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Linking mesopelagic prey abundance and distribution to the foraging behavior of a deep-diving predator, the northern elephant seal

Daisuke Saijo[a,1], Yoko Mitani[b,1,*], Takuzo Abe[c,2], Hiroko Sasaki[d], Chandra Goetsch[e], Daniel P. Costa[e], Kazushi Miyashita[b]

[a] *Graduate School of Environmental Science, Hokkaido University, 20-5 Bentencho, Hakodate, Hokkaido 040-0051, Japan*
[b] *Field Science Center for Northern Biosphere, Hokkaido University, 20-5 Bentencho, Hakodate, Hokkaido 040-0051, Japan*
[c] *School of Fisheries Science, Hokkaido University, 3-1-1 Minato cho, Hakodate, Hokkaido 041-8611, Japan*
[d] *Arctic Environment Research Center, National Institute of Polar Research, 10-3, Midori-cho, Tachikawa, Tokyo 190-8518, Japan*
[e] *Department of Ecology & Evolutionary Biology, University of California, Santa Cruz, CA 95060, United States*

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ABSTRACT

The Transition Zone in the eastern North Pacific is important foraging habitat for many marine predators. Further, the mesopelagic depths (200–1000 m) host an abundant prey resource known as the deep scattering layer that supports deep diving predators, such as northern elephant seals, beaked whales, and sperm whales. Female northern elephant seals (*Mirounga angustirostris*) undertake biannual foraging migrations to this region where they feed on mesopelagic fish and squid; however, *in situ* measurements of prey distribution and abundance, as well as the subsurface oceanographic features in the mesopelagic Transition Zone are limited. While concurrently tracking female elephant seals during their post-molt migration, we conducted a ship-based oceanographic and hydroacoustic survey and used mesopelagic mid-water trawls to sample the deep scattering layer. We found that the abundance of mesopelagic fish at 400–600 m depth zone was the highest in the 43 °N zone, the primary foraging area of female seals. We identified twenty-nine families of fishes from the mid-water trawls, with energy-rich myctophid fishes dominating by species number, individual number, and wet weight. Biomass of mesopelagic fishes is positively correlated to annual net primary productivity; however, at the temporal and spatial scale of our study, we found no relationship between satellite derived surface primary production and prey density. Instead, we found that the subsurface chlorophyll maximum correlated with the primary elephant seal foraging regions, indicating a stronger linkage between mesopelagic ecosystem dynamics and subsurface features rather than the surface features measured with satellites. Our study not only provides insights on prey distribution in a little-studied deep ocean ecosystem, but shows that northern elephant seals are targeting the dense, species-diverse mesopelagic ecosystem at the gyre-gyre boundary that was previously inferred from their diving behavior.

1. Introduction

The Transition Zone (TZ), which lies between subarctic and subtropical gyres in the eastern North Pacific (Roden, 1970), is an important foraging area for many marine predators, including albacore (*Thunnus alalunga*) and bluefin tuna (*T. thynnus*), loggerhead (*Caretta caretta*) and leatherback turtles (*Dermochelys coriacea*), neon flying squid (*Ommastrephes bartramii*), Laysan (*Phoebastria immutabilis*) and Black-footed albatrosses (*P. nigripes*), northern fur seals (*Callorhinus ursinus*), and sperm whales (*Physeter macrocephalus*) (Ayers and Lozier, 2010; Block et al. 2011; Ichii et al., 2009; Kappes et al., 2010; Mizroch and Rice, 2006, 2012; Polovina et al., 2001; 2015; Ream et al., 2005). While it has been difficult to observe these highly migratory predators within the off-shore regions, recent advances in electronic tags, such as light-based geolocation tags, satellite tags, and GPS tags, have made it possible to determine the movements and habits of these animals (Block et al., 2011; Costa et al. 2010a, 2010b, 2010c; Wilson et al., 2002). Remote sensing data combined with bio-logging tracking data have revealed relationships between predator distribution and physical and biological variables, such as sea-surface temperature, chlorophyll-*a*, and sea surface height (Polovina et al., 2001; Ream et al., 2005; Kappes et al., 2010). These

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[*] Corresponding author.
E-mail address: yo_mitani@fsc.hokudai.ac.jp (Y. Mitani).
[1] The first two authors contributed equally to this work.
[2] Present address: Minamisanriku Nature Center, 56-2 Numata, Minamisanriku-cho Shizugawa, Motoyoshi-gun, Miyagi, 986-0792, Japan.

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combined methods allow us to observe relationships between predator distributions and surface oceanographic features especially in the remote region of the Transition Zone. While these methods can provide coverage at ocean basin scales, satellite data cannot describe the subsurface oceanography nor the mesopelagic food web.

