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Title:

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

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Abstract

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

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

Introduction

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

Several stock assessment methods for fisheries resources have been proposed in terms of relative abundance measured by fisheries or research data [2, 3] or by population estimates using catch-at-age data [4, 5], among others. Stock assessments for a large number of fisheries resources can be conducted by an age-structured model, which has the advantage that population size, fishing mortality, and age and time structure can be estimated. Such estimates provide the basis for the evaluation of a stock-recruitment relationship and for the exploration of some technical management procedures. Catch-at-age data are indispensable in age-structured models for population estimates of northern shrimp.

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

Age and growth (age composition) of crustaceans is usually inferred from their length distribution, which is assumed to have a multi-normal distribution for each age and mean lengths at age, standard deviation, and frequency per age-at-length [17-21]. The method of Yamakawa and Matsumiya [21] can simultaneously analyze multiple length frequency data sets even when growth rates fluctuate between years, allowing all available information in the data to be used.

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

Materials and methods

Collecting samples for length frequency analysis

Carapace length (CL) frequency data of northern shrimp for length frequency analysis were collected by scientific surveys conducted every year from 1999 to 2011 by the scientific research vessel “Hokuyo-maru” (gross registered tonnage 237 t), which belongs to the Wakkanai Fisheries Research Institute (Table 1). Annual surveys were conducted during June and July every year at water depths of 200–600 m to cover the distribution of northern shrimp in the Sea of Japan, off western Hokkaido (Fig. 2). Sampling was conducted 6–18 times in each year using shrimp-pots with a mesh size of 5.33 mm bar length. The number of shrimp-pot employed per station was almost constant within a survey year, although it was varied from year to year. Collected northern shrimp were classified into four stages (male, transitional, non-ovigerous female, and ovigerous female), based on the shape of the first pleopod and the presence or absence of eggs in the abdomen. Oblique CL, which is the distance from the eye socket to the mid-posterior carapace edge, was measured to the nearest 0.1 mm with digital calipers. These measurements were made either on board immediately after the catch or at later at the laboratory.

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

The number of age groups was determined for length frequency analysis. The life history pattern of northern shrimp in the Sea of Japan, off western Hokkaido, was simplified based on the results of Nakame [8] as follows. The birth date of the shrimp was set to January 1. Males and transitional individuals were considered to be aged 1–5 years, non-ovigerous females were aged 7 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 yth 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 jth age group of growth stage s in the yth 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:

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

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

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

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

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

Constant: $$\sigma_j = a \qquad (3)$$

Liner: $$\sigma_j = aj + b \qquad (4)$$

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

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

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

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

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

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

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

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

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

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

$$\mathrm{AIC} = -2MLL' + 2m \qquad (10)$$

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

Estimation of catch-at-age in commercial landings

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:

$$N_{i,y} = \frac{M_{0,y}}{\sum_{t} M_{t,y}} \sum_{k} \sum_{t} \sum_{m} \frac{W_{k,m,t,y}}{\overline{w}_{k,m,t,y}} n_{i,k,m,t,y} \qquad (11)$$

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, $\overline{w}_{k,m,t,y}$ 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 calculate catch-at-age in year *y*, ALKs in year (*y*–1) or year *y* applied to catch-at-length class before or after molting, respectively, and after age 1 year were added to that before molting, and then both catch-at-age values were summed. Transitional individuals were considered to be age 5 after molting and age 6 before molting. Alternative estimation by a simple method, viz. an ACT without annual growth variation, was conducted using the same length frequency data (Table 2) [10].

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

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

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 standard deviation of *j*th age group during 2000–2011, respectively.

Results

Growth of northern shrimp

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

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

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

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

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

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

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

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

Multi-normal distributions estimated by the maximum likelihood method indicated a good fit to the length distributions (Fig. 5). Inter-annual variation of length-at-age was small, with standard deviations of 0.37–0.50 (Table 4). Regression analysis revealed significantly decreasing trends in mean length from ages 5–8 years ($p < 0.05$; Table 4).

Catch-at-age

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

ALKs were computed for every year according to the results of annual growth variation (Table 3). Catch-at-age computed by ALKs and ACT were similar in that the catch number at age 3, an age class of recruitment, represented a low proportion of the total catch. The catch number at age 7, i.e., 4 years after recruitment, was the highest of the total catch (Fig. 8). The catch of 6- and 8-year-old ovigerous females was smaller than the catch of 7- and 9-year-old non-ovigerous females (Fig. 8). The catch number of 6- and 7-year-old individuals computed by ALK was almost larger than that computed by ACT (Fig. 9). On the other hand, the number of, 9- and 10-year-old shrimp was almost smaller because of the compensation for the increased numbers of 6- and 7-year-old shrimp, which are the most abundant age groups of non-ovigerous and ovigerous females, respectively (Fig. 9). Moreover, the number of 11-year-old shrimp computed by ALK was smaller than that computed by ACT (Fig. 9).

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

Discussion

In this study, we used the method of Yamakawa and Matsumiya [21] for a length frequency analysis to estimate the growth and age composition of northern shrimp. Biologically reasonable results are not necessarily obtained when a multi-normal distribution is fit to a length distribution by a statistical method [23, 24]. To avoid such inconsistent results, the mean length and standard deviation in each age group are assumed in some models [23, 24]. ELEFAN and MULTIFAN [19, 20], which are commonly used methods for multiple length frequency analysis. However, these methods are only applicable without annual growth variation. We found that northern shrimp showed annual growth variation and a decreasing trend in growth in some age groups (Table 4). Consequently, it is appropriate to employ Yamakawa and Matsumiya's method [21] involving inter-annual growth variation.

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

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

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

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

On the other hand, fishing factors are also a possible reason, because age classes indicated 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 analysis, influenced the consistent decrease in the landings (Table 4).

