



# Numerical studies on snow crab (*Chionoecetes opilio*) larval survival and transport in the Sea of Japan

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## ABSTRACT

The snow crab *Chionoecetes opilio* is an important fishery species in Japan. Hydrodynamics are vital to the distribution, recruitment and settlement of crab larvae in nursery areas. In this study, we developed a survival and transport model of snow crab larvae to investigate the interannual variability in larval settlement in three fishing areas: west of Toyama (region A), west of Niigata (region B) and west of Hokkaido (region C). We found that the female crab stock abundance determined the modeled number of zoea in regions A and B, whereas water temperature played a major role in the initial number of zoea in region C. As for larval settlement, the ocean current impacted settlement in region B, and water temperature was vital to settlement in region C. Both female crab abundance and hydrodynamics contributed to variability in settlement in region A. The results revealed contrasting recruitment patterns in the three fishing areas. Self-recruitment was the primary form in regions A and C, whereas both self-recruitment and recruitment from upstream sources were important in region B.

## 1. Introduction

The snow crab *Chionoecetes opilio* is a spider crab that inhabits deep, cold waters in high latitudes in the northern hemisphere. It exists in the Sea of Japan, Okhotsk Sea, Bering Sea, and the northwest Atlantic Ocean (Charmantier and Charmantier-Daures, 1995). This is an important fishery species, particularly in Japan, Alaska, and Atlantic Canada. In the mid- and late 20th century, snow crab stocks declined drastically in the Sea of Japan and eastern Bering Sea due to overfishing (National Federation of Bottom Trawler's Union, 2006; North Pacific Fishery Management Council, 2000). To help stocks recover, a combination of permanent and seasonal marine protected areas was introduced following the management strategies of the snow crab bottom fishery off Kyoto Prefecture, Japan that began in 1983 (Makino, 2008). The 1999 landings recovered to the levels of the early 1970s (National Federation of Bottom Trawler's Union, 2006). For snow crab in the eastern Bering Sea, a rebuilding plan was enacted by the North Pacific Fishery Management Council (2000) to return mature male crab bio-

mass to a sustainable level within two consecutive years. The stock recovered in 2011, but then dropped again; however, it appears to have improved in more recent years (Szuwalski, 2018). Low recruitment below average was likely a contributing factor to the rebuilding failure before 2010 (Szuwalski and Punt, 2013).

As indicated by previous studies, ocean climate is thought to be the primary driver for the decline in the Newfoundland and Labrador snow crab stocks (Mullowney et al., 2014). However, crab stocks in Alaska and the eastern Bering Sea were not related to decadal shifts in climate and physical oceanography (Zheng and Kruse, 2000, 2006). Although several hypotheses of either climate forcing (bottom-up) or groundfish predation (top-down) for crab recruitment have been presented, all have failed to show significant relevance between snow crab and large-scale environmental indices. A piece-wise regression model was proposed by Szuwalski and Punt (2013) to successfully correlate the regime shift with snow crab recruitment in the eastern Bering Sea, but it was impossible to present spatial dynamics using that simple model. As Zheng and Kruse (2006) suggested, hydrodynamic simulations are

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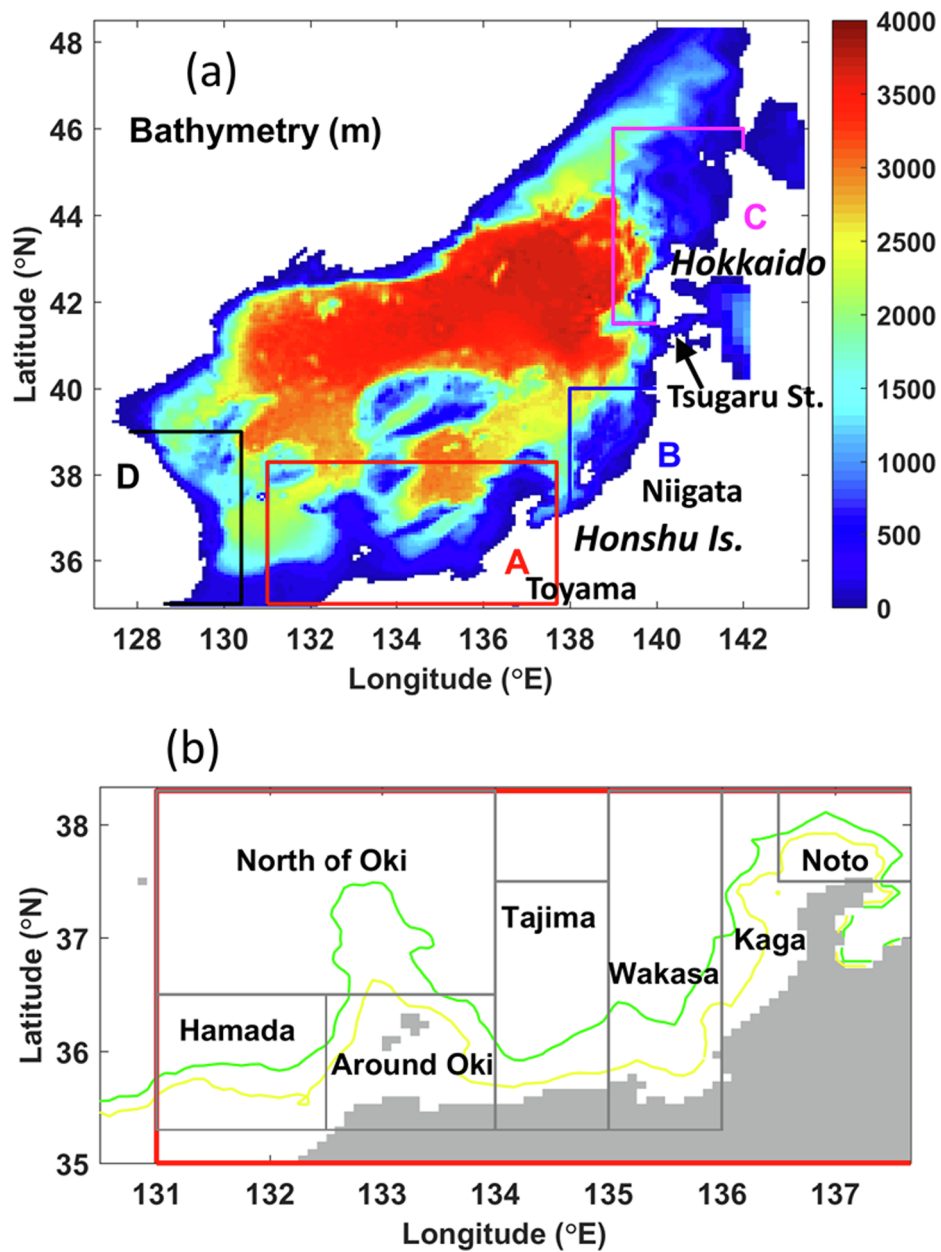


Fig. 1. Model domain and bathymetry. (a) Bathymetry of the Sea of Japan with regions A, B, C and D; (b) Magnification of region A: yellow and green lines are the isobaths of 200 m and 500 m, respectively. Seven subareas related to the distribution of initial larval density are separated by gray lines. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

needed to clarify crab larval distributions and settlement in nursery areas, which are two of the most critical processes for crab survival and recruitment (Kruse et al., 2007).

