

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

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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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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 grow 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.

186

187

188 **2 | MATERIALS AND METHODS**

189

190 **2.1 | Field sampling**

191 Samples of Japanese anchovy larvae and Pacific round herring larvae were collected
192 from the commercial catches by a trawler in the *shirasu* fishing grounds of the Kii
193 Channel, Japan, during July 2021 to April 2022 (Table 1, Figure 1). A trawler with a
194 cod end mesh size of approximately 1.5–2.0 mm was towed once or twice during the
195 morning hours (08:00–10:30) to target the larvae of approximately 13–30 mm in
196 standard length (SL) (Yasue and Takasuka, 2009). The samples of anchovy and round
197 herring larvae were randomly selected from the commercial catches and were frozen at
198 –20°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.

225

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 Ciechowski, 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).

244 The status of feeding success was defined by presence/absence of any food items in
245 the gut of each larva by visual observation under a binocular stereo microscope. The
246 main prey items of anchovy and round herring larvae are copepods. For example, a gut
247 content analysis showed that copepods represented the vast majority of prey items
248 (90–99% and 74–95% for anchovy and round herring, respectively) based on the
249 samples in the Kii Channel from December to March (Yasue et al., 2011). These
250 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
293 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.,
295 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 | Mechanism tests**

311 Somatic size, age, and growth rate were compared between the feeding and
312 non-feeding larvae to understand the general differences in growth characteristics
313 between the two groups for the respective samples. First, relationships of SL to daily
314 age (i.e., size-at-age data) were described and compared between the two groups. Then,
315 the three growth–feeding mechanisms were tested in the context of the direct or
316 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.

341 The "morphological development" mechanism was tested by comparing
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**

364

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 ($p <$

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) ($p < 0.001$).

403

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
412 regressions differed between feeding and non-feeding larvae ($p < 0.001$) and thus the
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 \ln -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 t -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 \ln -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).

463

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

465 The results of the tests of the three mechanisms are summarized in Table 2. Overall,
466 the “somatic size” mechanism was supported for all of 6 samples for anchovy larvae
467 and 3 of 4 samples for round herring larvae. The “growth rate” mechanism was
468 supported for 2 of 6 samples for anchovy larvae and 1 of 4 samples for round herring
469 larvae. The “morphological development” mechanism was supported at least in any of
470 the head length, head height, lower jaw length, and eye diameter for 3 of 4 samples for
471 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

526 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

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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
639 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

650 **REFERENCES**

651

652 Anderson, J. T. (1988). A review of size dependent survival during pre-recruit stages of
653 fishes in relation to recruitment. *Journal of Northwest Atlantic Fishery Science*, 8,
654 55–66. <https://doi.org/10.2960/J.v8.a6>

655 Bailey, K. M., & Houde, E. D. (1989). Predation on eggs and larvae of marine fishes
656 and the recruitment problem. *Advances in Marine Biology*, 25, 1–83.
657 [https://doi.org/10.1016/S0065-2881\(08\)60187-X](https://doi.org/10.1016/S0065-2881(08)60187-X)

658 Baumann, H., Pepin, P., Davidson, F. J. M., Mowbray, F., Schnack, D., & Dower, J. F.
659 (2003). Reconstruction of environmental histories to investigate patterns of larval
660 radiated shanny (*Ulvaria subbifurcata*) growth and selective survival in a large bay
661 of Newfoundland. *ICES Journal of Marine Science*, 60, 243–258.
662 [https://doi.org/10.1016/S1054-3139\(03\)00019-5](https://doi.org/10.1016/S1054-3139(03)00019-5)

663 Blaxter, J. H. S., & Hunter, J. R. (1982). The biology of the clupeoid fishes. *Advances*
664 *in Marine Biology*, 20, 1–223.
665 [https://doi.org/https://doi.org/10.1016/S0065-2881\(08\)60140-6](https://doi.org/https://doi.org/10.1016/S0065-2881(08)60140-6)

666 Burns, C. M., Pepin, P., Plourde, S., Veillet, G., Sirois, P., & Robert, D. (2021).
667 Revealing the relationship between feeding and growth of larval redfish (*Sebastes*
668 sp.) in the Gulf of St. Lawrence. *ICES Journal of Marine Science*, 78, 3757–3766.
669 <https://doi.org/10.1093/icesjms/fsab221>

670 Campana, S. E. (1990). How reliable are growth back-calculations based on otoliths?
671 *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 2219–2227.
672 <https://doi.org/10.1139/f90-246>

673 Catalán, I. A., Alemany, F., Morillas, A., & Morales-Nin, B. (2007). Diet of larval
674 albacore *Thunnus alalunga* (Bonnaterre, 1788) off Mallorca Island (NW
675 Mediterranean). *Scientia Marina*, 71, 347–354.

- 676 <https://doi.org/10.3989/scimar.2007.71n2347>
- 677 Chambers, R. C., & Leggett, W. C. (1987). Size and age at metamorphosis in marine
678 fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes*
679 *americanus*) with a review of variation in other species. *Canadian Journal of*
680 *Fisheries and Aquatic Sciences*, 44, 1936–1947. <https://doi.org/10.1139/f87-238>
- 681 Chick, J. H., & Van Den Avyle, M. J. (2000). Effects of feeding ration on larval
682 swimming speed and responsiveness to predator attacks: implications for cohort
683 survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 106–115.
684 <https://doi.org/10.1139/f99-185>
- 685 Cushing, D. H. (1975). *Marine ecology and fisheries*. Cambridge: Cambridge
686 University Press.
- 687 Cushing, D. H. (1990). Plankton production and year-class strength in fish populations:
688 an update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26,
689 249–293. [https://doi.org/10.1016/S0065-2881\(08\)60202-3](https://doi.org/10.1016/S0065-2881(08)60202-3)
- 690 de Ciechomski, J. D. (1966). Investigations of food and feeding habits of larvae and
691 juveniles of the Argentine anchovy *Engraulis anchoita*. *California Cooperative*
692 *Oceanic Fisheries Investigations Reports*, 11, 72–81.
- 693 Dower, J. F., Pepin, P., & Kim, G.-C. (2009). Covariation in feeding success,
694 size-at-age and growth in larval radiated shanny (*Ulvaria subbifurcata*): insights
695 based on individuals. *Journal of Plankton Research*, 31, 235–247.
696 <https://doi.org/10.1093/plankt/fbn118>
- 697 Folkvord, A., Blom, G., Johannessen, A., & Moksness, E. (2000). Growth-dependent
698 age estimation in herring (*Clupea harengus* L.) larvae. *Fisheries Research*, 46,
699 91–103. [https://doi.org/10.1016/S0165-7836\(00\)00136-3](https://doi.org/10.1016/S0165-7836(00)00136-3).
- 700 Fuiman, L. A., & Magurran, A. E. (1994). Development of predator defences in fishes.

