Daily growth rate model of Japanese anchovy larvae *Engraulis japonicus* in Hiuchi-nada Sea, central Seto Inland Sea

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Received: 22 December 2011 / Accepted: 28 June 2012 / Published online: 31 July 2012
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Abstract In the present study, we developed a larval anchovy growth model in relation to sea temperature and food availability via food consumption and metabolic process terms, based on biological data from previous laboratory experiments and field surveys from 2003 to 2006 in Hiuchi-nada Sea, central part of Seto Inland Sea, Japan. To investigate when food shortage for larval anchovy and then recruitment failure occur in Hiuchi-nada Sea, anchovy food requirements were estimated by using the growth model, and we compared the food requirement with anchovy food availability. We applied an estimation method for growth model parameters, Hewett–Johnson p and Q_{10} , by minimizing the sum of squares of difference between mass-specific growth rates estimated by the models and those by otolith growth analysis. Parameter p was 0.86, slightly higher than typical values, and Q_{10} was 2.11, close to the value used for the biological model of larval northern anchovy. Food shortage for anchovy larvae did not occur in Hiuchi-nada Sea, although it was indicated that low food availability led to a low reproductive success rate. The newly developed growth model is considered optimal at present and useful to link environmental conditions and larval growth.

Keywords Anchovy larvae · Growth model · Hiuchi-nada Sea · Otolith growth analysis · Seto Inland Sea

Introduction

The Seto Inland Sea is well known for its high fish production [1]. Japanese anchovy *Engraulis japonicus* is an important commercial species, accounting for 34 % of the total fish production of 67×10^3 tons in the Seto Inland Sea in 2009. Hiuchi-nada Sea is located in the central part of the Seto Inland Sea between Kurushima Strait and Bisan Strait, a semi-enclosed narrow sea (Fig. 1). It has a size of about $50 \times 30 \text{ km}^2$ and an average depth of about 20 m, being a major spawning and fishing ground of Japanese anchovy. Total catch of anchovy in Hiuchi-nada Sea was 15×10^3 tons in 2005, accounting for 27 % of the total anchovy catch in the entire Seto Inland Sea. In this area, forecasting the degree of recruitment populations of *shirasu* (larval anchovy in Japanese, body length: ca. 20–35 mm) to the fishery stock is required for efficient exploitation [2]. Recruitment forecasting however has generally not been successful [3], because it is difficult to forecast the survival rate (or mortality rate) from the prerecruitment stage to the recruitment stage.

In recent years, individual-based models have been developed to understand how physical or biological factors affect larval anchovy survival or recruitment [4–6]. These models require algorithms for the growth process. In Zenitani et al. [2], the authors already found that the growth rate for larval anchovy was dependent on temperature, food availability, and larval size. However, a detailed growth model to describe the relation to sea temperature and food availability has not been developed for larval anchovy in the Seto Inland Sea. The aims of the present study are to (1) develop a larval anchovy growth model in relation to sea temperature and food availability via food consumption and metabolic process terms in Hiuchi-nada

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Fig. 1 Survey stations of plankton sampling in Hiuchi-nada Sea, Seto Inland Sea, Japan

Sea and (2) investigate if a food shortage for larval anchovy occurs and detect any recruitment failure of year-class in this study area. We developed a growth model for larval anchovy, based mainly on information from Japanese anchovy and northern anchovy *E. mordax*. In the past, anchovy were popular experimental organisms, cultured to understand their growth [7, 8], physiology [9], capacity to survive starvation [10], and swimming behavior [2, 11]. Yokota et al. [12] and Uotani [13] studied feeding behavior in the Seto Inland Sea or waters along the Pacific coast of Japan. These studies provide a rich source of information which can be used to formulate and calibrate the growth model. This manuscript presents a method for estimating parameters of the growth model by linking otolith growth analysis, laboratory experiments, and field survey data in Hiuchi-nada Sea.

A possible key factor in the regulation of anchovy population levels is the fluctuations in abundance of the copepod assemblage, and the crucial period for recruitment of anchovy in Hiuchi-nada Sea would be the period just before the anchovy recruitment to the *shirasu* fishery [14]. To investigate when food shortage for larval anchovy and recruitment failure occur in Hiuchi-nada Sea, anchovy food requirements were estimated by

using the growth model, and we compared the food requirement with anchovy food availability in Hiuchi-nada Sea.

Materials and methods

Otolith growth

The mass-specific growth rate of an individual anchovy *l* was determined by otolith growth analysis, as follows [2]:

Anchovy were sampled from commercial catches (seine net fishery) at Kanonji Port in Hiuchi-nada Sea (Fig. 1) on 18 July 2003, 6 July and 6 August 2004, 27 June 2005, and 24 June 2006. A subsample of 50–100 anchovy larvae and juveniles was taken randomly from each commercial catch and preserved in 99 % ethanol. Each fish was measured for standard length (SL) to the nearest 0.1 mm with digital calipers. Sagittal otoliths of the larvae and juveniles (30.2–44.6 mm SL in 2003, 37.4–64.5 mm SL in 2004, 17.7–33.0 mm SL in 2005, 23.7–32.0 mm SL in 2006) were dissected out, cleaned under a binocular dissecting microscope, and mounted on a glass slide with epoxy resin. Measurement of otolith daily increments was conducted

along core–posterior margin axis using the otolith measurement system (Ratoc System Engineering Inc., Tokyo, Japan) under a light microscope at 100–200× magnification.

