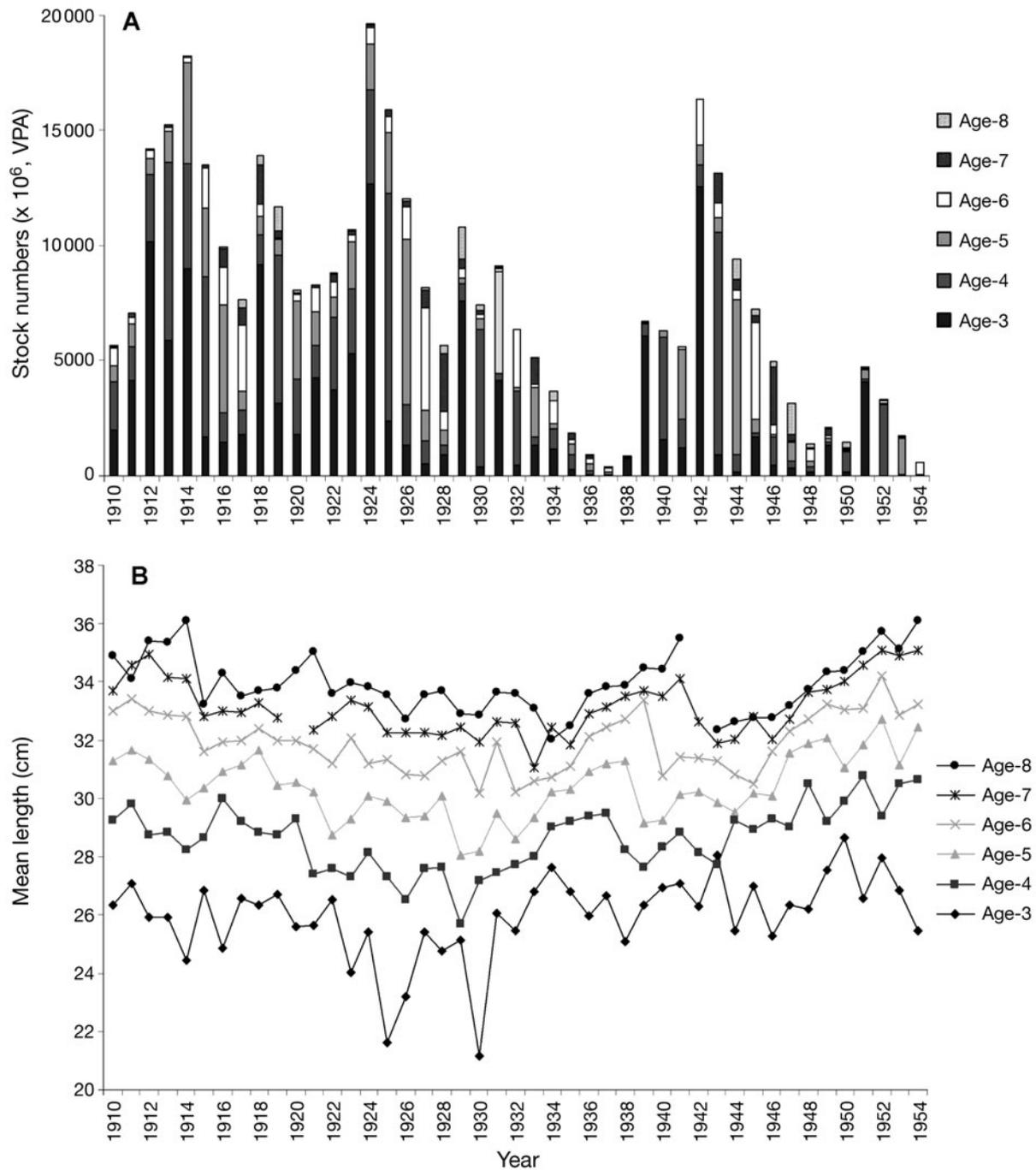


Fig. 1. *Clupea pallasii*. (A) Stock numbers at age of Hokkaido spring spawning (HSS) herring (virtual population analysis estimates). (B) Mean length at age of HSS herring caught at the spawning grounds

increase in temperature will increase the metabolism, which will lead to an increased demand for prey. If prey abundance is a limiting factor, this will result in density-dependent growth (i.e. lower growth at high abundances).