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

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

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

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

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Figure captions

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

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

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

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

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

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

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

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

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

Fig. 10 Z values of catch-at-age of northern shrimp calculated by a) age-length key and b) 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									
	$L_{\inf y}$	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

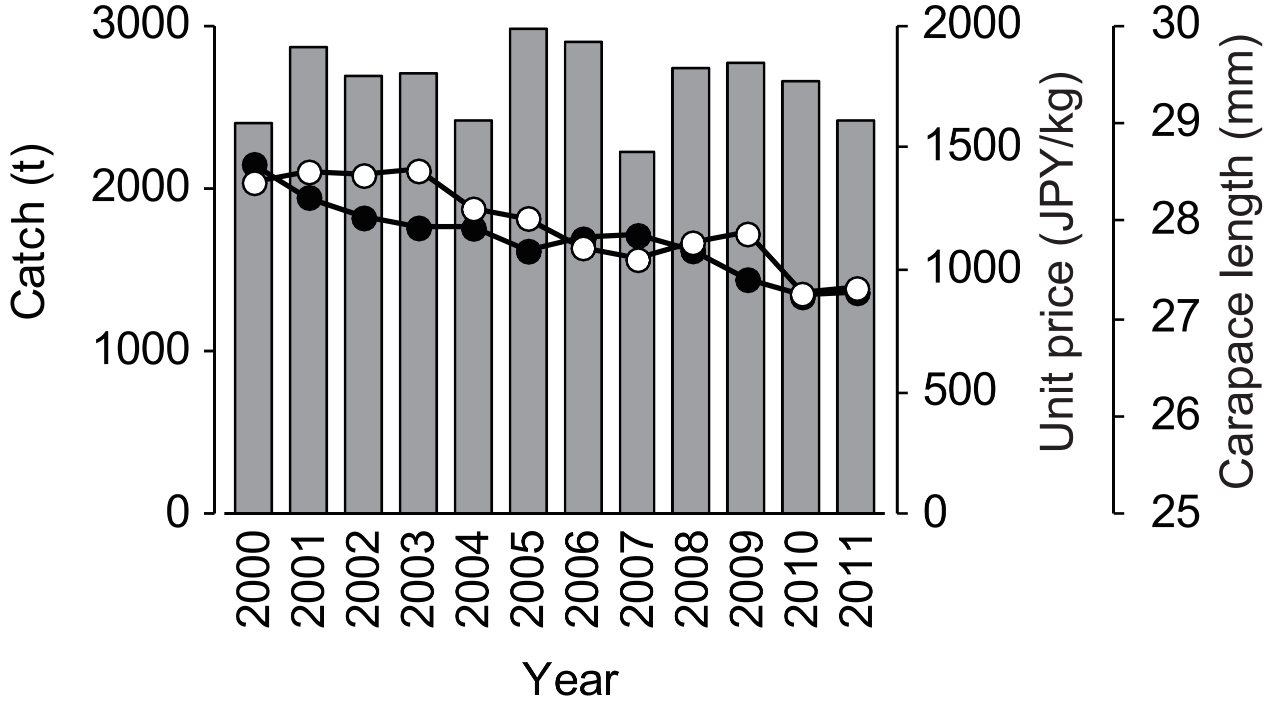
Catch (t)
3000
2000
1000
0
2000
1500
1000
500
0
Unit price (JPY/kg)
30
29
28
27
26
25
Carapace length (mm)
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year

Figure 1

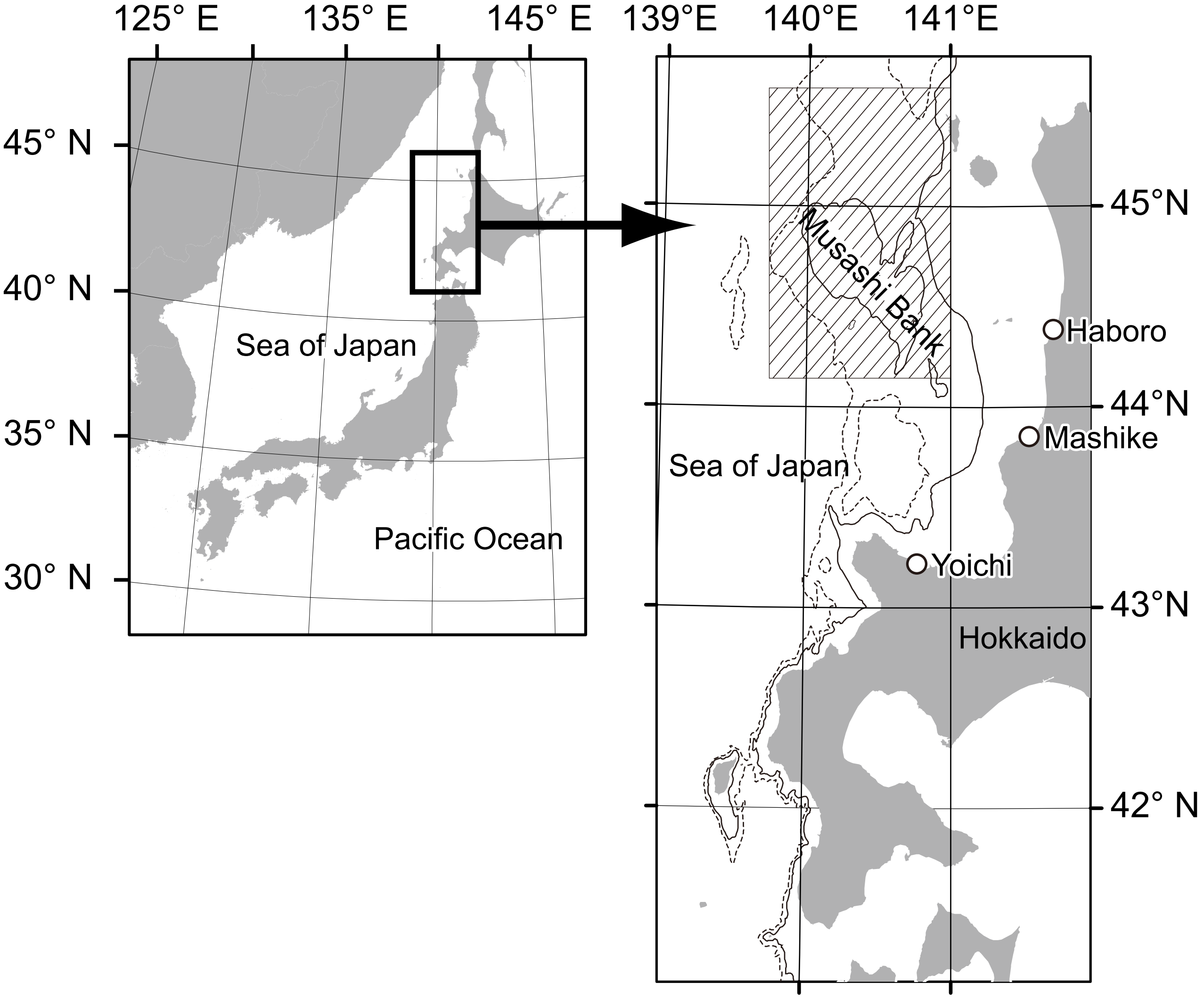
125° E
135° E
145° E
45° N
40° N
35° N
30° N
Sea of Japan
Pacific Ocean
139°E
140°E
141°E
45°N
44°N
43°N
42° N
Musashi Bank
Haboro
Mashike
Yoichi
Sea of Japan
Hokkaido