When the relation between otolith radius and fish size is predictable, growth rates can be calculated based on otolith increment widths [2, 15–18]. According to previous experimental studies on Japanese anchovy, the daily growth increment is deposited at the start of external feeding, 3–4 days after hatching [8], and SL at completion of yolk absorption is 5.6 mm [19]. Daily age of each anchovy was calculated, therefore, as the number of rings plus 3. SL at each daily age was back-calculated by the biological intercept method [20, 21], with SL at the first deposition of the daily growth increment fixed at 5.6 mm as the biological intercept at the individual level. We assumed that the relationship of otolith radius $OR(l, m)$ (μm) and SL $[=L_a(l, m)]$ (mm) of individual anchovy l of the m th ring formation can be expressed by an allometric formula for the individual. Hence, $L_a(l, m)$ of each anchovy was back-calculated by substituting $OR(l, m)$ (μm) for $L_a(l, m)$ using the allometric relationship,

$$L_a(l, m) = a(l) \times OR(l, m)^{b(l)}, \quad (1)$$

where $a(l)$ and $b(l)$ are parameters determined for each anchovy by solving the two equations

$$L_a(l, 1) = a(l) \times OR(l, 1)^{b(l)} \quad (2)$$

and

$$L_a(l, m_{\max}(l)) = a(l) \times OR(l, m_{\max}(l))^{b(l)}, \quad (3)$$

where $m_{\max}(l)$ is the maximum number of rings of individual anchovy l , and $L_a(l, 1)$ of 5.6 mm, $OR(l, 1)$, $L_a(l, m_{\max}(l))$, and $OR(l, m_{\max}(l))$ are the SL at the first daily growth increment deposition, measured radius of the first daily ring, SL at sampling day $d_s(l)$, and measured radius at sampling day $d_s(l)$, respectively.

The relationship between body mass, $W_a(l, m)$ (mgC), and SL of Japanese anchovy larvae [22] has been found as

$$W_a(l, m) = 2.045 \times 10^{-4} \times L_a(l, m)^{3.385} \times 0.43, \quad (4)$$

where 0.43 is a multiplier to convert to carbon weight from dry weight [23].

The mass-specific growth rate $\hat{G}(l, m(i, l))$ (day^{-1}) for individual anchovy l at $m(i, l)$ th ring formation was estimated from the change in the back-calculated weight for individual anchovy l in plankton survey cruise i as

$$\hat{G}(l, m(i, l)) = \frac{W_a(l, m(i, l) + \Delta t) - W_a(l, m(i, l))}{\Delta t \times W_a(l, m(i, l))}, \quad (5)$$

$$m(i, l) = m_{\max}(l) - (d_s(l) - d_c(i)) \times \text{number of rings} \times \text{day}^{-1}, \quad (6)$$

where $d_c(i)$ is the first day of plankton survey cruise i . In our study, Δt is the period of time for a cruise, $\Delta t = 3$ days. The metamorphosing stage of Japanese anchovy, defined as the stage of guanine deposition on the peritoneal and trunk surface, occurs from 31 to 37 mm SL, while the juvenile stage occurs from ca. 40 mm SL [24]. Based on this study of anchovy development stages, we supposed a larval-stage SL range of 5.6–31.0 mm, and then estimated the growth rate in this range.

Plankton survey

From spring to early summer, in 2003–2006, a total of 14 daytime cruises of R.V. *Shirafuji maru*, National Research Institute of Fisheries and Environment of Inland Sea, were conducted to sample plankton at 13 stations over 4-day survey periods, as follows (Fig. 1; Table 1, Zenitani et al. [2]):

At each station, a hydrographic cast was made using a Niel Brown CTD (Cataumet, MA, USA) in 2003 and a compact CTD (ACL 208-PDK Alec Electronics, Kobe, Japan) in 2004–2006. Water samples for determining copepod nauplii density were collected with a 20-l Van Dorn water sampler (Rigo, Tokyo, Japan) from 10 m depth. Since previous studies in Seto Inland Sea [25, 26] have demonstrated that larval anchovies are distributed mainly in the 5–20 m depth strata, predominantly at 10 m depth, we selected 10 m as a representative depth.

For copepod nauplii abundance, 1 l of the water sample was filtered aboard with a cellulose nitrate membrane filter (pore size 5.0 μm ; Toyo Roshi Kaisha, Tokyo, Japan), and copepod nauplii on the filters were resuspended and preserved in 5–10 % formalin in a 10-ml test tube. After nauplii were stained by adding 0.1–0.2 ml Rose Bengal, they were enumerated on a counting plate. Body length was measured for all the nauplii.

