

Vertical Migratory Behavior of Jumbo Flying Squid (*Dosidicus gigas*) off Peru: Records of Acoustic and Pop-up Tags

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Abstract

The vertical migratory behavior of jumbo flying squid (*Dosidicus gigas*) was recorded in the Humboldt Current region off Peru in 2007 by ship-based tracking with acoustic tags for two days and a pop-up archival transmitting (PAT) tag for two weeks. Two squid (measuring 74.0 cm and 110.5 cm in dorsal mantle length, respectively) were tagged with acoustic tags. The larger one was also tagged with a PAT tag. Tracking data indicated that both squid dived to a depth of 1200 m in the daytime. Although the PAT tag was not recovered, its seven-day summary data that was recovered via the Argos satellite system suggest that *D. gigas* off Peru engage in diel vertical migration, where the squid also migrate to near the sea surface at night. Conversely, two daytime migration patterns were observed: migration to mid-waters above the oxygen minimum zone (OMZ) at depths between 200 and 800 m, and migration to deeper waters. During descents to 1200 m, the squid increased its descending velocity in the OMZ. We also discuss the biological implications of that diel vertical migration.

Discipline: Fisheries

Additional key words: biotelemetry, oxygen minimum zone, Humboldt Current system, diel vertical migration

Introduction

Since 1999, jumbo flying squid (*Dosidicus gigas*) have simultaneously shown larger body size at maturity and an abundant population, and also expanded their spatial distribution (Zeidberg & Robison 2007, Argüelles et al. 2008). The biomass of jumbo flying squid is potentially concentrated in the Humboldt Current region off Peru and Chile, as 90% of the world's commercial catch of jumbo flying squid is obtained there (FAO 2015).

The population of jumbo flying squid in the Humboldt Current region was affected by distinct ocean-atmosphere

events in the form of El Niño in 1997-1998 and La Niña in 1996-1997 and 1999-2000 (Waluda et al. 2006, Argüelles et al. 2008), prior to the growth seen in the years since 1999. Between the El Niño and La Niña events, the commercial catch and catch per unit effort (CPUE) of jumbo flying squid off Peru drastically decreased, with the fluctuations in both apparently being closely associated with those events. However, CPUE had been decreasing since 1995, even before these events according to Taipe et al. (2001). One possible factor is provided by data on fluctuations in the abundance of a mesopelagic fish (*Vinciguerria lucetia*), the primary prey of squid in the Humboldt Current region

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off Peru (Argüelles et al. 2008). Moreover, a study on the diel vertical distribution patterns of prey fish in the region (Cornejo & Koppelman 2006) showed that the vertical distribution of *V. lucetia* is restricted to the oxygen minimum zone (OMZ). Conversely, the diel vertical distribution of *D. gigas* in the region remains unclear. Yatsu et al. (1999) suggested diving to waters deeper than 1200 m through the OMZ in the daytime using acoustic tracking off Peru and in the Costa Rica Dome area. However, a conclusion remains pending as the acoustic signal was lost beyond the depth limit of transmission (1200 m). Dives deeper than 2000 m by *D. gigas* have been reported in California's Monterey Bay based on ROV observations (Zeidberg & Robison 2007).

Gilly et al. (2006) recently conducted intensive studies over long periods by using electronic tagging methods on the vertical migration of another population of *D. gigas* in the Gulf of California. According to their studies, the squid clearly engaged in diel vertical migration in the depth range from near the sea surface down to depths of 250-400 m, which mark the upper boundary of a midwater hypoxic zone. From a biological standpoint as well as for conducting daytime catch fishery activities using a 150-m jig line off Peru (Y. Ochi pers. comm.), clarifying whether the migratory behavior of squid in Monterey Bay and the Gulf of California is the same as that of squid in the waters off Peru poses a very interesting challenge.

The diel vertical migration of other ommastrephid squids, particularly larger species (i.e., *Ommastrephes bartramii*, *Sthenoteuthis pteropus*, *S. oualaniensis*, *Todarodes sagittatus*), has been well studied by employing acoustic tracking or observations using manned submersibles (Nakamura 1991, Nakamura 1993, Tanaka 2001, Sakai et al. 2006, Moiseev 1991). These studies showed that the squid engage in diel vertical migration and deep-water dives beyond 800-1000 m.

