

# Roles of vertical behavior in the open-ocean migration of teleplanic larvae: a modeling approach to the larval transport of Japanese spiny lobster

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**ABSTRACT:** The vertical behavior of planktonic larvae has been increasingly recognized as an important factor in their transport. However, little is known about the roles of this behavior in open-ocean migration of teleplanic larvae. Using Japanese spiny lobster *Panulirus japonicus* in the western North Pacific and adjacent waters as a model species, we aimed to clarify (1) the effect of vertical behavior of larvae on transport success, (2) migration pathways of larvae, and (3) mechanisms that enable larvae to approach adult habitats before metamorphosing into competent swimmers (pueruli). Larval transport was simulated using an individual-based model with 10 different vertical behavior types (VBTs) and mortality caused by exposure to water temperatures outside the range (19–30°C) at which wild larvae appear. The VBTs that started transport at a shallow depth (1 m) had significantly higher transport success than those that started at greater depths ( $\geq 25$  m). Of the successful VBTs, those with ontogenetic vertical migration (OVM) showed greater detrainment of particles from the Kuroshio Extension (KE) and facilitated southwestward transport of particles in the recirculation region. Furthermore, the results indicate that phyllosoma larvae are transported by the Kuroshio, KE, and Kuroshio Countercurrent. Our study suggested that (1) detrainment of phyllosoma larvae from the KE to the recirculation region is facilitated by OVM and cross-frontal exchange at the meander trough, and (2) southwestward transport to adult habitats and avoidance of the low-temperature water shifting southward in winter are facilitated by OVM and the beta spiral. These findings highlight the importance of vertical behavior in open-ocean migration of teleplanic larvae.

**KEY WORDS:** *Panulirus japonicus* · Phyllosoma · Individual-based model · Cross-frontal exchange · Beta spiral · Kuroshio · Detrainment

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## INTRODUCTION

The vertical behavior of planktonic larvae has been increasingly recognized as an important factor in the transport of marine species (Cowen et al. 2007, Pineda et al. 2007, Werner et al. 2007, Cowen & Sponaugle 2009). Ontogenetic behavioral changes of

larvae potentially influence their dispersal (Scheltema 1986a), and growing numbers of studies suggest that ontogenetic vertical migration (OVM) can affect the scale of dispersal (e.g. Paris & Cowen 2004, Butler et al. 2011). For coastal species, the effect of vertical behavior has been investigated extensively (e.g. Paris & Cowen 2004, North et al. 2008). How-

ever, only a few species that extend their larval transport to the open ocean have been studied (e.g. Scheltema 1966, 1968), and little is known about the roles of vertical behavior in relation to the migration of teleplanic larvae in the open ocean.

A variety of marine animals disperse as plankton in their early life stages, and some of them have teleplanic larvae capable of dispersal over long distances because of their long larval period (e.g. Arthropoda, Phillips & McWilliam 1986; Asteroidea, Villalobos et al. 2006; Gastropoda, Scheltema 1966; Polychaeta, Scheltema 1986b). Teleplanic larvae start dispersal from shoal waters, and their pelagic larval duration lasts for several months to a year (Scheltema 1972). Palinurid lobsters (spiny or rock lobsters) have this type of larva. The lobster larva, called phyllosoma, has a transparent leaf-like body, and its pelagic larval stage lasts for months to years (Lipcius & Eggleston 2000), whereas its postlarva, called puerulus, has a transparent adult-like shape, and this stage lasts for weeks to months (Booth & Phillips 1994). Phyllosoma larvae do not have a strong ability to swim horizontally, whereas pueruli have the ability to swim toward nursery habitats (Booth & Phillips 1994).

Knowledge of larval transport is essential for understanding recruitment variability, which is important for stock management and sustainable use of fisheries resources. Transport of phyllosoma larvae has been studied worldwide using Lagrangian models. This method has been applied to *Panulirus marginatus* (Polovina 1999), *P. cygnus* (Griffin et al. 2001, Feng et al. 2011), *Jasus edwardsii* (Chiswell et al. 2003, Chiswell & Booth 2008), *Sagmariasus verreauxi* (Chiswell et al. 2003), *P. argus* (Briones-Fourzan et al. 2008, Butler et al. 2011), and tropical Atlantic *Panulirus* spp. (Rudorff et al. 2009), some incorporating vertical behaviors of larvae into the models (Griffin et al. 2001, Butler et al. 2011, Feng et al. 2011). Furthermore, larval transport modeling has been applied to evaluate marine reserves for *P. argus* (Lipcius et al. 2001, Kough et al. 2013). Despite worldwide applications of a modeling approach to the studies of larval transport of spiny lobsters and the commercial importance of the Japanese spiny lobster *P. japonicus* in East Asia (i.e. Japan and Taiwan; Sekiguchi 1997, Sekiguchi & Inoue 2002), no studies have employed Lagrangian models to investigate larval transport in this species.

Based on the distribution of phyllosoma larvae and pueruli together with hydrodynamic features in the western North Pacific (Sekiguchi 1985, 1997, Inoue & Sekiguchi 2001), Sekiguchi & Inoue (2002) proposed an early-life migratory route of *P. japonicus* by which phyllosoma larvae are transported from

coastal waters into the Kuroshio Current, and then enter the Kuroshio Countercurrent (KCC). The larvae reach sub-final, final, and puerulus stages east of the Ryukyu Archipelago and Taiwan, reenter the Kuroshio, and finally return to coastal waters. The above-mentioned transport route was supported by *in situ* larval distributions of late- to final-stage larvae (Chow et al. 2006b) and pueruli off southern Kyushu (Yoshimura et al. 1999). Chow et al. (2006 a,b) demonstrated a method for molecular species identification of phyllosoma larvae of the genus *Panulirus* from the western North Pacific, and the distributions of mid- to final-stage larvae of *P. japonicus* revealed by this method supported the hypothesized transport route. The route hypothesized by Sekiguchi & Inoue (2002) is well supported by *in situ* larval distributions; however, the distribution range has recently been found to be wider (AFFRC 2010, Chow et al. 2011). Furthermore, mechanisms involved in the larval transport remain unsolved (Sekiguchi & Inoue 2002).

Rimmer & Phillips (1979) studied vertical migration of *P. cygnus* larvae off the west coast of Australia and hypothesized that the vertical positioning of larvae is an important mechanism for successful migration. Phillips & McWilliam (1986) emphasized the significance of OVM and oceanography in larval transport mechanisms and recruitment processes in palinurid species. The importance of vertical behavior has been emphasized for transport success of *P. argus* to nurseries in the Caribbean Sea (Butler et al. 2011). As proposed by Sekiguchi & Inoue (2002), *P. japonicus* is likely to utilize the circulation in the western North Pacific. However, the roles of vertical behavior have yet to be clarified in regard to utilization of ocean circulation. For Japanese eels *Anguilla japonica*, Kimura et al. (1994) hypothesized that the vertical migration of leptocephali is a key to successful larval transport from the North Equatorial Current to the Kuroshio. Little information is available on how the vertical behavior of teleplanic larvae is related to their utilization of oceanographic features and how this facilitates their open-ocean migration. Thus, we simulated transport of *P. japonicus* phyllosoma larvae using a modeling approach and investigated the mechanisms for their successful migration. In the present study, we aimed to clarify (1) the effect of the vertical behavior of *P. japonicus* larvae on transport success, (2) migration pathways of larvae, and (3) mechanisms that enable larvae to approach adult habitats before metamorphosing into pueruli. Using *P. japonicus* as a model species, this study contributes to our understanding of the roles of vertical behavior in open-ocean migration of teleplanic larvae.

## MATERIALS AND METHODS

### Larval transport simulations

Larval transport simulations were performed using the FRA-JCOPE2.1 (1993–2013) reanalysis data and an individual-based model. During this data period, the Kuroshio mainly took non-large-meander paths, although it took large-meander paths from July 2004 to August 2005 (Japan Meteorological Agency, [www.data.jma.go.jp/kaiyou/data/shindan/b\\_2/kuroshio\\_stream/kuroshio\\_stream.html](http://www.data.jma.go.jp/kaiyou/data/shindan/b_2/kuroshio_stream/kuroshio_stream.html)). The reanalysis data set is from the JCOPE2 ocean forecast system, which is based on the Princeton Ocean Model with generalized sigma coordinates, and driven by NCEP/NCAR (National Centers for Environmental Prediction/National Center for Atmospheric Research) reanalysis data (Miyazawa et al. 2009, 2010). From this system with assimilation of satellite and *in situ* data, the reanalysis data were created to describe the oceanic variability associated with the Kuroshio–Kuroshio Extension, the Oyashio, and the mesoscale eddies in the western North Pacific (Miyazawa et al. 2009). *In situ* data from the World Ocean Database 2009 and from Japanese coasts provided by the Fishery Research Agency of Japan (FRA) are also assimilated for the generation of the FRA-JCOPE2 reanalysis data (Soeyanto et al. 2014). The reanalysis data provide daily mean data of east–west and north–south

current velocities, sea surface height, potential temperature, and salinity with a horizontal resolution of  $1/12^\circ$  and a vertical resolution of 47 sigma levels. The model assimilates the *in situ* data with the 3DVAR assimilation scheme using temperature–salinity coupling empirical orthogonal function (EOF) modes, and the model reproduces enhanced Kuroshio front (i.e. the front between the Kuroshio and the coastal water) variations and phenomena consistent with observations (Miyazawa et al. 2010). Miyazawa et al. (2008) demonstrated that their reanalysis data successfully simulated a large meander formation of the Kuroshio. From the reanalysis data, the east–west and north–south components of current velocity and water temperature in the region around Japan ( $115\text{--}160^\circ\text{E}$ ,  $15\text{--}40^\circ\text{N}$ ) were used, and the vertical layers were adjusted to horizontally constant thicknesses (i.e. z-layers) by linear interpolation for larval transport simulations.