Mean length at age of HSS herring was analyzed using generalized additive models (GAM). Length

estimates were yearly mean values of herring caught at the spawning grounds along the coast of Hokkaido Island, Japan, during the period 1910 to 1954. The variation in mean length at age was analyzed with respect to 2 hypotheses: (1) length growth in HSS herring is density dependent, and (2) high water temperature has a negative effect on growth.

MATERIALS AND METHODS

HSS herring were caught by set nets in the spawning grounds along the coast of Hokkaido Island during the spawning season from April to June by commercial fishermen. Between 700 and 10 000 individual fish were sampled each year during the period 1910 to 1954. Total length, age determined by scale reading, and body weight are among the measurements that were collected for each individual. Mean lengths at age for each year were calculated based on data given by Kitahama (1955), who summarized numbers of fish in 1 cm length classes. Based on catch in numbers at age, first published by Hanamura (1963), we recalculated the mean length at ages 3 to 8 of HSS herring (Fig. 1b) and estimated stock numbers (Fig. 1a) by VPA (Gavaris 1988).

The stock size of HSS herring has varied extensively throughout the period with a collapse in the late 1930s and a final collapse in the 1950s. The mean lengths at age decreased slightly in the first half of the period (until the 1930s) and increased slightly in the second half (Fig. 1b). The annual variation was large, in general larger than the long-term trends, and the annual variation was largest for the youngest age-classes.

The temperature data were sea-surface temperatures (SST) from 2 areas in the Sea of Japan (Fig. 2) averaged over seasons and year. The SST data were composed of the historical Comprehensive Ocean-Atmosphere Data Set (COADS) and Kobe Collection in a 1° grid (latitude × longitude) for the area around Japan (20–45°N, 110–160°E) during the period of the last century (Tomosada 2005). Area 1 (41–44°N, 138–141°E) and Area 2 (44–47°N, 138–141°E) are approximately separated by Ishikari Bay, the main spawning and fishing grounds of HSS herring, and are generally considered to represent the effect of the Tsushima Warm Current and subarctic cold water, respectively. There were only small long-term trends in the temperature data in Area 1, with a slight decrease in the 1930s and early 1940s, and then an increase from the mid 1940s (Fig. 3a). The temperatures were 2 to 3° above the temperatures in Area 2. Area 2 showed a slight increase in temperatures in the beginning of the period (until the late 1920s) and then a slight decrease (Fig. 3b). For each area, we used SST data lagged by 1 yr and averaged by season (winter, spring, summer, and fall) or year. Each season lasts for 3 mo, starting with the winter season from January to March. The temperatures were lagged because they are thought to affect prey abundance and growth in the feeding season (summer) preceding the spawning in spring.

Our analyses were done using the generalized additive model (GAM) in the R (version 2.4.1) package

mgcv (Wood & Augustin 2002). Let $L_{a,t}$ be the mean length at age a at time t and let $\mathbf{E}_{j,t-1}$ be a vector of environmental variables at time $t-1$, where the subscript j identifies the single components. Let f , g , and h_j be nonparametric, smoothing functions specifying the effect of mean length the previous year, population abundance (N_{t-1}), and environmental forcing on the mean length at the following age a , respectively. The generalized additive formulation for mean length at age a then becomes:

$$L_{a,t} = \alpha_a + f(\bar{L}_{a-1,t-1}) + g(N_{t-1}) + \sum_j h_j(\mathbf{E}_{j,t-1}) + \varepsilon_t \quad (1)$$

The coefficient α_a is the intercept of the model equal to the average length at age a , and the term ε is a random error assumed to be normally distributed. Note that each smooth function is assumed to be centered (i.e. of 0 mean over the data) for model identifiability.

