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Skipjack migration in the western central Pacific Ocean estimated from the particle tracking simulation with dynamic energy budget model

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Abstract

In this document, particle tracking simulation and Dynamic Energy Budget (DEB) model were combined to investigate skipjack migration from main hatching areas in the tropical areas, while verifying whether their growth through the migration is reasonable. Coupling two models provide us additional information of the migration for skipjack especially in small size which is not suitable for tagging. Our results demonstrated that part of skipjack in tropical migrated to near Japanese water through subtropical area (20 - 25°N, 125 - 150°E), where the fork lengths calculated by DEB model was the similar size composition with the observed length. The subtropical area is suggested to be a key area for skipjack migration in terms of connecting the tropical and near Japanese water, while it is also an important area for Japanese fisheries. Hence, spatial structure along the skipjack migration through their life cycle should be considered in the stock assessment.

Introduction

Recent skipjack tuna abundance (2004 - 2015) in Japanese coastal areas has declined from the higher period (1990 - 2003) (Kiyofuji *et al*. 2015a). According to Kiyofuji *et al*. 2014, high catches in equatorial area may cause range contraction of skipjack tuna in the Western Central Pacific Ocean, thereby causing a reduction of catch at higher latitude area such as Japan. To test this hypothesis, migration needs to be investigated from spawning area through the egg to young skipjack, which is difficult to be observed from tagging experiments.

Particle track simulation is a useful tool to evaluate the migration especially in small size fish which has not been tagged due to possibility of high mortality rate by tagging itself, difficulties in finding fish schools and its non-target size for fisheries. One of the issues of the particle tracking is lacking reliable method to verify the validity of the simulated results, especially in biological aspect. Bioenergetic models such as Dynamic Energy Budget (DEB) model have been used for estimation of the growth of organisms in recent years (Kooijman 2010). Coupling the two models of particle tracking and DEB model enables us to compare body sizes in the case fish habits where the particles arrive to observed sizes by fishery, which helps us to verify the validity of particle track simulations (Fig. 1). In this document, we demonstrate whether the movement from tropical area to near Japanese water occurs or not, and suggest that the successful movement from tropical to near Japanese water by using different models, particle tracking and calculated growth history.

Materials and Methods

Particle tracking with Hybrid coordinate ocean model

Particle tracking was employed with Hybrid coordinate ocean model (HYCOM) + Navy Coupled Ocean Data Assimilation (HYCOM + NCODA Global 1/12° Reanalysis; https://hycom.org/data/glbu0pt08/expt-19pt1). In the particle tracking simulation here, the HYCOM data of temperature, eastward ocean current and northward ocean current in area between 120°E - 100°W and 30°S - 60°N at the depth at 0 m and 50 m were extracted from the original global data. The grid interval is 1/12°.

Particle tracking simulation setup

In the particle tracking simulation, we located a particle in each one 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, 2010 and particles were added every 15 days until February 15, 2011, which is based on the historical larvae sampling research (Kiyofuji *et al*., 2015b). In a case of landing on the shore, we terminated the simulation for the particle.

Particle tracking simulation with passive transport

First simulation for the particle tracking was conducted in the condition assuming fish migrates only by the passive transport. Although this simulation is not realistic considering swimming ability of skipjack, it is an effective way to check whether skipjack can actually migrate toward north only by current transportation or not. In this simulation, calculation period was from November 1st, 2010 to March 1st, 2012.

Particle tracking simulation with active transport

Second simulation for the particle tracking was conducted in the condition assuming fish migrates by the passive transport and active swimming. Active swimming was set to start at the first day of juvenile stage (Matsumoto *et al*. 1984) corresponding to the 11 days after hatching based on growth curve by Kayama (2006). Swimming speed was set to be one to four body length (BL) /sec based on swimming speed of juvenile skipjack tuna estimated from an archival tag data (Fig. 2). Daily body length was referred to Kayama (2006) for fish of until 62 days after hatching and Ochi *et al*. (2016) for those of 62 to 1077 days after hatching. Direction of the swimming was defined as the coolest direction among surrounding grids in daily temperature field, i.e., the inverse direction of temperature gradient at particle position. Regarding to swimming depth, 0 m and 50 m was applied. In this simulation, calculation period was from November 1st, 2010 to June 30th, 2012.

In total, we simulated 8 scenarios for active tracking simulation (i.e., 4 types of swimming speed for 2 types of swimming depth). To evaluate the validity of the active tracking simulation among 8 scenarios, we checked whether the estimated growth by DEB model (described later) referring each simulate result have the similar length to the observed length or not. After we checked the suitable swimming depth, ratio of particle crossing over 20°N until March 1st, 2012 (the same period of passive simulation) was calculated for each latitude to compare the ratio between passive and active simulations.

we also evaluated the migration ratio among areas that is used in general stock assessment in the condition of throughout life stage vs specific period, 1st (January to March) and 2nd (April to June) quarter in 2012 as representative.