Larval transport was simulated using an individual-based particle-tracking model. Transport of simulated phyllosoma larvae (i.e. particles) was calculated using the current velocities from the above-mentioned reanalysis data and a 3-dimensional advection-diffusion scheme (Kim et al. 2007). The coefficient for the horizontal diffusivity of particles was set at  $100\text{ m}^2\text{ s}^{-1}$ . Positions of particles were calculated with a time step of 900 s. Particles were released in the range of the adult distribution

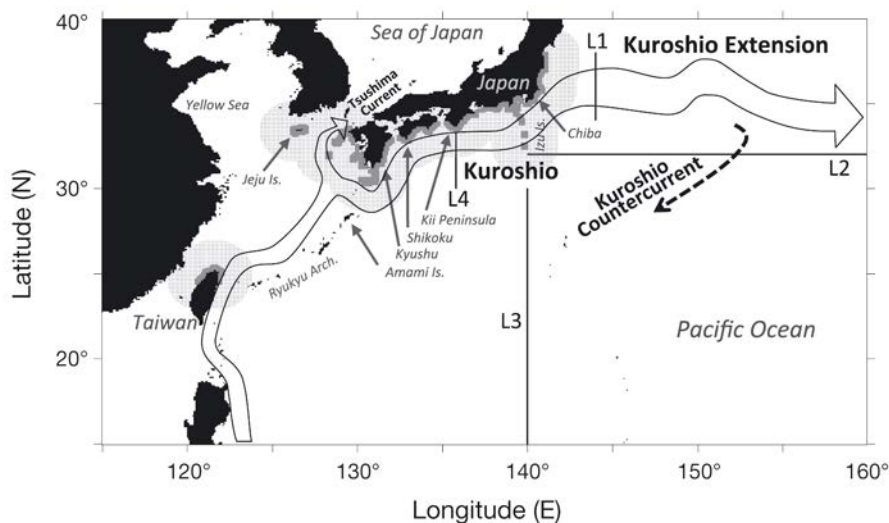


Fig. 1. Range of the model domain with currents in the western North Pacific. Land is shown in black; seas and locations are in *italics*; currents (**bold**) are indicated by curved arrows; particle release sites are in dark gray; and areas for transport success are crosshatched. Straight lines indicate Line 1 (L1:  $34\text{--}38^\circ\text{N}$ ,  $144^\circ\text{E}$ ), L2 ( $32^\circ\text{N}$ ,  $140\text{--}160^\circ\text{E}$ ), L3 ( $15\text{--}30^\circ\text{N}$ ,  $140^\circ\text{E}$ ), and L4 ( $30\text{--}33.5^\circ\text{N}$ ,  $135.8^\circ\text{E}$ ). The number of particles that crossed these lines during the simulation periods was counted for quantitative analysis of transport. Southward larval detrainment from the Kuroshio Extension (KE) was estimated based on particles that crossed both L1 and L2. Southwestward transport in the recirculation region of the Kuroshio and KE was estimated based on particles that crossed both L2 and L3. To find the main migration pathways of phyllosoma larvae, successfully transported particles that crossed L1, and particles that crossed L4 without crossing L1, were counted

described by Sekiguchi & Inoue (2002) (Fig. 1), except for Amami Island, where at least 90 % of spiny lobster species are not *Panulirus japonicus* (Sekiguchi 1997). Within this distribution range, the northern limit of the distribution along the Pacific coast is Chiba Prefecture (Fig. 1). However, Fukushima and Ibaraki Prefectures, located north of Chiba Prefecture, were additionally included for particle release because catches of adults in these prefectures have recently been increasing. The release sites consisted of grid cells ( $1/12^\circ \times 1/12^\circ$ ) next to land since *P. japonicus* inhabits shallow waters, and particles were released with  $1/60^\circ$  intervals in each grid cell (except its edges) within the release sites (25 particles per grid cell). This number of released particles was considered sufficient since the transport success and mortality (both arcsine-square-root transformed) of vertical behavior type (VBT) 1 did not significantly change when the number of released particles was increased 5-fold (paired-samples *t*-test,  $p = 0.889$  for transport success and  $0.353$  for mortality; transport success and mortality are discussed in this sub-section and 'Statistical analysis', and VBT1 is discussed in this sub-section). The number of released particles in each grid cell was fixed due to limited knowledge of spatial differences in adult density. Egg incubation by female adults and appearances of newly hatched phyllosoma larvae in coastal waters mainly take place from June to August (Harada 1957, Fushimi 1978). Therefore, particles were released on the first days of these 3 months between 1993 and 2012. In total, 38 700 particles were released in each year, and particles were tracked up to October in the year following particle release (i.e. the end of recruitment period: see below for details). Particles that were transported onto land were returned back to the previous position.

Phyllosoma larvae of spiny lobsters exhibit phototaxis (Ritz 1972b, Matsuda et al. 2006, Butler et al. 2011) and distribute in the shallower layer in early stages, in contrast to the deeper distribution in late stages (Chittleborough & Thomas 1969, Lesser 1978, Rimmer & Phillips 1979, Bradford et al. 2005, Butler et al. 2011). Newly hatched phyllosoma larvae of *P. japonicus* show positive phototaxis (Saisho 1966, Matsuda & Takenouchi 2006) and appear near the sea surface (Harada 1957). Early-stage phyllosoma larvae of this species mainly distribute in the water column shallower than 80 m during both day and night, and the center of distribution of middle-stage larvae tends to be less than 50 m during the night and 50–100 m during the day (AFFRC 2010), indicating the start of diel vertical migration (DVM) from the middle stages. In order to compare the effects of

Table 1. Particle depths of each vertical behavior type (VBT) and period (Period 1: up to 90 d; Period 2: 91–180 d; Period 3: 181 d or later following release) in larval transport simulations (D: dark period, i.e. first and fourth quarters of the day, L: light period, remainder of the day)

VBT	Particle depth (m)		
	Period 1	Period 2	Period 3
1	1	1	1
2	50	50	50
3	100	100	100
4	D: 25, L: 75	D: 25, L: 75	D: 25, L: 75
5	1	D: 25, L: 75	D: 25, L: 75
6	1	D: 25, L: 75	D: 25, L: 100
7	40	D: 25, L: 75	D: 25, L: 75
8	40	D: 25, L: 75	D: 25, L: 100
9	1–40 <sup>a</sup>	D: 25, L: 75	D: 25, L: 75
10	1–40 <sup>a</sup>	D: 25, L: 75	D: 25, L: 100

<sup>a</sup>Depth was set to linearly increase with time

different vertical behaviors of larvae on transport success and migration pathways, simulations with 10 different VBTs were performed (Table 1).

In VBTs 1, 2, and 3, the depths of particles were fixed at 1, 50, and 100 m deep, respectively. In addition to these fixed depth runs, DVM was simulated by alternatively moving particles to a depth of 25 m (dark period: first and fourth quarters of the day) and 75 m (light period: rest of the day; VBT 4). These depths (25 and 75 m) were determined based on the vertical distribution of middle-stage larvae during the night (<50 m) and day (50–100 m) in the natural environment mentioned above.

For ontogenetically changing vertical behavior of larvae, simulations were also performed by setting particles at a depth of 1 m for the first 3 mo (up to 90 d), and changing the depth to 25 m (dark) and 75 m (light) for the rest of the simulation period (VBT 5), or 1 m for the first 3 mo, 25 m (dark) and 75 m (light) for the following 3 mo, and 25 m (dark) and 100 m (light) for the rest of the simulation periods (VBT 6). In these cases, particles were fixed at 1 m deep for the first 3 mo because larvae show positive phototaxis up to 5 mm body length (BL; Matsuda & Takenouchi 2006), which corresponds with the BL of stage V in coastal areas, i.e. about 3 mo old (Yoshimura et al. 2009, AFFRC 2010, Hamasaki et al. 2012). However, early-stage phyllosoma larvae reportedly distribute above 80 m deep in the field (AFFRC 2010). Thus, simulations with a vertical distribution at 40 m deep for the first 3 mo (VBTs 7 and 8) were also performed. The length of the second period was also set to 3 mo, since stage VI larvae distribute at depths of <50 m (dark) and 50–100 m (light) in the autumn (AFFRC 2010), which is in the range of ap-

proximately 4 to 6 mo from the earliest release of particles (June). The depth during the dark period in and after the second 3 mo period was kept constant because the depth of the night distribution may not ontogenetically change between these periods (Ritz 1972a), although the day distribution may become deeper (Rimmer & Phillips 1979, Bradford et al. 2005). Positive phototaxis of phyllosoma larvae may gradually disappear in the early stage (Matsuda & Takenouchi 2006), and therefore linearly deepening behavior (1–40 m deep in the first 3 mo) was also simulated (VBTs 9 and 10). In cases where the depth of the particle was greater than that of the bottom, particle was set at 1 m above the bottom.

