**Western and**
**Central Pacific**
**Fisheries**
**Commission**

**SCIENTIFIC COMMITTEE**
**FOURTEENTH REGULAR SESSION**

**Busan, Republic of Korea**
**8-16 August 2018**

**Annual trend in migration rate of skipjack from spawning grounds to off Japan**

**WCPFC-SC14-2018/ SA-IP-05**

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**Abstract**

1. The DEB-IBM model (Individual Based Model (IBM) based on Dynamic Energy Budget (DEB) model) was applied to investigate the annual trend (2002-2010) in the migration rate of skipjack from their spawning grounds to off Japan.
2. Model settings in the IBM part assuming the averaged vertical distribution of skipjack to be 50 m was used for the replication of the skipjack migration as the estimated body length composition obtained with the setting in the preliminary experiment explained the composition around off Japan well.
3. In terms of spawning ability, the annual migration rate and its effect on the recent decline of skipjack catch around off Japan are discussed.

**Introduction**

Understanding the basic biology of skipjack (*Katsuwonus pelamis*) is necessary for their stock assessments in the context of biological settings in the stock assessment model and interpretations of the model outputs. However, their complex migratory life-cycle makes biological assumptions for area definition and connectivity among the areas more difficult. One way to compromise this situation is simplification of their migration areas. The simplicity might well explain the overall stock trend but still lacks the local trend when it comes to the stock in the western north Pacific Ocean. In fact, the discrepancy between the overall stock trend of increase and the recent decline in the higher latitude area (around off Japan) has been reported with the possibility of range contraction (Kiyofuji et al. 2014). One problem in the current model assumption arises from little connections between tropical areas and off Japan. However, there are little ways to confirm the connections between conventional areas because of the lack of information on skipjack migration via the life cycle (Phillips et al., 2018).

Individual Based Model (IBM) shed a light on the reevaluation of the connections between the conventional areas (Aoki et al., 2017; Phillips et al., 2018). The connections based on the biological evidence would provide better explanations for the biological settings in the stock assessment model. In conjunction with the skipjack migration among areas, other biological settings such as growth and reproduction are expected to have different trends in each area. Dynamic Energy Budget (DEB) model is a useful framework in terms of environment-dependent estimates of individual's growth and reproduction (Kooijman, 2010). The two models of IBM and DEB have a good affinity because the IBM can estimate temperature and food prey environments on the tracks, and the environments can be passed into the DEB as an input data for estimation of the fork length, body weight, batch fecundity through the times (Martin et al., 2012; Aoki et al., 2017). Aoki et al., (2017) devised a framework of combination of these models, which is called as DEB-IBM model for skipjack in the western north Pacific Ocean, and the models successfully reproduce their body size composition around off Japan. The framework can give us the environmentally driven estimates of the growth curve, and batch fecundity in each conventional region or newly proposed region (Kiyofuji et al., 2015a) while updating them.

In this document, we revisited the biological assumptions of the connections and reproduction through the years from 2002 to 2010 by using DEB-IBM model, and then compared reproductive traits among each latitude. Finally, we discussed these results to fill the gap between overall and local trends focusing on the recent catch decline around off Japan.

**Materials and methods**

*Model outline*

Because a comprehensive model setting is lengthy and has been already described in the literature (Aoki et al., 2017), the model descriptions are briefly mentioned here. This model constitutes the Individual Based Model (IBM) based on the Dynamic Energy Budget model (DEB).

The IBM part was employed with a condition assuming fish migrates by passive transport and active swimming which was set to start at the beginning of the juvenile stage. Swimming speed and depth was set to be one body length (BL) /sec, and 50 m, respectively, because the body length composition around off Japan was well explained with this setting (Aoki et al., 2017). Direction of the swimming was defined as the coolest direction among surrounding grids in daily temperature field. Oceanic environmental data of temperature, eastward and northward ocean currents at the depth of 50 m were used from the Hybrid coordinate ocean model (HYCOM) + Navy Coupled Ocean Data Assimilation (HYCOM + NCODA Global 1/12° Reanalysis; https://hycom.org/data/glbu0pt08/expt-19pt1).

