

Growth–feeding linkage in small pelagic fish larvae in the Kii Channel, Japan

メタデータ	言語: English
	出版者:
	公開日: 2024-06-25
	キーワード (Ja):
	キーワード (En): anchovy; feeding success; growth rate;
	larvae; morphological development; otolith; round
	herring; somatic size
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URL	https://fra.repo.nii.ac.jp/records/2008602

1	ORIGINAL ARTICLE
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3	Growth-feeding linkage in small pelagic fish larvae in the Kii
4	Channel, Japan
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26 **Funding information** 27 Japan Society for the Promotion of Science, Grant/Award Number: 21H04737 and 28 20K20455. 29 30 Running title: Growth and feeding of fish larvae 31 32 Abstract 33 The linkage between growth rate and feeding success has been shown to strengthen the 34 effects of early growth rate on later growth rate in the early life history of fish. 35 However, the growth-feeding linkage largely remains to be tested at the individual 36 level within the same populations/cohorts. We examined the growth-feeding linkage 37 for multiple populations/cohorts in Japanese anchovy Engraulis japonicus larvae and 38 Pacific round herring Etrumeus micropus larvae, through otolith microstructure 39 analysis, based on samples collected from the commercial fishery for larval fish in the 40 Kii Channel, Japan. The three growth-feeding mechanisms, which are based on the 41 respective potential advantages of larger somatic size, higher growth rate, and earlier 42 morphological development for achieving feeding success, were tested to understand 43 how growth rate relates to feeding success. The "somatic size" mechanism was 44 supported for all of 6 samples for anchovy larvae and 3 of 4 samples for round herring 45 larvae. The "growth rate" mechanism was supported for 2 of 6 samples for anchovy 46 larvae and 3 of 4 samples for round herring larvae. The "morphological development" 47 mechanism was supported for 3 of 4 samples for anchovy larvae and all of 3 samples 48 for round herring larvae. Overall, the present analysis supported the growth-feeding 49 linkage but revealed the dynamics of the growth-feeding mechanisms. All the 50 mechanisms were shown to operate at least for certain populations/cohorts, but none of

51	them were universally effective over all populations/cohorts across the two species.
52	Understanding the dynamics of the growth-feeding mechanisms would provide
53	precious hints for considering strategies of predicting recruitment dynamics.
54	
55	KEYWORDS
56	anchovy, feeding success, growth rate, larvae, morphological development, otolith,
57	round herring, somatic size
58	
59	1 INTRODUCTION
60	
61	Growth and survival dynamics during the early life stages have been a central issue in
62	studies on recruitment mechanisms of fish. The "growth-survival" paradigm, taking its
63	roots from the concept of growth-dependent mortality (Cushing, 1975) and later coined
64	as the "growth-mortality" hypothesis (Anderson 1988), postulates that larger and/or
65	faster-growing individuals will have higher probabilities of survival than smaller
66	and/or slower-growing conspecifics. This paradigm comprises three functional
67	mechanisms linking higher growth rate to survival advantages: "bigger is better",
68	"growth-selective predation", and "stage duration" mechanisms (Hare and Cowen,
69	1997; Searcy and Sponaugle, 2001; Houde, 2008; Leggett and Frank, 2008; Plaza &
70	Ishida, 2008; Takasuka et al., 2017). The "bigger is better" mechanism (Miller et al.,
71	1988) focuses on survival advantages linked to larger somatic size. Faster-growing
72	individuals are characterized by a larger somatic size than slower-growing conspecifics
73	at a given age. This size-based mechanism works when larger larvae have higher
74	growth rates in the population and larvae experience negative size-selective mortality
75	(selectivity against smaller size). The "growth-selective predation" mechanism

76	(Takasuka et al., 2003, 2004a,b) links growth rates per se to survival directly.
77	Slower-growing individuals generally display poorer physiological conditions and thus
78	have a lower potential in antipredator behaviors (Chick & Van Den Avyle, 2000;
79	Fuiman and Magurran, 1994; Skajaa et al., 2003). The mechanism works when
80	slower-growing individuals are more vulnerable to predation mortality than
81	faster-growing conspecifics at the same somatic size. The higher vulnerability of
82	slower-growing individuals can result from lower locomotor activities (Nakamura et al.,
83	2022). The "stage duration" mechanism (Chambers and Leggett, 1987; Houde, 1987)
84	focuses on the effects of growth rates on the timing of metamorphosis. This time-based
85	mechanism works when higher growth rates accelerate the timing of the
86	metamorphosis from larval to juvenile stages and faster-growing individuals
87	experience a shorter duration of the high-mortality larval stage. The three
88	growth-survival mechanisms are independent of and synergistic with one another in
89	operation (Takasuka et al., 2003, 2017).
90	The earlier studies on recruitment mechanisms of fish focused on the initial feeding
91	success following yolk exhaustion (Hjort, 1914; Cushing, 1975, 1990; Lasker, 1975,
92	1978). As the origin of fisheries oceanography, the "critical period" hypothesis
93	postulated that feeding success/failure at the start of external feeding largely
94	determines year-class strength of fish populations (Hjort, 1914). This concept was then
95	extended to the "match/mismatch" and "ocean stability" hypotheses, which are based
96	on the critical roles of starvation in regulating recruitment (Cushing, 1975, 1990;
97	Lasker, 1975, 1978). Nonetheless, several review papers (Anderson, 1988; Leggett and
98	DeBlois, 1994) contended that these hypotheses focusing on the feeding success at the
99	start of external feeding have rarely been supported in the field. The current
100	understanding holds that recruitment is determined by cumulative survival/mortality

101	throughout the larval to juvenile stages rather than a sole episodic starvation event
102	immediately after hatching (Sissenwine, 1984; Watanabe et al., 1995; Houde, 2008;
103	Robert et al., 2023). Furthermore, predation is recognized as the major and direct
104	source of mortality throughout early life, whereas starvation is an important direct
105	source mortality only during the short first-feeding period (Bailey and Houde, 1989).
106	The extended timing over which mortality operates during early life thus constitutes a
107	major departure from the classic hypothesis of Hjort (1914).
108	Growth rate is autocorrelated by nature, which was often confirmed in daily
109	increments recorded in the otolith microstructure (Campana, 1990; Folkvord et al.,
110	2000; Dower et al., 2009; Pepin et al., 2015). Growth autocorrelation is stronger when
111	faster- and slower-growing individuals continue to growth faster and slower,
112	respectively. To the contrary, growth autocorrelation is weaker when individual growth
113	rate is variable or random throughout early development. The extent of growth
114	autocorrelation has been evaluated at the group level by determining the correlation
115	coefficient between combinations of daily otolith increment widths (proxies for daily
116	growth rates), corresponding to two different ages (Dower et al., 2009; Robert et al.,
117	2014a; Pepin et al., 2015; Burns et al., 2021; Primo et al, 2021; Tanaka et al., 2023).
118	Pepin et al. (2015) proposed to use the extent of growth autocorrelation as a tool for
119	considering potential effects of early growth rate on later growth rate in the life history
120	of fish.
121	A potential mechanism underlying the growth autocorrelation is attributable to the
122	linkage between growth rate and feeding success/failure (hereafter, growth-feeding
123	linkage) (Dower et al., 2009; Robert et al., 2014a; Pepin et al., 2015). In theory,
124	faster-growing larvae are characterized by higher probabilities of feeding success on
125	which they rely to maintain higher growth rate levels (positive feedback loop);

