Impact of paralarvae and juveniles feeding environment on the neon flying squid (*Ommastrephes bartramii*) winter–spring cohort stock

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ABSTRACT

In this study, we found that there were significant positive correlations between the catch per unit effort (CPUE, a squid abundance index) for the neon flying squid (*Ommastrephes bartramii*) winter–spring cohort and the satellite-derived chlorophyll a concentrations in their spawning grounds located at 140–160°E where 21°C < sea surface temperature < 25°C from February to May. The spawning grounds of the winter–spring cohort are located in a quiet stream region, and a particle tracking experiment, based on the velocity field obtained from an ocean data assimilation system, showed that paralarvae and juveniles aged <90 days remained in their spawning grounds and the chlorophyll a concentration in their habitat had a significant positive correlation with the CPUE. A backward particle tracking experiment also showed that the chlorophyll a concentration in the spawning grounds had a significant positive correlation with the autumn–winter mixed layer depth. Based on these results, we hypothesize that the CPUE interannual variability is caused by variations in the feeding environment of the paralarvae and juveniles, which may be linked to autumn–winter mixed layer depth variations.

Key words: neon flying squid, ocean data assimilation system, particle tracking experiment, stock fluctuation

INTRODUCTION

The neon flying squid (*Ommastrephes bartramii*) is an oceanic squid that lives in the subtropical and temperate waters of the world’s oceans (Roper et al., 1984). The optimum spawning zone for this species is defined by a sea surface temperature (SST) range of 21–25°C (Bower, 1994; Ichii et al., 2004) and the squid migrate between their spawning grounds in the subtropical waters and feeding grounds in the subarctic waters (Fig. 1). The North Pacific population comprises an autumn cohort and a winter–spring cohort (Yatsu et al., 1997, 1998). Recently, the catches and stock levels of the winter–spring cohort have varied drastically from year to year. In 2009, the catch in Japan during the winter fishing season was 11 500 t. By contrast, the catch in 2010 was <20% of its 2009 level. A year later, in 2011, the catch recovered to 60% of that in 2009 (Fisheries Agency and Fisheries Research Agency of Japan, 2011).

For the autumn cohort, the food availability for juvenile neon flying squid may be critical for the level of stock recruitment (Ichii et al., 2011). It was found that the winter position of the transition zone chlorophyll front (TZCF) in the nursery grounds of the autumn cohort could predict the change in the catch per unit effort (CPUE). In a high stock regime, a high chlorophyll concentration zone was found in vast parts of the main spawning and nursery grounds due to the southward expansion of the TZCF. Thus, the feeding environment is an important factor that determines the autumn cohort recruitment.

For the winter–spring cohort, the variability in recruitment was explained by variation in the SST. Chen et al. (2007) found that the SST rises by 1°C in a La Niña year compared with the normal level, and a
higher SST resulted in unfavorable recruitment conditions. In an El Niño year, however, the SST was almost the same as that in a normal year, thereby leading to favorable conditions for recruitment. Cao et al. (2009) suggested that a high SST reduced the proportion of favorable SST areas in the spawning grounds during a La Niña year. However, it must be noted that variation in the SST should not influence the feeding environment directly during the early life stages of the squid. Roberts (2005) found significant negative correlations between the chokka squid (Loligo vulgaris reynaudii) catch and the SST near the spawning grounds. A low SST is caused by mesoscale upwelling, and the movement of nutrient-rich deep layers toward the surface stimulates a nutritional condition that should cause a proliferation of copepods, which are the main forage of the chokka squid paralarvae. Thus, previous studies of the neon flying squid winter–spring cohort stock show that their recruitment may be affected by the feeding conditions in their nursery grounds.

In the present study, we calculated the CPUE, which is assumed to reflect the squid stock level, and investigated the possible feeding conditions in the nursery grounds that may have affected winter–spring cohort recruitment based on a correlation analysis between the CPUE and satellite chlorophyll a (Chl-a) data to try to understand why the feeding environment varied among years. It is known that the paralarvae and juveniles feed on dissolved organic material and/or zooplankton (Uchikawa et al., 2009), but long-term dissolved organic material and zooplankton biomass data were not available for the nursery grounds. However, satellite-derived Chl-a data have been collected continuously in a form that is suitable for statistical analysis and mapping. The spatial distribution and abundance of zooplankton are driven by concomitant primary production, so satellite Chl-a data were used previously to estimate the productivity in the chokka squid paralarvae feeding grounds (Roberts, 2005). Thus, we used satellite Chl-a data as an index of the feeding conditions in the present study.