The DEB part was applied to estimate the growth of skipjack tuna based on the trajectory environments obtained from the particle tracking of the IBM. As the DEB model derives metabolic process of an organism as a function of temperature ($T$) and food environment ($f$, $0 < f < 1$) from the first principles (i.e., mass-energy conservation laws and homeostasis of organisms, etc., Kooijman, 2010), fork length and batch fecundity on each track can be estimated through the simulation periods. Detailed model descriptions for tuna DEB model have been previously reported (e.g. Jusup *et al*. 2011) and all the settings including the food environment follows the previous document (Aoki et al., 2017).

*Simulation setting*

In the particle tracking simulation, we located a particle in each grid ranging from 120°E - 180°E and 20°S - 20°N (1°×1°, 2400 particles in total). Position of each particle was calculated every 3 hours. Release of particles started from November 1st of study year and particles were added every month until February, which is based on the historical larvae sampling research (Kiyofuji *et al*., 2015b). In total, we simulated four releases per released year, and its annual trend in the migration was explored through years from 2002 to 2010. In a case of landing on the shore, we terminated the simulation for the particle.

We selected the particles released in the northern hemisphere (0 to 20 °N) for analysis to focus on the migration in the north western Pacific. The changes in

environments of temperature and food, physiology of growth and reproduction were evaluated in each 5 degrees of latitude by averaging these values in released locations of 0 to 5°N, 5 to 10°N, 10 to 15°N, and 15 to 20°N.

**Results and Discussion**

*Annual trends in the migration rate from spawning grounds to off Japan*

Tracks of the particles can capture the potential migration routes from the spawning grounds to off Japan through the years from 2002 to 2010 (Fig 1). Overall, the higher the latitude of the original released locations, the more particles reached to off Japan. The annual trend drastically changes through the years (Fig. 1). For example, particles released from 0-5°N in 2002, 2003, 2004, 2009 moved to north-west directions and relatively large number of the particles reached to the areas over 20°N (Fig. 1a). On the other hand, it showed the west-direction movement in 2006, 2007, 2008, and 2010, which results in the small number of the particles reaching to the areas over 20 °N.

Aside from the qualitative understanding, we quantified the proportions of particle origins reaching to off Japan (Fig. 2). Almost 50% of the particles were from the closest area (15-20°N), and the proportions of particles decreased with the released latitude decrease. It should be mentioned that the particles released from the tropical areas (0-10°N) can reach to off Japan through the study years, which is also consistent with the recently estimated connections by different models (Senina et al., 2017; Phillips et al., 2018). These lead to the undoubted connections between the tropical areas and off Japan.

Turning attention to the annual proportions of the particles released from the tropical areas (0-10°N), the numbers gradually decreased from 2002 (20%) to 2010 (10%) with the lowest record (8%) in 2007. Given that it takes approximately 1.5 years to be a fishery target size (>40 cm) after hatching, the cohort of the lowest record hatched in Nov 2007 to Feb 2008 can be seen in the fishery from April to July 2009. Incidentally, this is the period of the worst catch recorded in the coastal fishery in off Japan (Nihira 2012). The coincidence may suggest that the impacts from the tropical areas on the catch in Japan is not negligible, even though the proportion is low.

*Reproductive biology in each released region*

Reproduction is one of the key factors affecting population dynamics. Here, the impacts of released locations on the batch fecundity as a function of body length were investigated (Fig. 3). No remarkable difference was found between released locations until 55 cm FL (Fig. 3), and the batch fecundity in the lower latitude areas (0-10°N) slightly increased over 55 cm. It is worth noting that the lower the latitudinal locations, the larger the fork

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length and batch fecundity in the same simulation time. These provide a first indication of the physiology having different trends in each released location.

We subsequently made more detailed comparisons between the released locations by looking at the fork length and batch fecundity as functions of time (Fig. 4). The higher the latitude in the released locations, the lower the fork length and batch fecundity expected. This was also confirmed by the time reaching to maturity at puberty (beginning of energy investment into the reproduction) in each released area showing the 239 days (0-5°N), 251 days (5-10°N), 269 days (10-15°N), 306 days (15-20°N) on median (Fig. 5). A key message here is that the reproductive traits would differ depending on the area as showing relatively low reproductive potentials in subtropical areas (10-20°N) compared to that in the tropical areas (0-10°N). However, we have little information to support the latitudinal difference in reproductive potential based on the comprehensive observed data of batch fecundity vs. age for now. Even though the large parts of the particles derive from the subtropical areas (Fig. 2), it needs reasonable and convincing explanations for how the low productivity of the subtropical areas can support the whole catch around off Japan.

