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Author(s)	Kishi, Michio J.; Nakajima, Kazuto; Fujii, Masahiko; Hashioka, Taketo
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Environmental factors which affect growth of Japanese common squid, *Todarodes pacificus,* analyzed by a bioenergetics model coupled with a lower trophic ecosystem model

Michio J. Kishi[1,2], Kazuto Nakajima[3], Masahiko Fujii[4], and Taketo Hashioka[2]

[1] *Hokkaido University, Faculty of Fisheries Sciences, c/o Cho-tatsu-ka, N13W8, Sapporo, Hokkaido, 060-0813, Japan*
[2] *Ecosystem Change Research Program, Frontier Research Center for Global Change, Japan Agency for Marine-Earth Science and Technology, 3173-25, Showa-machi, Kanazawa-ku, Yokohama, Kanagawa, 236-0001, Japan*
[3] *Hokkaido University, Graduate School of Environmental Science, N10W5, Sapporo, Hokkaido 060-0810, Japan*
[4]*Sustainability Governance Project, Center for Sustainability Science, Hokkaido University, N9W8, Kita-ku, Sapporo, Hokkaido 060-0809, Japan*

Abstract

Bioenergetics model is applied to Japanese common squid, *Todarodes pacificus*. The temporal change of wet weight of common squid, which migrates in the Sea of Japan, is simulated. The time dependent horizontal distribution of prey is calculated a priori by 3-D coupled physical-biological model. The biological model NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) is used to simulate the lower-trophic ecosystem including three kinds of zooplankton biomass two of which is used as prey of common squid. A bioenergetics model reproduced appropriate growth curve of common squid, migrating in the North Pacific and the Sea of Japan. The results show that the wet weight of common squid in the northern Sea of Japan is heavier than that migrating in the central Sea of Japan, because prey density of the northern Sea of Japan is higher than that of the central Sea of Japan. We also investigate the wet weight anomaly for a global warming scenario. In this case, wet weight of common squid decreases because water temperature exceeds the optimum temperature for common squid. This result indicates that migration route and spawning area of common squid might change with global warming.

Key words: NEMURO, Bioenergetics model, *Todarodes pacificus*, Japanese common squid.

Introduction

Japanese common squid, *Todarodes pacificus*, is classified into three groups based on hatching season, i.e., winter-spawned group, summer-spawned group and fall-spawned group (Araya, 1972; Okutani, 1983; Kidokoro and Hiyama, 1996).

Winter-spawned group migrates widely to the Sea of Japan, Yellow Sea and North Pacific. This group is the main fisheries target inshore of the Sea of Japan and its resource was the highest amongst the three groups until 1970s. Its larvae appear mainly in the northern East China Sea and juveniles are transported to northward by the Tsushima Current from March to June (Watanabe, 1965; Murata, 1989). Young common squids, which are main squid fisheries targets, migrate along warm branch of the Tsushima Current up to the Polar Front (PF) and also into the North Pacific from June to July. They start southward migration in September and October (Murata, 1989). Based on Tameishi (1992), it also migrates along the Pacific coast of Japan and this migration route plays important role in their maintenance of biomass.

Summer group distributes inshore of middle and south of the Sea of Japan. The resource is the least amongst the three groups. This group spawns from May to August.

Fall group mainly distributes offshore of the Sea of Japan and is the main fisheries target since 1970s. Larvae appear in north of the East China Sea up to southwest part of the Sea of Japan from September to November. Young common squids mainly distribute from warm region of the Tsushima Current to south of PF from May to June. Adult common squids distribute from PF to near the coast of Japan from July to August. The northward migration is related to location of PF and sea surface temperature (SST) of Liman Current (Kasahara and Ito, 1972; Naganuma, 1967). Southward migration begins in August and September when mating becomes active. Then common squids that migrate to north of PF (called as the subarctic group (SG)) move westerly along Liman current and reach offshore of east coast of the Korean Peninsula. Common squids that stay in south of PF (called as the Tsushima group (TG)) move the eastern Sea of Japan along the coast of Japan. Kidokoro and Hiyama (1996) found that the growth of SG is better than that of TG, because of the difference of prey in the migration area.

The purpose of the present study is: (1) to construct a common squid bioenergetics model by improving Rudstam (1988)'s model and NEMURO.FISH (North Pacific Ecosystem Model for Understanding Regional Oceanography for Including Saury and Herring; Ito et al. 2004; Megrey et al, 2007), which embedded a fish bioenergetics model into a lower-trophic ecosystem model, (2) demonstrate that the bioenergetics model can reproduce the growth of common squids, regardless of the spawning areas and migration routes, (3) elucidate factors which cause the difference of growth between the subarctic group (SG) and the Tsushima group (TG) for the fall-spawned group, (4) discuss the difference of growth depending on migration routes for winter-spawned group, and (5) evaluate the response to global warming.

Model description

We used 3-D coupled physical-biological model results by Hashioka and Yamanaka (2007a) as input data necessary for the bioenergetics model of common squids. Hashioka and Yamanaka (2007a) used the CCSR-COCO (Center for Climate System Research, University of Tokyo, Ocean Component model; Hasumi, 2000) as a physical model and the NEMURO (Kishi et al., 2007) as a biological model. The two models were coupled and were run for the northwestern Pacific. The NEMURO has three categories of zooplankton, which are small zooplankton (ZS), large zooplankton (ZL) which corresponds to copepods, and predatory plankton (ZP) which corresponds to krill and/or salpa. The modeled common squid preys ZS and ZP as described below.

The daily growth rate of an individual common squid is described as the difference between the consumption and losses due to the respiration, specific dynamic action, egestion and excretion (Eq. (1)). Formulas and parameters for the individual components in the bioenergetics model follow terminology and symbols used in the Wisconsin bioenergetics models (Hanson et al., 1997) and Atlantic herring (*C. harengus*) model by Rudstam (1988).

Growth

The growth rate of an individual common squid is calculated as wet weight (W) increment per wet weight per day:

$$\frac{dW}{W \cdot dt} = [C - (R + SDA + F + E)] \cdot \frac{CAL_z}{CAL_f} \qquad (1)$$

where C is the consumption (g prey g squid^{-1} day^{-1}), R is the respiration or losses through metabolism (g prey g squid^{-1} day^{-1}), SDA is the specific dynamic action or losses due to energy costs of digesting food (g prey g squid^{-1} day^{-1}), F is the egestion or losses due to feces (g prey g squid^{-1} day^{-1}), E is the excretion or losses of nitrogenous excretory wastes (g prey g squid^{-1} day^{-1}), and $\mathrm{CAL_z}$ and $\mathrm{CAL_f}$ are the caloric equivalent of zooplankton (cal g zooplankton^{-1}) and common squid (cal g squid^{-1}), respectively. $\mathrm{CAL_z}$ is 617.00 (cal g prey^{-1}), which is the same value as that of Megrey et al. (2002) used for pelagic fish in the North Pacific. CAL_f is the mean caloric equivalent of seven sample squids that were estimated by Nishiyama and Hamaoka (1989) and is set to be 1526.14 (cal g squid^{-1}). All the units for the weight show the wet weight in this study.

Consumption (C)

Daily consumption rate (g prey g squid^{-1} day^{-1}) was determined as the proportion of available consumption rate that depends on prey density, the maximum daily consumption rate that depends on the common squid wet weight, and the water temperature:

$$C = C_r \cdot f_c(T) \quad (2)$$

$$C_r = \sum_{j=1}^{n} C_j \quad (3)$$

$$C_j = \frac{C_{MAX} \cdot \frac{PD_{ij} \cdot v_{ij}}{K_{ij}}}{1 + \sum_{k=1}^{n} \frac{PD_{ik} \cdot v_{ik}}{K_{ik}}} \quad (4)$$

$$C_{MAX} = a_c W \ + b_c \quad (5)$$

where C_r is the total available consumption rate without temperature effects (g prey g squid^{-1} day^{-1}), $f_c(T)$ is the temperature dependence function for the consumption, T is the water temperature (°C), j and k are the prey types (ZS or ZP, see Table 2 in detail), i is the predator type (life stage of common squid), C_{MAX} is the maximum consumption rate dependant on the common squid wet weight (g prey g squid^{-1} day^{-1}), PD_{ij} is the density of prey type j (g wet weight m^{-3}), υ_{ij} is the vulnerability of prey type j to predator i (0 or 1; dimensionless), K_{ij} is the half saturation constant (g wet weight m^{-3}) for individual predator type i feeding on prey type k, and a_c and b_c are the intercept and slope of the allometric mass function for consumption, respectively. The formula for C_{MAX} is different from that in Megrey et al. (2007) for simplicity.