Copepods (copepodites and adults) were collected with a plankton net (mouth diameter 0.45 m, length 1.95 m, mesh opening 100 μm , fitted with a Rigosha flowmeter; Rigo), which was pulled vertically from 2 m above the sea bottom to the surface. After the net was retrieved, the zooplankton were immediately preserved in 5–10 % formalin-sea water solution. Later the sample was split into 1/32–1/256 subsamples, from which copepods were enumerated under a stereoscopic microscope. To estimate the length–frequency distribution from cruise i , up to 100 copepods for each genus were randomly sorted from each sample and their prosome length was measured to the nearest 0.1 mm.

Table 1 Mean temperature, copepod nauplii abundance, small-size (0.25–0.50 mm prosome length) copepod abundance, and large-size (over 0.50 mm prosome length) copepod abundance in Hiuchi-nada Sea in 2003–2006

Cruise	Date	Mean temperature ($\pm$ SD) ($^{\circ}$ C)	Copepod nauplii mean concentration ($\pm$ SD) (10^3 individuals m^{-3})	Small-size copepods mean concentration ($\pm$ SD) (10^3 individuals m^{-3})	Large-size copepods mean concentration ($\pm$ SD) (10^6 individuals m^{-3})
1	21–24 May 2003	16.3 ± 0.5	33.2 ± 17.6	12.3 ± 37.4	3.4 ± 18.5
2	11–14 June 2003	19.0 ± 0.4	22.8 ± 12.9	19.8 ± 62.5	1.6 ± 8.8
3	27–30 June 2003	20.8 ± 0.8	25.1 ± 13.3	12.2 ± 36.9	2.2 ± 12.1
4	6–9 May 2004	15.9 ± 0.6	15.5 ± 9.4	11.3 ± 35.0	2.9 ± 15.8
5	18–21 May 2004	17.5 ± 0.6	23.8 ± 12.7	14.7 ± 44.8	2.2 ± 12.0
6	6–9 June 2004	19.8 ± 0.6	16.2 ± 9.0	4.5 ± 13.7	0.4 ± 2.0
7	1–4 July 2004	22.5 ± 0.7	18.9 ± 9.8	5.0 ± 15.5	1.1 ± 5.9
8	13–16 July 2004	24.3 ± 0.9	52.9 ± 17.8	20.9 ± 64.2	2.1 ± 11.1
9	9–12 May 2005	15.7 ± 0.6	23.0 ± 15.1	11.0 ± 34.1	2.4 ± 12.9
10	19–22 May 2005	16.7 ± 0.5	34.6 ± 20.5	13.3 ± 41.4	2.8 ± 15.1
11	6–9 June 2005	18.3 ± 0.5	38.3 ± 23.1	20.0 ± 61.2	3.6 ± 19.2
12	22–25 June 2005	20.4 ± 0.9	25.1 ± 13.3	19.8 ± 60.3	1.9 ± 10.1
13	23–26 May 2006	15.6 ± 0.6	15.2 ± 10.1	8.1 ± 24.5	2.4 ± 12.6
14	13–16 June 2006	18.4 ± 0.5	16.6 ± 9.7	10.4 ± 31.9	2.3 ± 12.2

We classified the copepods into three stages

$$j = \begin{cases} 1 & \text{nauplius stage (<0.25 mm in body length)} \\ 2 & \text{small-size stage (0.25–0.50 mm in prosome length, mode 0.37 mm)} \\ 3 & \text{large-size stage (> 0.50 mm in prosome length)} \end{cases} \quad (7)$$

We calculated the mean body length $L_c(i, 1)$ (mm) for a copepod nauplii from cruise i , and then the carbon content $W_c(i, 1)$ (mgC) was calculated from the mean body length as [27]

$$W_c(i, 1) = 1.51 \times 10^{-14} \times (L_c(i, 1) \times 10^3)^{2.94}. \quad (8)$$

Prosome length $L_c(i, j, k)$ (mm) of taxonomic group k of stage j ($=2, 3$) of copepod from cruise i was converted to body carbon weight using the length–carbon weight regression equation [23, 28, 29]

$$W_c(i, j, k) = 10^{-c(k)} \times 10^{-3} \times (L_c(i, j, k) \times 10^3)^{d(k)}. \quad (9)$$

$W_c(i, j, k)$ (mgC) is the carbon weight of taxonomic group k of stage j of copepod from cruise i . The taxonomic groups were $k = 1$, *Acartia*; $k = 2$, *Calanus*; $k = 3$, *Centropages*; $k = 4$, *Microsetella*; $k = 5$, *Oithona*; $k = 6$, *Paracalanus*; $k = 7$, others (*Corycaeus*, *Oncaea*, etc.). $c(k)$ and $d(k)$ are parameters of the taxonomic group k (Tables 2; Zenitani et al. [2]).

