



Title	Validation of otolith daily increments for larval and juvenile Japanese halfbeak <i>Hyporhamphus sajori</i>
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Title: Verification of growth dependent survival in early life history of Pacific saury *Cololabis saira* using laboratory experiment.

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Keywords: growth dependent survival; metamorphosis; Pacific saury; Survival

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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.

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3 1 **Verification of growth dependent survival in early life history of Pacific saury**

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6 2 ***Cololabis saira* using laboratory experiment**

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

28 **Keywords** Growth dependent survival • Metamorphosis • Pacific saury • Survival

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3 **37 Introduction**
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6 38 The Pacific saury *Cololabis saira* (Brevoort) is an important pelagic commercial fish. Although the
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9 39 stock is currently at a high level (Tian *et al.*, 2003: Annual catches of Pacific saury in Japan have
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12 40 fluctuated from 572,000 metric tons (t) in 1958 to 63,000t in 1969 with an annual average of about
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15 41 257,000t over the last half century), landings in Japan and the body size distribution of catch have
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18 42 fluctuated from year by year (Fukushima *et al.*, 1990; Watanabe *et al.*, 1997). To determine the factors
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21 43 causing the fluctuations, at first we need to get information about the life history, age and growth, and
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24 44 reproduction process. Hotta (1964) and Kosaka (2000) outlined the life history, and sampling continues
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27 45 to clarify details of the life history. However reasons for the dramatic fluctuations in the stock are still
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30 46 not clear, this being partly due to the broad distribution of this species in the northwestern Pacific (Hubbs
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33 47 and Wisner, 1980).

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35 48 The sampling of eggs, larvae, and juveniles using plankton nets has also continued since the 1950's.
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38 49 For nearshore Japan, many studies have been carried out on the growth and survival of Pacific saury in
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41 50 the early life stages (Watanabe *et al.*; 1988, 1997, 2003), and it is estimated that the body size when
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44 51 high levels of mortality stabilize is approximately 40 mm knob length (KnL: a special unit of body length;
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47 52 detailed below). In addition, catch efficiency of Pacific saury larger than this size by existent sampling
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50 53 gears show much fluctuation presumably due to gear avoidance. Thus, currently the abundance of 40
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53 54 mm KnL is used as an index of the recruitment for each cohort. Nonetheless minimal evidence has been
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56 55 obtained to examine how differences in growth between individuals that fail to survive and individuals
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59 56 that are able to survive metamorphosis in the field.
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3 57 The cause of early life mortality of fish is due to various incremental factors ,and predation is generally
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6 58 the final factor (Bailey and Houde, 1989). To clarify these factors, comparison of the growth rate
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9 59 between individuals that survive and those that die during the period of high mortality (generally related
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12 60 to metamorphosis) is one potential method. In the case of Japanese anchovy, the growth rates analyzed
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15 61 by otolith microstructure have directly been compared between larvae from the stomach contents of
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18 62 predators and otoliths from the larvae taken by sampling nets in the field, and consequently, the
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21 63 growth-selective predation hypothesis has been proposed (Takasuka *et al.*, 2003). However, this is only
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24 64 a rare case, for most fish species including Pacific saury, non-surviving larvae and juveniles have not
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27 65 been sampled in the field, and therefore comparison of the growth rates between non-surviving and the
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30 66 surviving individuals has not been carried out. During the period of metamorphosis, high mortality due
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33 67 to dramatic changes of the body is often observed (e.g. Tanaka *et al.*, 1989). Metamorphosis was
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36 68 defined using the full completion of fins and morphometric ratio change (Kendall *et al.*, 1984). In this
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39 69 study, we observed the metamorphosis process, and then the growth rates were compared between
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42 70 individuals that died and those that survived (growth dependent survival) by otolith microstructure
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45 71 analysis. Using the above results, we verified whether the criterion of body size (40 mm KnL) as an
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48 72 index of recruitment is appropriate for estimates of abundance or not. The research assesses the: (1)
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51 73 growth and survival processes in the early life stage, (2) processes of morphological change, and (3)
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54 74 growth comparison of individuals that survived and those that died during the high level mortality
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77 **Methods**

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79 Egg collection

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81 Fertilized eggs of the Pacific saury, attached to drifting brown algae, were collected by RV ‘Tankai’
82 offshore of Kushiro, Hokkaido Prefecture on August 5, 2004 (1st Batch: 1B) and RV ‘Asama’ in
83 Kumano-nada, Mie Prefecture, Pacific Ocean, Japan on March 4 (2nd Batch: 2B), April 21–23 (3rd Batch:
84 3B), and April 25 (4th Batch: 4B), 2005. The eggs were kept in plastic bags containing 10 liters of
85 ambient seawater (17 °C) with oxygen and then transported to Hokkaido National Fisheries Research
86 Institute, Fisheries Research Agency, Akkeshi by vehicle and plane. The eggs were stocked and then
87 incubated with running seawater (exchange rate of 120 % / day) in 500 liters black colored polyethylene
88 circular tanks or a 20,000 liters green color painted concrete rectangular tank at temperatures of
89 approximately 17 °C until hatching.