126 reversely, slower-growing larvae are characterized by lower probabilities of feeding 127 success and thus keep lower growth rate levels (negative feedback loop). The strength 128 of these positive and negative feedback loops would be linked to the level of growth 129 autocorrelation in a given species. Previous studies have shown that the level of growth 130 autocorrelation differs among species with a general trend that faster-growing species 131 display higher growth autocorrelation than slower-growing species (Pepin et al., 2015; 132 Tanaka et al., 2023). These lines of evidence have led to the idea that feeding failure 133 after the start of external feeding, even if it does not result in starvation mortality 134 immediately, could continue to influence survival potential during the later life stages, 135 especially in faster-growing species. In this sense, the effects of growth autocorrelation 136 on survival potential could reconcile the classic recruitment hypotheses (importance of 137 the first feeding stage) and the current "growth-survival" paradigm (importance of 138 growth performance throughout early life), as argued by Tanaka et al. (2023). 139 Despite the potential importance of the growth-feeding linkage, previous studies on 140 this topic presented major limitations. First, the growth-feeding linkage was examined 141 based on the data pooled over various samples originating from different populations 142 and/or cohorts (regions and seasons). Second, the samples included only early larval 143 stages. These limitations were mainly due to the difficulty to obtain a sufficient number 144 of fish larvae, particularly late larvae, by a single plankton gear tow at a given station 145 of a research survey. Hence, the growth-feeding linkage largely remains to be tested at 146 the individual level within the same populations/cohorts. Growth-survival 147 relationships have been shown to be more variable and dynamic than previously 148 recognized when comparing growth and survival dynamics among different 149 populations/cohorts (Robert et al., 2007; Takasuka et al., 2017). Here emerged a need 150 to investigate the dynamics of the growth-feeding relationships among different

151 populations/cohorts in the field.

152 Japan waters host a unique commercial fishery in which postlarval stages of small 153 pelagic fish (called *shirasu*) are commercially captured by trawlers for food resources 154 (e.g., raw fish for *sushi* and dried fish for snacks or cooking ingredients). The *shirasu* 155 fishing grounds are typically formed in the shallow waters of coastal areas. One of the 156 major *shirasu* fishing grounds is formed in the Kii Channel (Figure 1), where 157 commercial catches include Japanese anchovy Engraulis japonicus (throughout the 158 year), Japanese sardine Sardinops melanostictus (late autumn to mid-spring), and 159 Pacific round herring Etrumeus micropus (late autumn to mid-summer) (Yasue et al., 160 2011). Previous studies used multiple samples collected from the commercial catches 161 to study growth, development, feeding, and trophodynamics during the early life stages 162 of small pelagic fish in the Kii Channel (Yasue and Takasuka, 2009; Yasue et al., 2011, 163 2014, 2016). The commercial fishery provides the unique opportunity to obtain large 164 sample sizes of larvae from the same populations/cohorts, allowing us to examine 165 variability in the relationships linking growth characteristics to feeding success at the 166 individual level within the same populations/cohorts. 167 In the present study, we examined the linkage between growth rate and feeding 168 success at the individual level within the same populations/cohorts in Japanese 169 anchovy larvae and Pacific round herring larvae, through otolith microstructure 170 analysis, based on multiple samples collected from the *shirasu* fishery in the Kii 171 Channel, Japan. As an analogy of the three functional mechanisms of the 172 growth-survival paradigm, we considered three functional mechanisms linking growth 173 rate to feeding success as hypotheses to test: "somatic size", "growth rate", and 174 "morphological development" mechanisms, which are based on the respective 175 potential advantages of larger somatic size, higher growth rate, and earlier

176	morphological development for achieving feeding success. The "somatic size"
177	mechanism hypothesizes that somatic size influences feeding success: larger
178	individuals have higher probabilities of feeding success at a given age. The "growth
179	rate" mechanism hypothesizes that growth rate directly influences feeding success:
180	faster-growing individuals have higher probabilities of feeding success at a given
181	somatic size. The "morphological development" mechanism hypothesizes that
182	morphological development influences feeding success: more morphologically
183	developed individuals have higher probabilities of feeding success at a given age. The
184	three growth-feeding mechanisms were tested to understand how growth rate relates to
185	feeding success.
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- $198 -20^{\circ}$ C in a freezer. Sardine larvae were also included in the catches in winter but were
- 199 not considered for the present study, as they only represented a minor proportion of
- 200 catches.

201 Japanese anchovy spawn almost throughout the year with a peak from May to July, 202 and Pacific round herring spawn mainly from October to July off the Pacific coast of 203 Japan (Oozeki et al., 2007). In the Kii Channel, anchovy larvae occur almost 204 throughout the year, and round herring larvae occur mainly from November to July 205 (Yasue et al., 2011). Larval sampling was conducted in different months to collect 206 larval samples with various growth and morphological characteristics. The present 207 sampling design intended to reveal the dynamics of the growth-feeding mechanisms 208 by taking advantage of the seasonal variability in growth and morphological 209 characteristics. 210 A total of 6 samples comprising 1,889 individuals and 4 samples comprising 1,214 211 individuals were collected and analyzed for anchovy and round herring, respectively 212 (Table 1). Each sample included > 200 individuals (> 300 individuals in most cases) of 213 anchovy or round herring larvae. Note that "sample" here refers to a group of larvae 214 collected simultaneously during a given net tow. The larvae within each sample were 215 assumed to have hatched during a certain period and experienced similar 216 environmental conditions, at least at the time of sampling. Even with relatively wide 217 age ranges (thus wide hatching date ranges) within each sample (Table 1), different 218 samples were interpreted as different populations/cohorts. The samples covered a 219 variety of seasonal populations/cohorts with a substantial variability of sea temperature 220 at 10 m depth near the trawling areas in the fishing ground (Figure 1), which was 221 measured by a self-registering thermometer attached to an observation station 222 (Shirahama Oceanographic Observatory, Disaster Prevention Research Institute, Kyoto 223 University, Wakayama, Japan). The thermometer was located < 5 km from the trawling 224 areas.

