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Title	Growth and age composition of northern shrimp <i>Pandalus eous</i> estimated by multiple length frequency analysis
Author(s)	Yamaguchi, Hiroshi; Goto, Yoko; Hoshino, Noboru et al.
Citation	Fisheries Science, 80(4), 665-678 https://doi.org/10.1007/s12562-014-0758-2
Issue Date	2014-07
Doc URL	https://hdl.handle.net/2115/57042
Type	journal article
File Information	Northern_shrim.pdf



1 Title:

2 Growth and age composition of northern shrimp *Pandalus eous* estimated by multiple length
3 frequency analysis

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20 Abstract

21 We examined growth of northern shrimp *Pandalus eous* in the Sea of Japan, off western Hokkaido,
22 to improve estimations of catch-at-age for stock assessment. Multiple length frequency analysis
23 based on length frequency data collected by a scientific research vessel was conducted to examine
24 length-at-age in the shrimp population. Multi-normal distributions estimated using maximum
25 likelihood indicated a good fit to length distributions. AIC values and regression analyses revealed
26 annual growth variation and a decreasing trend in the length at several age classes in the shrimp
27 population. We revised the method for estimating catch-at-age from age-conversion table (ACT),
28 which is a simple method for age determination, to age-length keys (ALK) calculated from the
29 results of multiple length frequency analysis. Abundant year classes caught successively year after
30 year could be more easily identified from the catch-at-age data computed using ALK than by using
31 ACT. Our results suggested not only that the mean size of commercial landings fluctuated based on
32 changes in age composition but also that decrease in the length-at-age in the population influenced
33 the consistent size decrease of commercial landings.

34

35 Key words: northern shrimp, *Pandalus eous*, length frequency analysis, age and growth, age-length
36 key, catch-at-age

37

38 **Introduction**

39 The northern shrimp *Pandalus eous*, which is widely distributed in the northern parts of the Pacific
40 Ocean, the Sea of Japan, the Okhotsk and Bering Seas, and along the coasts of Alaska and Canada,
41 is a commercially important species. Northern shrimp in the Sea of Japan, off western Hokkaido,
42 are largely caught by a shrimp-pot fishery operating through a year other than February. Although
43 the commercial catch has remained stable between 2000 and 3000 t over the past decade, fishermen
44 have been facing financial difficulty with a decline in the price of shrimp, which is partly caused by
45 decreases in the mean size of the commercial landings (Fig. 1). The size decrease of commercial
46 landings may be caused by biological factors (such as recruitment of strong year classes or
47 decreasing growth rates) or fishing-related factors (e.g., over-harvesting) [1]. However, the mean
48 size derived from fishery-dependent data is biased by changes in the target size or selectivity of
49 fishing gear. To elucidate such causal relationships, fluctuations in the mean size at age in the
50 population should be examined using fishery-independent data. Subsequently, based on these results,
51 age composition of commercial landings should be estimated to conduct a stock assessment to
52 examine fluctuations in recruitment and the influences of fishing on the population.

53 Several stock assessment methods for fisheries resources have been proposed in terms of
54 relative abundance measured by fisheries or research data [2, 3] or by population estimates using
55 catch-at-age data [4, 5], among others. Stock assessments for a large number of fisheries resources
56 can be conducted by an age-structured model, which has the advantage that population size, fishing
57 mortality, and age and time structure can be estimated. Such estimates provide the basis for the

58 evaluation of a stock-recruitment relationship and for the exploration of some technical
59 management procedures. Catch-at-age data are indispensable in age-structured models for
60 population estimates of northern shrimp.

61 For crustaceans, for which age is difficult to determine because of the lack of ageing
62 characters, estimation of catch-at-age based on cohort slicing or age-length keys may prevent
63 precise population estimates in cases when annual growth variation is evident [6, 7]. Age and
64 growth of northern shrimp in Japan were examined from the end of the 1980s to the beginning of
65 the 1990s in two areas within the Sea of Japan: the northern part of the Sea of Japan around the
66 Musashi Bank, off western Hokkaido [8], which is the same area investigated in our study, and the
67 central part of the Sea of Japan, off the Noto Peninsula [9]. Growth and catch-at-age data of
68 northern shrimp in the Sea of Japan, off western Hokkaido, have been estimated by discriminating
69 modal classes of carapace length distributions [8], and by cohort slicing based on an age-conversion
70 table (ACT) to catch-at-length classes in commercial landings without considering the growth
71 variation [10], respectively. However, given that a size decrease has been observed in commercial
72 landings, catch-at-age data may be estimated incorrectly when using methods that do not account
73 for variation in growth. In the northern Atlantic Ocean, several studies have reported size decreases
74 in northern shrimp *Pandalus borealis*, a closely related species to *P. eous*, associated with annual
75 growth variation [11-16].

76 Age and growth (age composition) of crustaceans is usually inferred from their length
77 distribution, which is assumed to have a multi-normal distribution for each age and mean lengths at

78 age, standard deviation, and frequency per age-at-length [17-21]. The method of Yamakawa and
79 Matsumiya [21] can simultaneously analyze multiple length frequency data sets even when growth
80 rates fluctuate between years, allowing all available information in the data to be used.

81 Here we examined length-at-age in a northern shrimp population based on
82 fishery-independent data, and improved the estimation of catch-at-age for stock assessment using an
83 age-structured model. For this purpose, multiple length frequency analysis based on length
84 frequency data collected by a scientific research vessel was conducted to examine growth and
85 annual variation. We then estimated catch-at-age from catch-at-length classes of commercial
86 landings using age-length keys (ALKs) calculated from the results of multiple length frequency
87 analysis.

88

89 **Materials and methods**

90

91 **Collecting samples for length frequency analysis**

92

93 Carapace length (CL) frequency data of northern shrimp for length frequency analysis were
94 collected by scientific surveys conducted every year from 1999 to 2011 by the scientific research
95 vessel “Hokuyo-maru” (gross registered tonnage 237 t), which belongs to the Wakkanai Fisheries
96 Research Institute (Table 1). Annual surveys were conducted during June and July every year at
97 water depths of 200–600 m to cover the distribution of northern shrimp in the Sea of Japan, off
98 western Hokkaido (Fig. 2). Sampling was conducted 6–18 times in each year using shrimp-pots

99 with a mesh size of 5.33 mm bar length. The number of shrimp-pot employed per station was
100 almost constant within a survey year, although it was varied from year to year. Collected northern
101 shrimp were classified into four stages (male, transitional, non-ovigerous female, and ovigerous
102 female), based on the shape of the first pleopod and the presence or absence of eggs in the abdomen.
103 Oblique CL, which is the distance from the eye socket to the mid-posterior carapace edge, was
104 measured to the nearest 0.1 mm with digital calipers. These measurements were made either on
105 board immediately after the catch or at later at the laboratory.

106 Nakame [8] investigated the reproductive cycle and growth of northern shrimp in the Sea
107 of Japan, off western Hokkaido (Fig. 3). The life history of northern shrimp is characterized by
108 protandric hermaphroditism and a long life span. Globally, northern shrimp have the longest
109 recorded life span, ca. 11 years, in the Sea of Japan. All shrimp hatch as males, and a sex change
110 from male to female usually occurs in autumn at age 5. Females incubate eggs for ca. 10 months
111 after spawning in spring at age 6, and they spawn two or three times every other year during their
112 life time. Molt frequency is not clear in males, but in females, molting occurs once a year, during
113 April and May.

114 The number of age groups was determined for length frequency analysis. The life history
115 pattern of northern shrimp in the Sea of Japan, off western Hokkaido, was simplified based on the
116 results of Nakame [8] as follows. The birth date of the shrimp was set to January 1. Males and
117 transitional individuals were considered to be aged 1–5 years, non-ovigerous females were aged 7
118 and 9 years, and ovigerous females were aged 6, 8, and 10 years. Length frequency distributions, in

0.5-mm length intervals, of males and transitional individuals, non-ovigerous females, and ovigerous females were divided into five, two, and three age groups, respectively. Transitional individuals were seldom collected because the surveys were conducted before the sex-change season (Table 1). Consequently, males and transitional individuals were combined into the same growth stage. Age 11, the terminal age, was not added to the age classes for length frequency analysis, because individuals of this age have been almost depleted in June after the third hatching [8].

Multiple length frequency analysis

Multiple length frequency analysis was conducted based on a method applied to Japanese spiny lobster *Panulirus japonicus* by Yamakawa and Matsumiya [21] as follows. We assumed that length frequency data were sampled randomly and that the measurement errors were negligible; $Q_{i,s,y}$ is the probability when an individual randomly sampled from the y th length frequency data set belongs to growth stage s ($s = mt$: male and transitional, nof : non-ovigerous female, of : ovigerous female) and length class i . Assuming that the frequency distribution of the j th age group of growth stage s in the y th data set follows a normal distribution $N(L_{j,s,y}, \sigma_j)$, $Q_{i,s,y}$ can be expressed as a multi-normal distribution:

$$Q_{i,s,y} = \sum_j \frac{p_{j,y} \omega}{\sqrt{2\pi\sigma_j^2}} \exp\left\{-\frac{(l_i - L_{j,s,y})^2}{2\sigma_j^2}\right\} \quad (1)$$

138 where ω is the width of the length class, l_i is the middle length of the i th length class, $L_{j,s,y}$ is the
 139 mean length of the j th age group at growth stage s in the y th data set, σ_j is the standard deviation of
 140 length in the j th age group, $p_{j,y}$ is proportion of the j th age group in the y th data set, and $\sum_j p_{j,y} = 1$
 141 ($p_{j,y} > 0$).