Of interest here are female northern elephant seals (*Mirounga angustirostris*) that travel to this gyre-gyre boundary, over 3000 km from the rookery during their migrations and forage at depths averaging 600 m during the day and 450 m at night (Le Boeuf et al., 2000; Simmons et al. 2010; Robinson et al. 2012). Such a diel pattern indicates that elephant seals track the vertical migrations of prey within the deep-scattering layer (Robinson et al., 2012). They undertake two foraging migrations after breeding (February to May) and after molting (June to January) to replenish their energy reserves (i.e. blubber stores) that are depleted while they were fasting on land breeding and molting (Costa et al. 1986; Crocker et al. 2001). Most female elephant seals gain energy in the Transition Zone, north of gyre-gyre boundary (Robinson et al., 2012). Further, jaw movement data from accelerometers indicate that the feeding events occurred deeper than 450 m in the Transition Zone (Naito et al., 2013). Digital camera loggers (still and video) deployed on migrating female seals have captured when the seals feed on mesopelagic fishes, such as myctophids, and squid (Naito et al., 2013 and Naito, unpublished data). Therefore, foraging success of seals can be used as proxy of abundance of mesopelagic biomass, and sensors such as temperature, conductivity, and light level attached on the seals can reveal subsurface oceanographic features linked with the prey field.

Instrumented elephant seals are a suitable platform to gather oceanographic measurements within their foraging environments; however, not all features of the prey field are sampled. Furthermore, this approach only samples the prey-rich regions and does not provide information on where the seals do not forage. Thus, monitoring across different water masses where seals are and are not foraging is necessary to characterize the features responsible for aggregating prey. In situ surveys, such as trawling and hydroacoustic sampling have been used to study mesopelagic ecosystems. The world biomass of the mesopelagic fish has been estimated to be 1000 million tons (Gjosaeter and Kawaguchi, 1980; Lam and Pauly, 2005) surveyed using micronekton sampling gear, which mesopelagic fish can avoid (Kaartvedt et al., 2012). Whereas hydroacoustic monitoring, using an echosounder, provides a continuous data set without avoidance reactions and can measure prey presence and density at high resolution throughout the water column along the ship track (Croll et al., 1998; Murase et al., 2002). Recent hydroacoustic observations show that mesopelagic fish biomass has been underestimated by as much as 10,000 million tons or more (Irigoien et al. 2014). This represents a significant proportion of the world's ocean biomass, and may be critically important for global ocean biogeochemical cycles and nutrient recycling.

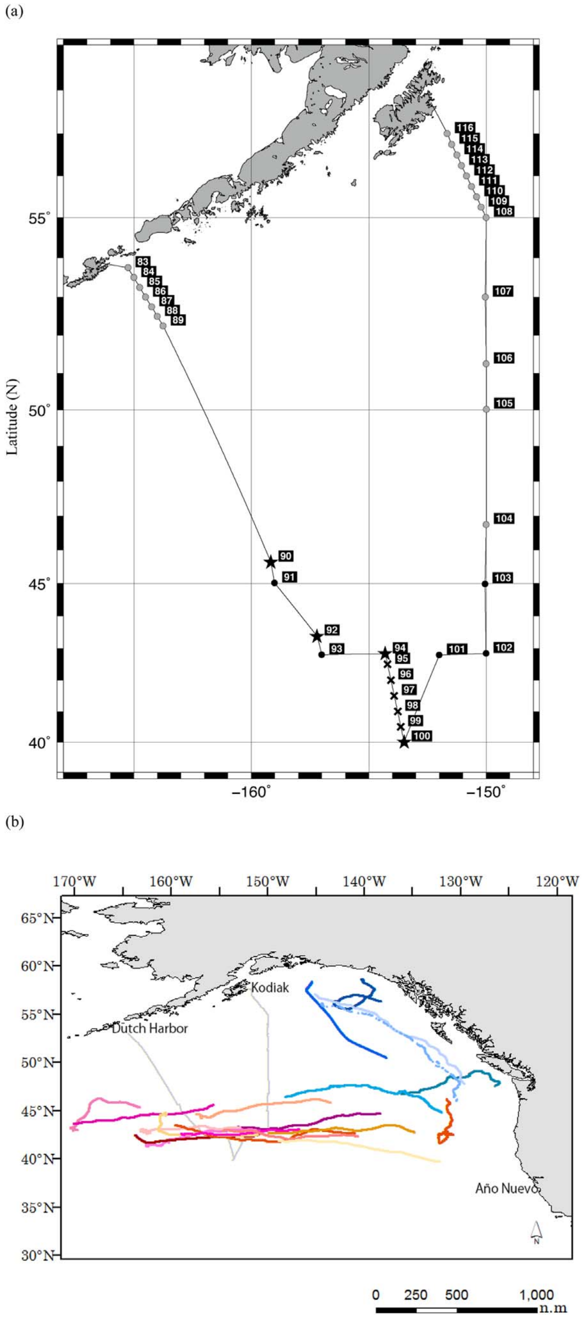

Fig. 1. (a) Sampling stations in the northeast Pacific Ocean (filled circle: CTD, X: XCTD and stars: mid-water trawl and CTD). Black symbols show stations in the Transition Zone, and gray symbols in the Subarctic Gyre as shown in Fig. 2. (b) The track lines of 20 northern elephant seal females during July 1–19. Fourteen seals spent time in the Transition Zone were represented in warm colors, whereas six seals in the subarctic water were represented in cool colors. Grey line shows track line of T/S Oshoro-Maru.