This paper mainly describes the vertical movement of *D. gigas* off Peru using both ship-based tracking with acoustic tags and archived trajectory with a Pop-up Archival Transmitting (PAT) tag. We intended to obtain evidence on whether *D. gigas* (especially the largest individuals) dives beyond the OMZ (as is seen in the Humboldt Current region off Peru) and migrates down to depths exceeding 1200 m.

Material and methods

This study was conducted in November and December 2007 (austral early summer) at two locations in the center of the Humboldt Current region off Peru (at 10-20°S / 79-82°W as shown in Fig. 1) during a research cruise aboard the R/V *Kaiyo Maru* (2942 GT) of the Fisheries Agency of Japan. We conducted two biotelemetry experiments for two large females, measuring 74.0 cm (Squid 1) and 110.5 cm

(Squid 2) in dorsal mantle length (ML), respectively (Table 1). These individuals were captured by hand-line fishing with commercial jigs for neon flying squid, using a jig 40 cm in length. Jigged squids were raised using a ring net (2 m in diameter) from the sea surface to the deck. The large squids landed were generally very calm in air due to their heavy bodies. ML was measured to the nearest 1 mm for all the squids captured. To assess sex and maturity, we observed the presence or absence of both the hectocotylus in the fourth arm and the spermatangium and seminal receptacles in the buccal area. All candidates of vigorous squid, with mantle cavity muscles pulsating rhythmically and not inking, were carefully treated. We pumped fresh seawater into the mantle cavity during all procedures conducted in air. We released the two squids within nine minutes after attaching their tags, using a scooper net to lower them to the sea surface. The local time used in this study was UTC-5 hrs. The water temperature (°C), dissolved oxygen (DO, ml l⁻¹), and salinity (psu) were measured by casts of a CTD profiler with a DO sensor (SBE 9 plus, Sea Bird Electronics) down to 3000 m and an XCTD probe (XCTD-4, Tsurumi Seiki Co.) casts down to 1950 m in the study area. According to Helly and Levin (2004), we defined the low dissolved oxygen concentrations (< 0.5 ml l⁻¹) at midwater depths as the oxygen minimum zone (OMZ). Squid body weight was estimated based on the length-weight relationship shown below (our unpublished data). $BW = 0.053ML^3 - 2.227ML^2 + 65.496ML - 614.66$ (n = 1106, r² = 0.989)

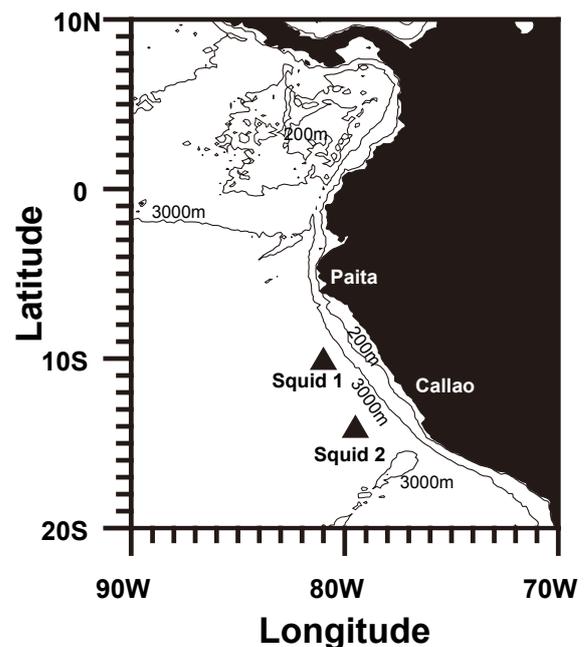


Fig. 1. Map of the study area in the Humboldt Current system off Peru. The black triangles indicate the experimental sites.