To date, three numerical studies have simulated snow crab larval

transport (Parada et al., 2010a, b; Okuno et al., 2010). Parada et al. (2010a) built a preliminary coupled model of circulation and crab larval drift in the eastern Bering Sea, covering the zoea I, zoea II and megalopal larval stages. They later improved their simulation by using

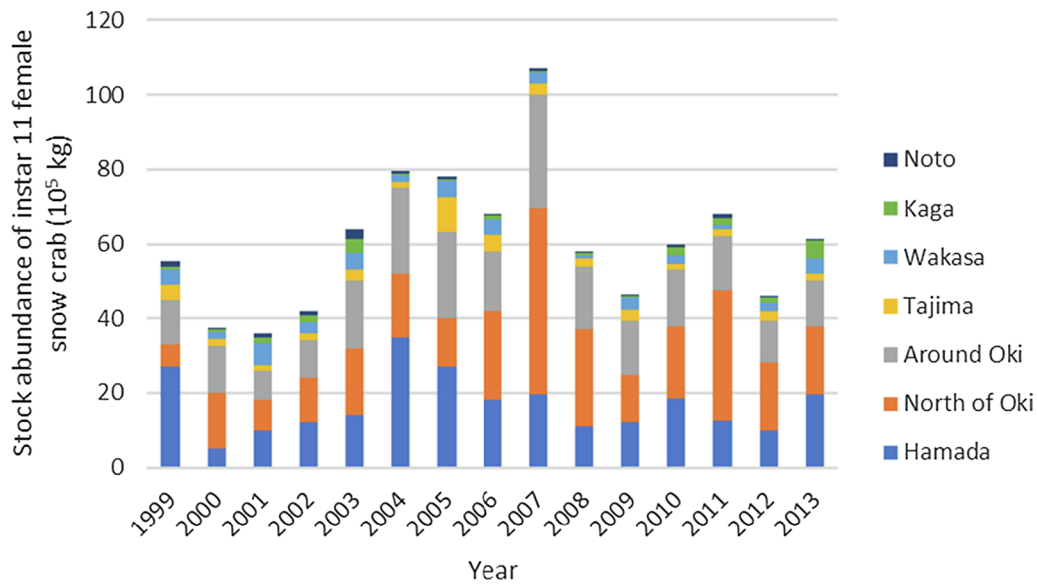


Fig. 2. Annual stock ( $10^5$  kg) of instar 11 female snow crab in the seven subareas of region A during 1999–2013. Data are digitized from Supplementary Fig. 3-3 in Ueda et al. (2017).

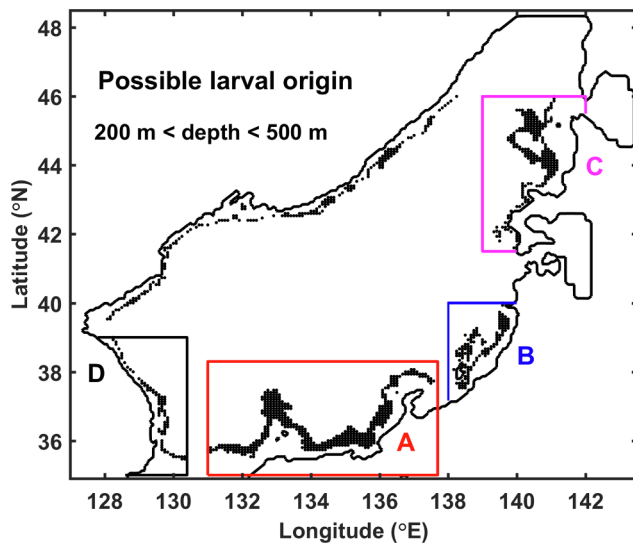


Fig. 3. Spatial locations of particle origins.

realistic initial conditions of each year from 1978 to 2003 and developing a spatial index of larval abundance for each modeled year based on mature female abundance, fecundity-at-size, clutch fullness index and annual/biennial reproductive schedule (Parada et al., 2010b). Another improvement was to vary the duration of the pelagic stage, i.e. explicitly modeling zoea I and zoea II stage durations based on water

temperature (Parada et al., 2010b). In Okuno et al. (2010), larval transport was simulated only in the southern part of the Sea of Japan and no consideration was given to survival processes. In the present study, we aimed to build a larval survival and transport model in the Sea of Japan and to investigate the factors leading to interannual variability in larval settlement, as well as recruitment patterns.

## 2. Model description and configuration

### 2.1. Life history basis for snow crab model in the Sea of Japan

*C. opilio* eggs remain attached to the pleopods of the female crab for at least 1 year (Ito, 1967), and prezoa are hatched from February to April on the seabed at water depths of 225–275 m (Kon, 1980). They rise toward the surface by phototaxis in less than 1 h, and develop into the zoea I stage before reaching the surface (Kon, 1967).

Most of the first zoea are distributed in the 0–50 m layer right above the hatching site. It takes 20–30 days to develop into zoea II, which is accompanied by horizontal transport and sinking to depths shallower than 150 m. The zoea II stage lasts another 30 days and then the larval crab turns into megalopa and sinks down to depths of 150–200 m beginning in early April. Megalopa gradually concentrate in the layer deeper than 200 m where the water temperature is less than 6–7 °C, and settlement generally occurs in June when the megalopa metamorphose into first stage benthic crabs (Kon, 1980; Kon et al., 2003). It is estimated that the total duration of the pelagic larval stage in the water column is approximately 100–130 days.

Kon et al. (2003) partially addressed diurnal vertical migration

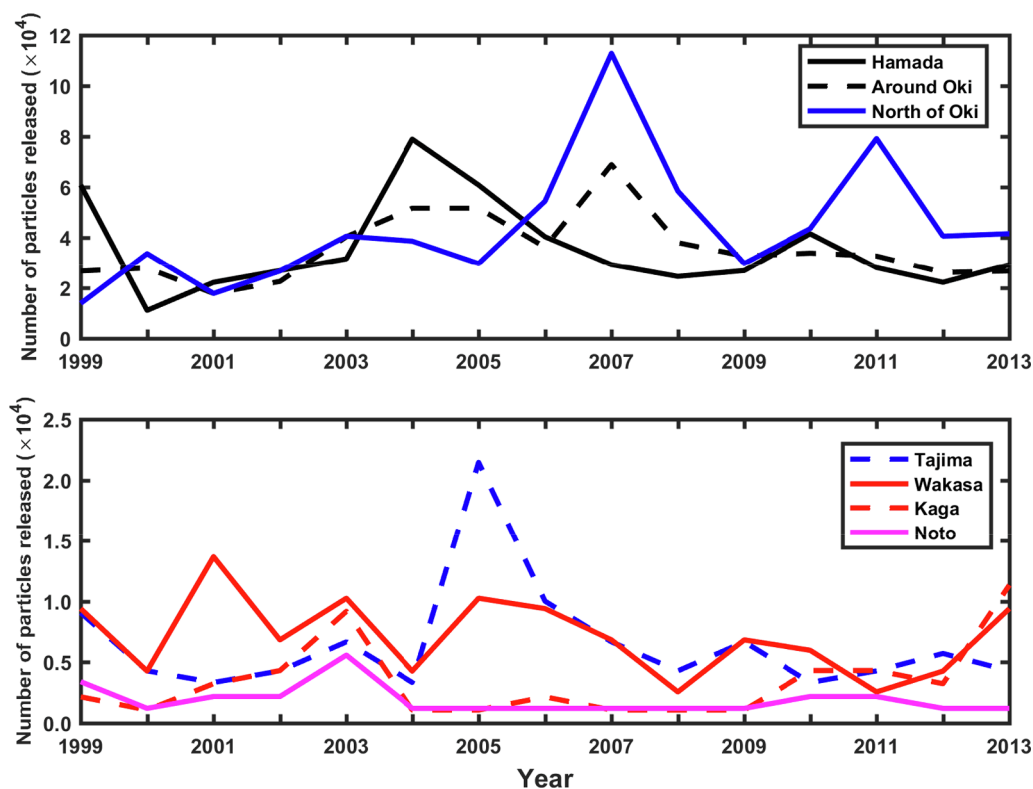


Fig. 4. Time-series of released number of particles in seven subareas during 1999–2013.