Table 1
Trawl sampling stations (start point), shown as stars in Fig. 1 and as triangles in Fig. 3.

Station	Date	Latitude	Longitude	Max depth
90	2016.7.6	45 °39' N	159 °22' E	730
92	2016.7.6	43 °21' N	157 °28' E	650
94	2016.7.7	42 °48' N	154 °29' E	650
100	2016.7.9	39 °59' N	153 °30' E	720

Variation of ocean processes, such as shifting mesoscale eddies, fronts, and thermoclines, determines prey distribution and abundance both at the surface and in the deep scattering layers. Therefore, combining biological data from trawls or hydroacoustic surveys with oceanographic data from CTD (Conductivity-Temperature-Depth) measurements allows us to link the mesopelagic ecosystem with subsurface oceanographic features. As for northern elephant seals, several studies have linked female foraging success with reproductive success through variation in animal condition, so changes in the prey base in the Transition Zone related to climate events, such as El Niño could have population-level consequences (Crocker et al. 2006; Le Boeuf and Crocker, 2005; Costa et al., 2016). However, investigation of the links between mesopelagic foraging areas and the associated oceanographic conditions and the composition of prey in the deep scattering layer is challenging (Kloser et al., 2009; Young et al., 2015). Meanwhile, the deep scattering layers represent a high-density prey resource that links the mesopelagic food web from phytoplankton to top predators (Hazen and Johnston, 2010). Further, a recent global hydroacoustic survey confirmed that the abundance of mesopelagic fishes is correlated with satellite-derived primary production measurements (Irigoien et al., 2014), suggesting that satellite remotely sensed

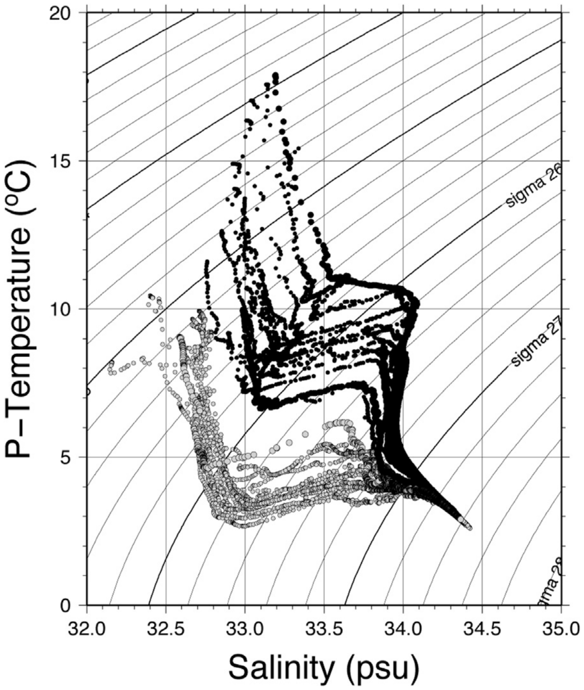

Fig. 2. Potential temperature plotted vs. salinity (T-S diagram) for data from stations in the northeast Pacific Ocean. Each color indicates a different water type (black: Transition Zone and gray: Subarctic Gyre).

surface chlorophyll-*a* concentration can be used to predict the abundance of mesopelagic fishes.

To test whether there is a link between primary production, mesopelagic prey and top predators, we conducted a ship-based oceanographic and hydroacoustic survey. This included concurrent mesopelagic net sampling while we tracked foraging female elephant seals. We tested the hypothesis that northern elephant seal females forage in regions based on the availability of prey and examined how these mesopelagic prey communities of the Transition Zone correlate with hydrographic features. We tested whether mesopelagic fish abundance correlated with remotely sensed primary production data.

2. Methods

2.1. Study area

The study was conducted on the T/S Oshoro-Maru (Hokkaido University, 72.85 m length, 1779 gross tonnage) 2012 summer cruise between 2 to 19 July, as part of Leg 2 (from Dutch Harbor to Kodiak, USA), crossing the Subarctic Gyre and the TZ (Fig. 1). The track line and net sampling positions were determined at the beginning of Leg 2 using position data of satellite-tracked females transmitted between 28 June and 4 July, and adjusted while at sea in response to the near-real time Argos positions until 10 July, 2012. The vessel cruised the lines at a speed of 10 knots (18.52 km/h).