To dig in the main factors affecting the difference in the biological traits among the released locations, experienced environments of temperature and food since hatching were investigated (Fig. 6). The temperature in the tropical areas (0-10°N) was constantly higher than that in the subtropical areas (10-20°N). As for the food availability, on the other hand, the particles released in the subtropical areas experienced richer food environment compared to those released in the tropical areas with the peak around 300 to 600 days. Briefly, each area is characterized as high (low) temperatures and poor (rich) food environment in the tropical (subtropical) area. Given that the growth and the reproduction in the tropical area showed greater magnitude than that in the subtropical area, the effect of environment on the physiology is probably derived more from the temperature than the food availability.

*Conclusion*

We revisited the skipjack biology of migration and reproduction by using the DEB-IBM model and emphasized that the annual difference in the migration from the tropical area to off Japan, and the potential difference in reproductivity between tropical and subtropical areas. We demonstrated that:

1) The annual trends of the particle proportions originally from the tropical areas reached to off Japan ranged from 8 to 20% with the lowest record in 2007. Taking into account the time (1.5 years) needed to grow as large as the target size of the coastal fisheries in

Japan, the lowest year coincides with the worst skipjack catch year (2009) around off Japan. This may suggest that the impact of the reproduction occurred in the tropical areas on the catch around off Japan is not trivial enough to be negligible.

2) The reproductive potential in the tropical areas (0-10°N) was always higher than that in the subtropical areas (10-20°N) because of their accelerated metabolic activity due to the high ambient temperature. Thinking with the underlying low batch fecundity in the subtropical areas, the overall catch around off Japan may not be supported by only the local reproduction.