(DVM) for the second zoea and megalopa stages. Zoea II were mainly distributed at 0–50 m at night, and at 100–150 m at noon, migrating approximately  $100 \text{ m day}^{-1}$ . The full DVM range of megalopa was not assessed, due to constraints on water depth at the stations in the study.

After megalopa settle on the seabed, snow crabs do not migrate long distances in the Sea of Japan (Yamamoto et al., 2014). Juvenile crabs gather on the seabed at depths of more than 250 m before growing into instar 7, and then move to the seabed shallower than 250 m. The instar of crab increases with molting, and the gender is not resolved until the eleventh molt. In instar 9 and 10 stages, they assemble on the seabed at depths of approximately 225 m, where female crabs undergo a terminal molt to maturity and males live until molting to instar 11. After that, males begin moving to depths of 275–400 m and will stay there on the seabed for up to 6 years (Kon, 1980).

## 2.2. Model description

Hydrodynamics play an important role in the larval planktonic phase (Kon, 1970, 1973; Davidson and Chin, 1991), in addition to the availability of food (Kon, 1979; Squires and Dawe, 2003) and predation (Forward, 2009). In this study, daily reanalysis from the Data Assimilation Research of the East Asian Marine System (DREAMS) (Hirose et al., 2013) datasets were used to provide 3-D water velocity and water

temperature data in the Sea of Japan from 1999 to 2013. The model domain is shown in Fig. 1a. The horizontal resolution is  $(1/12)^\circ$  in the zonal direction and  $(1/15)^\circ$  in the meridional direction. There are 38 layers in the vertical direction (4 m, 10 m, 15 m, 22 m, 30 m, 39 m, 50 m, 64 m, 81 m, 100 m, 120 m, ..., 5674 m).

Nine larval release-drift events were simulated every year from 1999 to 2013 at 10-day intervals beginning on February 1st. Each event lasted 120 days. The durations of the zoea I, zoea II and megalopa stages were hypothesized to be 30, 30 and 60 days, respectively (Yamamoto et al., 2014, 2015).

Particles representing zoea I were released at the sea surface between isobaths of 200 m and 500 m (Ueda et al., 2017) when the sea surface temperature (SST) was within the range of  $5^\circ\text{C}$  to  $16^\circ\text{C}$  (Yamamoto et al., 2014). Once the larvae were released, they were transported by ocean currents. The particle tracking method used in our model was as follows:

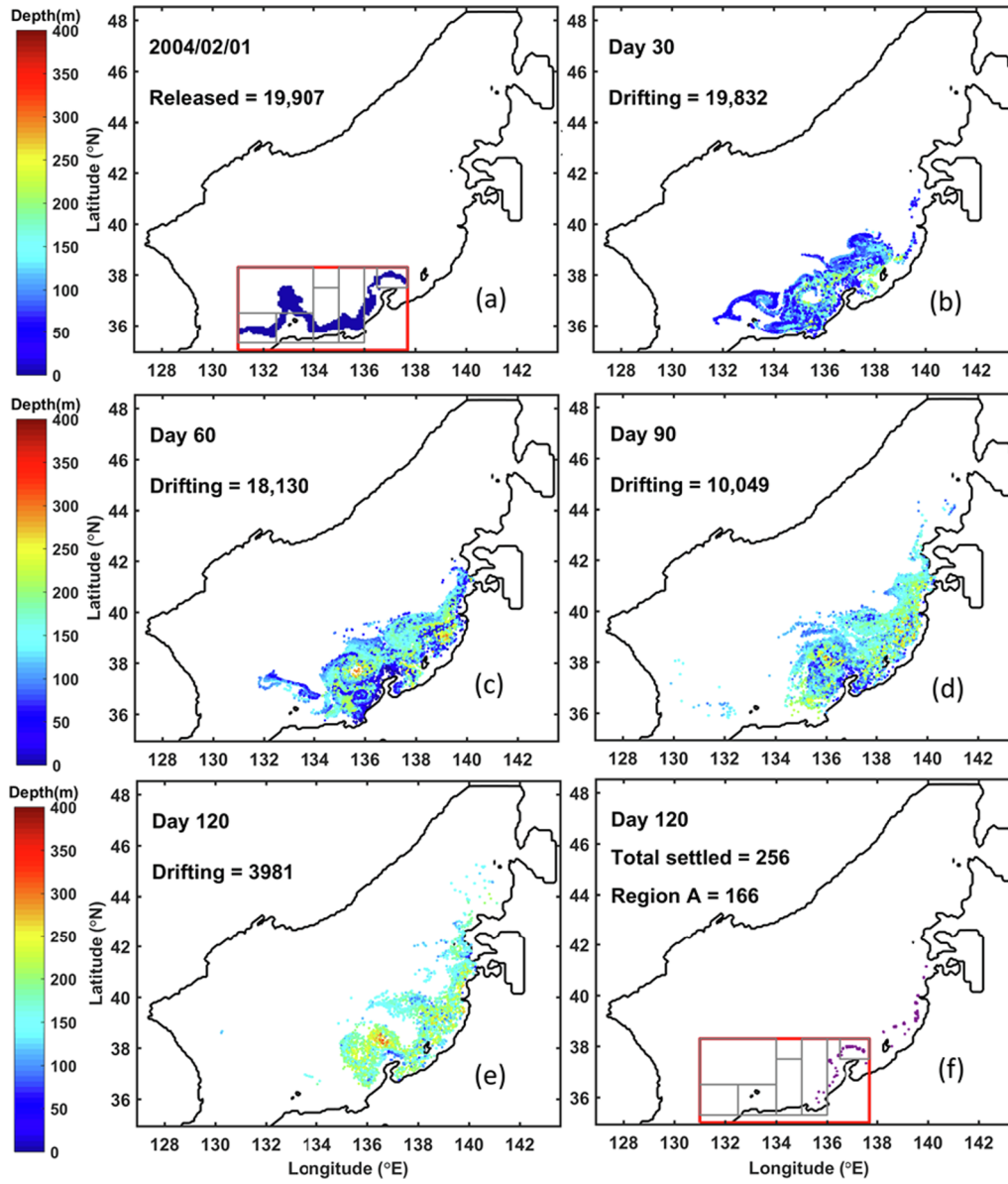
$$x(t + \Delta t) = x(t) + u\Delta t + \xi\sqrt{2A_H\Delta t} \tag{1}$$

$$y(t + \Delta t) = y(t) + v\Delta t + \xi\sqrt{2A_H\Delta t} \tag{2}$$

$$z(t + \Delta t) = z(t) + w\Delta t + ws\Delta t + D(t)\Delta t \tag{3}$$

where  $(u, v, w)$  is the velocity vector and  $(x, y, z)$  denotes the particle's position at moment  $t$  or  $t + \Delta t$ .  $\Delta t$  denotes the time step, which is set





**Fig. 5.** Larval distribution during one release-drift event with a 30-day interval. (a) The initial distribution of larvae. Start date and number of released particles are shown in the top left; (b)–(e) The distribution of drifting larvae on day 30, 60, 90 and 120. Both the time and number of drifting particles are shown in the top left and the depth of existing particles is indicated by color; (f) The distribution of successfully settled larvae within the depth of 200–500 m. The number of settled larvae is shown in the top left.