Dynamic Energy Budget model

Dynamic Energy Budget (DEB) model was applied to estimate growth of skipjack tuna based on trajectory environment of the particle tracking. In the DEB model, fork length can be estimated through the environment temperature (T) and food environment (f, $0<f<1$). Detailed model descriptions for tuna DEB model have been previously reported (e.g. Jusup *et al*. 2011), and only brief description will be given here. The DEB model describes the rate at which the organism assimilates into the reserve and utilizes the energy from the reserve for somatic and maturity part. The ratio of the somatic and maturity is constant. Energy flow allocated to somatic and maturity is used for each maintenance flow, and the rest of each flow is allocated to growth and maturity/reproduction, respectively. Aoki (2017) reviewed literature of the skipjack tuna, and obtained a reliable estimate of the model parameters. We refer to that study for the model construction and parameter settings for skipjack tuna.

Converting primary production to food availability

To evaluate the food availability for each particle, ocean net primary production (NPP) was used as an index of food availability for skipjack tuna, which is based on Vertically Generalized Production Model (Behrenfeld and Falkowski 1997). The NPP data with the time span of 8 day and the grid interval of 1/5° were downloaded from the Ocean Productivity Home Page (http://www.science.oregonstate.edu/ocean.productivity/). The NPP value at each particle position was estimated with bilinear interpolation from the nearest four NPP data. According to Aoki (2017), DEB model for tuna was constructed under the condition of food availability (f) of 0.8 for skipjack tuna in tropical and subtropical, and we converted the NPP obtained from particles to 0.8 by using the equation below.

$$f = 0.00025\times(\text{NPP} - 200) + 0.8 \ (0<\text{NPP}\leq 1000),\quad 1 \ (1000<\text{NPP})$$

Results

Particle tracking simulation with passive transport

Detailed examples of tracking trajectory that crossed 20°N from 0°N - 2°N were shown in Fig. 3. Particles released at the east side moved toward north-west until they reach to 20 °N, and some particles continued to move further north-west, while the others move to the north-east direction. Table 1 shows the ratio of the particles that crossed 20°N from each released latitude. The particles reached to 20°N was derived from particles released in north hemisphere (Table 1). In tropical area (5°S - 10°N), the ratio ranged from 27.4% to 39.9% depending on release date.

Particle tracking simulation with active transport

We calculated the difference in searching area size due to different growth trajectories of literature and ours. Growth curve estimated from particles that arrived subtropical area (20°N - 25°N, 125°E - 150°E) in January was compared with the curve from literatures (Kayama 2006; Ochi *et al*. 2016, Fig.4). In the case of swimming depth at 0 m, maximum difference in body length ranged from 2.6 to 3.0 cm between our results and literatures, and those were found at age of 453 to 467 days. We obtained the daily difference in movement distances of 2.3 km, 4.6 km, 7.2 km, 10.4 km for 1 to 4 BL/s scenarios. Regarding the case of swimming depth at 50 m, maximum body length difference ranged from 3.3 - 3.8 cm, and those were found at age of 246 - 258 days. The daily difference in movement distance was 2.8 km, 6.4 km, 9.8 km, 12.4 km for 1 to 4 BL/s scenarios. Among scenarios in each swimming depth, swimming speed of 1 BL/s is the least effected scenario by growth difference in respect of movement distance.

we checked the validity of swimming depth by comparing the size composition estimated from DEB model with the observed length (Fig. 5, Table 2). As for the swimming depth at 0 m, the first quartile, median, and third quartile were 44 - 45 cm, 47 - 48 cm, 49 - 50 cm, respectively. Regarding the scenario with swimming depth at 50 m, the first quartile, median, and third quartile are 41 - 42 cm, 43 - 44 cm, 46 - 47 cm, respectively. The median for the swimming depth at 0 m tends to be larger than that in depth at 50 m, although the difference among swimming speed was not large. In the observed data, the first quartile, median, and third quartile are 42.6 cm, 43.7 cm, 45.2 cm, respectively, which is close to the those of swimming depth at 50 m.

In the case of swimming depth at 50 m, the ratio of the particles crossing 20°N in each latitude was shown in Table 3. Nearly half percentage of particles came from 15°N - 20°N area, and the ratio of particles from tropical area (5°S-10°N) ranged from 5.8 to 21.1%. In each swimming speed, average percentage from the tropical area was 15.4%, 9.1%, 10.0%, 12.3% for 1 to 4 BL/s, respectively.

Figure 6 shows that the examples of trajectory in each particle released in latitude from 0°N to 10°N with estimated track by archival tag released in February to March 2012 for the swimming depth at 50 m and swimming speed of 1 BL/s. In the area between 0°N - 2.5°N and 2.5°N - 5.0°N, some particles moved to near Japanese water. In the latitude of 5.0°N - 7.5°N and 7.5°N - 10°N, overlapping of particles trajectory with tagged skipjack are found.

Figure 7 shows that migration ratio among areas in conventional segmentation for stock assessment, comparing calculations throughout life stages vs specific periods (1st and 2nd quarters) for swimming depth at 50 m and swimming speed 1 BL/s. In the 1st quarter (Fig.7 upper panel), particles reaching to Region 1 (stock assessment area definition in 2016) of 89%, 6%. 2%, 3% is derived from the original region of 1 and other regions of 2, 3, and 4, respectively. Similarly, in the 2nd quarter (middle panel), particles reaching to Region 1 of the 83%, 4%, 1%, 12% is derived from the original region of 1 and other regions of 2, 3, and 4. Almost all of particles in Region 1 stayed at the same Region of 1. On the other hand, the case considering movement in longer period that is throughout egg to adult, migration to Region 1 is 61%, 31%, 8% from Region 2, 3, and 4.