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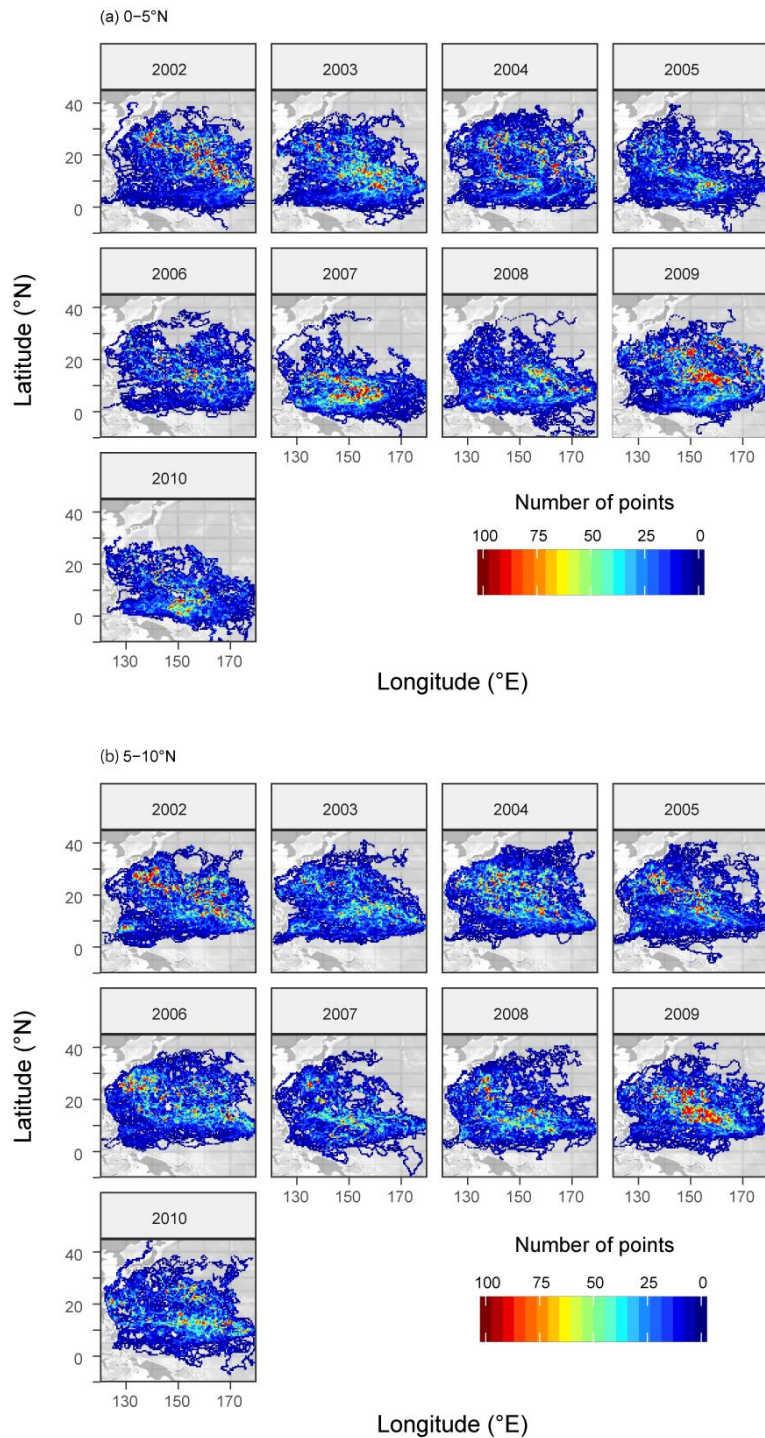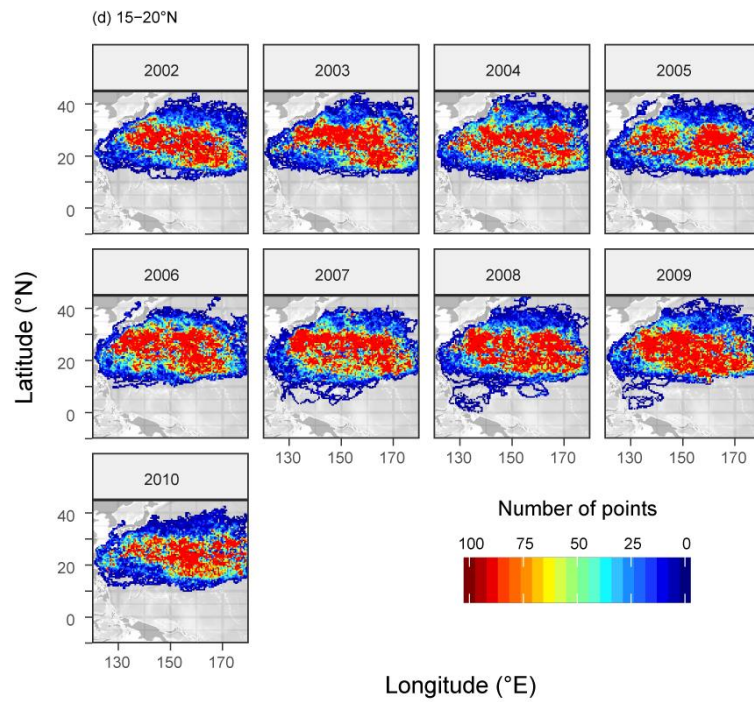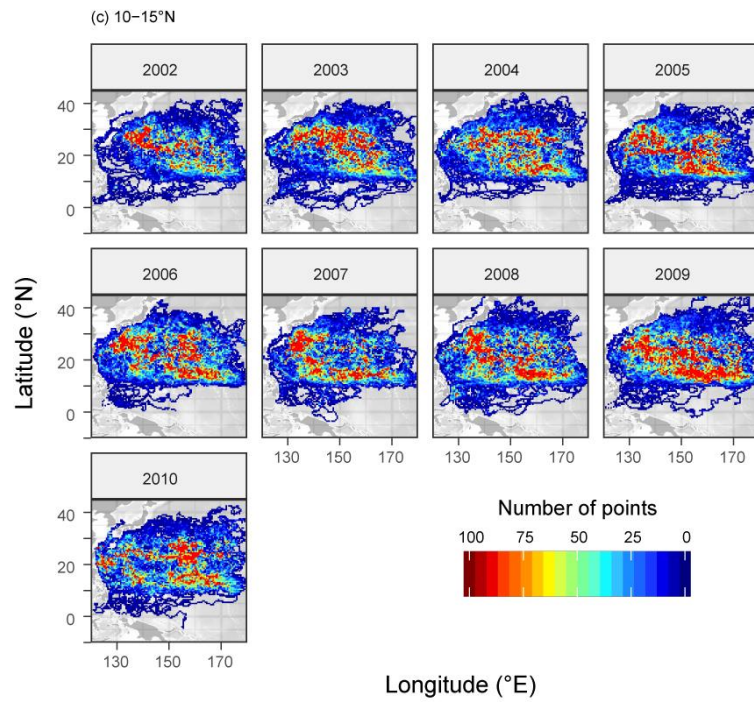
Figure 1. Estimated positions of particles released from latitudes of (a) 0 to 5°N, (b) 5 to 10°N, (c) 10 to 15°N, and (d) 15 to 20°N from 2002 to 2010. The locations of the particles every calculated time