The sinking speed of phyllosoma larvae of *P. japonicus* is in the range of approximately 2 to 10 mm s<sup>-1</sup>, increasing with growth (Hamasaki et al. 2012). Rimmer & Phillips (1979) estimated the rates of vertical movement of *P. cygnus* larvae during diurnal vertical migration and found that the ascending and descending rates did not differ greatly. Thus, the vertical swimming speed of particles (both ascending and descending) was linearly increased from 2 to 10 mm s<sup>-1</sup> up to 9 mo (average number of months between particle release and the month before the recruitment period; 270 d) from particle release.

The areas for transport success of larvae were estimated based on the swimming speed (14.5 cm s<sup>-1</sup>; Murakami 2011) and the length of the puerulus stage (approximately 2 wk; Kittaka & Kimura 1989, Yamakawa et al. 1989, Sekine et al. 2000). This information allowed us to estimate the maximum distance pueruli can swim, which is about 175.4 km, assuming there is no influence of water flow. This swimming distance was consistent with the distance from shore of the location where *P. cygnus* metamorphose into pueruli (161 km; Ritz 1972a) and was within the estimated swimming range of *Jasus edwardsii* pueruli based on their lipid content (200 km; Jeffs et al. 2001). Thus, we assumed that grid cells within the radius of the above-mentioned distance from particle release grid cells were the transport success areas, except those areas in the Sea of Japan that are unlikely to be inhabited by Japanese spiny lobsters (Sekiguchi 1988a,b). The larval duration of *P. japonicus* phyllosoma larvae in rearing environments can vary from about 6 mo (Murakami 2011) to 14 mo (Sekine et al. 2000), and recruitment of pueruli takes place from April to October (Fushimi 1978). Taking these factors into account, only particles that reached transport success areas (Fig. 1) between April and October in the year following particle release (i.e. recruitment period) were considered to have been successfully transported.

Phyllosoma larvae can be found in the natural environment in water temperature between approximately 19 and 30°C (AFFRC 2010), and they are also reared inside this range (Kittaka & Kimura 1989, Yamakawa et al. 1989, Matsuda & Yamakawa 1997, Matsuda 2006). Larvae may survive for a short period of time even in water temperature outside this range (12–15 h at 15°C and 12 h at 35°C for early-stage larvae; Saisho 1966). Therefore, particles that were exposed to water temperature outside this window (19–30°C) for longer than 12 h were considered dead (recorded as mortalities).

The predicted distribution of each VBT of phyllosoma larvae during their migration was calculated as follows. The number of particles in each grid cell, which was vertically integrated, was added daily for the simulation periods. For normalization, the number in the grid cell was then divided by the total of the number of particles added daily inside the model domain. Additionally, the same method was performed by counting only the particles which were successfully transported. In this case, the number of particles were added daily until successfully transported. The same was done for the visualization of the monthly distribution. These predicted distributions are hereafter referred to as relative distributions.

### Statistical analysis

Transport success of each VBT in every simulation year was obtained by dividing the number of particles transported into the transport success areas during the recruitment period by the number of released particles (38 700 particles each year). Mortality was also calculated by dividing the number of particles that died following >12 h exposure to water temperature outside the 19–30°C window by the number of released particles. Particles that died due to water temperature after reaching the transport success areas during the recruitment period were not included as mortalities.

For quantitative analysis of transport, the number of particles that crossed Lines 1, 2, and 3 (L1, L2, and L3) during the simulation periods (i.e. from particle release to the end of the recruitment period) was counted (see Fig. 1 for locations of these lines). These lines were placed based on the hydrodynamic field in the surface layer, which was obtained by averaging the current data from the FRA-JCOPE2.1 reanalysis data for the entire simulation period (June 1993 to October 2013). In this analysis, the simulation results



without mortality (i.e. particles not dying due to water temperature) were used in order to analyze the transport of particles only. For estimating detrainment of particles from the Kuroshio Extension (KE), the percentages of the particles that crossed L2 southward among those that previously passed L1 eastward (i.e. detrainment from the KE after being entrained by it) were calculated. The percentages of the particles that crossed L3 westward among those that previously crossed L2 southward were also calculated in order to estimate southwestward transport in the recirculation region of the Kuroshio and KE (hereafter, recirculation region).

Transport success, mortality, and line crossing of particles were compared among VBTs using 1-way repeated measures ANOVA with a Bonferroni post hoc test. Before all statistical analyses, arcsine-square-root transformation was performed (Sokal & Rohlf 2009). In addition, normality and sphericity were tested using Shapiro-Wilk and Mauchly's tests, respectively. For all analyses, the assumption of normality was met, but the assumption of sphericity was violated. Therefore, a Greenhouse-Geisser adjustment of degrees of freedom was applied to all analyses. No outliers were detected in the data when assessed by inspecting a boxplot.

To find the migration pathways of phyllosoma larvae that would successfully approach adult habitats, the percentage of successfully transported particles that passed L1 eastward (passing the KE before

transport success) was calculated for each VBT. The same was done for the successfully transported particles that passed L4 (Fig. 1) eastward but did not pass L1 eastward, to investigate the percentage of successfully transported particles that directly detrain from the Kuroshio (between the area off Kii Peninsula and KE) into the recirculation region. The mean difference between these 2 indices was tested for each VBT using the paired-samples *t*-test after performing arcsine-square-root transformation. The test was performed only when the differences between these two met the assumptions of normal distribution, assessed by a Shapiro-Wilk test, and no outliers, assessed by inspecting a boxplot. For all statistical analyses, we used IBM SPSS Statistics Version 22.

## RESULTS

### Larval migration pathways

Regardless of VBTs, the relative distribution of particles showed frequent passage in the regions along the Kuroshio and KE (Fig. 2), indicating that particles tended to be entrained and subsequently transported eastward by these currents. The relative distribution of VBT 3 appeared to differ due to different hydrodynamics (e.g. northward transport from Taiwan) and high mortality in the deeper layer (see 'Transport success and mortality' below).

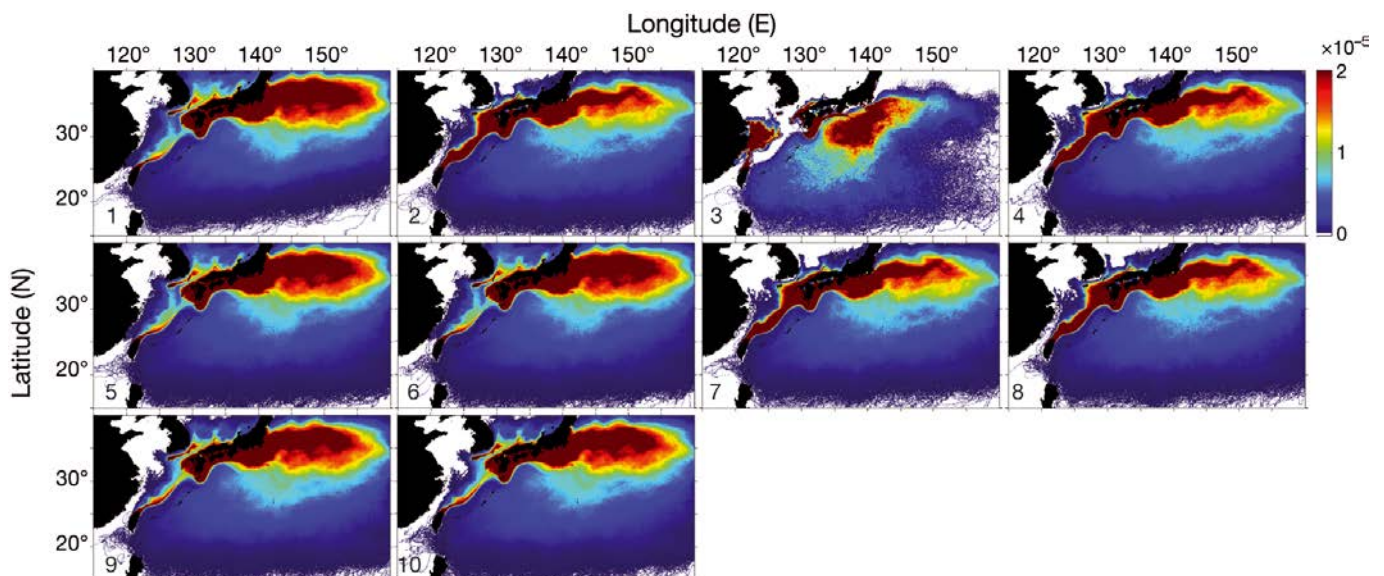


Fig. 2. Relative distribution of all particles between the release and the end of the simulation periods for 1993–2012 simulations of 10 vertical behavior types (VBTs, numbers in bottom left corners of panels). Colors indicate the number of particles added daily within a  $1/12^\circ \times 1/12^\circ$  grid cell divided by the total number of particles added daily within the model domain. Land is in black; areas where no particles passed during the simulation are white

The relative distribution of successfully transported particles indicated the distribution of phyllosoma larvae along successful migration pathways (Fig. 3). Regardless of VBTs, the results showed an oval-shaped distribution, formed by the Kuroshio, KE, and KCC, although the distribution of VBT 3 did not extend eastward as far as the other VBTs. The relative distribution was mainly found between 120 and 155°E, indicating that phyllosoma larvae that start southward transport before 155°E are subsequently transported southwestward by the KCC.