Discussions

Our coupled models provide new insight with respect to the horizontal movement of skipjack and growth throughout life cycle from egg to adult. Estimated growth curve was favorably fit to the literature value, suggesting that the effect on the movement distance due to using different growth curve was small, especially in the swimming speed of 1 BL/s. In addition, size composition in swimming depth at 50 m shows good fits to the observed size better compared to the scenario with swimming depth at 0m. This is also supported by the fact that the sampling depth for skipjack larva (>10 mm) ranged from 40 m to 120 m (Tanabe *et al*. 2017), and that age-0 skipjack tuna in subtropical area distributed at a depth of 30 m to 70 m in daytime based on archival tag data (Okamoto *et al*. 2013). Further, particle trajectory and estimated track based on archival tag data did not contradict. These results suggested that coupling active tracking simulation (with swimming depth and speed: 50 m and 1 BL/s) and DEB model is suitable enough to discuss the realistic movement and growth of skipjack tuna.

In this document, we strongly suggest that the fish movement from tropical to near Japanese water should be considered in the stock assessment. In both passive and active particle tracking simulation, particles released in tropical area crossed over 20°N. In the active simulation, the movement preference of skipjack was defined to seek for the coolest point among neighboring grids where they can search in a day. This preference of environment seems to let particles move toward cooler grid such as north region. However, the result of passive tracking simulation provides us with the fact that the particles released in tropical area was transported to cross 20°N over the North Equatorial Current (NEC) from east to west around 10°N, and the ratio of transportation from tropical area (5°S - 10°N) is higher than that in active tracking simulation.

Regarding the ratio of particles crossing 20°N in the active tracking simulation, at least 15.4% of the particles are found in the case of swimming depth 50 m and swimming speed of 1 BL/s. In reality, this ratio would be affected by difference in egg mass released in each latitude. It should be emphasized that we set the uniform number of particles through the study area (20°S - 20°N, 120°E - 180°E) so that we could detect the existence of migration to near Japanese water from hatching areas. Although the relationships between egg and spawning individual remain unknown for this species, we need to consider the spatial difference of spawning individuals, especially the difference in tropical and subtropical areas. According to William and Terawasi (2016), catch of skipjack tuna was spatially concentrated in 5°S - 5°N. In the case of weighting the number of eggs in released positions by the catch of spawning individuals in the same area, the contribution from tropical area to near Japanese water would increase, thus the ratio we showed in this document would be one of the most pessimistic case of the ratio.

Movement rate among regions that used in the stock assessment drastically differed between the cases of considering specific periods and the whole life cycle. In cases considering specific periods, almost all of the regions were dominated by the particles that stay at the region they originally exist, which is used as an indicator of movement rate in the stock assessment, while based on results of movement through egg to adult, the ratio of particles that keep staying in the original region was different from that of the specific periods. These results indicate that movement rate among regions used in the stock assessment is biased by the movement of young skipjack which is suitable for tagging research. Hence, the movement rate based on the whole life cycle should be considered.

For precise stock assessment of skipjack tuna, our model which can evaluate the movement from hatching area is suitable. However, our coupled-model approach still contains some problems for further analysis. For example, there is lack of information about the directions of skipjack movement from biological aspect. We need to test other cases of the preference in movement such as maximizing food availability, and so on. We should compare the simplest case of random walk with our results shown in this document. This model is practical tool for the purpose of recreating the northward migration in the aspects of movement and growth of fish, while there is a need to make some adjustments for the southward migration during the spawning seasons by using information such as maturity level of individuals. DEB model can also estimate the maturity level, and the direction of particle movement in the tracking simulation can be determined by the maturity level in the future (i.e., maximizing extra energy for young fish and maximizing maturity energy for adult fish). Setting food availability in this model is crucial. We used primary production for their food as an index due to the lack of high resolution of information about their prey distribution such as anchovy, sardine, and squid. In our tracking simulations, we terminated the simulation if the particle is on the land, which would cause underestimate of the movement ratio around lands. However, this model is still good enough to understand the overall summary of the skipjack movement in basin scale.

Summary

In the passive tracking simulation, particles released in tropical area crossed north equatorial current and reached to near Japanese water, suggesting that the skipjack hatched in tropical area can migrate to the near Japanese water.

In the active tracking simulation with dynamic energy budget model, particles in swimming depth at 50 m reaching to subtropical area had the similar size composition with observed length in the same area and period, supporting the validity of active tracking simulation in terms of movement and growth.

Based on the active tracking simulation in a depth at 50 m, migration ratio among areas, especially from tropical to near Japanese water, was low if we see relatively short, segmented periods, but in the case regarding lifetime throughout egg to adult, the migration ratio from tropical to near Japanese water increased. Thus, spatial structure along the skipjack migration through their life cycle should be considered in the stock assessment.

