

Feeding habits of sperm whales (*Physeter macrocephalus*) in the western North Pacific in spring and summer

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ABSTRACT

The stomach contents of 56 sperm whales (*Physeter macrocephalus*) sampled in the western North Pacific by the Second Phase of the Japanese Whale Research Program under Special Permit in the western North Pacific (JARPNII) from May to September of the years 2000 to 2013, were examined. A total of 49 undigested and half-digested prey items were found, including 28 species of cephalopods and six species of fish. The Index of Relative Importance (IRI) showed that *Belonella borealis* and *Histioteuthis* spp. were the dominant prey in the Subarctic Region, while *B. borealis* and *Galiteuthis phyllura* were the dominant prey in the Transitional Domain. *B. borealis* and *Taningia danae* were the dominant prey in the Northern part of the Transition Zone, while *T. danae* and *Histioteuthis* spp. were the dominant prey in the Southern part of the Transition Zone. In the Kuroshio Zone, *T. danae* and *Octopoteuthis* spp. were the dominant preys. The composition of prey items changed in relation to transitional change between north and south. Canonical Correspondence Analysis (CCA) indicated that environmental and biological factors significantly contributed to the prey composition of sperm whales. Our study demonstrated that sperm whales moved along waters with different oceanographic conditions, feeding on a variety of prey species. Larger whales tend to feed at offshore waters. This flexibility and different size distribution in sperm whale seems to be important to maintain large body size and large abundance in the western North Pacific. The commercially important Neon flying squid *O. bartrami* was not an important prey of sperm whales in spring and summer.

KEYWORDS: SPERM WHALE; FOOD/PREY; SQUID; NORTH PACIFIC; SCIENTIFIC PERMITS

INTRODUCTION

The sperm whale (*Physeter macrocephalus*) is the largest species among odontocete with remarkable sexual dimorphism that males attain 18.3m and females attain 12.5m as maximum length. Sperm whale ranges throughout all deep oceans of the world from the equator to the edges of the polar pack ice (Rice, 1989), however mature males migrate at higher latitudes, while females and younger males generally occurring at south of 40-50°N in the Northern Hemisphere, so to speak sexual geographical segregation (Ohsumi, 1966; Rice, 1989). Sperm whales dive to mesopelagic waters (Aoki *et al.*, 2007, Amano and Yoshioka, 2003), and the most important food items are meso- and bathypelagic squids (Berzin, 1972, Kawakami, 1980, Clarke, 1996). For these reason, sperm whales play an important role in the ecosystem at deeper layer because of its high abundance.

In the western North Pacific subarctic and subtropical fronts converge, and this confluence leads to a Transition Region (Kawai, 1972), where oceanographic conditions are complex and of high productivity. This region is important feeding area for cetaceans (Tamura *et al.*, 1998, Tamura and Fujise, 2002, Ohizumi *et al.*, 2003, Murase *et al.*, 2007, Konishi *et al.*, 2009, Watanabe *et al.*, 2012).

There are few diet studies of sperm whale in the western North Pacific that only report whales feed almost on squids (Mizue, 1951, Omura, 1950), and *Histioteuthis dolfleini*, *Ommastrephes bartrami*, *Octopoteuthis* sp., *Moroteuthis robusta* are important prey species during autumn and winter (Kawakami, 1976, Okutani *et al.*, 1976, Okutani and Satake, 1978). However, studies on sperm whale feeding habits are extremely limited.

Distribution patterns of mesopelagic fishes and squids, which are prey species for sperm whale, are related to water masses (Brodeur and Yamamura, 2005, Jefferts, 1988, Watanabe, 2006). However, the information on this relationship is still limited.

The purposes of this study were to (1) to describe the diet of sperm whales, and (2) examines the sperm whales feeding habits, in the western North Pacific, based on samples and data collected by the JARPNII since 2000

MATERIALS AND METHODS

Research area and sampling of whales

The sampling area was comprised between the Pacific coast of Japan and 170°E, in the latitudinal range between 35°N and 50°N (Figure 1). A total 56 sperm whales were sampled by JARPNII from May to September during 2000-2013. The sampling of sperm whales was restricted to animals of body length < 13 m because of logistical reasons (capacity of research base vessel) in the operation. The sampled whales were transported to a research base vessel where biological survey was conducted. All whales were measured, weighed, and their reproductive organs were examined to determine sexual maturity.

Stomach contents analyses

The stomach contents were removed from each compartments, (*i.e.* forestomach, fundic, pyloric and duodenal ampulla, see Hosokawa and Kamiya, 1971, Olsen *et al.*, 1994), and were weighted to the nearest 0.1kg. Stomach contents were frozen for further analysis in the laboratory. In the case when large fresh preys were found in the stomach, their body lengths (BL): standard or total length (SL, TL) for fishes, mantle length or dorsal mantle length (ML, DML) for cephalopods and wet body weight (BW) were measured. Buccal mass (beaks with surrounded muscle) or head (head and arms including buccal mass) and whole undigested prey were sampled.