Table 1. Two *D. gigas* deployed for the telemetry studies

No.	Release date & time	Latitude/Longitude	ML cm (BW, kg)	Maturity and sex	Tag type	Tag/BW ratio (%)
1	30 Nov 2007 21:52	10°04'S/80°55'W	74.0 (13.5)	Copulated female	V22P-5XS-EP	0.6
2	13 Dec 2007 22:51	14°03'S/79°18'W	110.5 (50.9)	Copulated female	V22P-5XS-EP & PAT	0.3

1. Acoustic tag

The acoustic telemetry system (VEMCO Ltd.) employed in the present study consisted of directional hydrophones (VH41) attached to the bottom of a stainless steel pipe (9 m in length, 13 cm in diameter) placed alongside the ship, a receiver (VR28), a PC running “TRACK 28” software, and a 50-kHz ultrasonic transmitter “pinger” (V22P-5XS-EP, VEMCO Ltd.), measuring 120 mm in length and 22 mm in diameter, and with 40 g of mass in water and 84 g in the air. The nominal life span of the pinger is 11 d with a maximum working pressure at a depth of approximately 1000 m (pressure-resistant down to 1500 m). Its pressure sensor accuracy is 5%. We adopted two methods of attaching the pinger to the two squids: attachment to the forward part of the dorsal mantle, near the head, and firmly penetrated by two cable-ties (see Yano et al. 2000) (Fig. 2-A) for Squid 1, and attachment to the dorsal surface of a fin adjacent to the mantle with two cable-ties and a washer for Squid 2 (Fig. 2-B).

The signal was received onboard by the VR28 ultrasonic receiver that provides 360 degrees of monitoring coverage so that the transmitter bearing can be determined. All data received concerning depth, heading, position, speed, and position dilution of precision were digitally recorded by the PC, and then used to monitor vertical movement and horizontal direction. The ship followed the tagged squids as closely as possible, judging from the relative strength of the pinger signal and bearing indicator of the VR28 system.

2. PAT tag

A pop-up archival tag (PAT; Mk10, Wildlife Computers; 18 cm in length; 85 g of mass in air; specific gravity (i.e., the ratio of tag density to water density) < 1)) with an antenna 13-cm long was attached to Squid 2 in addition to a pinger (Fig. 2-B), thereby modifying the method described by Gilly et al. (2006). Prior to deployment, we programmed a histogram collection of summarized time-at-depth data for 14 bins (at 0, 10, 20, 50, 100, 150, 200, 300, 400, 600, 800, 1000, 1200 and deeper than 1200 m) at six-hours intervals in order to save the battery. The PAT tag was released from the squid at a designated time (after seven days) by electrolysis of a metal pin. After floating to the sea surface, the tag began transmitting the archived summary data, time-at-depth/time-at-temperature histograms, and depth and temperature ranges for each period via the ARGOS satellite