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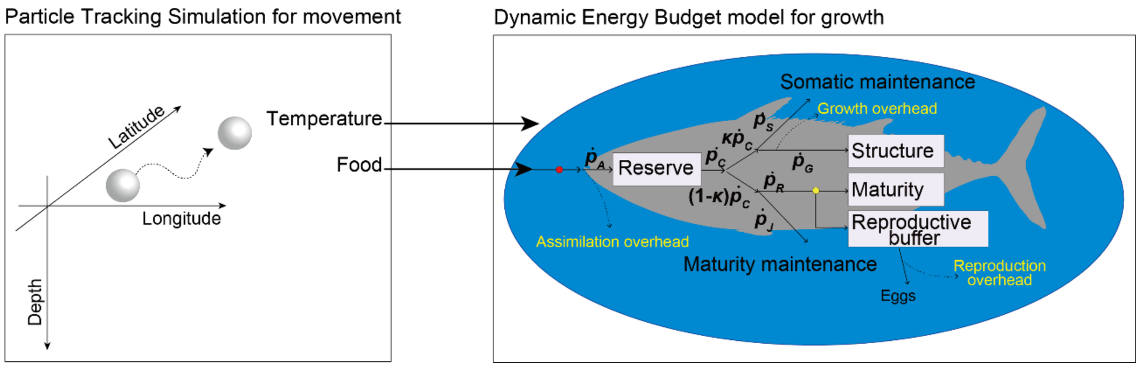

Fig.1. Schematic relationships between particle tracking simulation and Dynamic Energy Budget (DEB) model. Temperature and food in each particle is passed to DEB model as an input data for estimation growth.

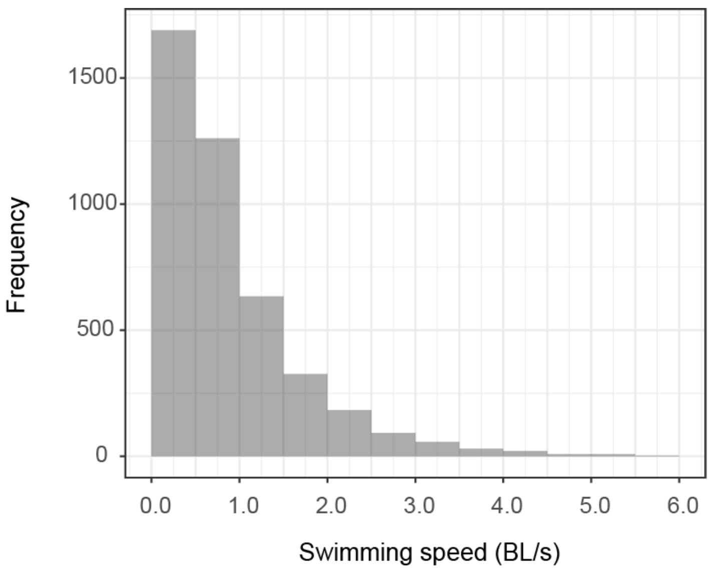

Fig.2. Frequency of swimming speed (Body Length/sec) estimated from daily movement distances based on archival tag data (in preparation). The swimming speed was calculated by dividing daily horizontal movement by average length of tagged skipjack tuna (45cm).

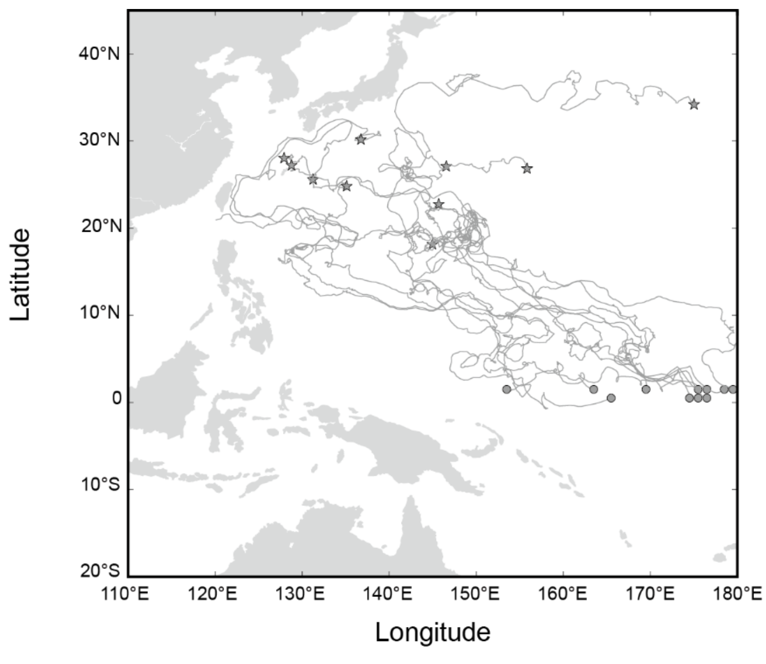

Fig. 3. Example of particle trajectory released in 0-2°N for passive tracking. Start and end points are shown as circle and star marks, respectively.