- 701 *Reviews in Fish Biology and Fisheries*, 4, 145–183.
702 <https://doi.org/10.1007/bf00044127>
- 703 Fukuhara, O. (1983). Development and growth of laboratory reared *Engraulis japonica*
704 (Houttuyn) larvae. *Journal of Fish Biology*, 23, 641–652.
705 <https://doi.org/10.1111/j.1095-8649.1983.tb02943.x>
- 706 Fukuhara, O., & Takao, K. (1988). Growth and larval behaviour of *Engraulis japonica*
707 in captivity. *Journal of Applied Ichthyology*, 4, 158–167.
708 <https://doi.org/10.1111/j.1439-0426.1988.tb00556.x>
- 709 Garrido, S., Marçalo, A., Zwolinski, J., & van der Lingen, C. D. (2007). Laboratory
710 investigations on the effect of prey size and concentration on the feeding behaviour
711 of *Sardina pilchardus*. *Marine Ecology Progress Series*, 330, 189–199.
712 <https://doi.org/10.3354/meps330189>
- 713 Gisbert, E., Conklin, D. B., & Piedrahita, R. H. (2004). Effects of delayed first feeding
714 on the nutritional condition and mortality of California halibut larvae. *Journal of*
715 *Fish Biology*, 64, 116–132. <https://doi.org/10.1111/j.1095-8649.2004.00289.x>
- 716 Hare, J. A., & Cowen, R. K. (1997). Size, growth, development, and survival of the
717 planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). *Ecology*, 78,
718 2415–2431. [https://doi.org/10.1890/0012-9658\(1997\)078\[2415:SGDASO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2415:SGDASO]2.0.CO;2)
- 719 Hayashi, A., & Kawaguchi, K. (1994). Growth and daily otolith increments of reared
720 round herring *Etrumeus teles* larvae. *Fisheries Science*, 60, 619–619.
721 <https://doi.org/10.2331/fishsci.60.619>
- 722 Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in the
723 light of biological research. *Rapports et Procès-Verbaux des Réunions du Conseil*
724 *Permanent International pour l'Exploration de la Mer*, 20, 1–228.
- 725 Houde, E. D. (1987). Fish early life dynamics and recruitment variability. *American*

- 726 *Fisheries Society Symposium*, 2, 17–29.
- 727 Houde, E. D. (2008). Emerging from Hjort's shadow. *Journal of Northwest Atlantic*
728 *Fishery Science*, 41, 53–70. <https://doi.org/10.2960/J.v41.m634>
- 729 Hovenkamp, F. (1992). Growth-dependent mortality of larval plaice *Pleuronectes*
730 *platessa* in the North Sea. *Marine Ecology Progress Series*, 82, 95–101.
- 731 Hunter, J. R. (1972). Swimming and feeding behavior of larval anchovy *Engraulis*
732 *mordax*. *Fishery Bulletin*, 70, 821–838.
- 733 James, A. G., & Findlay, K. P. (1989). Effect of particle size and concentration on
734 feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy
735 *Engraulis capensis*. *Marine Ecology Progress Series*, 50, 275–294.
- 736 Lasker, R. (1975). Field criteria for survival of anchovy larvae: the relation between
737 inshore chlorophyll maximum layers and successful first feeding. *Fishery Bulletin*,
738 73, 453–462.
- 739 Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy
740 food in the California Current: identification of factors contributing to recruitment
741 failure. *Rapports et Procès-Verbaux des Réunions du Conseil Permanent*
742 *International pour l'Exploration de la Mer*, 173, 212–230.
- 743 Leggett, W. C., & DeBlois, E. (1994). Recruitment in marine fishes: Is it regulated by
744 starvation and predation in the egg and larval stages? *Netherlands Journal of Sea*
745 *Research*, 32, 119–134. [https://doi.org/10.1016/0077-7579\(94\)90036-1](https://doi.org/10.1016/0077-7579(94)90036-1)
- 746 Leggett, W. C., & Frank, K. T. (2008). Paradigms in fisheries oceanography.
747 *Oceanography and Marine Biology: An Annual Review*, 46, 331–363.
748 <https://doi.org/10.1201/9781420065756>
- 749 Llopiz, J. K., Cowen, R. K., Hauff, M. J., Ji, R., Munday, P. L., Muhling, B. A., Peck,
750 M. A., Richardson, D. E., Sogard, S., & Sponaugle, S. (2014). Early life history and

- 751 fisheries oceanography: New questions in a changing world. *Oceanography*, 27,
752 26–41. <https://doi.org/10.5670/oceanog.2014.84>
- 753 Miller, T. J., Crowder, L. B., Rice, J. A., & Marschall, E. A. (1988). Larval size and
754 recruitment mechanisms in fishes: toward a conceptual framework. *Canadian*
755 *Journal of Fisheries and Aquatic Sciences*, 45, 1657–1670.
756 <https://doi.org/10.1139/f88-197>
- 757 Morote, E., Olivar, M. P., Pankhurst, P. M., Villate, F., & Uriarte, I. (2008). Trophic
758 ecology of bullet tuna *Auxis rochei* larvae and ontogeny of feeding-related organs.
759 *Marine Ecology Progress Series*, 353, 243–254. <https://doi.org/10.3354/meps07206>
- 760 Nakamura, M., Yoneda, M., Morioka, T., Takasuka, A., & Nishiumi, N. (2022).
761 Positive effects of fast growth on locomotor performance in pelagic fish juveniles.
762 *Oecologia*, 199, 589–597. <https://doi.org/10.1007/s00442-022-05216-6>
- 763 Oozeki, Y., Takasuka, A., Kubota, H., & Barange, M. (2007). Characterizing spawning
764 habitats of Japanese sardine (*Sardinops melanostictus*), Japanese anchovy
765 (*Engraulis japonicus*), and Pacific round herring (*Etrumeus teres*) in the
766 northwestern Pacific. *California Cooperative Oceanic Fisheries Investigations*
767 *Reports*, 48, 191–203.
- 768 Peck, M. A., Herrmann, J.-P., Ewest, B., Stäcker, S., & Temming, A. (2015).
769 Relationships between feeding, growth and swimming activity of European sprat
770 (*Sprattus sprattus* L.) post-larvae in the laboratory. *Environmental Biology of Fishes*,
771 98, 1117–1127. <https://doi.org/10.1007/s10641-014-0345-5>
- 772 Pepin, P. (2023). Feeding by larval fish: how taxonomy, body length, mouth size, and
773 behaviour contribute to differences among individuals and species from a coastal
774 ecosystem. *ICES Journal of Marine Science*, 80, 91–106.
775 <https://doi.org/10.1093/icesjms/fsac215>