90

91 Rearing of larvae

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93 Hatched larvae (initial stock density of batches 1–4 were 0.9, 2.5, 5.0, and 2.9 inds. / liter, respectively)
94 were reared in the same tank at a temperature of approximately 20°C, which has been shown to produce
95 the best growth and survival for Pacific saury (for larvae and juvenile (Oozeki and Watanabe, 2000), and
96 from larvae to adult (Tsuzaki, 2000a, b, 2001a, b)). Illumination of the tank was via natural daylight and

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97 light intensity was reduced by covering the tank with a black plastic sheet. The fish were fed to almost
98 satiation (rotifers *Brachionus* spp. and *Artemia* sp. nauplii: two times a day (08:00–09:00, 15:00–16:00) ,
99 frozen copepods (Miyabi No. 1 (300–700µm), and No. 2 (1000–1500µm): JCK Co. Ltd): three times a
100 day (08:00–09:00, 11:00–12:00, 15:00–16:00) , and artificial feed (Otohime A, B1, and B2: Marubeni
101 Nishiin Feed Co., well mixed): 15–22 times a day (depending on their appetite using a self feeding
102 machine) during 06:00–17:00). Details of the feeding and environmental conditions are shown in Table
103 1. From 08:00 to 09:00, the bottom of the tanks was cleaned, dead individuals collected, and then the
104 water temperature was measured.

105
106 Sampling of fish

107
108 Samples of over 20 individuals were collected randomly every 5 days from 0 to 40 days after hatching
109 (DAH), and then 20–30 individuals were collected randomly at 10 days intervals, twice on 50 and 60
110 DAH. The sampling was undertaken at feeding time when the fish could be caught easily without
111 causing excess stress. During feeding, when the fish were swimming at the surface of the tank, is a
112 period when they are least wary.

113 The samples were preserved in 80% ethanol after being anaesthetized with FA-100 (Dainippon
114 Pharma)(50–100ppm). Knob length (KnL: a special unit of body length represented by the length
115 from the anterior edge of the lower jaw to the posterior edge of the silver flesh which is protruded on the
116 base of the tail fin; the measurement with least bias for Pacific saury (Kimura, 1956)) were measured to

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117 the nearest 0.1mm. According to Oozeki et al. (1991), for fish preserved in 80 % ethanol we used a
118 correction factor of 1.08 for fish smaller than 9.9 mm KnL and 0.98 for those larger than 10.0 mm KnL.
119 Body weight (BW) of the individuals was measured to the nearest 0.01g. In addition, their total length
120 (TL), head length (HL), pre-anal length (PAL), eye diameter (ED), lower jaw length (LJL), body depth
121 (BD), and head depth (HD) were measured, and also their fin rays (pectoral (P1), pelvic (P2), anal (A),
122 dorsal (D), and caudal (C)) were counted for each sample. Thereafter the otoliths were extracted under a
123 stereomicroscope.

124

125 Growth analysis

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

132 The image data for measuring the number of otolith increments and the otolith increment widths were
133 obtained using a light microscope (400–1000 x) with a camera connected. They were analyzed on a
134 monitor of a computer using image-analyzing software (Adobe Photoshop 7.0). These measurements
135 were repeated at least three times by different researchers without knowledge of the previous results.

136 These data were adopted when two or more counts agreed. The first growth increment for Pacific saury

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137 has been reported to begin at 4 to 6 days before hatching (Watanabe and Kuji, 1991): 4–5, mean 4.81;
138 Suyama *et al.* (1996), middle North Pacific Ocean: mean 6.1, western North Pacific Ocean: mean 5.6;
139 Oozeki and Watanabe (2000): mean 6.37) and posterior radius of hatching check are 20–35 μm (Watanabe
140 *et al.* (1988), about 27 μm ; Watanabe and Kuji, (1991), 31 μm ; Suyama *et al.* (1996), 25.8 \pm 3.9 μm
141 (western North Pacific Ocean); Suyama (2002), 28.1 \pm 5.0 μm (middle North Pacific Ocean)). Therefore,
142 we measured the width of the hatching check as 20–35 μm distant from the center of the focus and
143 counted the daily growth increments to the last distinct increment (posterior radius). KnL and daily
144 growth rate at each age were back-calculated by the biological intercept method (Campana 1990) in order
145 to obtain the growth trajectories and histories of individual larvae. Average KnL on 0 DAH was 7.33
146 mm.