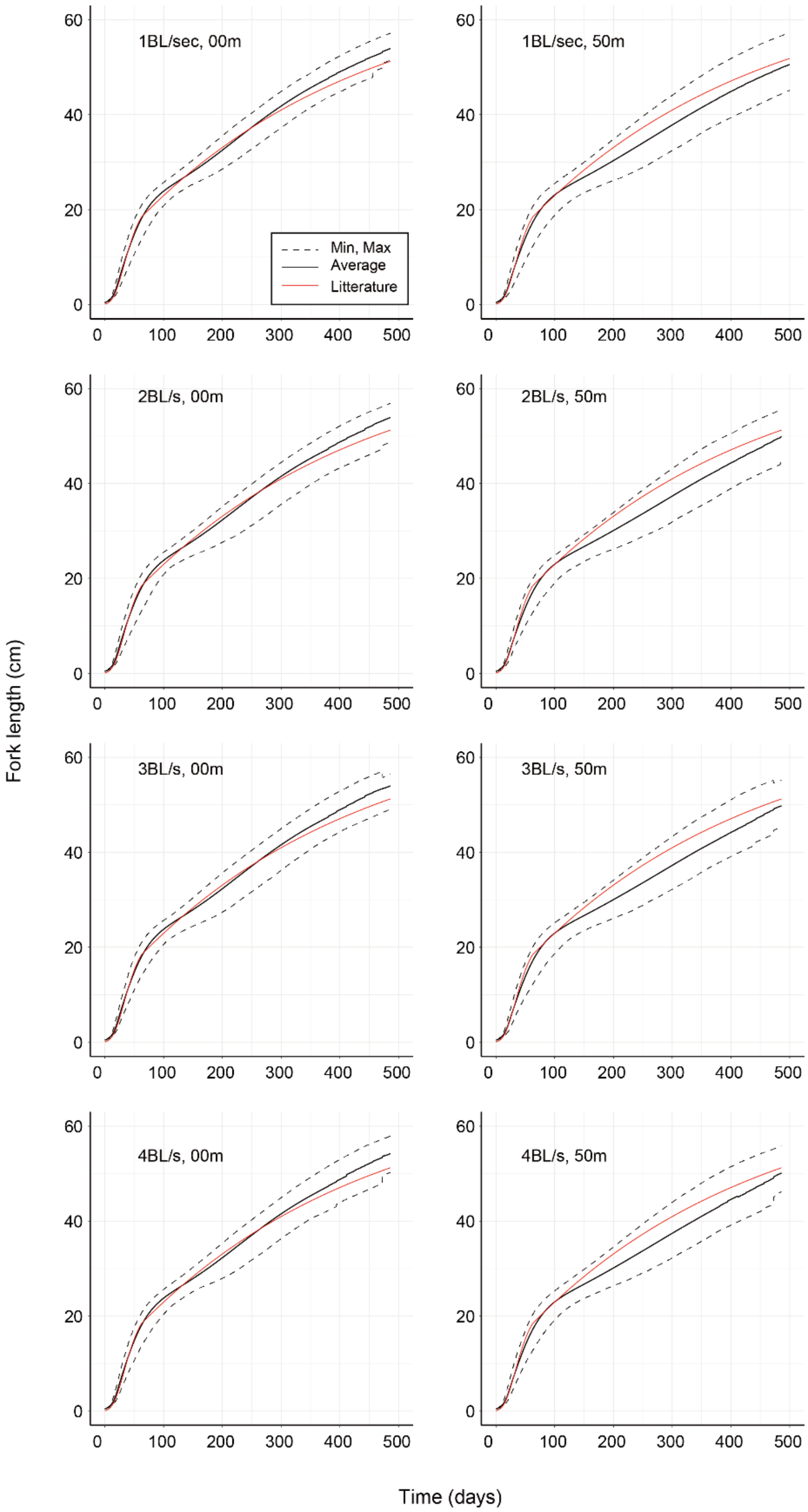

Fig. 4. Comparison of estimated growth curve with that of literature (Kayama 2006 and Ochi *et al.* 2016). Left and right panels show the cases of swimming depth at 0 m and 50 m for 1BL/s.to 4BL/s from top to the bottom.