- 776 Pepin, P. (2024). Foraging by larval fish: a full stomach is indicative of high
777 performance but random encounters with prey are also important. *ICES Journal of*
778 *Marine Science*. <https://doi.org/10.1093/icesjms/fsae037>
- 779 Pepin, P., Robert, D., Bouchard, C., Dower, J. F., Falardeau, M., Fortier, L., Jenkins, G.
780 P., Leclerc, V., Levesque, K., Llopiz, J. K., Meekan, M. G., Murphy, H. M.,
781 Ringuette, M., Sirois, P., & Sponaugle, S. (2015). Once upon a larva: revisiting the
782 relationship between feeding success and growth in fish larvae. *ICES Journal of*
783 *Marine Science*, 72, 359–373. <https://doi.org/10.1093/icesjms/fsu201>
- 784 Plaza, G., & Ishida, M. (2008). The growth–mortality relationship in larval cohorts of
785 *Sardinops melanostictus*, revealed by using two new approaches to analyse
786 longitudinal data from otoliths. *Journal of Fish Biology*, 73, 1531–1553.
787 <https://doi.org/10.1111/j.1095-8649.2008.02012.x>
- 788 Primo, A. L., Vaz, A. C., Crespo, D., Costa, F., Pardal, M., & Martinho, F. (2021).
789 Contrasting links between growth and survival in the early life stages of two flatfish
790 species. *Estuarine, Coastal and Shelf Science*, 254, 107314.
791 <https://doi.org/10.1016/j.ecss.2021.107314>
- 792 Robert, D., Castonguay, M., & Fortier, L. (2007). Early growth and recruitment in
793 Atlantic mackerel *Scomber scombrus*: discriminating the effects of fast growth and
794 selection for fast growth. *Marine Ecology Progress Series*, 337, 209–219.
795 <https://doi.org/10.3354/meps337209>
- 796 Robert, D., Pepin, P., Dower, J. F., & Fortier, L. (2014a). Individual growth history of
797 larval Atlantic mackerel is reflected in daily condition indices. *ICES Journal of*
798 *Marine Science*, 71, 1001–1009. <https://doi.org/10.1093/icesjms/fst011>
- 799 Robert, D., Murphy, H. M., Jenkins, G. P., & Fortier, L. (2014b). Poor taxonomical
800 knowledge of larval fish prey preference is impeding our ability to assess the

- 801 existence of a “critical period” driving year-class strength. *ICES Journal of Marine*
802 *Science*, 71, 2042–2052. <https://doi.org/10.1093/icesjms/fst198>
- 803 Robert, D., Shoji, J., Sirois, P., Takasuka, A., Catalán, I. A., Folkvord, A., Ludsin, S. A.,
804 Peck, M. A., Sponaugle, S., Ayón, P. M., Brodeur, R. D., Campbell, E. Y.,
805 D'Alessandro, E. K., Dower, J. F., Fortier, L., García, A. G., Huebert, K. B., Hufnagl,
806 M., Ito, S., Joh, M., Juanes, F., Nyuji, M., Oozeki, Y., Plaza, G., Takahashi, M.,
807 Tanaka, Y., Tojo, N., Watari, S., Yasue, N., & Pepin, P. (2023). Life in the fast lane:
808 Revisiting the fast growth–high survival paradigm during the early life stages of
809 fishes. *Fish and Fisheries*, 24, 863–888. <https://doi.org/10.1111/faf.12774>
- 810 Sabatés, A., & Saiz, E. (2000). Intra- and interspecific variability in prey size and niche
811 breadth of myctophiform fish larvae. *Marine Ecology Progress Series*, 201, 261–271.
812 <https://doi.org/10.3354/meps201261>
- 813 Schneider, C. A., Rasband, W. S., and Eliceiri, K. W. (2012). NIH Image to ImageJ: 25
814 years of image analysis. *Nature Methods*, 9, 671–675.
815 <https://doi.org/10.1038/nmeth.2089>
- 816 Searcy, S. P., & Sponaugle, S. (2001). Selective mortality during the larval–juvenile
817 transition in two coral reef fishes. *Ecology*, 82, 2452–2470.
818 [https://doi.org/10.1890/0012-9658\(2001\)082\[2452:SMDTLJ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2452:SMDTLJ]2.0.CO;2)
- 819 Sissenwine, M. P. (1984). Why do fish populations vary? In R. M. May (Ed.),
820 *Exploitation of marine communities* (pp. 59–94). Berlin: Springer-Verlag.
- 821 Skajaa, K., Fernö, A., & Folkvord, A. (2003). Swimming, feeding and predator
822 avoidance in cod larvae (*Gadus morhua* L.): trade-offs between hunger and
823 predation risk. In H. I. Browman, & A. B. Skiftesvik (Eds.), *The Big Fish Bang:*
824 *Proceedings of the 26th Annual Larval Fish Conference* (pp. 105–121). Bergen,
825 Norway: The Institute of Marine Research.

- 826 Takasuka, A., Aoki, I., & Mitani, I. (2003). Evidence of growth-selective predation on
827 larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. *Marine Ecology*
828 *Progress Series*, 252, 223–238. <https://doi.org/10.3354/meps252223>
- 829 Takasuka, A., Aoki, I., & Mitani, I. (2004a). Three synergistic growth-related
830 mechanisms in the short-term survival of larval Japanese anchovy *Engraulis*
831 *japonicus* in Sagami Bay. *Marine Ecology Progress Series*, 270, 217–228.
832 <https://doi.org/10.3354/meps270217>
- 833 Takasuka, A., Oozeki, Y., Kimura, R., Kubota, H., & Aoki, I. (2004b).
834 Growth-selective predation hypothesis revisited for larval anchovy in offshore
835 waters: cannibalism by juveniles versus predation by skipjack tunas. *Marine*
836 *Ecology Progress Series*, 278, 297–302. <https://doi.org/10.3354/meps278297>
- 837 Takasuka, A., Aoki, I., & Oozeki, Y. (2007). Predator-specific growth-selective
838 predation on larval Japanese anchovy *Engraulis japonicus*. *Marine Ecology*
839 *Progress Series*, 350, 99–107. <https://doi.org/10.3354/meps07158>
- 840 Takasuka, A., Oozeki, Y., Aoki, I., Kimura, R., Kubota, H., Sugisaki, H., & Akamine, T.
841 (2008). Growth effect on the otolith and somatic size relationship in Japanese
842 anchovy and sardine larvae. *Fisheries Science*, 74, 308–313.
843 <https://doi.org/10.1111/j.1444-2906.2008.01519.x>
- 844 Takasuka, A., Sakai, A., & Aoki, I. (2017). Dynamics of growth-based survival
845 mechanisms in Japanese anchovy (*Engraulis japonicus*) larvae. *Canadian Journal of*
846 *Fisheries and Aquatic Sciences*, 74, 812–823.
847 <https://doi.org/10.1139/cjfas-2016-0120>
- 848 Tanaka, S., Togoshi, S., Yasue, N., Burns, C. M., Robert, D., & Takasuka, A. (2023).
849 Revisiting the role of early life growth for survival potential in three clupeoid
850 species. *Fisheries Oceanography*, 32, 245–254. <https://doi.org/10.1111/fog.12626>