148 Numerical value analysis

149
150 Death of Pacific saury were recorded daily during the experiment. Daily instantaneous mortality rate
151 (IMR) were derived (Ricker 1958) at 5 day intervals. Mortality rates were calculated using the
152 following equation.

153
$$\text{IMR} = (\text{Ln}N_i - \text{Ln}N_{i+1}) / 5$$

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

156 In order to calculate the morphometric variation at 5 mm KnL intervals, the morphometric characters

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

$$163 \quad MV = ((MC / KnL)_i - (MC / KnL)_{i+1}) / \Sigma(MC / KnL) / n$$

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

166

167 **Statistical analysis**

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

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174 **Results**

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176 **Growth and survival processes**

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178 Growth of larval and juvenile Pacific saury is shown in Fig. 1. Their KnL at 20, 40, and 60 DAH was
179 16.1 ± 1.90 , 39.3 ± 4.31 , and 65.9 ± 10.51 (mean \pm SD), respectively. The number of dead individuals
180 until 9 DAH could not be counted accurately because of their small and weak bodies which decomposed
181 rapidly. Consequently, specific mortality rates (SMR) (% / day) are shown using data from individuals
182 that died from 10–60 DAH (Table 2). After 10 DAH, a high mortality rate usually started from 11 DAH,
183 and continued until 20 DAH (the highest mean SMR time interval: 15–19 DAH). Then the mortality
184 rate stabilized, however it increased again and continued until 33 DAH (the second highest mean SMR
185 time interval: 25–29 DAH). After 40 DAH, the SMR decreased drastically. Such a mortality process
186 pattern was observed regardless of the different batches of eggs and rearing conditions. Therefore this
187 process probably reflects changes in internal physiological factors during the early life history of Pacific
188 saury.

189

190 Metamorphosis

191

192 Relationships between DAH and number of fin rays are shown in Fig. 2. In the case of the caudal (C)
193 and dorsal (D) fins, notable increases were observed 0–5 DAH. Such increases were also observed for
194 the anal (A) fin 0–10 DAH, pectoral (P1) fin 5–10 DAH, and pelvic (P2) fin 20–30 DAH. Almost all
195 them had already reached their stable ray number by 40 DAH (D: 12–15, A: 18–21, P1: 12–16, P2: 6, C:
196 19–21 as detailed by Nakabo (2000), and Nakaya *et al.* (2007)). Relationships between KnL and percent

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197 that had reached a stable number for each fin rays are shown in Table 3. By 15.0–19.9 mm KnL the
198 number of D rays had already reached a stable number. P1 and P2 rays reached the stable number of
199 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
200 fin rays reached the stable number before reaching 40.0 mm KnL.

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

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

210

211 Comparison of growth between survived and dead individuals

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213 During 10–60 DAH, two periods of high mortality were observed. We compared the back-calculated
214 growth rate among dead individuals during these periods (the highest mean SMR time interval: 15–19
215 DAH (D1) , the second highest mean SMR time interval: 25–29 DAH (D2)), and surviving individuals
216 collected at 60 DAH (SV) using otolith microstructure analysis (Fig. 5). As a result, there were

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217 significant differences (One-way ANOVA, $P<0.01$) among them since 1 DAH. Although no significant
218 difference was observed between D1 and D2 (Scheffe's test, $P=0.82$), there were significant differences
219 (Scheffe's test, $P<0.01$) between SV and D1, D2 since 1 DAH. These (D1, D2) lower growth continued
220 until death.

221

222 **Discussion**

223

224 Natural mortality rates of fish are generally highest in early life. Fishes may die from many causes
225 (endogenous factors (maternal effects: e.g. Solemdal (1997)) such as insufficient endogenous nutrition
226 and physical disorders, and exogenous factors such as poor-nutrition, disease, and unfavorable
227 environmental conditions), nonetheless predation is usually the critical agent for mortality (Houde, 1997).
228 In general, the mortality rate is high until the end of metamorphosis and after that tends to be more
229 gradual. Metamorphosis was defined using the full completion of fins and morphometric ratio change
230 (Kendall *et al.*, 1984). In this study, we observed the development of fin rays and the relative growth of
231 each body part. The first inflection point was observed at 5–9 DAH (<10 mm KnL). This point
232 corresponds to the period when a change of nutrition from endogenous to exogenous occurs (20°C:
233 Nakaya *et al.*, 2009). The second inflection point was observed at about 30 DAH, and most of the fin
234 rays were completely formed before 40 DAH (over 40 mm KnL). Consequently, the second inflection
235 point (about 30 DAH) was considered to be the end of the metamorphosis period for this species. We
236 directly examined the growth process between surviving and dead individuals of larval and juvenile

