

Effects of hydrographic conditions on the transport of neon flying squid *Ommastrephes bartramii* larvae in the North Pacific Ocean

Efecto de las condiciones hidrográficas en el transporte de las larvas de calamar rojo *Ommastrephes bartramii* en el Océano Pacífico Norte

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ABSTRACT

The neon flying squid, *Ommastrephes bartramii*, is widespread in subtropical and temperate regions. In the North Pacific Ocean, the species is comprised of two spawning cohorts; an autumn cohort and a winter-spring cohort. Interestingly, despite their apparently contiguous hatching periods, there is a marked disparity in the mantle length of both cohorts. We hypothesized that differences in the ambient temperature during larval development were responsible for the observed disparity in mantle size. Numerical simulations of ambient temperature revealed that water temperatures were approximately 1 °C higher in areas inhabited by the autumn cohort than they were in areas inhabited by the winter-spring cohort. The findings imply that differences in ambient water temperature and nutrient condition may be responsible for the observed differences in the growth of the autumn and winter-spring cohorts.

Key words: Ambient temperature, neon flying squid, spawning cohort, 4D-VAR.

RESUMEN

El calamar neón, *Ommastrephes bartramii*, está muy extendido en las regiones subtropicales y templadas. En el Pacífico Norte, la especie se compone de dos cohortes de desove, la de otoño y la de invierno y primavera. Curiosamente, a pesar de sus períodos de incubación contiguos, al parecer hay una clara diferencia en la longitud del manto de ambas cohortes. La hipótesis es que son las diferencias en la temperatura ambiental durante el desarrollo larval fueron las responsables de las diferencias observadas en el crecimiento del manto. Las simulaciones numéricas de la temperatura ambiente en la cohorte de otoño, revelaron que la temperatura del agua fue aproximadamente 1 °C más alta que en la de invierno y primavera, lo que implica que las diferencias en la temperatura del agua es la responsable de las diferencias observadas en el crecimiento durante el otoño y las cohortes de invierno y primavera de *O. bartramii*.

Palabras clave: Calamar rojo, cohorte desovante, temperatura ambiente, 4D-VAR.

INTRODUCTION

The neon flying squid, *Ommastrephes bartramii* (Lesueur, 1821), is widespread in subtropical and temperate regions (Roper *et al.*, 1984). This economically important oceanic squid species has been harvested commercially by Japan since 1974, and subsequently by Korea and China. The north Pacific population is comprised of two spawning cohorts; an autumn cohort and a winter-spring cohort (Yatsu *et al.*, 1997; 1998). Interestingly, despite their apparently contiguous hatching periods, there is a marked difference in the mantle length of both cohorts. Stock levels of the autumn-spawning cohort, which is important in the fishery economy because of its large size, were low when large-scale driftnet fishing was widely practiced (1979-1992). After an international moratorium on all large-scale pelagic drift net fishing at the end of 1992, squid stocks increased rapidly (Yatsu *et al.*, 1998; Ichii *et al.*, 2009).

Field observations have shown that both cohorts have a lifespan of one year (O'Dor 1998), and that they migrate between their spawning grounds in subtropical waters (30-35 °N) to their feeding grounds in subarctic waters (40-45 °N) (Ichii *et al.*, 2011; Yatsu *et al.*, 1997, 1998; Chen & Chiu, 2003). Although the migration routes of juvenile neon flying squid have been inferred based on ambient sea temperatures and fisheries data obtained for both cohorts (Murata *et al.*, 1985; Yatsu *et al.*, 1998; Ichii *et al.*, 2006), relatively little is known about the migration events undertaken before the juvenile stage. Thus, to elucidate the effects of hydrographic conditions on the migration and distribution of neon flying squid larvae in the North Pacific Ocean, numerical experiments were conducted using a Lagrangian particle-tracking model.

Numerical modeling has recently been employed to clarify the larval transport mechanisms of a variety of fish species in the open ocean (Kimura *et al.*, 1999; Kim *et al.*, 2007; Kitagawa *et al.*, 2010). These simulations of larval-juvenile dispersal have shown that oversimplification of the biological characteristics and ecological phenomena by models can markedly reduce their applicability to real systems.