Figure 2

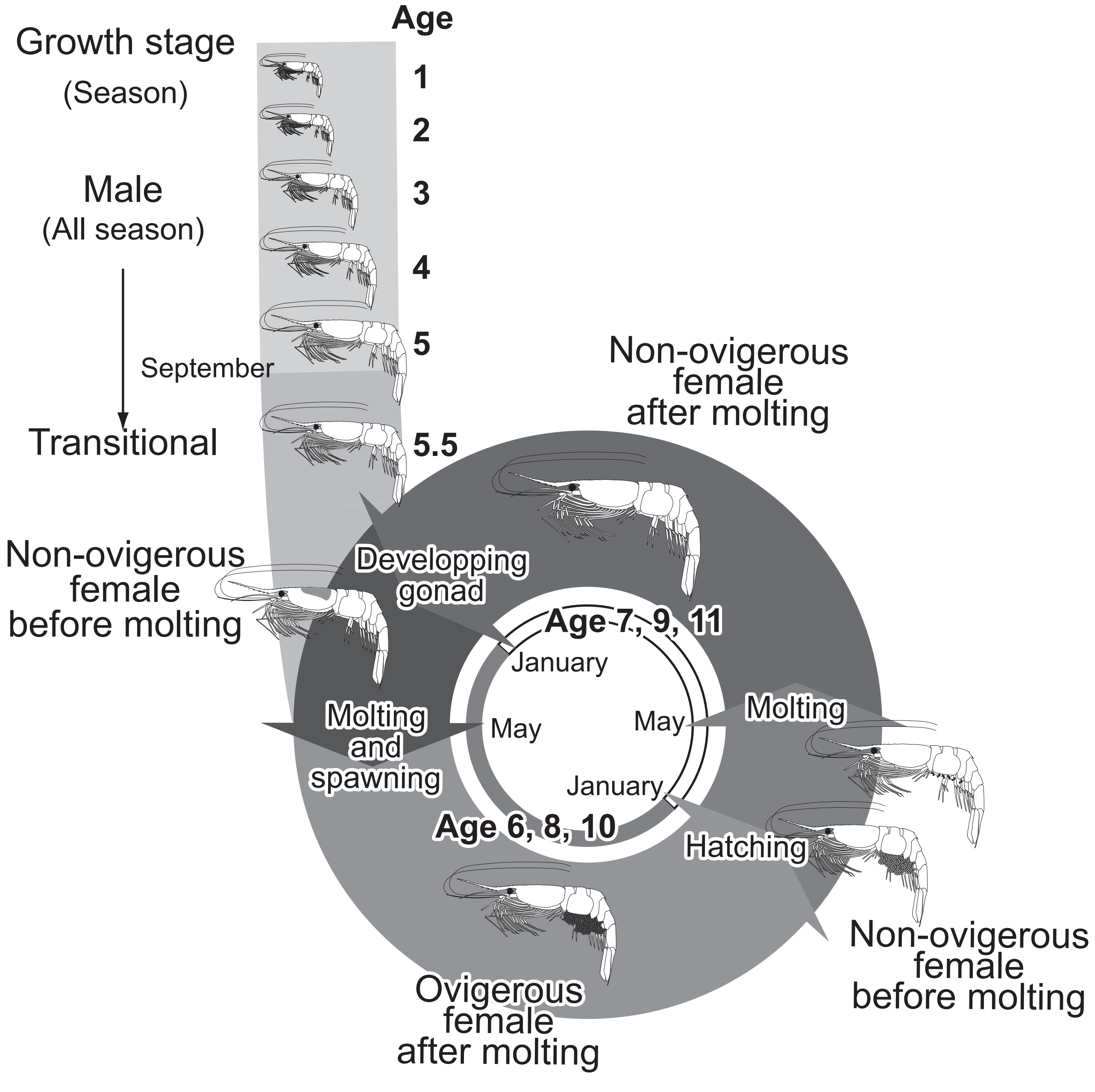
Age
Growth stage
(Season)
1
2
Male
(All season)
3
4
5
September
Transitional
5.5
Non-ovigerous
female
after molting
Non-ovigerous
female
before molting
Developping
gonad
Age 7, 9, 11
January
Molting
and
spawning
May
May
Molting
January
Age 6, 8, 10
Hatching
Non-ovigerous
female
before molting
Ovigerous
female
after molting

