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Verification of growth dependent survival in early life history of Pacific saury

*Cololabis saira* using laboratory experiment

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Abstract  To understand the survival processes in Pacific saury during the early life stages, growth histories were compared between individuals that died and those that survived under laboratory conditions. The morphology of Pacific saury drastically changed by 40 days after hatching (DAH) under 20 °C, and during this period most individuals reached the juvenile stage (40 mm knob length (KnL)). From hatch to this period, high levels of mortality were observed. The back-calculated growth rates analyzed from otolith microstructure were compared among individuals that died and those that survived this period of metamorphosis. Growth rates of individuals that died were significantly lower since 1 DAH than surviving individuals. Factors contributing to mortality are considered to be cumulative effects of their delayed growth and other unfavorable body conditions (growth dependent survival). The body size (40 mm KnL) that is currently used to estimate the recruitment is concluded to be valid for evaluating the recruitment in the field.

Keywords  Growth dependent survival • Metamorphosis • Pacific saury • Survival
Introduction

The Pacific saury *Cololabis saira* (Brevoort) is an important pelagic commercial fish. Although the stock is currently at a high level (Tian et al., 2003: Annual catches of Pacific saury in Japan have fluctuated from 572,000 metric tons (t) in 1958 to 63,000t in 1969 with an annual average of about 257,000t over the last half century), landings in Japan and the body size distribution of catch have fluctuated from year by year (Fukushima et al., 1990; Watanabe et al., 1997). To determine the factors causing the fluctuations, at first we need to get information about the life history, age and growth, and reproduction process. Hotta (1964) and Kosaka (2000) outlined the life history, and sampling continues to clarify details of the life history. However reasons for the dramatic fluctuations in the stock are still not clear, this being partly due to the broad distribution of this species in the northwestern Pacific (Hubbs and Wisner, 1980).

The sampling of eggs, larvae, and juveniles using plankton nets has also continued since the 1950’s. For nearshore Japan, many studies have been carried out on the growth and survival of Pacific saury in the early life stages (Watanabe et al., 1988, 1997, 2003), and it is estimated that the body size when high levels of mortality stabilize is approximately 40 mm knob length (KnL: a special unit of body length; detailed below). In addition, catch efficiency of Pacific saury larger than this size by existent sampling gears show much fluctuation presumably due to gear avoidance. Thus, currently the abundance of 40 mm KnL is used as an index of the recruitment for each cohort. Nonetheless minimal evidence has been obtained to examine how differences in growth between individuals that fail to survive and individuals that are able to survive metamorphosis in the field.
The cause of early life mortality of fish is due to various incremental factors, and predation is generally the final factor (Bailey and Houde, 1989). To clarify these factors, comparison of the growth rate between individuals that survive and those that die during the period of high mortality (generally related to metamorphosis) is one potential method. In the case of Japanese anchovy, the growth rates analyzed by otolith microstructure have directly been compared between larvae from the stomach contents of predators and otoliths from the larvae taken by sampling nets in the field, and consequently, the growth-selective predation hypothesis has been proposed (Takasuka et al., 2003). However, this is only a rare case, for most fish species including Pacific saury, non-surviving larvae and juveniles have not been sampled in the field, and therefore comparison of the growth rates between non-surviving and the surviving individuals has not been carried out. During the period of metamorphosis, high mortality due to dramatic changes of the body is often observed (e.g. Tanaka et al., 1989). Metamorphosis was defined using the full completion of fins and morphometric ratio change (Kendall et al., 1984). In this study, we observed the metamorphosis process, and then the growth rates were compared between individuals that died and those that survived (growth dependent survival) by otolith microstructure analysis. Using the above results, we verified whether the criterion of body size (40 mm KnL) as an index of recruitment is appropriate for estimates of abundance or not. The research assesses the: (1) growth and survival processes in the early life stage, (2) processes of morphological change, and (3) growth comparison of individuals that survived and those that died during the high level mortality periods.
Methods

