Deep–Sea Research Part II 140 (2017) 25–35

Contents lists available at ScienceDirect

Deep–Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Reconstruction of historical changes in northern fur seal prey availability and diversity in the western North Pacific through individual-based analysis of dietary records

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ARTICLE INFO

Keywords:
Diets
Feeding migrations
Long-term changes
Marine mammals
Pelagic environment

ABSTRACT

We analyzed long-term dietary records of northern fur seals (*Callorhinus ursinus*) to reconstruct historical changes in prey availability and diversity in the western North Pacific off northeastern Japan. The nominal relationships between the occurrence frequencies of fishes or squids in fur seal stomachs and the sampling locations reflected the spatial heterogeneity of fish and squid distributions along the shelf–slope–offshore continuum off northeastern Japan, whereas changes in the temporal occurrence frequencies reflected mainly the migration and foraging patterns of the fur seals. The occurrence probabilities of fishes and squids in fur seal stomachs were standardized by using generalized linear models to compensate for sampling biases in space and time. The reconstructed historical trends revealed decadal shifts in relatively high prey abundance—from mackerels in the 1970s to Japanese sardine in the 1980s and myctophids/sparkling enope squids in the 1990s—that were related to decadal shifts in the oceanographic regime. The sequential increase in mackerel and Japanese sardine abundances coincided with the annual catch trends of commercial fisheries. The index of overall prey availability calculated from the standardized occurrence probabilities of fishes and squids in fur seal stomachs was fairly stable over the decades.

1. Introduction

There is growing concern about global changes in marine ecosystems resulting from climate and anthropogenic impacts. To evaluate these ecosystem changes, an understanding of ecosystem status relative to long-term shifts from past to present is very important (Pauly, 1995). However, ecosystem monitoring is time and labor intensive and long-term data from the open ocean are generally lacking. Commercial fisheries provide time-series data on multiple species, but sampling is neither random nor systematic and is affected by many factors, including fishing strategies and market demands (Yonezaki et al., 2015). Examination of fisheries-independent data is preferable if available (Branch et al., 2010).

Top predators such as marine mammals and seabirds are useful indicators of marine ecosystems (Boyd et al., 2006; Piatt and Sydeman, 2007; Moore, 2008) as their diets can provide information about the abundance, composition, and distribution of prey resources over extensive areas (Le Boeuf and Crocker, 2005; Iverson et al., 2007). Their individual and population performances (e.g., growth, body condition, reproduction, and population dynamics) may be proxies that reflect integrated ecosystem functions acting through food webs and the physical environment (Boyd and Murray, 2001; Diamond and Devlin, 2003; Weimerskirch et al., 2003). However, the population dynamics of these predators are affected by multiple factors and are therefore difficult to interpret. Before we can use such top predators as ecological indicators we need to gain a better understanding of their habitats and diets.

Northern fur seals (*Callorhinus ursinus*) breed on several remote islands in the North Pacific Ocean (Gentry, 1998) and are distributed over the subarctic waters of the North Pacific during the non-breeding season. In winter, many northern fur seals migrate along areas offshore of the Pacific coasts of Eastern Asia and North America (Bigg, 1990; Gentry, 1998). The Kuroshio–Oyashio mixture zone off northeastern Japan provides an important winter feeding area in the western North Pacific (Wada, 1969).

In 1957, pelagic sampling of northern fur seals was initiated to monitor their stock status, migration, and foraging ecology as a part of scientific surveys under the former Interim Convention on Conservation of North Pacific Fur Seals (Roppel, 1984). This sampling provided basic information on the seals' migration and feeding ecology

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http://dx.doi.org/10.1016/j.dsr2.2017.02.005

Available online 24 February 2017
0967-0645/

at sea (Wada, 1969, 1971; Perez and Bigg 1986). Early stomach contents analyses revealed that they are opportunistic feeders that consume the small schooling fishes, neritic and oceanic squids, and bathypelagic or demersal fishes that are available in their foraging habitats (Kajimura, 1985). Unfortunately, these surveys were terminated in 1988, but additional sampling was conducted sporadically during subsequent years and provided further information on prey composition and selection (Sinclair et al. 1994, 1996, 2008; Yonezaki et al. 2003).

The long-term dietary records of northern fur seals can be an important source of fishery-independent time-series information on marine ecosystems. However, the primary aim of the historical sampling of northern fur seals in the western Pacific was to assess the distribution, abundance, reproductive condition and food habits of wintering fur seals (Fisheries Agency of Japan, 1959). Sample collection was designed to cover the whole wintering area and season around northern Japan in several successive years (North Pacific Fur Seal Commission, 1969,1975, 1980). The wintering area extends over the continental shelf, slope, and offshore areas across the cold Oyashio and Kuroshio–Oyashio mixed water masses and northward from as far south as 35°N to up into the waters off the Kurile islands and in the Sea of Okhotsk. The prey species found in the fur seals' stomachs changed according to the sampling location and season.