In our GAM analysis, length and year class strength at $t-1$, spawning stock abundance (SSN) in the age-3

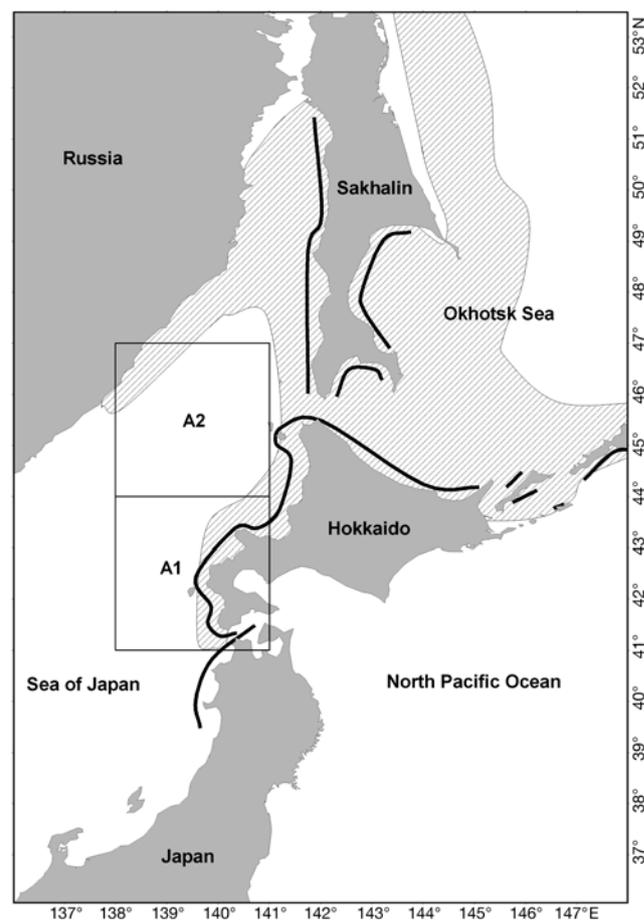


Fig. 2. *Clupea pallasii*. Distribution ranges (hatched area) and spawning grounds (thick lines) of Hokkaido spring spawning herring (redrawn from Nagasawa 2001). A1 and A2 show the areas where sea-surface temperatures (SST) were collected