2.2. Elephant seal behavior

We deployed ARGOS satellite transmitters (Wildlife Computers, Belleview, WA, USA: SPOT4, SPOT5, MK10-AF) and time-depth recorders (Wildlife Computers MK9 or MK10) on adult female elephant seals at Año Nuevo State Reserve, California, USA (37° 5’ N, 122° 16’ W, n=19) at the end the 2012 molting season (May-June 2012), using standard protocols for chemical immobilization and instrument attachment (Le Boeuf et al., 1988, 2000; Robinson et al., 2012). The data from these tags were extracted from July 1–19 to compare with the environmental data collected on the Oshoro-Maru. Raw Argos tracking data (n=18) transmitted from July 1–19 were analyzed using the CRAWL package in R (Johnson et al., 2008), and GPS data (n=2) were analyzed following Robinson et al. (2012). Dive depth data were sampled at least once every 8 s, and dives were divided into day (4:30–19:30, GMT-10 h) and night (19:30–4:30, GMT-10 h). Diving data were processed in MatLab using the purpose-built IKNOS toolbox (Y. Tremblay, unpublished), with and maximum dive depth were used for analysis.

2.3. At-sea oceanographic and prey sampling

Oceanographic observations were conducted with a conductivity-temperature-depth profiler (CTD; model SBE9Plus and SBE-19, Sea-Bird, Bellevue, WA) or with an expendable conductivity temperature depth probe (XCTD; model XCTD-2, Tsurumi-Seiki, Yokohama, Japan)

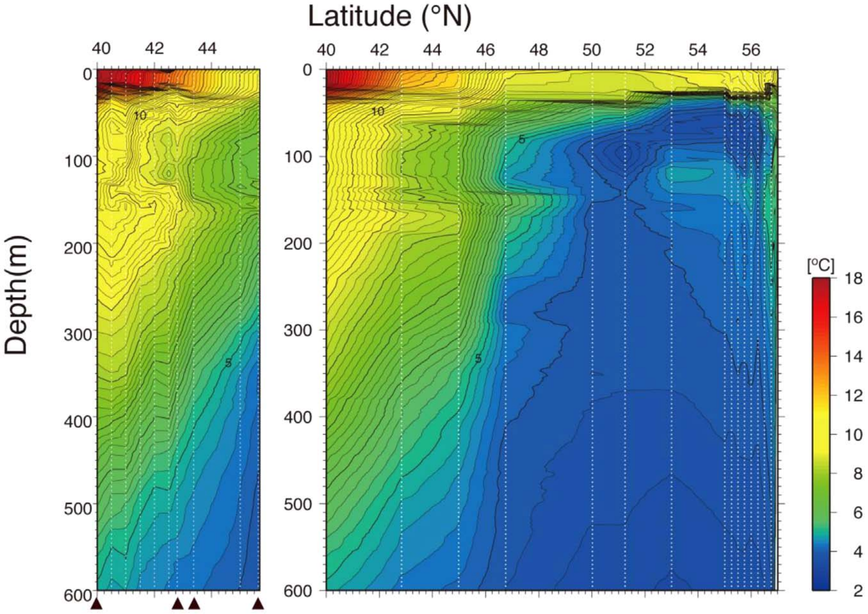

Fig. 3. Contours of temperature along the southward (left, St. 90–100) and the northward (right, St. 100–116) cruise track in Fig. 1. The white dots indicate stations where temperature data were obtained. Triangles below the left panel shows the mid-water trawl stations shown in Table 1, and stars in Fig. 1.