period were counted as number of points in each 1°×1° grid.
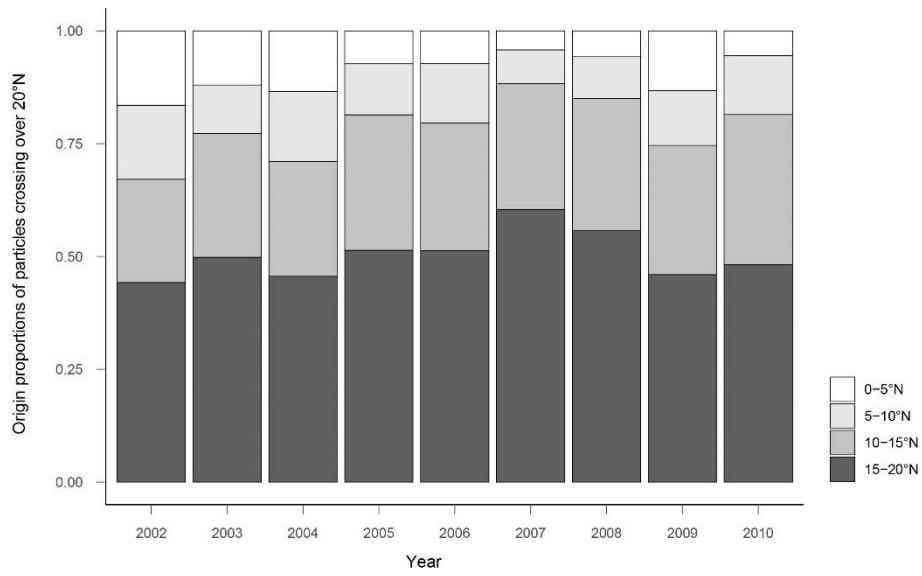
(Continued) Figure 1. Estimated positions of particles released from latitudes of (a) 0 to 5°N, (b) 5 to 10°N, (c) 10 to 15°N, and (d) 15 to 20°N from 2002 to 2010. The locations of the particles every calculated time period were counted as number of points in each 1°×1° grid.