142 Mean length $L_{j,s,y}$ were expressed by von Bertalanffy's growth formula as follow:

$$143 \quad L_{j,s,y} = L_{\inf y} [1 - \exp\{-K_y(j - j_{0y})\}] \quad (2)$$

144 where $L_{\inf}$, K_y , and j_{0y} are asymptotic length, growth coefficient, and age at which length
 145 extrapolates back to zero along the curve, respectively. Following four equations are considered for
 146 the model of standard deviation σ_j :

$$147 \quad \text{Constant:} \quad \sigma_j = a \quad (3)$$

$$148 \quad \text{Liner:} \quad \sigma_j = aj + b \quad (4)$$

$$149 \quad \text{Logistic:} \quad \sigma_j = \frac{c}{1 + \exp\{a(1 - bj)\}} \quad (5)$$

$$150 \quad \text{Tanaka and Tanaka [22]:} \quad \sigma_j = \left[a + \frac{b}{2K_y} \{1 - \exp(-2K_y j)\} \right]^{1/2} \quad (6)$$

151 where a , b , and c are parameters to be estimated.

152 Parameters were estimated by a maximum likelihood method. The probability P of
 153 obtaining $f_{i,s,y}$ individuals in the i th length interval of growth stage s in the y th data set is equal to the
 154 constant multiplied by the expression:

$$155 \quad P = \prod_y \prod_s \left(\frac{F_{s,y}!}{\prod_i f_{i,s,y}!} \prod_i Q_{i,s,y}^{f_{i,s,y}} \right) \quad (7)$$

156 where $F_{s,y}$ is the total number of individuals of growth stage s in the y th data set. The objective
 157 function to maximize is the log-likelihood LL ,

$$158 \quad LL = \sum_y \sum_s \left\{ \ln(F_{s,y}!) - \sum_i \ln(f_{i,s,y}!) + \sum_i f_{i,s,y} \ln(Q_{i,s,y}) \right\} \quad (8)$$

159 In actually, it was difficult to carry out factorial calculations of large sample size in this study. We
 160 used LL' as the alternative objective function of the log-likelihood for parameter estimation as
 161 follow.

$$162 \quad LL' = \sum_y \sum_s \sum_i f_{i,s,y} \ln(Q_{i,s,y}) \quad (9)$$

163 To estimate average growth during 1999–2011, optimal model of standard deviation σ_j was
 164 selected with common parameters of von Bertalanffy to all survey years (Case 1–1 to 1–4) (Table3).
 165 Next, we considered the fluctuation in growth rate between years. If the growth rate varied between
 166 years, parameters of the growth formula and age composition of all data sets were estimated with
 167 model selection of standard deviation σ_j (Case 2–1 to 2–4) (Table 3). Selection of the optimal model
 168 was performed by Akaike's Information Criterion (AIC),

$$169 \quad AIC = -2MLL' + 2m \quad (10)$$

170 where MLL' and m denote the maximum log-likelihood of LL' and the number of free parameters,
 171 respectively. We selected the model with the lowest AIC value.

172

173 Estimation of catch-at-age in commercial landings

174

175 To estimate annual catch-at-age data of northern shrimp during 2000–2011 on a calendar year basis,

commercial landings in the Sea of Japan, off western Hokkaido, were represented by the landings from the shrimp-pot fishery reported at the ports of Haboro, Mashike, and Yoichi. Stratified samples of landings were collected for each market size category, time, and port to estimate size frequencies. Carapace length and body weight of these samples were measured, and sex was discriminated by the shape of the first pleopod. Shrimp were distinguished before or after molting by sampling month or external characters following Figure 4, because catch-at-length classes in commercial landings before or after molting must be determined from different ALKs, respectively. Molt timing of male was assumed to be the same as that of female. From 1999 to 2005, evidence of hatching was not confirmed in non-ovigerous females without head roe caught in March; however, based on confirmed samples caught in 2006 and later, these individuals were regarded as having all hatched. Catch-at-length classes of the commercial landings $N_{i,y}$ before or after molting were estimated in weighted strata of market size category, port, and time as follows:

$$N_{i,y} = \frac{M_{0,y}}{\sum_t M_{t,y}} \sum_k \sum_t \sum_m \frac{W_{k,m,t,y}}{w_{k,m,t,y}} n_{i,k,m,t,y} \quad (11)$$

where $n_{i,k,m,t,y}$ is catch number on length-class i at port k of market size category m at time t , in year y , $\bar{w}_{k,m,t,y}$ is mean body weight of market size category m at time t , in year y , $W_{k,m,t,y}$ is catch weight at port k of market size category m at time t , in year y , $M_{t,y}$ is total catch weight of sampling ports, Haboro, Mashike and Yoichi, at time t , in year y , $M_{0,y}$ is total catch in year y during January and April or May to December in the Sea of Japan, western Hokkaido, respectively.

ALKs were computed from the age composition obtained by length frequency analysis. To

195 calculate catch-at-age in year y , ALKs in year $(y-1)$ or year y applied to catch-at-length class before
 196 or after molting, respectively, and after age 1 year were added to that before molting, and then both
 197 catch-at-age values were summed. Transitional individuals were considered to be age 5 after
 198 molting and age 6 before molting. Alternative estimation by a simple method, viz. an ACT without
 199 annual growth variation, was conducted using the same length frequency data (Table 2) [10].

200 To compare catch-at-age estimated by ALKs and ACT, z values $z_{y,j}$, which are standardized
 201 values representing the distance between catch number at age in a given year and the mean over the
 202 whole research period, were calculated as follow,

$$203 \quad z_{y,j} = \frac{C_{y,j} - \overline{C_j}}{sd_j} \quad (12)$$

204 where $C_{y,j}$ is catch number in year y of j th age group, $\overline{C_j}$ and sd_j are mean catch number and
 205 standard deviation of j th age group during 2000–2011, respectively.

206

207 **Results**

208

209 **Growth of northern shrimp**

210

211 The number of northern shrimp collected by scientific surveys in each year ranged from 3,985 to
 212 21,799 (Table 1). Carapace length of shrimp collected in these surveys ranged from 3.3 to 30.7 mm
 213 in males and transitional individuals, from 21.5 to 37.2 mm in non-ovigerous females, and from

214 20.6 to 37.1 mm in ovigerous females (Table 1). Four or five modes were observed in length
 215 frequencies of males and transitionals in each year (Fig. 5). Length frequencies of females generally
 216 showed a single peak, or occasionally an indistinct one, unlike the distributions of males and
 217 transitionals. In this study, the first peak at 9–10 mm in length was regarded as age 1, according to
 218 the results of previous studies in the same study area and off the Noto Peninsula [8, 9] (Fig. 5).

219 Comparing AIC values in Case 1–1 to 1–4 for estimating average growth during 1999–
 220 2011, logistic model (Case 1–3) was selected for the optimal model for standard deviation σ_j (Table
 221 3). Mean length and standard deviations of average growth were expressed as follows (Table 4, Fig.
 222 6):

$$223 \quad L_j = 35.877[1 - \exp\{-0.208(j + 0.492)\}] \quad (13)$$

$$224 \quad \sigma_j = \frac{1.434}{1 + \exp\{14.928(1 - 1.068j)\}} \quad (14)$$

225 Comparing AIC values in all cases to consider the annual growth variation, AIC values
 226 were smaller in cases with annual growth variation (Case 2–1 to 2–4) than in those with common
 227 growth parameters (Case 1–1 to 1–4) (Table 3). Case 2–3 was selected for optimal model with von
 228 Bertalanffy parameters estimated for every year and logistic model for standard deviation σ_j as
 229 follow.

$$230 \quad \sigma_j = \frac{1.393}{1 + \exp\{13.873(1 - 1.071j)\}} \quad (15)$$

231 The estimates of growth parameters in Case 2-3 are shown in Table 4.

232 Multi-normal distributions estimated by the maximum likelihood method indicated a good
 233 fit to the length distributions (Fig. 5). Inter-annual variation of length-at-age was small, with

234 standard deviations of 0.37–0.50 (Table 4). Regression analysis revealed significantly decreasing
235 trends in mean length from ages 5–8 years ($p < 0.05$; Table 4).

236

237 Catch-at-age

238

239 Most of the commercial landings were from 20 to 35 mm in CL, with modes between 26 and 29
240 mm CL (Fig. 7). The difference in the size range between scientific survey samples and commercial
241 landings was caused by the difference in the shrimp-pot mesh size between the surveys and the
242 fishery (Fig. 5). In the shrimp-pot fishery in the Sea of Japan, off western Hokkaido, the mesh size
243 is regulated to >17 mm bar length by the Hokkaido government. Length distributions had a single
244 major peak, with one or more smaller peaks. The proportion of males and transitionals to total
245 individuals was low, viz. 13.5–22.5% (Fig. 7).

246 ALKs were computed for every year according to the results of annual growth variation
247 (Table 3). Catch-at-age computed by ALKs and ACT were similar in that the catch number at age 3,
248 an age class of recruitment, represented a low proportion of the total catch. The catch number at age
249 7, i.e., 4 years after recruitment, was the highest of the total catch (Fig. 8). The catch of 6- and
250 8-year-old ovigerous females was smaller than the catch of 7- and 9-year-old non-ovigerous females
251 (Fig. 8). The catch number of 6- and 7-year-old individuals computed by ALK was almost larger
252 than that computed by ACT (Fig. 9). On the other hand, the number of, 9- and 10-year-old shrimp
253 was almost smaller because of the compensation for the increased numbers of 6- and 7-year-old

254 shrimp, which are the most abundant age groups of non-ovigerous and ovigerous females,
255 respectively (Fig. 9). Moreover, the number of 11-year-old shrimp computed by ALK was smaller
256 than that computed by ACT (Fig. 9).