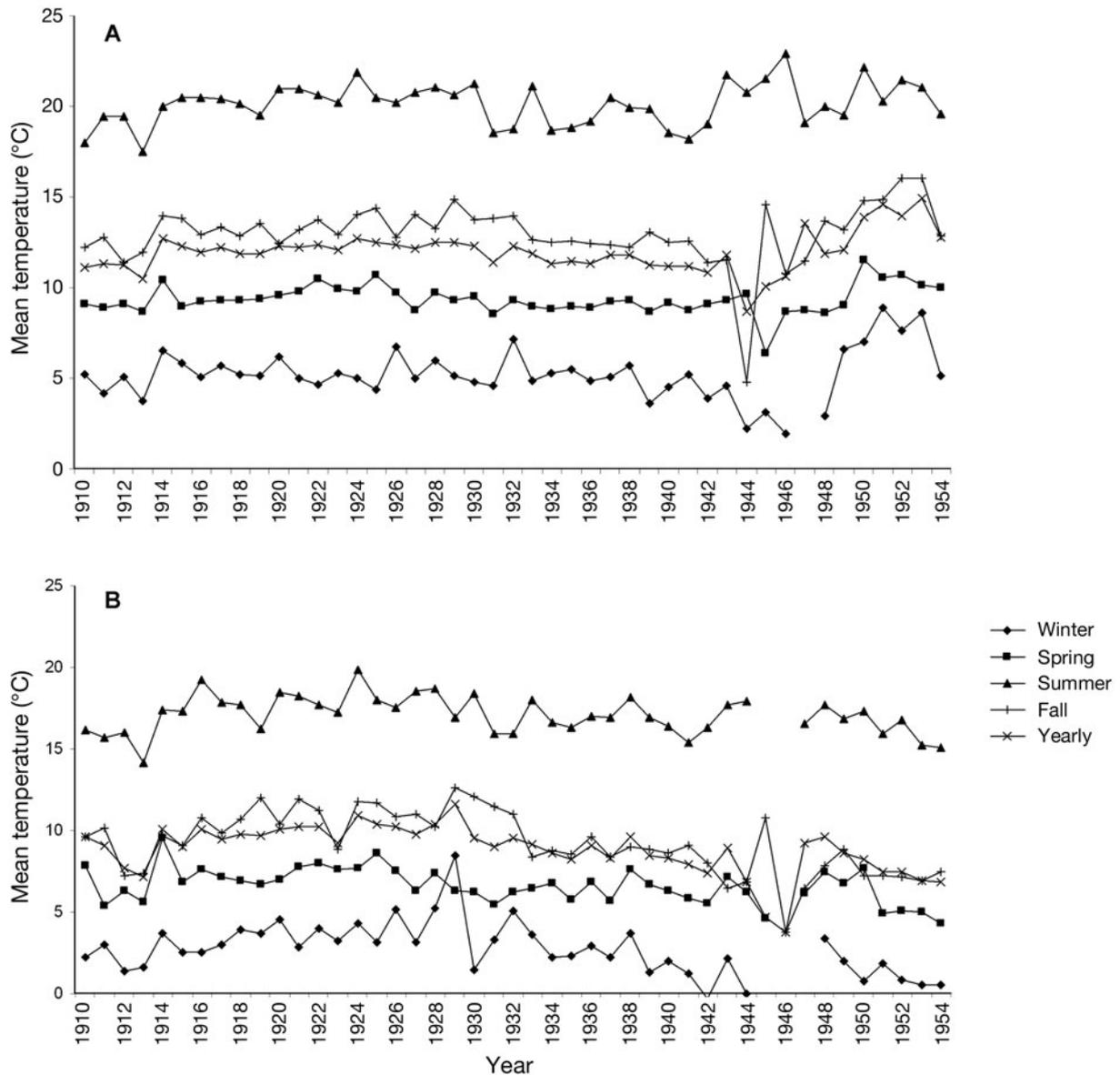


Fig. 3. Sea-surface temperature time-series from (A) Area 1 and (B) Area 2. Gaps represent missing data

model, were used as covariates in a start model. We then applied a forward selection strategy to decide which environmental covariates to retain in the final models. Specifically, we ran a GAM model including each of the environmental covariates (one at a time) considered relevant to a specific modeled age, and retained the most significant (lowest p-value) covariate. We then added covariates one at a time, using the same procedure, until the generalized cross validation score (GCV, a measure of the leave-one-out mean squared prediction error) was minimized or no additional covariates were significant. We used a forward selection strategy because of its advantages when the ratio between predictor values and potential covariates is small.

RESULTS AND DISCUSSION

The final GAM formulations are listed in Table 1, and the effects of the different covariates are visualized in Fig. 4. The GAM models indicated weak density-dependent growth, but this effect was only significant in the model of age-7. For age-4 to age-8, lengths in the previous year explained most of the variation, and high winter temperatures ($t-1$) in Area 2 had a negative effect. In general, the models performed quite well and explained most of the variation in mean lengths ($R^2 = 0.72$ to 0.87), except for age-3 ($R^2 = 0.60$).

Factors determining size at age are different in Pacific and Atlantic herring. Tanasichuk (1997) found that

size of age-3 recruits of the Pacific herring *Clupea pallasii* is negatively related to parental biomass. He interpreted this as a pre-recruit effect exerted in the first year of life. Toresen (1990) found that length at age of Norwegian spring spawning herring *C. harengus* in the 1950s with large spawning stock biomass (SSB) was substantially smaller than in the 1980s with reduced SSB. In the case of Norwegian herring, length at age-0 was not much different across the year classes examined, but increased later in life. Slow growth in strong year-classes was explained by both density-dependent growth in fjords and reduced growth due to the migration of juveniles to the cold Barents Sea (Toresen 1990). Hay (2001) reported that in the large 1977 year class of Pacific herring *C. pallasii* in British Columbia (Canada) and Alaska (USA), body length at age-4 and older fish was distinctly smaller than the neighboring year classes, but not at age-2, indicating that the growth deceleration occurred after first maturation.