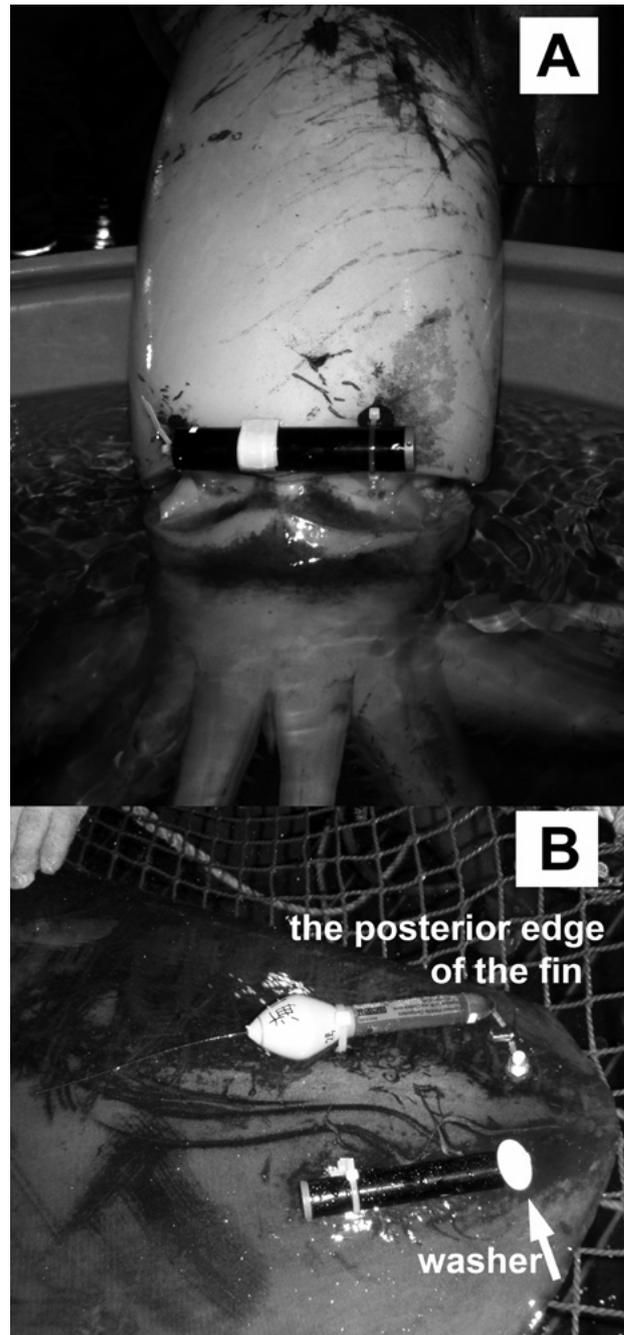


Fig. 2. Methods of attaching acoustic tags (pinger) and a pop-up archival transmitting (PAT) tag.

(A) Pinger tags were attached forward of the mantle with cable ties. (B) Pinger and PAT tags were attached to the dorsal surface of each fin with cable ties and a washer. See the text for details.

network. The Mk10-PAT tag uses a mechanical “guillotine” as a release device (RD1800) that prevents the tag from being crushed at intolerable depths beyond 1800 m. We did not recover the floating tag due to time limitations for this research cruise. Consequently, we could only obtain the archived time-series data.

Results

1. Hydrographic feature

The water temperature in the study areas decreased from 20°C on the sea surface to about 4°C at a depth of 1200 m, with a subsurface thermocline at depths of 50-200 m (Fig. 3). In contrast, the dissolved oxygen decreased drastically from the subsurface down to 200 m, especially at 125 to 175 m. The lowest dissolved oxygen layer (< 0.1 ml l⁻¹) was observed in the depth range of 220-400 m. And the oxygen minimum zone (OMZ) characterized by dissolved oxygen < 0.5 ml l⁻¹ (~20 μmol kg⁻¹ as defined as the upper boundary of the OMZ by Stewart et al. 2013) was distinct in the depth range of 200-800 m (Fig. 3). Beyond a depth of 500 m, however, a gradual increase in dissolved oxygen was observed from 0.17 ml l⁻¹ at 500 m to 1.45 ml l⁻¹ at 1200 m.

2. Telemetry by acoustic tags

Squid 1 was captured at 21:52 on 30 November 2007, and then was released and tracked for 11 hours. During the tracking, the moon’s age was 20.7 days. While the squid stayed in the subsurface layer at a depth of 6 to 14 m during the night, about 40 min. before sunrise the squid suddenly began a deep-sea dive (Fig. 4). The average speed of steepest descent was 16.8 ± 9.0 m min⁻¹ (SD) from the sea surface (almost 0 m in depth) to a depth of 650 m, and then decreased to 3.1 ± 2.8 m min⁻¹ (SD) in deeper waters. The squid reached a deeper layer at a depth of 1200 m and then migrated horizontally. Unfortunately, we had to abandon further tracking due to a long-line fishing boat blocking our

tracking course.

For the second tracking experiment, Squid 2 was caught at 22:51 on 13 December and then immediately released after tagging. During the tracking, the moon’s age ranged from 4 to 15 days. We tracked the squid for 36 hours (Fig. 5). And during the night tracking, we observed two descents down to depths of 100-200 m, 30-40 minutes before sunrise. The squid mainly stayed in the layer at depths of 150-200 m during the day, and mainly stayed in the subsurface layer at depths of 10-50 m at night (Fig. 6). On the second night of tracking, a descent to a depth of 200 m was observed 40 min. before sunrise. Finally around noon, we observed a sudden descent into deeper water. The

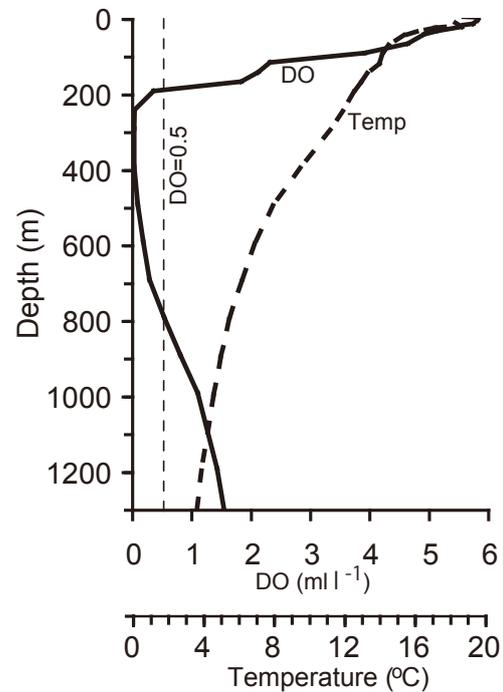


Fig. 3. Temperature and dissolved oxygen (DO) profiles at 14°S/79.5°W on 12 December 2007.