For further clarification of the migration pathways of phyllosoma larvae, the monthly relative distribution of all particles (Fig. 4) and successfully transported particles (Fig. 5) of the most successful VBT with vertical migration (VBT 9; see ‘Transport success and mortality’ for details) were visualized. The relative distribution of all particles (Fig. 4) shows that particles were distributed near the release sites after being discharged from these sites and were then transported mainly along the Kuroshio and KE. Particles in the KE were subsequently detrained southward from the current. The relative distribution shifted southwestward as time passed. The relative distribution of successfully transported particles differed from that of all particles in the transport pathways, and in the first few months showed transport along the Kuroshio and KE, a southward shift from the KE, and direct transport from the Kuroshio and Izu Islands into the recirculation region (Fig. 5). From then on, the southern edge of the distribution stretched southwestward (toward the southeast of Taiwan), and the eastern edge of the high concentration patch also shifted westward until particles disap-

peared due to their transport success. In comparison with the relative distributions of all particles (Fig. 4), those of successfully transported particles (Fig. 5) more rapidly shifted southward from the KE and southwestward in the KCC, indicating that transport success requires earlier transport toward the southwestern part of the recirculation region.

The mean percentages of successfully transported particles of VBTs were over 40 % for those that crossed L1, except VBT3, and lower than 40 % for those that crossed L4 but did not cross L1 (Fig. 6). For VBTs 1, 2, 5, 6, 9, and 10, the differences between these 2 indices met the assumptions of a paired-samples *t*-test. The means were significantly higher in the percentages of successfully transported particles that crossed L1 in VBTs 2, 9, and 10 ( $p < 0.05$ ). These results indicate that the KE could be the main pathway for successfully transported particles before entering the recirculation region, although particles also detrained from the Kuroshio into the recirculation region. Successfully transported particles appeared to mainly detrain from the KE at the meander trough (Fig. 7).

### Transport success and mortality

Transport success was significantly different among VBTs ( $F_{1,694, 32.186} = 59.664$ ,  $p < 0.001$ ; Table 2). The transport success of VBTs 1, 5, 6, 9, and 10 (means 0.9–1.1 %) did not differ significantly among them ( $p > 0.05$ ); however, they were significantly higher than those of the other VBTs (means 0.1–0.5 %,  $p < 0.01$ ; Fig. 8a). Thus, the VBTs that started transport at