257 Consecutive cohorts are difficult to discriminate in catch-at-age of time series (Fig 8). Note
258 the successive cohorts with relatively high z values calculated using ALK. The year class 1992 had
259 high z values above 1.0 in 2001 and 2002, and positive values in 2000 and 2003 (Fig. 10). In spite
260 of the negative z values above age 9, z values of the year class 1996 showed consistently positive
261 values of 0.28–0.98 from 2000 to 2004. The year classes 2000 and 2001 had positive values
262 successively year after year. In particular, z values of the year class 2001 were positive values from
263 2005 to 2009. In contrast, for the year classes 1992, 1996, 2000, and 2001, the relatively high z
264 values successively calculated by ALK were only in accordance with year class 2001 calculated by
265 ACT.

266

267 **Discussion**

268 In this study, we used the method of Yamakawa and Matsumiya [21] for a length frequency analysis
269 to estimate the growth and age composition of northern shrimp. Biologically reasonable results are
270 not necessarily obtained when a multi-normal distribution is fit to a length distribution by a
271 statistical method [23, 24]. To avoid such inconsistent results, the mean length and standard
272 deviation in each age group are assumed in some models [23, 24]. ELEFAN and MULTIFAN [19,
273 20], which are commonly used methods for multiple length frequency analysis. However, these

274 methods are only applicable without annual growth variation. We found that northern shrimp
275 showed annual growth variation and a decreasing trend in growth in some age groups (Table 4).
276 Consequently, it is appropriate to employ Yamakawa and Matsumiya's method [21] involving
277 inter-annual growth variation.

278 Based on previous studies [8, 9] of the relationship between age and growth stage in the
279 Sea of Japan, we simplified the life history pattern for the length frequency analyses (Fig. 3). The
280 theoretical optimum age of sex change of northern shrimp was calculated to be around 5 years old
281 in the waters off the Noto Peninsula, in the Sea of Japan [25]. The variation in the age at sex change
282 estimated based on survey data from 1987 to 1993 was small [25]. Therefore, it is appropriate to
283 assume that sex change generally occurs at age 5. In addition, Sadakata [9] reported that the
284 proportion of early-matured females was quite low, around 0.05%. Consequently, the simplification
285 of the life history pattern in this study was reasonable because of the consistent timing of sex
286 change.

287 A logistic model for standard deviation σ_j of length-at-age was selected statistically, though
288 the number of parameters estimated is the most in all models (Table 3). Standard deviations of each
289 age group resulted in 2 values calculated by Eq. 15 of which age 1 and the older were 1.014 and
290 1.393, respectively. Possible causes include: if standard deviations are potentially constant in all age
291 groups, mesh selectivity of shrimp-pot employed in scientific surveys might influence on the shape
292 of length distribution of age 1.

293 Despite the different data and methods used, we found that the average growth estimated

294 using multiple length frequency analyses by using length frequency data combined during 1999 to
295 2011 was not very different from the conventional growth values measured in the waters off the
296 Noto Peninsula [9] and in a previous study in our study area [8] (Fig. 6); further, the parameters of
297 length frequency analysis were estimated consistently (Table 4). Age determination for long-lived
298 crustacean species is difficult to decompose the length distribution because of high overlap in length
299 between successive ages owing to their slow growth rate [26]. It was difficult to decompose length
300 distributions of northern shrimp to multi-normal distributions in multiple length frequency analyses,
301 because the length distribution of females (>6 years old) showed a single peak (Fig. 5). Several
302 reasons may explain why we obtained consistent results in our length frequency analyses. First,
303 mean length and standard deviation were assumed from von Bertalanffy and logistic models,
304 respectively. If models are not assumed, then a large number of parameters, including mean lengths,
305 standard deviations, and age compositions, in each of 10 age groups (i.e., 29 parameters in one data
306 set) must be estimated simultaneously. The number of parameters could be reduced to 15 by the
307 MS-EXCEL solver function. Second, length distributions of males and transitional individuals were
308 considered ‘good’ data for length frequency analysis because of clear peaks [24]. Mean lengths at
309 ages 1–5 years could be estimated precisely; consequently, parameters of females of older age
310 classes might be robustly estimated. Third, females with overlap in length distributions at age were
311 assigned age groups based on whether they contained eggs, because they spawn every other year.
312 Therefore, the number of age groups could be reduced, in which non-ovigerous female were divided
313 into two age groups, and ovigerous female into three. This reduction might contribute to a

314 consistent estimation of growth parameters and age compositions in each year.

315 Annual growth variation was detected in multiple length frequency analyses comparing
316 AIC values between cases where the von Bertalanffy parameters were or were not the same as
317 average growth (Table 4). Moreover, lengths-at-age in several age classes showed significantly
318 decreasing trends (Table 4). This size decrease could be caused by fishing and/or environmental
319 factors. Environmental factors may be involved, because the decreasing transition size and
320 commercial landings of the related northern shrimp *P. borealis* in the North Atlantic Ocean were
321 reported to be caused by environmental factors [11-16]. In these study, the size decrease could be
322 caused by increasing metabolic demands as direct factors and by density-dependent effect as
323 indirect factors due to bottom-temperature increase [15, 16]. It follows from these previous studies
324 that annual growth variation could be caused by bottom temperatures as direct or indirect factors. In
325 the Sea of Japan, the potential water temperature of the Japan Sea Proper Water, which northern
326 shrimp occupy, indicates an increasing trend (Japan Meteorological Agency:
327 http://www.data.kishou.go.jp/kaiyou/shindan/e_2/maizuru_koyusui/JSPW_THETA.txt, accessed
328 3/9/2013). The decrease in length-at-age observed in this study, thus, could be caused directly or
329 indirectly by an increase in temperature similar to the case of *P. borealis* in the North Atlantic
330 Ocean. Density-dependent effects, which are indirect factors in the size decrease of shrimp in the
331 North Atlantic Ocean, should be examined after the stock size is estimated in the future study.

332 On the other hand, fishing factors are also a possible reason, because age classes indicated
333 a decrease in mean length after the recruitment ages of 5–8 years. It is questionable that

environment factors, temperature or density-dependent effect, can equally influenced on the growth in not only ages of 5–8 years but all age groups. In northeastern Newfoundland and the Labrador shelf, a mechanism of decreasing mean size of many groundfish species associated with declines in abundance caused by overfishing has been proposed, i.e., selective removal of large individuals as targets of the fishery for commercial species and the capture and discarding of non-commercial species [27]. To support the fishing factor hypothesis, data on the abundance and fishing intensity of northern shrimp are required.

Consider the effect of age composition on the decrease in the mean CL of commercial landings (Fig. 1). Our results suggest not only that the mean size of commercial landings fluctuated corresponding with the change in the age composition, but also that the decrease in length-at-age in the population influenced the consistent size decrease of commercial landings. The reason why the mean CL decreased from 2003 to 2007 is that fewer shrimp in older age classes (>age 9) were caught compared to 2001–2002, and that more individuals of younger age classes were caught from 2005 to 2007 (Figs. 1, 10). On the other hand, the reason why the mean length slightly increased from 2008 to 2009 is that the 2000 and 2001 year classes, which were relatively abundant, recruited to the main fishing target size (Fig. 10). Subsequently, from 2010 to 2011, the mean length decreased again, because 2000 and 2001 year classes, which neared the end of their life span, no longer comprised the majority of the landings. Even if relative abundant year classes, e.g., 2000 and 2001, recruited, the mean length consistently decreased. The decrease in length-at-age in the main age classes of commercial landings, i.e., from ages 5–8 years, resulting from length frequency

354 analysis, influenced the consistent decrease in the landings (Table 4).

355 The number of ovigerous females at ages 6 and 8 years was low compared to that of 7- and
356 9-year-old non-ovigerous females, despite the small age difference (Fig. 8). The catch number of
357 ovigerous females was lower than that of non-ovigerous females, likely because swimming or
358 feeding activity of ovigerous females was low compared to that of non-ovigerous females [28].
359 Since the shrimp-pot fishery, which contributes more than 90% of the total catch of northern shrimp
360 in the Sea of Japan, off western Hokkaido, is a passive fishing method, low activity levels would
361 prevent ovigerous females from being caught.

362 We found that abundant year classes caught successively year after year were more readily
363 identified in z values of catch-at-age data computed by ALKs than by ACT (Fig. 10). In ACT, all
364 individuals within a certain range of length classes were considered an age group (Table 2).
365 Therefore, the number of individuals in the abundant age class was underestimated because
366 individuals outside of a designated length class were counted in successive age classes on both sides.
367 On the other hand, the number of individuals in less common age classes was overestimated; in
368 particular, adjacent age classes would influence each other. In ALKs, age compositions in length
369 classes that overlapped were estimated by fitting normal distributions, which largely reduced the
370 bias affected by abundant age classes. In 2009 and 2010, catch number of age 6 estimated by ALKs
371 were smaller than by ACT, because of the replacement of abundant age classes by year classes of
372 2000 and 2001 (Fig. 9). Consequently, using ALKs computed by multiple length frequency analyses,
373 catch-at-age would be improved, both practically and theoretically. It is generally recognized that

374 ALKs generate a bias in computing catch-at-age from length frequency [6, 7]. In particular,
375 Westrheim and Ricker examined the factors that introduce bias when catch-at-age is computed from
376 length frequency using ALKs [6]. They reported that the age composition of a parental sample in
377 the ALK influences that of a filial sample in the ALK. The bias becomes larger when length
378 distributions are much more overlapped between successive age groups. Consequently, they
379 concluded that a parental sample for ALK should be collected from the same population at the same
380 time to compute catch-at-age irrespective of fishing gear. In our study, catch-at-age was computed
381 using ALKs estimated every year to prevent introducing a bias caused by annual growth variation.
382 Thus, the computed catch-at-age should not be affected by bias corresponding to sampling year. If it
383 is necessary to estimate catch-at-age even more precisely, then the ageing problem must be solved.
384 Technical developments are expected for the direct determination of age in crustaceans, including
385 routinely examining lipofuscin accumulation or growth bands of the eyestalk [29-31].