In HSS herring, we found that the length at age is highly dependent on the length at the previous age. This indicates that growth early in life, before first maturation at age 3 or 4, largely determines the length at older ages, in contrast to Pacific herring along the west coast of northern North America (Hay 2001) and the Norwegian spring spawning herring (Toresen 1990). Our results also indicate weak density-dependent effects of year-class strength. A case similar to HSS herring was reported for the western North Pacific chub mackerel *Scomber japonicus*, where body lengths at age-1 and older were highly dependent on growth in the first year of life and negatively correlated with year-class strength (Watanabe & Yatsu 2004).

The effect of length in the models for age-5 and age-6 indicate compensatory growth (Fig. 4). Slow-growing year classes up to age-3 to age-4 tended to grow faster

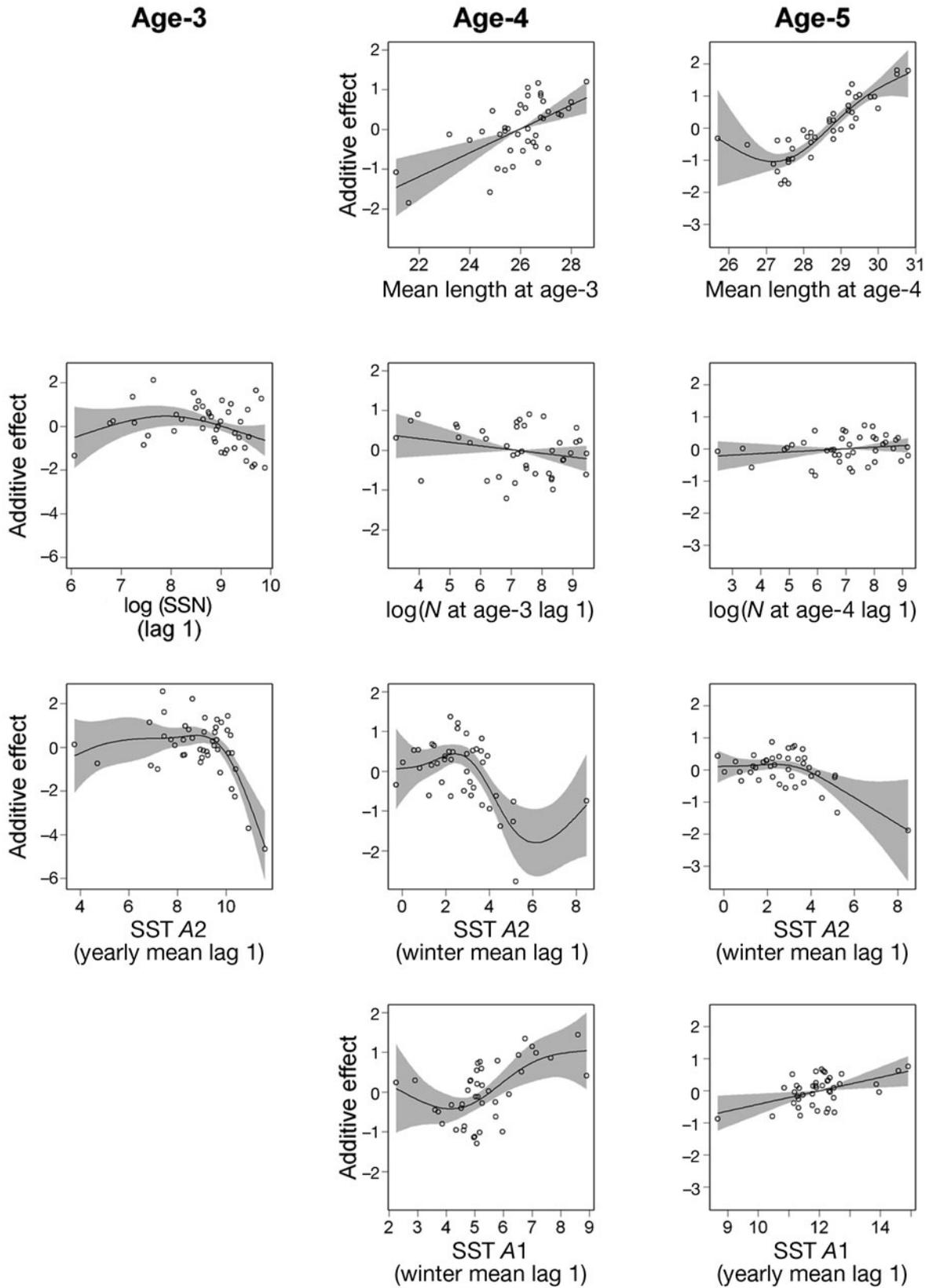
in the following years. Similar growth history is found in chub mackerel in the Kuroshio-Oyashio area in the western North Pacific (Watanabe & Yatsu 2004). This phenomenon may be explained by asymptotic growth trajectory in these fishes caused by a reduction in growth after maturation. However, in Norwegian spring spawning herring, length difference at age-4 do not decrease in older ages up to age-10 (Toresen 1990). Growth trajectories are asymptotic for fish in general, but the determination of finite body length may be different among fish species or populations.