We set the mean length of stage 2 copepods, $L_c(i, 2, k)$, at 0.37 mm, and calculated the mean length $L_c(i, 3)$ (mm)

in stage 3 copepods and mean weight $W_c(i, j)$ (mgC) in stage 2 and 3 copepods by the following equations:

$$L_c(i, 3) = \frac{\sum_{k=1}^7 (L_c(i, j, k) \times A_c(i, j, k))}{\sum_{k=1}^7 A_c(i, j, k)}, \quad (10)$$

$$W_c(i, j) = \frac{\sum_{k=1}^7 (W_c(i, j, k) \times A_c(i, j, k))}{\sum_{k=1}^7 A_c(i, j, k)} \quad (j = 2, 3), \quad (11)$$

where $A_c(i, j, k)$ (10^3 individuals m^{-3}) is the mean abundance of taxonomic group k of stage j of copepod from cruise i .

Consumption

The mass-specific food consumption rate was determined by an individual-based model for each individual anchovy of given size at a temperature and abundance of prey as follows (Fig. 2; Zenitani et al. [2]):

Copepods are the main prey items for anchovy larvae. At the first feeding stage, larval anchovy eat mainly

Table 2 Parameters of regression equation of carbon weight against length for copepods collected in the Seto Inland Sea

k	Taxonomic group	$c(k)$	$d(k)$
1	<i>Acartia</i>	8.51	3.08
2	<i>Calanus</i>	7.00	2.64
3	<i>Centropages</i>	8.19	2.97
4	<i>Microsetella</i>	5.58	1.95
5	<i>Oithona</i>	3.90	1.13
6	<i>Paracalanus</i>	8.45	3.13
7	Others (<i>Corycaeus</i> , <i>Oncaea</i> , etc.)	8.37	3.07

naupliar copepods, then with increasing size, the larvae eat copepodites and adult copepods [12, 30]. The food availability $C_c(l, m(i, l))$ (mgC day⁻¹) of individual anchovy l on copepods at $m(i, l)$ th ring formation was calculated as

$$C_c(l, m(i, l)) = \sum_{j=1}^3 (E_m(i, j, l) \times W_c(i, j)), \quad (12)$$

where $E_m(i, j, l)$ is the number of encounters between stage j copepods and individual anchovy l that resulted in successful capture of stage j copepods during cruise i . The number of encounters $E(i, j, l)$ (day⁻¹) between stage j copepods and individual anchovy l in cruise i was based on the Gerritsen and Strickler [31] model for randomly moving organisms in a three-dimensional space, such that

$$E(i, j, l) = \begin{cases} \pi \times D_E \times C_E \times A_c(i, j) \times R_T(i, j, l)^2 \\ \quad \times \left(\frac{3 \times V_a(i, l)^2 + V_c(j)^2}{3 \times V_a(i, l)} \right) \\ \quad \text{for } V_a(i, l) \geq V_c(j) \\ \pi \times D_E \times C_E \times A_c(i, j) \times R_T(i, j, l)^2 \\ \quad \times \left(\frac{3 \times V_c(j)^2 + V_a(i, l)^2}{3 \times V_c(j)} \right) \\ \quad \text{for } V_c(j) > V_a(i, l), \end{cases} \quad (13)$$

where D_E is the proportion of daylight hours in a day (12/24 h), C_E is a conversion factor (8.64×10^{-4} s day⁻¹), $A_c(i, j)$ (individuals m⁻³) is the abundance of stage j copepods from cruise i ,

$$A_c(i, j) = \sum_{k=1}^7 A_c(i, j, k), \quad (14)$$

and $R_T(i, j, l)$ (mm) is the total encounter radius. $V_a(i, l)$ (mm s⁻¹) and $V_c(j)$ (mm s⁻¹) are the swimming speeds of individual anchovy l in cruise i and stage j copepods, respectively. The total encounter radius was assumed to be equal to the sum of the mean encounter radius $R_c(i, j)$ (mm) of stage j copepods and the mean encounter radius $R_a(i, l)$

(mm) of individual anchovy l in cruise i , as Bailey and Batty [32] estimated,

$$R_T(i, j, l) = R_c(i, j) + R_a(i, l), \quad (15)$$

$$R_c(i, j) = \frac{2 \times L_c(i, j)}{\pi^2}, \quad (16)$$

$$R_a(i, l) = \frac{2 \times L_a(l, m(i, l))}{\pi^2}. \quad (17)$$

The swimming speed $V_a(i, l)$ (mm s⁻¹) of individual anchovy l in cruise i was calculated as

$$V_a(i, l) = L_a(l, m(i, l)) \times (0.076 \times T(i) - 0.52), \quad (18)$$

where $T(i)$ (°C) is the mean water temperature at 10 m depth in cruise i in Hiuchi-nada Sea (Zenitani et al. [2]).