MATERIALS AND METHODS

Squid CPUE data
We use CPUE (raw catch kg per vessel per day) data as an index of squid abundance (stock level). The CPUEs of commercial jigging vessels from 2001 to 2011 were calculated using a dataset (daily catch per vessel) collected by the Fisheries Research Institute, Aomori Prefectural Industrial Technology Research Center. Commercial jigging vessels operate off the coast of northeast Japan from 140° to 150°E and 35° to 42°N in the winter from January to March, targeting the winter–spring spawning cohort. Almost all of the vessels in the database were categorized as the medium class size, from 138 to 183 GT, and they were equipped with about 24 automatic jigging machines with double reels.

Chlorophyll a data
The Chl-a data were derived using Standard Mapped Image products (Level-3) from the ocean color sensor known as MODIS, on board the Aqua satellites (NASA). These data are available from the following site: http://oceandata.sci.gsfc.nasa.gov/MODISA/ Mapped/ [accessed 30 July 2011]. Monthly data were used for the correlation analysis and 8-day interval data were used for the particle tracking experiments. The horizontal resolution of the Chl-a data was 9 km and the study period was 2003–2010.
Oceanographic data
We estimated the distributions of paralarvae and juveniles using particle tracking experiments. To facilitate the release of particles and to determine the spawning grounds, we used velocity data, SST, and mixed layer depth (MLD) information, which were obtained from an ocean data assimilation system, MOVE/MRI.COM-WNP (Usui et al., 2006). MLD is defined as the depth where the density is 0.125 kg m\(^{-3}\) higher than that at the surface. The ocean data assimilation system comprised an ocean general circulation model (OGCM) and a variational analysis scheme.

The OGCM was the MRI Community Ocean Model (MRI.COM) described by Tsujino et al. (2010). The model domain encompassed 117°E to 160°W zonally and from 15°N to 65°N meridionally. The horizontal resolution was variable: 1/10° from 117°E to 160°E, and 1/6° from 160°E to 160°W, zonally; and 1/10° from 15°N to 50°N, and 1/6° from 50°N to 65°N, meridionally. There were 54 vertical levels with increasing thicknesses from 1 m at the surface to 600 m near the bottom. The assimilation part of the system was the western North Pacific version of the MRI Multivariate Ocean Variational Estimation (MOVE-WNP; Usui et al., 2006) system. MOVE-WNP estimates the temperature and salinity fields using a multivariate 3DVAR scheme with a vertically coupled temperature–salinity empirical orthogonal function modal decomposition (Fujii and Kamachi, 2003).

Correlation analysis
In the present study, the correlation coefficient was Pearson’s product–moment correlation coefficient. The data were assumed to be normally distributed and Pearson’s product–moment correlation coefficient is generally used for relational analyses between environment factors and squid stocks (e.g., Chen et al., 2012). We determined the correlation coefficients of two spatial distributions. One was the correlation between the Chl-a concentration and CPUE with respect to the longitude–latitude coordinates. In this analysis, the Chl-a concentration obtained from MODIS was interpolated to a 1° × 1° horizontal resolution. The other was the correlation between the Chl-a concentration and CPUE with respect to the longitude–SST coordinates. In this coordinate system, the meridional position was replaced by the SST at each longitude. The correlation analysis was performed by comparing the CPUE with the Chl-a concentration, which was averaged in the 20° longitude × 1°C SST box on the longitude–SST coordinates system. We defined a significant correlation as \(P < 0.05\). In both analyses, we compared CPUE against the previous year’s Chl-a concentration. This is because the vessels caught adult squid born in the previous year.