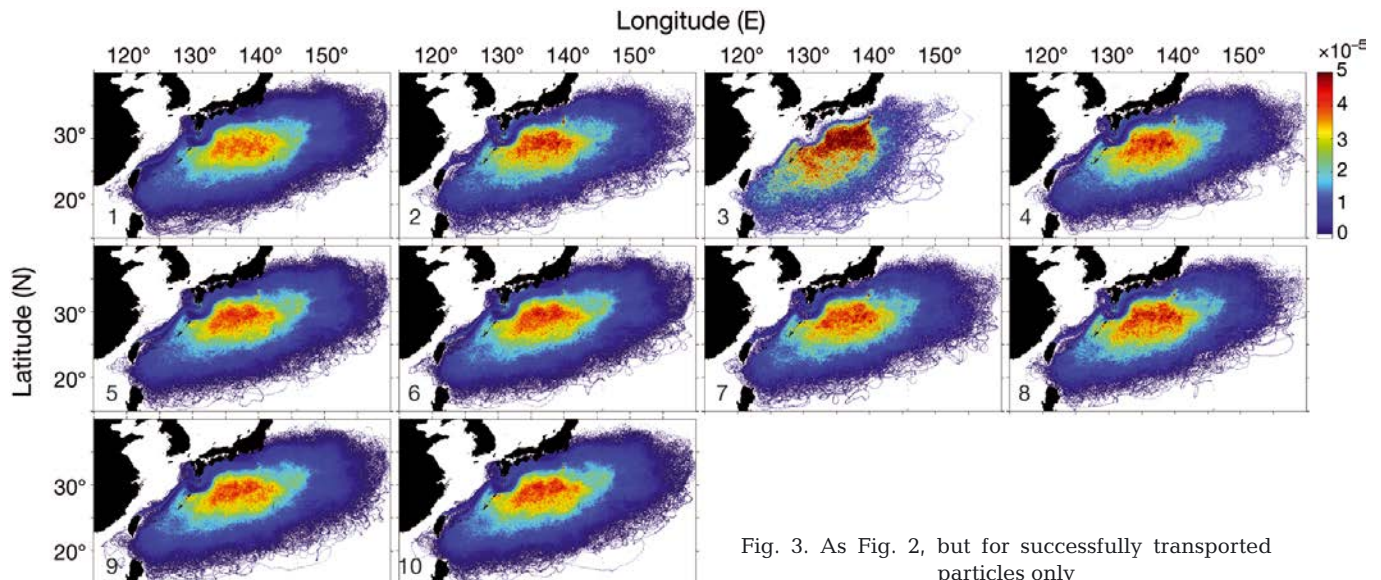


Fig. 3. As Fig. 2, but for successfully transported particles only



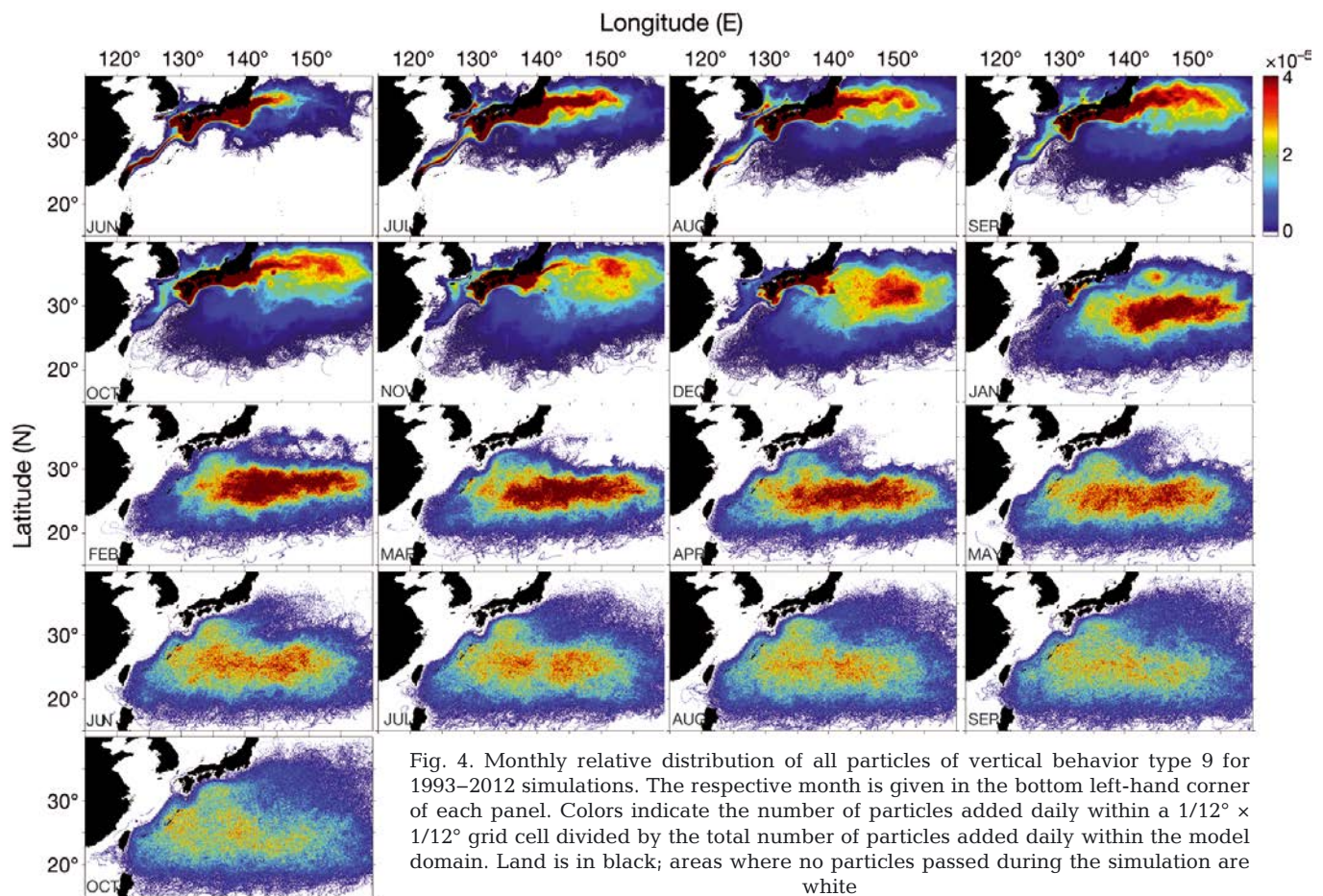


Fig. 4. Monthly relative distribution of all particles of vertical behavior type 9 for 1993–2012 simulations. The respective month is given in the bottom left-hand corner of each panel. Colors indicate the number of particles added daily within a  $1/12^\circ \times 1/12^\circ$  grid cell divided by the total number of particles added daily within the model domain. Land is in black; areas where no particles passed during the simulation are white

the shallow depth (1 m) had significantly higher transport success than those that started at greater depths ( $\geq 25$  m).

Mortality due to water temperature was high (means 65.4–99.8 %; Fig. 8b) and differed significantly among VBTs ( $F_{1.667, 31.677} = 731.609$ ,  $p < 0.001$ ; Table 2). Mortality was mainly caused by the low water temperature (means 97.5–99.9 % of mortalities). Transport success appeared to reflect mortality (i.e. low transport success reflected high mortality). However, there were significant differences in mortality among the behavior types with high transport success (VBTs 1, 5, 6, 9, and 10), although transport success was not significantly different. To further investigate the roles of vertical behavior in migration, transport of particles was statistically compared among VBTs.

Percentages of the particles that passed L2 after L1 during the simulation period were significantly different among VBTs ( $F_{1.168, 22.200} = 8.389$ ,  $p < 0.01$ ; Table 2). Percentages of the particles for VBTs that started at 1 m depth and moved deeper as they developed (VBTs 5, 6, 9, and 10; hereafter, referred to as VBTs with OVM starting near the surface) were

significantly higher than for VBT 1 ( $p < 0.01$ ), indicating greater detrainment from the KE by OVM (Fig. 9a). Percentages of particles that crossed L3 after L2 were also significantly different among VBTs ( $F_{1.624, 30.852} = 25.106$ ,  $p < 0.001$ ; Table 2). Percentages of particles for the VBTs with OVM starting near the surface were significantly higher than for VBT 1 ( $p < 0.001$ ), indicating facilitated southwestward transport in the recirculation region by OVM (Fig. 9b). These results suggest the existence of mechanisms by which OVM can facilitate the detrainment of phyllosoma larvae from the KE and their southwestward transport (toward adult habitats) in the recirculation region.

#### Oceanographic characteristics of the western North Pacific

The temporally averaged hydrodynamic field showed the formation of anticyclonic circulation off Shikoku (Fig. 10). The location of this circulation pattern corresponded to a high concentration in the rel-



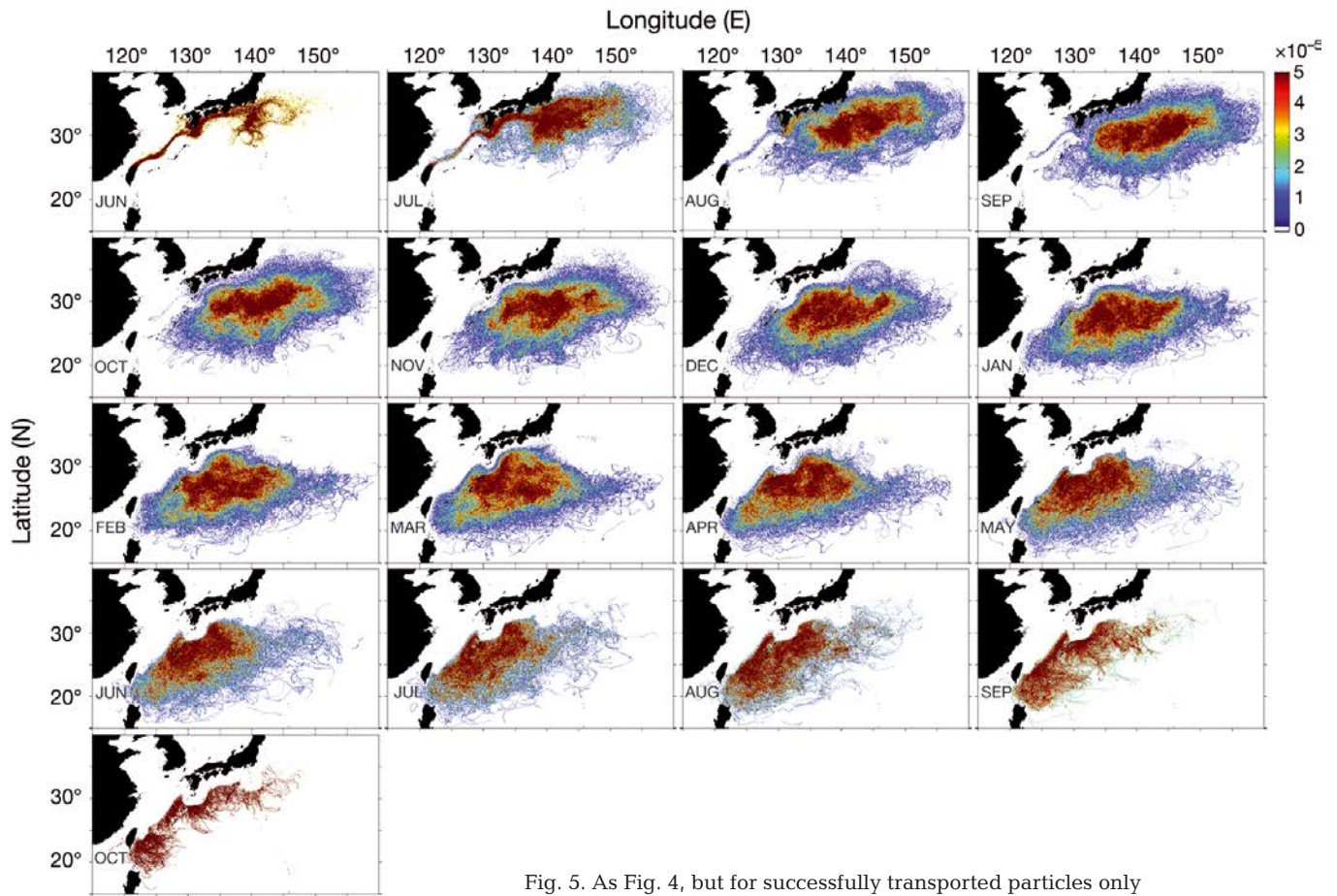


Fig. 5. As Fig. 4, but for successfully transported particles only

ative distribution of successfully transported particles (Fig. 3). In the recirculation region, southwestward flows in mid- and low latitude areas of the model domain became increasingly prominent at greater depths (Fig. 10), indicating boosted southwestward

transport of particles at greater depths. There was a wider distribution of southwestward flows at the surface layer during winter than in the other seasons (Fig. 11). However, this distribution became wider at greater depths in all seasons, and therefore the

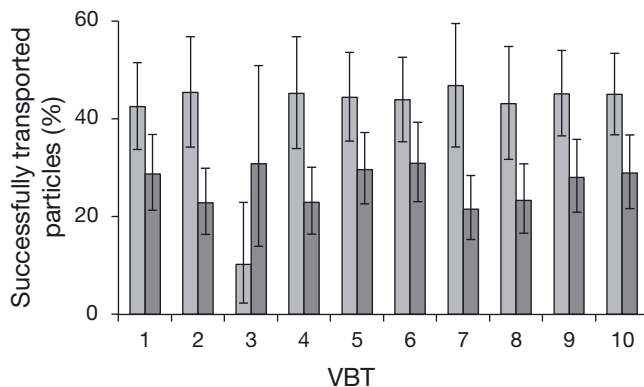


Fig. 6. Percentages of successfully transported particles (back-transformed) that crossed L1 (light gray; see Fig. 1), and that crossed L4 without crossing L1 (dark gray) of 10 vertical behavior types (VBTs) from 1993–2012 simulations. Error bars indicate 95 % confidence intervals