- 851 Tanaka, S., Togoshi, S., Yasue, N., & Takasuka, A. (2024). Seasonal variability in the
852 otolith and somatic size relationship of Japanese anchovy larvae: Counter effects of
853 somatic growth and temperature. *Fisheries Research*, 275, 107027.
854 <https://doi.org/10.1016/j.fishres.2024.107027>
- 855 Tsuji, S., & Aoyama, T. (1984). Daily growth increments in otoliths of Japanese
856 anchovy larvae *Engraulis japonica*. *Bulletin of the Japanese Society of Scientific*
857 *Fisheries*, 50, 1105–1108. <https://doi.org/10.2331/suisan.50.1105>
- 858 Uotani, I., Izuha, A., & Asai, K. (1978). Food habits and selective feeding of anchovy
859 larvae (*Engraulis japonica*). *Bulletin of the Japanese Society of Scientific Fisheries*,
860 44, 427–434.
- 861 Watanabe, Y., Zenitani, H., & Kimura, R. (1995). Population decline of the Japanese
862 sardine *Sardinops melanostictus* owing to recruitment failures. *Canadian Journal of*
863 *Fisheries and Aquatic Sciences*, 52, 1609–1616. <https://doi.org/10.1139/f95-154>
- 864 Yasue, N., & Takasuka, A. (2009). Seasonal variability in growth of larval Japanese
865 anchovy *Engraulis japonicus* driven by fluctuations in sea temperature in the Kii
866 Channel, Japan. *Journal of Fish Biology*, 74, 2250–2268.
867 <https://doi.org/10.1111/j.1095-8649.2009.02238.x>
- 868 Yasue, N., Doiuchi, R., Yoshimoto, Y., & Takeuchi, T. (2010). Diet of late larval
869 Japanese anchovy *Engraulis japonicus* in the Kii Channel, Japan. *Fisheries Science*,
870 76, 63–73. <https://doi.org/10.1007/s12562-009-0181-2>
- 871 Yasue, N., Takasuka, A., & Shirakihara, K. (2011). Interspecific comparisons of growth
872 and diet among late larvae of three co-occurring clupeoid species in the Kii Channel,
873 Japan. *Marine Biology*, 158, 1709–1720. <https://doi.org/10.1007/s00227-011-1685-8>
- 874 Yasue, N., Doiuchi, R., & Takasuka, A. (2014). Trophodynamic similarities of three
875 sympatric clupeoid species throughout their life histories in the Kii Channel as

876 revealed by stable isotope approach. *ICES Journal of Marine Science*, 71, 44–55.

877 <https://doi.org/10.1093/icesjms/fst128>

878 Yasue, N., Harada, S., & Takasuka, A. (2016). Seasonal variability in the development

879 of Japanese anchovy during the transition from larval to juvenile stages. *Marine*

880 *Ecology Progress Series*, 562, 135–146. <https://doi.org/10.3354/meps11942>

881

882 **SUPPORTING INFORMATION**

883 Additional supporting information can be found online in the Supporting Information

884 section at the end of this article.

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886

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

Sample	Date of capture	ST (°C)	Category	n	SL (mm)		Age (days)		Recent GR (mm/day)		Mean GR (mm/day)	
					Range	Mean	Range	Mean	Range	Mean	Range	Mean
Anchovy												
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
Round herring												
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	23.9	19–60	35	0.26–0.82	0.43	0.41–0.85	0.55

ST: sea temperature; SL: standard length; Recent GR: recent 3-day mean growth rate directly before capture; Mean GR: mean growth rate from hatching to capture

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 length	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 herring							
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

893

894 **Figure captions**

895

896 **FIGURE 1** Sampling area for Japanese anchovy *Engraulis japonicus* larvae and
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 t -test or Welch's t -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 *Etrumeus micropus* (R2–R4). Head length proportion is defined
932 as the proportion of head length to standard length. Linear regressions of
933 \ln -transformed head length proportion on \ln -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 t -test or Welch's t -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 *Etrumeus micropus* (R2–R4). Head height proportion is defined

944 as the proportion of head length to standard length. Linear regressions of
945 \ln -transformed head height proportion on \ln -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 t -test or Welch's t -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 \ln -transformed lower jaw length proportion on \ln -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 t -test
961 or Welch's t -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 *ln*-transformed eye diameter proportion on *ln*-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 *t*-test or
973 Welch's *t*-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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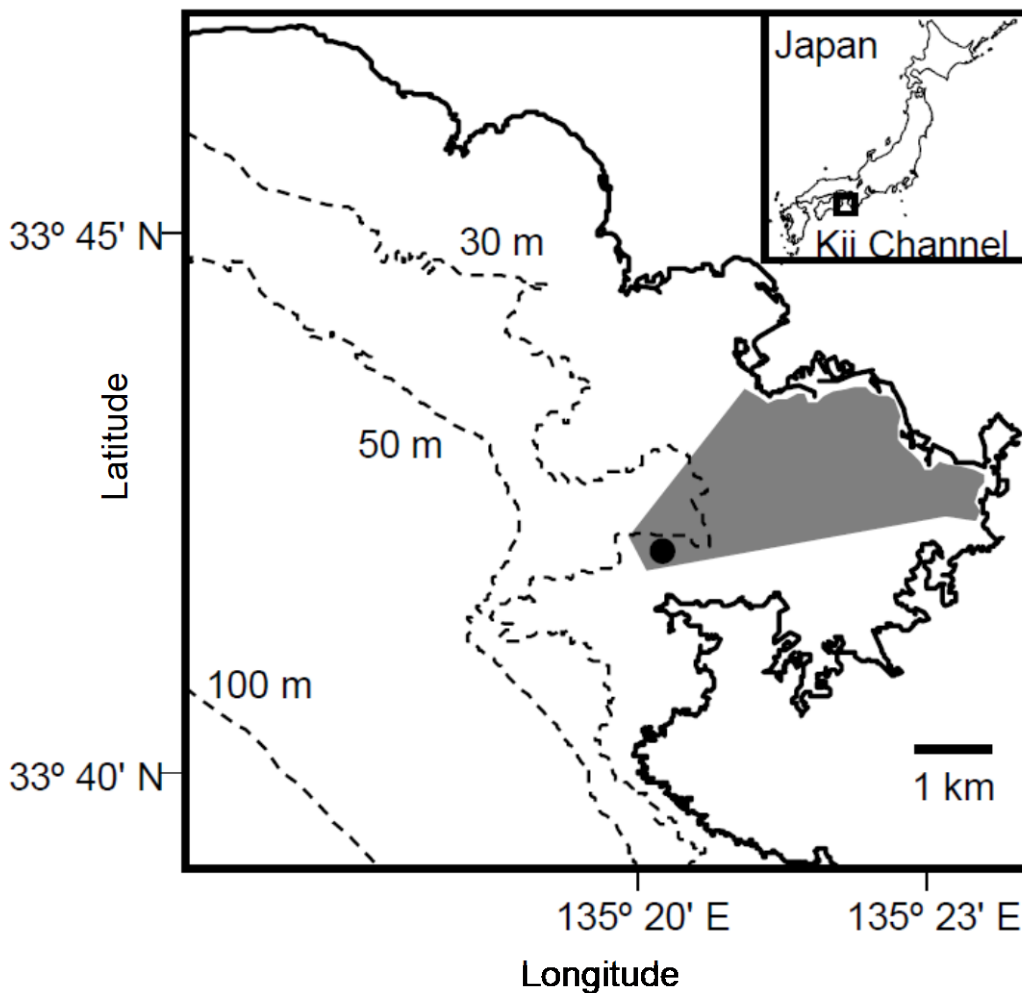
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FIGURE 1