Particle tracking experiment
We conducted two particle tracking experiments: (i) forward particle tracking to analyze the feeding environment of the paralarvae; and (ii) backward particle tracking to analyze the MLD history of the feeding grounds. The particle locations were traced according to the following formula (Awaji et al., 1980):

If a particle moves from an initial position \(x_0\) at time \(t_0\) to a new position \(x = x_0 + \Delta x\) at time \(t\), then its Lagrangian velocity \(u(x_0, t; t_0)\) is given as

\[
\begin{align*}
\mathbf{x}(x_0, t; t_0) &= \mathbf{x}(x_0, t) \\
\mathbf{u}(x_0, t; t_0) &= \mathbf{u}(x_0, t) + \Delta \mathbf{x} \cdot \nabla_H \mathbf{u}(x_0, t)
\end{align*}
\]

(1)

where \(\mathbf{x}\) is the three-dimensional position vector and \(\mathbf{u}\) is the three-dimensional velocity vector in the Eulerian system. The new velocity of the particle depends on the space gradient of the velocity field. If \(\Delta \mathbf{x}\) is very small compared with the local length scale of the velocity field \(\mathbf{u}\), \(\Delta \mathbf{x}\) can be given as

\[
\Delta \mathbf{x} = \int_{t_0}^{t} \mathbf{u}(x_0, t) \, dt
\]

(2)

Thus, the new position \(\mathbf{x}(x_0, t; t_0)\) is defined by

\[
\begin{align*}
\mathbf{x}(x_0, t; t_0) &= \mathbf{x}_0 \\
&+ \int_{t_0}^{t} \left\{ \mathbf{u}(x_0, t; t_0') + \int_{t_0}^{t} \mathbf{u}(x_0, t; t_0') \mathbf{d}t' \right\} \cdot \nabla_H \mathbf{u}(x_0, t)
\end{align*}
\]

(3)

which is obtained by integrating Eqn (1) over a small time interval \(\Delta t = t - t_0\). We did not consider diffusion in this study.

The correlation analysis between the Chl-a concentration in the spawning grounds and the CPUE could not clarify how long the feeding environment affected the CPUE. If the eggs were flushed rapidly from the spawning grounds by strong current, the CPUE may be determined based on the feeding environment immediately after hatching, which is similar to the critical period hypothesis (Hjort, 1914), whereas the cumulative feeding environment would have affected the CPUE if the eggs, paralarvae and juveniles remained in the spawning grounds for a long time. The neon flying squid hatch within 3–4 days after spawning and they are transported passively like

particles for at least 1 week. The development of the swimming ability of paralarvae and juveniles is unclear, so we assumed that the duration of the passive transport period was 0–30, 0–60 and 0–90 days after the eggs were spawned. The particles were placed in the spawning grounds at 0.2° latitude and longitude intervals and released on days 3, 11, 19 and 27 in each month from December to May during 2003 to 2010, which corresponded to the winter–spring spawning season (Okutani, 1968; Yatsu et al., 1997). The spawning grounds are defined by a favorable spawning SST range of 21–25°C (Bower, 1994; Ichii et al., 2004) within the area bounded by the 117°E–160°W longitudes. The distribution of the early life stage may have an upper limit of 50 m (Okutani, 1968; Young and Hirota, 1990; Saito and Kubodera, 1993). Based on a previous particle tracking experiment with paralarvae (Kato et al., 2014), the particles were released at depths of 4 and 50 m in a horizontal velocity field. We temporally interpolated the original 5-day interval snapshot velocity data and 8-day interval Chl-a data to obtain a per-day resolution. There were occasional missing data points because of cloud in the 8-day interval Chl-a data. In these cases, we used the monthly Chl-a data. Particles correlated with Chl-a concentration after day 90 were not included in the particle number estimates.

To analyze the MLD history of waters in the feeding grounds, the particles were placed in the feeding grounds at 0.2° latitude and longitude intervals from 2000 to 2010: in areas located at 140–160°E where 21°C < SST < 24°C on February 15; in the areas located at 140–160°E where 21°C < SST < 24°C on March 15; in the areas located at 140–160°E where 22°C < SST < 25°C on April 15; and in areas located at 140–160°E where 21°C < SST < 25°C on May 15. The MLD and Chl-a data were recorded along the particle trajectories for 9 months. We wanted to determine the origins of waters that appeared at the surface layer in the feeding grounds, so the particles were released at a 4-m depth in a three-dimensional velocity field. Note that this experiment involved backward tracking.