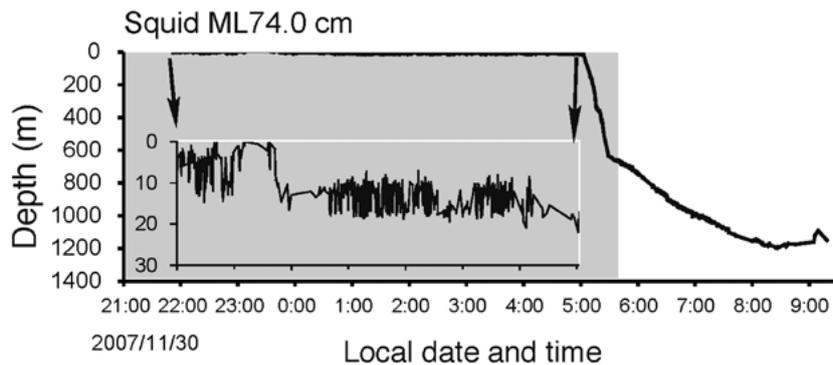


Fig. 4. Vertical tracking profiles of Squid 1 (ML 74.0 cm) from 21:52 on 30 November 2007 to 09:19 on 1 December 2007. Nighttime hours are shaded.

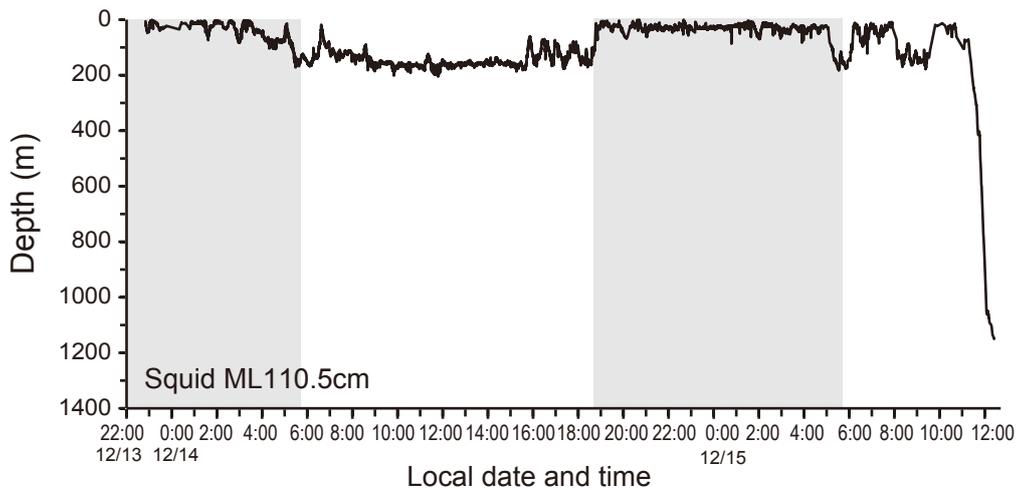


Fig. 5. Vertical tracking profile of Squid 2 (ML 110.5 cm) from 22:00 on 13 December 2007 to 15 December 2007. Nighttime hours are shaded.

squid dived down to 1100 m, beyond the maximum nominal working pressure at approximately 1000 m (Fig. 5). We continued monitoring the squid's behavior in descent until 1148 m, beyond which we lost continuous tracking signals and consequently completed the tracking.