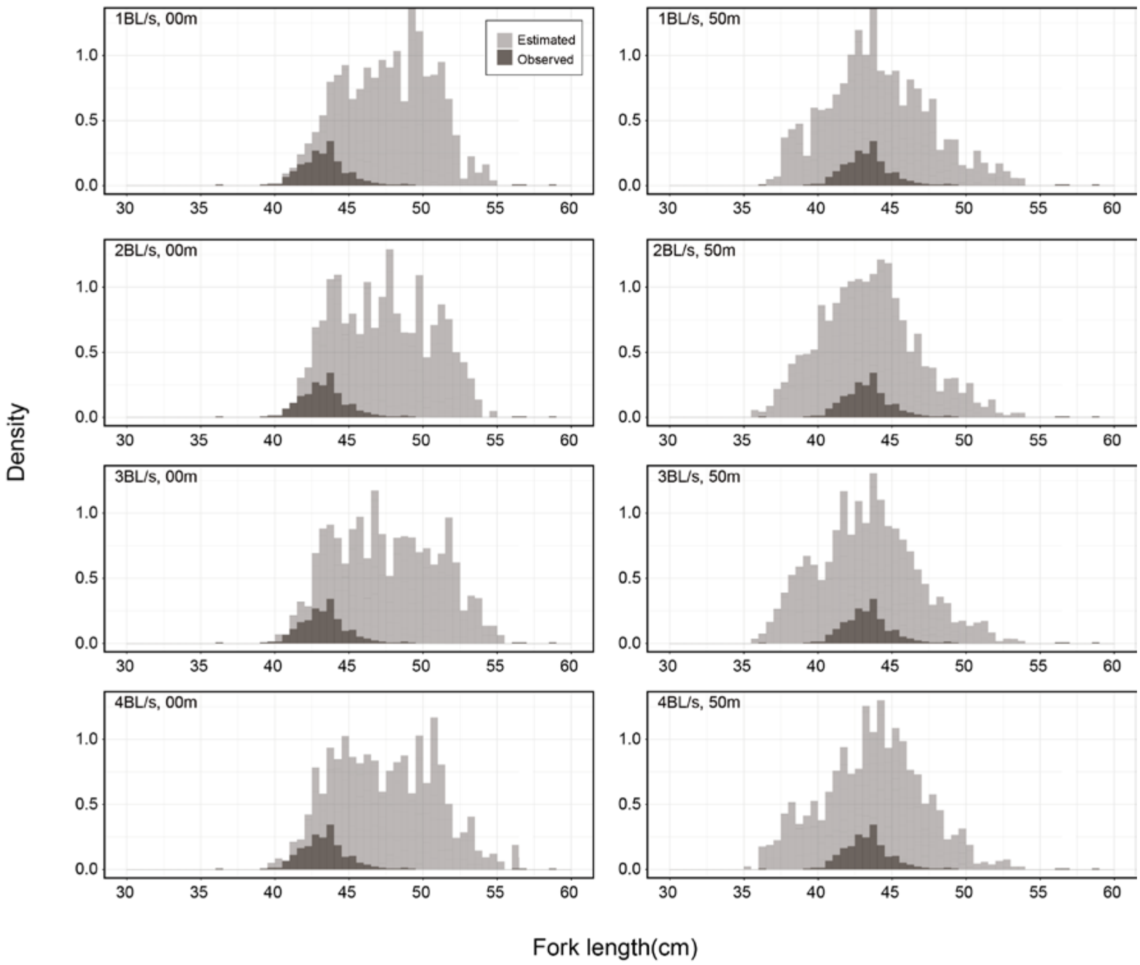

Fig. 5. Estimated (gray) and observed (black) size composition in subtropical area (20 - 25°N, 125 - 150°E) on January. Left and right panels show the cases of swimming depth at 0 m and 50 m for 1BL/s to 4BL/s from top to the bottom.

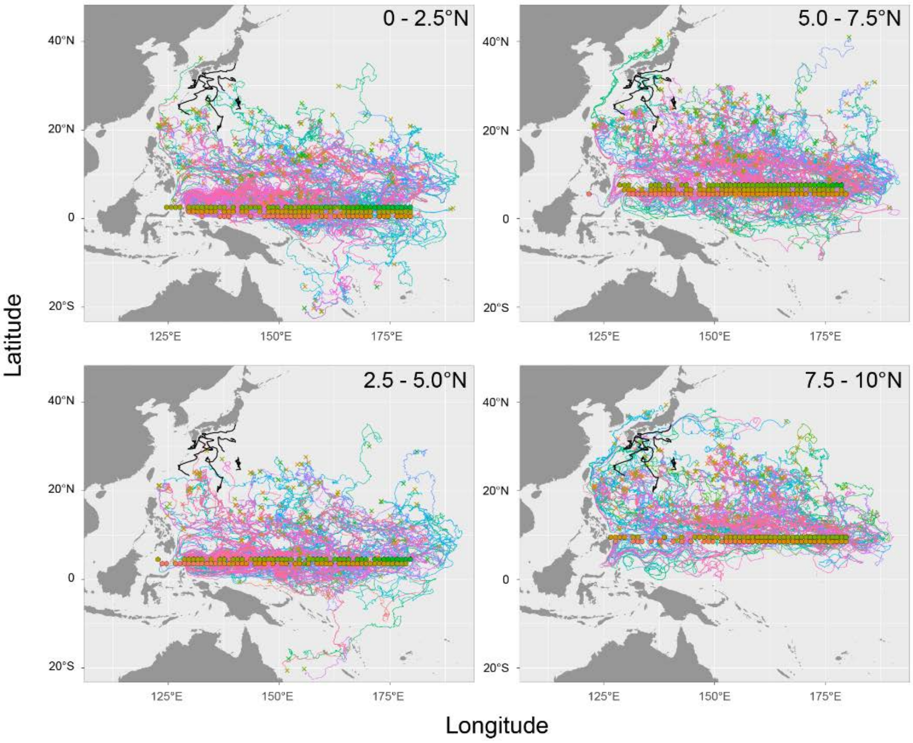

Fig. 6. Examples of particle trajectory released in 0 - 2.5°N, 2.5 - 5.0°N, 5.0 - 7.5°N, and 7.5 - 10°N for active tracking simulation (parameter settings: swimming depth at 50 m and swimming speed 1BL/sec). Colors indicate the difference in release date and longitude. Estimated track (black line) by archival tag released in February to March 2012 (black line). Start and end points are shown in circle and x marks.