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237 Pacific saury in laboratory conditions by otolith microstructure analysis, and observed significant
238 differences among them already at 1 DAH. Though newly hatched Pacific saury can survive for 5–10
239 days (50% mortality period) without feeding in 10–25°C (Nakaya *et al.*, 2009), if larvae of Pacific saury
240 can not encounter appropriate environmental conditions by 5–9 DAH, their survival rate may be low in
241 the field as they will become more prone to predation. Survival in this species in the early life stage may
242 be determined soon after hatching, although predation effects should also be considered further for
243 precise evaluations of natural mortality rates.

244 The relationship between growth rates and larval duration (to metamorphosis) has been a focus of study
245 especially for a variety of coral reef fishes (Victor, 1986; Victor and Wellington, 2000; McCormick *et al.*,
246 2002; Shima and Findlay, 2002) and for flatfishes (Hovenkamp, 1992; Bertram *et al.*, 1997) that are
247 characterized by settlement through metamorphosis. Takasuka *et al.* (2004) suggested that a growth
248 selective survival mechanism might apply to pelagic fish (Japanese anchovy), and our present results are
249 consistent with their study. In general, the critical period for fishes is species specific, and in cold water
250 species, tends to be long and gradual (e.g. in Japanese anchovy *Engraulis japonicus*: the growth and
251 developmental rate-dependent mortality occurred at 50–60 days (Takahashi and Watanabe, 2004), and in
252 Atlantic cod *Gadus morhua*, growth selective mortality occurred at 41–80 days (Meekan and Fortier,
253 1996)). On the other hand, the period of warm water species tends to be short (e.g. in bluefish
254 *Pomatomus saltatrix* at 10–15 days (Hare and Cowen, 1997), at 0–5 days in the common coral wrasse
255 *Halichoeres bivittatus* (Searcy and Sponaugle, 2001), at 7–10 days in damselfish *Stegastes partitus*
256 (Wilson and Meekan, 2002), and within 2 weeks of hatching was crucial for survival to recruitment in

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257 Pacific bluefin tuna *Thunnus orientalis* (Tanaka *et al.*, 2006)). The present study suggests that the body
258 conditions and environmental conditions at the start of the feeding period in Pacific saury may be more
259 related to survival than for other warm water species reported previously. We could compare directly
260 between individuals that died during the metamorphosis period and the surviving individuals, and thus,
261 obtained evidence that growth dependent survival strategy occurs in Pacific saury. Maternal effects and
262 the environmental conditions (variance in feed and temperature conditions) at the start of the feeding
263 period might be closely related to survival during the metamorphosis period (e.g. Houde, 1997).
264 Hereafter we need to further study the relationships between maternal effect and the growth-survival for
265 larval and juvenile stages.

266 According to Watanabe and Kuji (1991), Pacific saury starts schooling behavior when they attain
267 45–50 mm KnL. The density of juveniles after mass mortality can be used as a quantitative index of the
268 recruiting cohort, therefore the 40 mm KnL juvenile density has been used as an index of recruitment.
269 The present study found that the high rate of mortality stabilized after 40mm KnL for Pacific saury
270 under non-predation conditions. Therefore, we consider that using density of 40 mm KnL of Pacific
271 saury collected by net is valid for estimating the wild recruitment amount.

272

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382 Fig. 1 Relationships between days after hatching (DAH) and knob length (KnL) of Pacific saury.

383 Open circles and closed squares show the individual score and mean value at each date, respectively.

384 Fig. 2 Relationships between days after hatching (DAH) and number of fin rays for each fin of Pacific

385 saury. Open circles and closed squares show the individual scores and the mean value at each date,

386 respectively. The stable number of rays for each fin is shown with oblique lines area and / or dashed

387 lines.

388 Fig. 3 Relationships between days after hatching (DAH) and relative length of body parts (% KnL) of

389 Pacific saury. Open circles and closed squares show the individual scores and the mean value at each

390 date, respectively.

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

392 Fig. 5 Relationships between days after hatching (DAH) and estimated knob length (KnL) using otolith

393 microstructure data for three kinds of individuals (dead individuals during their periods (15–19 DAH

394 (D1) , 25–29 DAH (D2)) and surviving individuals collected at 60 DAH individuals (SV)) of Pacific

395 saury. Vertical lines show the standard deviation (SD).