Figure 3

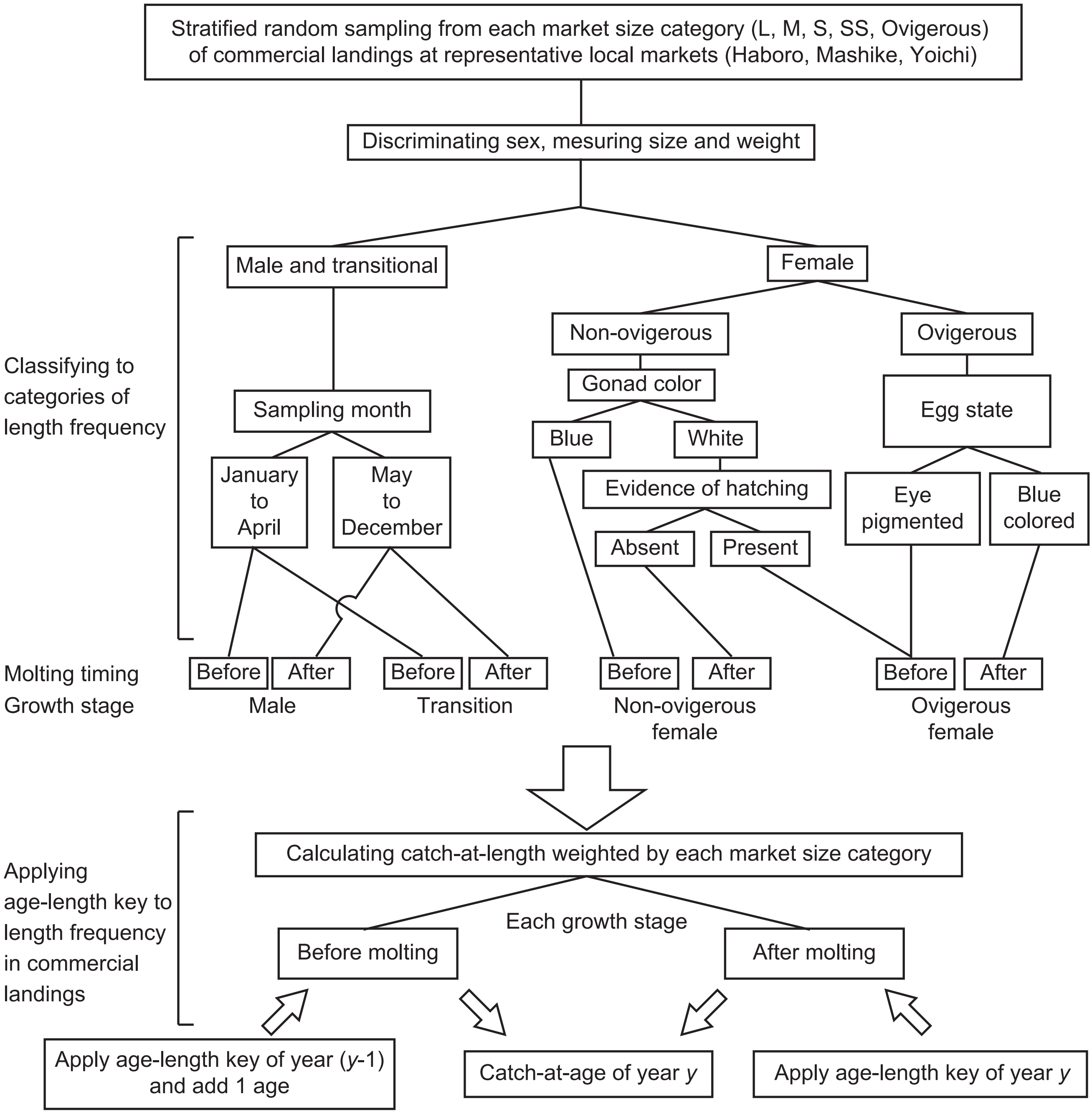
Stratified random sampling from each market size category (L, M, S, SS, Ovigerous) of commercial landings at representative local markets (Haboro, Mashike, Yoichi)
Discriminating sex, mesuring size and weight
Classifying to categories of length frequency
Male and transitional
Sampling month
January to April
May to December
Female
Non-ovigerous
Gonad color
Blue
White
Evidence of hatching
Absent
Present
Ovigerous
Egg state
Eye pigmented
Blue colored
Molting timing
Growth stage
Before
After
Before
After
Before
After
Before
After
Male
Transition
Non-ovigerous female
Ovigerous female
Applying age-length key to length frequency in commercial landings
Calculating catch-at-length weighted by each market size category
Each growth stage
Before molting
After molting
Apply age-length key of year (y-1) and add 1 age
Catch-at-age of year y
Apply age-length key of year y