At the laboratory, stomach contents were sorted into the following categories, (1) undigested: nearly intact whole body or body with little digestion effects, include fishes when most of muscle was still attached to the bone (2) partially digested: head containing buccal masses with beaks in cephalopods and sagittal otoliths in fishes, head was detached from mantle or vertebra, (3) isolated buccal mass with beaks, (4) digested: isolated beaks and sagittal otoliths, (5) other remains and parasites. The BL and BW were measured for undigested items. There are many beaks remained in the stomachs because these parts are hard and need long time to digest or broken. Therefore following two categories which reflect recent feeding, were used (1) undigested items, (2) partially digested items and buccal mass with beaks in the analyses.

Cephalopods and fishes were identified to the lowest taxonomic level as possible based on the morphology of their lower beaks and sagittal otoliths, respectively (Clarke, 1986; Kubodera and Furuhashi, 1987; Kubodera, 2005, and the beak reference collection at the National Science Museum, Tokyo), as well as on external morphology in regards to undigested items (Nesis, 1987; Okutani, 1995, 2005; Nakabo, 2000). The rostral length of the lower beak (LRL) of cephalopods was measured using vernier calipers to the nearest 0.1 mm and previously published equations (Wolff, 1982; Clarke, 1986; Jackson, 1995; Kubodera, 2005; Lu and Ickeringill, 2002; Orlov, 2007) were used to estimate DML or ML and body weight.

Restoration of prey weight

To examine total prey weight fed by sperm whale, two step calculation to restore weight from digested prey from hard parts remained. We made equations to restore dorsal mantle length (DML) or body weight (BW) for some squid species. For example, to estimate DML or BW, lower rostral length of beak (LRL) of *Taningia danae* were used on 34 undigested items. Existing equations of the same genus or family were adapted for the estimates of some cephalopod species for which the equations have not reported. BW and ML were then calculated from BL or DML by equations of Orlov (2007), Lu and Ickeringill (2002), Clarke and Young (1998) and Watanabe *et al.* (1999).

Oceanography

Positions of oceanographic boundary and water masses were examined to know at which water mass whale feed on the prey species. From mixed Layer data set of Argo by JAMSTEC (Japan Agency for Marine-Earth Science and Technology) (Hosoda *et al.*, 2010), water temperature and salinity from 2001 to 2013 were visualized using software Ocean Data View (Schlitzer, R., Ocean Data View, <http://odv.awi.de>, 2014). Monthly mean of temperature in 2000 were obtained by Japan Meteorological Agency (JMA) and Japan Oceanographic Data Center (JODC) (http://near-goops1.jodc.go.jp/index_j.html; accessed 26 August 2014) and Off Tohoku Temperature Field by Tohoku National Fisheries Research Institute (TNFRI) (<http://tnfri.fra.affrc.go.jp/kaiyo/temp/temp.html>; accessed 27 August 2014).

Then water mass was determined using above dataset into 5 areas based on the definition by Yasuda (2003) and Brodeur and Yamamura (2005) as follows: Subarctic Region (SA), Transitional Domain (TD), Northern part of Transition Zone (NTZ), Southern part of Transition Zone (STZ) and Kuroshio Zone (KZ) (see Figure 1).

Data analysis

The composition of each prey items was calculated as percent by number (%N), percent by weight (%W), and percent by frequency of occurrence (%F). %N is the total number of a single prey item/the total number of all prey items $\times 100$; %W is the total wet weight of a single prey item/the total wet weight of all prey items $\times 100$; %F is the total number of stomachs including a single prey item/the total number of stomachs examined (excluding heavily damaged stomach by harpoon or no undigested and partially digested prey items) $\times 100$. The Index of Relative Importance IRI (Pinkas *et al.* 1971) was calculated as $IRI = (%N + \%W) \times \%F$. The IRI expressed as a percent basis was also calculated.

Canonical Correspondence Analysis (CCA), which is categorized as one of the habitat models (Redfern *et al.*, 2006), and is a powerful tool that can identify features within diet compositions and habitat use, together with biological and environmental factors (Guisan and Zimmermann, 2000, Redfern *et al.*, 2006). CCA of number and weight data for the most important prey items (frequency $>5\%$ in 49 whales and whales occurring in $>10\%$ of all prey types) was conducted after $\ln(x+1)$ transformation to examine diet composition in relation to environmental variables (latitude, longitude, sampled date, depth of sampled site) and biological variables (body length, sex, sexual maturity), using the ‘vegan’ package (ver.2.3-0, Oksanen *et al.*, 2015) in R (<http://www.r-project.org>). According to the preliminary CCA, collinear environmental variables with high variance inflation factors ($VIF > 20$) were eliminated from further analyses. The variable excluded was body weight, which was correlated positively to body length. Each environmental and biological factors was tested by 1,000 permutations and considered significant at the 5% level.

Distribution of sperm whales

This study used sighting data collected from JARPNII from 2000-2013. Density Index by 0.5 degree mesh (number of whales found per n.mile) of sperm whales distribution in the research area was calculated by month.

RESULTS

Whales examined

A total of 56 sperm whales were examined. Biological data of sperm whales in this study were summarized by oceanographic features (Table 1). Body length ranged from 7.4 to 13.7m (average 10.1m) and body weight ranged from 4.1 to 32.7t (average 15.5t). The sample of sperm whales was composed of eight immature females, seven immature males, 32 mature females, one mature male and eight males in puberty. In the case of three whales (TD: one whale, STZ: two whales) the stomachs were largely damaged by the harpoon. In the case of four whales (STZ: two whales, KZ: two whales) undigested, partially digested and buccal mass with beaks items were not found in the stomachs. Those seven whales were excluded from the analyses. Although the sample size is small and sampling was restricted to sperm whales with body length of 13m or smaller, the samples obtained were widely distributed in the western North Pacific.