The consumption is linearly dependent on the wet weight and nonlinearly dependent on the prey zooplankton density and temperature, according to equations above. The detailed values of the parameters are shown in Table 1. The maximum consumption rate is referred to experimental data by Sakurai et al (1993). Their data showed that the maximum daily feeding rate was 38.2g of food ingested by a 186g common squid, or 20.5% of the body wet weight. Equation (5) was derived from a relationship between the maximum daily feeding rate and estimated body wet weight in each common squid for weights ranging from 141 to 413g during a 4-day experiment from 8 to 12 August, 1990 (Sakurai et al 1993). The adapted curve of the maximum consumption w*C_{max} (g prey day^{-1}) is shown in Fig.1. Model results of ZS and ZP biomass from NEMURO were used as prey for common squids. Modeled water temperature by Hashioka and Yamanaka (2007a) was applied to this study.

Temperature dependence in the bioenergetics model f_c is generally modeled as a dome-shaped curve proposed by Thornton and Lessem (1978). The Thornton and Lessem function is the product of two sigmoid curves: one fits the increasing segment (gcta) and the other fits the decreasing segment (gctb) of the temperature dependence function:

$$f_c(T) = gcta \cdot gctb \quad (6)$$

(The increasing segment)

$$gcta = \frac{(xk1 \cdot t4)}{(1.0 + xk1 \cdot (t4 - 1.0))} \quad (7)$$

$$t4 = e^{[t5 \cdot (T - te1)]} \quad (8)$$

$$t5 = tt5 \cdot a\log\left[0.98 \cdot \frac{(1.0 - xk1)}{(0.02 \cdot xk1)}\right] \quad (9)$$

$$tt5 = \frac{1}{(te2 - te1)} \quad (10)$$

(The decreasing segment)

$$gctb = \frac{(xk4 \cdot t6)}{(1.0 + xk4 \cdot (t6 - 1.0))} \quad (11)$$

$$t6 = e^{[t7 \cdot (te4 - T)]} \quad (12)$$

$$t7 = tt7 \cdot a\log\left[0.98 \cdot \frac{(1.0 - xk4)}{(0.02 \cdot xk4)}\right] \quad (13)$$

$$tt7 = \frac{1}{(te4 - te3)} \quad (14)$$

where *te1* and *te2* is the lower and higher water temperature in the increasing segment at which the temperature dependence is the small fraction *xk1* (0.1) and the large fraction *xk2* (0.98) of the maximum consumption rate, respectively. *te3* and *te4* is the lower and higher water temperature in the decreasing segment at which the temperature dependence is the large fraction *xk3* (0.98) and the small fraction *xk4* (0.1) of the maximum consumption rate, respectively. See Table 1 for values of xk1, te1, te2, xk4, te4, and te3. The preferable temperature for the common squid habitat is obtained from Kasahara (1989). Although experiments to investigate the temperature effect on the consumption rate must be conducted, we have no data at this moment. Therefore, we speculated the curve using habitat temperature of common squid. The maximum temperature te4 at which common squids can survive was set to be 23ºC (Sakurai, personal communication based on laboratory experiment). Consequently, we set te1 through te4, as is shown in Table 1 and Fig. 2 (Sakurai, personal communication).

Respiration rate (R)

The respiration nonlinearly depends on the wet weight and the temperature, and the swimming speed dependant on the wet weight,

$$R = a_R \cdot W^{b_R} \cdot c_R{}^T \cdot f_R(U) \cdot 2.629 \qquad (15)$$

$$f_R(U) = e^{(d_R \cdot U)} \qquad (16)$$

$$U = a_A \cdot W^{b_A} \qquad (17)$$

where a_R is the intercept of the allometric mass function and represents the specific weight of the oxygen consumption rate of a 1g common squid at 0 ºC without activity (g O_2 g squid^{-1} day^{-1}), $f_R(U)$ is the swimming dependence function for the respiration, U is the swimming speed (cm s^{-1}), b_R is the slope of the allometric mass function for the standard metabolism, c_R is the coefficient relating temperature to the metabolism, d_R is the coefficient relating the swimming speed to the metabolism, a_A is the intercept of the allometric mass function, b_A is the slope of the allometric mass function with the standard swimming speed.

The coefficient of 2.629 is used to convert (g O_2 g squid^{-1} day^{-1}) into (g prey g squid^{-1} day^{-1}):

$$\frac{6{,}780\,joules}{gO_2} \cdot \frac{1cal}{4.18\,joules} \cdot \frac{1gwetweight}{617cal} = 2.629 \qquad (18)$$

Demont and O'dor (1984) introduced a relation between the respiration and water temperature as well as the activity using *Illex illecebrosus,* which is an open ocean species of squids and its ecological characteristics such as life cycles are similar to Japanese common squid *Todarodes pacificus*. (Hatanaka et al., 1985)

The respiration nonlinearly depends on the body wet weight, temperature and swimming speed which also depends on the wet weight. The energy loss due to the respiration of squids is not known for the Japanese common squid, but a pelagic squid *Illex illecebrosus* can be substituted for the Japanese common squid. In this study, the equation of oxygen consumption for *Illex illecebrosus* was used for the Japanese common squid (Demont and O'Dor, 1984) by modifying the parameters. The water temperature does not play an important role in the respiration of the Japanese common squid compared with *Illex illecebrosus* (Sakurai, personal communication). Consequently, c_R in Eq. (15) is set to be smaller than that of *Illex illecebrosus.* Fig. 3 shows (A) a relationship between the wet weight on the water temperature at 15ºC and the respiration rate per day (g prey g squid^{-1} day^{-1}), and (B) the respiration (g prey day^{-1}) in the case of 15ºC water temperature. Oxygen consumption of the Japanese common squid was estimated at 470mg O_2 kg^{-1} h^{-1} (=0.0589 g prey g squid^{-1} day^{-1}) for a 300g squid, which coincides with an experimental value (HITEC, 2001).

Specific dynamic action (SDA), excretion (E), egestion or loss due to feces (F)

Specific dynamic action is part of the total respiration and represents the energy allocated to not only the digestive processes of food, principally the deamination of proteins but also the absorption, transportation, and deposition of food (Beamish, 1974). We formulated the specific dynamic action as:

$$SDA = S \cdot (C - F), \quad (20)$$

where S is the proportion of assimilated energy by the specific dynamic action, C is the consumption and F is the egestion or loss due to feces. The egestion (F) is modeled as a constant proportion a_F of consumption and the excretion (E) is as a constant proportion a_E of (C-F).

$$F = a_F C, \quad (21)$$

$$E = a_E \cdot (C - F). \quad (22)$$

Migration and stages

Kasahara (1989) divided life history of the common squid in the Sea of Japan into five stages based on its mantle length. We divided 5th stages into two categories, before and after the migration for spawning. Based on Okutani (1983), fall-spawned common squid is hatched at the beginning of November. In our model, the date of hatching out is supposed to be on 1st of November. This date is not strict, because we interpolated 10-day averaged model outputs of NEMURO (Hashioka and Yamanaka, 2007a) to daily and used in this study, as mentioned in the following subsection. The relation between the day from the hatching out and the stage is based on the relation between mantle length and age by Kidokoro et al. (1999) and shown in Table 2. The migration route of common squids in the Sea of Japan is suggested by Fujii et al. (2004), in which they simulated the migration route supposing a squid as a passive tracer, and by Ikeda et al. (2003) in which they monitored the migration route using the relation between the Sr:Ca ratio of statolith and the growth. The spawning ground of the fall-spawned group has been considered to extend from the southwestern part of the Sea of Japan to inshore of the northwestern Kyushu Island and also to the northern East China Sea (Kasahara and Ito, 1972, Shojima and Hotta, 1972). The wet weight of common squid increases rapidly from the age of five months and reaches its maximum weight at the age of eight or nine months (Kidokoro et al., 1999). Its main prey is zooplankton (*Themisto japonica* and *Euphausia pacifica),* which is pelagic species (Nishimura 1965). The life expectancy is exactly one year.