Figure 4

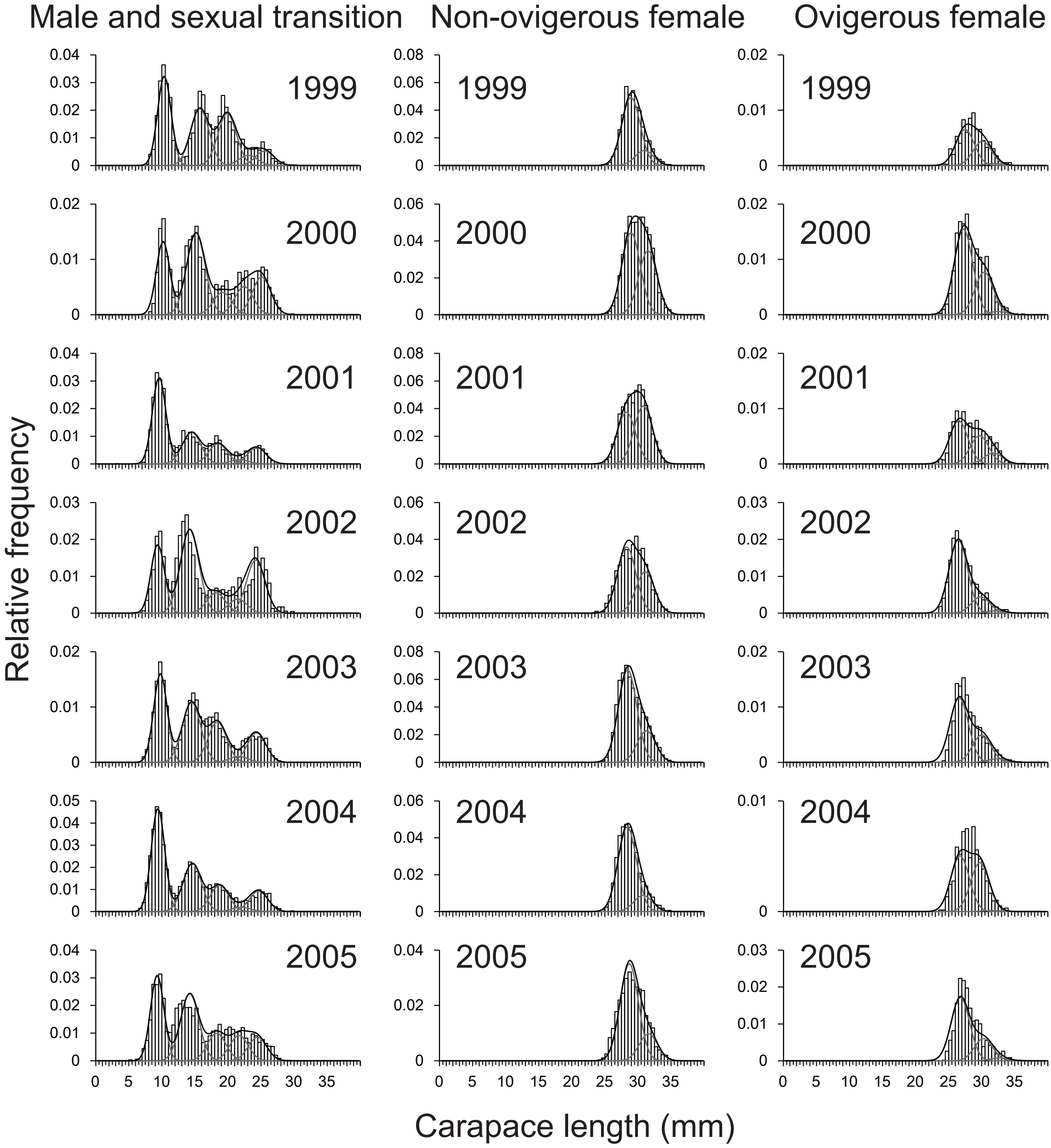
Male and sexual transition
Non-ovigerous female
Ovigerous female
1999
2000
2001
2002
2003
2004
2005
Relative frequency
Carapace length (mm)
0
5
10
15
20
25
30
35
0.01
0.02
0.03
0.04
0.05
0.06
0.08

Figure 5

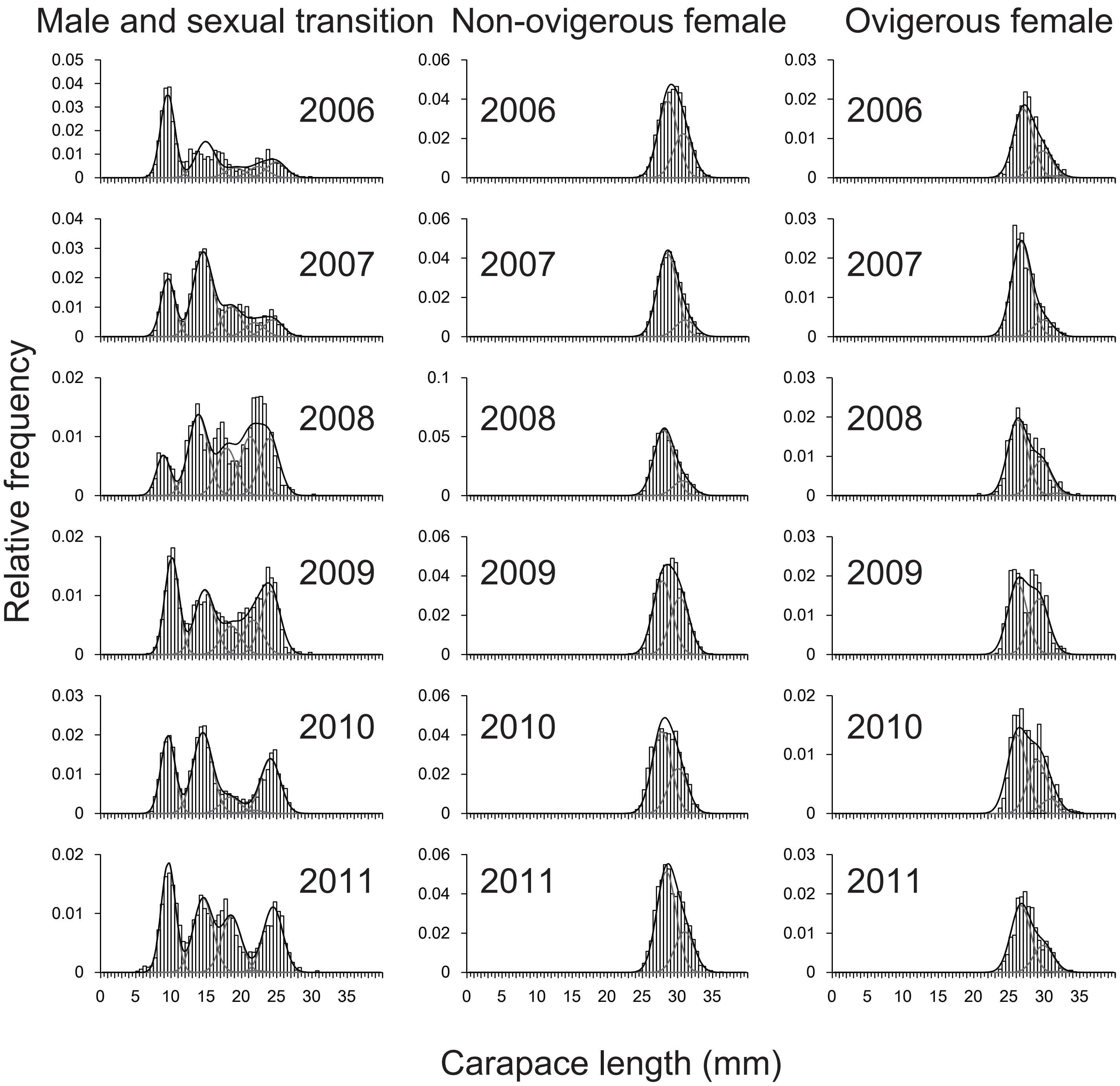

Figure 5 (Continued)