RESULTS

Spatial distributions of the correlations between CPUE and Chl-a concentration

There were positive correlations between the CPUE and the previous year’s Chl-a concentration in the area located at 140–160°E and 20–30°N from December to February and in the area located at 140°E–160°W and 20–35°N from March to May (2004–2011, Fig. 2). Based on a comparison of the location of the long-term mean SST of the 21°C and 25°C contour lines, which correspond to the lower and upper limits of optimum spawning temperature for the neon flying squid, the area bounded by the 140–160°E longitudes and 20–30°N latitudes from January to May overlapped with the spawning grounds (Fig. 2b–f). During February and March, in particular, the positive correlations were focused in the spawning grounds from 140 to 160°E (Fig. 2c,d).

The spawning grounds depend on SST, so we rearranged the correlation coefficient distribution in the longitude–SST coordinate system where latitude was replaced by SST. In this coordinate system, spatially continuous positive correlations were observed in the area where the SST ranged from 21° to 24°C in February, from 21° to 24°C in March, from 22° to 25°C in

Figure 2. Distributions of the correlation coefficients between: (a) the CPUE of the neon flying squid winter–spring cohort during the period 2005–2011 and December Chl-a concentration during the period 2003–2009; and (b–f) CPUE during the period 2004–2011 and the Chl-a concentration in January to May during the period 2003–2010. The contour lines denote the long-term mean SST of 21°C and 25°C, which correspond to the lower and upper limits of the optimum spawning temperature range. Note that the correlation coefficients are shown based on the 90%, 95%, and 99% confidence intervals (d.f. = 6 for all except (a), where d.f. = 5, t-test).

April, and from 21° to 25°C in May at 140–160°E (Fig. 3c–f). The longitude–SST coordinates clearly had positive correlations near the spawning grounds (21°C < SST < 25°C) in April and May, which could not be identified easily in Figure 2.

The correlation coefficients in the area with an SST of 22°C in February, 25°C in April, and 24°C in May were not significant (0.05 < P < 0.1, d.f. = 6, t-test; Fig. 3c,e,f). However, the correlation coefficients were significant between the CPUE and averaged Chl-a concentration in the regions with spatially continuous positive correlations (shown in Fig. 3): r = 0.75 (P = 0.03) in February; r = 0.84 (P = 0.009) in March; r = 0.70 (P = 0.05) in April; and r = 0.79 (P = 0.02) in May (Fig. 3b–f). The time-series data detected a clear relationship between the Chl-a concentration and CPUE, where the average Chl-a concentrations near the spawning grounds were high in high CPUE years (2004–2006 and 2008–2009) and low in low CPUE years (2007 and 2010–2011; Fig. 4). These results suggest that the CPUE can be affected by the Chl-a concentration immediately after spawning.

We also found significant positive correlations between the CPUE and Chl-a concentration from 160°E to 160°W in May (Fig. 3f), when the SST was lower than the optimum spawning temperature. This result is discussed in the Discussion section.

**CPUE and Chl-a concentrations in the feeding grounds**

To estimate how long the feeding environment of the early life stage affected the CPUE, we investigated the Chl-a concentration during the passive transport stage (henceforth, the ambient Chl-a) with particle tracking experiments. In these experiments, the particles represented eggs, paralarvae and juveniles. We found that there were significant positive correlations between the CPUE and the ambient Chl-a concentration, which were averaged along the particle tracks during the periods 0–30, 0–60 and 0–90 days after the eggs were released from December to May (Fig. 5). In particular, for the paralarvae and juveniles that originated

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**Figure 3.** This figure is the same as Figure 2, except the y-axis is changed from latitude to SST. The solid lines indicate the optimal spawning SST range. The correlation coefficient was defined as described in Figure 2.
from the January–April spawning grounds in the area bounded by the 140°–160°E longitudes, we detected significant positive correlations between the CPUE and the ambient Chl-a concentration (Fig. 5b–e). The eggs were released at 8-day intervals and at depths of 4 and 50 m, but the results did not depend on 8-day release interval or the depth. Figure 5 shows the results for the eggs we released on the 11th day of the month at a depth of 4 m, which are typical of the results obtained each month.