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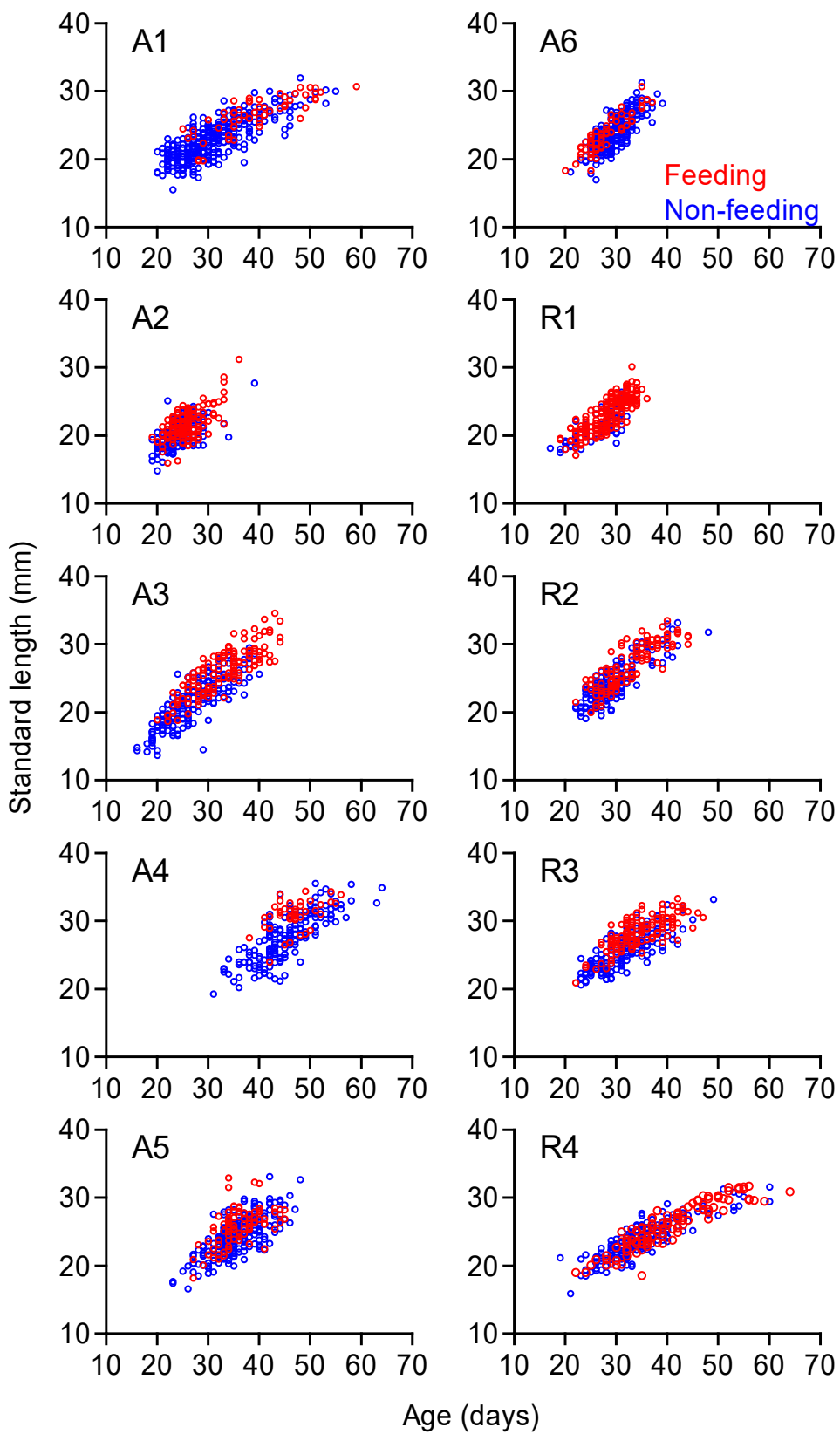
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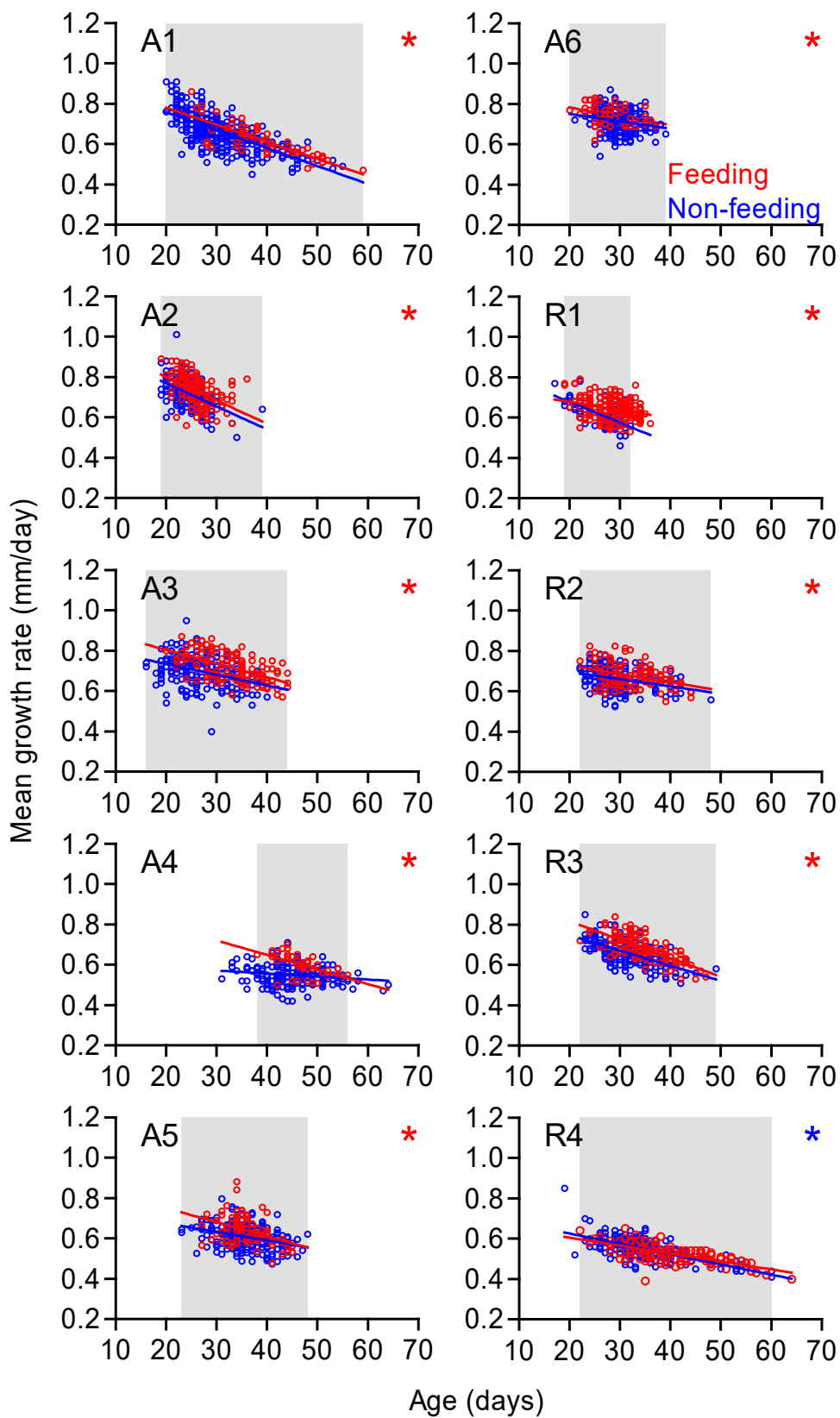
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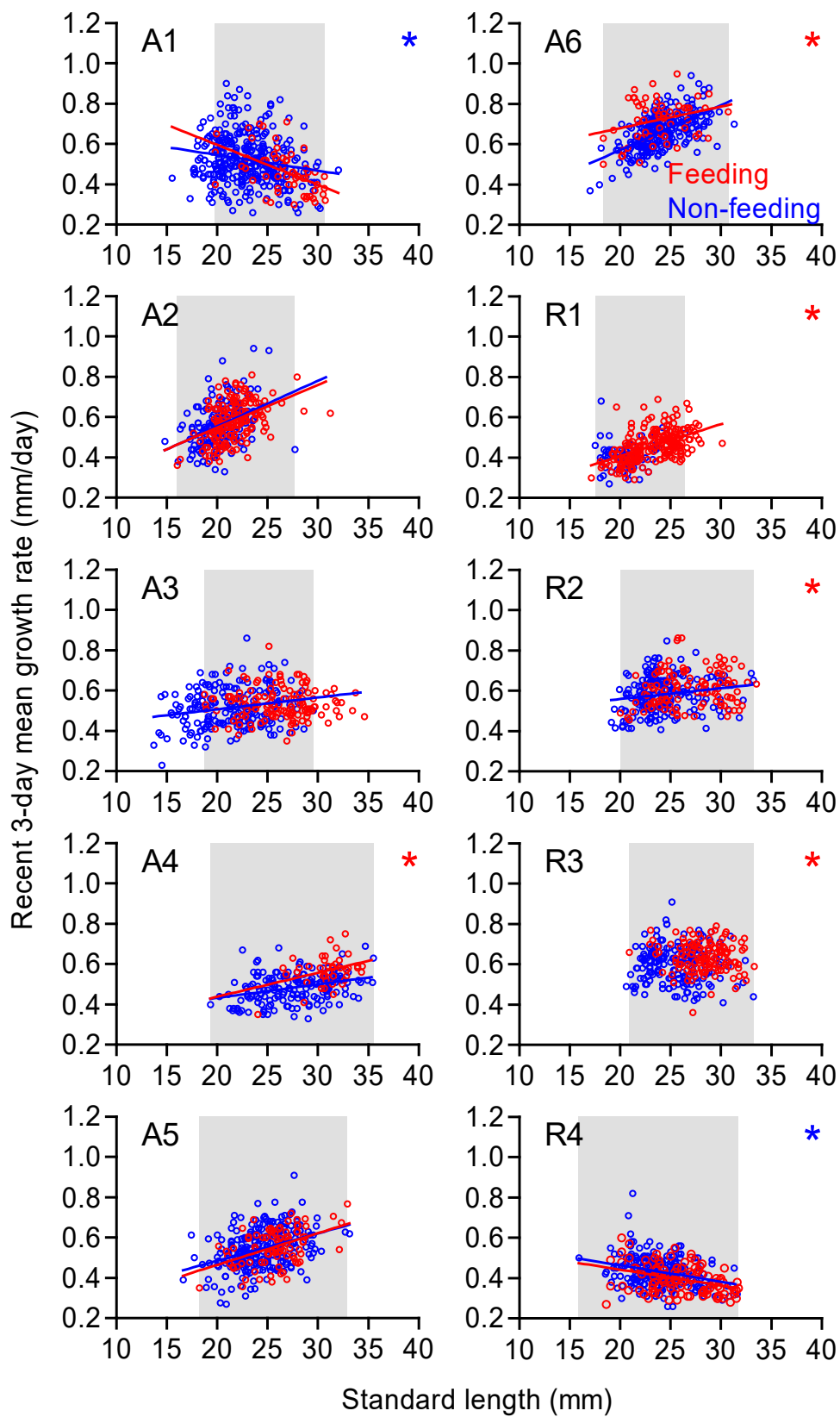
FIGURE 2