386 We were able to construct an age-structured model by estimating catch-at-age.
387 Subsequently, the causal relationship between the decrease in length-at-age in a population and
388 fishing impacts or population density could be discussed. Moreover, we propose the effective
389 utilization of recruitment, e.g., yield per recruit (YPR) and spawning per recruit (SPR) analyses.
390 Particularly for northern shrimp in the Sea of Japan, off western Hokkaido, most landings are
391 caught by the shrimp-pot fishery, which can readily control the size of the harvested shrimp by
392 changing the mesh size without bycatch of small northern shrimp [32]. Based on YPR and SPR
393 analyses, it would be possible to propose an optimal mesh size of the shrimp-pots that is compatible

394 both for the sustainable utilization of the resource and for increased production value.

395

396 **Acknowledgements**

397 We would like to thank the crew of “Hokuyo-maru”, scientific research vessel of Wakkanai
398 Fisheries Research Institute, Hokkaido Research Organization, for their support in the shrimp-pot
399 survey. We also thanks Dr. H. Miyake, Dr. O. Shida and Dr. K. Baba, Central Fisheries Research
400 Institute, Hokkaido Research Organization for many helpful comments. We are grateful to the
401 scientist of shrimps in Hokkaido Research Organization for their successive data collection.

402

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485

486 Figure captions

487 **Fig. 1** Fluctuations in the total catch, unit price, and mean carapace length of commercial landings
488 of northern shrimp in the Sea of Japan, off western Hokkaido (columns show total catch in
489 weight, closed circles show unit price, and open circles show mean carapace length). Total catch
490 and unit price data were obtained from fisheries statistics of the Hokkaido government; mean
491 carapace length was calculated from catch-at-length classes as described in the Materials and
492 Methods

493 **Fig. 2** Shrimp-pot survey area (oblique lines) covered during 1999–2011 by a scientific research
494 vessel collecting northern shrimp for length frequency analyses (solid lines show 200 m water
495 depth; dotted lines show 600 m water depth)

496 **Fig. 3** Life history of northern shrimp in the Sea of Japan, off western Hokkaido

497 **Fig. 4** Flow chart for discriminating growth stages before or after molting of commercial landings
498 of northern shrimp for estimating catch-at-length

499 **Fig. 5** Carapace length and normal distributions of each growth stage of northern shrimp estimated
500 by length frequency analyses in each year (bars show frequencies in each length class, black
501 lines show multi-normal distributions, gray lines show normal distributions in each age class)

502 **Fig. 6** Age and growth of northern shrimp estimated using common von Bertalanffy parameter
503 every year in length frequency analysis (closed circles show results of this study; crosses show
504 results of a previous study, conducted around the Musashi bank [8]; asterisks show results from
505 waters off the Noto Peninsula [9])

506 **Fig. 7** Length distributions of northern shrimp caught by commercial fisheries in the Sea of Japan,
507 off western Hokkaido. Black: males, dark gray: transitional individuals, gray: non-ovigerous
508 females, white: ovigerous females

509 **Fig. 8** Catch-at-age of northern shrimp calculated by a) age-length key and b) age-conversion table

510 **Fig. 9** Difference values in catch-at-age of northern shrimp estimated by ALK and by ACT

511 **Fig. 10** Z values of catch-at-age of northern shrimp calculated by a) age-length key and b)
512 age-conversion table

Table 1 Summary of shrimp-pot surveys conducted by a scientific research vessel for multiple length frequency analyses

Year	Date	Number of stations	Number of shrimp-pots	Depth (m)	Number of individuals in each growth stage					Range of carapace length (mm)
					M	T	NOF	OF	Total	
1999	6–14 July	10	100	318 - 510	1,999	1	1,671	314	3,985	7.4-35.0
2000	4–10 July	11	110	301 - 506	2,060	0	4,037	1,211	7,308	8.1-36.5
2001	3–9 July	6	180	405 - 495	2,786	0	4,495	846	8,127	3.3-36.9
2002	3–6 July	7	420	346 - 498	3,954	0	3,845	1,648	9,447	5.6-37.2
2003	3–10 July	12	720	264 - 589	5,045	2	12,479	2,405	19,931	5.9-36.4
2004	1–8 July	10	600	303 - 595	8,611	0	5,960	1,042	15,613	6.1-35.8
2005	30 Jun–6 July	8	480	248 - 497	11,313	0	6,826	3,660	21,799	5.1-35.6
2006	17–24 Jun	18	524	251 - 512	5,235	0	5,658	2,288	13,181	6.4-34.4
2007	15–28 Jun	16	461	240 - 506	6,346	0	5,077	2,831	14,254	4.2-35.1
2008	6–18 Jun	14	416	258 - 517	2,596	0	3,814	1,611	8,021	5.9-34.7
2009	25 Jun–2 July	16	478	270 - 517	5,353	0	8,004	3,938	17,295	6.4-34.7
2010	8–15 Jun	16	384	241 - 520	7,391	0	8,840	3,394	19,625	5.3-35.3
2011	7–14 Jun	16	384	212 - 517	5,971	0	9,123	3,061	18,155	4.9-36.0

M: male, T: transitional, NOF: non-ovigerous female, OF: ovigerous female

Table 2 Age-conversion table for calculating catch-at-age from catch-at-length classes of commercial northern shrimp landings

Age	Carapace length class and growth stage
1	0–13 mm male
2	14–16 mm male
3	17–19 mm male
4	20–22 mm male
5	more than 23 mm male or all size transitional
6	less than 28 mm ovigerous female
7	less than 29 mm non-ovigerous female
8	28–30 mm ovigerous female
9	29–31mm non-ovigerous female
10	more than 31mm ovigerous female
11	more than 32 mm non-ovigerous female

Modified from Nakame and Mitsuhashi [10]

Table 3 Results of the model selection of growth parameter and standard deviation σ_j in multiple length frequency analysis

Case	von Bertalanffy parameters	model of standard deviation σ_j	m	AIC value
1-1	common	constant	121	1,431,632
1-2	common	liner	122	1,431,076
1-3	common	logistic	123	1,430,154 *
1-4	common	Tanaka and Tanaka [22]	122	1,430,815
2-1	variable	constant	157	1,428,738
2-2	variable	liner	158	1,428,207
2-3	variable	logistic	159	1,427,153 **
2-4	variable	Tanaka and Tanaka	158	1,427,805

Single asterisk shows the selected model for estimation of average growth

Double asterisk shows the selected model for estimation of growth with annual growth variation

m indicates the number of free parameters

Table 4 von Bertalanffy growth model parameters and mean carapace length at each age of northern shrimp estimated using multiple length frequency analysis

Survey year	von Bertalanffy parameters			Mean carapace length (mm) in each age									
	$L_{\infty y}$	K_y	j_{0y}	1	2	3	4	5°	6°	7°	8°	9	10
1999-2011	35.877	0.208	-0.492	9.58	14.51	18.52	21.79	24.44	26.60	28.36	29.79	30.95	31.90
1999	33.984	0.258	-0.413	10.37	15.73	19.88	23.08	25.56	27.47	28.95	30.09	30.98	31.66
2000	36.387	0.210	-0.560	10.17	15.15	19.17	22.44	25.08	27.23	28.96	30.37	31.51	32.44
2001	35.783	0.208	-0.500	9.58	14.50	18.49	21.73	24.37	26.51	28.25	29.66	30.81	31.74
2002	37.066	0.192	-0.519	9.36	14.20	18.19	21.48	24.20	26.44	28.30	29.83	31.09	32.13
2003	37.616	0.185	-0.625	9.77	14.47	18.38	21.63	24.33	26.58	28.44	29.99	31.28	32.35
2004	34.920	0.227	-0.383	9.41	14.59	18.72	22.01	24.63	26.72	28.39	29.71	30.77	31.61
2005	37.935	0.188	-0.491	9.29	14.21	18.28	21.66	24.45	26.77	28.69	30.28	31.59	32.68
2006	34.051	0.248	-0.323	9.51	14.89	19.09	22.37	24.93	26.93	28.49	29.71	30.66	31.41
2007	35.901	0.210	-0.476	9.55	14.53	18.57	21.85	24.50	26.66	28.40	29.82	30.97	31.90
2008	36.363	0.199	-0.414	8.90	13.85	17.90	21.22	23.95	26.18	28.02	29.52	30.75	31.76
2009	35.196	0.205	-0.653	10.10	14.74	18.53	21.61	24.13	26.18	27.84	29.21	30.31	31.22
2010	34.135	0.224	-0.464	9.55	14.49	18.44	21.59	24.11	26.13	27.73	29.02	30.05	30.87
2011	36.091	0.206	-0.503	9.61	14.54	18.55	21.82	24.48	26.64	28.40	29.83	31.00	31.95

Open circles show age classes which decreased in carapace length significantly ($p < 0.05$) by regression analysis