Egg collection

Fertilized eggs of the Pacific saury, attached to drifting brown algae, were collected by RV ‘Tankai’ offshore of Kushiro, Hokkaido Prefecture on August 5, 2004 (1st Batch: 1B) and RV ‘Asama’ in Kumano-nada, Mie Prefecture, Pacific Ocean, Japan on March 4 (2nd Batch: 2B), April 21–23 (3rd Batch: 3B), and April 25 (4th Batch: 4B), 2005. The eggs were kept in plastic bags containing 10 liters of ambient seawater (17 ºC) with oxygen and then transported to Hokkaido National Fisheries Research Institute, Fisheries Research Agency, Akkeshi by vehicle and plane. The eggs were stocked and then incubated with running seawater (exchange rate of 120 % / day) in 500 liters black colored polyethylene circular tanks or a 20,000 liters green color painted concrete rectangular tank at temperatures of approximately 17 ºC until hatching.

Rearing of larvae

Hatched larvae (initial stock density of batches 1–4 were 0.9, 2.5, 5.0, and 2.9 inds. / liter, respectively) were reared in the same tank at a temperature of approximately 20ºC, which has been shown to produce the best growth and survival for Pacific saury (for larvae and juvenile (Oozeki and Watanabe, 2000), and from larvae to adult (Tsuzaki, 2000a, b, 2001a, b)). Illumination of the tank was via natural daylight and
light intensity was reduced by covering the tank with a black plastic sheet. The fish were fed to almost satiation (rotifers *Brachionus* spp. and *Artemia* sp. nauplii: two times a day (08:00–09:00, 15:00–16:00),

frozen copepods (Miyabi No. 1 (300–700µm), and No. 2 (1000–1500µm): JCK Co. Ltd): three times a day (08:00–09:00, 11:00–12:00, 15:00–16:00), and artificial feed (Otohime A, B1, and B2: Marubeni Nishiin Feed Co., well mixed): 15–22 times a day (depending on their appetite using a self feeding machine) during 06:00–17:00). Details of the feeding and environmental conditions are shown in Table 1. From 08:00 to 09:00, the bottom of the tanks was cleaned, dead individuals collected, and then the water temperature was measured.

**Sampling of fish**

Samples of over 20 individuals were collected randomly every 5 days from 0 to 40 days after hatching (DAH), and then 20–30 individuals were collected randomly at 10 days intervals, twice on 50 and 60 DAH. The sampling was undertaken at feeding time when the fish could be caught easily without causing excess stress. During feeding, when the fish were swimming at the surface of the tank, is a period when they are least wary.

The samples were preserved in 80% ethanol after being anaesthetized with FA-100 (Dainippon Pharma)(50–100ppm). Knob length (KnL: a special unit of body length represented by the length from the anterior edge of the lower jaw to the posterior edge of the silver flesh which is protruded on the base of the tail fin; the measurement with least bias for Pacific saury (Kimura, 1956)) were measured to
the nearest 0.1mm. According to Oozeki et al. (1991), for fish preserved in 80% ethanol we used a
correction factor of 1.08 for fish smaller than 9.9 mm KnL and 0.98 for those larger than 10.0 mm KnL.

Body weight (BW) of the individuals was measured to the nearest 0.01g. In addition, their total length
(TL), head length (HL), pre-anal length (PAL), eye diameter (ED), lower jaw length (LJL), body depth
(BD), and head depth (HD) were measured, and also their fin rays (pectoral (P1), pelvic (P2), anal (A),
dorsal (D), and caudal (C)) were counted for each sample. Thereafter the otoliths were extracted under a
stereomicroscope.

Growth analysis

The left (primarily) or the right (if the left one was lost or broken) otolith was mounted on a glass slide
using epoxy enamel. The mounted otolith was allowed to set for over 24 hours. Thereafter, the
proximal side of the otolith was polished with lapping films of grit sizes of 1, 3, and 9 µm. Since the
posterior otolith radius is more suitable for back-calculation of KnL (Oozeki and Watanabe, 2000), the
number of otolith increments and the otolith increment widths were measured for the posterior part.