Kidokoro and Hiyama (1996) reported that the growth of common squids is different between those caught at the south of PF and those caught at the north of PF, although the spawning ground is in the same region. Consequently, the common squid's growth and distribution are closely related to the structure of the Sea of Japan (Araya 1967). The common squid which migrates up to PF is called the Tsushima group (TG) and one which crosses PF and migrates up to the northern Sea of Japan is called the subarctic group (SG). As is shown in Fig. 4, TG migrates along the coast of Japan and begins to come back to the spawning ground in July, SG migrates along the coast of the Korean Peninsula and comes back southward along the continent as well (Araya 1967). The winter-spawned group comes up to the east coast of Hokkaido in summer and comes down to the south coast of Kyushu in winter, migrating along the coast of Japan in the Pacific.

Inputs from NEMURO

Inputs from the coupled physical-ecological model from Hashioka and Yamanaka (2007a) were used as the physical condition and prey density. The ten-day averaged model results were interpolated to daily and were used for our simulation. The water temperature was averaged within the water column from the surface to 50m depth, because squids daily migrate down to 50~100m. Zooplankton concentrations were averaged from the surface to 20m depth, considering that the modeled zooplankton concentrates within upper 20m. Adult of common squid preys not only zooplankton but also small fish (Sakurai et al., 1993). NEMURO does not include explicitly fish, but ZP (predatory zooplankton) includes implicitly higher trophics as well since ZP is the highest trophic in NEMURO. We assumed in the model that adult common squids prey ZP.

Hashioka and Yamanaka (2007b) simulated responses of the lower-trophic levels to global warming, using simulated fields according to the IPCC IS92a global warming scenario as boundary condition at the sea surface. These physical fields are obtained from global warming experiment of the CCSR/NIES coupled ocean-atmosphere model (Nozawa et al., 2001). We used the outputs from Hashioka and Yamanaka (2007b) for simulating responses of the common squid to global warming.

The bioenergetic model is integrated with a time step of one day. The starting points of migration are indicated in Fig.4. The initial wet weight of a squid in the model was supposed to be 0.2 g and simulations start on November 1st and January 1st for fall spawning and winter spawning group respectively. The outputs of water temperature and prey density are laniary interpolated in time and space between each migration point shown in Fig.4.

RESULTS AND DISCUSSIONS

Growth of fall-spawning Subarctic group (SG) and Tsushima group (TG)

Fig. 5 shows simulated time dependent features of (A) prey density along the migration route, (B) water temperature along the migration route and (C) wet weight of common squid. The prey density along the migration route increases in April for SG and in May for TG, respectively. The prey density for TG reaches its maximum in June and then decreases. That for SG, on the other hand, maintains its high level from the end of April to August. The difference of prey density between the two groups is 0.22 μmol N l^{-1} in April and 0.05μmol N l^{-1} in June. The difference of the water temperature becomes clear after May, while the growth shows clear difference after April, when the SG begins to cross the PF. The growth saturates in late August in both groups.

According to Kidokoro and Hiyama (1996), the clear difference of body size was observed during common squid investigations of the Sea of Japan from late June to early July 1994. The averaged wet weight of common squids caught at the south of the PF is 190g and that at the north of the PF is 267g, the ages of which were almost 240 days. The simulated wet weight on 240 days after the hatch (at the beginning of July) is around 230g for TG and 320g for SG, respectively (Fig. 5 (C)). The modeled wet weight overestimates the observation by about 20% and the modeled growth rate is considered faster than the observed one. However, the difference in the wet weight between TG and SG is around 40% in both observation and simulation, showing good performance of the model in reproducing the difference of the wet weight and growth rate between the two groups. Overall, the simulated sigmoid-shaped growth curve captures well the observed features by Kidokoro et al. (1999), and therefore, the model could reproduce well the growth of squids, although the simulated wet weight slightly overestimate and underestimate the observation before Stage 4 and after Stage 5, respectively. The time dependent features of the wet weight and the mantle length based on Kidokoro et al. (1999) is shown in Fig. 6. Kidokoro et al. (1999) examined the growth of mantle length, and mantle length was converted to body weight using the relation, logW=-9.27+2.72logL (W:wet weight, L:mantle length), which was observed by Araya(1967). According to Fig.6, we can conclude that our simulation shows a good agreement with the observation.

Figure 5 (A) suggests that the difference of the growth between two groups is caused by the difference of the prey density. In NEMURO, ZL which corresponds to copepods, behaves ontogenetic vertical migration. It ascends shallower layer in April to prey bloomed phytoplankton and descends to deeper layer in September. The reason why the prey density increases in April is due to the vertical migration of ZL, which brings increase of ZP as well. The growth of ZL and ZP is better in the subarctic regions than in the southern part of the Sea of Japan, because the spring bloom of phytoplankton is larger in the north of the PF due to the deep convection during winter. This causes the difference of the prey density between the two groups. Figure 7 shows the observed zooplankton concentration along the migration route, rewritten from Hirota and Hasegawa (1999). The observed zooplankton density supports our results as well as Hashioka and Yamanaka (2007a).

On the other hand, the water temperature gives a different effect on the growth. Fiure 8 shows $f_c(T)$ of Eqs. (2) and (6), which is the temperature dependence function for the consumption. This shows that the water temperature is more preferable for the growth of TG than that of SG from April to August. In addition, the energy loss by the respiration does not show clear difference between the two groups (not shown). These results show that the physical environment, represented solely by the water temperature, is more preferable in TG than in SG, but the difference of prey density plays much more important role in the common squid growth. This is the hypothesis also pointed out by Kidokoro and Hiyama (1996).

Growth of winter-spawning group which migrates the Pacific coast

Fig. 9 denotes modeled time series of (A) prey density of winter-spawning group and (B) the water temperature on the migration route, and (C) wet weight of winter-spawning group from January to December, estimated by using the bioenergetics model. The prey density on the migration route has two peaks which appear in April and September through November. The maximum of prey density for winter-spawning group is 0.192 μmolN l^{-1}, as high as that for TG (Fig. 5 (A)). The prey density is high from the first stage of common squid's life history and is variable with time. The water temperature on the migration route of winter-spawning group is around 20°C from January to July, and has its minimum in September. The minimum temperature for winter-spawning group is 13.8°C, close to that for fall-spawning groups. The modeled wet weight of winter-spawning group is 292.2g, which is close to that of TG (Figs. 5 (C) and 9 (C)). The wet weight increases rapidly after July when food consumption of the winter-spawning group starts to be relatively active, and show signs of leveling off after mid-October. As the modeled increase curve of wet weight follows reasonably a sigmoid-shaped curve which is characteristic for the growth of common squids, the model result can be considered to reproduce realistically the growth of common squids. The growth of the modeled winter-spawned group is similar to that of the modeled TG, because the prey density for winter-spawned group in June through October is 0.192μmolN l^{-1}, as high as for TG. The higher energy loss caused by the respiration in migrating in the warm region during early stages is considered to be made up by feeding on plentiful preys from April to June.

For simplicity, winter-spawning group in the Pacific Ocean in the model is set to migrate from spawning areas toward the east coast of Hokkaido along the coast of Japan. In reality, on the other hand, common squids in the eastern coast of Hokkaido migrate in the warm Kuroshio water advecting northward. The migration to the eastern coast of Hokkaido is considered to restrict in years when the cold Oyashio water is dominant and intrusion of the warm Kuroshio water is interrupted (Mori and Nakamura, 2001). Therefore, we examined how migration routes affect the growth of winter-spawning group, by comparing model results obtained by three experiments with different migration routes of P-1, P-2 and P-3 (Table 3). P-1 is a route described above as a standard experiment, on which common squids migrate northward along the coast of Japan and reach the east coast of Hokkaido (42.5°N, 146.5°E). P-2 is a route that common squids migrate along the coast of Japan but do not reach the east coast of

Hokkaido and stay at 39.5°N, 144.5°E. P-3 is a route on which common squids reach the east coast of Hokkaido (42.5°N, 146.5°E) but migrate through the offshore area of Japan (along 142.5°E) since June. On any of the three routes, common squids are set to hatch out at 30.5°N, 128.5°E on January 1 and migrate northward along the coast of Japan until the end of May.