Table. 2 Specific mortality rate (%/day) of Pacific saury for different batch treatments and time intervals

Time interval (days after hatching)	Batch treatment				
	1st	2nd	3rd	4th	Mean
10–14	6.74	0	11.96	1.24	4.98
15–19	32.16	12.25	7.93	3.86	14.05
20–24	0	5.24	3.54	2.04	2.70
25–29	8.18	10.23	0.66	2.56	5.41
30–34	13.65	0	2.11	0.49	4.06
35–39	–	0	6.00	0.27	2.09
40–44	–	0	0.51	0.07	0.19
45–49	–	0	1.05	0.14	0.40
50–54	–	0	0.55	0.38	0.31
55–59	–	0	0.56	0.14	0.23

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

KnL size interval (mm)	Anal (A)	Caudal (C)	Dorsal (D)	Pectoral (P1)	Pelvic (P2)	No. samples
5.0–9.9	0	0	3	0	0	50
10.0–14.9	0	0	12	0	0	34
15.0–19.9	0	0	100	0	0	28
20.0–24.9	0	0	100	100	100	20
25.0–29.9	8	0	100	100	100	13
30.0–34.9	75	92	100	100	100	12
35.0–39.9	100	100	100	100	100	19
40.0–44.9	100	100	100	100	100	11
45.0–49.9	100	100	100	100	100	10
50.0–54.9	100	100	100	100	100	6
55.0–59.9	100	100	100	100	100	7
60.0–64.9	100	100	100	100	100	5
65.0–69.9	100	100	100	100	100	2
70.0–74.9	100	100	100	100	100	6
75.0–79.9	100	100	100	100	100	2