During the deep-water dive, we monitored the descending velocity down to 1148 m (Fig. 7). The velocity fluctuated between 5-35 m min⁻¹. As the squid started diving, its velocity increased until the squid reached the upper boundary of the OMZ. And as the squid descended through the lowest oxygen dissolved layer at depths of 200-300 m in the OMZ, the descending velocity remained constant at about 15 m min⁻¹. As the squid dived to a deeper layer (> 400 m), the descending velocity sharply increased and the maximum velocity (35 m min⁻¹) was observed in the layer at a depth of 500 m. In even deeper layers (> 800 m) where the oxygen concentration increased above 0.5 ml l⁻¹, the descending velocity of the squid began to gradually decrease to 5 m min⁻¹ below 1000 m (Fig. 7). No direct relationship was observed between the fluctuations in descending velocity and ambient temperature at depth (Fig. 3).

3. PAT

The trajectory data for Squid 2 was recorded over eight days until midnight on 21 December at the designated pop-up time. Range and mean depths calculated from the histogram of the PAT tag data were plotted at six-hour intervals (Fig. 8). The trajectory indicated by the PAT tag agreed with that of the acoustic tag. The PAT tag trajectory recorded a continuous deep-water dive (near a depth of 1300 m) during the day. After that, we lost the acoustic signal when the squid reached a depth of 1148 m; the PAT tag recorded

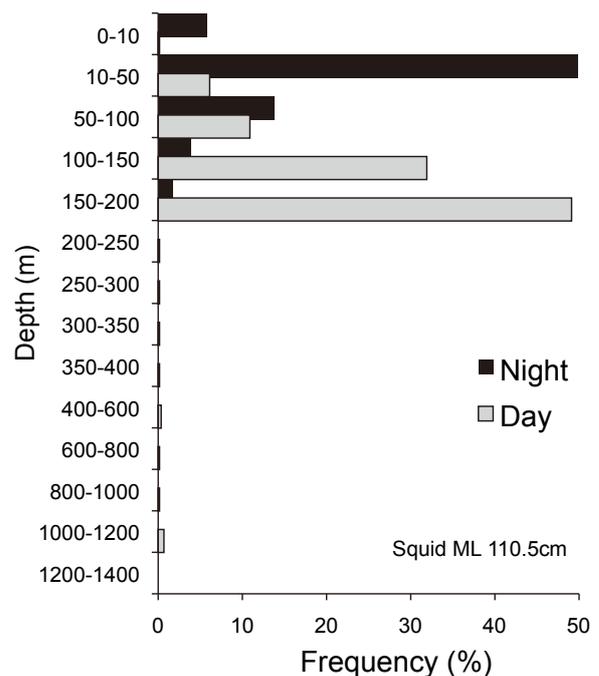


Fig. 6. Frequency of vertical distribution of Squid 2 (ML 110.5 cm) by day and night.

the dive during the day on December 15. At dawn, the tag trajectory showed an ascent to subsurface water, thereby suggesting continuous migratory behavior. If the squid died after making a deep descent, its body should drop to the sea bottom (> 3000 m) and the mechanical "guillotine" should work at a depth of 1800 m. In such case, the PAT tag should float to the sea surface and commence data transmission earlier than the designated date (midnight on December 21).

After December 16, the tag trajectory showed stable migration near the sea-surface migration except for two descent marks near midnight on December 17 and 21.

Discussion

The first trials of biotelemetry experiments for small-size jumbo flying squid (measuring 35-43 cm in ML) were made using acoustic tags in 1997 (Yatsu et al. 1999), prior to the change in their population structure that began in 1999. Since 1999, the stock of jumbo flying squid increased along with enlarged body size and an expanded distribution range (Keyl et al. 2008). The trials suggested that the squid migrated vertically beyond a depth of 1,000 m during the

day, but sufficient reproducibility remained unclear as all tracking signals were lost after the deep dives. In the present study, deep-water dives down to a depth exceeding 1200 m during the day were demonstrated by the combined use of acoustic tags and the PAT tag. The squid (measuring 74 cm in ML) engaged in stable swimming in the layer at a depth of 1200 m for more than one hour until a fishing boat disturbed our tracking course. The trajectory of the other squid (measuring 110.5 cm in ML) obtained from the PAT tag summary data agreed with that of the acoustic tag.

According to the hypothesis proposed by Stewart et al. (2013), deep-water diving (> 1000 m) utilizing hypoxic and suboxic waters below the OMZ during the day might offer combined advantages for the animal, such as avoiding predators and foraging with minimal effort. These waters might provide a refuge zone from large predators with high oxygen requirements (Seibel 2011, Stramma et al. 2012, Bianchi et al. 2013). The high descending velocity observed across the OMZ in the squid's descent trajectory down to 1200 m (Fig. 7) would thus be due to adaptive behavior for the purpose of reaching the refuge zone.