Another important finding of our results in the HSS herring is that only a weak density-dependent effect was detected in growth. Limited food resources cause density-dependent growth, i.e. decreased growth at high abundances. The weak density-dependent growth in this stock is in contrast to Atlantic (Toresen 1990) and Pacific herring (Tanasichuk 1997, Hay 2001). Distinct density-dependent growth is also found in other small pelagic fishes in the western North Pacific, such as chub mackerel mentioned above and Japanese sardine *Sardinops melanostictus*. Body length in Japanese sardine is negatively correlated with total biomass, and length was sharply reduced at age-0 in the strong 1980 year class (Wada et al. 1995). In this study, we found only weak indications of density-dependent growth. Length at age-3 was partly influenced by the spawning stock abundance 1 yr before the given year-class first recruited to the spawning stock. However, the effect was weak and did not seem to be a major determinant of length at age-3. While we found some density-dependent effects in length at older ages, this does not seem to have large implications in the HSS herring ecology. We have no clear explanation for the ecological mechanism of this weak density-dependent growth in HSS herring. Density dependency in growth might be ecologically insignificant in this stock.

The winter temperature in Area 2 may have an indirect effect on growth through trophic interaction. We do not have historical time series data for zooplankton for the study area to show the relationship between zooplankton biomass and temperature in the first half of the 20th century. However, Japan Meteorological Agency oceanographic monitoring data for the Sea of Japan since 1965 indicate a correlation between increases in temperatures of the Japan Sea Proper Water (at depth from 500 to 2000 m) and declines in the dissolved oxygen (Minami et al. 1999, Ishikawa et al. 2003). These changes in physical

Table 1. *Clupea pallasii*. Final generalized additive modeling (GAM) formulations and R^2 (i.e. proportion of variance explained) of the best models for length (L) at age of Hokkaido spring spawning herring. SSN: spawning stock numbers, N : abundance at age, SST: sea-surface temperature. A1 and A2 = Area 1 and Area 2, respectively. Winter, spring, and yearly = the seasons that data are averaged over