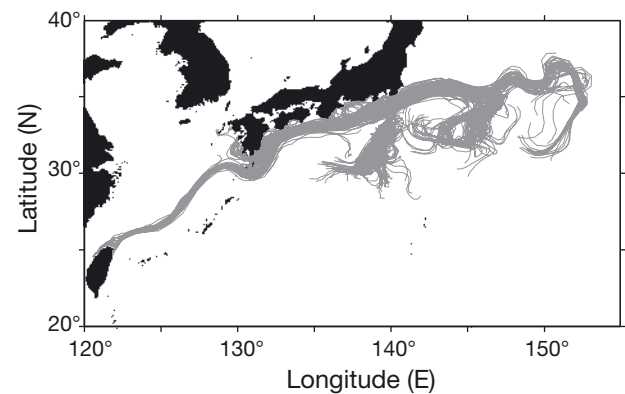


Fig. 7. Example of transport pathways of successfully transported particles up to 1 mo after release. The gray lines indicate the pathways of vertical behavior type (VBT) 9 (the most successful VBT with vertical migration) particles that were released in June–August 2010. Land is shown in black

Table 2. Results of 1-way repeated measures ANOVA on arcsine-square-root-transformed transport success, mortality, percentages of particles that passed Line 2 (L2; see Fig. 1) after L1, and percentages of particles that passed L3 after L2, testing the effects of different vertical behavior types (VBTs). Greenhouse-Geisser adjustment of degrees of freedom was applied. Results were considered significant at  $p < 0.05$

	Source	df	MS	F	p
Transport success	VBTs	1.694	0.053	59.664	<0.001
	Error	32.186	0.001		
Mortality	VBTs	1.667	3.460	731.609	<0.001
	Error	31.677	0.005		
Particles passing L2 after L1	VBTs	1.168	0.058	8.389	<0.01
	Error	22.200	0.007		
Particles passing L3 after L2	VBTs	1.624	0.047	25.106	<0.001
	Error	30.852	0.002		

facilitated southwestward transport at deeper layers is not seasonal. The distribution of the low water temperature in the model domain started to shift southward from the north in October (Fig. 12). From February to April, the 19°C isotherm (lower limit of the temperature window for particles) shifted southward in the eastern part of the model domain, whereas it remained relatively high in latitude near

the southern coast of Japan due to the warm water of the Kuroshio. Therefore, mortality due to the seasonal change in the distribution of water temperature as well as transport caused the southwestward shift of the relative distribution of particles (Figs. 4 & 5).

## DISCUSSION

In the present study, larval transport of *Panulirus japonicus* was investigated using an individual-based model with different vertical behaviors and mortality due to water temperature. Our findings suggest a potential migration pathway of phyllosoma larvae, which has not been proposed previously, and the vertical behavior of larvae can affect their open-ocean migration by interacting with oceanographic features of the western North Pacific.

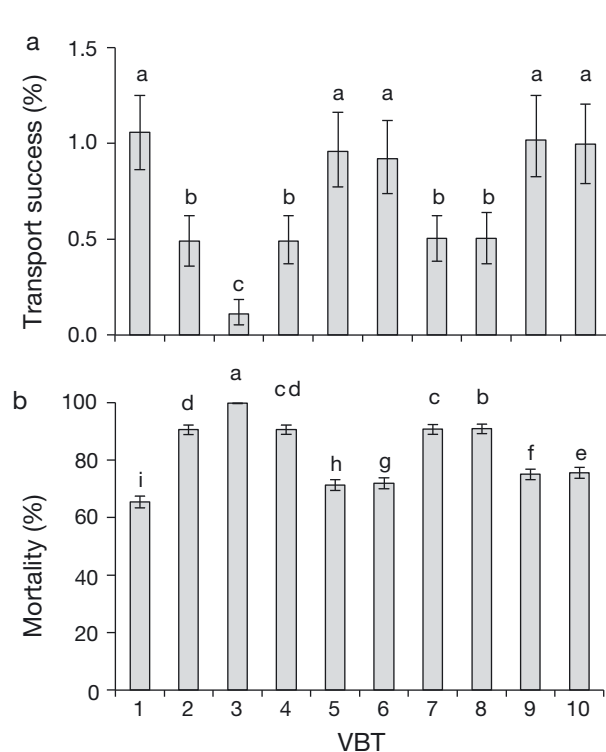


Fig. 8. (a) Transport success and (b) mortality (back-transformed) for 10 vertical behavior types (VBTs) from 1993–2012 simulations (for definitions of transport success and mortality, see ‘Statistical analysis’ in ‘Materials and methods’). Error bars indicate 95% confidence intervals, and different letters indicate significant differences (1-way repeated measures ANOVA with Bonferroni post hoc test)

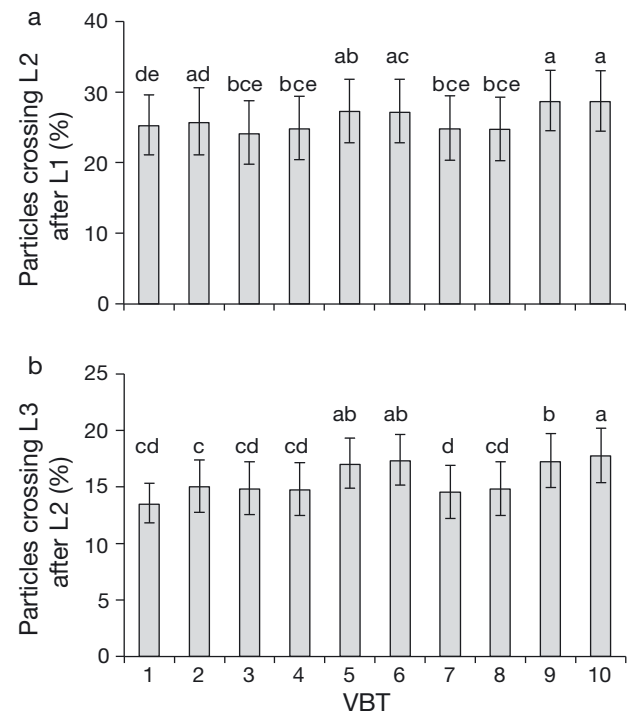


Fig. 9. (a) Percentages of particles that passed L2 (see Fig. 1) southward among those that previously passed L1 eastward, and (b) percentages of particles that passed L3 westward among those that previously passed L2 southward, for 10 vertical behavior types (VBTs) from 1993–2012 simulations. Percentages are back-transformed. Error bars indicate 95% confidence intervals, and different letters indicate significant differences ( $p < 0.05$ ; 1-way repeated measures ANOVA with Bonferroni post hoc test)

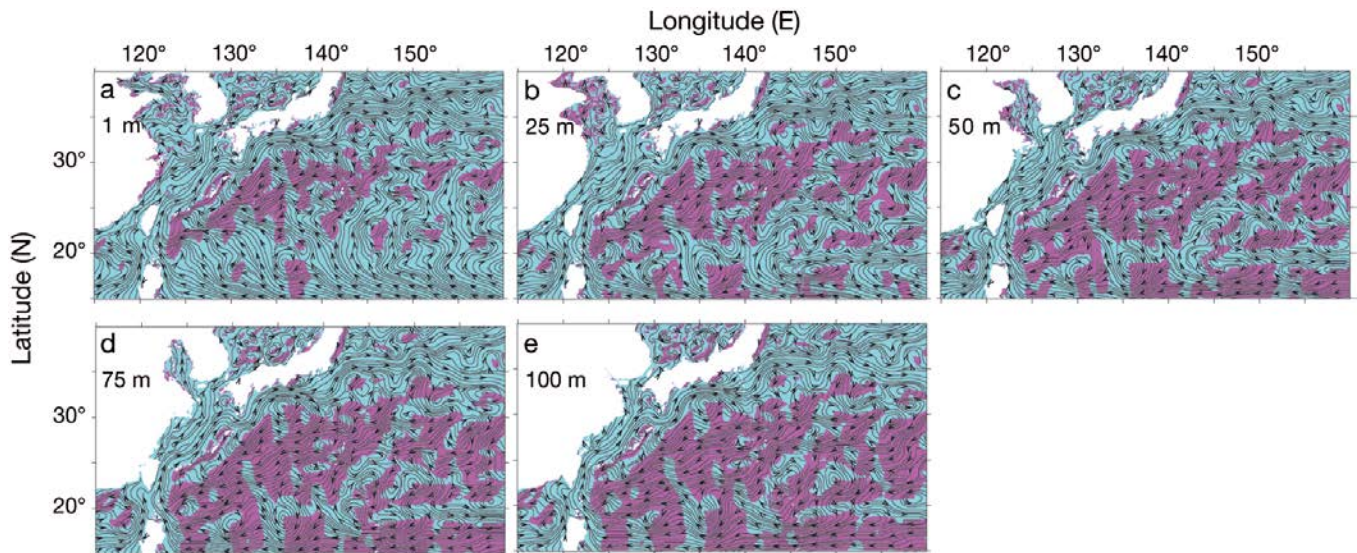


Fig. 10. Vertically changing directions of horizontal currents, averaged for the entire simulation period (June 1993–October 2013). Each panel shows the mean hydrodynamic environment at layers corresponding to the vertical positions (1, 25, 50, 75, 100 m depth) of particles during the simulations. Black lines are streamlines of currents; arrowheads indicate current directions. The distribution of currents whose directions are within  $\pm 45^\circ$  from southwest (i.e.  $180\text{--}270^\circ$  from north) is indicated by magenta; currents in the other directions are indicated by cyan. Land is shown in white