3600 s. Both  $\xi$  and  $A_H$  are parameters related to turbulence.  $\xi$  is a random number in the range of  $[-1, 1]$ , and  $A_H$  is the horizontal eddy diffusivity, recalculated by the Smagorinsky scheme (Smagorinsky, 1963) using the horizontal water velocity data.  $w_s$  denotes the sinking velocity. Based on Kon et al. (2003), the distribution of larval crab increases 50–60 m in depth in each month from zoea I to megalopa. Therefore,  $w_s$  is set as  $2 \text{ m day}^{-1}$  in the model.  $D(t)$  represents the DVM speed and is set as a piecewise function of time  $t$  with unit of  $\text{m hour}^{-1}$  and a positive downward direction.

$$D(t) = \begin{cases} 0 & 0 < \text{day} \leq 30 \\ 5 & \text{hour}=23 \text{ or } 0 \leq \text{hour} < 9, 30 < \text{day} \leq 60 \\ 12.5 & 9 \leq \text{hour} < 13, 30 < \text{day} \leq 60 \\ -10 & 13 \leq \text{hour} < 23, 30 < \text{day} \leq 60 \\ 0 & 60 < \text{day} \leq 120 \end{cases} \quad (4)$$

During larval transport, we set the following water temperature range as a survival condition: 5–16 °C for zoea development (first 60 days in each cycle), and 5–14 °C for megalopa stage (second 60 days)

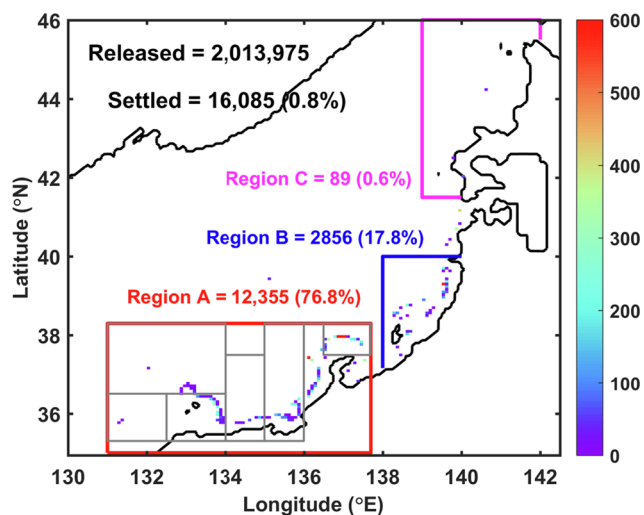


Fig. 6. Distribution of the total settled particles (shading) over 1999–2013 in the hindcast simulation. The number of released particles in the Sea of Japan was 2,013,975, among which 16,085 particles successfully settled.

based on Yamamoto et al. (2014). If one larva stayed out of the proper temperature range for 24 consecutive hours, it “died” and was removed from the model simulation. Considering that snow crab larvae in the Sea of Japan do not experience large salinity fluctuations (Kon, 1980), we did not take salinity into account. This was also supported by the laboratory study of Yamamoto et al. (2015), in which crab larval

survival was highest at a salinity between 20 and 38.

As for settlement on the seabed, there are two conditions for crab larvae. The first is that the larvae have been transported for longer than 90 days (Kon et al., 2003), meaning that they are in the late megalopa stage and are getting ready to settle on the seabed. The second is that the larvae must be hyperbenthic and located horizontally between isobaths of 200 m and 500 m.

### 2.3. Model configurations

#### (1) Hindcast calculation for 1999–2013

Since the fishery in western Toyama Prefecture accounts for the highest snow crab catches in the Sea of Japan, a 15-year hindcast was carried out in this zone (referred as region A in this study). Following Ueda et al. (2017), we divided this area into seven subareas: Hamada, around Oki, north of Oki, Tajima, Wakasa, Kaga and Noto (Fig. 1b). In the model, for grids where depth and temperature meet the conditions mentioned above, the modeled number of zoea was set as a spatio-temporal variable proportional to annual mature female abundance. More specifically, seven spatial density indices were introduced in each modeled year, based on the stock abundance of instar 11 female crab, which were digitized from Supplementary Fig. 3-3 in Ueda et al. (2017) (Fig. 2). The number of particles released in one grid was set as the product of 25 and the density index.

#### (2) Sensitivity experiments

In addition to the hindcast simulation, additional three experiments

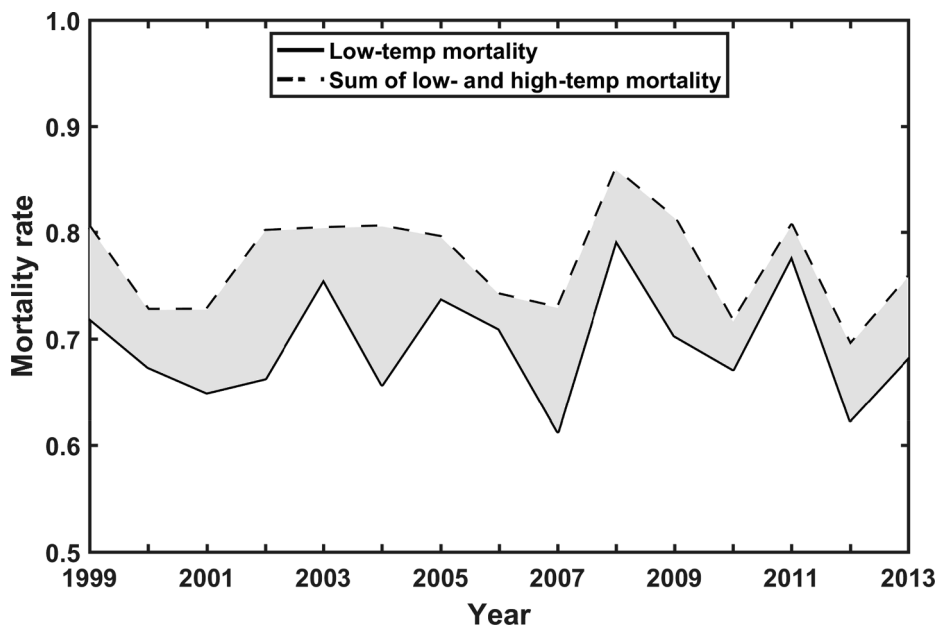


Fig. 7. Annual mortality rate in the 1999–2013 hindcast simulation. Shading denotes mortality rate with water temperatures > 16 °C (zoea) or > 14 °C (megalopa), solid line denotes mortality rate with water temperatures < 5 °C; dashed line denotes total mortality rate.

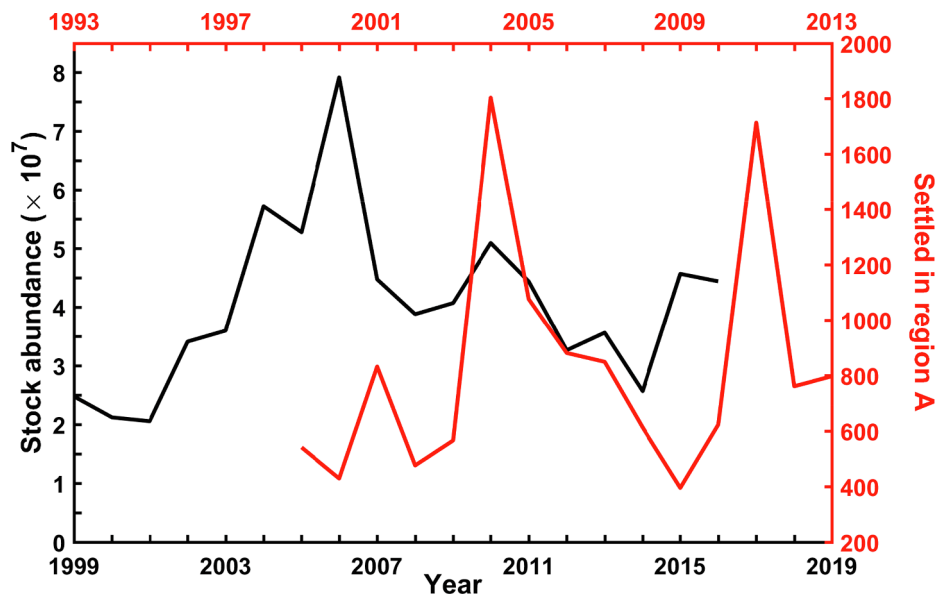


Fig. 8. Number of settled particles (red line) and stock abundance of instar 10 snow crab (black line, from Ueda et al., 2017) in region A. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