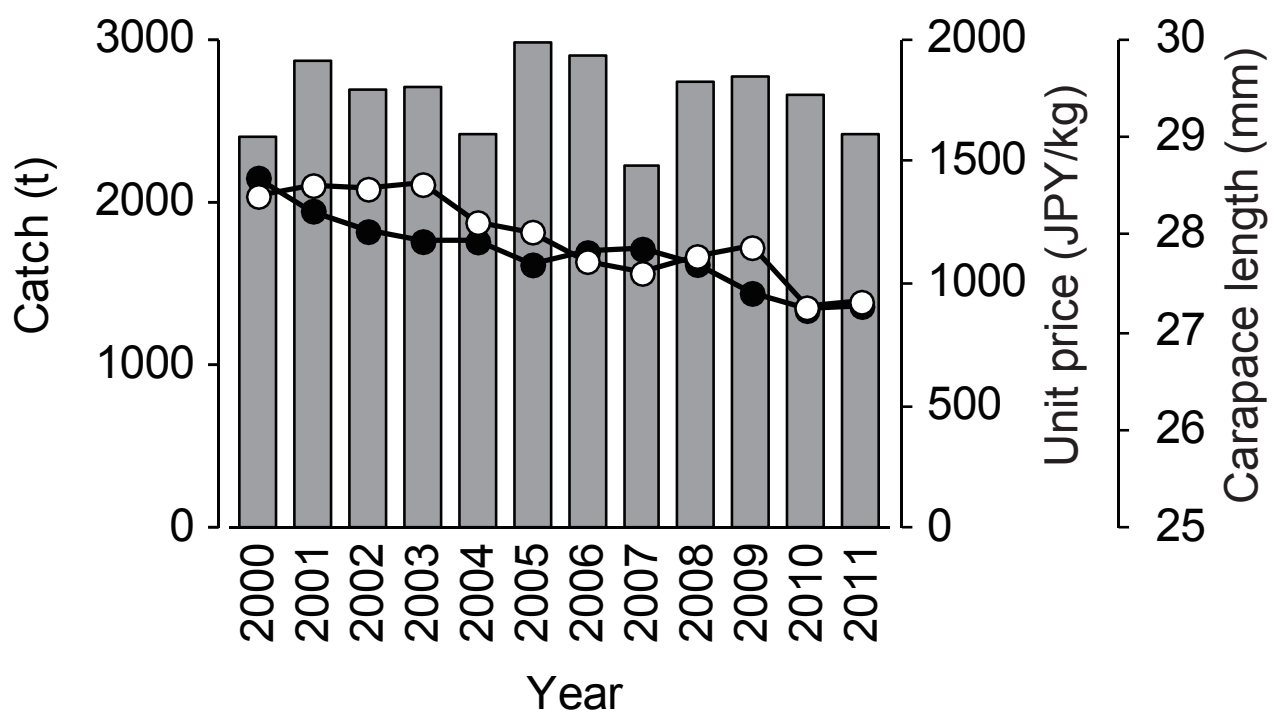


Figure 1

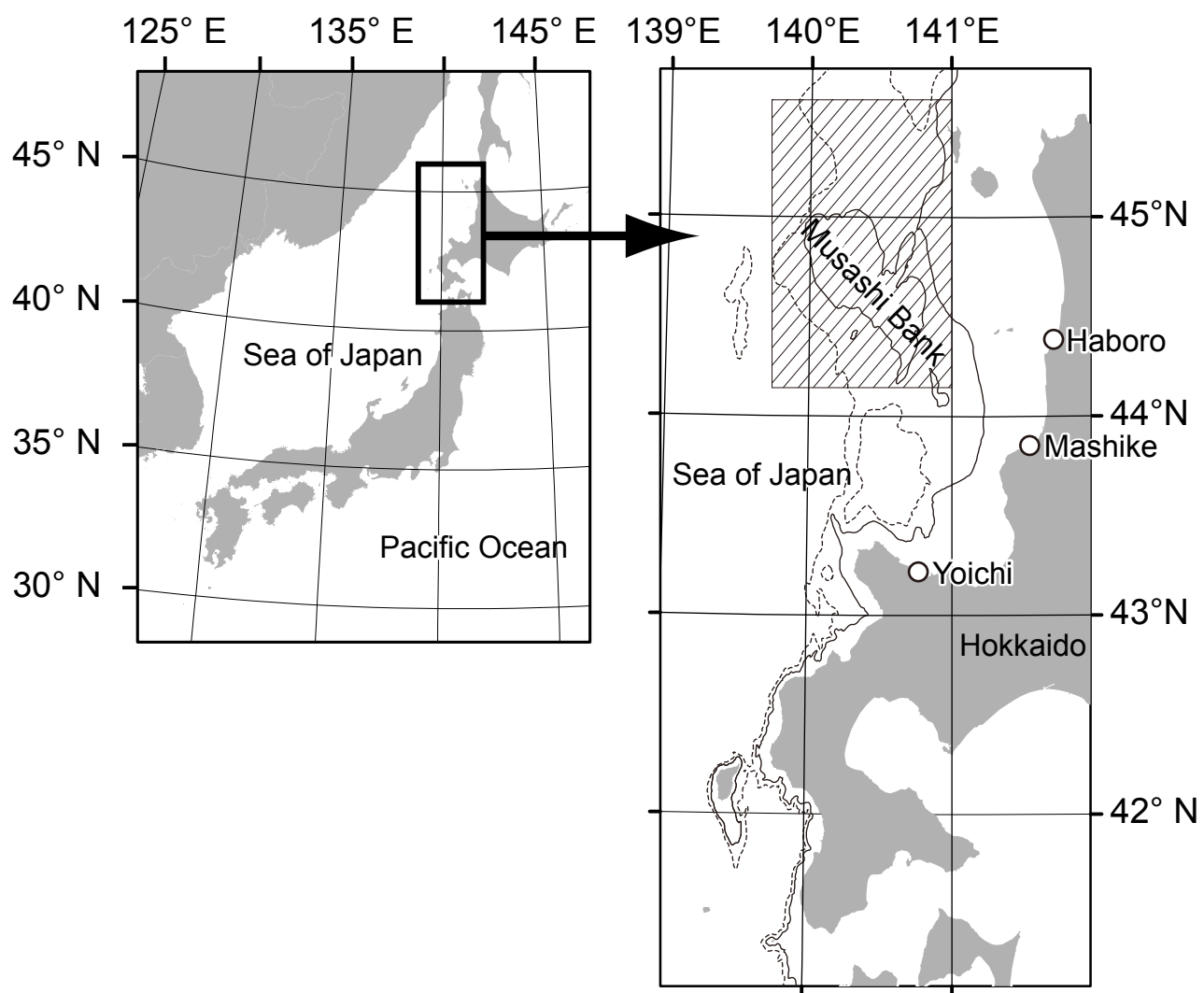


Figure 2

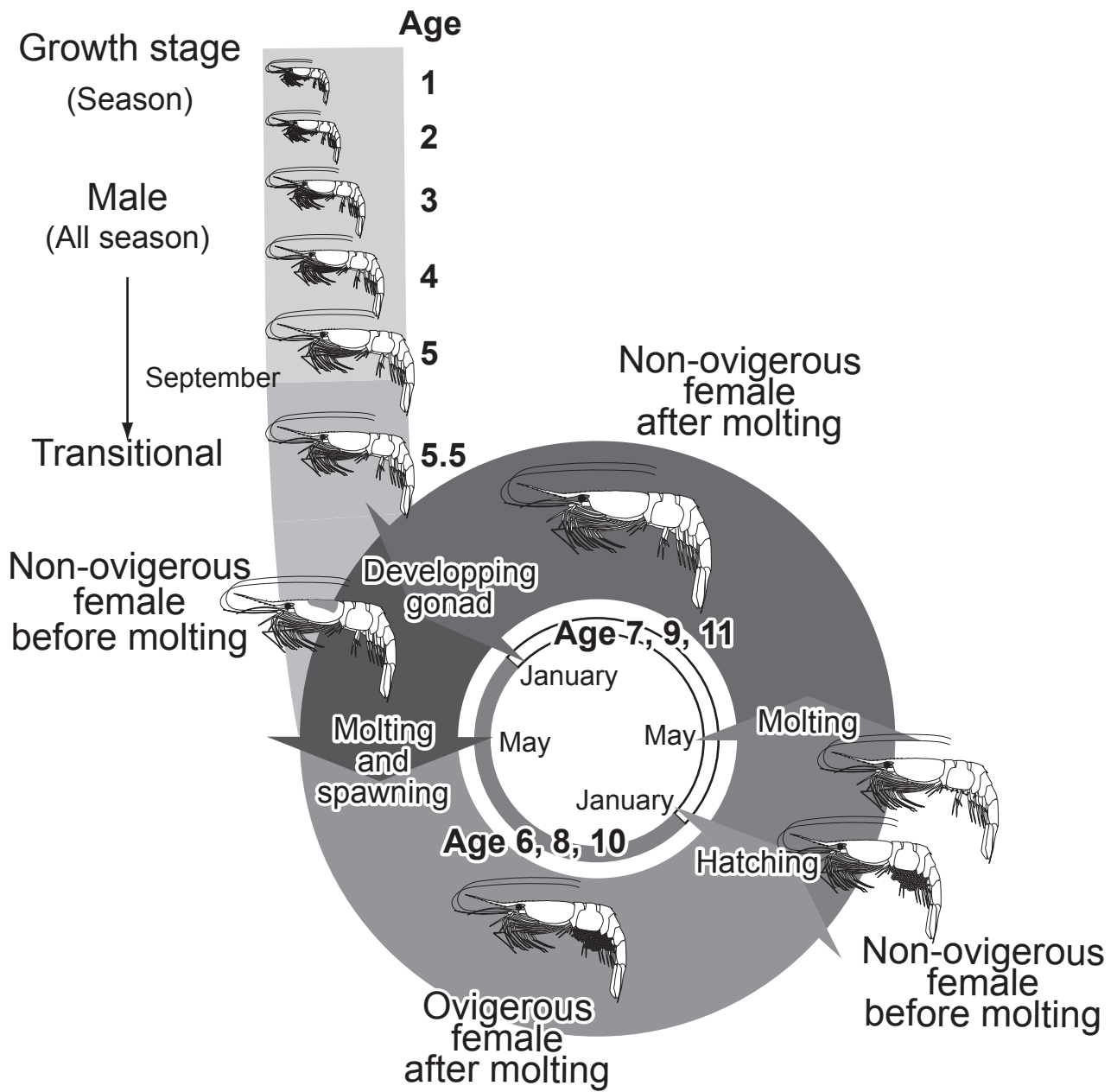