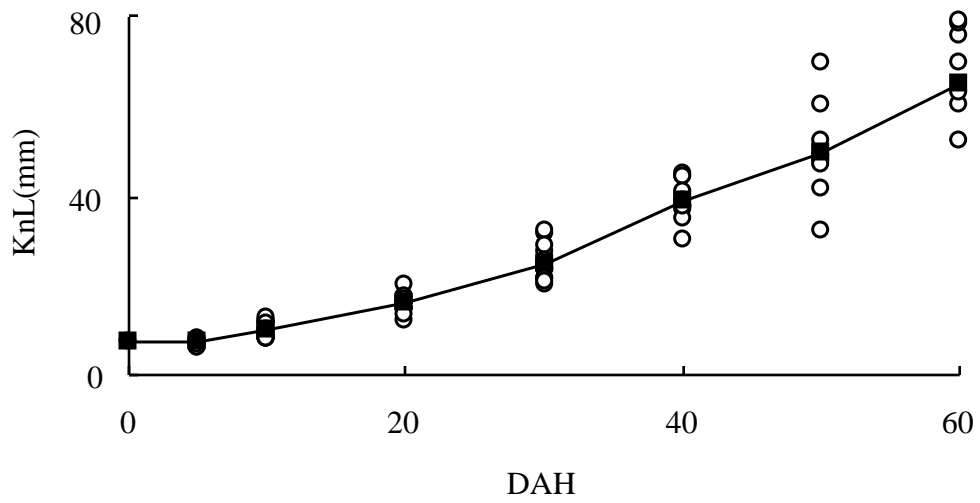


Fig. 1 Nakaya *et al.*

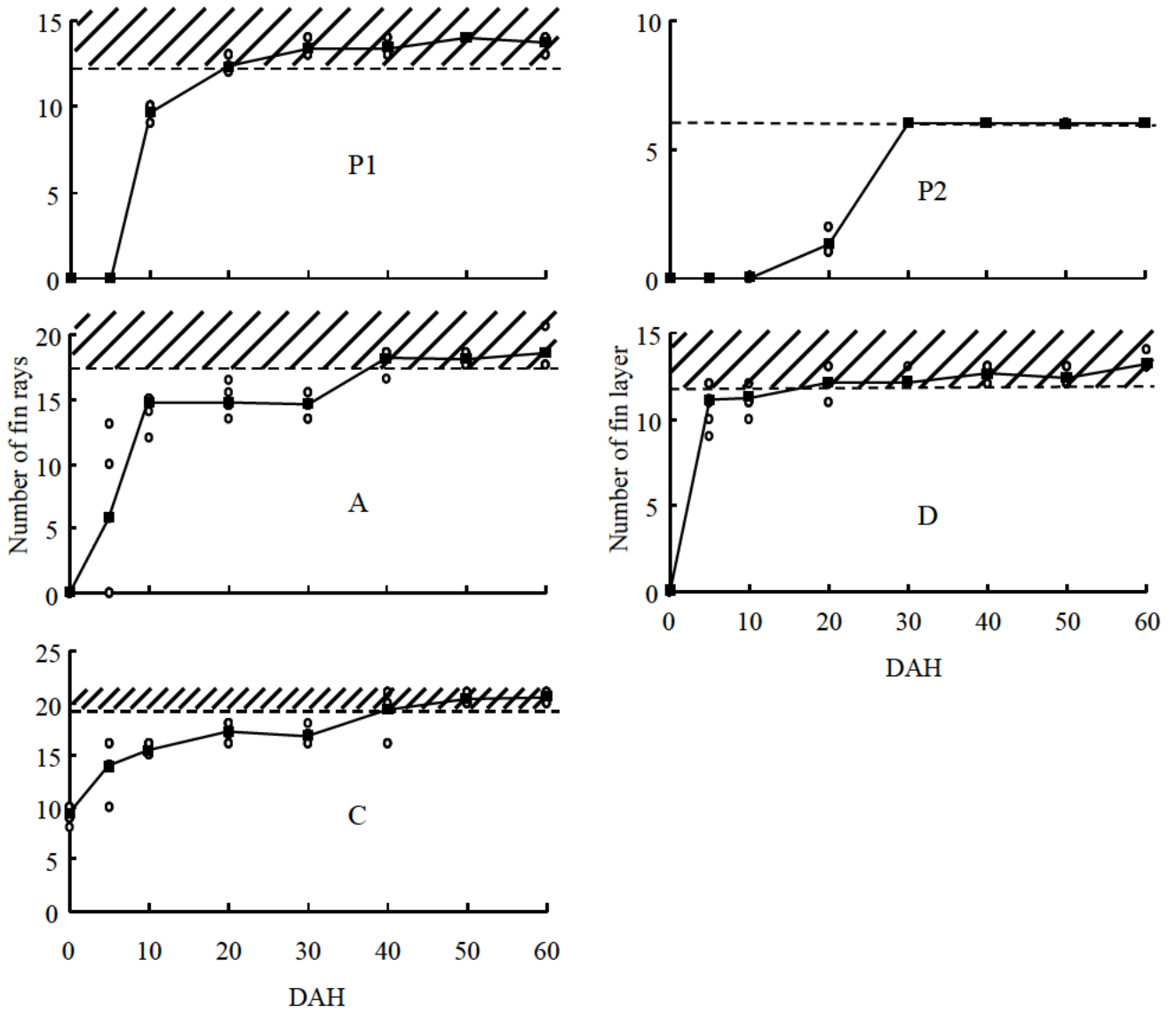