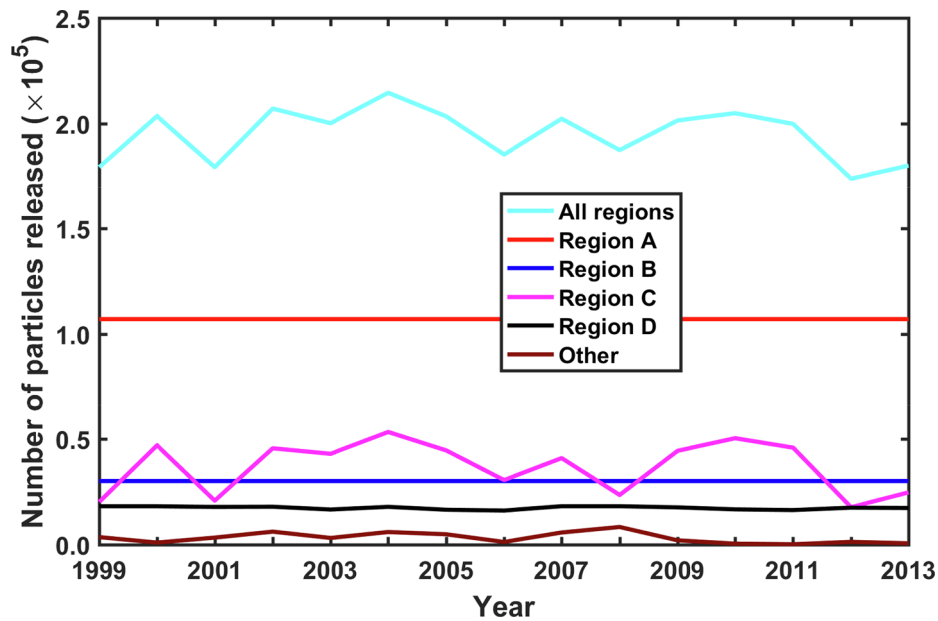


Fig. 9. Time-series of released number of particles in different regions in case “JS”.

were carried out to evaluate effects of female crab abundance, water temperature and ocean circulation on crab larvae.

The first experiment was simulated for the Japan Sea (case “JS”), in which a uniform distribution of released particles was adopted all around the Sea of Japan. Specifically, 25 particles were regularly

distributed in the surface layer of one grid that met the water depth preconditions of crab larval survival (200–500 m). As long as the SST of the grid fell within the range of 5–16 °C, the particles could be released from five zones, i.e. regions A, B, C, D and Other (Fig. 3). Regions B and C, following Ueda et al. (2017), are two other important snow crab

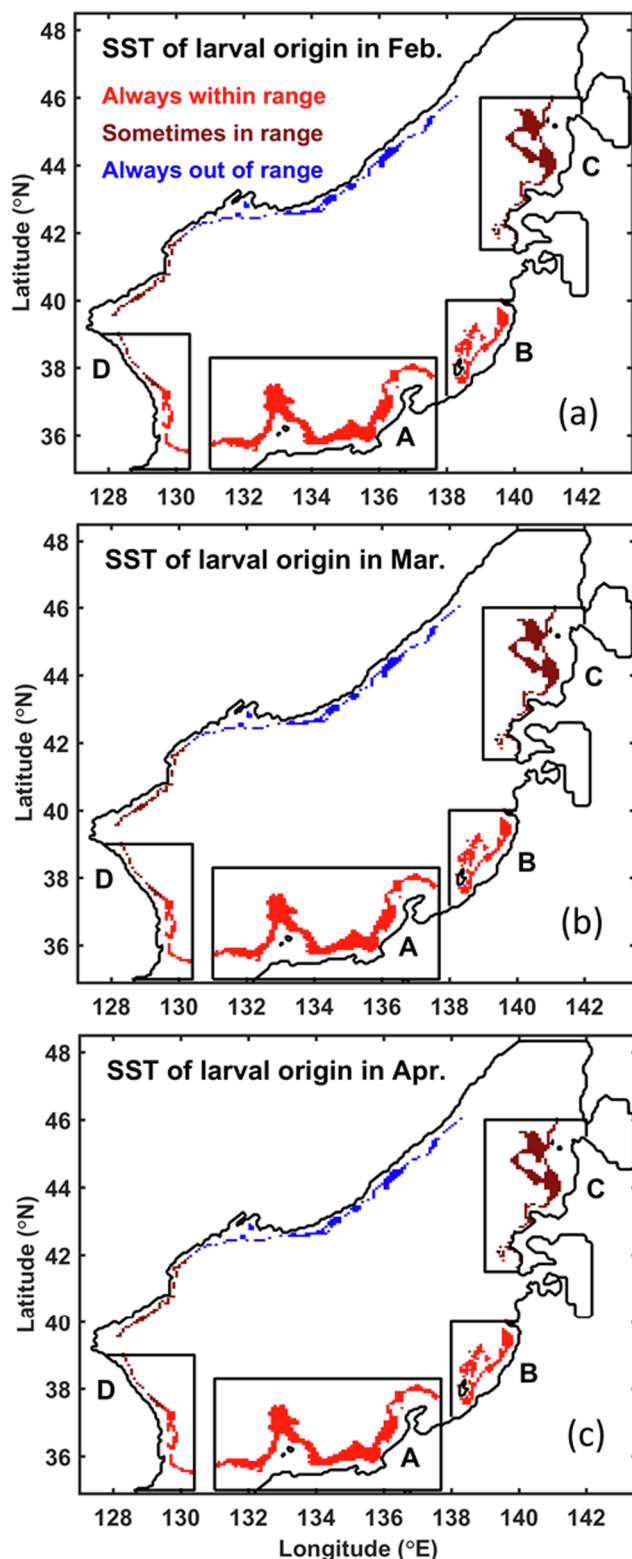


Fig. 10. Classification of interannual SST variation in (a) February, (b) March and (c) April. The color red indicated that the SST within the grid always fell in the suitable temperature range (5–16 °C) during 1999–2013; the color brown indicated that the SST within the grid was out of the suitable range in some years; the color blue indicated that the SST within the grid was always out of the suitable range. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

fishing areas in the Sea of Japan, located in western Niigata Prefecture and western Hokkaido Prefecture, respectively. Region D is east of the Korean Peninsula; crab larvae from this area were speculated to drift with the Ulleung Warm Eddy and Tsushima Warm Current (TWC) and settle in region A (Hogan and Hurlburt, 2006; Kim et al., 2008). The fifth zone, “Other”, is the northwest region in the Sea of Japan (Fig. 3).

The other two experiments were initialized the same as case “JS”. One of these was named “Tclim”, in which the actual water temperature field was replaced by the multi-year mean temperature field, i.e., removing interannual variation in water temperature during 1999–2013. The other was named “UVclim”, in which the actual current field was replaced by multi-year mean current field, i.e. removing interannual variation in current field during 1999–2013. The multi-year climatology was a 366-day dataset obtained by averaging 15-year of DREAMS data at the same calendar day.

### 3. Hindcast results for 1999–2013

The annual number of zoea released from the seven subareas during 1999–2013 is shown in Fig. 4. More particles were released from subareas west of Tajima than from the other subareas. After release, most particles moved northeastward following the TWC and were gradually widely distributed near middle and northern Honshu Island (Fig. 5). Vertically, larva kept settling to deeper layers over time. Mean depth of larval distribution increased from 4 m at release (Fig. 5a) to approximately 90 m at day 30 (Fig. 5b), 130 m at day 60 (Fig. 5c) and 160 m at day 90 (Fig. 5d), which is consistent with Kon et al. (2003). At the end of the calculation for the 2004/02/01 release-drift event, 20% of the particles remained drifting in the ocean, and 1.3% settled on the seabed, 3/5 of which settled in region A (Fig. 5f). “Dead” particles caused by temperatures that were too-low or too-high accounted for 3/4 of all released particles.