### Migration pathways of phyllosoma larvae

The model results suggest that larvae hatched in coastal areas are transported into the Kuroshio. After entrainment into this current, the main migration pathway of larvae is apparently connected to the KE, and larvae are subsequently transported eastward. This is consistent with Chow et al. (2011) who found *P. japonicus* larvae in the eastern reach of the KE ( $30^\circ 59' \text{--} 34^\circ 9' \text{N}$ ,  $165^\circ \text{E}$ ). The pathways indicated by the relative distribution of successfully transported particles (Fig. 3) were strikingly similar to the route proposed by Sekiguchi & Inoue (2002). The main difference was that our model results suggested that the KE is part of the migration pathways and that the larvae are detrained from this current, whereas Sekiguchi & Inoue (2002) assumed that larvae only leave the Kuroshio and are directly transported into the KCC. Furthermore, our results suggested that detrainment from the KE mainly takes place before reaching  $155^\circ \text{E}$ , which is the origin of the KCC (Hasunuma & Yoshida 1978).

### Transport mechanisms for the successful migration of phyllosoma larvae

Transport success was not significantly different between the behaviors of particles that stayed near the surface and those of particles which exhibited

OVM but started near the surface, although the latter showed significantly higher mortality. This result suggests that, in terms of transport alone, the OVM that deepens the vertical position of larvae from the surface positively affects larval transport. Furthermore, staying near the surface for the entire larval period is not a realistic behavior for phyllosoma larvae, and transport success in that case would be much lower than that shown by our results because zooplankton are thought to exhibit DVM for evading predation (Lampert 1989). Thus, OVM of *P. japonicus* larvae appears to be the mechanism that increases transport success.

Transport from the spawning grounds in coastal areas to the Kuroshio, or the offshore edge of this western boundary current, may be facilitated by the shallow distribution of larvae. This allows them to use the greater current speed near the surface and the eastward Ekman transport ( $45^\circ$  clockwise rotation from the wind direction at the surface) due to the summer southwesterly wind over East Asia (Zhao et al. 2007) that coincides with the spawning season of *P. japonicus*. It resembles the wind-induced offshore transport mechanism of early-stage phyllosoma larvae of *P. cygnus* in western Australia (Chittleborough & Thomas 1969, Rimmer & Phillips 1979, Feng et al. 2011). The deep position can cause mortality due to the low water temperature at depth, or slower transport to the Kuroshio. Particles that stayed in the coastal areas were killed by the low water tempera-



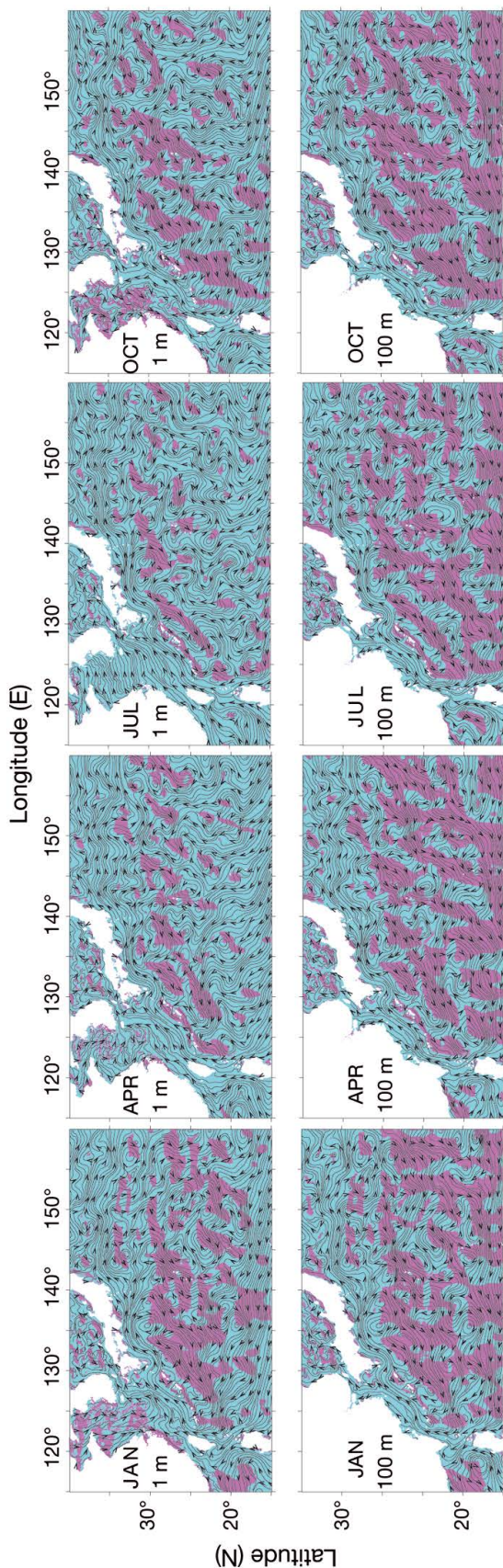


Fig. 11. Seasonal and vertical comparison of southward currents, averaged for January, April, July, and October in the simulation period. Upper and lower panels show the mean hydrodynamic environment at layers corresponding to the vertical positions of particles at 1 m and 100 m depths, respectively, during the simulations. See Fig. 10 for details

ture ( $<19^{\circ}\text{C}$ ) during winter as shown by the disappearance of particles in coastal areas (Fig. 4), and thus the delayed transport into the Kuroshio could be fatal to the larvae.

Detrainment of phyllosoma larvae from the KE to the recirculation region may be facilitated by OVM and cross-frontal exchange at a trough between 2 meanders of the KE. There are 2 quasi-stationary meanders in the KE (ridges at  $144^{\circ}$  and  $150^{\circ}$  E; Qiu 2002), and a trough is located between these ridges. Bower & Rossby (1989) proposed a cross-frontal fluid exchange induced by meanders of the Gulf Stream. Ito et al. (2000) suggested the cross-frontal flow of KE to be a possible mechanism for larval and juvenile fish to enter the mixed-water zone to the north of KE. The southward cross-frontal exchange also exists at the meander trough of the KE (Howe et al. 2009). In the Gulf Stream, the floats at shallower depth are retained in the stream for longer distances than the ones at greater depth (Bower & Rossby 1989). This may be the reason why OVM worked positively for southward detrainment. Sekiguchi & Inoue (2002) hypothesized that larvae transfer from the Kuroshio to the KCC. Although some phyllosoma larvae are likely to be transported directly from the Kuroshio or Izu Islands into the KCC, the synergistic effect between OVM and cross-frontal exchange at the meander trough may be the mechanism responsible for detaining phyllosoma larvae from the KE to the recirculation region, and consequently enhancing transport success.

Southwestward transport of phyllosoma larvae in the recirculation region may be facilitated by OVM and the beta spiral. The wider distribution of southwestward currents at the surface layer of the reanalysis data (FRA-JCOPE2.1) during winter may be due to Ekman transport, driven by the northwest wind prevailing over the study area during winter (Weng et al. 2009). However, the wider distribution of southwestward currents at greater depths was not limited to winter. Horizontal current vectors in subtropical gyres (where a downward vertical component of velocity can be expected) in the northern hemisphere are rotated clockwise with increasing depth by a property called the beta spiral (Stommel & Schott 1977, Schott & Stommel 1978). This property has been demonstrated in our study region (North Pacific) using an ocean general circulation model (Kubokawa & Inui 1999). Therefore, the hydrodynamic fields from the reanalysis data showed the wider distribution of southwestward currents at greater depths in the western North Pacific, possibly due to the beta spiral. For some marine species, OVM of lar-