Figure 2. Proportion of particles migrated from the released locations of 0-5°N, 5-10°N, 10-15°N, and 15-20°N to off Japan area (>20°N) in the studied years from 2002 to 2010.
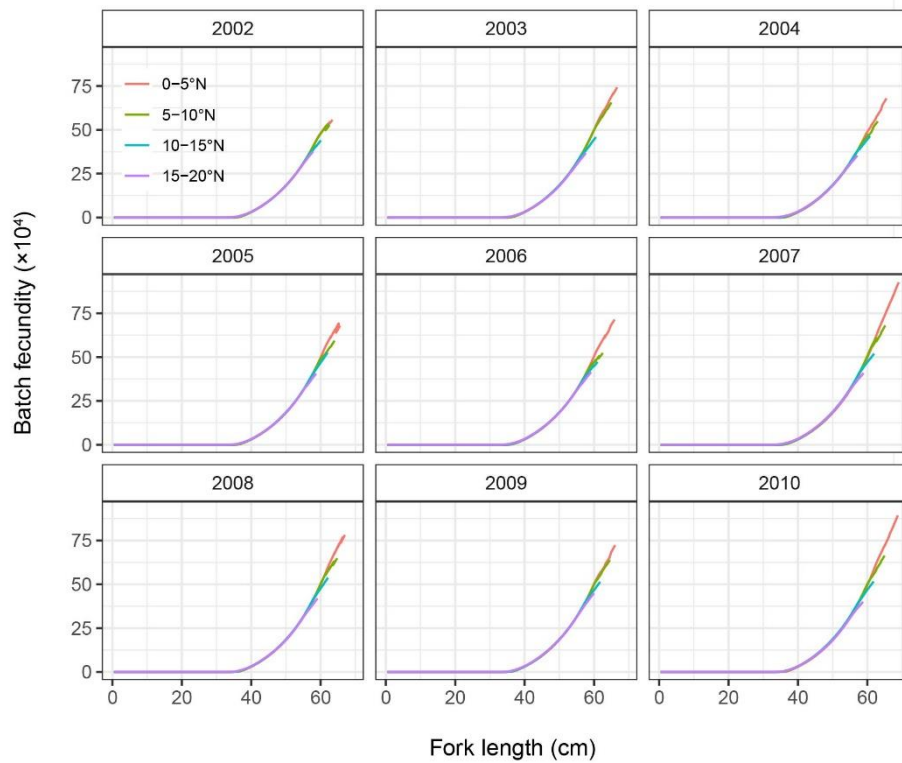
Figure 3. Model estimates of batch fecundity as the functions of fork length from 2002 to 2010. The colored lines represented the averages for the released locations of 0 to 5°N, 5 to 10°N, 10 to 15°N, and 15 to 20°N.