Among the 2 million particles released over the 15-year simulation period, approximately 16,000 particles successfully settled on the seabed (settling rate, 0.8%), with settlement in regions A and B accounting for 76.8% and 17.8%, respectively (Fig. 6). Both regions A and B are known as typical nursery areas of young snow crab in the Sea of Japan. The remaining particles settled west of the Tsugaru Strait and west of Hokkaido. As for the larval mortality (Fig. 7), more than 3/4 of the released particles “died” due to improper water temperatures. The maximum mortality rate was 86% in 2008, and the minimum was 69% in 2012. The change in mortality rate was certainly related to variability in water temperature, but was also affected by that in the flow field. Additionally, as shown in Fig. 7, low temperatures induced more deaths than did high temperatures.

Due to a lack of information on in-situ settlement numbers of crab larvae, it was difficult to directly verify our larval model results using field data. Nevertheless, we have annual stock abundance of instar 10 snow crab at hand. In general, it takes benthic crab 6–7 years to undergo ten molts (Kyoto Prefectural Agriculture, Forestry and Fisheries Technology Center, 1994). Consequently, we compared the estimated stock abundances of instar 10 snow crab from Ueda et al. (2017) with the simulated settlement 6 years earlier in Fig. 8. Stock abundance from 2007 to 2014 followed the same trend as simulated settlement 6 years earlier from 2001 to 2008, but the other years did not. The peak in 2006 and trough in 2014 in the stock series seemed to represent a 5-year lag of extreme values in the settlement series. Although the model evaluation is not enough, we assume that the model results reflect major variation in transport and survival of crab larvae in the Sea of Japan and will discuss these factors in the next session.

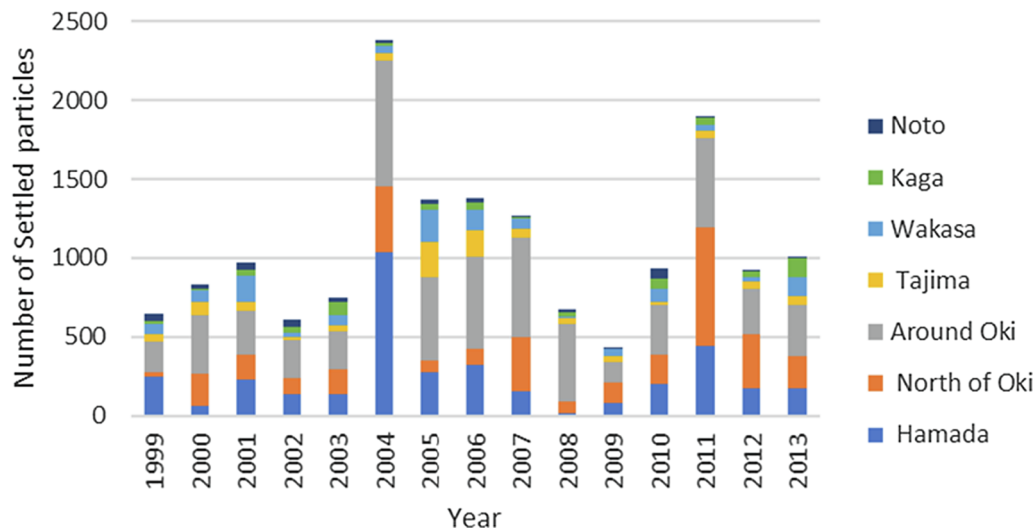


Fig. 11. Number of settled particles sorted by its origin in the hindcast simulation.

Table 1

Numbers of settled particles sorted by origin and destination in the hindcast simulation from 1999 to 2013.

Origin	Destination							Region A	Region B	Region C
	Hamada	North of Oki	Around Oki	Tajima	Wakasa	Kaga	Noto			
Hamada	10	49	538	125	413	593	1473	3201	347	18
North of Oki	0	41	241	63	263	462	1126	2196	750	48
Around Oki	0	67	1092	84	570	1227	1950	4990	800	17
Tajima	0	0	46	12	90	259	326	733	199	4
Wakasa	0	0	44	1	92	247	452	836	244	1
Kaga	0	0	3	0	13	31	283	330	205	0
Noto	0	0	0	0	0	0	69	69	311	1
<b>Sum</b>	<b>10</b>	<b>157</b>	<b>1964</b>	<b>285</b>	<b>1441</b>	<b>2819</b>	<b>5679</b>	<b>12,355</b>	<b>2856</b>	<b>89</b>

#### 4. Discussion

##### 4.1. Initial number of crab larvae

In case “JS”, the modeled number of zoea was set irrelevant of the abundance of female crab. The numbers of particles released in regions A and B did not change throughout the 15 years during 1999–2013 (Fig. 9), because the SST of these two regions in February, March and April were always within the range of 5–16 °C (labeled in red in Fig. 10). Considering the modeled number of zoea did not vary in case “JS”, in which the water temperature and velocity had interannual variations, it can be inferred that the interannual variation in crab spawning in regions A and B in hindcast simulation depended entirely

on the variation in the abundance of female crabs. Additionally, there was little variation in the number of particles released in region D, while the relative variation in the higher-latitude zone (regions C and Other) reached more than 50%, obviously affected by the interannual change in SST in spring (Fig. 10).

##### 4.2. Controlling factors for settlement

To link the initial number of zoea with final megalopa settlement, we sorted settlements of the hindcast simulation by the origins of the particles (Fig. 11). Settlement peaked in 2004 and 2011 due to higher initial numbers in those years than in the other years (Fig. 2). Settlement was positively related to the initial number of particles in some



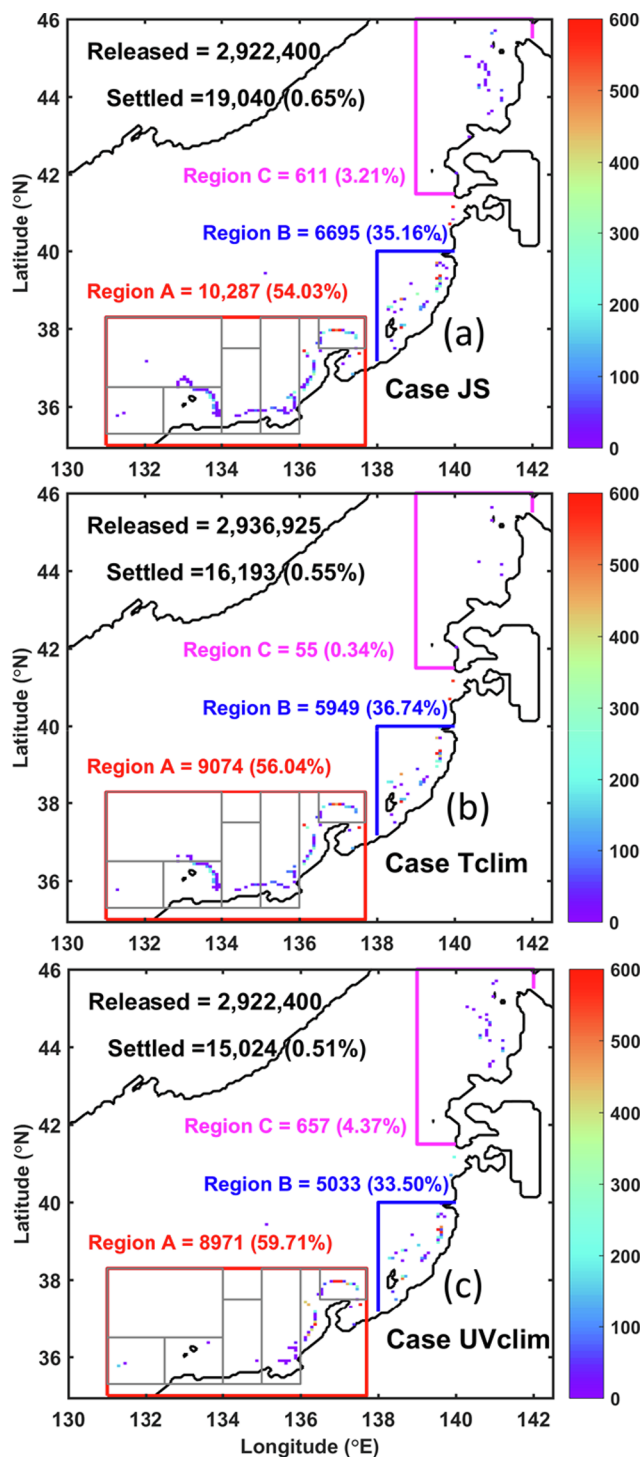


Fig. 12. Distribution of settled particles in case “JS”, “Tclim” and “UVclim”. The values inside each panel have the same meaning as those in Fig. 6.