Formulation	R^2 (%)
$L_{3,t} = \alpha_3 + g[\log(\text{SSN}_{t-1})] + h(\text{SST}_{A2\text{yearly},t-1}) + \epsilon_t$	60
$L_{4,t} = \alpha_4 + f(\bar{L}_{3,t-1}) + g[\log(N_{3,t-1})] + h_1(\text{SST}_{A2\text{winter},t-1}) + h_2(\text{SST}_{A1\text{winter},t-1}) + \epsilon_t$	74
$L_{5,t} = \alpha_5 + f(\bar{L}_{4,t-1}) + g[\log(N_{4,t-1})] + h_1(\text{SST}_{A2\text{winter},t-1}) + h_2(\text{SST}_{A1\text{yearly},t-1}) + \epsilon_t$	87
$L_{6,t} = \alpha_6 + f(\bar{L}_{5,t-1}) + g[\log(N_{5,t-1})] + h_1(\text{SST}_{A2\text{winter},t-1}) + h_2(\text{SST}_{A1\text{yearly},t-1}) + \epsilon_t$	84
$L_{7,t} = \alpha_7 + f(\bar{L}_{6,t-1}) + g[\log(N_{6,t-1})] + h(\text{SST}_{A2\text{winter},t-1}) + \epsilon_t$	72
$L_{8,t} = \alpha_8 + f(\bar{L}_{7,t-1}) + g[\log(N_{7,t-1})] + h_1(\text{SST}_{A2\text{spring},t-1}) + \epsilon_t$	75