226 **2.2** | Measurement and observation

227 SL was measured to the nearest 0.1 mm for each larva using a digital caliper, after a 228 sample of frozen larvae was thawed. A photograph of each larva was taken by a digital 229 camera for subsequent morphological measurements. On a photograph, head length, 230 head height, lower jaw length, and orbit diameter (eye diameter) were measured to the 231 nearest 0.01 mm, using ImageJ software (Schneider et al., 2012; https://imagej.net/, 232 RRID: SCR 003070). These morphological characteristics were selected as factors 233 which are potentially related to feeding activity and ability (Sabatés and Saiz, 2000; 234 Gisbert et al., 2004; Catalán et al., 2007; Morote et al., 2008). Head and jaw 235 morphology could be influential in feeding, since mouth size has previously been 236 shown to influence feeding success (Blaxter and Hunter, 1982). In general, clupeoid 237 fish larvae are visual predators that feed through a particulate-feeding mode, until they 238 alternate between particulate-feeding and filter-feeding modes with their gill raker 239 development (de Ciechomski, 1966; Uotani et al., 1978; James and Findlay, 1989; 240 Garrido et al., 2007). Thus, eye diameter could also be a potential factor influencing 241 feeding success. Note that the photographs of larvae and the data of morphological 242 characteristics were available only for 4 of 6 samples and 3 of 4 samples for anchovy 243 and round herring, respectively (Table S1).

The status of feeding success was defined by presence/absence of any food items in the gut of each larva by visual observation under a binocular stereo microscope. The main prey items of anchovy and round herring larvae are copepods. For example, a gut content analysis showed that copepods represented the vast majority of prey items (90–99% and 74–95% for anchovy and round herring, respectively) based on the samples in the Kii Channel from December to March (Yasue et al., 2011). These copepods are highly visible as they are colored with the astaxanthin red pigment.

251	Given this characteristic, we were able to externally detect the presence of ingested
252	copepods in the relatively transparent, linear digestive tractus of the larvae. If any
253	copepods were visible in the guts of a given individual by external observation, that
254	larva was identified as "feeding larva"; if no copepod was detected in a given
255	individual, it was identified as "non-feeding larva". This identification method
256	indicates the status of feeding success a few hours prior to capture but does not reflect
257	feeding history.
258	
259	2.3 Growth analysis
260	Sagittal otoliths were dissected from each larva and then mounted on a glass slide with
261	enamel resin. Either the left or the right sagitta was used based on the assumption of
262	symmetry between both otoliths. A series of otolith measurements were conducted by
263	an otolith measurement system (RATOC System Engineering, Tokyo, Japan), which is
264	composed of a transmitted light microscope with a video camera connected to a
265	computer and monitor. This system enables measuring an otolith on a live image under
266	different focal points. On a monitor, a measurement transect was set from the nucleus
267	to the outermost posterior margin of the otolith. Along the measurement transect,
268	maximum otolith radius (OR) and each daily increment width were measured to the
269	nearest 0.1 µm.
270	The first increment is deposited 3 to 4 days after hatching for anchovy (Tsuji and
271	Aoyama, 1984) and 2 days after hatching for round herring (Hayashi and Kawaguchi,
272	1994) in rearing conditions. Thus, age in days (daily age) was determined as the
273	number of daily growth increments plus 3 and plus 1 for anchovy and round herring,
274	respectively. Hatching date was determined by date of capture and daily age. SL at the
275	time of hatching was 2.9 mm for anchovy (Fukuhara and Takao, 1988) and 5.0 mm for

276 round herring (Hayashi and Kawaguchi, 1994). Mean growth rate from hatching to 277 capture was calculated by dividing SL minus the SL at the time of hatching by daily 278 age. SL and daily growth rate at each age were back-calculated by the biological 279 intercept method (Campana 1990). The relationships between OR and SL were well 280 expressed as allometric relationships for anchovy and round herring larvae (Takasuka 281 et al., 2008; Yasue et al., 2011). Thus, an allometric formula was determined separately 282 for each larva with SL at the first growth increment deposition fixed at 5.6 mm for 283 anchovy (Fukuhara, 1983) and 6.0 mm for round herring (Hayashi and Kawaguchi, 284 1994) as the biological intercepts in the back-calculation. In the back-calculated 285 growth history, the growth rate based on the distance from the last increment to the 286 outermost margin was excluded, as it does not necessarily correspond to the daily 287 growth rate. Note that the growth rate data were available for all the individuals of 6 288 samples and 4 samples for anchovy and round herring, respectively (Table 1), and that 289 the 6 anchovy samples and their growth rate data were also used in Tanaka et al. (2024), 290 which detailed seasonal variability in the otolith and somatic size relationship for 291 anchovy larvae. 292 If any uncoupling in the OR–SL relationship occurs, it could be a possible source of

biases in the back-calculation (Campana 1990). For example, growth effects on the

294 OR–SL relationship were observed for anchovy and sardine larvae (Takasuka et al.,

2008; Tanaka et al., 2024) as in many species. Therefore, the fitness of the allometric

296 formula was a concern. In the present samples, the values of coefficient of

297 determination (r^2) of allometric formula in the OR–SL relationships were 0.500 and

- 298 0.688 for the overall samples of anchovy and round herring, respectively. These
- 299 coefficients were relatively low because of the substantial variability among samples.
- 300 At the sample level, however, the r^2 value ranged from 0.821 to 0.949 and from 0.893

301 to 0.922 for anchovy and round herring, respectively. These values were high enough 302 to ensure reliable back-calculation based on the allometric relationships, compared to 303 the cases of several previous studies (e.g., Takasuka et al., 2008 and references therein). 304 Note that the processes and calculation methods for otolith microstructure analysis in 305 the present study are consistent with those in the previous studies on growth-survival 306 dynamics for anchovy and round herring larvae (e.g., Takasuka et al., 2003, 2004a,b; 307 Yasue and Takasuka, 2009; Yasue et al., 2011; Takasuka et al., 2017; Tanaka et al., 308 2024). 309

310 **2.4**

2.4 | Mechanism tests

Somatic size, age, and growth rate were compared between the feeding and non-feeding larvae to understand the general differences in growth characteristics between the two groups for the respective samples. First, relationships of SL to daily age (i.e., size-at-age data) were described and compared between the two groups. Then, the three growth–feeding mechanisms were tested in the context of the direct or indirect effects of growth rate in a more rigorous manner.

317 The "somatic size" mechanism was tested by comparing growth rate between the 318 feeding and non-feeding larvae at the same daily age. Mean growth rate from hatching 319 to capture was adopted as a proxy for growth rate since somatic size is a cumulative 320 consequence of growth rate from hatching to capture (Takasuka et al., 2003, 2008). A 321 linear regression analysis was applied to the relationships of mean growth rate to daily 322 age for the feeding and non-feeding larvae, respectively. When linear regressions were 323 statistically significant for both groups and their slopes were parallel, an analysis of 324 covariance (ANCOVA) was applied to the data with daily age as a covariate to test for 325 any differences in the intercepts of the regressions. When linear regressions were not