Figure 6 shows time-series plots of the CPUE and the ambient Chl-a concentration, which were averaged for the periods 0–30, 0–60 and 0–90 days after the eggs were released on March 11 at a depth of 4 m. Each ambient Chl-a varied corresponding to the CPUE interannual variation and there were significant correlations between the two values. These results suggest that the CPUE was affected by the cumulative feeding environment of the 1- to 3-month-old paralarvae and juveniles spawned in the area from 140° to 160°E.

The distances between the spawning grounds and the locations of 30-, 60-, and 90-day-old paralarvae and juveniles spawned in the area from 140° to 160°E are shown in Figure 7. The longitudinal and latitudinal differences were within ±0.6° at 30 days (Fig. 7a), within ±1.2° at 60 days (Fig. 7b) and within ±1.8° at 90 days (Fig. 7c). These differences did not depend on the release depth. The paralarvae and juveniles tended to be distributed in the southwestern part of the spawning grounds from December to February, and in the northeastern part of the spawning grounds from March to May. This seasonal tendency may be related to seasonal monsoons because the release depth was in the surface Ekman layer. In conclusion, the paralarvae and juveniles spawned in the area of 140°–160°E between January and April remained in the area, and there were positive correlations between the CPUE and Chl-a concentrations until 90 days of age (and the 140°–160°E spawning grounds from February to May), as shown in Figures 3 and 4.

**Chl-a concentration and MLD history of waters in the feeding grounds**

The results suggested that the February–May Chl-a concentration in the area bounded by the 140°–160°E longitudes affected the CPUE via the feeding environment of the paralarvae and juveniles. One of the
Factors that controlled the Chl-a concentration was the autumn–winter MLD interannual variation (e.g., Sverdrup, 1953). This is because the mixed layer deepened from autumn to winter and supplied nutrients to the surface layer. Therefore, we investigated the MLD history of the waters located in the February–May spawning grounds from 140° to 160°E, which roughly corresponded to the feeding grounds of the paralarvae and juveniles, and we compared them with the Chl-a concentrations during the February–May feeding season.

We found positive correlations between the Chl-a concentration and MLD history from September (in the previous year) to January and from February to March (Table 1). Some examples of the Chl-a concentration and the autumn/winter MLD history

Figure 5. Release points of all eggs located in the optimum spawning SST range of 21–25°C (gray dots) and release points of the eggs where the ambient Chl-a concentration had significant positive correlations with the CPUE (black dots). The release dates were: (a) December 11, (b) January 11, (c) February 11, (d) March 11, (e) April 11 and (f) May 11. The Chl-a concentration was averaged for the periods: (i) 0–30 days after the eggs were released; (ii) 0–60 days after the eggs were released; and (iii) 0–90 days after the eggs were released.

Figure 6. Time-series of CPUE (solid line with closed circles) and the ambient Chl-a concentration (broken line with open squares) for the paralarvae and juveniles, which were averaged for the period: (a) 0–30 days after the eggs were released, (b) 0–60 days after the eggs were released, and (c) 0–90 days after the eggs were released. The eggs were released at 155.4°E and 24.6°N at a depth of 4 m on March 11. Note that the Chl-a concentration lags 1 yr behind the CPUE. r Denotes the correlation coefficient and P denotes probability value.

Figure 8. The Chl-a concentration was high in the years when the autumn/winter mixed layer was deep. This relationship suggests that the autumn/winter MLD interannual variation affects the Chl-a concentration in the feeding grounds via the nutrient supply.

CPUE and MLD history of waters in the feeding grounds

The Chl-a data were available from MODIS from 2003, so we compared the Chl-a from 2003 to 2010 with the CPUE from 2004 to 2011. However, the CPUE data were available from 2001, whereas the ocean environment data from the assimilation system were available from 1999. If the MLD interannual variation affects the CPUE via the feeding environment, there should be positive correlations between the MLD and CPUE. Therefore, we investigated the MLD history of the waters in the feeding grounds from 1999 and compared them with the CPUE from 2001 to 2011.