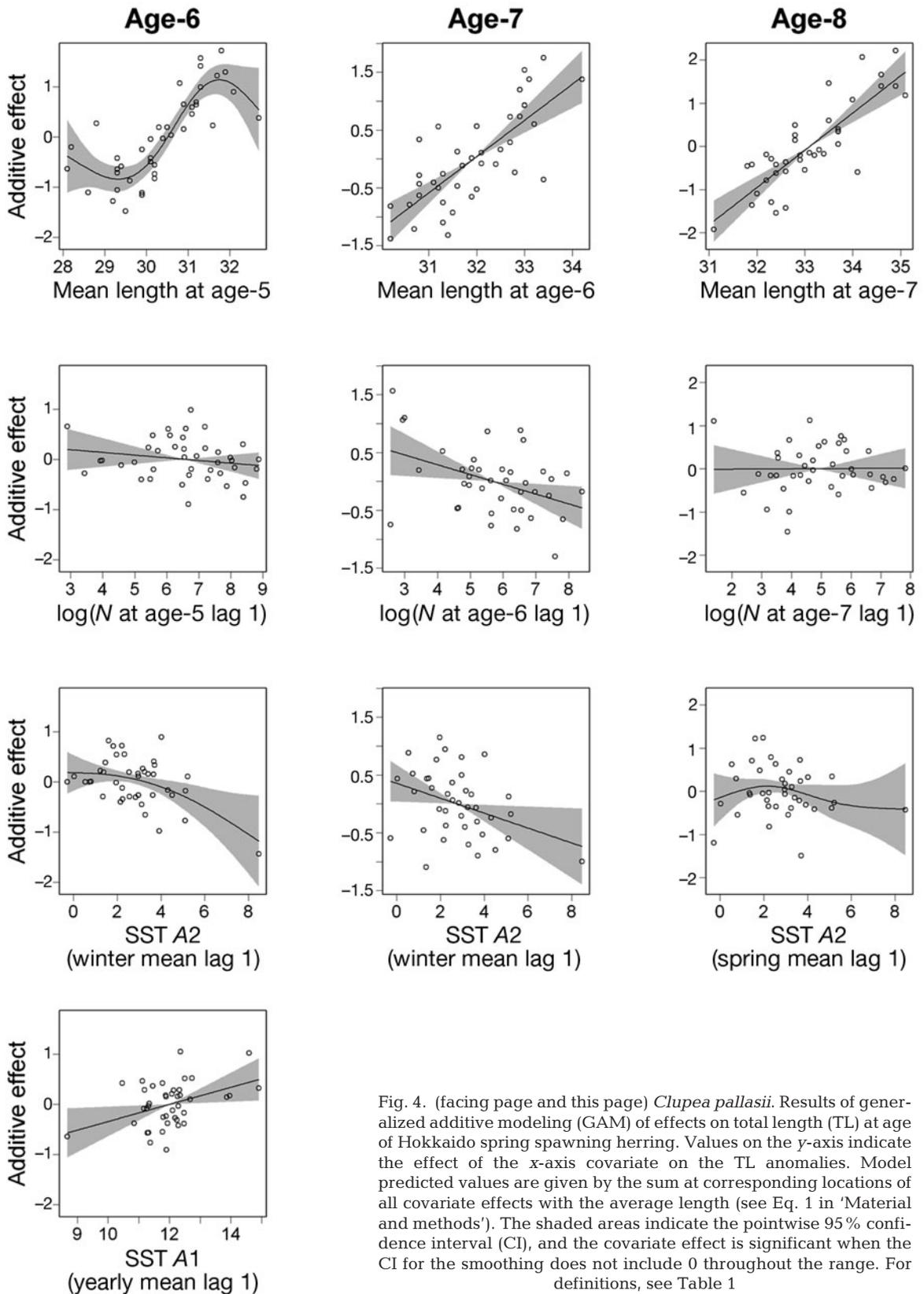


Fig. 4. (facing page and this page) *Clupea pallasii*. Results of generalized additive modeling (GAM) of effects on total length (TL) at age of Hokkaido spring spawning herring. Values on the y-axis indicate the effect of the x-axis covariate on the TL anomalies. Model predicted values are given by the sum at corresponding locations of all covariate effects with the average length (see Eq. 1 in 'Material and methods'). The shaded areas indicate the pointwise 95% confidence interval (CI), and the covariate effect is significant when the CI for the smoothing does not include 0 throughout the range. For definitions, see Table 1

and chemical components affect the biological process such as species composition of diatoms (Kubo & Ebara 1992). Variation in winter temperatures determine the mixed layer nutrient concentration and then affect the timing and magnitude of spring phytoplankton blooms (Chiba & Saino 2002, Yamada et al. 2004), which control the zooplankton production. The diet of herring consists mainly of zooplankton, and zooplankton production can have a profound effect on growth. Thus, the negative effects of increased temperatures may also be caused by a decrease in prey abundance at high temperatures, either through a decrease in prey abundance at high temperatures or through an increase in competition for food caused by higher prey demand at high temperatures to maintain the metabolism.

Water temperature may also have a direct effect on growth. Because HSS herring are found at the southern boundary of the Pacific herring distribution, an increase in temperature may have a negative effect on growth. Thus, the temperatures during spring and summer may have a direct negative effect on growth because increased temperatures will cause increased metabolism and less energy will be available for growth. The temperatures may also have a negative effect on the year-class survival and limit the southward migration, distribution, and fishing ground formation along the coast of Hokkaido (Nagasawa 2001, Tanaka 2002). European herring at the southern boundary such as the stock in the English Channel are also negatively affected by the temperature, while the northern stocks such as Norwegian herring respond positively to the increased water temperature (Ottersen et al. 2004).

We detected weak density dependence in length at age-3, and a large proportion of the variability in length at this age was determined by environmental factors (represented by SST in this study) independent of population density. Because of the large variability in the environment in the northern area of the western North Pacific, variability in vital parameters such as growth, mortality rates in early life history stages, and eventual recruitment tend to be large in these waters (Watanabe et al. 2003, Watanabe 2007). Juvenile HSS herring up to age at first maturation are considered to have experienced large inter-annual variations in environment in their spawning and nursery grounds in the northern Sea of Japan, the Sea of Okhotsk, and the Pacific waters off Hokkaido and the Kurile Islands (Ishida 1952). This seems to be reflected in the large variability in length at age-3 of this herring population. It is important to remember that these fish were sampled at the spawning grounds and thus only mature fish were sampled. The mean lengths at age-3 and to a certain degree age-4 are therefore positively biased since only the largest fish at these ages have matured and migrated to the spawning grounds in the coastal waters.

CONCLUSIONS

HSS herring are distributed at the southern boundary of the distribution range of Pacific herring, and we hypothesized that increasing temperatures would have a negative effect on their growth. Our results show that increasing temperatures preceding the feeding season had a negative effect on growth, supporting our hypothesis. We also hypothesized that growth in HSS herring is density dependent. However, our results did not support this hypothesis. Thus, most of the variability in length was explained by length the previous year, and the length of HSS herring was highly dependent on growth early in life.

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