In this study, we examined the effect of the ambient water temperature during larval period on differences in the size of the two cohorts using cutting-edge physical simulation data sets.

MATERIALS AND METHODS

Circulation model. Since Lagrangian particle-tracking models require hydrographic data, such as current velocity and water temperature, we employed a four-dimensional variational (4D-VAR) data assimilation system to more accurately define the mean seasonal state of the North Pacific Ocean. The 4D-VAR system is a synthesis of observational records and a sophisticated general circulation model that produces dynamically consistent time-vary-

ing data. The system is capable of realistically representing global ocean circulation patterns and requires no artificial temperature sources or sinks, or salinity fields. The resulting dataset enabled us to clarify both water mass formation and movement processes at a horizontal resolution of one degree with 27 vertical levels at monthly intervals (Masuda *et al.*, 2006).

Particle tracking. To estimate the extent of larval transport to temperate waters, simulated larva particles were released in the paralarval distribution range and tracked as passive tracers for a 30-day period. It was assumed that the swimming ability of paralarvae and juveniles is relatively poor. For the particle tracking model, the following equations were applied discretely to individual particles at each time step, starting from an initial condition:

$$\begin{aligned} \vec{dX}/dt &= \vec{v}_{adv} + \vec{v}_{dif}, \quad \vec{X}/dt = \vec{v}_{adv} + \vec{v}_{dif}, \\ \vec{v}_{dif} &= RC_{horcon} \sqrt{u_x^2 + v_y^2 + u_y v_x}, \end{aligned}$$

where \vec{v}_{adv} is the ocean current velocity obtained from the ocean general circulation model, 4D-VAR, \vec{v}_{dif} is a random velocity associated with horizontal oceanic diffusion and expressed by the Smagorinsky scheme, R is a random number between -1 and 1 generated at each time step for each individual particle, and C_{horcon} is the Smagorinsky constant and is assumed to have a value of 0.05.

RESULTS

In this study, the particles were released in two domains within the areas shown in Figure 1. These areas were selected based on the seasonal distributions of neon flying squid paralarvae that were estimated previously by observations conducted from 1993 to 2001 (Ichii *et al.*, 2004; Mori *et al.* 1999). Based on observations of the vertical distribution of paralarvae and juveniles in the wild (Okutani, 1968; Young & Hirota, 1990; Saito & Kubodera, 1993), particles were released at depths of 4 m in a horizontal velocity field with no-diffusion. The vertical distribution of the particles was fixed to a depth of 4 m for the duration of the simulation because the distribution of neon flying squid larvae appears to be restricted to near the ocean surface (Saito & Kubodera, 1993; Bower, 1996). Particles simulating the autumn cohort were released on October 1 and November 1 from 1993 to 2001, while particles simulating the winter-spring cohort were released on February 1 and May 1 from 1993 to 2001.

Figure 2 shows the distribution of particles, which remained very close to their initial positions and exhibited very little year-on-year variation. The particles of the autumn cohort moved eastward for approximately 120 nautical miles (220 kilometers), while the particles of the winter-spring cohort moved northward for approximately 120 nautical miles. The track followed by the particles