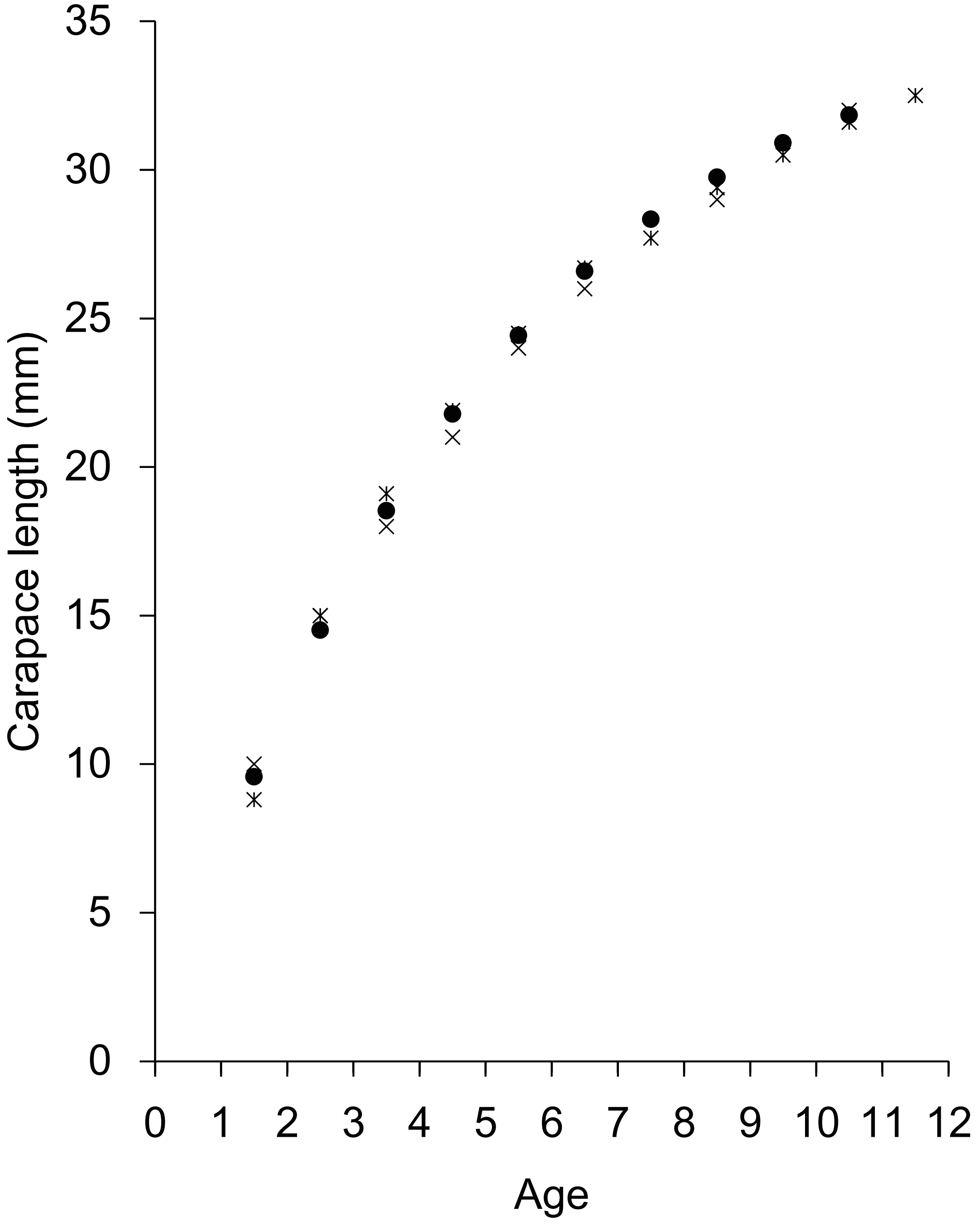

Figure 6

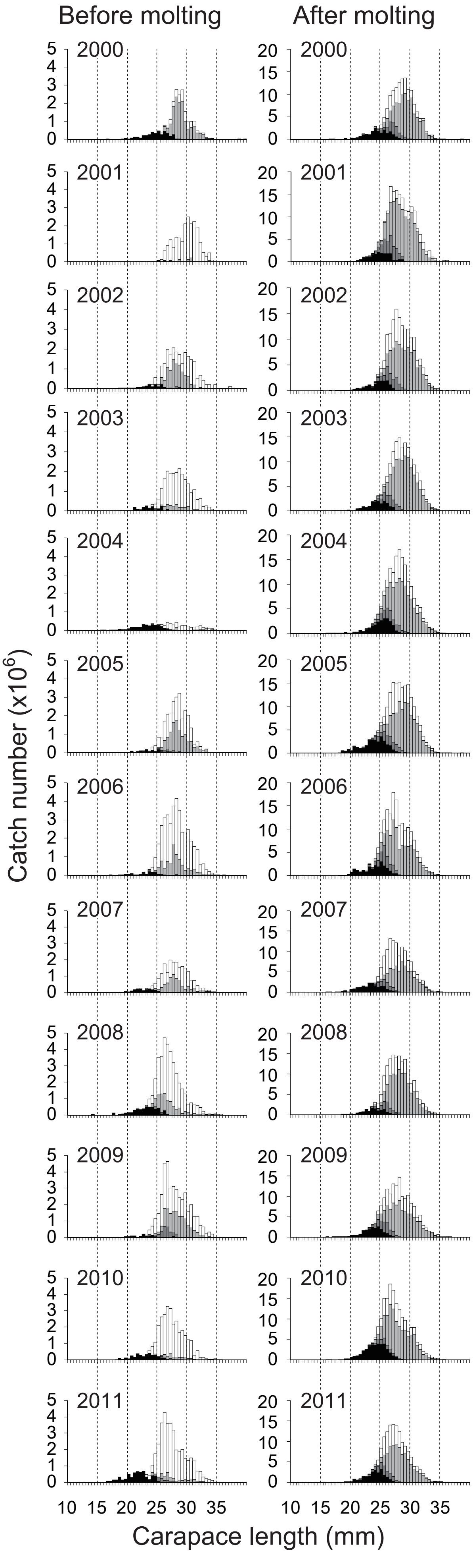
Before molting
After molting
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
0
1
2
3
4
5
0
5
10
15
20
Catch number (x10^6)
10
15
20
25
30
35
Carapace length (mm)