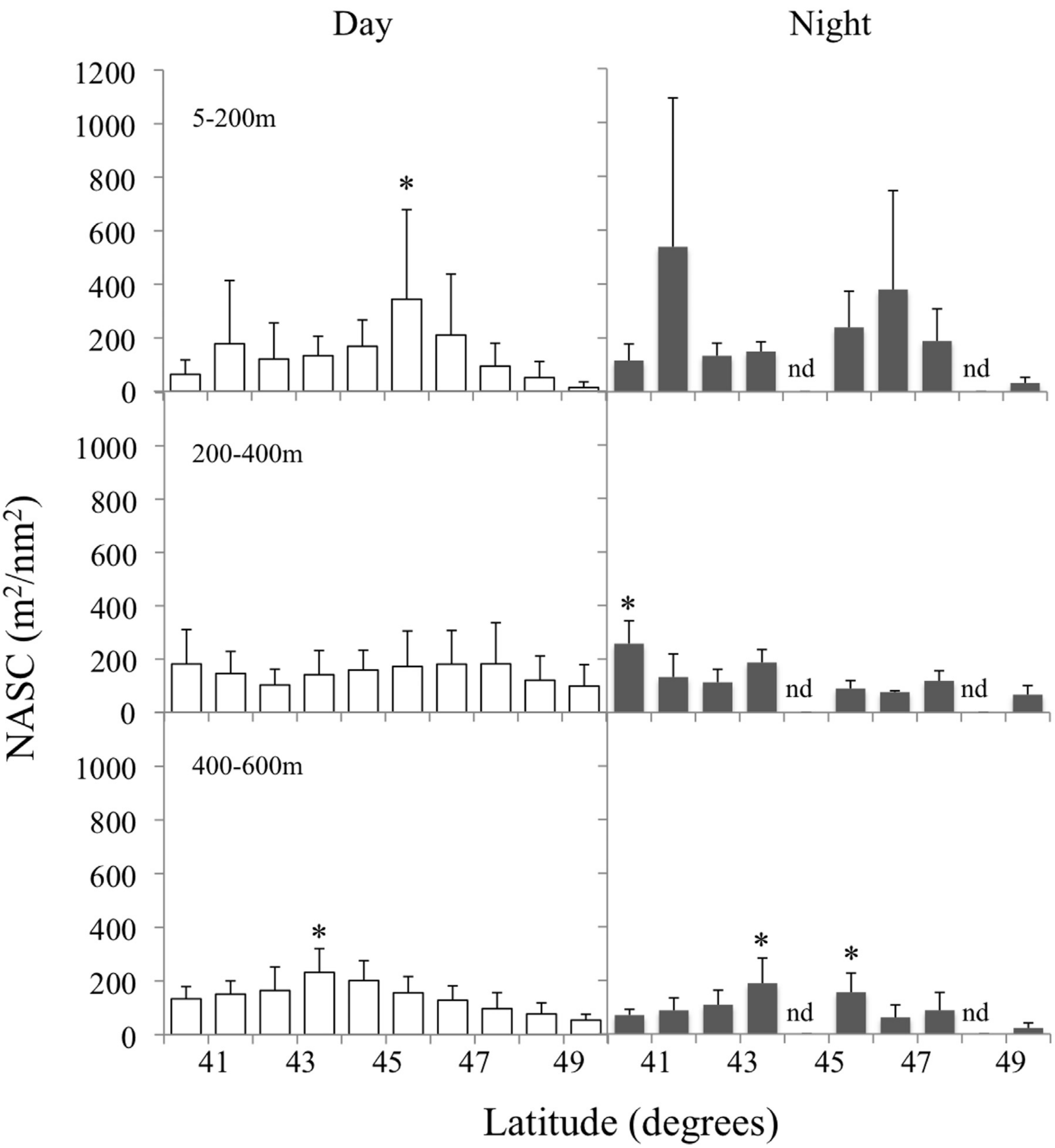

Fig. 4. Latitudinal change of relative prey density (Nautical Area Scattering Coefficient, NASC, m^2/nm^2) (upper: epipelagic, 5–200 m, middle: intermediate, 200–400 m, and lower: foraging depth, 400–600 m in water depth). White and black bars show day and night, respectively. Stars show statistically significant peaks (Tukey-Kramer test, $p < 0.05$).

to obtain the temperature and salinity, and as for CTD, fluorescence was also obtained. Seawater samples for fluorescence analyses were collected at 11 depths (5, 10, 20, 30, 40, 50, 60, 100, 125, 150, and 200 m) with Niskin bottles during CTD casts, and surface water collected. A 200-mL sample of the surface seawater was filtered through a glass fiber filter (Whatman GF/F) for fluorometric determination of chlorophyll *a* concentration. The filter was immediately soaked in *N*, *N*-dimethylformamide (DMF), and phytoplankton pigments on filter were extracted for 24 h in the dark at -20 °C (Suzuki and Ishimaru, 1990). Chlorophyll *a* concentration was determined by fluorometric method (Welschmeyer, 1994) using fluorescent intensity measured with a Turner Designs 10AU fluorometer calibrated against a pure chlorophyll-*a* standard (Sigma), and chlorophyll-*a* concentration was calculated according to the non-acidification method and used to correct the fluorescence data obtained from the CTD. The interpolation and contouring of temperature and chlorophyll data were computed using the Generic Mapping Tool (GMT) (Wessel and Smith, 1998).

A quantitative echosounder, EK60 (Simrad, Norway) with an operating frequency of 38 kHz from the hull-mounted transducer was used to record hydroacoustic data to 1,000 m continuously throughout the survey track, however, > 700 m were excluded from the analysis because of noise. We used this frequency because of the greater range achieved using lower frequency sonars, which is necessary to sample mesopelagic fishes (Yasuma et al., 2010). These data were analyzed using Echoview version 4.90 (Myriax, Hobart, Tasmania, Australia). Hydroacoustic backscatter data were expressed as the nautical area scattering coefficient (NASC; m^2/nmi), a relative measure of prey density. The NASC values were integrated over 1 nm-length intervals and 100 m depth bins up to 600 m depth, except < 5 m below the surface to exclude surface noise. Latitudinal differences of NASC values within three depth strata (epipelagic: 5–200 m, intermediate: 200–400 m, and foraging depth: 400–600 m) and differences in vertical distribution of NASC values within day and night periods in Subarctic water and the Transition Zone were tested using ANOVA followed by a Tukey-Kramer test.