326 significant for either or both groups or their slopes were not parallel given significance, 327 differences in mean growth rate were tested by Student's t-test or Welch's t-test, 328 depending on the normality and homoscedasticity, between the feeding and 329 non-feeding larvae within their common ranges of daily age. 330 The "growth rate" mechanism was tested by comparing growth rate between the 331 feeding and non-feeding larvae at the same somatic size. Recent 3-day mean growth 332 rate directly before capture in the back-calculated growth history was adopted as a 333 proxy for growth rate since it represents an instantaneous status of growth rate 334 (Takasuka et al., 2007, 2017). A linear regression analysis was applied to the 335 relationships of recent 3-day mean growth rate to SL for the feeding and non-feeding 336 larvae, respectively. When linear regressions were statistically significant for both 337 groups and their slopes were parallel, an ANCOVA was applied to the data with SL as 338 a covariate. Otherwise, differences in recent 3-day mean growth rate were tested by 339 Student's t-test or Welch's t-test between the feeding and non-feeding larvae within 340 their common ranges of SL. The "morphological development" mechanism was tested by comparing 341 342 morphological characteristics (head length, head height, lower jaw length, and eye 343 diameter) between the feeding and non-feeding larvae at the same daily age. The 344 morphological characteristics were expressed in proportion to SL since they increased 345 with SL (Figures S1–S4). Allometric relationships fitted to the relationships of the 346 morphological characteristics (in proportion to SL) to daily age. Thus, a linear 347 regression analysis was applied to the relationships of the morphological 348 characteristics to daily age in *ln*-transformed data. When linear regressions were 349 statistically significant for both groups and their slopes were parallel, an ANCOVA was 350 applied to the data with daily age as a covariate. Otherwise, differences in

351 morphological characteristics were tested by Student's *t*-test or Welch's *t*-test between 352 the feeding and non-feeding larvae within their common ranges of daily age. The 353 effects of growth rate on morphological characteristics were also examined for the 354 respective samples. Mean growth rate from hatching to capture was adopted as a proxy 355 for growth rate since morphological characteristics are potentially a cumulative 356 consequence of growth rate from hatching to capture. As both growth rate and 357 morphological characteristics were related to daily age (see Results), both factors were 358 standardized by daily age. Residuals of linear regressions of growth rate on daily age 359 and those of morphological characteristics on daily age (in *ln*-transformed data) were 360 used to describe the relationships of morphological characteristics to growth rate. Then, 361 a linear regression analysis was applied to those relationships.

362

- 363 3 **RESULTS**
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- 365

3.1 | Growth characteristics

366 Profiles of the samples are summarized in Table 1. For anchovy larvae, a total of 6 367 samples (A1-A6) comprising 1,889 individuals were collected from July 12, 2021 to 368 April 28, 2022, under the sea temperature range of 16.5–26.9°C. The number of 369 individuals ranged from 213 (Sample A4) to 388 (Sample A1). The SL of anchovy 370 larvae ranged from 13.7 to 35.5 mm, and the daily age ranged from 16 to 64 days. 371 Mean growth rate from hatching to capture and recent 3-day mean growth rate showed 372 substantial variability within and among samples. The fraction of feeding larvae 373 fluctuated between 14.1% and 48.3% depending on the samples. Note that any samples 374 including less than 20 individuals of feeding larvae were not considered in the present 375 study as the sample size was considered insufficient to ensure statistical reliability. For

376	round herring larvae, a total of 4 samples (R1-R4) comprising 1,214 individuals were
377	collected from July 29, 2021 to April 14, 2022, under the temperature range
378	16.5–26.8°C. The number of individuals ranged from 273 (Sample R1) to 322 (Sample
379	R4). The SL of round herring larvae ranged from 15.9 to 33.5 mm; the daily age
380	ranged from 17 to 64 days. Mean growth rate from hatching to capture and recent
381	3-day mean growth rate showed substantial variability within and among the samples.
382	The fraction of feeding larvae fluctuated between 32.6% and 76.9%.
383	The relationships of SL to daily age (size-at-age data) varied among the samples
384	both for anchovy larvae and round herring larvae (Figure 2). The ranges of SL and
385	daily age substantially overlapped between feeding and non-feeding larvae. However,
386	the feeding larvae tended to be larger and older than the non-feeding larvae.
387	

388 3.2 | Somatic size mechanism

389 Mean growth rate from hatching to capture decreased with daily age both for anchovy 390 larvae and round herring larvae (Figure 3). Negative linear regressions were fitted to 391 the relationships of mean growth rate to daily age for feeding larvae and non-feeding 392 larvae for all samples (p < 0.05). The slopes of the regressions differed between 393 feeding and non-feeding larvae (p < 0.001) and thus the mean growth rates were 394 compared between the two groups by Student's t-tests within the common daily age 395 ranges for Samples A4 (anchovy), R1, and R4 (round herring). The slopes of the 396 regressions were parallel and thus the intercepts were compared between the two 397 groups by ANCOVAs for Samples A1, A2, A3, A5, A6 (anchovy), R2, and R3 (round 398 herring). Mean growth rates were significantly higher in feeding larvae than in 399 non-feeding larvae at the same daily age for all of 6 samples (Samples A1-A6) for 400 anchovy larvae and 3 of 4 samples (Samples R1–R3) for round herring larvae (p < p

401	0.01). As an exception, mean growth rates were significantly lower in feeding larvae
402	than in non-feeding larvae for Sample R4 (round herring) ($p < 0.001$).

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- 404

3.3 | Growth rate mechanism

405 Recent 3-day mean growth rate directly before capture increased, decreased, or did not 406 relate with SL, depending on the samples, for anchovy larvae and round herring larvae 407 (Figure 4). Positive or negative linear regressions were fitted to the relationships of 408 recent growth rate to SL for both of feeding and non-feeding larvae for Samples A1, 409 A2, A4, A5, A6 (anchovy), and R4 (round herring) (p < 0.05) but not for Samples A3 410 and R1–R3 (round herring) (p > 0.05). The linear regressions were not significant for 411 either or both of feeding and non-feeding larvae (p > 0.05) or the slopes of the linear regressions differed between feeding and non-feeding larvae (p < 0.001) and thus the 412 413 recent growth rates were compared between the two groups by Student's t-tests within 414 the common SL ranges for Samples A1, A2, A3, A5, A6 (anchovy), and R1-R3 (round 415 herring). The slopes of the regressions were parallel and thus the intercepts were 416 compared between the two groups by ANCOVAs for Samples A4 (anchovy) and R4 417 (round herring). Recent 3-day mean growth rates were significantly higher in feeding 418 larvae than in non-feeding larvae at the same somatic size for 2 of 6 samples (Samples 419 A4 and A6) for anchovy larvae and 3 of 4 samples (Samples R1-R3) for round herring 420 larvae (p < 0.01). As exceptions, recent 3-day mean growth rates were significantly 421 lower in feeding larvae than in non-feeding larvae for Samples A1 (anchovy) and R4 422 (round herring) (p < 0.05).