The subsurface (0-50 m) migration of the squid at night agreed with previous studies conducted in the northern California Current System (CCS) or in the Gulf of California (GOC) in the Northern Hemisphere (Gilly et al. 2006, Stewart et al. 2013) (Table 2). During the day, we observed two different patterns: 1) migration to deep water through the OMZ (> 1000 m) and 2) migration in the upper layers of the OMZ (150-200 m). The deep-water dive pattern was also occasionally observed in the CCS and the GOC (Stewart et al. 2013). In the pattern of upper layer migration, however, the depth layer (150-200 m) in the present study was shallower than in the GOC (200-400 m; Gilly et al. 2006, Stewart et al. 2013) and CCS where the depth

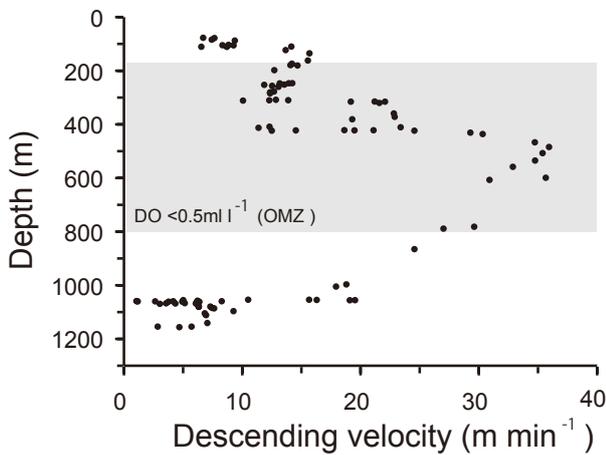


Fig. 7. Vertical trajectory of Squid 2.
The small white squares indicate mean recorded depth by a PAT tag with ranges; gray lines indicate the pinger tracking trajectory. Nighttime hours are shaded.

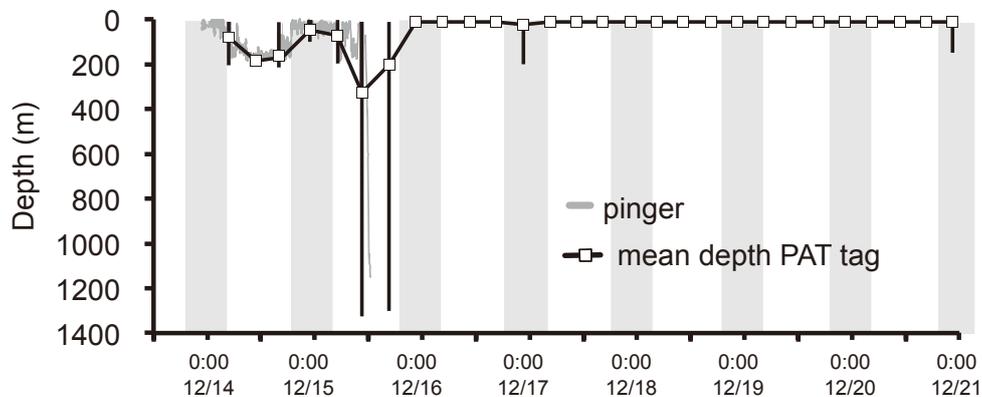


Fig. 8. Fluctuations in descending velocity (m min⁻¹) of *D. gigas* (Squid 2, ML 110.5 cm) during periods of descending migration from the sea surface down to 1200 m from 11:00 to 12:30 on 15 December 2007. Shaded and darker shaded areas are indicated as the OMZ in lower dissolved oxygen layers less than 0.5 ml l⁻¹.

Table 2. Comparison of vertical distribution range of *D. gigas* and depth range of the OMZ (< 0.5 ml l⁻¹) between areas.