Fig. 2 Nakaya *et al.*

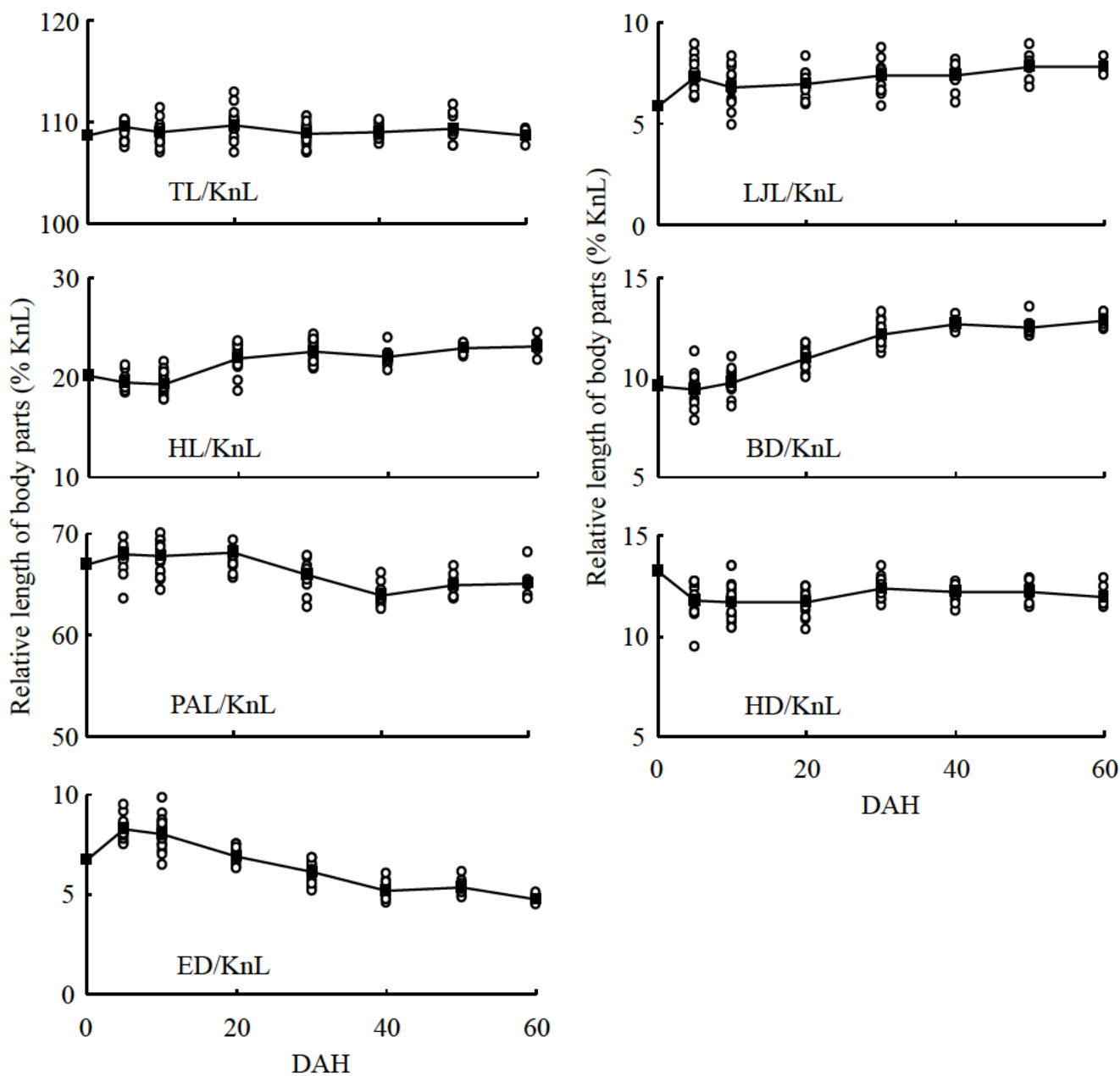


Fig. 3 Nakaya *et al.*

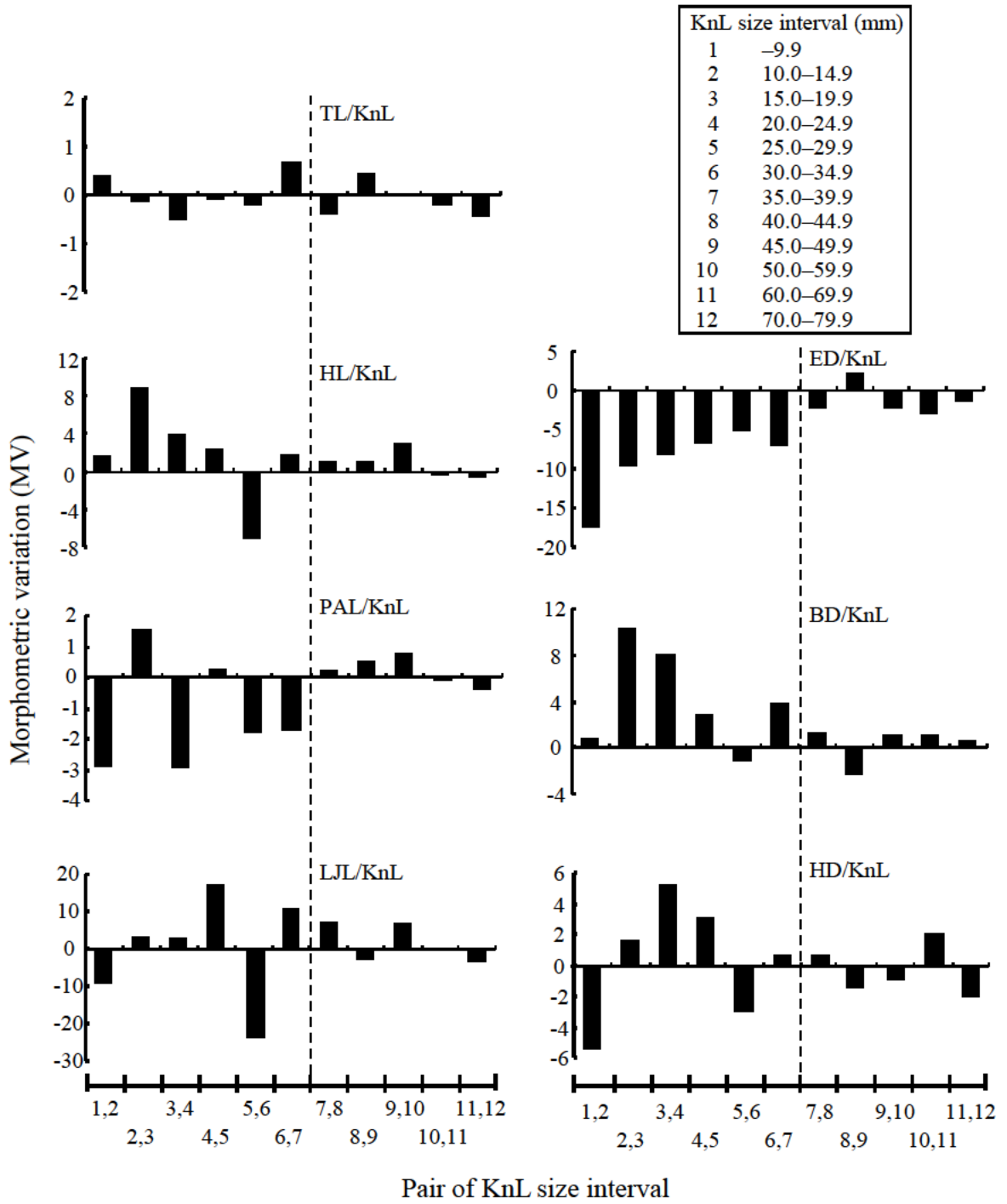