423

424 **3.4** | Morphological development mechanism

425 The proportions of head length, head height, lower jaw length, and eye diameter to SL

426	increased with daily age in general (Figures 5-8). Linear regressions were fitted to the
427	relationships of the head length proportions to daily age in <i>ln</i> -transformed data for both
428	of feeding larvae and non-feeding larvae for Samples A3, A4 (anchovy), and R2-R4
429	(round herring) ($p < 0.05$) but not for Samples A5 and A6 (anchovy) ($p > 0.05$) (Figure
430	5). The linear regressions were not significant for either or both of feeding and
431	non-feeding larvae ($p > 0.05$) or the slopes of the linear regressions differed between
432	feeding and non-feeding larvae ($p < 0.001$) and thus the head length proportions were
433	compared between the two groups by Student's <i>t</i> -tests within the common daily age
434	ranges for Samples A5, A6 (anchovy), R3, and R4 (round herring). The slopes of the
435	regressions were parallel and thus the intercepts were compared between the two
436	groups by ANCOVAs for Samples A3, A4 (anchovy), and R2 (round herring). The
437	head length proportions were significantly higher in feeding larvae than in non-feeding
438	larvae at the same daily age for 2 of 4 samples (Samples A3 and A4) for anchovy
439	larvae and all of 3 samples (Samples R2–R4) for round herring larvae ($p < 0.01$)
440	(Figure 5).
441	Differences in the head height, lower jaw length, and eye diameter proportions to
442	daily age (in <i>ln</i> -transformed data) between feeding and non-feeding larvae were tested
443	in a similar manner to the head length proportions. The head height and lower jaw
444	length proportions were significantly higher in feeding larvae than in non-feeding
445	larvae at the same daily age for 3 of 4 samples (Samples A3-A5) for anchovy larvae
446	and all of 3 samples (Samples R2–R4) for round herring larvae ($p < 0.05$) (Figures 6
447	and 7). The eye diameter proportions were significantly higher in feeding larvae than
448	in non-feeding larvae at the same daily age for 1 of 4 samples (Sample A3) for
449	anchovy larvae and all of 3 samples (Samples R2–R4) for round herring larvae ($p <$
450	0.01) (Figure 8).

451	The head length proportions (standardized by daily age) were positively related to
452	mean growth rate from hatching to capture (standardized by daily age) for 3 of 4
453	samples (Samples A3–A5) for anchovy larvae and 2 of 3 samples (Samples R2 and R3)
454	for round herring larvae (linear regression analysis, $p < 0.01$) (Supplementary Figure
455	S5). The head height proportions (standardized by daily age) were positively related to
456	mean growth rate (standardized by daily age) for all of 4 samples (Samples A3–A6) for
457	anchovy larvae and all of 3 samples for round herring larvae (linear regression analysis,
458	p < 0.01) (Supplementary Figure S6). The lower jaw length and eye diameter
459	proportions (standardized by daily age) were positively related to mean growth rate
460	(standardized by daily age) for all of 4 samples (Samples A3–A6) for anchovy larvae
461	and 2 of 3 samples (Samples R2 and R3) for round herring larvae (linear regression
462	analysis, $p < 0.05$) (Supplementary Figures S7 and S8).
462	

464 **3.5** | Three growth–feeding mechanisms

The results of the tests of the three mechanisms are summarized in Table 2. Overall, the "somatic size" mechanism was supported for all of 6 samples for anchovy larvae and 3 of 4 samples for round herring larvae. The "growth rate" mechanism was supported for 2 of 6 samples for anchovy larvae and 1 of 4 samples for round herring larvae. The "morphological development" mechanism was supported at least in any of the head length, head height, lower jaw length, and eye diameter for 3 of 4 samples for anchovy larvae and all of 3 samples for round herring larvae.

472

473 4 | DISCUSSION

474

475 Growth-feeding linkage was examined for Japanese anchovy larvae and Pacific round

476	herring larvae by testing the three underlying functional mechanisms. The present
477	study led to advances in testing the growth-feeding linkage from several viewpoints.
478	First, the growth-feeding linkage was tested at the individual level for multiple
479	populations/cohorts separately. Second, the samples covered broad ranges of age and
480	somatic size of larvae. These advances were realized by taking advantage of the
481	present samples including multiple populations/cohorts with substantial sample sizes
482	from the shirasu fishing ground. Lastly, theoretical progress lies in testing the
483	growth-feeding linkage in terms of functional mechanisms. In reality, the actual
484	processes of the different mechanisms could be interconnected or interactive.
485	Nonetheless, a conceptual distinction in theory is useful to understand the roles of
486	growth characteristics in the feeding success, as in the growth-survival mechanisms
487	(Hovenkamp, 1992; Takasuka et al., 2017). In this context, the growth-feeding
488	mechanisms were tested under a clearly defined theoretical framework.
489	The "somatic size" mechanism was supported for the majority of tested samples of
490	different populations/cohorts. It is natural that larger larvae feed more than smaller
491	larvae in general, which was obvious in the comparison of somatic size between the
492	feeding and non-feeding larvae. Hence, this mechanism becomes an axiomatic truth if
493	broader larval size ranges are considered. Nonetheless, of note here is the fact that
494	somatic size variability influenced feeding success even at the same age: the larger
495	larvae showed higher feeding success even among individuals of the same age (and
496	thus the same hatch date). In general, larger larvae show higher levels of activity and
497	thus higher levels of feeding and antipredator behaviors (Miller et al., 1988). Higher
498	growth rate leads to larger somatic size at the same age. The advantages of larger
499	somatic size are likely to be evident in somatic size variability among the larvae
500	hatching on the same date, which is a consequence of higher growth rate (i.e., indirect

501 effects of growth rate).

502 The "growth rate" mechanism was supported only for the minority of tested samples. 503 The tests for multiple populations/cohorts showed that this mechanism is possible, 504 even though it was not universal as the "somatic size" mechanism. Faster-growing 505 larvae would be less vulnerable to predation mortality as they are characterized by 506 higher physiological conditions, which are generally linked to more elaborated 507 antipredator behaviors among the larvae of the same somatic size (Fuiman and 508 Magurran, 1994; Skajaa et al., 2003; Takasuka et al., 2003, 2004a,b). Similarly, 509 faster-growing larvae generally display enhanced feeding behaviors at a given somatic 510 size. Thus, growth rate could have direct effects on feeding success regardless of 511 somatic size or morphological development.