The average swimming speed of the copepod *Temora longicornis* was 1.5 mm s⁻¹ for nauplii and young copepodid stage (<0.4 mm in body length), about 5 mm s⁻¹ in female adult stage, and 9 mm s⁻¹ in male adult stage [33]. According to Yen [34], *Euchaeta rimana* has a typical swimming speed of roughly 7 mm s⁻¹. We assumed that the swimming speed in the nauplii, small copepods, and large copepods was 1.5, 1.5, and 7 mm s⁻¹, respectively.

The number of encounters between stage j copepods and individual anchovy l in cruise i , in which individual anchovy l successfully captured stage j copepods, was determined from a binomial distribution $B_N(E(i, j, l), P(i, j, l))$, and the mean number of encounters $E_m(i, j, l)$ (day⁻¹) is

$$E_m(i, j, l) = E(i, j, l) \times P(i, j, l), \quad (19)$$

where $P(i, j, l)$ is the capture success probability of individual anchovy l for stage j copepods in cruise i

$$P(i, j, l) = \begin{cases} 1 & \text{for } L_{\min}(i, l) \leq L_c(i, j) \leq L_{\max}(i, l) \\ 0 & \text{for } L_c(i, j) < L_{\min}(i, l) \text{ or } L_{\max}(i, l) < L_c(i, j). \end{cases} \quad (20)$$

The minimum and maximum length of copepods that anchovy larvae were able to capture, $L_{\min}(i, l)$ (mm) and $L_{\max}(i, l)$ (mm), were

$$L_{\min}(i, l) = \begin{cases} 0.15 & \text{for } 5.6 \text{ mm} \leq L_a(l, m(i, l)) < 9.0 \text{ mm} \\ 0.20 & \text{for } 9.0 \text{ mm} \leq L_a(l, m(i, l)) \end{cases} \quad (21)$$

and

$$L_{\max}(i, l) = 0.434 \times \exp(0.105 \times L_a(l, m(i, l))), \quad (22)$$

after Fig. 5-1 in Yokota et al. [12] and Fig. 6 in Uotani [13].

The mass-specific food consumption rate $C(l, m(i, l))$ (day⁻¹) of individual anchovy l on copepods at $m(i, l)$ th ring formation is defined as a function of feeding rate for copepods and a proportionality constant parameter, Hewett-Johnson p value [35], having values of zero to one.

Table 3 Back-calculated mass-specific growth rate and food availability of anchovy in Hiuchi-nada Sea in 2003–2006

Cruise	Date	Sampling or back-calculation	Mass-specific growth rate as weight increment per unit weight ($\pm$ SD) (day^{-1})	Mass-specific food availability per unit weight ($\pm$ SD) (day^{-1})	Back-calculated SL ($\pm$ SD)	Ratio of food availability to minimum food requirement, λ	Sample size
1	21–24 May 2003	Back-calculation	0.27 ± 0.05	0.72 ± 0.10	12.0 ± 2.2	6.82	5
2	11–14 June 2003	Back-calculation	0.17 ± 0.11	0.34 ± 0.07	18.4 ± 4.8	3.30	38
3	27–30 June 2003	Back-calculation	0.10 ± 0.06	0.31 ± 0.04	24.0 ± 4.2	3.07	50
	18 July 2003	Sampling					58
4	6–9 May 2004	Back-calculation	0.16 ± 0.09	0.23 ± 0.06	17.5 ± 5.1	2.80	9
5	18–21 May 2004	Back-calculation	0.15 ± 0.08	0.23 ± 0.05	19.7 ± 5.5	2.66	20
6	6–9 June 2004	Back-calculation	0.17 ± 0.11	0.45 ± 0.09	18.8 ± 5.9	4.22	42
7	1–4 July 2004	Back-calculation	0.09 ± 0.03	0.14 ± 0.01	26.7 ± 4.0	1.27	18
	6 July 2004	Sampling					14
8	13–16 July 2004	Back-calculation	0.09 ± 0.04	0.36 ± 0.01	28.7 ± 1.3	3.03	6
	6 August 2004	Sampling					50
9	9–12 May 2005	Back-calculation	0.26 ± 0.17	0.51 ± 0.26	11.8 ± 6.3	4.97	2
10	19–22 May 2005	Back-calculation	0.27 ± 0.15	0.44 ± 0.11	12.0 ± 3.6	4.05	18
11	6–9 June 2005	Back-calculation	0.13 ± 0.09	0.47 ± 0.10	18.6 ± 4.4	4.90	46
12	22–25 June 2005	Back-calculation	0.07 ± 0.03	0.24 ± 0.03	25.3 ± 4.4	2.55	49
	27 June 2005	Sampling					50
13	23–26 May 2005	Back-calculation	0.18 ± 0.06	0.22 ± 0.04	12.6 ± 3.2	2.24	15
14	13–16 June 2006	Back-calculation	0.09 ± 0.02	0.23 ± 0.01	22.3 ± 1.8	2.56	98
	24 June 2006	Sampling					98

$$C(l, m(i, l)) = p \times C_c(l, m(i, l)) \times W_a(l, m(i, l))^{-1}. \quad (23)$$