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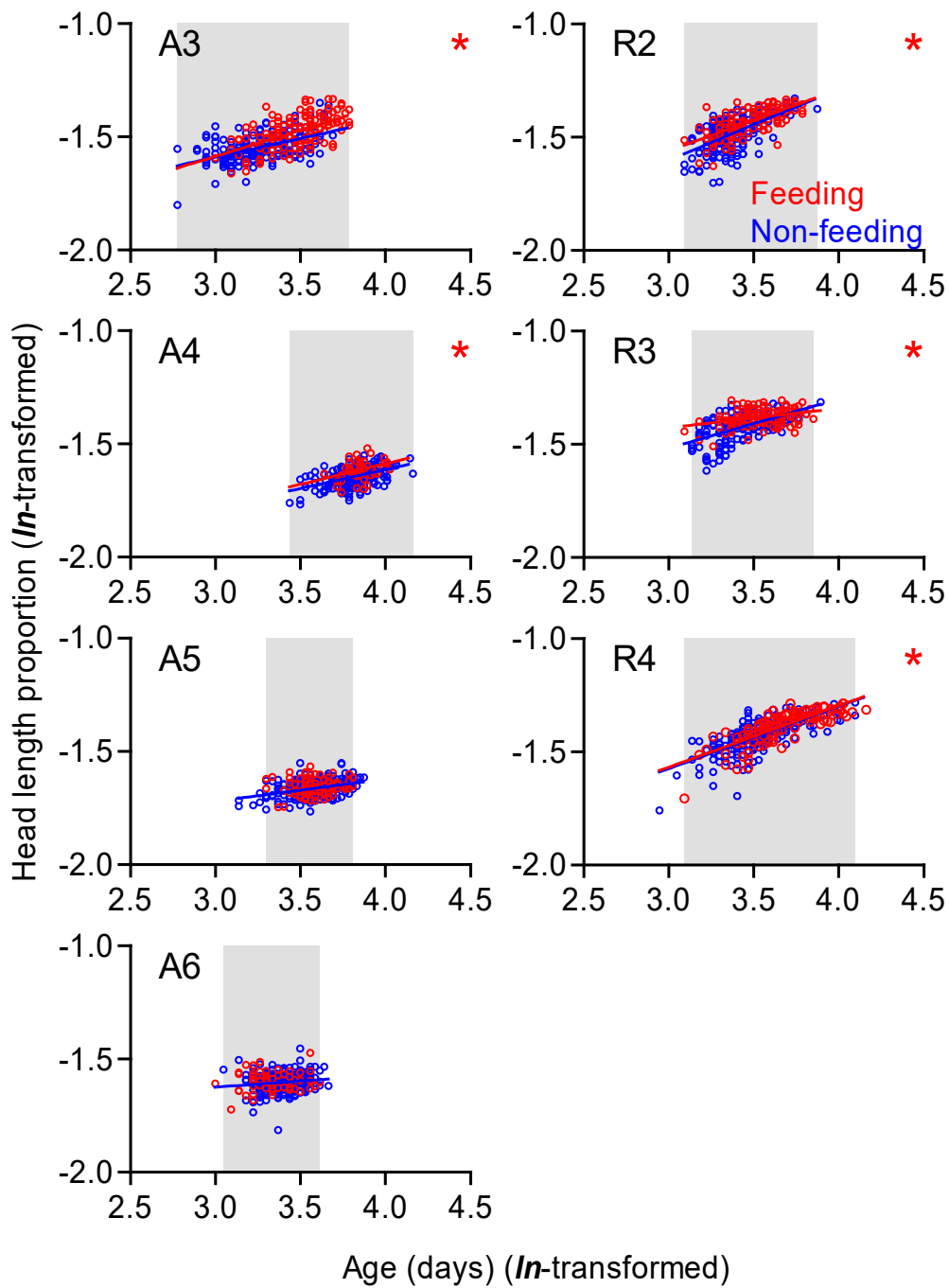
FIGURE 3