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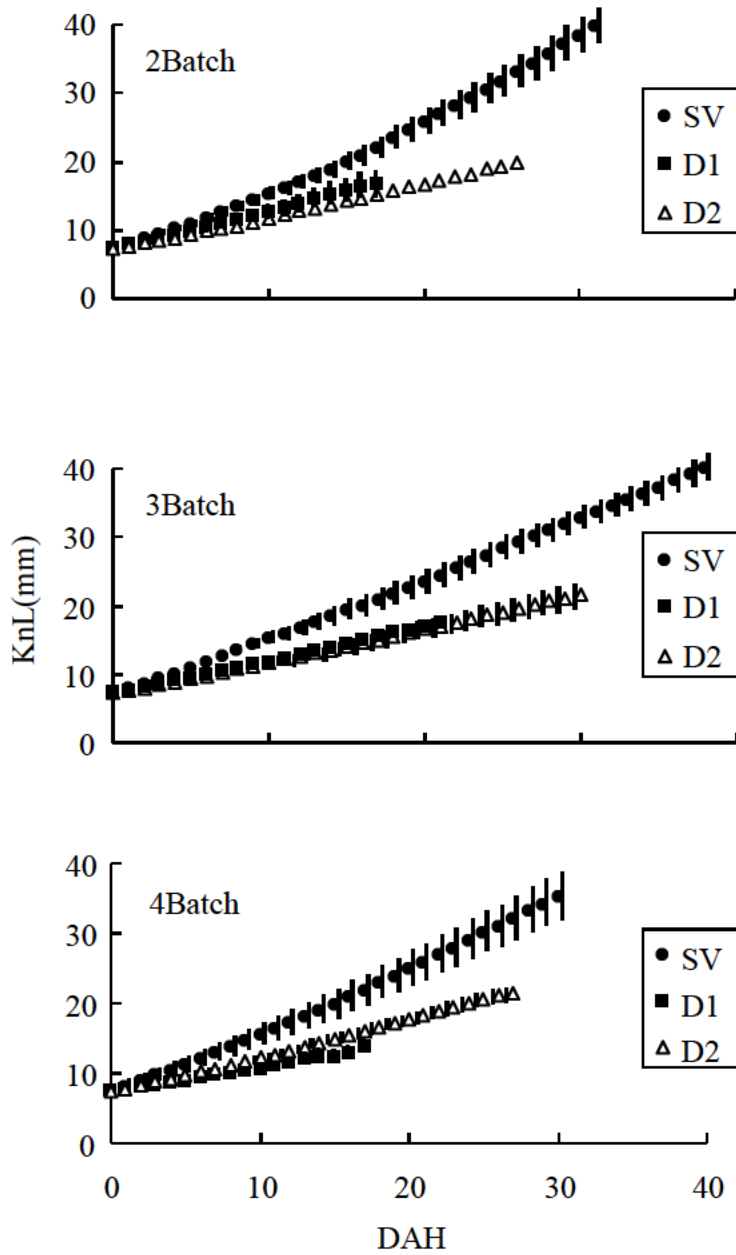


Fig. 5 Nakaya *et al.*