Diet composition

A total of 49 types of prey items were found, including 28 species of cephalopods and 6 species of fish (Table 2). Indices of Relative Importance (IRI) for prey items of sperm whales in water masses are shown in Figure 2.

Subarctic Region (SA)

Belonella borealis was the most important prey item by number (26.4%), weight (24.8%) and frequency of occurrence (100%), followed by *Histioteuthis* spp. (30.5%, 14.5% and 100.0%, respectively). Weight of *Onikia* (*Onikia robusta*) was the highest (27.8%), however its number (1.4%) and frequency of occurrence (50.0%) were lower than in *B. borealis* and *Histioteuthis* spp.. The %IRI was in the following order: *B. borealis* (30.9%), *Histioteuthis* spp. (27.2%), *O. (Onikia) robusta* (8.8%), *Gonatopsis* aff. *makko* (7.5%), *Gonatus* spp. (7.5%), *Histioteuthis dofleini* (7.3%), *Galiteuthis phyllura* (5.9%) and *Chiroteuthis calyx* (1.9%).

Transitional Domain (TD)

B. borealis was the most important prey item by number (36.6%), weight (27.9%) and frequency of occurrence (100%), followed by *G. phyllura* (25.7%, 8.4% and 85.7%, respectively). Weight of *O. (Onikia) robusta* (26.9%) was almost the same as in *B. borealis*, but its number (2.1%) and frequency of occurrence (28.6%) were lower. The %IRI was in the following order: *B. borealis* (47.4%), *G. phyllura* (21.4%), *Histioteuthis* spp.

(10.3%), *O. (Onikia) robusta* (6.1%), *Taningia danae* (3.7%), *Gonatopsis borealis* (3.6%), *C. calyx* (1.6%) and *G. aff. makko* (1.4%).

Northern part of Transition Zone (NTZ)

The most important species were *B. borealis* in number (35.9%) and *T. danae* in weight (51.5%). However, number of *T. danae* was very low (5.2%). The frequency of occurrence in *Histioteuthis* spp., *G. phyllura* and *G. borealis* were 82.4%, 88.2% and 76.5%, respectively, higher than *B. borealis* (58.8%) and *T. danae* (47.1%). The %IRI was in the following order: *B. borealis* (30.1%), *T. danae* (22.8%), *Histioteuthis* spp. (13.8%), *G. phyllura* (11.6%), *G. borealis* (7.3%), *H. dofleini* (3.5%), *Gonatus berryi* (3.2%) and *Gonatus* spp. (3.1%).

Southern part of Transition Zone (STZ)

The most important species were *Histioteuthis* spp. in number and frequency of occurrence (37.2% and 88.2%, respectively) and *T. danae* in weight and frequency of occurrence (58.6% and 64.7%, respectively), while the weight of *Histioteuthis* spp. and number of *T. danae* were low (9.7% and 8.6%, respectively). The %IRI was in the following order: *T. danae* (36.6%), *Histioteuthis* spp. (34.8%), *H. dofleini* (7.6%), *O. (Onikia) robusta* (5.5%), *Ancistrocheirus lesueurii* (5.0%), *G. phyllura* (2.0%), *Megalocranchis* sp. (1.6%) and *B. borealis* (1.4%).

Kuroshio Zone (KZ)

The common species in number were *Octopoteuthis* spp. (15.9%), followed by *Gonatus* spp. (14.2%) and *Histioteuthis* spp. (14.2%). The common species in weight were *T. danae* (32.1%), followed by *Octopoteuthis* spp. (15.7%). The most common species in frequency of occurrence were *B. borealis*, *H. dofleini* and *Gonatus* spp. (75.0%, 75.0% and 75.0%, respectively) and *Histioteuthis* spp. (75.0%). The %IRI was in the following order: *T. danae* (19.7%), *Octopoteuthis* spp. (15.9%), *Gonatus* spp. (14.2%), *A. lesueurii* (10.7%), *B. borealis* (10.2%) and *Histioteuthis* spp. (9.7%). *Trachipterus* spp. as a fish prey was ranked 3.2%, and this differed from other water masses.

Prey compositions by environmental and biological factors

The CCA analyses for correlation between prey items of weight and environmental factors (Longitude, Latitude, Date, Sex, Depth, Maturity and Body length) had eigenvalues of 0.200 and 0.093, explaining 41.1% and 19.1% of the species-environment variance (Figure 3). Within above seven variables, “latitude” and sampled “date” were significant at $p<0.001$ and $P<0.05$, respectively. Positive scores of Axis 1 (longitudinal axis (a) in Figure 3) was explained by higher latitude and later day. “Longitude”, “maturity” and “body length” were also significant values at $p<0.01$, $p<0.01$ and $p<0.01$, respectively. On the second axis 2 represents larger whale and maturity.