Figure 10 shows the modeled wet weight of winter-spawning group that migrates along P-1, P-2 and P-3 route, respectively. The difference of the growth in July through September among the three cases is considered to be due to difference of the prey density. On the other hand, the wet weight increases up to 300g and is similar eventually in any cases. This suggests that the bioenergetics model modified to fit common squids by this study can reproduce the growth of winter-spawning common squids regardless of migration routes. In this study, only one southward migration route of winter spawning group is considered, that is, a route along the coast of Japan in the Pacific Ocean. This is because the water temperature in the Sea of Japan in southward migrating period exceeds the maximum temperature of 23℃ at which common squids can survive (Sakurai, personal communication). However, as common squids carry out actively the diurnal vertical migration, it is possible that common squids also reach the spawning region through the Sea of Japan, where is the other migration route of WG, by passing through the deep water with lower temperature and migrating southward. The possible southward migration is not taken into account in this study. We might need to incorporate ecological knowledge of common squids such as the vertical migration and habitat depth into future bioenergetics models.

As well as fall-spawned common squid, the growth of winter-spawned common squids is also considered to depend strongly on the prey density. The bioenergetics model modified in this study can be applied to various common squids that migrate the coasts of Japan regardless of spawning periods and migration routes.

Possible effects of global warming on the growth of fall-spawning groups

We examined how common squids are affected by global warming, by comparing model results with and without changes in the water temperature and prey density, both of which are presumably caused by global warming. Fig. 11 shows the model results of (A) the prey density, (B) water temperature and (C) wet weight for SG and TG under the influence of global warming. The prey density increases rapidly in April for SG and in May for TG, similar to the corresponding result without global warming effects (Fig. 5 (A)). However, the peak of the prey density for TG would appear earlier by 10 days and the prey density for SG from the end of April to August will be more fluctuant as global warming proceeds.

The water temperature on the migration route of common squids under the influence of global warming decreases after the start of migration and has their minimum in April for TG and in August for SG, respectively. The water temperature on the migration route of TG is predicted to increase by 4ºC on the entire migration route by global warming. The water temperature on the migration route of SG, by contrast, raises by 2ºC from November to July, but does not after August in which common squids migrate for hatching, by global warming.

The wet weight of SG is estimated to be 393.4g by the bioenergetics model, similar with or without the influence of global warming. The modeled wet weight of TG, on the other hand, is estimated to be 145.3g with global warming, much lower than that without global warming. It also should be noted that the wet weight of TG will decrease in August through the end of September in which common squids migrate for hatching if global warming proceeds. This is because the water temperature on the migration route exceeds the maximum temperature of 23ºC at which common squids can survive (Sakurai, personal communication) under the influence of global warming.

The model results above reveal that the growth of TG can be significantly inhibited by global warming while the effect of global warming to the growth of SG is relatively minor. The inhibition of the growth of TG by global warming is primarily due to higher water temperature because the prey density is similar with or without the influence of global warming.

Model results show that the energy loss by the respiration is notably higher for TG than for SG in April though July (Fig. 12) when the growth rate of fall-spawned group is relatively high. The energy loss by the respiration is strongly dependent on the water temperature (Eq. 15), and therefore, the energy loss is high during the period when the water temperature is relatively high.

The model results suggest that global warming presumably affects the growth of common squids with higher water temperature, especially for TG. Global warming may yield the water temperature on the migration route which is closer to, or even higher than the maximum water temperature for the growth of common squids in rapidly-growing larvae, juvenile, young and adult stages (Table 2) in summer. The rise in the water temperature may result in future changes in the migration route and spawning regions of common squids. The southernmost region which meets the maximum water temperature for common squid's spawning predicted by the model is off Niigata pref. (38.5~39.5N, 137.5~138.5E), which is consistent with a potential spawning region suggested by Sakurai et al. (2002) estimated by the water temperature distribution and bottom topography.

Conclusion

We conclude: (1) a bioenergetics model that was modified for common squids by this study can be applied to various common squids migrating around the coasts of Japan, regardless of the spawning season and migration route, (2) difference in growth of fall-spawning common squids with different migration route is resulting from different prey density on the migration route, and (3) possibility of future inhibited growth of the Tsushima group and changes in the migration routes and spawning areas of common squids, caused by rise in the water temperature as effect of global warming.

The vertical migration and horizontal migration route are simplified in the model. Some parameters for the common squid's respiration were needed to be modified from values obtained from previous studies and be used in the model. We may need to solve the problems in developing the bioenergetics model by incorporating various important ecological processes for common squids, such as the specific dynamic action, fecal excretion and nitrogenous egestion, into the model for more accurate assessment and prediction of the common squid's growth.

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Figure captions

Fig. 1. Relationship between the wet weight (g) and maximum consumption rate w^*C_{max} (g prey day^{-1}).

Fig. 2. Temperature dependence function of the consumption $f_c(T)$ for each stage of common squids.

Fig. 3. Relationship between the wet weight at the water temperature of 15ºC and (A) the respiration rate (g prey g squid^{-1} day^{-1}) and (B) the respiration (g prey day^{-1}).

Fig. 4. Migration routes of common squids in this study: fall-spawned subarctic group (SG) (squares), fall-spawned Tsushima group (TG) (circles), and winter-spawned Pacific migration route (diamonds). Dotted lines indicate migration routes. Open symbols indicate northward migration and black symbols indicate southward migration. The numerals indicate the date when common squid arrives at the point.

Fig. 5. Calculated seasonal variations of (A) the prey density (sum of prey as is indicated in Table 2), (B) the water temperature and (C) the wet weight of fall-spawned common squids. Solid and dotted lines are for subarctic group (SG) and Tsushima group (TG), respectively.

Fig. 6. Observed wet weight and mantle length by Kidokoro et al. (1999)

Fig. 7. Observed zooplankton density along the migration route after Hirota and Hasegawa(1999) converted from biomass into nitrogen using the ratio by Tanaka and Omori(1969)

Fig. 8. Seasonal variation of $f_C(T)$ (the temperature dependence function for the consumption). A solid line is for subarctic group and a dotted line is for Tsushima group.

Fig. 9. Same as for Fig. 5 but for winter-spawning group.

Fig. 10. Modeled wet weight of winter-spawning groups with different migration routes. P-1 indicates northward migration along the coast of Japan, P-2 indicates northward migration along the coast of Japan (stay at 39.5°N), and P-3 indicates northward migration along the 142°E line (see Table 3).

Fig. 11. Same as for Fig. 5, but for global warming case.

Fig. 12. Energy loss through the respiration in global warming case. Solid and dotted lines are for subarctic group (SG) and Tsushima group (TG), respectively.

Table lists

Table 1. Biological parameter symbols and the values in a common squid bioenergetics model.

Table 2. Ecological conditions and parameters in each stage of common squids.

Table 3. Northward migration route and limit of northwan routes (P-1, P-2 and P-3).