Metabolic

In the growth model of larval northern anchovy, the metabolic rate, assumed as a function of an organism's body mass and temperature, is

$$R = 0.187 \times W_d^{0.834} \times \exp\left(\frac{\ln(Q_{10})}{10} \times (T - 16)\right), \quad (24)$$

where R ($\mu\text{g day}^{-1}$) is the metabolic rate, W_d (μg) is dry body weight, Q_{10} is defined as the increase in the rate of a physiological process resulting from a 10 °C increase in temperature, and T (°C) is temperature [36]. We assumed a simple and standard formulation for the mass-specific metabolic rate $U(l, m(i, l))$ (day^{-1}) of individual anchovy l at $m(i, l)$ th ring formation of

$$U(l, m(i, l)) = 0.187 \times \left(W_a(l, m(i, l)) \times \frac{10^3}{0.43}\right)^{0.834-1} \times \exp\left(\frac{\ln(Q_{10})}{10} \times (T(i) - 16)\right), \quad (25)$$

where $10^3/0.43$ is a multiplier to convert to carbon weight from dry weight. Urtizborea et al. [36] used the same Q_{10} (=2.2) as in bay anchovy *Anchoa mitchilli* larvae [37].

We estimated Q_{10} by the data fitting method (see “[Estimation of parameters](#)”).

Estimation of parameters

The mass-specific growth rate of an individual for nonre-producing fish is predicted as the weight increment per unit weight per time and defined by the following equation [38]

$$G = C - (M + F + E), \quad (26)$$

where the growth G over a time period is the difference between energy gained through food consumption C and the sum of energy costs and losses through metabolism M , egestion F , and excretion E . Metabolic costs are represented by standard metabolism U and the cost of dynamic action SDA

$$M = U + \text{SDA}, \quad (27)$$

as in Hansen et al. [39]. Values of F , E , and SDA in both the original and modified model were determined as

$$F = 0.104 \times C, \quad (28)$$

$$E = 0.068 \times (C - F), \quad (29)$$

and

Fig. 2 Flow diagram of the anchovy food availability calculation. Arrows indicate flow of data calculation

$$SDA = 0.172 \times (C - F). \quad (30)$$

Substituting Eqs. 27–30 into Eq. 26,

$$G = 0.68 \times C - U. \quad (31)$$

We assumed that the predicted mass-specific growth rate of each individual anchovy had an error term z , with a normal distribution

$$G(l, m(i, l)) = 0.68 \times C(l, m(i, l)) - U(l, m(i, l)) + z, \quad (32)$$

$$z \sim N(0, \sigma^2), \quad (33)$$

where $N(0, \sigma^2)$ is a normal distribution with mean zero and variance σ^2 .

In the model, p and Q_{10} were estimated by minimizing the sum of squares

$$SS(p, Q_{10}) = \sum_i \sum_l (G(l, m(i, l)) - \hat{G}(l, m(i, l)))^2. \quad (34)$$

The least-squares minimization was performed by the quasi-Newton method in Solver add-in software for MS-Excel (Microsoft Co. Ltd.). The least-squares minimization procedure was stopped if either of the two following conditions was satisfied:

- More than 1000 iterations were attempted, or
- The sum of squared residuals changed by less than 0.01 % between iterations.

Confidence intervals of the estimators were calculated through a likelihood ratio test. $\Theta = (\theta_1, \theta_2) = (p, Q_{10})$ is a parameter vector, $\hat{\Theta} = (\hat{p}, \hat{Q}_{10})$ is the estimated parameter vector which minimizes $SS(p, Q_{10})$, and $\Theta_m(\Theta_1 = (\theta_1, \hat{\theta}_2) = (p, \hat{Q}_{10}), \Theta_2 = (\hat{\theta}_1, \theta_2) = (\hat{p}, Q_{10}))$ is the parameter vector which minimizes $SS(p, Q_{10})$ with respect to the parameters except θ_m . The confidence interval for a certain parameter θ_m was given as the region which satisfied the inequality

$$2 \times \ln \left(\frac{L(\hat{\Theta})}{L(\Theta_m)} \right) \leq \chi^2(0.95, 1), \quad (35)$$

where L is the likelihood:

$$\ln(L(\Theta)) = -\frac{n}{2} \times \ln(2 \times \pi \times \sigma^2) - \frac{1}{2 \times \sigma^2} \times SS(p, Q_{10}), \quad (36)$$

and $\chi^2(0.95, 1)$ is the 95 % value of the χ^2 distribution with one degree of freedom.