From the plots of each whales, such as TD6 or NTZ1 etc., whales sampled at SA and TD had positive scores on Axis 1, while whales sampled in STZ and KZ had negative scores on Axis 1 except STZ2. Whales sampled in NTZ scores were plotted at positive and negative on the Axis 1. This result indicated sperm whales shift to northward at later days, large and mature sperm whales distribute offshore, and contrarily small and immature sperm whales distribute more inshore area.

The prey items could be separated into three groups along Axis 1 in Figure 3b. The first group (*e.g. G. madokai*, *G. middendorffi*, *G. aff. makko*, *O. borealijaponica*) appeared to have positive scores (>0.5) on Axis 1. The second group (*e.g. Architeuthis dux*, *C. akimushkini*, *Megalocranchia* sp., *Octopoteuthis* spp., *D. discus*, *Trachipterus* spp.) appear to have negative scores (<-0.5) on Axis 1. The third group with close to neutral scores (>-0.5 , <0.5), appeared between first and second group. In these prey items, *O. sicula*, *C. calyx*, *B. borealis*, *G. borealis*, *G. phyllura*, *G. berryi* and *Gonatus* spp. plotted positive scores on Axis 1, *A. lesueurii*, *T. danae*, *O. (Onikia) robusta*, *O. (Onikia) loennbergii*, *O. deletron* and *C. imperator* plotted negative scores on Axis 1. Genus *Histioteuthis* plotted almost neutral scores on Axis 1. This result indicated squids composition strongly affect by latitude. *G. madokai* and *O. (Onikia) loennbergii* plotted have largest positive score and most negative score on Axis 2, respectively. *G. madokai* distributed at most North and offshore area and *O. (Onikia) loennbergii* is distributed inshore.

Distribution patterns of sperm whales

Density index based on sighting survey data suggested that the sperm whales were widely distributed in the whole research area. However, sperm whales east of 150°E moved northward in July and August, while high density remained in northern Japan west of 150°E.

DISCUSSION

Sperm whales in the western North Pacific off Pacific coast of Japan fed upon a variety of mesopelagic squids throughout the whole study area. Prey items in the Subarctic Region and Transitional Domain were mainly composed by subarctic and subarctic-transitional squids. Contrarily, prey items in the Kuroshio Zone and Southern part of Transition Zone were mainly composed of subtropical and subtropical-transitional squids. Prey items in the northern part of the Transition Zone were composed of squids that mixed in Subarctic Region to Kuroshio Zone. The composition of prey items changed in relation to transitional change between north and south in the study area and *B. borealis*, genus *Histioteuthis* and *T. danae* were the most important prey species with high abundance.

Kuroshio Zone had unique prey composition, having a small number of prey types and IRI values of each prey types (not more than 20%). The Kuroshio Zone had prey squids at lower density and important prey squids like *B. borealis* and *T. danae* did not occur at water masses in the north of Kuroshio Extension Front. In the Townsend's American (Yankee) whaling charts which Mizroch and Rice (2013) showed, sperm whales were not distributed in the Kuroshio Current System and high density was observed on both side of Kuroshio Current System. Uda (1954) stated that whale school does not occur in the easterly rapid flowing Zone of warm current. Accordingly the whaling grounds are poorly found in the westerly drift wind current area (a branch of Kuroshio) in the North Pacific Ocean and Kuroshio itself. Low density of sperm whales in the Kuroshio Zone may reflect feeding environment as well as oceanographic factor.

Sperm whales have a general shift northward during the northern summer (Rice, 1989). East of northern Japan area whaling ground by Yankee whalers namely Cast of Japan Ground (Mizroch and Rice, 2013) and costal whaling (Kasuya and Miyashita, 1988) occurred. In this study, results of the CCA and distribution of sperm whales suggested similar patterns northward movement and high density area off northern Japan at west of 150°E. High density areas of the northern part of research area and east of 150°E probably corresponds to the Subarctic Region and west of Northern/Southern part of the Transition Zone, respectively. Mizroch and Rice (2013) concluded by analyzing whaling data and movement data of whales marked with Discovery marks that sperm whales appear to be nomadic, most likely traveling in response to the geographical and temporal variations in the abundance of medium- and large-sized pelagic squids, their primary food. We confirmed that sperm whales feed there. Feeding environment of Subarctic Region and west of Northern/Southern part of the Transition Zone may represent favourable situation for sperm whales.

Distribution depth in the daytime of most important prey, *B. borealis*, *H. dofleini* and *T. danae* is 500-700m, 500-700m, and 600-900m, respectively (Watanabe *et al.*, 2006, Kubodera *et al.*, 2007). *B. borealis* and *H. dofleini* is non-diel vertical migration squids (Watanabe *et al.*, 2006). Therefore it is suggested that the main feeding depth of sperm whales is around 500-700m, in the western North Pacific east of Japan. Important prey species in autumn and winter for sperm whales in the east coast of Japan were *H. dofleini*, *O. bartrami*, *Octopoteuthis* sp., *Moroteuthis robusta* (Kawakami, 1976, Okutani *et al.*, 1976, Okutani and Satake, 1978). These squids were identified in the present study, in particular *H. dofleini* and *O. robusta* were identified as important preys in this study. According to the result of Tamura *et al.* (2009) and the present study, *O. bartrami* was not important prey of sperm whales in spring and summer. *O. bartrami* in nearby Subarctic Front mainly distributed 0–40m depths during the night and 200–350m depths during the day in summer (Nakamura, 1995, Tanaka, 1999). Important prey squids of sperm whales distributed deeper than *O. bartrami*. *O. bartrami* was not an important prey for sperm whales from spring to summer probably because of differences between feeding depth of sperm whale and distribution depth of *O. bartrami*.