The image data for measuring the number of otolith increments and the otolith increment widths were
obtained using a light microscope (400–1000 x) with a camera connected. They were analyzed on a
monitor of a computer using image-analyzing software (Adobe Photoshop 7.0). These measurements
were repeated at least three times by different researchers without knowledge of the previous results.
These data were adopted when two or more counts agreed. The first growth increment for Pacific saury
has been reported to begin at 4 to 6 days before hatching (Watanabe and Kuji, 1991): 4–5, mean 4.81;
Suyama et al. (1996), middle North Pacific Ocean: mean 6.1, western North Pacific Ocean: mean 5.6;
oozeki and Watanabe (2000): mean 6.37 and posterior radius of hatching check are 20–35 μm (Watanabe
et al. (1988), about 27μm; Watanabe and Kuji, (1991), 31μm; Suyama et al. (1996), 25.8 ± 3.9μm
(western North Pacific Ocean); Suyama (2002), 28.1 ± 5.0μm (middle North Pacific Ocean)). Therefore,
we measured the width of the hatching check as 20–35μm distant from the center of the focus and
counted the daily growth increments to the last distinct increment (posterior radius). KnL and daily
growth rate at each age were back-calculated by the biological intercept method (Campana 1990) in order
to obtain the growth trajectories and histories of individual larvae. Average KnL on 0 DAH was 7.33
mm.

Numerical value analysis

Death of Pacific saury were recorded daily during the experiment. Daily instantaneous mortality rate
(IMR) were derived (Ricker 1958) at 5 day intervals. Mortality rates were calculated using the
following equation.

\[ \text{IMR} = \frac{\ln N_i - \ln N_{i+1}}{5} \]

where \( N_i, N_{i+1} \) are the number of survivors at the first date of time intervals. Specific mortality rates
(SMR) were calculated as IMR x 100.

In order to calculate the morphometric variation at 5 mm KnL intervals, the morphometric characters
(TL, HL, PAL, ED, LJL, BD, and HD) per KnL of Pacific saury were made on 1000 data chosen randomly from the available samples. This operation was repeated 1000 times (Bootstrap method), and the mean value of the morphometric character per KnL composition was estimated for each 5 mm KnL interval. This calculation involved the use of Microsoft Excel software. Morphometric variations (MV) among 5 mm KnL intervals (e.g. 10.0–14.9, 15.0–19.9 mm) were calculated using the following equation.

$$MV = \frac{(MC / KnL)_i - (MC / KnL)_{i+1}}{\sum(MC / KnL) / n}$$

where MC is the morphometric character, (MC / KnL)$_i$, (MC / KnL)$_{i+1}$ are the mean values of 5mm KnL size intervals i and i+1, respectively. $n$ is the number of 5 mm KnL size intervals.

Statistical analysis

One-way ANOVA was used to detect differences in the growth speed among surviving and dead individuals. If the variances determined were heteroscedastic as shown by a $F_{max}$-test, the values were log transformed. When a significant difference was detected, Scheffe’s test was used for comparisons thereafter. The level of significance was set at 1%.

Results

Growth and survival processes
Growth of larval and juvenile Pacific saury is shown in Fig. 1. Their KnL at 20, 40, and 60 DAH was 16.1 ± 1.90, 39.3 ± 4.31, and 65.9 ± 10.51 (mean ± SD), respectively. The number of dead individuals until 9 DAH could not be counted accurately because of their small and weak bodies which decomposed rapidly. Consequently, specific mortality rates (SMR) (% / day) are shown using data from individuals that died from 10–60 DAH (Table 2). After 10 DAH, a high mortality rate usually started from 11 DAH, and continued until 20 DAH (the highest mean SMR time interval: 15–19 DAH). Then the mortality rate stabilized, however it increased again and continued until 33 DAH (the second highest mean SMR time interval: 25–29 DAH). After 40 DAH, the SMR decreased drastically. Such a mortality process pattern was observed regardless of the different batches of eggs and rearing conditions. Therefore this process probably reflects changes in internal physiological factors during the early life history of Pacific saury.