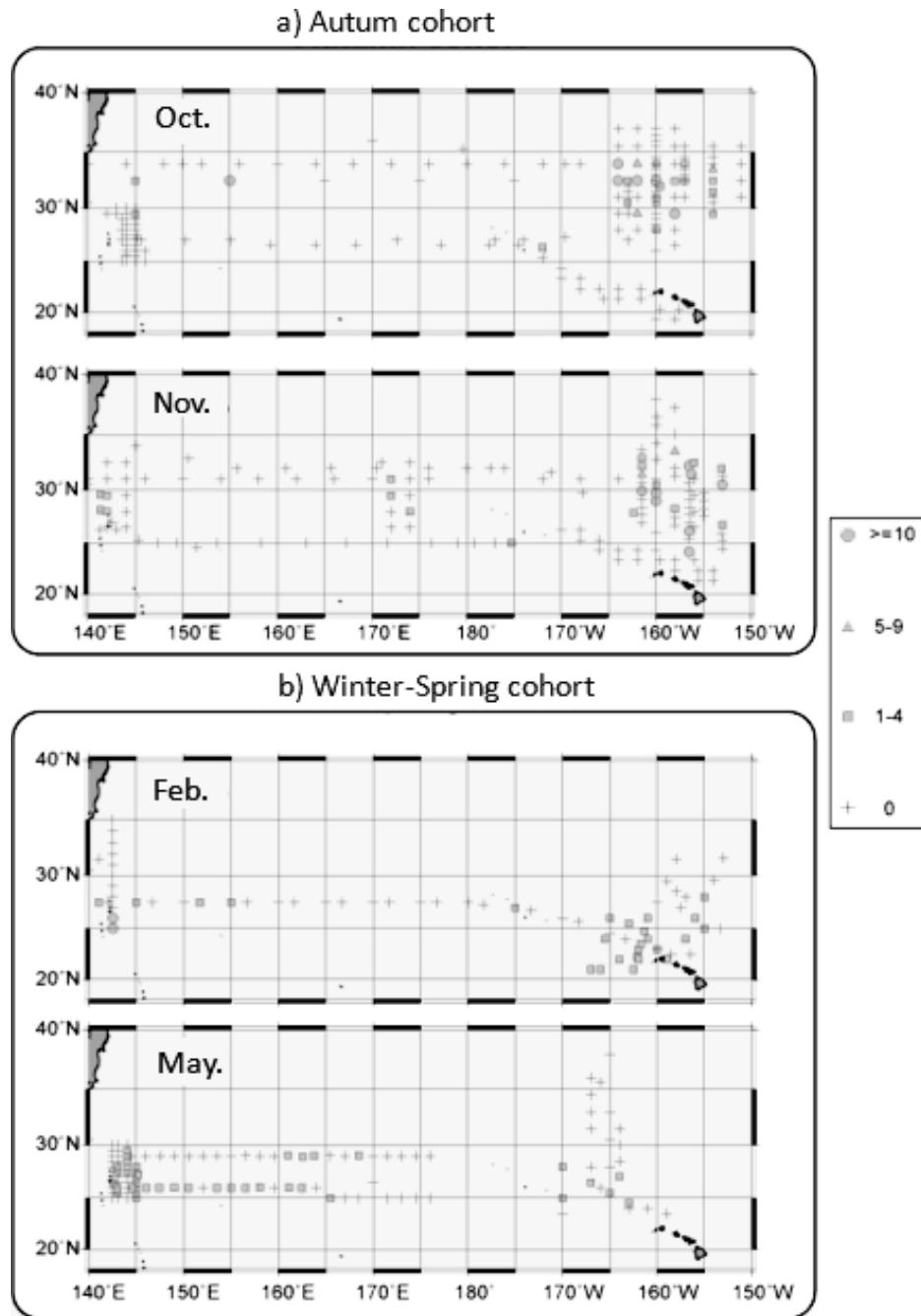


Figure 1a-b. Distribution of paralarval neon flying squid (redrawn from Ichii *et al.* 2004). Paralarval densities were standardized as the number of individuals caught per 20 min. using a using a ring net (diam: 2 m) and surface tow. Black boxes indicate the release of simulated particles. (a) Autumn cohort, (b) winter-spring cohort.

released in November, varied only slightly between years, and the particles that were released in November were typically present at low densities. Thus, horizontal diffusion of the particles was higher in November than in other months.