subareas. For example, the number released from Hamada in 2004 was the highest in the seven subareas, and the settled number was also the greatest, although most of the larvae settled in the other subareas, implied by the first line in Table 1. However, there were also exceptions. Settlement was considerably lower in 2005 than in 2004, with similar densities of female crab (Fig. 2), but 10% higher low-temperature mortality (Fig. 7). This suggests that hydrodynamics during larval transport can also influence final larval settlement.

With three sensitivity experiments (cases “JS”, “Tclim” and “UVclim”), the effects of hydrodynamics on larval transport and settlement were separated, neglecting the effects of female crab abundance. Settlement in regions A, B and C were compared spatially (Fig. 12) and temporally (Fig. 13). By removing the interannual variability in hydrodynamics, the number of settling megalopa decreased, especially in region C in case “Tclim” (Fig. 12b). Furthermore, the distribution of settlement in region A changed markedly in case “UVclim” (Fig. 12c). In the time-series (Fig. 13), the variability in the flow field seemed to have a great impact on settlement in region B, and that in water temperature was vital to settlement in region C. Both the interannual variations in water temperature and the flow field were related to the variation in settlement in region A.

The impact of the flow field upon the settlement in region A can also be confirmed from Table 1, which is a connectivity matrix of the settlement destination and release origin from the hindcast results. Larvae settling in one subarea were generally released from the TWC upstream areas, so the least settlement occurred in Hamada, which is in the most upstream (i.e. western) subarea of the seven subareas. The subarea around Oki was an exception, since the maximum proportion of larvae settling there originated from the same subarea, and larvae from downstream also made a positive contribution to settlement, particularly in 2005, 2007 and 2008, and less so in 2004 and 2009 (data not presented).

Taking the second release-drift event in 2007 and 2004 as examples, particles released from around Oki moved counterclockwise in 2007 (Fig. 14a), but they went much further northeastward in 2004, even reaching the vicinity of the Tsugaru Strait (Fig. 14c). Trajectories of particles released from Wakasa in 2007 were mainly westward, and then circled around counterclockwise at 134°E (Fig. 14b), whereas they moved more northeastward in 2004 (Fig. 14d) like the particles released from around Oki. A clockwise eddy existed in the layer shallower than 50 m in early spring of 2007, which was centered in Tajima around 37°N (Fig. 15a, b). Due to the southeastern half of the eddy, the particles released from Wakasa moved westward to 134°E, and were then restricted by local cyclonic circulation. The joint effect of the clockwise eddy and local cyclonic circulation resulted in the particle pathway shown in Fig. 14a and b. The clockwise eddy in early spring of 2004 was located more northeastward (Fig. 15c, d) and its center shifted to Wakasa and north of 37.5°N. Consequently, the particles released from around Oki, Tajima and Wakasa could easily leave region A and drift with the current towards the Tsugaru Strait (Fig. 14c, d).

### 4.3. Pattern of crab recruitment

The pattern of crab recruitment in the Sea of Japan could be obtained from case “JS” by distinguishing whether the settled particles in one region mainly originated from the region itself or not.



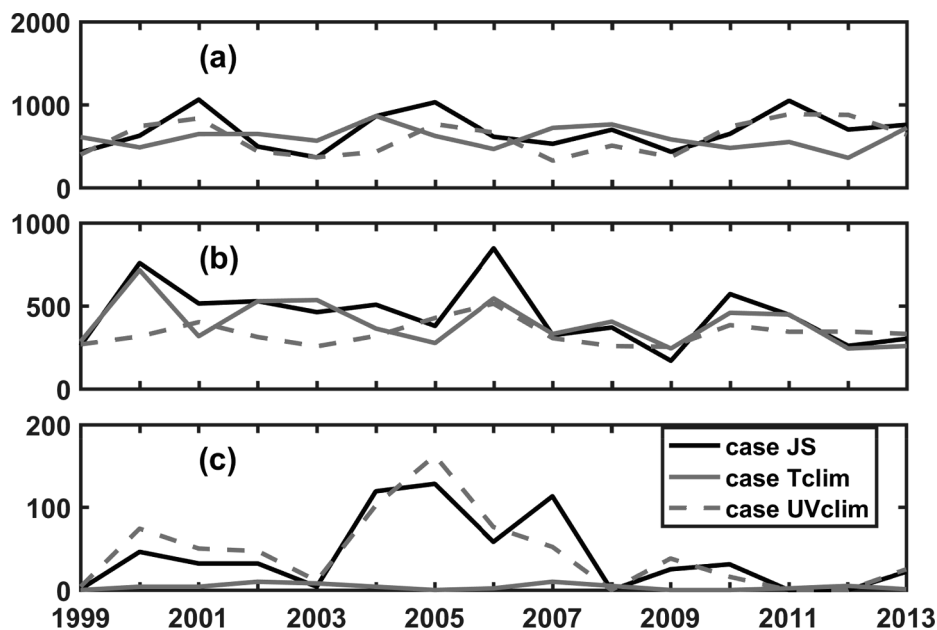


Fig. 13. Time-series of number of settled particles in regions (a) A, (b) B, and (c) C in cases “JS” (solid black line), “Tclim” (solid gray line) and “UVclim” (dashed gray line).