Metamorphosis

Relationships between DAH and number of fin rays are shown in Fig. 2. In the case of the caudal (C) and dorsal (D) fins, notable increases were observed 0–5 DAH. Such increases were also observed for the anal (A) fin 0–10 DAH, pectoral (P1) fin 5–10 DAH, and pelvic (P2) fin 20–30 DAH. Almost all them had already reached their stable ray number by 40 DAH (D: 12–15, A: 18–21, P1: 12–16, P2: 6, C: 19–21 as detailed by Nakabo (2000), and Nakaya et al. (2007)). Relationships between KnL and percent
that had reached a stable number for each fin rays are shown in Table 3. By 15.0–19.9 mm KnL the number of D rays had already reached a stable number. P1 and P2 rays reached the stable number of rays during 20.0–24.9 mm KnL. By 35.0–39.9 mm KnL the number of A and C rays was stable. All fin rays reached the stable number before reaching 40.0 mm KnL.

Fig. 3 shows the relationships between DAH and the proportion of total length (TL), head length (HL), pre-anal length (PAL), eye diameter (ED), lower jaw length (LJL), body depth (BD), and head depth (HD) to KnL. Morphometric variations (MV) among 5 mm KnL intervals are shown in Fig. 4. For all body proportions, the highest two MV values were observed by the KnL size range 35.0–39.9 mm KnL, after that the MV showed less fluctuation. Over 40 mm KnL, fluctuations in body proportions tended to be more gradual.

Before 39 DAH, the larvae swam only near the surface in the daytime, and were not observed to form schools in the tank. After 39 DAH, they swam not only near the surface but also in the middle to near bottom sections of the tank, and were observed to form a school.

Comparison of growth between survived and dead individuals

During 10–60 DAH, two periods of high mortality were observed. We compared the back-calculated growth rate among dead individuals during these periods (the highest mean SMR time interval: 15–19 DAH (D1), the second highest mean SMR time interval: 25–29 DAH (D2)), and surviving individuals collected at 60 DAH (SV) using otolith microstructure analysis (Fig. 5). As a result, there were
significant differences (One-way ANOVA, \( P<0.01 \)) among them since 1 DAH. Although no significant difference was observed between D1 and D2 (Scheffe’s test, \( P=0.82 \)), there were significant differences (Scheffe’s test, \( P<0.01 \)) between SV and D1, D2 since 1 DAH. These (D1, D2) lower growth continued until death.

Discussion

Natural mortality rates of fish are generally highest in early life. Fishes may die from many causes (endogenous factors (maternal effects: e.g. Solemdal (1997)) such as insufficient endogenous nutrition and physical disorders, and exogenous factors such as poor-nutrition, disease, and unfavorable environmental conditions), nonetheless predation is usually the critical agent for mortality (Houde, 1997). In general, the mortality rate is high until the end of metamorphosis and after that tends to be more gradual. Metamorphosis was defined using the full completion of fins and morphometric ratio change (Kendall et al., 1984). In this study, we observed the development of fin rays and the relative growth of each body part. The first inflection point was observed at 5–9 DAH (\(<10 \ \text{mm KnL} \)). This point corresponds to the period when a change of nutrition from endogenous to exogenous occurs (20°C: Nakaya et al., 2009). The second inflection point was observed at about 30 DAH, and most of the fin rays were completely formed before 40 DAH (over 40 mm KnL). Consequently, the second inflection point (about 30 DAH) was considered to be the end of the metamorphosis period for this species. We directly examined the growth process between surviving and dead individuals of larval and juvenile
Pacific saury in laboratory conditions by otolith microstructure analysis, and observed significant
differences among them already at 1 DAH. Though newly hatched Pacific saury can survive for 5–10
days (50% mortality period) without feeding in 10–25°C (Nakaya et al., 2009), if larvae of Pacific saury
can not encounter appropriate environmental conditions by 5–9 DAH, their survival rate may be low in
the field as they will become more prone to predation. Survival in this species in the early life stage may
be determined soon after hatching, although predation effects should also be considered further for
precise evaluations of natural mortality rates.