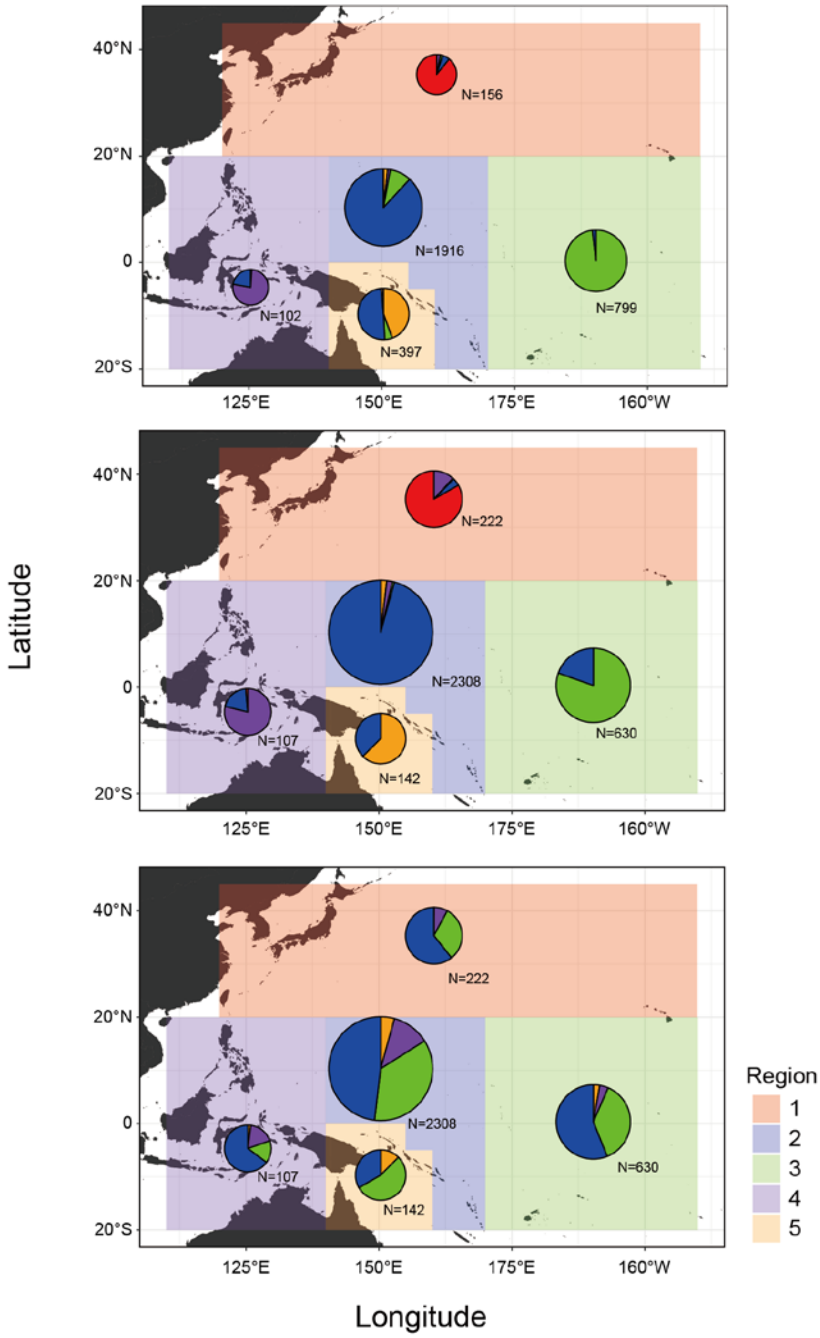

Fig. 7. Examples of migration ratio among areas in conventional region segmentation. Migration was calculated in 1st (upper) and 2nd (middle) quarters of 2012, and through the release dates to June 30th, 2012 (parameter settings: swimming depth at 50 m and swimming speed 1BL/sec). The size of pie charts shows the number of particles that reached in each region. Pie chart in each region expresses the ratio of reached particles colored by the original position on the first day of calculation.

Table 1. Ratios of particles that crossed 20°N toward north in the passive tracking simulation.

Release date	Number	15°N - 20°N	10°N - 15°N	5°N - 10°N	0 - 5°N	5°S - 0	10°S - 5°S	15°S - 10°S	20°S - 15°S
Nov. 1	570	44.9%	26.1%	17.0%	11.2%	0.7%	0.0%	0.0%	0.0%
Nov. 15	563	43.7%	28.8%	17.6%	9.1%	0.7%	0.2%	0.0%	0.0%
Dec. 1	599	40.1%	25.5%	19.9%	13.9%	0.7%	0.0%	0.0%	0.0%
Dec. 15	586	40.4%	26.8%	20.1%	11.4%	1.2%	0.0%	0.0%	0.0%
Jan. 1	615	38.4%	25.5%	21.8%	13.5%	0.8%	0.0%	0.0%	0.0%
Jan. 15	663	37.4%	25.5%	21.4%	14.5%	1.2%	0.0%	0.0%	0.0%
Feb. 1	746	34.6%	25.3%	20.9%	16.9%	2.1%	0.1%	0.0%	0.0%
Feb. 15	749	36.0%	25.8%	21.1%	14.6%	2.5%	0.0%	0.0%	0.0%

Table 2. Statistic information about estimated lengths for active tracking simulations. Abbreviation of Q indicates quartile in the boxplot.