Food shortage

Supposing that the zero growth rate state was under the minimum food requirement condition, setting the left-hand side of Eq. 31 to zero, the minimum food requirement of anchovy $C_{\min}$ (mgC day⁻¹) was calculated by

$$C_{\min} = 0.187 \times \left(W_a \times \frac{10^3}{0.43} \right)^{0.834} \times \exp \left(\frac{\ln(Q_{10})}{10} \times (T - 16) \right) \times \frac{0.43 \times 10^{-3}}{0.68 \times p}, \quad (37)$$

where W_a (mgC) is the body mass of an individual anchovy of body length L_a calculated by Eq. 4. If the food availability C_c (mgC day⁻¹) is evaluated, then we can judge whether the anchovy was under food shortage or not by using the ratio of C_c to $C_{\min}$, namely

$$\lambda = \frac{C_c}{C_{\min}} = \begin{cases} < 1 & \text{(as food shortage)} \\ \geq 1 & \text{(as not food shortage)} \end{cases} \quad (38)$$

We calculated λ from the average mass-specific food availability, body length, and temperature for each cruise and investigated whether a food shortage for anchovy larvae occurred or not in Hiuchi-nada Sea in 2003–2006.

Results

We could carry out back-calculation of the anchovy mass-specific growth rate, mass-specific food availability, and

Table 4 Estimated parameter values and 95 % confidence intervals (in parentheses) for the growth rate model equation

Parameters	σ^2	Log (L)	Sample size
p	Q_{10}		
0.86 (0.83–0.89)	2.11 (1.49–2.85)	0.0052	505
			416

SL in cruise 1–3 in 2003, 4–8 in 2004, 9–12 in 2005, and 13–14 in 2006 (Table 3). The range of average mass-specific growth rate, food availability, and SL was 0.07–0.27, 0.14–0.72 day⁻¹, and 11.8–28.7 mm, respectively. The estimated growth model parameters p and Q_{10} , their confidence intervals, the growth rate variance σ^2 , and the lognormal likelihood are summarized in Table 4. The goodness of fit between $\hat{G}(l, m(i, l))$ and

$$\begin{aligned}
 G(l, m(i, l)) &= 0.68 \times p \times C_c(l, m(i, l)) \times W_a(l, m(i, l))^{-1} \\
 &\quad - 0.187 \times \left(W_a(l, m(i, l)) \times \frac{10^3}{0.43} \right)^{0.834-1} \\
 &\quad \times \exp\left(\frac{\ln(Q_{10})}{10} \times (T(i) - 16)\right) \\
 &= 0.58 \times C_c(l, m(i, l)) \times W_a(l, m(i, l))^{-1} \\
 &\quad - 0.187 \times \left(W_a(l, m(i, l)) \times \frac{10^3}{0.43} \right)^{0.834-1} \\
 &\quad \times \exp\left(\frac{\ln(2.11)}{10} \times (T(i) - 16)\right) \quad (39)
 \end{aligned}$$

was significantly high (Fig. 3; $r^2 = 0.36$, $P < 0.001$). Regression analysis of predicted versus observed growth rates yielded a slope not significantly different from 1.0 (t test, $P < 0.05$). A plot of the difference between the observed and predicted mass-specific growth rate $\hat{G} - G$ against the back-calculated anchovy length and mass-specific food availability is shown in Fig. 4. The difference tends to decrease with increasing length and mass-specific food availability,

$$\hat{G} - G = -0.11 \times \ln(\text{SL}) + 0.33 \quad (r^2 = 0.23, P < 0.001), \quad (40)$$

$$\hat{G} - G = -0.045 \times \ln\left(\frac{C_c}{W_a}\right) - 0.021 \quad (r^2 = 0.43, P < 0.001). \quad (41)$$

The range of λ was 3.07–6.82 in 2003, 1.27–4.22 in 2004, 2.55–4.97 in 2005, and 2.24–2.56 in 2006. Food shortage for anchovy larvae did not occur, although λ in cruise 7 was close to the food shortage criteria value (Table 3).

Discussion

In this study, the estimated Q_{10} value was close to the value for bay anchovy larvae. Kono et al. [10] reared larvae for

Fig. 3 Goodness of fit between observed mass-specific growth rate estimated from otolith analysis and predicted mass-specific growth rate calculated from model of anchovy

up to 9 days after the first feeding stage at 20 and 25 °C. At 20 °C, the protein weight of larvae at 0, 2, and 3 days after first feeding day was 5.1, 3.8, and 2.8 µg, respectively, and at 25 °C, the weight of larvae at 0 and 2 days after first feeding day was 4.9 and 3.2 µg, respectively (after Fig. 4 in Kono et al. [10]). The mass-specific metabolic rate was calculated by the average decreasing rate in protein weight of unfed larvae reared at 20 and 25 °C. The mass-specific metabolic rate at 20 °C and at 25 °C was ((5.1 – 3.8 µg)/2 days/5.1 µg + (5.1 – 2.8 µg)/3 days/5.1 µg)/2 = 0.14 day⁻¹ and (4.9 – 3.2 µg)/2 days/4.9 µg = 0.17 day⁻¹, respectively. Calculating the mass-specific metabolic rate by using the second term on the right-hand side of Eq. 39, the rate of 5.6-mm larvae at 20 and 25 °C was 0.13 and 0.18 day⁻¹, respectively. The metabolic rate model adopted in this study should be appropriate, since the difference between the predicted and experimental value was small.