To reconstruct historical trends in prey availability from long-term dietary records such as these, data handling and analysis techniques that resolve the annual sampling biases are necessary. One approach is to aggregate the data over prolonged periods such as decades and examine broad patterns on the basis of the assumption that annual sampling biases in space and time are cancelled out by the data aggregation. Yonezaki et al. (2008) compiled annual summary tables of the fur seal stomach contents and detected the decadal shifts in major prey items from the 1950s to the 1980s although the validity of the data aggregation assumption has not been tested. It would be helpful if we could add more recent data and evaluate the historical changes in prey availability over longer periods. However, direct comparison of the historical and recent survey data is not straightforward. In recent surveys only small numbers of samples have been collected over a smaller area in shorter periods within a year. Therefore, especially in this case, decadal compilation of data may not be effective in alleviating the sampling bias.

Moreover, the recent improvement in the diet analysis technique may cause problems in reconstructing historical trends. In historical surveys up to the 1970s, only undigested fresh stomach contents were analyzed; digested trace materials were not subjected to species identification (Fisheries Agency of Japan, 1959). In this procedure, occurrence rates of prey items are affected by sampling time because northern fur seals actively forage at night and dawn and their stomachs contain fresh prey items in the early morning. Empty stomachs, with or without trace materials, are found more frequently in the afternoon (Wada, 1971). Since the late 1980s, as an improvement in the species identification technique, squid beaks and fish otoliths remaining in digested trace materials have also been analyzed for species identification as well as to estimate number and size. The increased prey item occurrences derived from analysis of the digested trace materials are not compatible with the old data. Moreover, stomach contents samples from early Japanese surveys are no longer available. However, individual-based records of stomach contents have been available since 1968 along with information on the age, sex, and other biological parameters of northern fur seals, with their catch location and time. It may be possible to extract long-term trends in prey availability by making use of these individual-based data through the application of statistical models to cancel the sample biases in space and time.

Our objective here was to reconstruct historical changes in prey availability by analyzing long-term dietary records of northern fur seals. We first examined the nominal relationships between the occurrence probabilities of prey categories and various factors, including sampling location and time, and fur seal age and sex, to screen for explanatory variables likely to affect the occurrence of each prey category in the seal's stomachs. We then applied generalized linear models (GLMs) to formulate the relationship between the occurrence probabilities of prey categories in fur seal stomachs and the explanatory variables. By using the GLMs, we standardized the annual occurrence probabilities of prey categories to extract the long-term shifts in prey availability away from the effects of sampling biases. We also proposed a new method to estimate indices of prey availability and diversity on the basis of the occurrence probabilities of prey items. Finally, we compared the resultant long-term trends in prey availability and diversity with commercial fisheries data and a climate index.

2. Methods

2.1. Northern fur seal dietary information

Japanese long-term northern fur seal data were used in this study. More than 10,000 northern fur seals were sampled in the western North Pacific Ocean, the Sea of Okhotsk and the Sea of Japan under the former Interim Convention on Conservation of North Pacific Fur Seals and during national scientific activities off northern Japan from 1968 to 2006. The biological data, stomach contents data and tissue samples from these surveys had been archived as the Miho collection (Yonezaki et al. 2015). We extracted the data on northern fur seals collected in the major winter foraging area off northeastern Japan to the south of 41°32′N and east of 140°50′ (N=5201; Fig. 1). The sampling date, time, location, and sea surface temperature (SST) of the sampling location had been recorded for each northern fur seal sample, although in the case of some individuals some data were missing. Seafloor depths at the sampling locations (recorded to the nearest minutes of the coordinates) were obtained from the JODC-Expert Grid data for Geography (J-EGG500 with 500 m grid resolution, http://www.jodc.go.jp/data_set/jodc/jegg_intro_detail.html, last accessed on 25 January 2016) and the General Bathymetric Chart of the Oceans (GEBCO) one-minute grid bathymetric data (http://www.bodc.ac.uk/data/online_delivery/gebco/, last accessed on 25 January 2016) with bilinear interpolation; they were classified into shelf (≤200 m depth), slope (201–1000 m), and offshore (> 1000 m). Midwater temperature at 100 m depth was also derived from the coordinates of the sampling locations by using the data set ds285.3 – Subsurface Temperature And Salinity Analyses V6.7, by Ishii et al. (2006); http://rda.ucar.edu/datasets/ds285.3/, last accessed on 25 January 2016) with a resolution of 1° and 1 month. Water masses at the sampling locations were classified into cold Oyashio water or Oyashio–Kuroshio mixed water with reference to the midwater Oyashio front temperature (5 °C from March to May, 6 °C in February, June, July and August, 7 °C in January September and October, and 8 °C in November and December) defined by Kawai (1972).

Fur seals were shot from the research vessels, retrieved onboard and measured. Most of the fur seals were sexed and were aged by examination of the annuli of the upper canine teeth (Scheffer, 1950; Anas, 1970). Seals younger than 4 years were classified as juveniles, whereas those 4 years or older were classified as adults. Subadult males which are socially excluded from reproduction were categorized as adults because they are physiologically mature and have larger bodies than females and juvenile males (Gentry, 1998).

During the historical surveys before 1988, the stomachs of the fur seals were removed onboard and stored in 10% formalin in sea water; the stomach contents were then analyzed in the laboratory within a few months. Total volume and weight of the stomach contents were measured, and prey species were identified on the basis of external morphology with supplementary use of typical body parts such as scales or bones (of fishes) and beaks or tentacular suckers and hooks (of squids) in the case of commercially important species. Digested trace materials (< 10 mL) were not used for species identification