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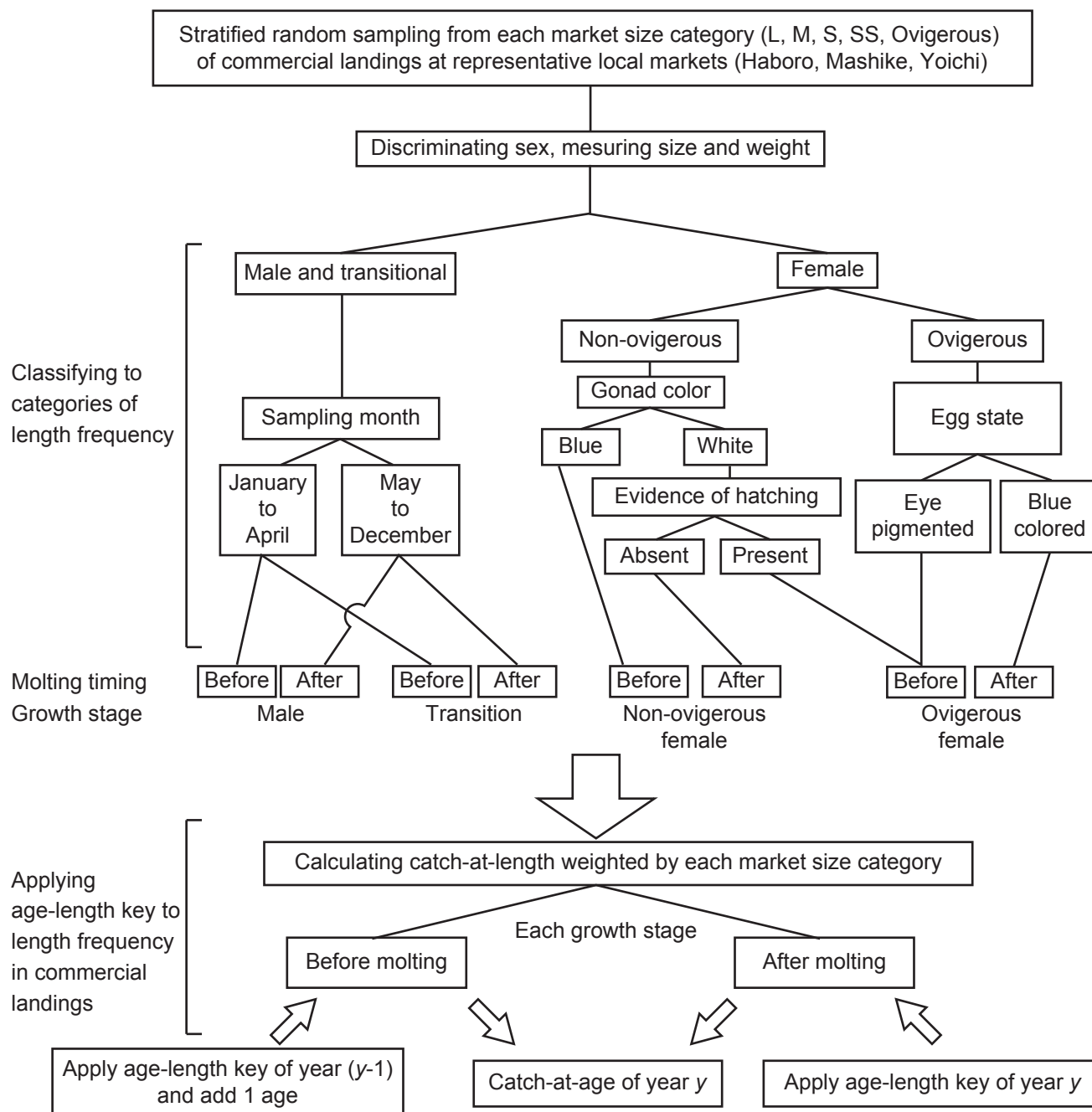


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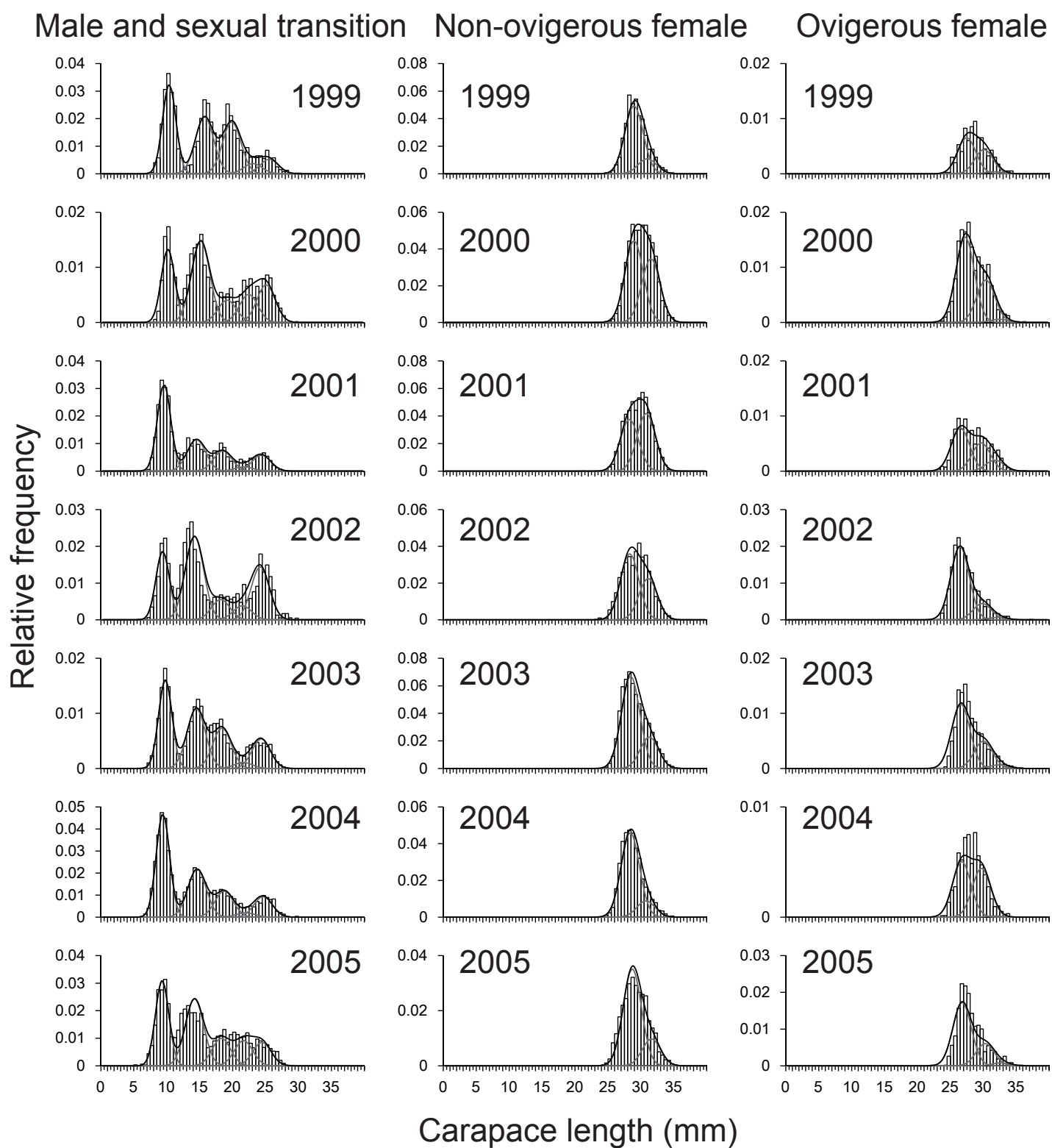