The relationship between growth rates and larval duration (to metamorphosis) has been a focus of study
epecially for a variety of coral reef fishes (Victor, 1986; Victor and Wellington, 2000; McCormick et al.,
2002; Shima and Findlay, 2002) and for flatfishes (Hovenkamp, 1992; Bertram et al., 1997) that are
characterized by settlement through metamorphosis. Takasuka et al. (2004) suggested that a growth
selective survival mechanism might apply to pelagic fish (Japanese anchovy), and our present results are
consistent with their study. In general, the critical period for fishes is species specific, and in cold water
species, tends to be long and gradual (e.g. in Japanese anchovy Engraulis japonicus: the growth and
developmental rate-dependent mortality occurred at 50–60 days (Takahashi and Watanabe, 2004), and in
Atlantic cod Gadus morhua, growth selective mortality occurred at 41–80 days (Meekan and Fortier,
1996)). On the other hand, the period of warm water species tends to be short (e.g. in bluefish Pomatomus saltatrix at 10–15 days (Hare and Cowen, 1997), at 0–5 days in the common coral wrasse
Halichoeres bivittatus (Searcy and Sponaugle, 2001), at 7–10 days in damselfish Stegastes partitus
(Wilson and Meekan, 2002), and within 2 weeks of hatching was crucial for survival to recruitment in
Pacific bluefin tuna *Thunnus orientalis* (Tanaka *et al.*, 2006)). The present study suggests that the body conditions and environmental conditions at the start of the feeding period in Pacific saury may be more related to survival than for other warm water species reported previously. We could compare directly between individuals that died during the metamorphosis period and the surviving individuals, and thus, obtained evidence that growth dependent survival strategy occurs in Pacific saury. Maternal effects and the environmental conditions (variance in feed and temperature conditions) at the start of the feeding period might be closely related to survival during the metamorphosis period (e.g. Houde, 1997). Hereafter we need to further study the relationships between maternal effect and the growth-survival for larval and juvenile stages.

According to Watanabe and Kuji (1991), Pacific saury starts schooling behavior when they attain 45–50 mm KnL. The density of juveniles after mass mortality can be used as a quantitative index of the recruiting cohort, therefore the 40 mm KnL juvenile density has been used as an index of recruitment. The present study found that the high rate of mortality stabilized after 40 mm KnL for Pacific saury under non-predation conditions. Therefore, we consider that using density of 40 mm KnL of Pacific saury collected by net is valid for estimating the wild recruitment amount.

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Fig. 1  Relationships between days after hatching (DAH) and knob length (KnL) of Pacific saury. Open circles and closed squares show the individual score and mean value at each date, respectively.

Fig. 2  Relationships between days after hatching (DAH) and number of fin rays for each fin of Pacific saury. Open circles and closed squares show the individual scores and the mean value at each date, respectively. The stable number of rays for each fin is shown with oblique lines area and / or dashed lines.

Fig. 3  Relationships between days after hatching (DAH) and relative length of body parts (% KnL) of Pacific saury. Open circles and closed squares show the individual scores and the mean value at each date, respectively.

Fig. 4  Morphometric variation (MV) in early life stage of Pacific saury among 5 mm KnL size intervals.

Fig. 5  Relationships between days after hatching (DAH) and estimated knob length (KnL) using otolith microstructure data for three kinds of individuals (dead individuals during their periods (15–19 DAH (D1), 25–29 DAH (D2)) and surviving individuals collected at 60 DAH individuals (SV)) of Pacific saury. Vertical lines show the standard deviation (SD).
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Table 2 Specific mortality rate (%/day) of Pacific saury for different batch treatments and time intervals

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Table 3  Percent of reached the stable number for each fin (%) of Pacific saury

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Fig. 1 Nakaya et al.
Fig. 5 Nakaya et al.