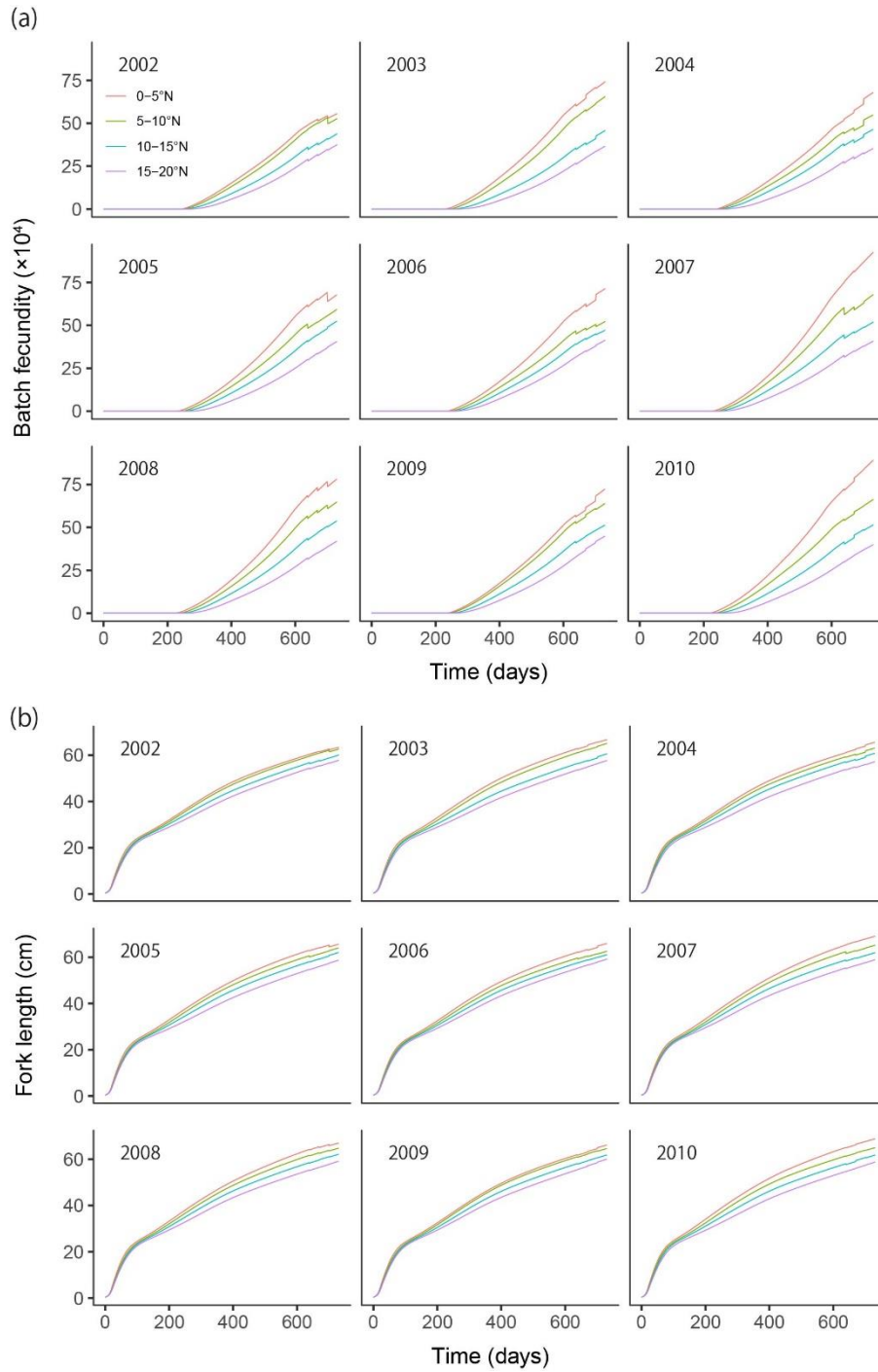
Figure 4. Model estimates of batch fecundity (a) and fork length (b) as the functions of time since hatching. Colored lines represented the averages for the released locations of 0 to 5°N, 5 to 10°N, 10 to 15°N, and 15 to 20°N.
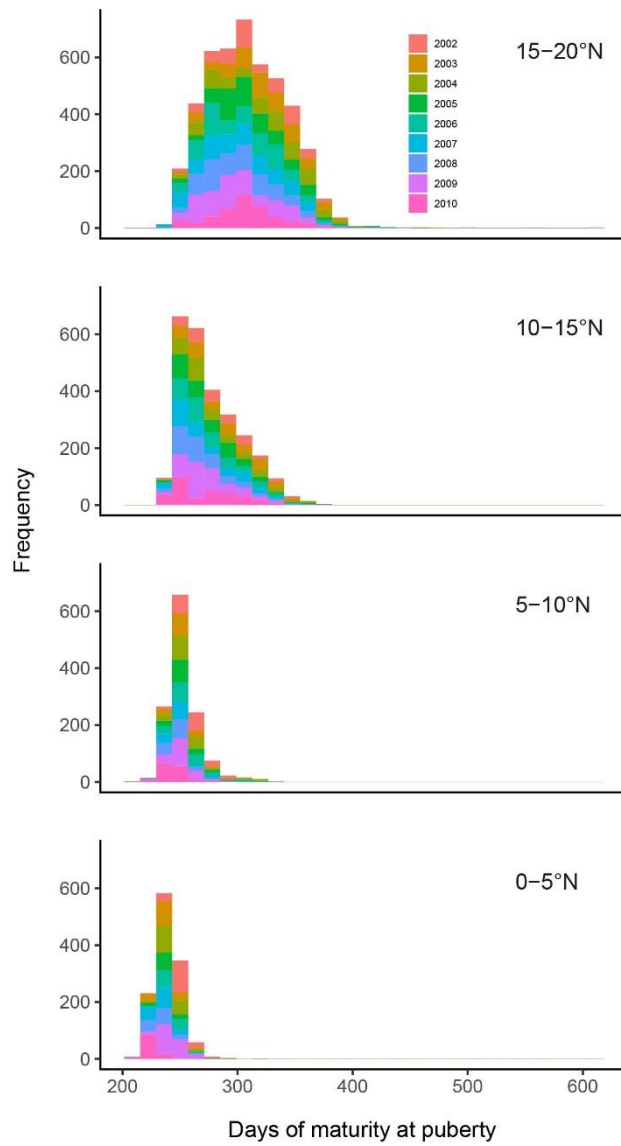
Figure 5. Model estimates of the days of maturity at puberty in each