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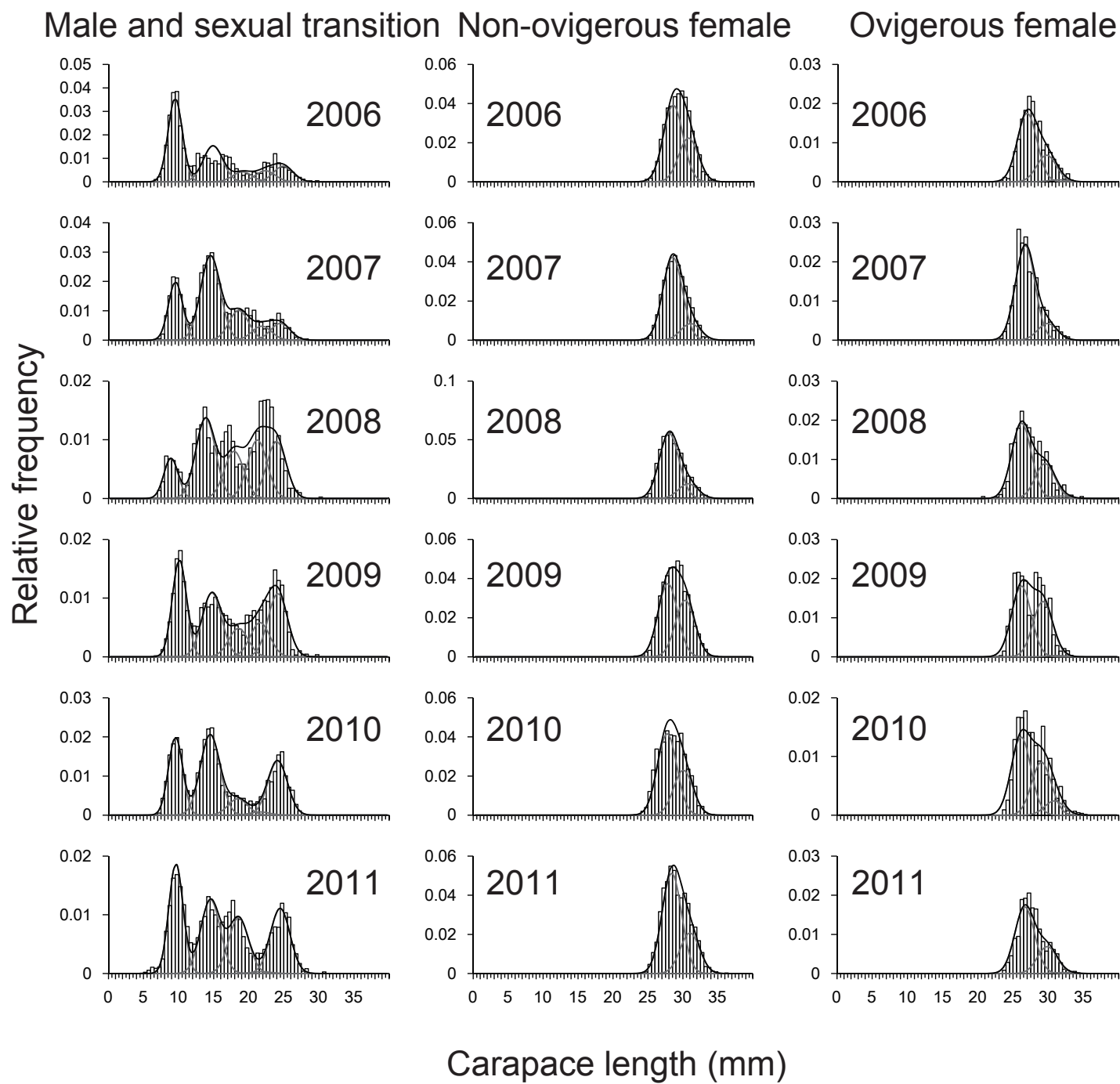


Figure 5 (Continued)

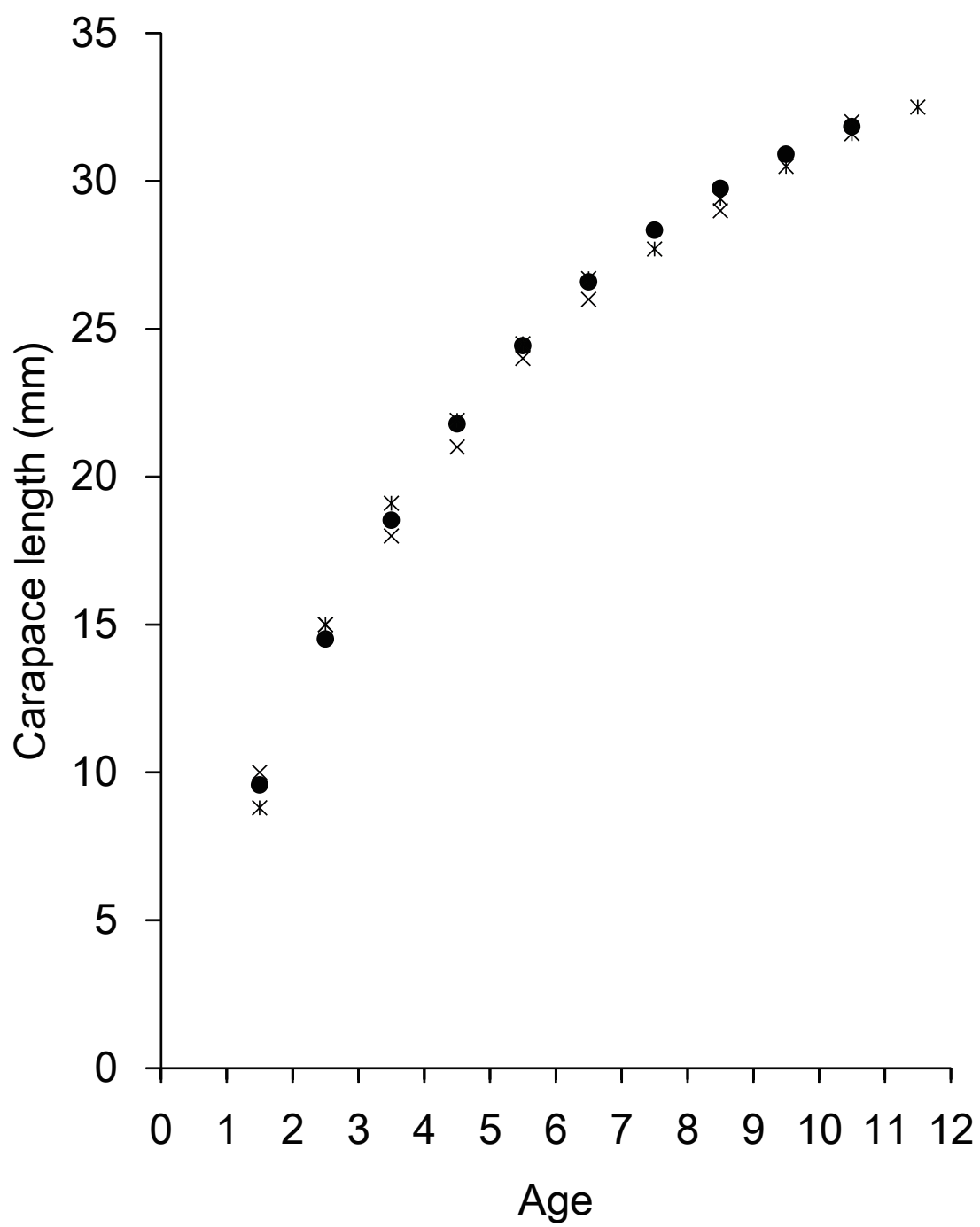


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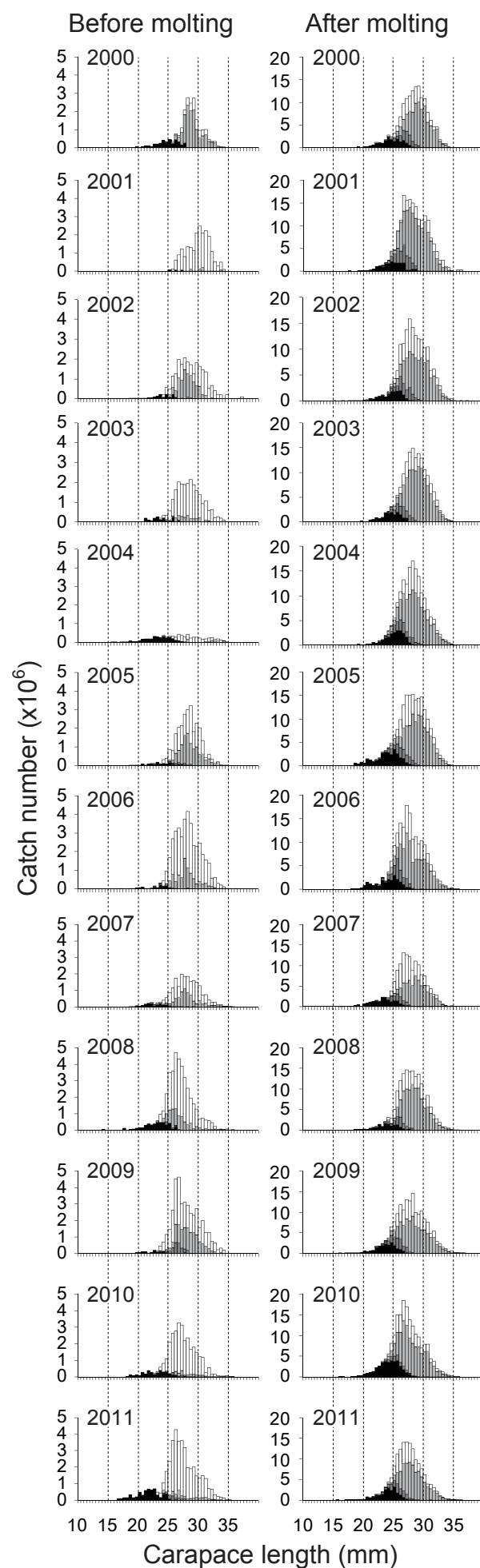