In 2000 to 2013 JARPNII, the large male sperm whales (Body length > 13m) could not obtain for technical reason. To understand more precisely the feeding habits of sperm whales, more samples, especially mature males are needed. However, food habit and consumption by sperm whale were used as input data for Ecopath & Ecosym type model to understand the role of sperm whale in the marine ecosystem (Mori *et al.*, 2009, Murase *et al.*, 2016: SC/F16/JR28).

In conclusion, our study suggest that the distribution and movement of sperm whales throughout Kuroshio to Subarctic Zone west of 170°E seems to reflect the abundance of mesopelagic squids in spring and summer, in particular *B. borealis*, genus *Histioteuthis* and *T. danae*. Larger whale likely feed at offshore waters which also be a factor of prey composition. This flexibility and different size distribution in sperm whale seems to be important to maintain large size of the body and high abundance in the North Pacific.

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Table 1. Biological data and stomach contents weight of sperm whales sampled from 2000 to 2013 in the western North Pacific. Sexual maturity of male was assigned based on summed weight of both testes as immature <1.2kg, puberty >1.2kg (Rice, 1989), sexually mature >4.85kg (Gambell, 1972). Sexual maturity of female was determined by the presence of at least one corpus luteum or corpus albicans in the ovaries and/or pregnancy. Stomach contents weight was the total net weight of forestomach and fundic compartment.

| | Subarctic Region (SA) | | Transitional Domain (TD) | | | Northern part of Transition Zone (NTZ) | | | | Southern part of Transition Zone (STZ) | | | | Kuroshio Zone (KZ) | | | | Total | |
|---|-----------------------|---------------|--------------------------|---------------|--------|--|---------------|-------------|---------------|--|------------------------|------------------------|---------|--------------------|---------------|----------|---------|--------------|--|
| | Female | | Male | | Female | | Male | | Female | | Male | | Female | | Male | | | | |
| | Mature | Puberty | Immature | Mature | Mature | Immature | Mature | Immature | Puberty | Immature | Mature | Immature | Puberty | Immature | Mature | Immature | Puberty | | |
| Number of whales | 1 | 3 | 3 | 4 | 1 | 2 | 10 | 2 | 3 | 2 | 14 | 4 | 1 | 1 | 3 | 1 | 1 | 56 | |
| Average body length (m) ± S.D. | 12.7 | 11.8 ± 0.56 | 8.6 ± 1.08 | 10.5 ± 0.61 | 13.7 | 8.5 ± 0.35 | 10.6 ± 0.50 | 8.6 ± 0.21 | 10.7 ± 1.87 | 8.8 ± 0.57 | 10.3 ± 0.86 | 9.3 ± 0.67 | 10.9 | 8.3 | 9.9 ± 0.25 | 7.9 | 10.2 | 10.1 ± 1.27 | |
| (Body length range) | - | (11.3 - 12.4) | (7.4 - 9.4) | (9.9 - 11.3) | - | (8.2 - 8.7) | (9.8 - 11.5) | (8.4 - 8.7) | (9.2 - 12.8) | (8.4 - 9.2) | (8.9 - 11.6) | (8.8 - 10.3) | - | - | (9.7 - 10.2) | - | - | (7.4 - 13.7) | |
| Average body weight (t) ± S.D. | 24.9 | 22.9 ± 4.10 | 9.0 ± 4.31 | 17.6 ± 4.28 | 32.7 | 8.0 ± 0.64 | 17.0 ± 4.34 | 9.3 ± 0.14 | 19.0 ± 9.91 | 9.5 ± 1.98 | 16.5 ± 3.74 | 11.4 ± 1.85 | 17.0 | 7.5 | 13.6 ± 2.32 | 6.3 | 14.4 | 15.5 ± 5.97 | |
| (Body weight range) | - | (19.7 - 27.5) | (4.1 - 12.2) | (13.5 - 23.5) | - | (7.5 - 8.4) | (13.0 - 26.2) | (9.2 - 9.4) | (12.4 - 30.4) | (8.1 - 10.9) | (10.2 - 22.0) | (10.2 - 14.1) | - | - | (11.8 - 16.2) | - | - | (4.1 - 32.7) | |
| Average stomach contents weight (kg) ± S.D. | 32.4 | 98.3±54.4 | 28.9 ^a | 19.1±21.2 | 179.1 | 41.1±3.8 | 67.5±58.1 | 56.8±48.8 | 40.7±17.1 | 49.6±57.0 | 50.5±44.0 ^b | 55.4±28.5 ^c | 54 | 16 | 21.6±17.7 | 4.1 | 6.7 | 51.4±46.2 | |
| (Stomach contents weight range) | - | (41.1-149.4) | - | (2.7-50.3) | - | (38.4-43.8) | (9.0-168.7) | (22.3-91.3) | (22.1-55.8) | (9.3-89.9) | (2.2-148.3) | (38.5-88.3) | - | - | (3.6-39.0) | - | - | (2.2-179.1) | |

^aTwo whales was excluded, for stomach was broken by harpoon and no stomach content weight data, respectively; ^band ^cOne whale was excluded, for stomach was broken by harpoon.