Similar to the correlations between the MLD history and Chl-a concentration, the autumn–winter MLD history had significant correlations with the CPUE (Table 2). The November–December MLD history of the waters from the February–May feeding grounds had particularly high (P < 0.01) positive correlations with the CPUE. Note that the MLD history of the waters from the February–April feeding grounds had significant positive correlations with the Chl-a concentration in the feeding grounds (Table 1). Furthermore, the time-series data detected a clear relationship in which the CPUE was high in the years with deep mixed layer depths (Fig. 9a–c). The November–December MLD history of waters from the February–May feeding grounds had a positive but insignificant correlation with the Chl-a concentration (r = 0.37, P = 0.14, Table 1), whereas the correlation between the MLD history and CPUE was significantly positive and the time-series data exhibited synchronous interannual variation (Fig. 9d). This discrepancy is discussed in the Discussion section. The February–March MLD history of the waters from the May feeding grounds had significant positive correlations with the Chl-a concentration and CPUE (Tables 1 and 2), and the MLD interannual variations also agreed well with that of the CPUE (Fig. 9e). Thus, our hypothesis that the autumn–winter MLD affects the CPUE via the feeding environment is a reasonable explanation for the CPUE interannual variability observed over the past 11 yr.

Figure 10 shows the locations of the waters for the MLD history recorded in Figure 9. The center of the distribution was located in the area at 140–160°E and 23–28°N from November to December (Fig. 10a–d), and in the area located at 140–160°E and 25–30°N from February to March (Fig. 10e). Based on a comparison of the center of the distribution with the initial position of the waters (feeding grounds), we found that the waters remained near the feeding grounds for a few months. As described in the previous section, feeding grounds were also formed near the spawning grounds. Thus, the feeding environment of the paralarvae and juveniles could be affected by the autumn–winter ocean environment near the spawning grounds.

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DISCUSSION

We detected significant positive correlations between the CPUE of the neon flying squid winter–spring cohort and the ambient Chl-a concentration in the areas where paralarvae and juveniles were spawned from January to April, which were bounded by the 140–160°E longitudes. The Chl-a concentration is a good index for the food availability for paralarvae and juveniles. There were also significant positive correlations between the Chl-a concentration in the feeding grounds and the autumn–winter MLD history of the waters in the feeding grounds. In general, the deep mixed layer supplies high volumes of nutrients to the surface layer, which activates photosynthesis. The winter deep mixed layer sometimes inhibits photosynthesis, but the winter Chl-a concentration was higher than the spring Chl-a concentration in the feeding grounds (Fig. 4). In this region, it is possible that the winter mixed layer was not sufficiently deep to inhibit photosynthesis and the most significant factor that controlled photosynthesis was the nutrient supply. Thus, the relationships between the CPUE and Chl-a concentration and between the Chl-a concentration and MLD suggest that deep autumn–winter mixed layer in the feeding grounds of the paralarvae and juveniles was linked to the higher nutrient concentrations, phytoplankton density, zooplankton density,

Table 1. Correlations between the Chl-a concentration of waters in the feeding grounds and the MLD history of waters in the feeding grounds. The first column shows the particle release date and the Chl-a concentration was recorded in the month. The first row shows the period over which the MLD history was averaged.

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<td>15 February released</td>
<td>0.62</td>
<td>0.78**</td>
<td>0.93**</td>
<td>0.86**</td>
<td>0.73*</td>
<td>0.69</td>
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<td>15 March released</td>
<td>0.85**</td>
<td>0.55</td>
<td>0.67</td>
<td>0.81*</td>
<td>0.78*</td>
<td>0.63</td>
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<tr>
<td>15 April released</td>
<td>0.03</td>
<td>0.66</td>
<td>0.38</td>
<td>0.71*</td>
<td>0.73*</td>
<td>0.50</td>
<td>0.37</td>
<td>0.56</td>
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<tr>
<td>15 May released</td>
<td>−0.15</td>
<td>0.64</td>
<td>0.91**</td>
<td>0.29</td>
<td>0.40</td>
<td>0.57</td>
<td>0.45</td>
<td>0.33</td>
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The single asterisk (*) denotes 0.01 < P < 0.05, and the double asterisk (**) denotes P < 0.01.
and dissolved organic material density via a bottom-up process, and that the good feeding conditions for the paralarvae and juveniles resulted in high CPUEs and vice versa. The significant positive correlations between the autumn–winter MLD and CPUE also support this hypothesis. Correlation analysis sometimes showed a slight discrepancy, such as the correlation between the MLD and CPUE was significant but correlation between the MLD and Chl-\(\alpha\) concentration was not significant for May feeding environment (Tables 1 and 2). This may be due to non-linear interactions between the Chl-\(\alpha\) concentration and dissolved organic material or zooplankton. We should confirm the posited bottom-up process by ecosystem model analysis in the future.