Figure 7

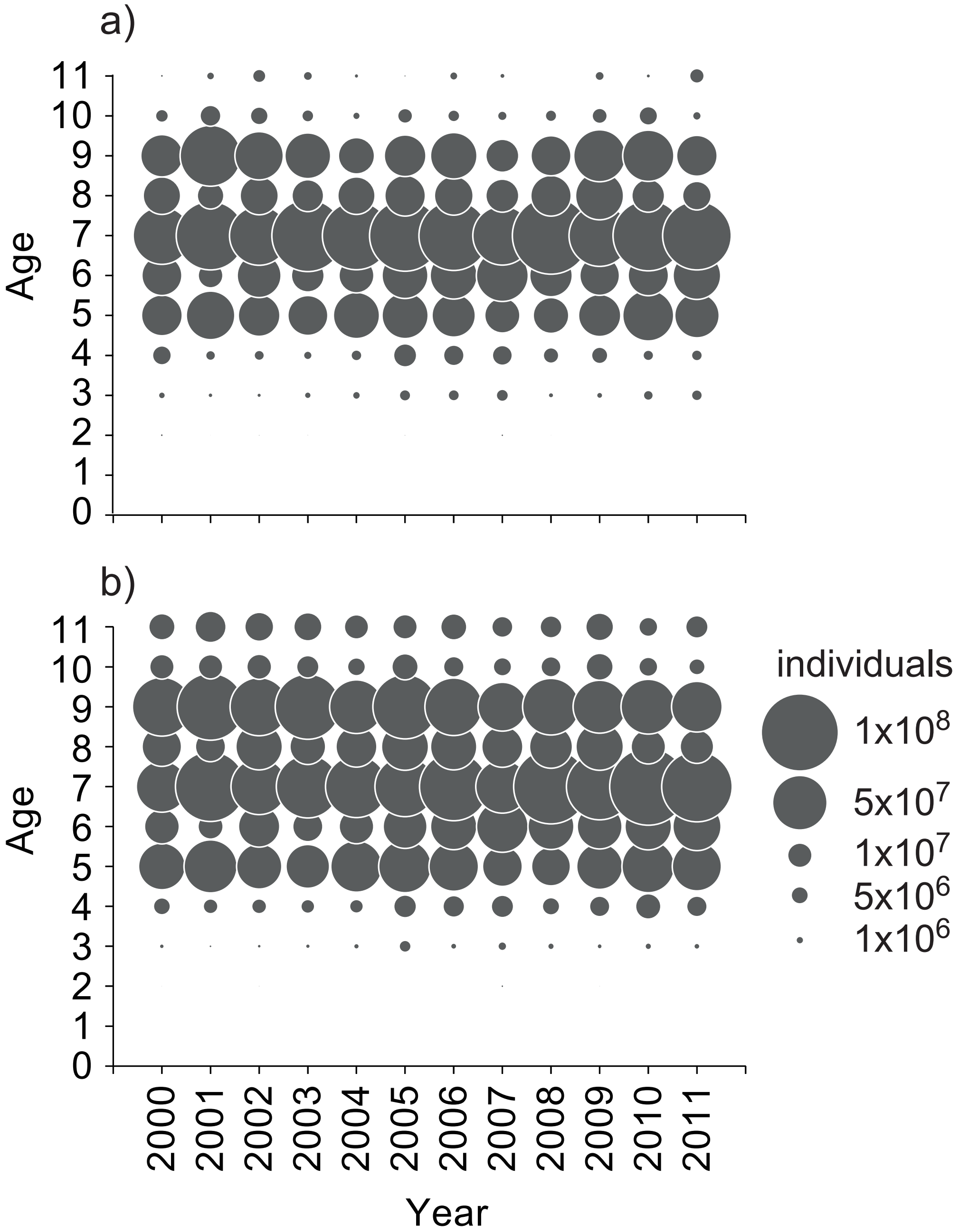
a)
Age
11
10
9
8
7
6
5
4
3
2
1
0
b)
individuals
1x10^8
5x10^7
1x10^7
5x10^6
1x10^6
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year