Table 2. Prey items compositions in the stomach contents from sperm whales sampled in the western North Pacific from 2000 to 2013.

| | | Subarctic Region (SA) n=4 | | | | Transitional Domain (TD) n=7 | | | | Northern part of Transition Zone (NTZ) n=17 | | | | Southern part of Transition Zone (STZ) n=17 | | | | Kuroshio Zone (KZ) n=4 | | | | |
|-------------------|--------------------------------------|------------------------------|------|-------|-------|---------------------------------|------|-------|-------|--|------|------|-------|--|------|------|-------|---------------------------|------|------|-------|--|
| | | % N | % W | % F | % IRI | % N | % W | % F | % IRI | % N | % W | % F | % IRI | % N | % W | % F | % IRI | % N | % W | % F | % IRI | |
| Cephalopods | | | | | | | | | | | | | | | | | | | | | | |
| Ancistrocheiridae | <i>Ancistrocheirus lesueurii</i> | 0.7 | 1.1 | 50.0 | 0.5 | - | - | - | - | 0.7 | 0.5 | 29.4 | 0.3 | 8.3 | 4.4 | 47.1 | 5.0 | 11.5 | 9.8 | 50.0 | 10.7 | |
| Enoplateuthidae | <i>Enoplateuthis chuni</i> | - | - | - | - | - | - | - | - | - | - | - | - | 0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| Onychoteuthidae | <i>Onychoteuthis borealijaponica</i> | - | - | - | - | 0.4 | 0.1 | 28.6 | 0.1 | 0.6 | 0.3 | 41.2 | 0.3 | 0.3 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| | <i>Onykia (Onykia) robusta</i> | 1.4 | 27.8 | 50.0 | 8.8 | 2.1 | 26.9 | 28.6 | 6.1 | 0.2 | 3.6 | 11.8 | 0.4 | 1.5 | 10.7 | 52.9 | 5.5 | - | - | - | - | |
| | <i>Onykia (Onykia) loennbergii</i> | - | - | - | - | - | - | - | - | - | - | - | - | 1.4 | 0.3 | 17.6 | 0.3 | - | - | - | - | |
| Gonatidae | <i>Gonatus berryi</i> | 1.0 | 0.4 | 75.0 | 0.6 | 1.9 | 0.6 | 57.1 | 1.1 | 6.1 | 1.1 | 52.9 | 3.2 | 1.0 | 0.2 | 29.4 | 0.3 | - | - | - | - | |
| | <i>Gonatus middendorffii</i> | 0.2 | <0.1 | 25.0 | <0.1 | 0.4 | 0.3 | 28.6 | 0.1 | 0.3 | <0.1 | 17.6 | <0.1 | 0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| | <i>Gonatus madokai</i> | 0.2 | 0.2 | 25.0 | <0.1 | - | - | - | - | 0.4 | 0.2 | 11.8 | <0.1 | - | - | - | - | - | - | - | - | |
| | <i>Gonatopsis aff. makko</i> | 4.1 | 8.3 | 100.0 | 7.5 | 1.2 | 3.1 | 42.9 | 1.4 | 0.5 | 1.0 | 17.6 | 0.2 | 0.1 | 0.1 | 5.9 | <0.1 | - | - | - | - | |
| | <i>Gonatopsis borealis</i> | 0.3 | 0.3 | 25.0 | <0.1 | 3.5 | 3.3 | 71.4 | 3.6 | 7.0 | 4.2 | 76.5 | 7.3 | 2.4 | 1.0 | 17.6 | 0.5 | - | - | - | - | |
| | <i>Berryteuthis magister</i> | 0.8 | 1.0 | 25.0 | 0.3 | - | - | - | - | <0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | - | - | - | - | |
| | <i>Gonatus</i> spp. | 8.1 | 8.4 | 75.0 | 7.5 | 1.4 | 1.6 | 57.1 | 1.3 | 3.9 | 0.9 | 76.5 | 3.1 | 1.3 | 0.5 | 47.1 | 0.7 | 14.2 | 4.7 | 75.0 | 14.2 | |
| | <i>Gonatopsis</i> sp. | 0.7 | 0.4 | 25.0 | 0.2 | - | - | - | - | 0.4 | <0.1 | 11.8 | <0.1 | - | - | - | - | - | - | - | - | |
| | <i>Gonatidae</i> sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| Octopoteuthidae | <i>Octopoteuthis sicula</i> | - | - | - | - | 0.2 | <0.1 | 14.3 | <0.1 | 0.2 | <0.1 | 17.6 | <0.1 | 0.4 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| | <i>Octopoteuthis deletron</i> | 0.7 | 0.3 | 50.0 | 0.3 | 0.7 | 0.5 | 28.6 | 0.2 | 1.5 | 0.8 | 35.3 | 0.7 | 1.5 | 0.4 | 29.4 | 0.5 | 3.5 | 3.2 | 25.0 | 1.7 | |
| | <i>Taningia danae</i> | 0.2 | 2.2 | 25.0 | 0.4 | 0.9 | 8.0 | 57.1 | 3.7 | 5.2 | 51.5 | 47.1 | 22.8 | 8.6 | 58.6 | 64.7 | 7.1 | 32.1 | 50.0 | 19.7 | | |
| | <i>Octopoteuthis</i> spp. | 0.5 | 0.2 | 50.0 | 0.2 | 0.2 | <0.1 | 14.3 | <0.1 | 0.1 | <0.1 | 11.8 | <0.1 | 2.6 | 0.7 | 35.3 | 1.0 | 15.9 | 15.7 | 50.0 | 15.9 | |
| Cycloteuthidae | <i>Cycloteuthis akimushikini</i> | - | - | - | - | - | - | - | - | <0.1 | <0.1 | 5.9 | <0.1 | 1.4 | 0.8 | 17.6 | 0.3 | 1.8 | 2.1 | 50.0 | 2.0 | |
| | <i>Discoteuthis discus</i> | - | - | - | - | - | - | - | - | <0.1 | <0.1 | 5.9 | <0.1 | 0.5 | <0.1 | 17.6 | <0.1 | - | - | - | - | |
| | <i>Cycloteuthidae</i> sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 2.7 | 2.1 | 25.0 | 1.2 | |