Area	Depth range of OMZ, m	Vertical distribution range, m		References
		Nighttime	Daytime (maximum depth)	
Off Peru	200-800	0-100	100-200 (1300)	This study
CCS	500-1000	50-100	334 (1447.9)	Stewart et al. (2013)
CCS	500	–	500	Stewart et al. (2014)
GOC	225- 600<	42-104, 85-301	200-400 (500)	Gilly et al. (2006)
GOC	250-1200	50-100	350 (1397.3)	Stewart et al. (2013)

(about 500 m) at which the squid spend the most time had somewhat higher oxygen concentrations than those in the OMZ proper (Stewart et al. 2014). This difference in depth may be caused by latitudinal variation regarding the vertical position and thickness of the OMZ between the Southern and Northern Hemispheres. According to Helly and Levin (2004), the upper-lower depth of the OMZ as an index of DO < 0.5 ml l⁻¹ was shallow and thick at 5-20°S (100-600 m), while the depth was deeper (500-700 m) and thinner at 25-40°N of the CCS. This suggests that the upper OMZ depth characteristics regulate the daytime migration depth. When considering squid behavior during the day in Peruvian waters, the OMZ characteristics would also affect squid fishery activities, such as information on a daytime catch using a 150-m jig line off Peru (Y. Ochi pers. comm.).

We still need to answer two questions: why do these squids dive to such a deep layer (> 1000 m) and why do they pass through the OMZ? The vertical distribution of *D. gigas* may be related to its trophic relationships. In Peruvian waters, a mesopelagic fish—*Vinciguerria lucetia*—is considered the main prey of squid (Argüelles et al. 2008). According to Cornejo and Koppelman (2006), the nocturnal vertical distribution of this mesopelagic fish is characterized by a single layer pattern of acoustic backscattering strength (at a depth of 50-60 m). During the night, complex layers were observed at depths of 60-90 m, 180-240 m and 260-340 m. The upper abundance peak (< 100 m) and the mid-water (200-400 m) coincide with the core of the OMZ (< 0.5 ml l⁻¹). The nocturnal migration of *D. gigas* in our study agreed with the diurnal vertical distribution of the prey fish. On the other hand, we categorized two patterns of diurnal migration for the squid: deep-water (> 1000 m) and mid-water (150-200 m). Both migration patterns agreed with the diurnal vertical distribution of the prey fish, except at 400 m and deeper depths. Thus, the nocturnal migration pattern of *D. gigas* reflects its feeding habits, while its diurnal patterns are apparently related to other factors.

The main predators for *D. gigas* are reportedly swordfish (Markaida & Sosa-Nishizaki, 1998), sperm whales

(Clarke 1986, Clarke & Paliza 2000), bluefin tuna, yellowfin tuna, bigeye tuna, dolphinfish, blue marlin, blue shark, northern fulmar, northern elephant seals, and spinner dolphins (reviewed by Markaida & Sosa-Nishizaki 1998). Swordfish and sperm whales are potentially the most important predators, given their relative size and diving behavior. Swordfish are generally reported to feed on ommastrephid squid (Stillwell & Kohler 1985, Bello 1991, Guerra et al. 1993). We assume that smaller *D. gigas*, which do not dive into deep waters, will face higher predatory pressure by the relatively abundant population of swordfish in the eastern Pacific Ocean (Hinton et al. 2005). According to biotelemetry studies on swordfish during the day, the swimming depth in the Pacific appeared limited to about 100 m in the OMZ (Carey & Robison 1980). Swordfish in the South Pacific typically spend most of their time in waters deeper than 400 m, but frequently spend maximum time at intermediate depths (150-250 m) (Abscal et al. 2010). Therefore, deeper descents beyond the OMZ of *D. gigas* as demonstrated in the present study support a means of possible escape from such large visual predators as swordfish. Sperm whales are apparently a more important predator of *D. gigas* (Clarke 1986, Clarke & Paliza 2000), and can dive down to a depth of 1200 m both during the day and at night (Watwood et al. 2006, Aoki et al. 2007). Unlike fish predators such as swordfish, sperm whales can dive into deep waters independently of OMZ distribution. As a result, this diving behavior of sperm whales will pose a threat to even the largest *D. gigas*, although the impact on squid behavior remains unknown.

In conclusion, our results on the relationship between the daytime migration depth of *D. gigas* and the upper OMZ depth characteristics in the Southern Hemisphere agreed with previous studies on the Northern Hemisphere. Our findings support the importance of the relationship between diurnal mid-water migration and thickness of the OMZ. Although expansion of the OMZ in eastern tropical oceans may reduce available habitats for tropical pelagic fish (Stramma et al. 2011), *D. gigas* would adapt to such OMZ expansion with its capability to dive beyond the OMZ.

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