Most bioenergetics models for fish have indicated that feeding rates, i.e., Hewett–Johnson p values, are around 0.3–0.4 [40–42]. Urtizbera et al. [36] assumed that p of northern anchovy increases from 0.42 to 0.78, proportionally to body mass. In our model, the estimated p value, 0.86, was slightly higher than the typical value range. Brylawski and Miller [42] indicated that Hewett–Johnson p values estimated for the blue crab *Callinectes sapidus* were different under different rearing conditions. Laboratory-reared crabs may have a low Hewett–Johnson p value ($p = 0.067$) because the food quality is much higher than in nature ($p = 0.35$). Higher p than the typical value indicates that the food quality for anchovy larvae in Hiuchi-nada Sea was lower than that for northern anchovy. However, this conclusion is not appropriate, since we could

Fig. 4 Difference between the predicted and observed mass-specific growth rate against back-calculated anchovy length and mass-specific food availability

not provide the “true value” of food availability for anchovy larvae in Hiuchi-nada Sea. Yamashita et al. [43] indicated that the naked dinoflagellates *Gyrodinium instriatum* and *Gymnodinium sanguineum* play a supplementary role under natural conditions of low microzooplankton density to sustain better survival and growth of first-feeding larval anchovy. Copepods outnumbered the meso- and macrozooplankton community in Hiuchi-nada Sea, with average compositions of about 87–100 and 53–71 % in April and June [44], the relative importance of copepods in this area being high, while copepod nauplii were less numerous in the microzooplankton (tintinnids, naked ciliates, copepod nauplii, etc.) community in Hiuchi-nada Sea in April and June [45]. This suggests that prey organisms other than copepod nauplii are important for survival and growth of first-feeding anchovy larvae, too. In our modeling analysis, anchovy was assumed to eat only copepods, therefore the food availability for anchovy may

be an underestimation. Moreover, our plankton survey did not consider the vertical distribution of copepod. When integrated over large spatial scales, estimates of prey abundance are generally considered to underestimate the effective concentrations of prey available to fish larvae [46]. We concluded that the estimation of food availability depends on the selected survey method and target prey organisms. In this study, the Hewett–Johnson p value was just a proportional constant value and not an assimilation rate. The underestimated food availability will lead to a higher estimated Hewett–Johnson p value, since there is a trade-off relationship between food availability and Hewett–Johnson p value. This is the main cause of the high estimated Hewett–Johnson p value in this study. Moreover, the growth model in this study underestimates the growth rate for smaller fish during the first-feeding stage or for low food availability (Fig. 4), and does not work well for larvae with SL smaller than about 10 mm. The main cause might be underestimation of food availability for smaller anchovy due to the exclusion of microzooplankton other than copepod nauplii. However, work on identification of microzooplankton other than copepod nauplii requires experience and is time consuming. To evaluate the survival or food condition of anchovy larvae during the first-feeding stage, we recommend that the 0 % growth criterion for RNA:DNA ratio be calculated against temperature [10].

The reproductive success rate (recruitment/larval abundance) in 2004 was lower than in 2003 and 2005 ($0.45 \times 10^{10} \text{ m}^3$ in 2003, $0.06 \times 10^{10} \text{ m}^3$ in 2004, $1.62 \times 10^{10} \text{ m}^3$ in 2005; Zenitani et al. [14]), and λ in the last 10 days of May 2004 was 2.26, lower than in the last 10 days of May 2003 and 2005, but not close to values corresponding to food shortage. It was possible that the low food availability in the last 10 days of May led to the low reproductive success rate in 2004. Our results for the food shortage criterion in this study support the suggestion of Zenitani et al. [14] that “periods of the last 10 days of May to first 10 days of June was the crucial period for recruitment of anchovy in Hiuchi-nada Sea.” Although the observed copepod density does not represent sufficient food availability for anchovy in some cases, the newly developed growth model is considered as optimal at present and useful to link environmental conditions and larval growth.

Acknowledgments We thank Dr. Tsukamoto, Mrs. Iguchi, Yoshida, Tani, Ueda, and Nakano for their kind assistance. We are also indebted to the captain and crew of the R.V. *Shirafuji maru* and company executives and staff of the Mekachi suisan Ltd. for their assistance with sampling. This work was supported in part by “Research for assessment and prediction of production rate in fishery ground,” the Fisheries Agency and “Study for the prediction and control of the population outbreak of the marine life in relation to environmental change (POMAL)-Studies on prediction and control of

Jellyfish outbreaks (STOPJELLY),” Agriculture, Forestry, and Fisheries Research Council (AFFRC).

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