| Histioteuthidae | <i>Histioteuthis dofleini</i> | 11.2 | 5.0 | 75.0 | 7.3 | 3.7 | 1.3 | 14.3 | 0.5 | 4.9 | 2.0 | 58.8 | 3.5 | 12.5 | 2.9 | 58.8 | 7.6 | 5.3 | 3.5 | 75.0 | 6.7 | |
| | <i>Histioteuthis corona inermis</i> | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| | <i>Histioteuthis</i> spp. | 30.5 | 14.5 | 100.0 | 27.2 | 17.3 | 7.2 | 57.1 | 10.3 | 14.5 | 5.2 | 82.4 | 13.8 | 37.2 | 9.7 | 88.2 | 34.8 | 14.2 | 5.1 | 50.0 | 9.7 | |
| Lepidoteuthidae | <i>Pholidoteuthis boschmai</i> | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.8 | 2.4 | 25.0 | 1.1 | | |
| Architeuthidae | <i>Architeuthis dux</i> | - | - | - | - | - | - | - | - | - | - | - | - | 0.6 | 5.4 | 23.5 | 1.2 | - | - | - | - | |
| Ommastrephidae | <i>Ommastrephes bartramii</i> | - | - | - | - | - | - | - | - | <0.1 | 0.2 | 5.9 | <0.1 | - | - | - | - | - | - | - | - | |
| Chiroteuthidae | <i>Chiroteuthis imperator</i> | 0.2 | <0.1 | 25.0 | <0.1 | - | - | - | - | 0.2 | <0.1 | 17.6 | <0.1 | 0.9 | <0.1 | 23.5 | 0.2 | - | - | - | - | |
| | <i>Chiroteuthis calyx</i> | 5.1 | 1.2 | 50.0 | 1.9 | 3.2 | 0.6 | 57.1 | 1.6 | 5.0 | 0.9 | 47.1 | 2.3 | 1.0 | 0.1 | 23.5 | 0.2 | 0.9 | 0.2 | 25.0 | 0.3 | |
| Mastigoteuthidae | <i>Asperoteuthis acanthoderma</i> | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.9 | 0.9 | 25.0 | 0.5 | | |
| Cranchiidae | <i>Mastigoteuthis</i> sp. | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.9 | <0.1 | 25.0 | 0.2 | | |
| | <i>Liocranchia reinhardtii</i> | - | - | - | - | - | - | - | - | - | - | - | - | 0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| | <i>Belonella borealis</i> | 26.4 | 24.8 | 100.0 | 30.9 | 36.6 | 27.9 | 100.0 | 47.4 | 35.9 | 23.9 | 58.8 | 30.1 | 3.0 | 0.9 | 41.2 | 1.4 | 8.8 | 4.7 | 75.0 | 10.2 | |
| | <i>Galiteuthis phyllura</i> | 6.9 | 2.9 | 100.0 | 5.9 | 25.7 | 8.4 | 85.7 | 21.4 | 11.9 | 3.4 | 88.2 | 11.6 | 5.9 | 0.8 | 35.3 | 2.0 | 4.4 | 1.6 | 25.0 | 1.5 | |
| | <i>Taonius</i> sp. | - | - | - | - | - | - | - | - | - | - | - | - | 1.1 | 0.1 | 5.9 | <0.1 | - | - | - | - | |
| | <i>Galiteuthis</i> sp. | - | - | - | - | - | - | - | - | - | - | - | - | 0.4 | 0.1 | 11.8 | <0.1 | - | - | - | - | |
| | <i>Megalocranchia</i> sp. | - | - | - | - | 0.2 | 0.4 | 14.3 | <0.1 | - | - | - | - | 3.9 | 0.6 | 41.2 | 1.6 | 1.8 | 0.6 | 50.0 | 1.2 | |
| Alloposidae | <i>Cranchiinae</i> spp. | 0.3 | <0.1 | 25.0 | <0.1 | - | - | - | - | - | - | - | - | 0.4 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| | <i>Haliphron atlanticus</i> | - | - | - | - | 0.2 | 0.1 | 14.3 | <0.1 | - | - | - | - | 0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| | Unidentified cephalopods | - | - | - | - | - | - | - | - | - | - | - | - | 0.3 | NA | 5.9 | NA | 2.7 | NA | 25.0 | NA | |
| Fishes | <i>Nannobrachium regale</i> | - | - | - | - | - | - | - | - | - | - | - | - | 0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| Moridae | <i>Laemonema longipes</i> | - | - | - | - | - | - | - | <0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | - | - | - | - | - | |
| | <i>Moridae</i> spp. | 0.2 | 0.2 | 25.0 | <0.1 | - | - | - | 0.1 | 0.2 | 5.9 | <0.1 | - | - | - | - | - | - | - | - | - | |
| Macrouridae | <i>Coryphaenoides pectoralis</i> | 0.3 | 0.9 | 25.0 | 0.2 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| Himantolophidae | <i>Himantolophus groenlandicus</i> | - | - | - | - | - | - | - | - | - | - | - | - | 0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| Diretmidae | <i>Diretmoides parini</i> | - | - | - | - | - | - | - | - | - | - | - | - | 0.1 | <0.1 | 5.9 | <0.1 | - | - | - | - | |
| Trachipteridae | <i>Trachipterus</i> spp. | - | - | - | - | - | - | - | - | - | - | - | - | 0.4 | 1.5 | 11.8 | 0.2 | 1.8 | 11.1 | 25.0 | 3.2 | |
| Icosteidae | <i>Icosteus aenigmaticus</i> | - | - | - | - | 0.2 | 9.7 | 14.3 | 1.0 | - | - | - | - | - | - | - | - | - | - | - | - | |
| | Unidentified fish | 0.2 | NA | 25.0 | NA | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | Total | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | 100 | |
| | Number of prey items | 591 | 590 | 565 | 565 | 1626 | 1626 | 793 | 791 | 113 | 110 | | | | | | | | | | | |