Biological samples were collected with a mid-water trawl net

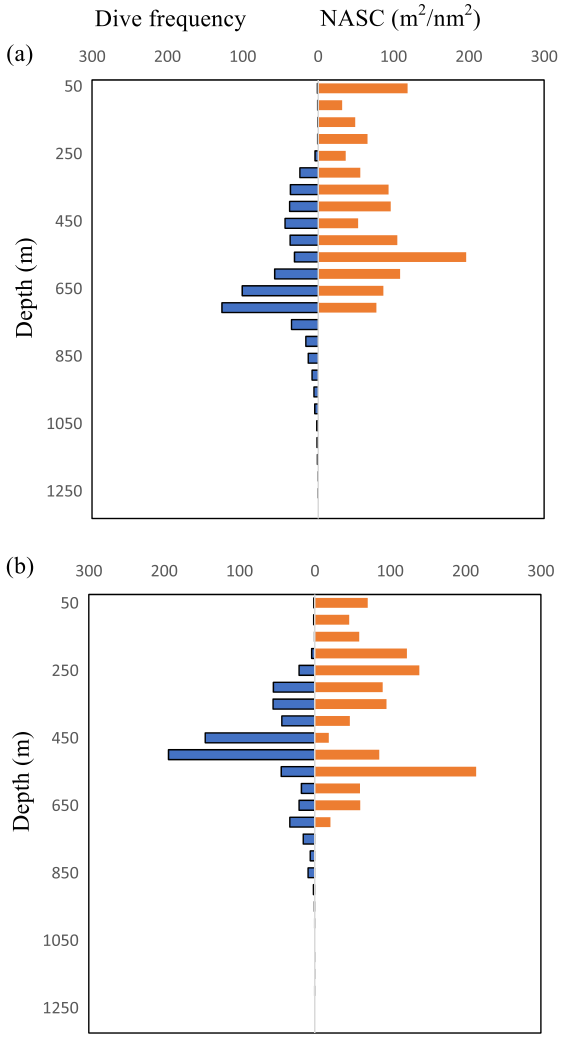

Fig. 5. Comparison of dive frequency of female northern elephant seals in the Transition Zone with average prey density (Nautical Area Scattering Coefficient, NASC, m^2/nm^2) in 43 °N zone (43.0–44.0 °N) as a function of depth during the day (a) and night (b).

(10 mm mesh size at inner cover of the cod end) at four stations within the foraging area of the seals as determined by their satellite locations (Table 1). The trawl net was towed obliquely from 650–730 m to the surface at a speed of approximately 2.5 knots. Prey samples were frozen and sub-samples sent to the *National Marine* Mammal Laboratory, NOAA-NMFS Seattle, WA. and to Hokkaido University. They were identified to family and genus or species whenever possible. At each station the number of each species and their abundance was recorded along with the wet weight of each sample. However, when many individuals of the same species were caught, we randomly selected a subset of individuals to measure average weight.

We retrieved satellite primary production data for July 2012 from the Oregon State University Ocean Productivity website (http://www.science.oregonstate.edu/ocean.productivity/index.php). All statistical analyses were conducted using the R statistical software v.3.0.1 (R Core Team, 2013).

3. Results

3.1. Oceanographic features of the transition zone and diving behavior of seals

Ship based oceanographic observations were conducted at 34 stations (CTD: 29 and XCTD: 5) and temperature-salinity profiles (T-S diagram) from the CTD data clearly showed two different hydrographic environments as previously reported (Talley, 1997): subarctic water (north from St. 104, 46 °45'N) and transition water (south from St. 90, 45 °38'N) (Fig. 2). The temperature profiles also revealed that the Subarctic Front was at 46 °N during July 2012 (Fig. 3), where a 5 °C vertical isotherm occurred below 100 m as described in Takasugi and Yasuda (1993) and Shimizu et al. (2001). We did not observe a 34.0 isohaline that stretched vertically, defining the subarctic boundary as described by Favorite et al. (1976). Therefore, we classified the Transition Zone as between 40 °N (southernmost station) and 46 °N. There was a distinct inversion layer at 100 m depth in the Transition Zone, and the thermocline was located at approximately 50 m depth at all stations (Fig. 3).

Fourteen of the 20 satellite-tagged seals spent their time at least more than 85% (98.2 ± 4.1%) of their time in the Transition Zone, whereas other 6 seals traveled in the subarctic water and spent no more than 15% (2.0 ± 4.8%) of their time in the Transition Zone during our cruise (Fig. 1b). Nine of these 14 seals returned with time-depth data, and they made 11,380 dives in total during July 1–20, 2012. Average dive depth during the day (573 ± 53 m) was significantly deeper than at night (453 ± 46 m) ($p < 0.05$, Welch's t test).