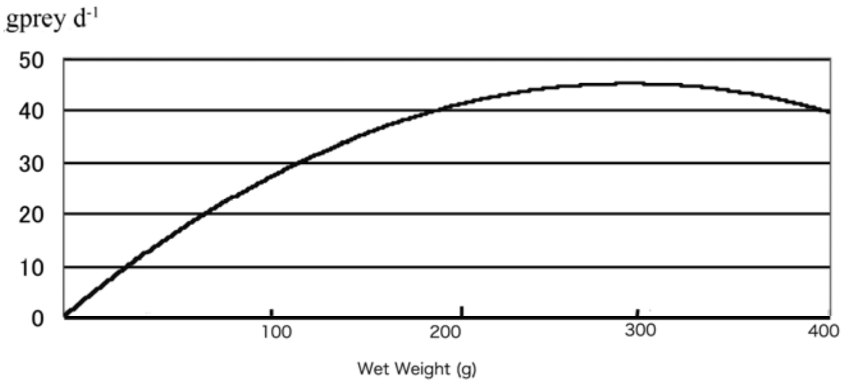


Fig. 1

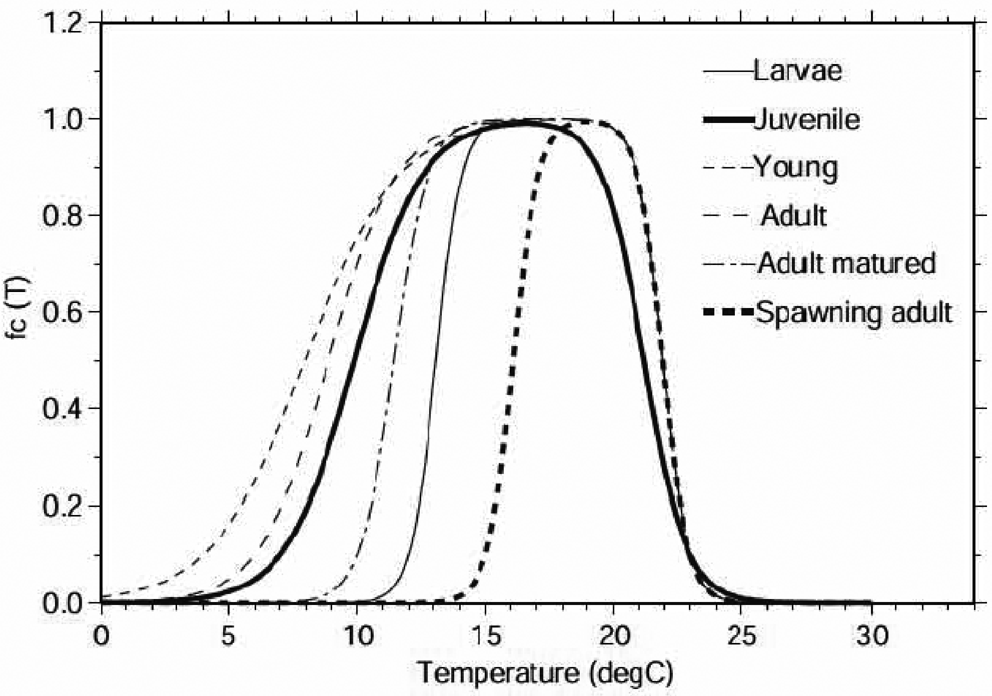

1.2
1.0
0.8
0.6
0.4
0.2
0.0
fc (T)
0
5
10
15
20
25
30
Temperature (degC)
Larvae
Juvenile
Young
Adult
Adult matured
Spawning adult

Fig.2

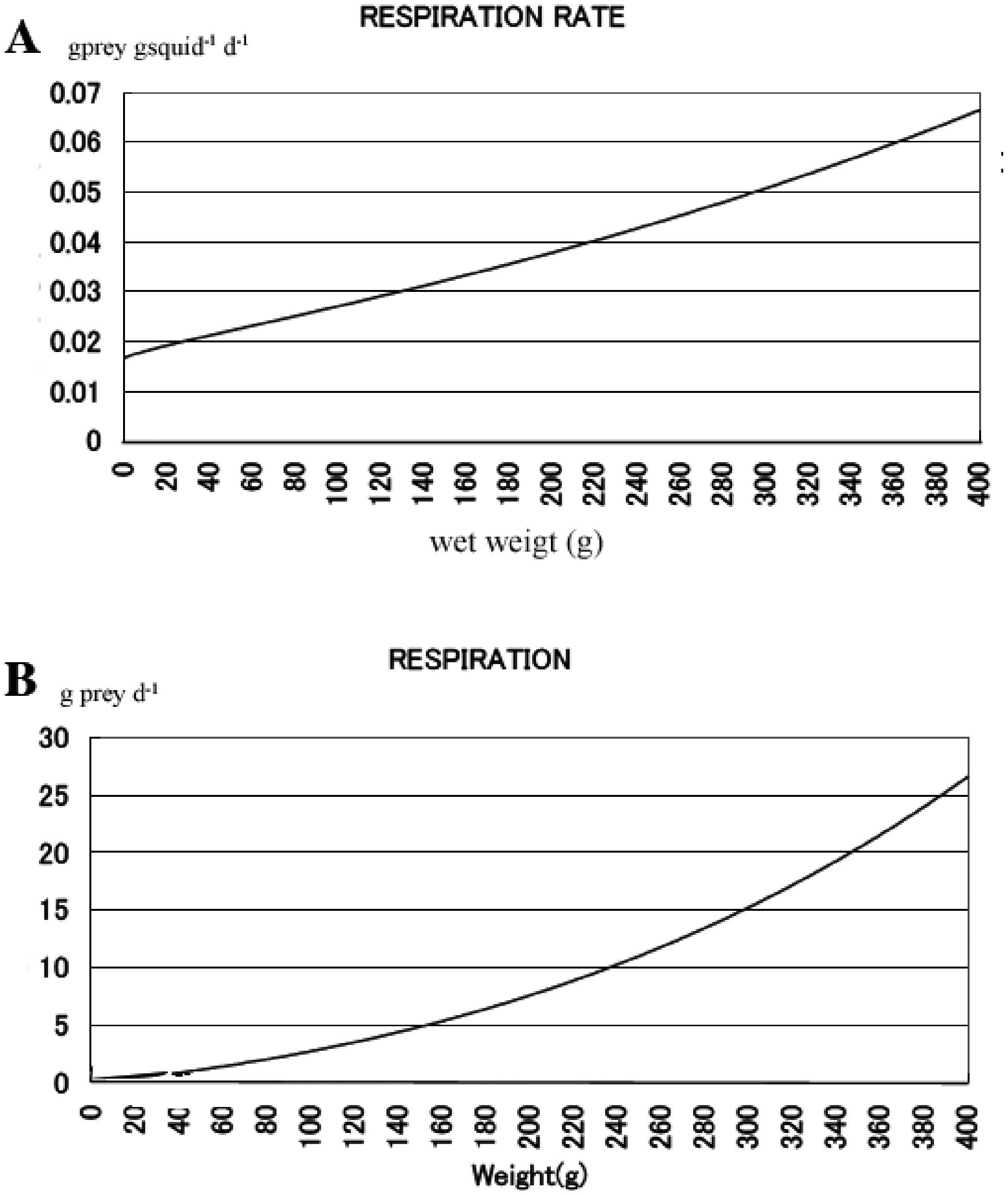

A
RESPIRATION RATE
gprey gsquid-1 d-1
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0 20 40 60 80 100 120 140 160 180 200 220 240 260 280 300 320 340 360 380 400
wet weigt (g)
B
RESPIRATION
g prey d-1
30
25
20
15
10
5
0
0 20 40 60 80 100 120 140 160 180 200 220 240 260 280 300 320 340 360 380 400
Weight(g)

Fig.3

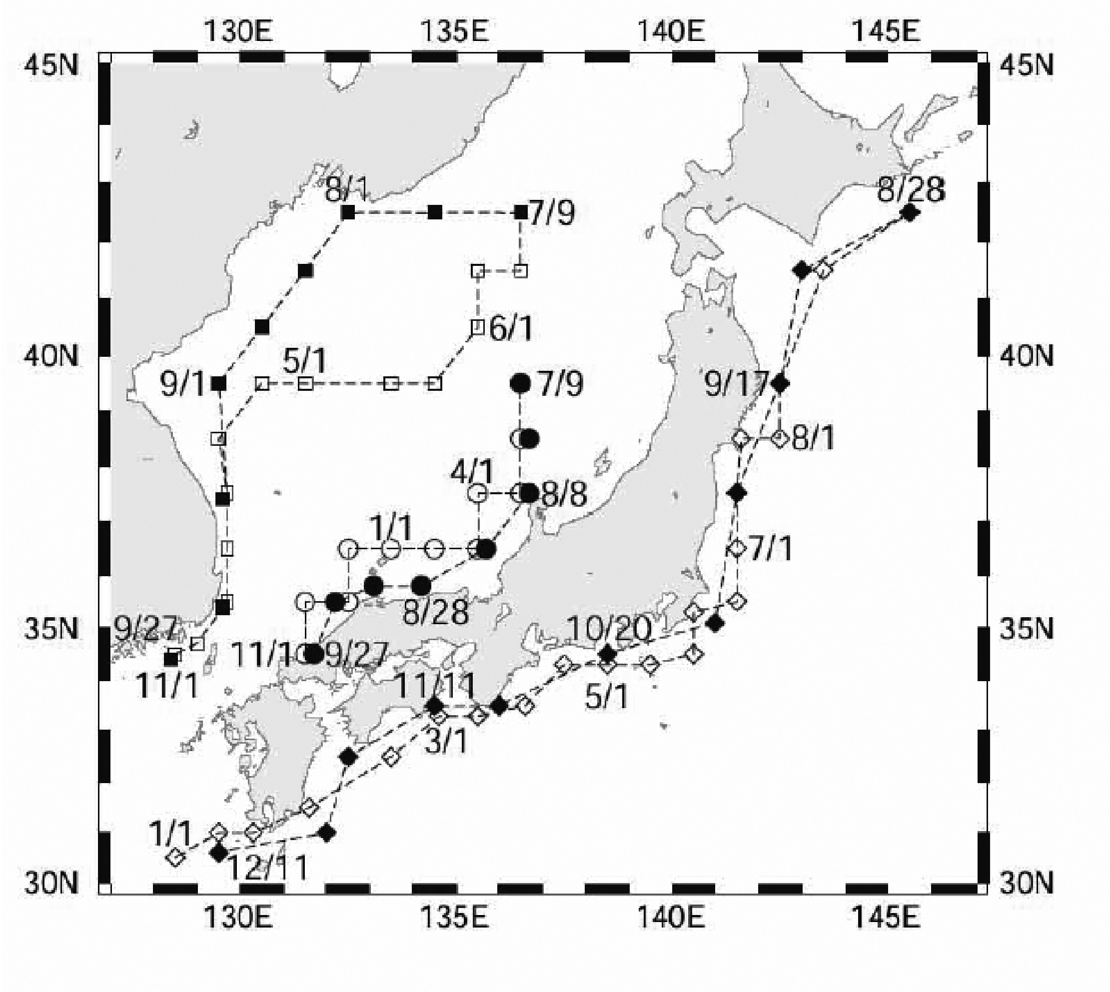

130E
135E
140E
145E
45N
40N
35N
30N
8/1
7/9
6/1
5/1
9/1
7/9
4/1
8/8
1/1
8/28
9/27
11/1
11/1
9/27
11/11
3/1
10/20
5/1
1/1
12/11
8/28
9/17
8/1
7/1