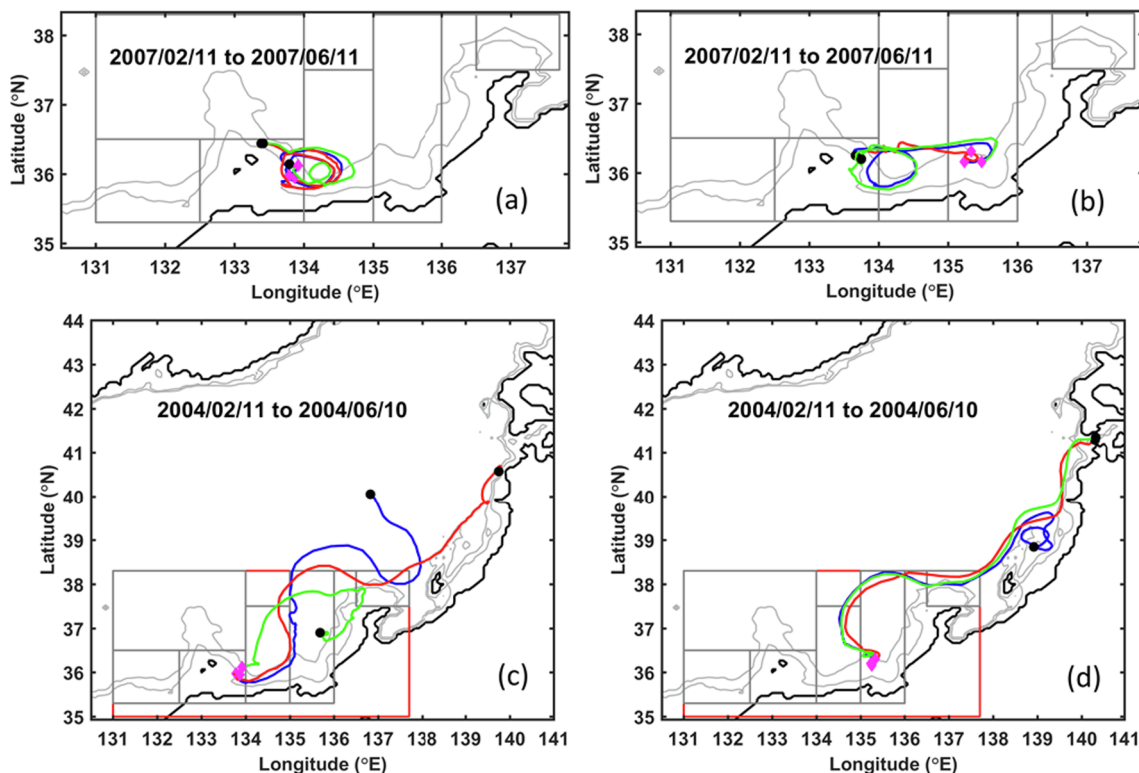


Fig. 14. Particle trajectories in two release-drift events: 2007/02/11–2007/06/11 (upper panels); 2004/02/11–2004/06/10 (lower panels), released from around Oki (left panels) and from Wakasa (right panels). Magenta diamonds denote the initial release location; red, blue and green lines are the trajectories of three particles; and black dots denote the final location of particles. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

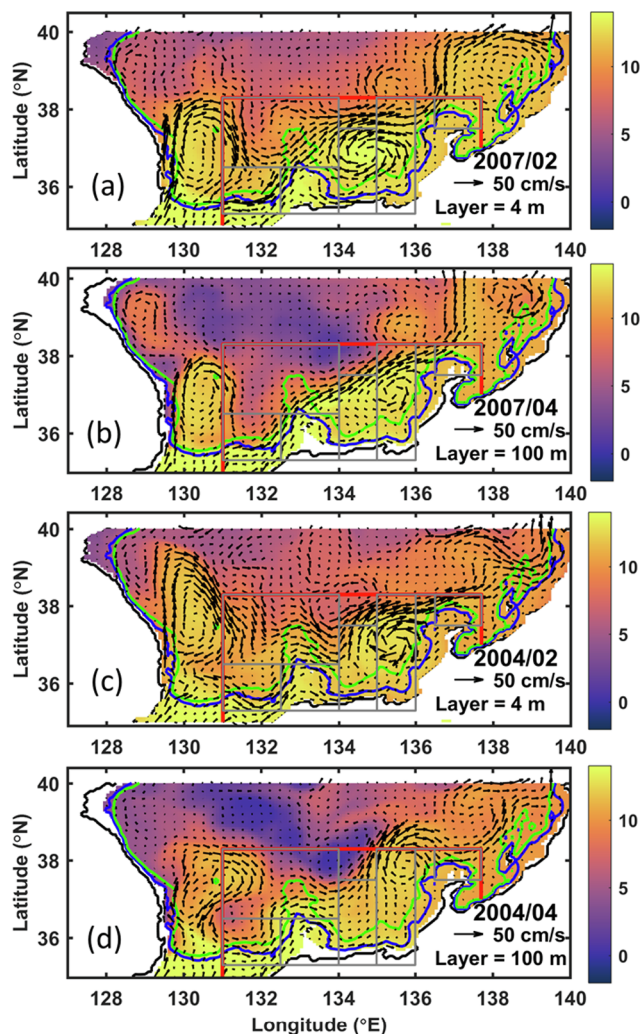


Fig. 15. Monthly-mean velocity (vector) and temperature (shading) in region A at 4 m in (a) 2007/02 and (c) 2004/02; and at 100 m in 2007/04 (b) and 2004/04 (d). Blue and green lines show the isobaths of 200 m and 500 m, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2

Numbers of released and settled particles in case “JS” sorted by particle origin and settlement region.

Origin	Region A	Region B	Region C	Region D	Other region	Sum
<b>Number of released particles</b>	<b>1,606,500</b>	<b>452,250</b>	<b>553,625</b>	<b>261,725</b>	<b>48,300</b>	<b>2,922,400</b>
Number of settled particles in region A	10,007	14	0	266	0	10,287
Number of settled particles in region B	4202	2478	0	15	0	6695
Number of settled particles in region C	10	11	590	0	0	611
Number of settled particles in other regions	883	522	32	10	0	1447
<b>Total settled</b>	<b>15,102</b>	<b>3025</b>	<b>622</b>	<b>291</b>	<b>0</b>	<b>19,040</b>
<b>Settling rate</b>	<b>0.9%</b>	<b>0.7%</b>	<b>0.1%</b>	<b>0.1%</b>	<b>0</b>	<b>0.7%</b>

Consequently, two patterns were observed: self-recruitment and recruitment from upstream sources, which we named “upstream-recruitment”. Both patterns play significant roles in the sustainability of the snow crab fishery in the Sea of Japan.

As shown in Table 2, particles released from region A accounted for 97.3% (10,007/10,287) of the settlement in the same region, while particles originating from upstream (region D) only accounted for 2.6%. Therefore, region A was regarded as having a self-recruitment pattern. This also suggested that crab larvae from east of the Korea Peninsula had little linkage to the benthic crab fishery in the area west of Toyama.

In settlement in region B, the ratio of particles released from upstream (regions A and D) to that from region B itself was roughly 1.7 ((4202 + 15)/2478), meaning the two patterns (self-recruitment and upstream-recruitment) were equally important to local recruitment. The pattern in region C was self-recruitment, because more than 96% of the particles settling there were released from the same area.

#### 4.4. Limitations of the present model

There are several limitations in the present larval model. The first is related to the initial number of zoea in each release-drift event. It might be inaccurate because higher stocks of instar 11 female crab do not necessarily mean that more larvae will be hatched (Kruse et al., 2007). Another limitation is that the duration of zoea I, zoea II and megalopa is fixed in the model, which is virtually variable with water temperature (Yamamoto et al., 2014). Thirdly, this study considered only temperature as the cause of larval mortality, but food availability and predation of crab larvae also affect survival in wild crab populations. Consequently, discrepancies are likely to exist between the simulated and actual settlement. Although the benthic phase of snow crab was excluded from the pelagic larval model, it should be stressed that predation of juvenile crab by benthic fish and cannibalism by elder crabs can lead to mortality of metamorphosed benthic crabs, which will probably reduce the 6-year lagged stock of adolescent crabs.

#### 5. Conclusion

In this study, we developed a transport and survival model for crab larvae in the Sea of Japan which considered DVM during the second zoea stage, and regarded water temperature as the sole factor affecting survival. The model can generally reproduce the distribution of larval drifting and settlement on the seabed. The settling rate of crab larvae was only about 1% of released particles. More than 3/4 of the released particles “died”, most of which were the result of low temperatures.

Sensitivity experiments revealed that variation in initial number of zoea in regions A and B depended entirely on the stock abundance of female crabs, while in the higher-latitude region C, modeled number of zoea varied with the water temperature on the interannual scale. As for larval settlement, the flow field likely had a great impact on settlement in region B and water temperature was vital to settlement in region C. Both variations in female crab abundance and hydrodynamics contributed to settlement in region A, where the influence of the flow field was significant, especially with respect to the clockwise eddy at Tajima-Wakasa. Finally, the recruitment patterns in the three fishing areas were presented. Regions A and C predominantly showed self-recruitment, while self- and upstream-recruitments played a major role in region B.

The numerical model can be improved in the future by considering effects of water temperature on the durations of the zoea and megalopa stages, and those of larval starvation and predation on survival conditions.

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