512 The "morphological development" mechanism was supported for the majority of 513 tested samples. Although the results differed among morphological characteristics, all 514 the characteristics were found to be potential drivers of feeding success. Head height 515 and lower jaw length would be particularly effective in anchovy larvae, whereas all 516 morphological characteristics would be effective in round herring larvae. The effects of 517 eye diameter were detected for round herring only, suggesting some species-specific 518 importance of the morphological characteristics in driving feeding. Visual detection 519 may play a more important role in the feeding behaviors of round herring relative to 520 anchovy. Larger proportions of head, jaw, and eye could be interpreted as factors 521 leading to enhanced feeding behaviors, which would improve the likeliness of feeding 522 success (Sabatés and Saiz, 2000; Gisbert et al., 2004; Catalán et al., 2007; Morote et al., 523 2008; Pepin, 2023, 2024). Furthermore, higher growth rate was shown to accelerate 524 morphological development in general. Thus, the advantages of larger head, longer jaw, 525 and larger eye relative to somatic size would also be a consequence of higher growth

rate (i.e., indirect effects of growth rate). As a note, all the measurements (somatic size 527 and morphological characteristics) were one-dimensional (length, height, or width), 528 and growth rate was originally defined as the increase of somatic length per unit time. 529 Hence, two- or three-dimensional measurements (e.g., body shape or weight) and 530 growth rate considering body mass may provide further advances in understanding the 531 "morphological development" mechanism in future studies. 532 Overall, the present analysis supported the growth-feeding linkage in anchovy 533 larvae and round herring larvae. At the same time, however, the tests for multiple 534 populations/cohorts revealed the dynamics of the growth-feeding mechanisms. All the 535 mechanisms were shown to operate at least for certain populations/cohorts, but none of 536 them were universally effective over all populations/cohorts across the two species. As 537 in the growth-survival mechanisms, the growth-feeding mechanisms are also 538 independent of and synergistic with one another. However, we found a marked contrast 539 in the relative importance of mechanisms based on somatic size and growth rate 540 between the growth-survival and growth-feeding mechanisms. The operation of the 541 growth-survival mechanisms was shown to be dynamic for multiple 542 populations/cohorts of anchovy in Sagami Bay, which is another *shirasu* fishing 543 ground (Takasuka et al., 2017). Although none of the three growth-survival 544 mechanisms were universally effective, the "growth-selective predation" mechanism 545 was identified to be the major mechanism regulating the growth-survival relationships, 546 whereas the "bigger is better" mechanism was identified to be a minor one. That is, the 547 effects of growth rate at a given size in survivorship were more generally detected than 548 those of somatic size at a given age. This significance of the "growth-selective 549 predation" mechanism relative to the "bigger is better" mechanism was theoretically 550 explained by the optimal foraging theory on the side of predators (Takasuka et al.,

551 2003, 2007). In short, smaller larvae are more easily captured by some types of 552 predators but are not necessarily optimal for the predators in terms of energy gain, 553 whereas slower-growing larvae are more easily captured by the predators without 554 sacrificing energy intake on the side of predators. To the contrary, the effects of 555 somatic size at a given age were more generally detected than those of growth rate at a 556 given size in the case of the growth-feeding mechanisms. This contrast is probably due 557 to the fact that feeding success of larvae is not related to any energy trade-off on the 558 side of the predators, given that there is no disadvantage of larger somatic size in 559 feeding success. For this reason, we argue that the effects of somatic size could be 560 detected more easily and markedly in the growth-feeding mechanisms than in the 561 growth-survival mechanisms.

562 The variability observed in the growth-feeding mechanisms in anchovy larvae and 563 round herring larvae could be attributed to spatial and temporal variability in the 564 characteristic of larval populations/cohorts driven by environmental factors. The size 565 and age composition and density of the larvae would differ depending on the 566 populations/cohorts. Moreover, these characteristics could vary temporally even within 567 the populations/cohorts. Physical factors (e.g., sea temperature and salinity) and 568 biological factors (e.g., prey and predator fields) would influence growth rate and 569 physiological conditions of the individual larvae and thus size and age composition and 570 density of the larval populations/cohorts (Baumann et al., 2003; Llopiz et al., 2014). 571 Such environmental factors would also influence feeding success itself. For example, 572 the substantial variability in the fraction of feeding larvae may be a consequence of 573 variability in food availability and intraspecific competition. Identifying the factors 574 responsible for the dynamics is outside the scope of the present study. As the dynamics 575 of these factors are highly complex in the field, a systematic and extensive monitoring

576 survey for the larval populations/cohorts and environmental factors will be required to 577 clarify how the potential factors are generating the variability in the growth-feeding 578 linkage and the operation of the growth-feeding mechanisms feeding mechanisms. 579 Several research avenues could be drawn from the present study. First, a quantitative 580 evaluation of feeding success would improve our understanding of the roles of the 581 growth-feeding mechanisms. Here, feeding success was evaluated by the 582 presence/absence of any number of prey items in the guts in a qualitative manner. The 583 present study intentionally avoided evaluating feeding success in a quantitative manner 584 because of lack of information on digestion and evacuation rates. However, growth rate 585 may also affect food consumption rate (Dower et al., 2009; Robert et al., 2014a; Pepin 586 et al., 2015). Any quantitative assessment based on the number and size of prey items 587 may improve understanding the roles of growth rate in feeding success. For example, 588 carbon content data converted from prey size and numbers would be useful in such an 589 assessment in future studies (Robert et al., 2014a; Pepin et al., 2015). Furthermore, 590 detailed taxonomical knowledge of prey selectivity by larvae may be needed to better 591 quantify feeding success (Robert et al., 2014b). In the Kii Channel, the main prey items 592 of anchovy larvae are copepods, but copepod prey composition shows major seasonal 593 shifts (Yasue et al., 2010). Reconstruction of carbon content data from the detailed 594 information on prey items may also enable an examination of feeding history, which 595 lacked in the present approach. Second, there will be a need to design a combination of 596 field and laboratory experiments. The present study discriminated the growth-feeding 597 mechanisms in theory. Yet, it is virtually impossible to exactly discriminate the effects 598 of the different factors, in consideration of the interconnective or interactive nature of 599 somatic size, growth rate, and morphological development. For example, the effects of 600 somatic size and morphological development cannot be quantitatively discriminated.

601	Likewise, it is difficult to specify how each factor actually influences the feeding
602	success in the field. Therefore, laboratory experiments will be needed to analyze
603	feeding behaviors in reared populations where age and size structures can be controlled,
604	as in previous studies on feeding success (Hunter, 1972; Blaxter and Hunter, 1982;
605	Chick & Van Den Avyle, 2000; Garrido et al., 2007; Peck et al., 2015). In this context,
606	the present field study provided a hypothetical framework of the growth-feeding
607	mechanisms by identifying potential key factors driving feeding success for future
608	experimental studies.
609	The positive and negative feedback loops in growth and feeding have been
610	considered to strengthen growth autocorrelation (Dower et al., 2009; Robert et al.,
611	2014a; Pepin et al., 2015). The extent of growth autocorrelation differed among
612	taxonomic groups and species (Pepin et al., 2015; Tanaka et al., 2023). Furthermore,
613	some intraspecific variability was observed among different cohorts in some species
614	(Pepin et al., 2015). Based on our results, we argue that the dynamics of the
615	growth-feeding mechanisms would generate such interspecific and intraspecific
616	variability in growth autocorrelation. The primary motivation behind the
617	"growth-survival" paradigm is predicting recruitment dynamics based on growth rate
618	during early life stages. In this context, the extent of the growth-feeding linkage can be
619	interpreted as an indicator of future survival potential based on early life stages.
620	Understanding the dynamics of the growth-feeding mechanisms for different species
621	and populations/cohorts would provide precious hints for considering strategies of
622	predicting recruitment dynamics in target species and populations.
623	