Fig.4

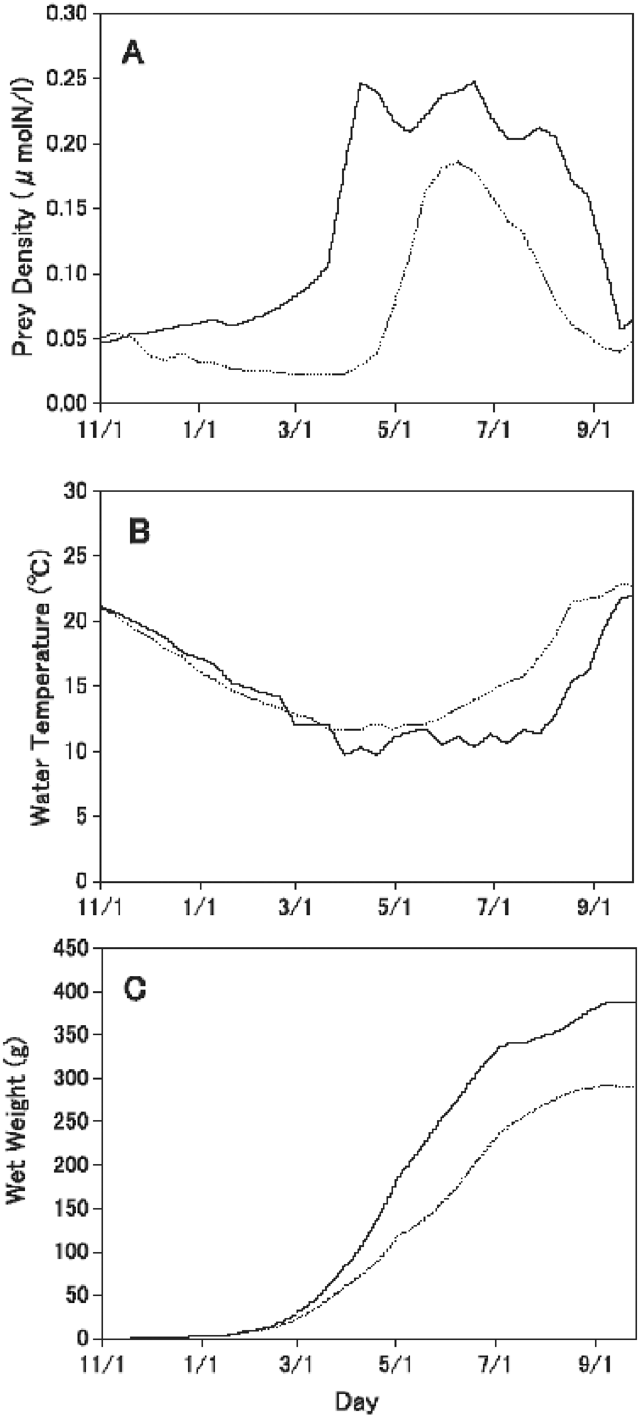

A
Prey Density (μmolN/l)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
11/1
1/1
3/1
5/1
7/1
9/1
B
Water Temperature (℃)
0
5
10
15
20
25
30
C
Wet Weight (g)
0
50
100
150
200
250
300
350
400
450
Day

Fig.5

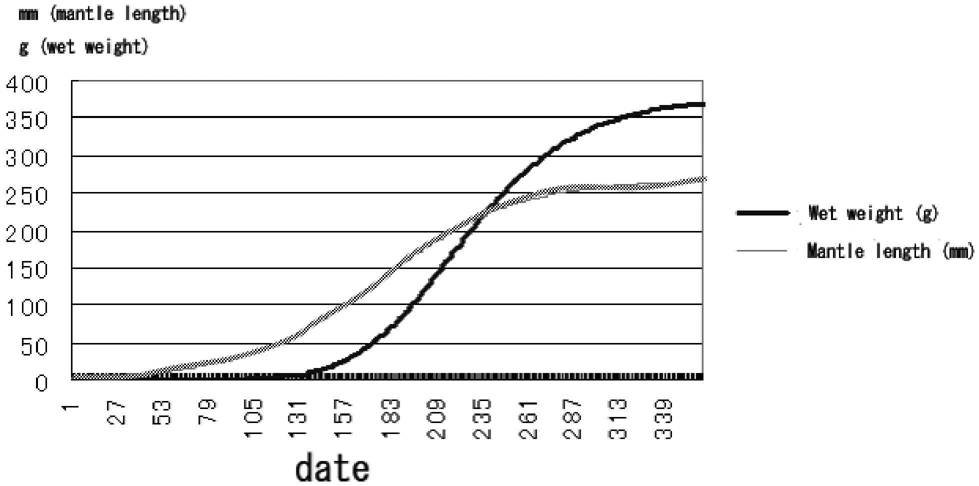

mm (mantle length)
g (wet weight)
400
350
300
250
200
150
100
50
0
1
27
53
79
105
131
157
183
209
235
261
287
313
339
date
Wet weight (g)
Mantle length (mm)