These results closely corroborate the changes observed in larval distribution at ambient water temperatures. Figure 3 shows

the variation in the ambient water temperature over time. The accumulated water temperature for a 30-day period can be calculated using the following equation:

$$T = \frac{1}{1000} \sum_{j=1}^{1000} \sum_{i=1}^{30} (t_{ij})$$

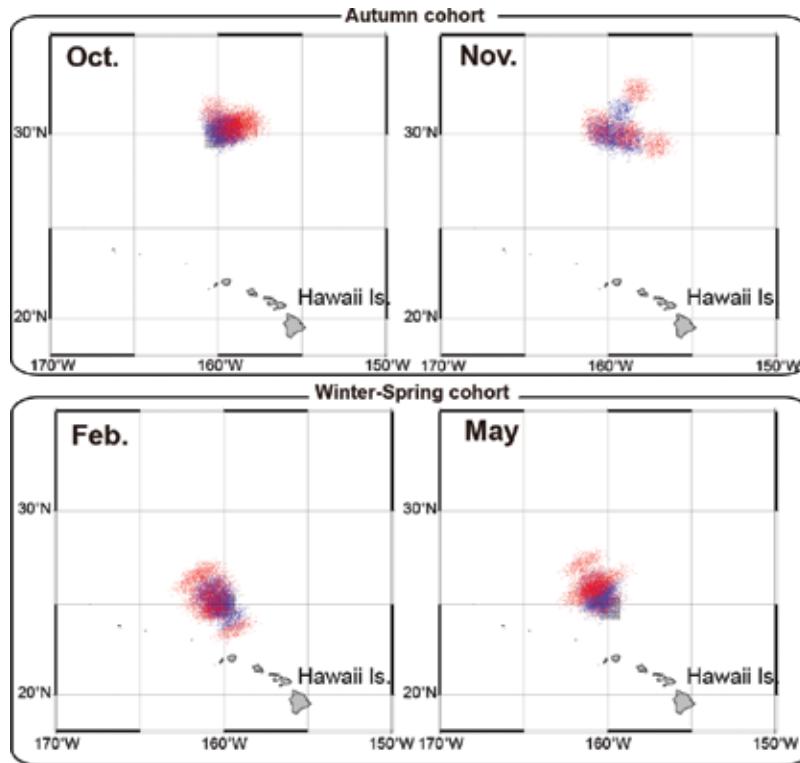


Figure 2. Distribution of particles calculated by an advection and diffusion model. Blue and red dots indicate particle distributions at 15 and 30 days, respectively.

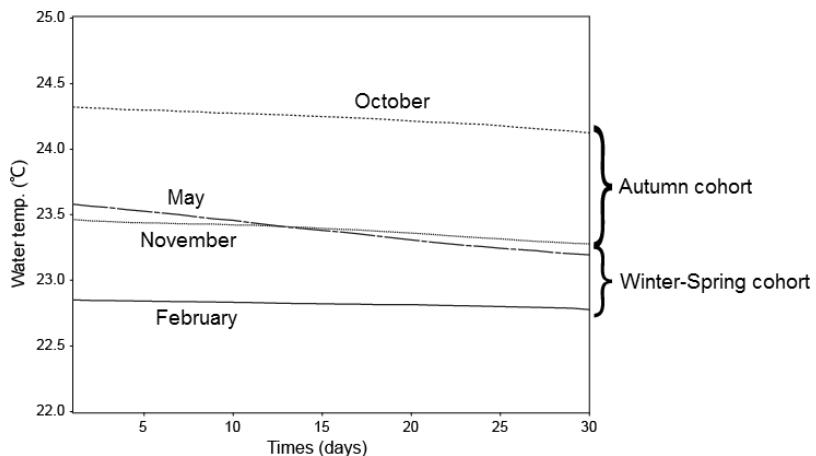


Figure 3. Ambient temperature on each larval particle release date calculated by 4D-VAR.

where t_{ij} is the ambient water temperature ($^{\circ}\text{C}$) of particle. j indicated particle identification number. One thousand particles were released at one experiment. i represented days after particles released. T is the accumulated water temperature ($^{\circ}\text{C}\cdot\text{day}$). There were large difference in the accumulated water temperature between the particles that were released in October and those that were released on February (Fig. 4). The value of difference was $42.5\text{ }^{\circ}\text{C}\cdot\text{day}$.