624 ACKNOWLEDGEMENTS

625 The sea temperature data were provided by Dr. Yasuyuki Baba (Kyoto University). The

- 626 study benefited from comments of Drs. Takashi Yamakawa, Mari Kuroki, and Yoko
- 627 Iwata (The University of Tokyo) on the earlier contents. The present work was
- 628 financially supported by Grant-in-Aid for Scientific Research (A) (KAKENHI No.
- 629 21H04737) and Challenging Research (Pioneering) (KAKENHI No. 20K20455) from
- 630 the Japan Society for the Promotion of Science (JSPS).
- 631

632 CONFLICT OF INTEREST

- 633 The authors declare no conflict of interest.
- 634

635 AUTHOR CONTRIBUTIONS

- 636 S. Togoshi led the overall study as a part of his master thesis. A. Takasuka and D.
- 637 Robert developed the original concept of the study. N. Yasue handled the sample
- 638 collection. S. Togoshi and S. Tanaka measured and analyzed the larval samples and
- otoliths. M. Nakamura designed the morphological measurements. A. Takasuka
- 640 redrafted the manuscript. All the authors contributed to elaborating the study processes,
- 641 interpreting the results, and developing the conclusions.
- 642

643 ETHICAL STATEMENT

- 644 Not applicable.
- 645

646 DATA AVAILABILITY STATEMENT

- 647 The data that support the findings of the present study are available from the
- 648 corresponding author upon reasonable request.
- 649

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882 SUPPORTING INFORMATION

- Additional supporting information can be found online in the Supporting Information
- 884 section at the end of this article.
- 885

Final version: May 2024

- 887 **TABLE 1** Profiles of samples of Japanese anchovy *Engraulis japonicus* and Pacific round herring *Etrumeus micropus* larvae collected in
- the Kii Channel during July 2021 to April 2022.

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Sample	Date of capture	ST (°C)	Category	п	SL (mm)		Age (days)		Recent GR (mm/day)		Mean GR (mm/day)	
					Range	Mean	Range	Mean	Range	Mean	Range	Mean
nchovy												
A1	Jul 12, 2021	24.1	All	388	15.5-32.0	23.5	20–59	32	0.26-0.90	0.51	0.45-0.91	0.65
			Feeding	55 (14.2%)	19.8-30.7	26.6	25–59	39	0.30-0.71	0.46	0.47-0.86	0.62
			Non-feeding	333 (85.8%)	15.5-32.0	23.0	20-55	31	0.26-0.90	0.52	0.45-0.91	0.66
A2	Jul 29, 2021	26.8	All	331	14.8-31.2	20.9	19–39	25	0.33-0.94	0.57	0.50-1.01	0.73
			Feeding	160 (48.3%)	16.0-31.2	21.6	19–36	26	0.36-0.81	0.58	0.56-0.89	0.73
			Non-feeding	171 (51.7%)	14.8-27.7	20.3	19–39	24	0.33-0.94	0.56	0.50-1.01	0.72
A3	Sep 9, 2021	26.9	All	313	13.7–34.6	23.4	16-44	29	0.23-0.86	0.52	0.40-0.95	0.71
			Feeding	131 (41.9%)	18.7–34.6	26.2	20-44	33	0.35-0.82	0.54	0.57-0.87	0.72
			Non-feeding	182 (58.1%)	13.7–29.5	21.3	16-40	27	0.23-0.86	0.51	0.40-0.87	0.70
A4	Mar 23, 2022	16.5	All	213	19.3–35.5	28.3	31-64	46	0.33-0.75	0.50	0.42-0.71	0.56
			Feeding	41 (19.2%)	24.0-34.4	30.9	38–56	47	0.35-0.75	0.57	0.50-0.70	0.60
			Non-feeding	172 (80.8%)	19.3-35.5	27.6	31-64	45	0.33-0.69	0.48	0.42-0.71	0.55
A5	Apr 14, 2022	18.9	All	341	16.6-33.1	24.8	23-48	36	0.27-0.91	0.55	0.47-0.88	0.62
			Feeding	86 (25.2%)	18.2-32.9	25.8	27–45	36	0.35-0.77	0.56	0.48-0.88	0.64
			Non-feeding	255 (74.8%)	16.6-33.1	24.4	23-48	36	0.27-0.91	0.54	0.47-0.80	0.61
A6	Apr 28, 2022	18.9	All	303	17.0-31.3	23.9	20–39	29	0.37-0.95	0.67	0.54-0.87	0.72
			Feeding	55 (18.2%)	18.3-30.7	23.8	20-37	28	0.50-0.95	0.72	0.62-0.83	0.75
			Non-feeding	248 (81.8%)	17.0-31.3	24.0	21-39	30	0.37-0.94	0.66	0.54-0.87	0.71
lound heri	ring											
R1	Jul 29, 2021	26.8	All	273	17.1-30.1	22.7	17–36	28	0.27-0.69	0.45	0.46-0.79	0.64
			Feeding	210 (76.9%)	17.1-30.1	23.3	19–36	29	0.29-0.69	0.46	0.53-0.79	0.64
			Non-feeding	63 (23.1%)	17.5-26.4	20.7	17-32	25	0.27-0.68	0.41	0.46-0.78	0.62
R2	Jan 19, 2022	17.4	All	314	19.1-33.5	25.2	22-48	30	0.41-0.86	0.59	0.52-0.83	0.67
			Feeding	113 (36.0%)	20.0-33.5	26.9	22-44	33	0.46-0.86	0.61	0.55-0.83	0.67
			Non-feeding	201 (64.0%)	19.1-33.2	24.3	22-48	29	0.41-0.85	0.58	0.52-0.78	0.66
R3	Mar 23, 2022	16.5	All	305	20.6-33.3	26.7	22–49	33	0.36-0.91	0.61	0.51-0.85	0.67
			Feeding	129 (42.3%)	20.9-33.3	28.4	22-47	35	0.36-0.79	0.64	0.53-0.84	0.68
			Non-feeding	176 (57.7%)	20.6-33.2	25.5	23-49	31	0.41-0.91	0.60	0.51-0.85	0.66
R4	Apr 14, 2022	18.9	All	322	15.9–31.7	24.6	19–64	37	0.26-0.82	0.42	0.39-0.85	0.54
			Feeding	105 (32.6%)	18.6–31.7	25.9	22-64	41	0.27-0.60	0.39	0.39-0.65	0.52
			Non-feeding	217 (67 4%)	15 9 31 6	23.0	19_60	35	0.26_0.82	0.43	0.41_0.85	0.55

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890 **TABLE 2** Summary of the test results of the "somatic size", "growth rate", and "morphological development" mechanisms for Japanese

891 anchovy *Engraulis japonicus* larvae and Pacific round herring *Etrumeus micropus* larvae.