Fig.6

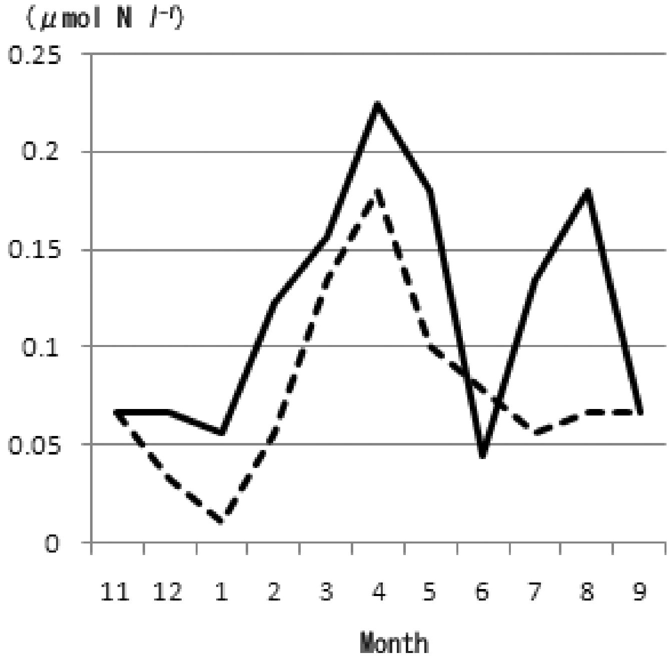


Fig.7

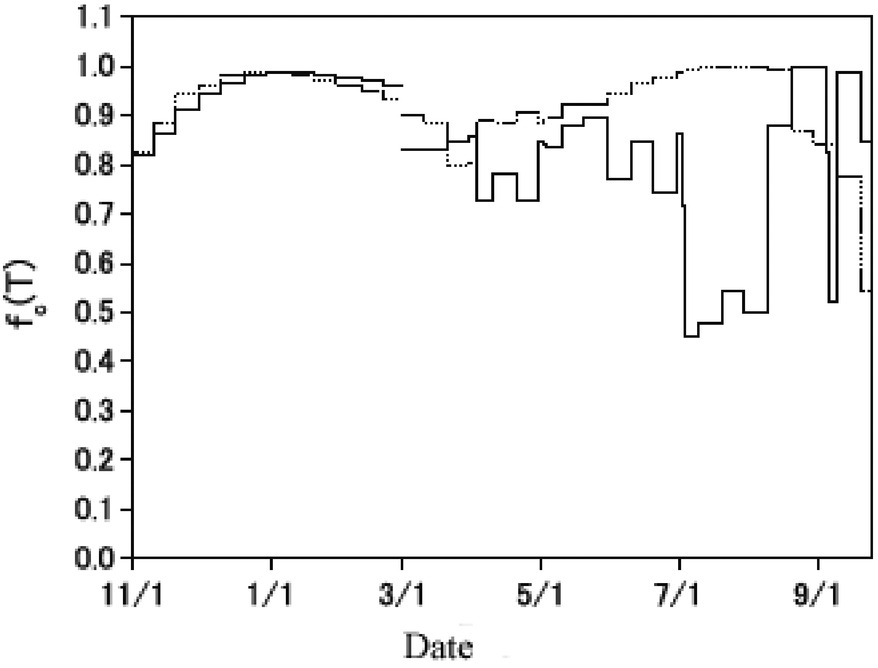


Fig.8

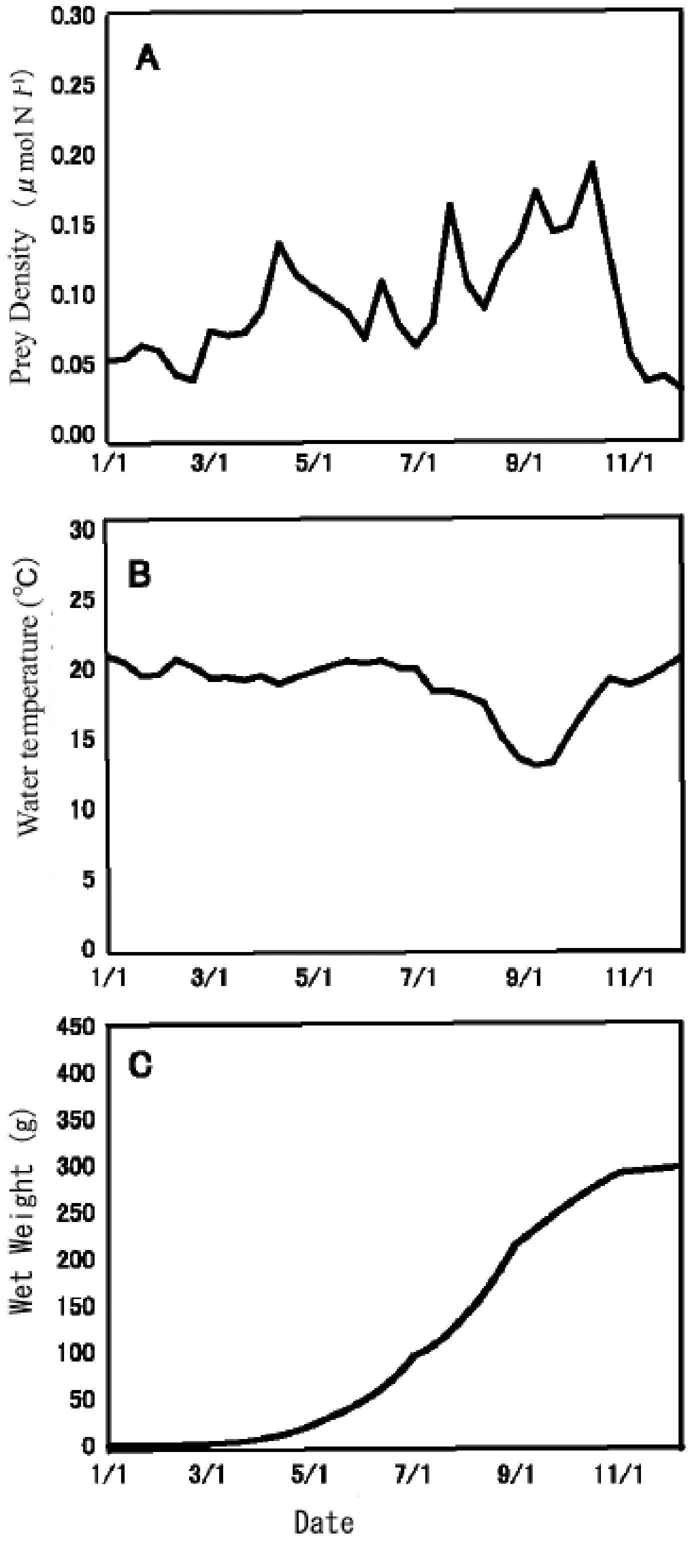
A
Prey Density（μ mol N l⁻¹）
0.30
0.25
0.20
0.15
0.10
0.05
0.00
1/1
3/1
5/1
7/1
9/1
11/1
B
Water temperature (°C)
30
25
20
15
10
5
0
1/1
3/1
5/1
7/1
9/1
11/1
C
Wet Weight (g)
450
400
350
300
250
200
150
100
50
0
1/1
3/1
5/1
7/1
9/1
11/1
Date

Fig.9

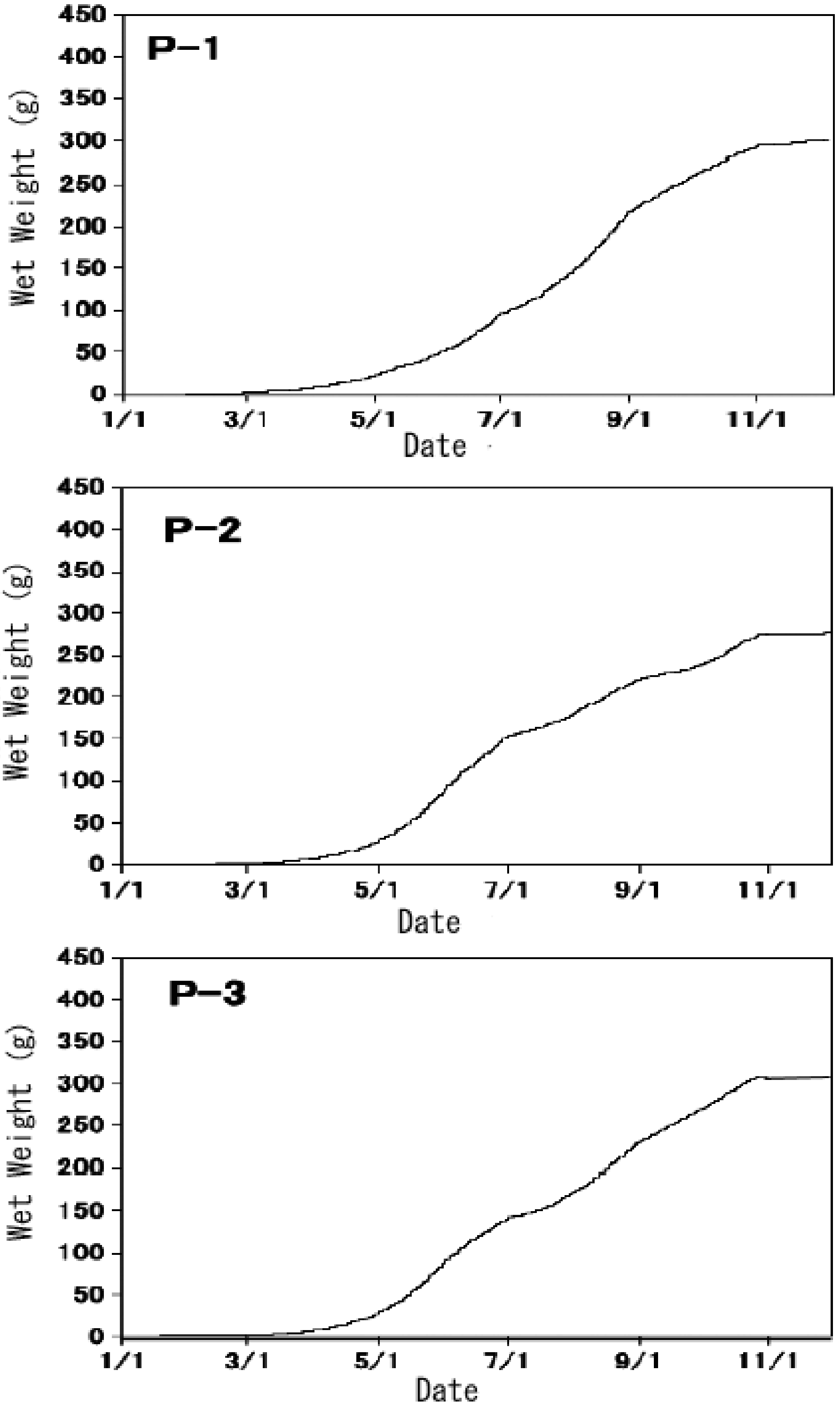

P-1
P-2
P-3
Wet Weight (g)
0
50
100
150
200
250
300
350
400
450
Date
1/1
3/1
5/1
7/1
9/1
11/1