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FIGURE 4



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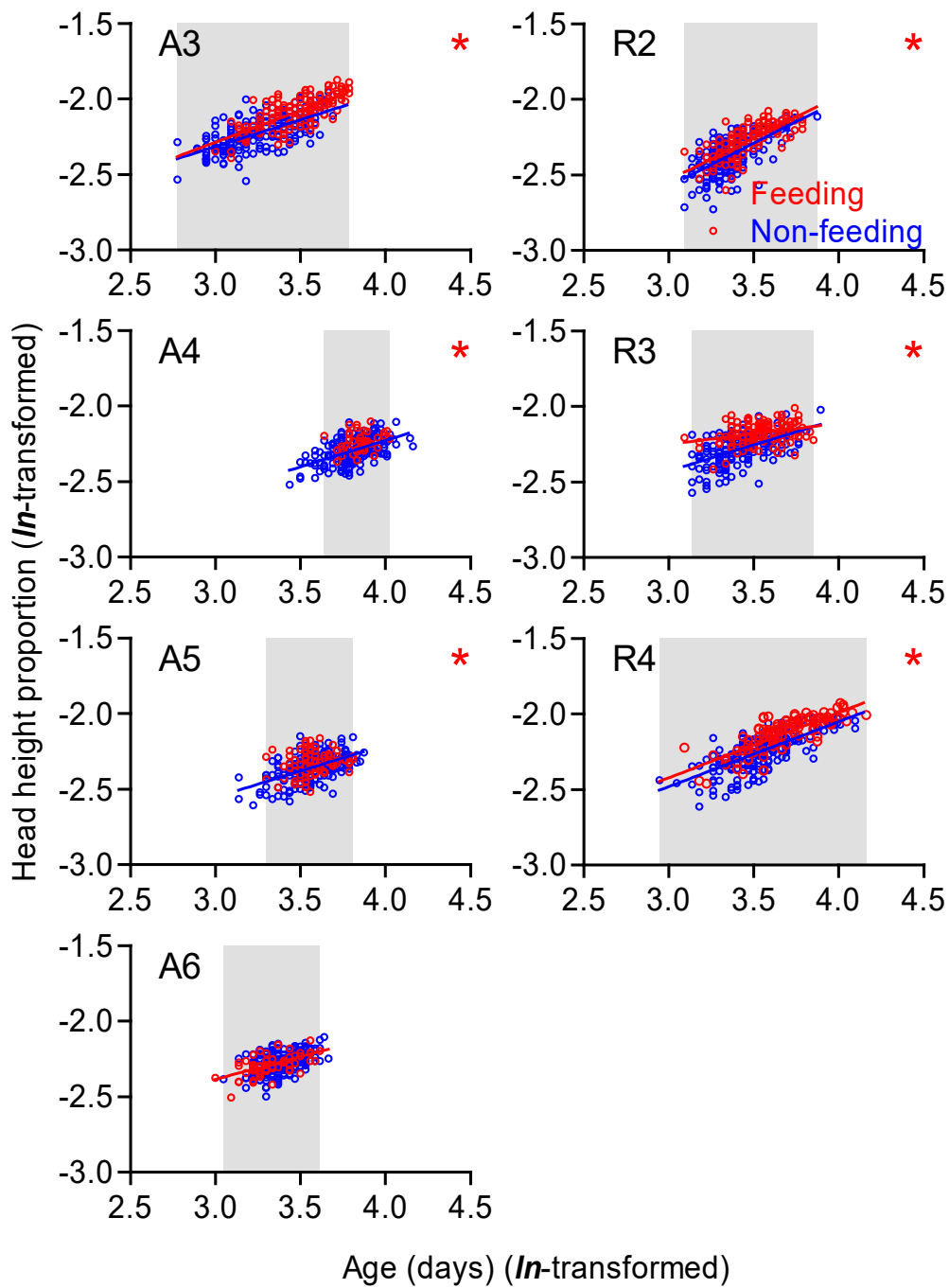
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FIGURE 5