We assumed that the passive transport period persisted for 30, 60, and 90 days based on the particle tracking experiments. The mantle length of the winter–spring spawning cohort at 90 days is about 100 mm (Chen and Chiu, 2003) so the passive transport period may be shorter than 90 days in reality. However, one of the authors (Mitsuo Sakai) observed that 2- to 3-month-old juveniles were distributed in the area with SST > 21°C, so these juveniles may remain near the spawning grounds voluntarily. Our findings that the particles did not move far from the

Table 2. Correlations between the CPUE and MLD history of waters in the feeding grounds. The first column shows the particle release date and the first row shows the period over which the MLD history was averaged.

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<th>15 January</th>
<th>December</th>
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<tr>
<td>15 February released</td>
<td>0.41</td>
<td>0.45</td>
<td>0.76**</td>
<td>0.75**</td>
<td>0.51</td>
<td>0.49</td>
<td></td>
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<tr>
<td>15 March released</td>
<td>0.51</td>
<td>0.51</td>
<td>0.61*</td>
<td>0.86**</td>
<td>0.85**</td>
<td>0.59</td>
<td>0.64*</td>
</tr>
<tr>
<td>15 April released</td>
<td>-0.08</td>
<td>0.59</td>
<td>0.54</td>
<td>0.84**</td>
<td>0.80**</td>
<td>0.48</td>
<td>0.63*</td>
</tr>
<tr>
<td>15 May released</td>
<td>0.14</td>
<td>0.29</td>
<td>0.72*</td>
<td>0.38</td>
<td>0.46</td>
<td>0.76**</td>
<td>0.77**</td>
</tr>
</tbody>
</table>

The single asterisk (*) denotes $0.01 < P < 0.05$, and the double asterisk (**) denotes $P < 0.01$.

Figure 9. Time-series of the CPUE (solid line with closed circles) and MLD history of waters in the feeding grounds (broken line with open squares). The starting months of the particle tracking experiments and MLD average periods are: (a) 15 February and 15 November–15 December, (b) 15 March and 15 November–15 December, (c) 15 April and 15 November–15 December, (d) 15 May and 15 November–15 December and (e) 15 May and 15 February–15 March. Note that the MLD history lags 1 yr behind the CPUE. $r$ Denotes the correlation coefficient and $P$ denotes the probability value (d.f. = 9, t-test).
spawning grounds within 90 days suggests that the current did not carry away the vulnerable neon flying squid, so they could feed on dissolved organic material and zooplankton in the spawning grounds until the age of 2–3 months. In conclusion, the important feeding grounds were centered on the spawning grounds bounded by the 140°–160°E longitudes, regardless of the duration of the passive transport period.

The paralarvae and juveniles remained near the spawning grounds, so we could not clarify whether there was a critical period shortly after hatching and at 0–30, 0–60 or 0–90 days after spawning based on the correlation analysis between the CPUE and Chl-a concentration. Previous studies offered some suggestions. Using individual-based model, Sinerchia et al. (2012) suggested that food availability during the early paralarvae stages (2–3 weeks after spawning) is generally important for squid recruitment. Laptikhovsky et al. (1993) found that remarkably high mortality rates due to starvation were recorded during the proboscis division stage (transformation of the paralarvae into juvenile) in Stenoteuthis pteropus because the proboscis is barely functional while division occurs. In the neon flying squid, transformation is complete around