892

Sample	Date of capture	Somatic size	Growth rate	Morphological development				
				Head legth	Head height	Lower jaw length	Eye diameter	
Anchovy								
A1	Jul 12, 2021	Effective	Contrary	_		_	_	
A2	Jul 29, 2021	Effective	NS	_		_	_	
A3	Sep 9, 2021	Effective	NS	Effective	Effective	Effective	Effective	
A4	Mar 23, 2022	Effective	Effective	Effective	Effective	Effective	NS	
A5	Apr 14, 2022	Effective	NS	NS	Effective	Effective	NS	
A6	Apr 28, 2022	Effective	Effective	NS	NS	NS	NS	
Round her	ring							
R1	Jul 29, 2021	Effective	Effective	_	_	_	_	
R2	Jan 19, 2022	Effective	Effective	Effective	Effective	Effective	Effective	
R3	Mar 23, 2022	Effective	Effective	Effective	Effective	Effective	Effective	
R4	Apr 14, 2022	Contrary	Contrary	Effective	Effective	Effective	Effective	

894 **Figure captions**

896 Sampling area for Japanese anchovy Engraulis japonicus larvae and FIGURE 1 897 Pacific round herring *Etrumeus micropus* larvae in the coastal fishing ground in the Kii 898 Channel, Japan, during July 2021 to April 2022. Shaded area indicates sampling area; 899 solid circle indicates the location of the observation station for the data of sea 900 temperature at 10 m depth. 901 902 FIGURE 2 Relationships of standard length to daily age (size-at-age) for the feeding 903 larvae versus non-feeding larvae of Japanese anchovy *Engraulis japonicus* (A1–A6) 904 and Pacific round herring *Etrumeus micropus* (R1–R4). 905 906 FIGURE 3 Relationships of mean growth rate from hatching to capture to daily age 907 for the feeding larvae and non-feeding larvae of Japanese anchovy Engraulis japonicus 908 (A1-A6) and Pacific round herring *Etrumeus micropus* (R1-R4). Linear regressions of 909 mean growth rate on daily age are shown when they were significant (equations not 910 shown, p < 0.05). Shaded areas indicate ranges of daily age for the feeding larvae and 911 non-feeding larvae for comparison. The comparison was limited to the common ranges 912 for A4, R1, and R4 by Student's *t*-test or Welch's *t*-test when analysis of variance 913 (ANCOVA) was not applicable and extended to the overall ranges for the other 914 samples by ANCOVA. *Mean growth rates were significantly higher in feeding larvae 915 (red asterisk) or non-feeding larvae (blue asterisk) (p < 0.01). 916 917 FIGURE 4 Relationships of recent 3-day mean growth rate directly before capture to 918 standard length for the feeding larvae and non-feeding larvae of Japanese anchovy

919	Engraulis japonicus (A1–A6) and Pacific round herring Etrumeus micropus (R1–R4).
920	Linear regressions of recent growth rate on standard length are shown when they were
921	significant (equations not shown, $p < 0.05$). Shaded areas indicate ranges of standard
922	length for the feeding larvae and non-feeding larvae for comparison. The comparison
923	was limited to the common ranges for A1, A2, A3, A5, A6, R1, R2, and R3 by
924	Student's <i>t</i> -test or Welch's <i>t</i> -test when analysis of variance (ANCOVA) was not
925	applicable and extended to the overall ranges for the other samples by ANCOVA.
926	*Recent 3-day mean growth rates were significantly higher in feeding larvae (red
927	asterisk) or non-feeding larvae (blue asterisk) ($p < 0.05$).
928	
929	FIGURE 5 Relationships of head length proportion to daily age for the feeding
930	larvae and non-feeding larvae of Japanese anchovy Engraulis japonicus (A3-A6) and
931	Pacific round herring <i>Etrumeus micropus</i> (R2–R4). Head length proportion is defined
932	as the proportion of head length to standard length. Linear regressions of
933	<i>ln</i> -transformed head length proportion on <i>ln</i> -transformed daily age are shown when
934	they were significant (equations not shown, $p < 0.05$). Shaded areas indicate ranges of
935	daily age for the feeding larvae and non-feeding larvae for comparison. The
936	comparison was limited to the common ranges for A5, A6, R3, and R4 by Student's
937	<i>t</i> -test or Welch's <i>t</i> -test when analysis of variance (ANCOVA) was not applicable and
938	extended to the overall ranges for the other samples by ANCOVA. *Head length
939	proportions were significantly higher in feeding larvae (red asterisk) ($p < 0.01$).
940	
941	FIGURE 6 Relationships of head height proportion to daily age for the feeding
942	larvae and non-feeding larvae of Japanese anchovy Engraulis japonicus (A3-A6) and
943	Pacific round herring <i>Etrumeus micropus</i> (R2–R4). Head height proportion is defined

944	as the proportion of head length to standard length. Linear regressions of
945	<i>ln</i> -transformed head height proportion on <i>ln</i> -transformed daily age are shown when
946	they were significant (equations not shown, $p < 0.01$). Shaded areas indicate ranges of
947	daily age for the feeding larvae and non-feeding larvae for comparison. The
948	comparison was limited to the common ranges for A4, A5, A6, and R3 by Student's
949	<i>t</i> -test or Welch's <i>t</i> -test when analysis of variance (ANCOVA) was not applicable and
950	extended to the overall ranges for the other samples by ANCOVA. *Head height
951	proportions were significantly higher in feeding larvae (red asterisk) ($p < 0.01$).
952	
953	FIGURE 7 Relationships of lower jaw length proportion to daily age for the feeding
954	larvae and non-feeding larvae of Japanese anchovy Engraulis japonicus (A3-A6) and
955	Pacific round herring Etrumeus micropus (R2-R4). Lower jaw length proportion is
956	defined as the proportion of lower jaw length to standard length. Linear regressions of
957	<i>ln</i> -transformed lower jaw length proportion on <i>ln</i> -transformed daily age are shown
958	when they were significant (equations not shown, $p < 0.01$). Shaded areas indicate
959	ranges of daily age for the feeding larvae and non-feeding larvae for comparison. The
960	comparison was limited to the common ranges for A4, A6, and R3 by Student's <i>t</i> -test
961	or Welch's <i>t</i> -test when analysis of variance (ANCOVA) was not applicable and
962	extended to the overall ranges for the other samples by ANCOVA. *Lower jaw length
963	proportions were significantly higher in feeding larvae (red asterisk) ($p < 0.05$).
964	
965	FIGURE 8 Relationships of eye diameter proportion to daily age for the feeding
966	larvae and non-feeding larvae of Japanese anchovy Engraulis japonicus (A3-A6) and
967	Pacific round herring Etrumeus micropus (R2-R4). Eye diameter proportion is defined

968 as the proportion of upper jaw length to standard length. Linear regressions of

969	<i>ln</i> -transformed eye diamete proportion on <i>ln</i> -transformed daily age are shown when
970	they were significant (equations not shown, $p < 0.05$). Shaded areas indicate ranges of
971	daily age for the feeding larvae and non-feeding larvae for comparison. The
972	comparison was limited to the common ranges for all the samples by Student's <i>t</i> -test or
973	Welch's <i>t</i> -test as analysis of variance (ANCOVA) was not applicable. *Eye diameter
974	proportions were significantly higher in feeding larvae (red asterisk) ($p < 0.01$).
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FIGURE 2

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FIGURE 3



FIGURE 4

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