Figure 8

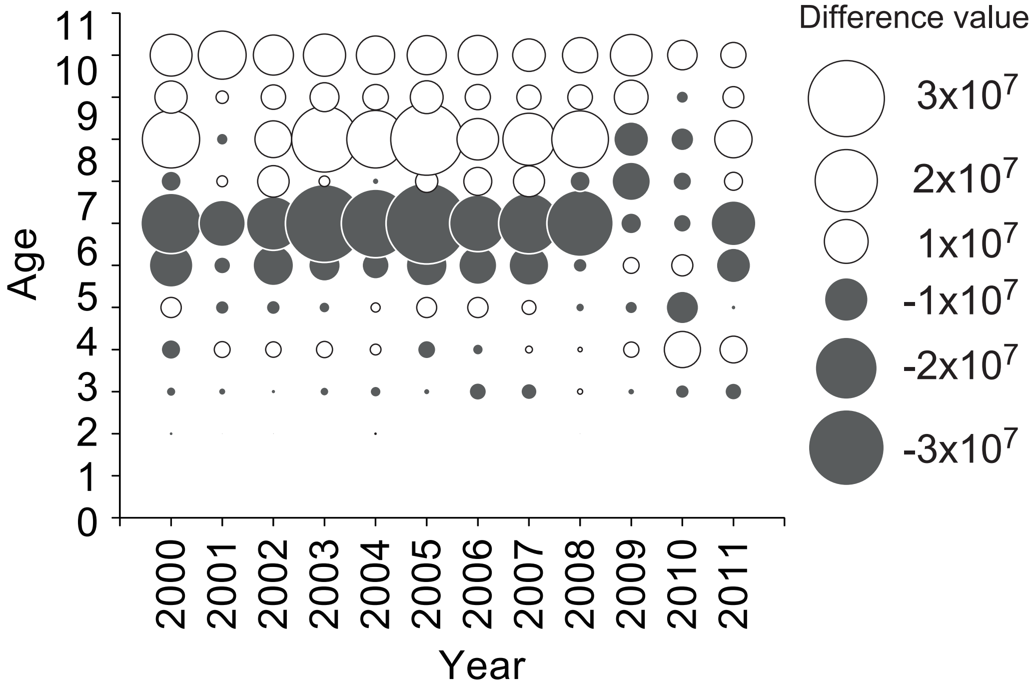
Difference value
3x10^7
2x10^7
1x10^7
-1x10^7
-2x10^7
-3x10^7
Age
0
1
2
3
4
5
6
7
8
9
10
11
Year
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011

Figure 9

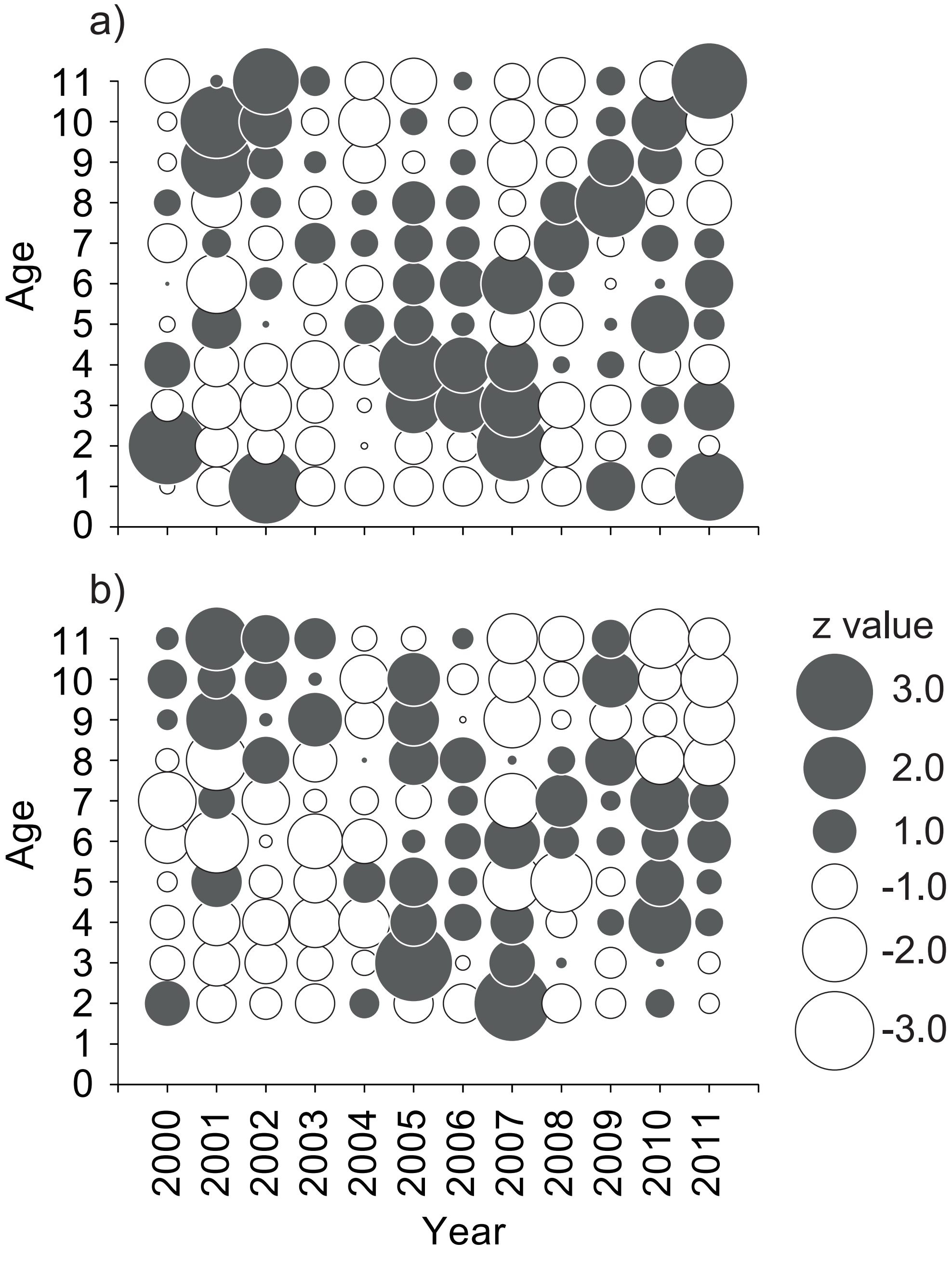
a)
b)
Age
Year
0
1
2
3
4
5
6
7
8
9
10
11
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
z value
3.0
2.0
1.0
-1.0
-2.0
-3.0

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

山口浩志（道中央水試）・後藤陽子（稚内水試）・星野昇（道中央水試）・宮下和士（北大 FSC）

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－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。