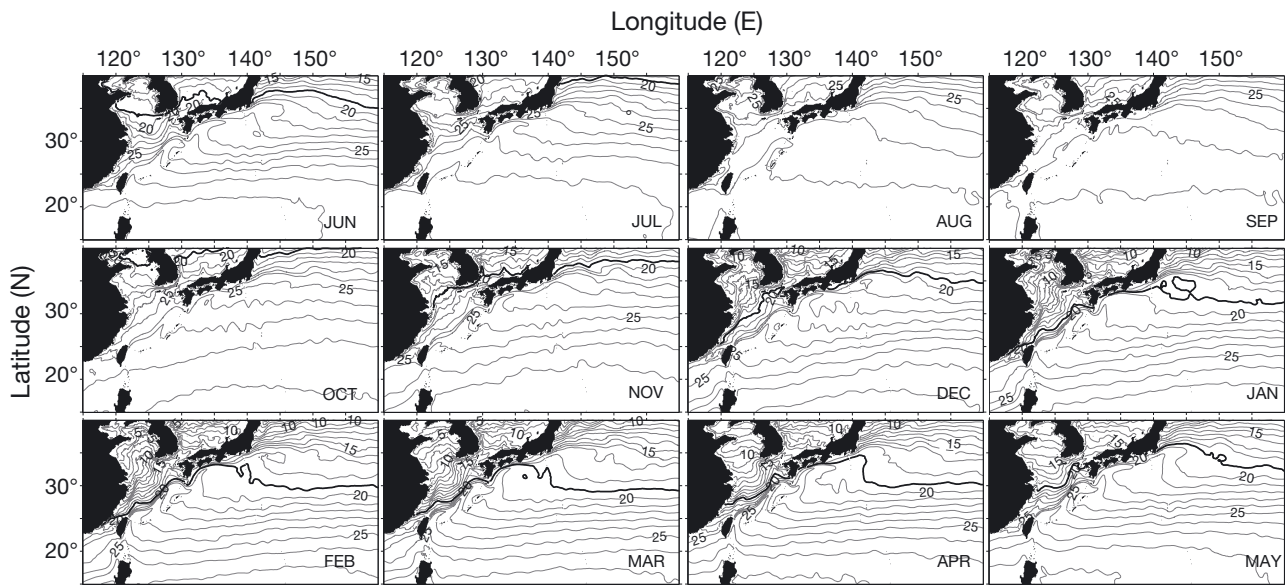


Fig. 12. Comparison of monthly distribution of water temperature at the surface layer (<5 m), averaged for the entire simulation period (June 1993–October 2013). Contour lines indicate the water temperature in 1°C intervals. Thick lines are 19°C contours, and numbers on the thin lines indicate the water temperature in 5°C intervals. Months are shown in the bottom right corners of the panels. Land is shown in black

vae can assist their retainment near, or return to, the natal habitats (e.g. Chittleborough & Thomas 1969, Cowen et al. 1993, Paris & Cowen 2004, Butler et al. 2011). In *P. japonicus*, OVM during the phyllosoma stage may help utilize the beta spiral for the southwestward migration (toward adult habitats) in the recirculation region. In addition, the wider distribution of the southwestward current at depth may help phyllosoma larvae avoid the low-temperature water, shifting from the north in winter.

### Study constraints

Incorporation of additional information from *in situ* data of phyllosoma larvae and ambient environment may improve our model. Unlike other modeled spiny lobster species such as *P. cygnus* (Griffin et al. 2001, Feng et al. 2011) and *P. argus* (Butler et al. 2011), little is known about the vertical behavior of phyllosoma larvae of Japanese spiny lobster *P. japonicus*. The vertical distribution of this species has been studied on a limited spatial scale (AFFRC 2010). Even in terms of horizontal coverage, larval distribution in the vicinity of the KE has not been sufficiently investigated. Both horizontal and vertical distributions of phyllosoma larvae need to be investigated to advance our understanding of larval migration mechanisms. Since the detailed density distributions of adults in nursery habitats are unknown, the numbers

of released particles in the present model were determined based on the numbers of grid cells next to coastlines in the known distribution of adults. In terms of interaction with other marine organisms, phyllosoma larvae of *Parribacus* sp. have been found in stomach contents of yellow fin albacore (Yoneyama & Takeda 1998). Since the present study was the first modeling study on larval transport of *P. japonicus*, the model was simplified for investigating the effect of vertical behavior on transport. Further incorporation of biological factors, such as adult distribution and predation on larvae, may improve the estimation of transport success and consequently allow us to predict the recruitment fluctuations.

### Future model application

The *P. japonicus* catch in the southern distribution of the species in Japan has declined (Yoshimura 2001, Inoue & Sekiguchi 2009), whereas that in the northern distribution has increased (Inoue & Sekiguchi 2009), potentially suggesting a northward shift of the distribution during the benthic period. This is similar to the southward distribution shift of rock lobsters *Jasus lalandii* in South Africa (Cockcroft et al. 2008), which has had an impact on the benthic community, including abalone *Haliotis midae* populations (Blamey et al. 2010). Since *P. japonicus* is a predator of abalone (Abe et al. 2013), its northward



distribution shift may impact the benthic community, including Ezo abalone *H. discus hannai* found off the Pacific coast of northern Japan (e.g. Miyake et al. 2011). The present stability of the catch of *P. japonicus* in Japan (Yoshimura 2001) may be altered by the northward shift in the distribution due to more likely transport of larvae into the region north of the KE and high mortality caused by the low water temperature there. This may lead to a decline in the population in the future, and marine reserves could be implemented as a protective measure. Larval transport simulations have been used for the evaluation of the effectiveness of reserves for benthic invertebrates in shoal waters (Miyake et al. 2009, 2010), and Lipcius et al. (2001) evaluated the effectiveness of reserve sites for *P. argus* in the Bahamas. The development of a population-dynamics model (Stockhausen et al. 2000, Stockhausen & Lipcius 2001) for *P. japonicus* may guide our decisions in fishery management and conservation in the future.

### Conclusion

The model results suggested the importance of OVM of phyllosoma larvae in open-ocean migration of *P. japonicus*. Possible mechanisms for larval transport of *P. japonicus* can be summarized as follows: (1) detrainment of phyllosoma larvae from the KE to the recirculation region is facilitated by OVM and cross-frontal exchange at the meander trough, and (2) southwestward transport toward adult habitats and avoidance of the low-temperature water shifting southward in winter are facilitated by OVM and the beta spiral. To our knowledge, this study is the first report on marine organisms that could utilize the beta spiral together with OVM for successful transport. We may conclude that 'meander trough detrainment' and 'beta spiral transport' are the mechanisms responsible for transporting phyllosoma larvae of *P. japonicus* near adult habitats before they metamorphose into pueruli (Fig. 13). These findings highlight the importance of vertical behavior for teleplanic larvae and their ontogenetic changes in utilization of oceanographic features in the open ocean. Our results were generally in agreement with the larval migration route of *P. japonicus* proposed by Sekiguchi & Inoue (2002). Phillips (1981) pointed out that

multiple mechanisms are involved in the larval transport of *P. cygnus*, and thus mechanisms that were not addressed in the present study may also be involved in the larval migration of *P. japonicus*. Surveys of the horizontal and vertical distribution of larvae based on the output of the present model study may provide stronger evidence for transport mechanisms of phyllosoma larvae of *P. japonicus*. The proposed mechanisms in the present study may not be limited to spiny lobster species in the western North Pacific. Numerous species disperse as teleplanic larvae, such as gastropods (Scheltema 1966, 1971), and, similar to *P. japonicus*, a number of spiny lobster species inhabit the continental shelf facing the open ocean (Lipcius & Eggleston 2000). The mechanisms may also be applicable to species that disperse as teleplanic larvae in the North Atlantic Ocean, since the cross-frontal exchange and beta spiral also exist there. Thus, these mechanisms may be utilized by larvae of a broad range of marine species with long pelagic larval durations.

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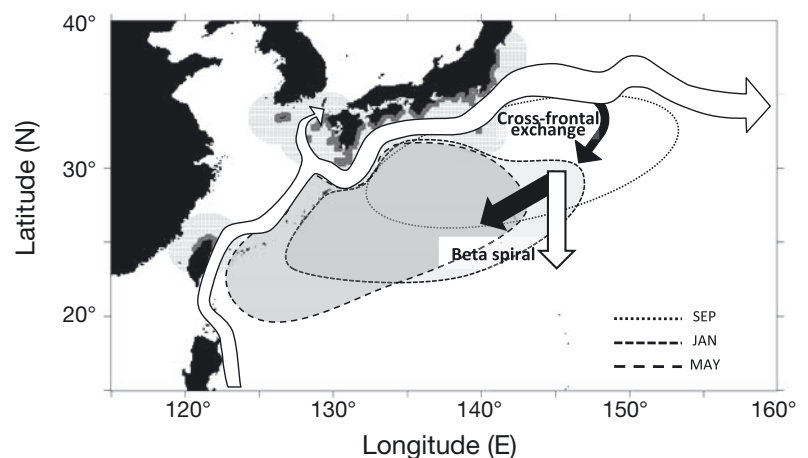


Fig. 13. Larval transport mechanisms of *Panulirus japonicus* in relation to vertical behavior. Arrows indicate directions of currents (white: surface; black: subsurface layer where phyllosoma larvae distribute). Ovals are based on the relative distributions of successfully transported particles of vertical behavior type 9 in September, January, and May (see Fig. 5), and indicate the southwestward shift of main larval distribution. Note that the distribution in May (within the recruitment period) does not overlap the transport success areas because particles that have reached those areas were not included. Black, dark gray, and crosshatched areas indicate land, particle release sites, and transport success areas, respectively



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