Fig.10

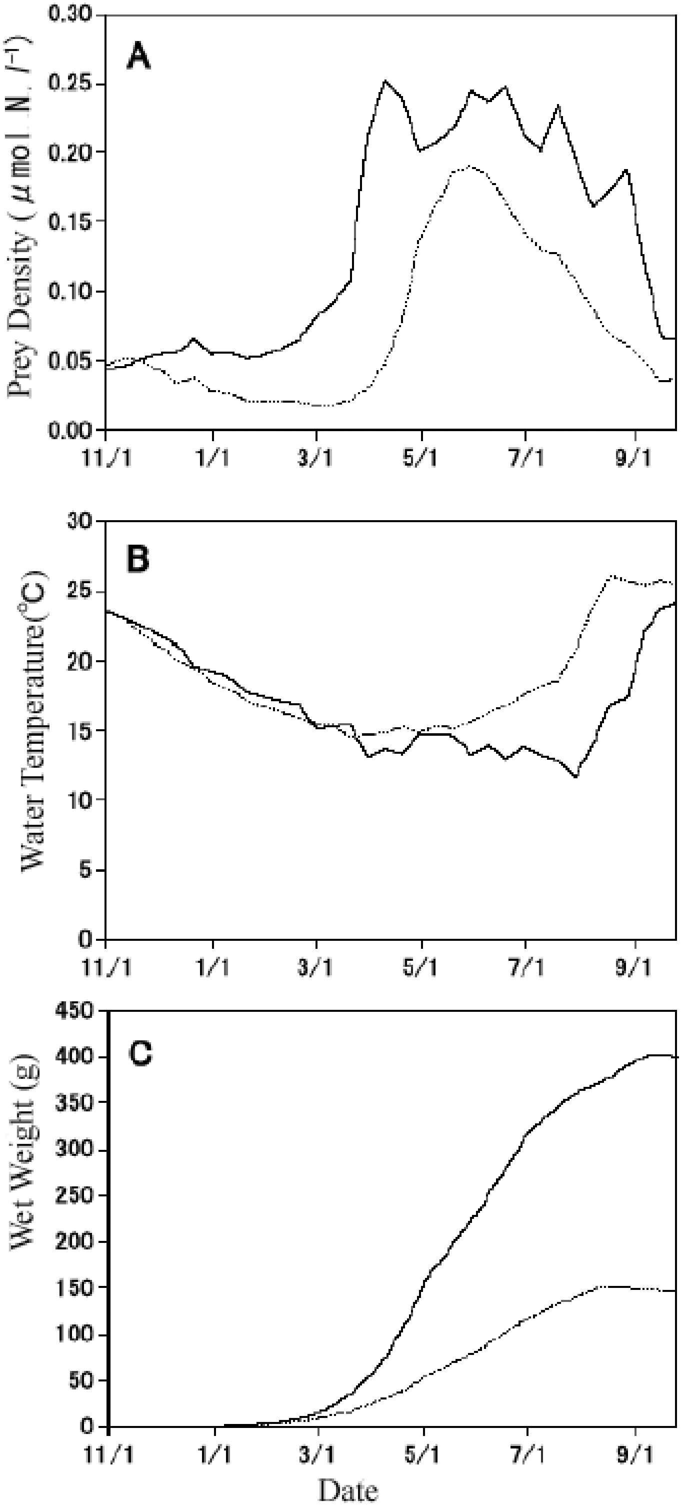
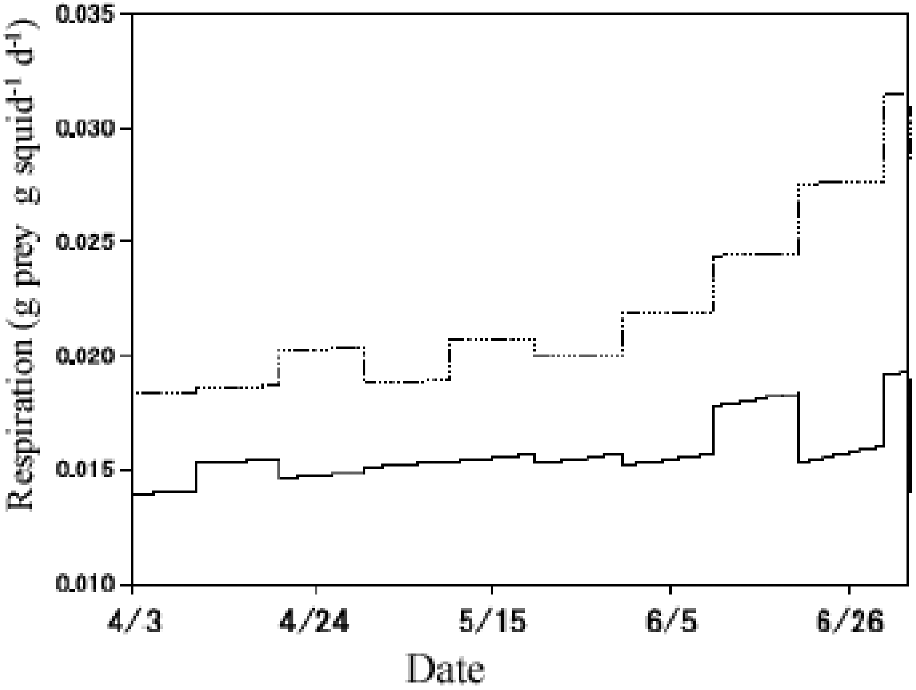

A
Prey Density (μ mol N l⁻¹)
0.00
0.05
0.10
0.15
0.20
0.25
0.30
B
Water Temperature(°C)
0
5
10
15
20
25
30
C
Wet Weight (g)
0
50
100
150
200
250
300
350
400
450
11/1
1/1
3/1
5/1
7/1
9/1
Date

Fig.11



Respiration (g prey g squid^{-1} d^{-1})
0.035
0.030
0.025
0.020
0.015
0.010
4/3
4/24
5/15
6/5
6/26
Date

Fig.12

Table1

Symbol	Value
consumption	
a_c	-0.00052
b_c	0.3048
te1(Stage1,Stage2,Stage3,Stage4,Stage6,Stage5)	12,7,4,6,10,15
te2(Stage1-3,Stage4-5,Stage6)	15,14,18
te3(Stage1-3,Stage4-6)	18,20
te4(for all stages)	23
xk1	0.1
xk2	0.98
xk3	0.98
xk4	0.1
Respiration	
a_R	0.000463
b_R	0.0
C_R	1.2
d_R	0.00972
Swimming speed	
a_A	1.6
b_A	0.75
Egestion and Excretion	
a_F	0.08
a_E	0.05

Table 2

Stage number	Stage name	Mantle length	Date		Prey
			(Fall-spawning)	(Winter-spawning)	
1	Larvae	less than 1.5 cm	Nov.1-Dec.15	Jan.1-Feb.15	ZS
2	Juvenile	1.5-12.0 cm	Dec.16-Apr.1	Feb.16-Jun.1	ZS+ZP
3	Young	12.1-20.0 cm	Apri.2-May1	Jun.2-Jul.1	ZP
4	Adult	20.1-23.0 cm	May2-Jul.2	Jul.2-Sep.2	ZP
5	Adult matured	more than 23.0 cm	Jul.3-Sep.3	Sep.3-Nov.3	ZP
6	Spawning adult	more than 23.0 cm	Sep.4-Oct.31	Nov.4-Dec.31	ZP

Table 3

Case	Northward migration route	Limit of northward migration (Stay period at the northernmost point)
P-1	Along the coast of Japan	42.5°N (8/28-9/27)
P-2	Along the coast of Japan	39.5°N (7/29-9/27)
P-3	Offshore area of Japan (Along 142.5°E line)	42.5°N (8/28-9/27)