DISCUSSION

The projections of the Lagrangian particle-tracking model employed in this study showed that larvae are not transported long distance during the larval period. In addition, the ambient water temperature during the larval period of the autumn cohort was estimated to be 1 to $1.5\text{ }^{\circ}\text{C}$ higher than it was during the larval period of the winter-spring cohort. Since individuals belonging to the au-

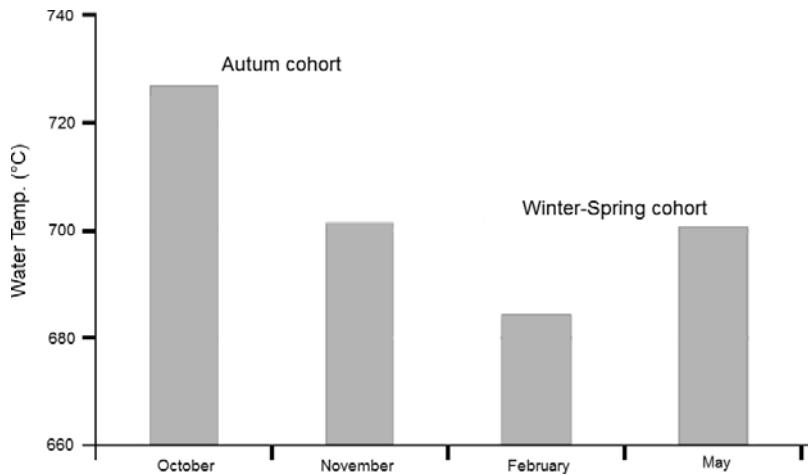


Figure 4. Accumulated water temperature during the larval period for each larval particle release date calculated by 4D-VAR.

tumn cohort were typically larger than those of the winter-spring cohort (Yatsu *et al.* 1997, 1998), it appears likely that the difference in ambient water temperature, especially in the accumulated water temperature, affects larval growth. Semmens and Moltschanowskyj (2000) concluded that the larger muscle blocks of loliginid squid *Sepioteuthis lessoniana* Lesson, 1830 affected both body size and individual growth rates. And larval growth in *S. lessoniana* was also influenced by environmental factors, population density, and, to some extent, genetic background. The presence of a continuous environmental parameter is also considered important for understanding growth dynamics in cephalopod. Stochastic analysis of wild-caught individuals revealed that growth was dependent on ambient temperature (Sakai *et al.*, 2004). Growth simulations by Forsythe (1993) revealed that even a 1 °C increase in average temperature during the 90-day exponential growth phase of larvae was capable of producing a two-fold increase in larval weight, while a 2 °C increase would result in a five-fold increase in larval weight over time. Grist and Clers (1999) reported that the body size of individual squid increases rapidly during the first stage of growth and that growth rate is temperature dependent. Andre *et al.* (2009) employed the model to investigate growth patterns occurring at different temperatures for 2 octopus species, *Octopus ocellatus* Gray, 1849 and *O. pallidus* Hoyle, 1885. The model projections were consistent with laboratory data and suggest that increases in temperature as small as 1 °C could have a significant influence on cephalopod growth, affecting the threshold body mass by up to 15.5% and the body mass at 100 d by up to 62.6%. From the above, difference of ambient water temperatures could be caused the difference of mantle length between autumn cohorts and winter-spring cohorts.

However the growth rate was also considered to be affected by nutrient conditions (Ichii *et al.*, 2004; Forsythe, 1993). Ichii *et al.* (2004) reported that the spawning grounds of the autumn cohort of *O. bartramii* are located within the subtropical frontal zone, which

is characterized by enhanced productivity in winter due to its proximity to the transition zone chlorophyll front (TZCF); a zone of surface convergence where cool surface waters with high chlorophyll a concentrations from the north sink beneath warm oligotrophic waters from the south (Polovina *et al.*, 2001). Conversely, the spawning grounds of the winter-spring cohort are located in the subtropical domain, which is less productive (Ichii *et al.*, 2009). Unlike their study, satellite chlorophyll data was not employed in this study because of the large spatiotemporal differences in the data resolution between the physical data of the model used in this study and that of satellite data. Future research will focus on the development of an ecosystem model capable of using high-resolution physical data to clarify the effect of ambient nutrient conditions on larval growth in *O. bartramii* in greater detail.

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