Depth (m)	Speed (BL/s)	1st Q. (cm)	Median (cm)	3rd Q. (cm)
0	1	45.8	48.0	49.9
0	2	44.8	47.2	49.6
0	3	45.2	47.5	50.2
0	4	44.9	47.3	50.0
50	1	41.9	44.1	46.8
50	2	40.9	43.3	45.5
50	3	40.6	43.1	45.6
50	4	41.1	43.7	46.0

Table 3. Ratios in origins of particles that crossed over 20°N toward north in the active tracking simulation with swimming depth at 50 m.

Speed (BL/s)	Release date	Num.	15°N-20°N	10°N-15°N	5°N-10°N	0-5°N	5°S-0	10°S-5°S	15°S-10°S	20°S-15°S
1	Nov. 1	488	54.7%	29.5%	11.9%	3.1%	0.6%	0.2%	0%	0%
1	Nov. 15	516	49.8%	34.1%	12.4%	2.5%	1.2%	0%	0%	0%
1	Dec. 1	491	53.2%	31.8%	11%	3.3%	0.6%	0.2	0%	0%
1	Dec. 15	519	51.1%	32%	12.1%	4%	0.8%	0%	0%	0%
1	Jan. 1	493	51.5%	33.1%	11.4%	3.4%	0.6%	0%	0%	0%
1	Jan. 15	487	52.6%	32.2%	10.3%	4.5%	0.4%	0%	0%	0%
1	Feb. 1	487	49.7%	34.9%	12.9%	2.1%	0.4%	0%	0%	0%
1	Feb. 15	487	53.4%	32.6%	11.1%	2.7%	0.2%	0%	0%	0%
2	Nov. 1	462	58.7%	28.6%	10.8%	1.9%	0%	0%	0%	0%
2	Nov. 15	446	57.4%	33.6%	7.6%	1.3%	0%	0%	0%	0%
2	Dec. 1	468	56%	33.1%	9.4%	1.5%	0%	0%	0%	0%
2	Dec. 15	475	56.4%	33.5%	8.8%	1.3%	0%	0%	0%	0%
2	Jan. 1	470	57.4%	34.5%	7.4%	0.4%	0.2%	0%	0%	0%
2	Jan. 15	460	56.7%	35.9%	6.3%	1.1%	0%	0%	0%	0%
2	Feb. 1	415	62.9%	30.4%	5.8%	1%	0%	0%	0%	0%
2	Feb. 15	424	60.1%	32.5%	6.4%	0.9%	0%	0%	0%	0%

(Continued) Table 3. Ratios in origins of particles that crossed over 20°N toward north in the active tracking simulation with swimming depth at 50 m.

Speed (BL/s)	Release date	Num.	15°N-20°N	10°N-15°N	5°N-10°N	0-5°N	5°S-0	10°S-5°S	15°S-10°S	20°S-15°S
3	Nov. 1	454	57.5%	31.3%	10.8%	0.4%	0%	0%	0%	0%
3	Nov. 15	458	55%	33.4%	10.5%	1.1%	0%	0%	0%	0%
3	Dec. 1	456	55.5%	32.9%	10.3%	1.3%	0%	0%	0%	0%
3	Dec. 15	470	56.8%	33.8%	8.7%	0.6%	0%	0%	0%	0%
3	Jan. 1	483	56.1%	32.3%	10.8%	0.8%	0%	0%	0%	0%
3	Jan. 15	459	57.1%	34.4%	7%	1.5%	0%	0%	0%	0%
3	Feb. 1	446	57.6%	32.5%	8.5%	0.9%	0.4%	0%	0%	0%
3	Feb. 15	414	61.6%	32.6%	5.6%	0.2%	0%	0%	0%	0%
4	Nov. 1	468	55.1%	30.1%	13.2%	1.5%	0%	0%	0%	0%
4	Nov. 15	458	57.4%	32.1%	8.5%	1.5%	0.2%	0.2%	0%	0%
4	Dec. 1	474	54.2%	34.4%	9.9%	1.5%	0%	0%	0%	0%
4	Dec. 15	492	54.5%	32.9%	11%	1.4%	0.2%	0%	0%	0%
4	Jan. 1	472	56.8%	33.7%	7.4%	1.9%	0.2%	0%	0%	0%
4	Jan. 15	544	46.3%	32.5%	14.5%	5.5%	1.1%	0%	0%	0%
4	Feb. 1	433	59.4%	31.2%	8.8%	0.7%	0%	0%	0%	0%
4	Feb. 15	432	58.6%	34.3%	6.3%	0.9%	0%	0%	0%	0%