3.2. Mesopelagic fishes in the deep scattering layer

NASC values, which we associated with the presence of prey, showed different latitudinal changes among the three depth strata (epipelagic: 5–200 m, intermediate: 200–400 m, and foraging depth: 400–600 m), and diel changes (Fig. 4). Significant peaks were measured during the day, (Tukey-Kramer test, $p < 0.05$) at 45.0–46.0 °N for the epipelagic layer and at 43.0–44.0 °N for the foraging depth layer. During the night, significant peaks (Tukey-Kramer test, $p < 0.05$) were observed at 40.0–41.0 °N for the intermediate layer and at 43.0–44.0 °N and 45.0–46.0 °N for the foraging depth layer.

Female northern elephant seals dove deeper than peak NASC values during the daytime, whereas they dove shallower during the nighttime in the Transition Zone (43.0–44.0 °N) (Fig. 5).

A total 29 families of fishes were identified in the foraging areas of the seals (Supplemental Table S1). Of these, myctophid fishes were dominant in the samples by species number (18 species), individual number (71.7% of all individuals) and fish wet weight (38.6% of the total weight, Supplemental Table S2). In addition, most samples (91.2% of all individuals) were less than 20 g wet weight. There was no relationship between surface primary production and NASC values between 200–600 m (Pearson's $r = 0.05$, $P = 0.82$). A subsurface chlorophyll maximum was observed south of 45 °N along the southward line, and at all stations along the northward line (Fig. 6).

4. Discussion

The distribution of the female elephant seals observed in this study was comparable to previous reports (Le Boeuf et al., 2000; Robinson et al., 2012). Robinson et al. (2012) found that most of the seals focused their foraging effort in the Transition Zone, especially along the 43 °N zone, where temperature inversions occur between 150 to 200 m. During our ship based survey our CTD measurements placed the boundary between the Transition Zone and the Subarctic Zone at 46.0 °N, which places the middle of the Transition Zone at 43 °N. Following the 8–9 °C isotherm we found temperature inversions at depths of 150 to 200 m between 42.0–44.0 °N. Our hydroacoustic survey revealed that the 43 °N zone showed the highest relative prey density (NASC) in the 400–600 m depth layer both in the day and night. Surface chlorophyll-*a* concentration was 0.2–0.4 mg/m^{-3}. We observed the subsurface chlorophyll maximum at 50 m.

While the relationship between top predators and the deep scattering layer (DSL) has not been reported for our study area, Hazen and Johnston (2010) showed that the distribution of toothed

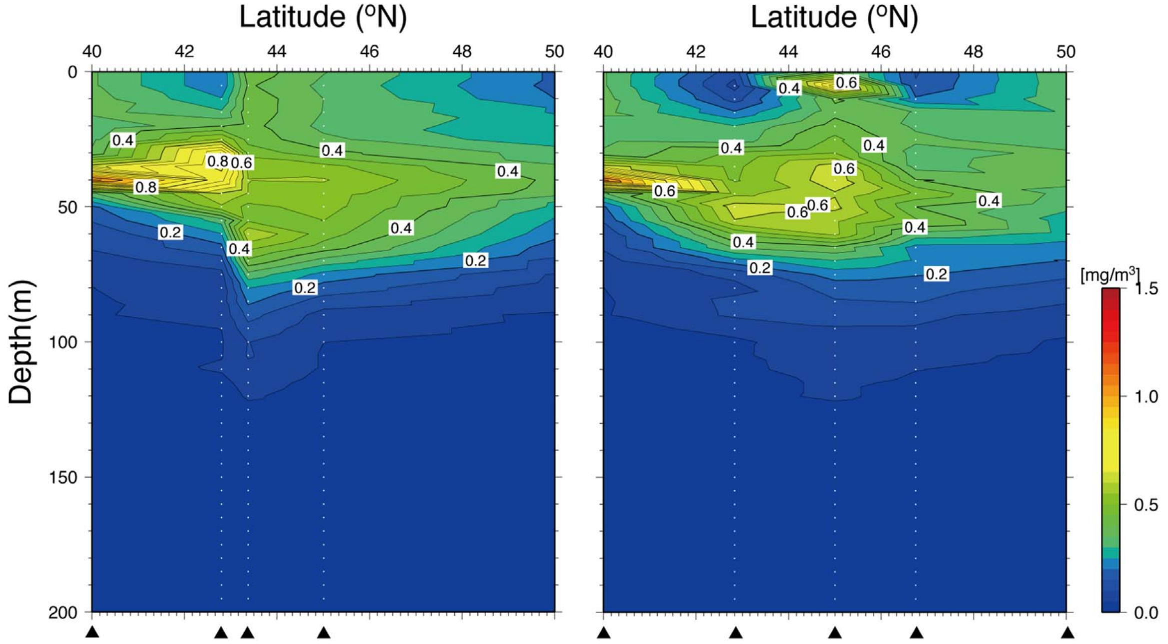

Fig. 6. Chlorophyll-a concentration (mg/m^{-3}) along the southward (Stn. 91–94, 100, left), and northward (Stn. 100–105, right) cruise track in Fig. 1. The stations are shown as black triangles.