released region. The colors of bars represented the released years from 2002 to 2010.
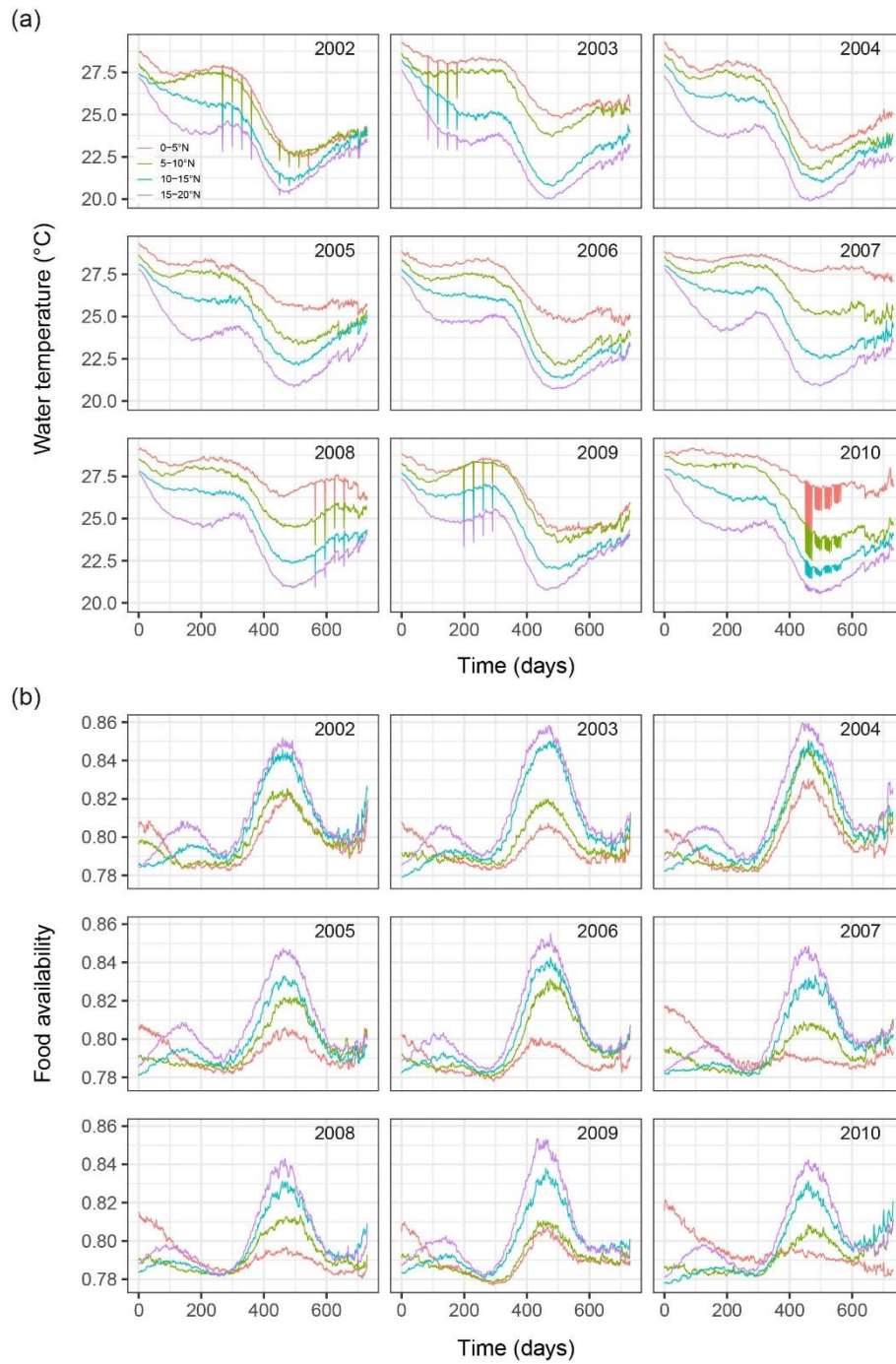
Figure 6. Annual environments of ambient temperature (a) and food environment (b) on the tracks from 2002 to 2010. The colored lines show the averages for the released locations of 0 to 5°N, 5 to 10°N, 10 to 15°N, and 15 to 20°N.

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