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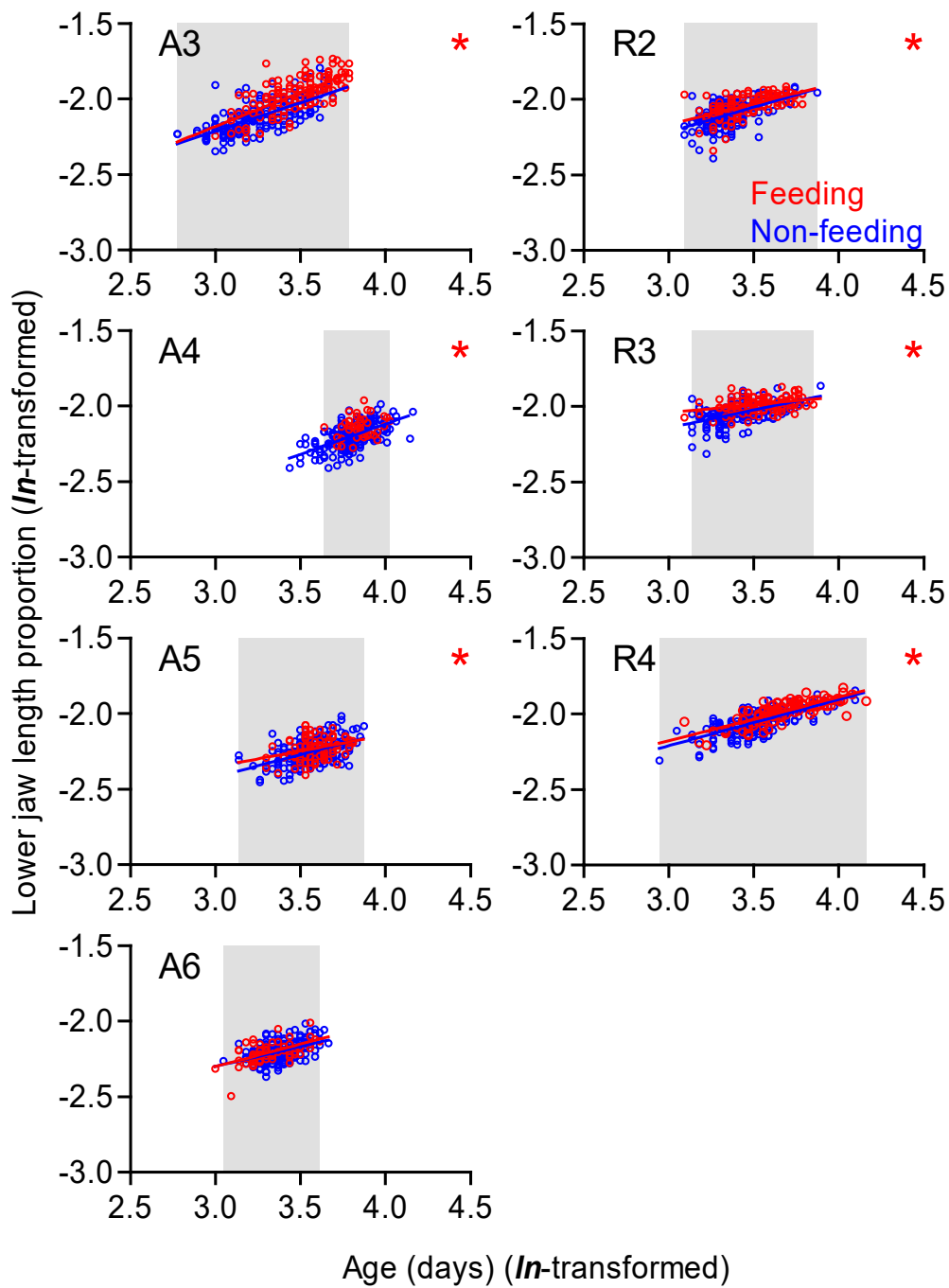
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FIGURE 6



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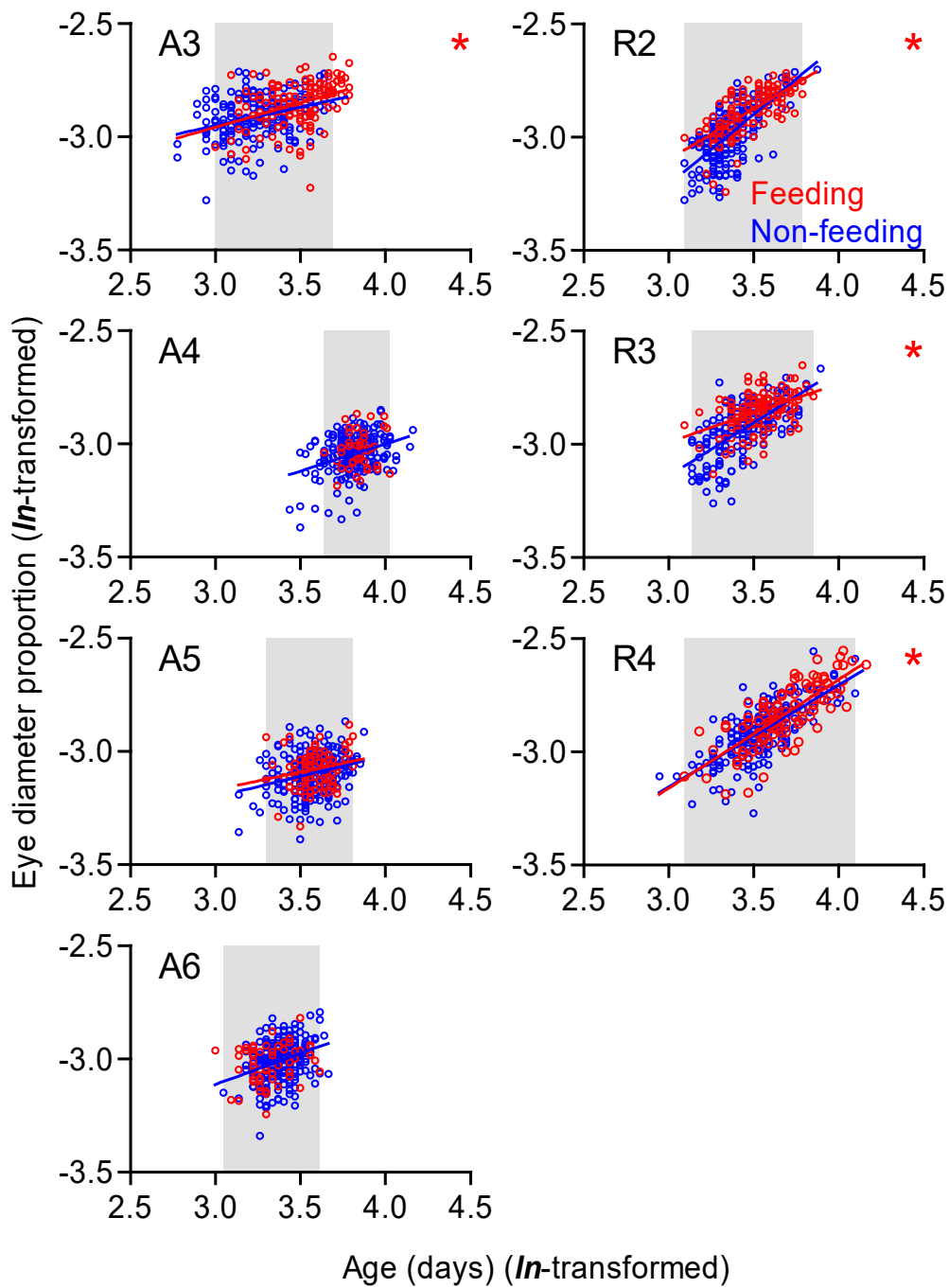
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FIGURE 7



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FIGURE 8