Figure 7

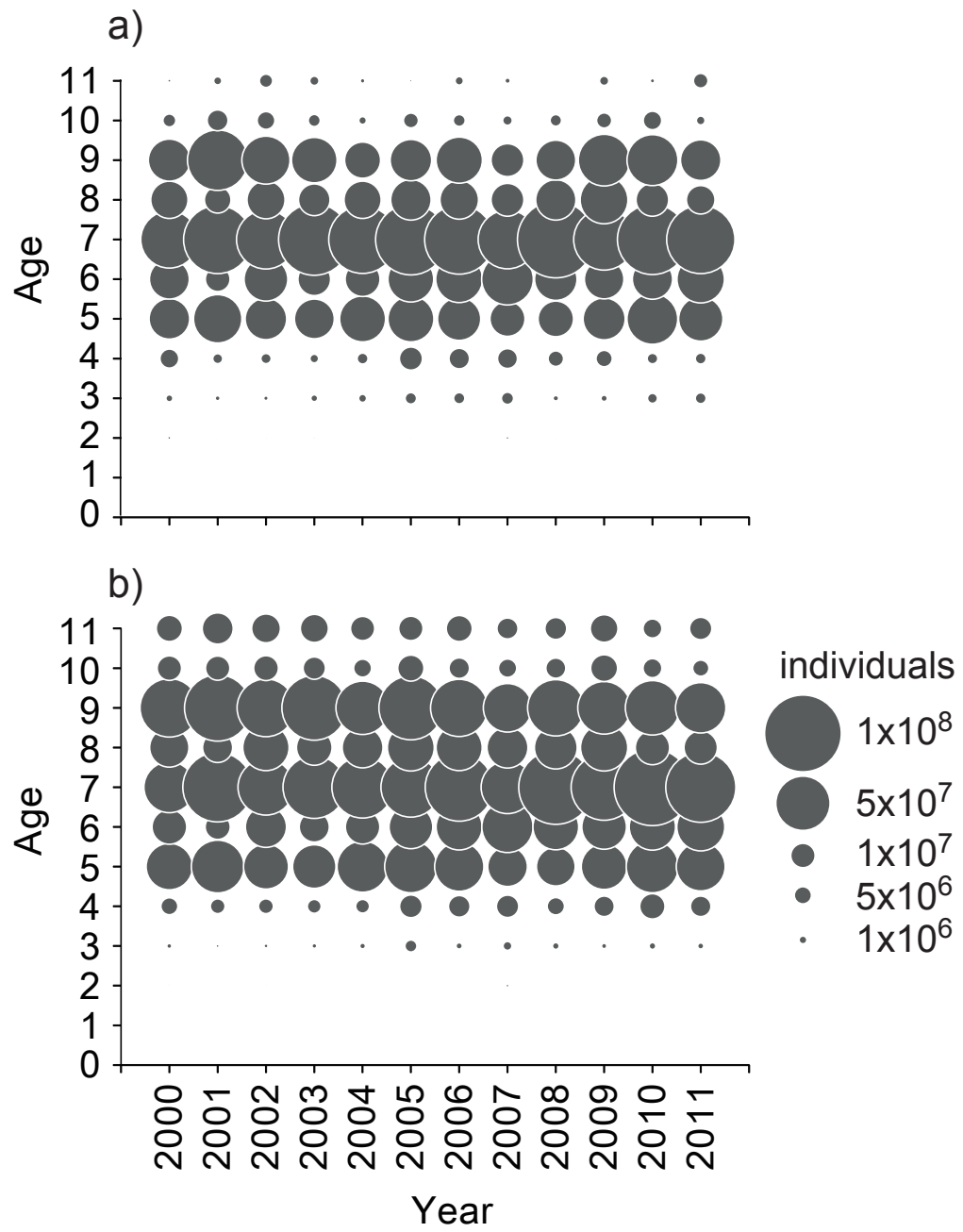


Figure 8

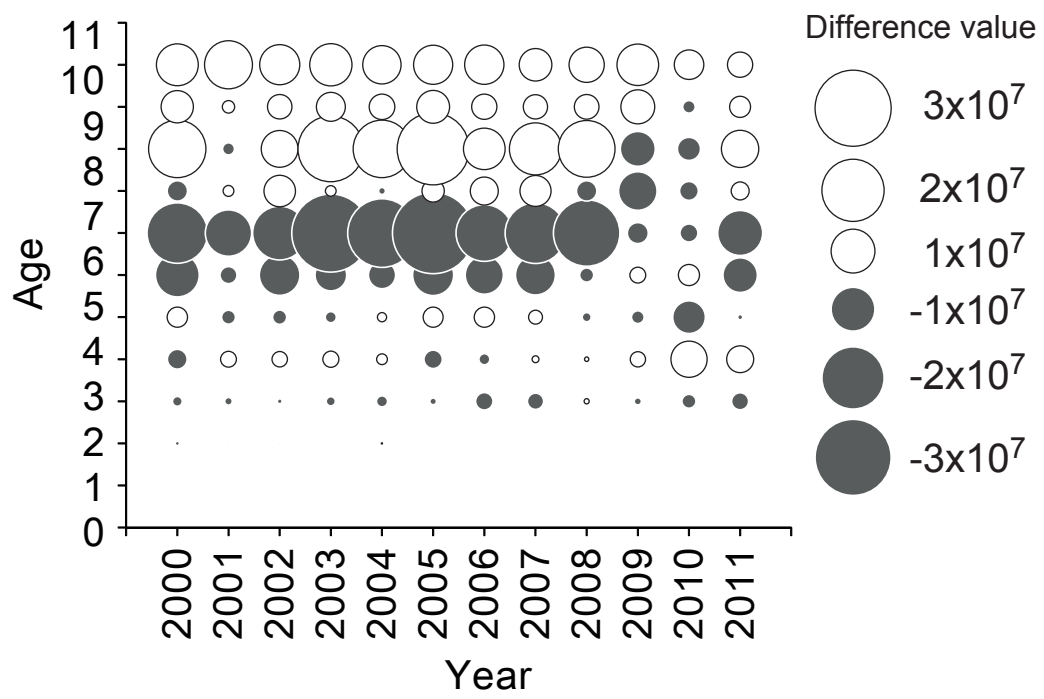


Figure 9

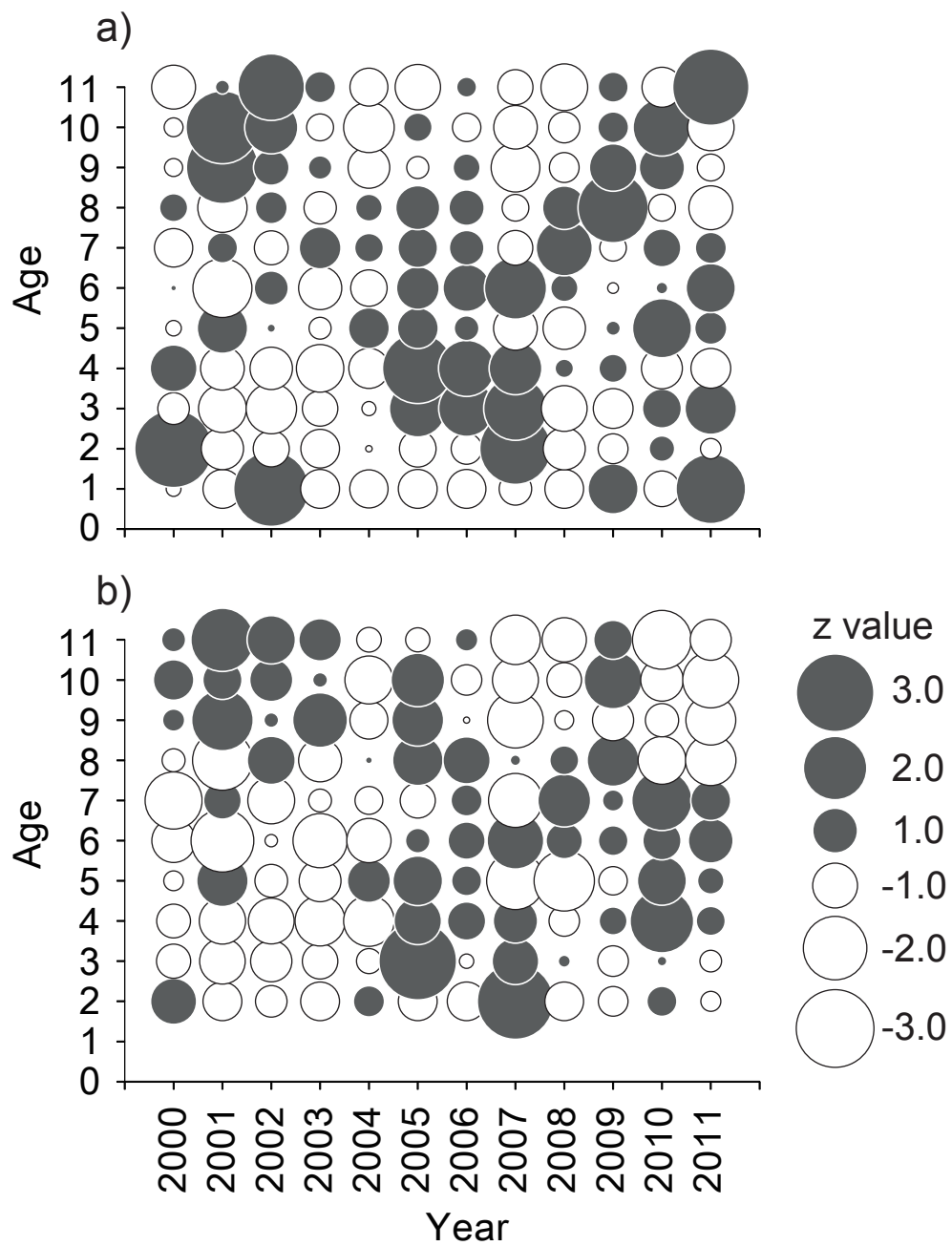


Figure 10

甲長組成解析によって推定されたホッコクアカエビの成長と年齢組成

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北海道西部日本海海域におけるホッコクアカエビの成長と年齢別漁獲尾数を推定するため、調査船標本にもとづく甲長組成解析を行い、年齢別サイズを調べた。解析結果から、成長の年変動と年齢別サイズの減少傾向が認められた。年齢別漁獲尾数の推定方法を、従来の甲長一年齢変換テーブル(ACT)から、age-length key(ALK)による方法に改良した。また、近年の漁獲物の小型化は、年齢組成の変動だけではなく、年齢別サイズの減少の影響を受けていることを明らかにした。