whales (Odontocete) was coincident with higher acoustic densities of their forage base in the central equatorial Pacific, where primarily myctophid fish (Bertrand et al., 1999) characterize the DSL. The distribution of seals corresponded with the regions where the relative prey density was highest in the mesopelagic depth range where they foraged. This is also the region where myctophid fish were most abundant in the net tows. As the mean caloric density of mesopelagic prey is high (Benoit-Bird, 2004), we can infer that seals focus on the Transition Zone, especially in the 43 °N zone, to forage on this abundant, high caloric prey.

Jaw motion detectors indicate that female seals exhibit high feeding rates (80–91% of the dives) during their migration and these feeding rates are particularly frequent in the mesopelagic zone (the ratio of dives with jaw-motion events; 450–500 m: 70–90% dives, and > 500 m: almost 100%. Naito et al., 2013). The peaks of dive depths during our study in July 2012 were 700–750 m during the daytime and 500–550 m during the nighttime. Our finding that most of the mesopelagic fishes collected in the trawls were less than 20 g wet weight supports the hypothesis by Naito et al. (2013) that elephant seals feed primarily on small fishes (9.9–21.1 g).

Although the peaks in prey density (NASC) were between 500–550 m in both the day and night, a second peak was observed between 200 and 250 m during nighttime. This secondary peak corresponds to the diel vertical migration of a subset of mesopelagic fishes. However, the peak in prey density and the peak in dive depth were not consistent, as the seals dove deeper than the peak depth of NASC during daytime, whereas they dove between the peaks during nighttime. Echosounders are biased towards fish with air-filled swim bladders, as acoustic backscatter from fish with gas-filled swimbladders is higher than those without swimbladders and/or fat-invested swimbladders (Yasuma et al., 2008). In our net tow samples, for example, Warming's lantern fish *Ceratoscopelus warmingii* has a gas-filled swimbladder (Badcock and Araújo, 1988), whereas the swimbladder of Garnet lanternfish *Stenobrachius nannochir* become fat-invested with age (Butler and Pearcy, 1972). It is, therefore, likely that the inconsistency between peak dive depths and peak NASC values is due to seals targeting prey without gas-filled swimbladders. Unfortunately, we were not able to collect samples stratified by depth, thus making it difficult to test this hypothesis. Another possible explanation is that deeper dives are advantageous for seals. Previous studies which analyzed the stratified samples collected with the multiple net Tucker trawl revealed that populations of each myctophid species tended to be vertically stratified by age or size, with larger individuals occurring progressively deeper (Frost and McCrone, 1979). In our net tow samples, for example, *Stenobrachius leucopsaurus*, one of the most common mesopelagic fishes in the North Pacific, is a semi-migrant species (Brodeur and Yamamura, 2005). Small size fish (19–82 mm) swim up to the 20–200 m layer during the night, whereas large size fish (90–112 mm) remain at a deeper than 330–440 m depth at night (Frost and McCrone, 1979). During the daytime, small size class fishes were distributed around 300 m, whereas at two of three stations, larger size classes were not observed above 440 m (Frost and McCrone, 1979). Therefore, seals may dive to depths deeper than peak NASC values to feed on larger myctophid fishes.

Mesopelagic fishes play an important role in oceanic ecosystems and global ocean biogeochemical cycles (Beamish et al., 1999; Irigoien et al., 2014). The biomass of mesopelagic fishes in the northeast Pacific Ocean (off the continental USA west to longitude 141 °W) and in the global ocean (but not including the North Pacific) are known to be positively related to annual net primary productivity (Davison et al., 2013; Irigoien et al., 2014). Primary production derived from satellite remote sensing data was used to estimate mesopelagic prey biomass (Irigoien et al., 2014). While remote sensing is a powerful tool that provides global data almost in real time, we found no significant relationship between the biomass of mesopelagic fishes and primary production in our study area (150–165 °W). One possible explanation is a time lag between surface primary production and mid-trophic level organisms, such as myctophids (Lehodey et al., 2010). Another possibility is that the subsurface chlorophyll maximum was around 50 m depth along our survey track, which is not detectable by remote sensing. In the central equatorial Pacific, the increased DSL scattering intensity was correlated with a deeper depth of maximum fluorescence and with a deeper thermocline (Hazen and Johnston, 2010). If this subsurface chlorophyll maximum supports metabolism of mesopelagic fishes in this area, subsurface monitoring may be necessary to obtain a more accurate biomass estimate of mesopelagic fishes.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2016.11.007.

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