Figure 10. Distribution density of particles (waters), which correspond to the MLD records shown in Figure 9. The density was the average for 2000–2010. The initial position of the waters were from 140° to 160°E and between the contour lines, which denote the long-term mean SST of: (a) 21° and 24°C in February, (b) 21° and 24°C in March, (c) 22° and 25°C in April, and (d, e) 21° and 25°C in May.
30 days after spawning (Wakabayashi et al., 2002; Shea, 2005). Based on the model experiment and morphological knowledge, the likely critical period is 0–30 days after spawning. It is interesting that the importance of the earliest feeding condition was not contradicted by our study. Survival during the first month of another cohort of neon flying squid and other squids in the same family did not contribute to the interannual variation in recruitment. The critical period for the neon flying squid autumn cohorts is at 2–3 months (Ichii et al., 2011), whereas the critical period of the Japanese common squid (Todarodes pacificus) winter cohort, which is distributed in the North Pacific, is 1 month after spawning (Mori, 2006). One possible explanation for the difference in the critical period is that both the neon flying squid autumn cohort and the Japanese common squid winter cohort experience drastic feeding environment fluctuations after 1 month of age relative to the neon flying squid winter–spring cohort. The feeding environment of the 2–3-month-old neon flying squid autumn cohort is strongly affected by the southward shift of the TZCF, which is defined as a Chl-a concentration of 0.2 mg m$^{-3}$ (Ichii et al., 2011). However, because the feeding grounds of the 2–3-month-old winter–spring cohort is in oligotrophic ocean, where the Chl-a concentration is <0.1 mg m$^{-3}$ (Fig. 6), the range of fluctuations in the Chl-a concentration is also smaller than that in the TZCF region. The neon flying squid winter–spring cohort remained in their spawning grounds until 3 months after spawning, whereas the Japanese common squid winter cohort is transported by the Kuroshio from their spawning grounds in the East China Sea to the Kuroshio Extension within 1 month (Mori, 2006). The fluctuations in the Chl-a concentration in the Kuroshio Extension are larger than those experienced in the East China Sea because both the Kuroshio and the Oyashio influence the Kuroshio Extension directly (e.g., nutrient and plankton advection from the eutrophic Oyashio region, and short-term drastic changes in the oceanic structure due to the collision of the Oyashio and the Kuroshio). By contrast, the spawning grounds of the neon flying squid winter–spring cohort are located in the gap between two subtropical countercurrents (Fig. 11), so the paralarvae and juveniles can remain in moderate environments until they are 3 months of age. Thus, the importance of the early feeding environment for the recruitment of the neon flying squid winter–spring cohort may be relatively greater than that for the autumn cohort and the Japanese common squid winter cohort.

Neon flying squid are cosmopolitan and the only restriction on their spawning is temperature. However, based on the differences in the occurrence of parasites, the winter–spring cohort in the North Pacific can be divided into two populations at 170°E: one from the western region and the other from the central-eastern region (Nagasawa et al., 1998). The westernmost point for the capture of paralarvae was off Okinawa island (Saito and Kubodera, 1993). Thus, the winter–spring cohort caught off the coast of northeast Japan are assumed to be distributed from 130° to 170°E. We found significant positive correlations between the CPUE and winter–spring Chl-a concentration in the area where the SST ranged from 21° to 25°C and from 140°E to 160°W (Figs 2 and 3), which are consistent with previous observations. We also found significant positive correlations between the CPUE and Chl-a concentration in the area where the SST ranges from 15° to 20°C and from 160°E to 160°W during May (Fig. 3f). The winter–spring cohort is distributed in

**Figure 11.** Eastward component of the surface velocity and the 21° and 25°C SST contour lines in February 2002. The locations of the two subtropical countercurrents (STCC) overlap with the SST contour lines. The remarkable eastward current to the north of STCC is the Kuroshio and the other strong eastward current to the south of STCC is the Hawaiian Lee Countercurrent (HLCC). The locations of STCC and HLCC were determined by Kobashi and Kawamura (2002).
the area where the SST ranges from 12° to 18°C during May (Ichii et al., 2004), so this significant positive correlation may suggest the effect of the feeding environment during the northward migration stage on the CPUE. However, it is doubtful that 160°E–160°W contains the actual feeding grounds of the western region cohort.

This correlation analysis cannot explain the CPUE interannual variation completely. This is partly because the CPUE is not necessarily an exact reflection of the stock levels. The winter–spring cohort is the main target of the Chinese jigging fishery that operates between 150°E–165°E and 38°N–46°N from August to November (Chen et al., 2008), which is before the Japanese survey and fishing season starts. The CPUE also depends on the formation of fishing grounds in the east of Japan, which are affected by the climate and ocean conditions. However, it is true that the CPUE depends on the stock level and our results support the hypothesis that the feeding environment of the early life stages is an important factor that affects stock fluctuations.

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