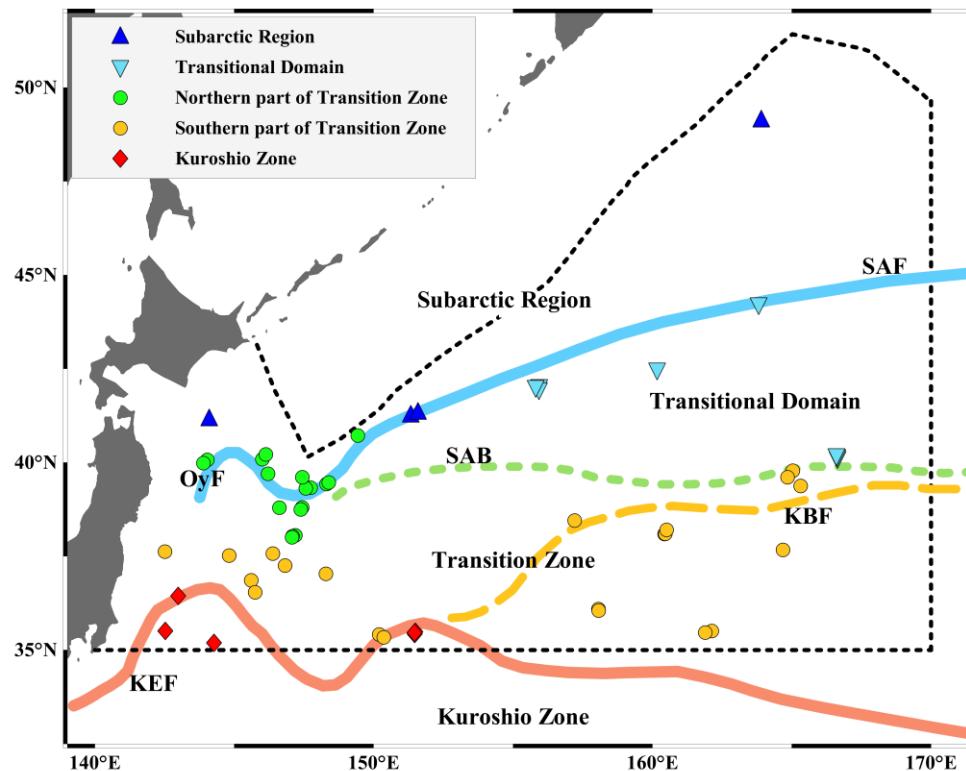


Figure 1. Sampling positions of sperm whales from 2000 to 2013 and schematic illustration of front and water mass structures in western North Pacific. Schematic illustration of front and water mass structures was determined according to Yasuda (2003) and Brodeur and Yamamura (2005) as follows. Subarctic Region (SA); north of the Oyashio Front (OyF) which is defined as a 5°C isotherm at 100 m depth at west of approximately 155°E and the Subarctic Front (SAF) is defined as the 4°C isotherm at 100 m depth at east of approximately 155°E. Transitional Domain (TD); area of between the Oyashio Front/the Subarctic Front and the Subarctic Boundary (SAB), which is defined as a near-surface salinity front (salinity of 34 psu). SAF (OyF) and SAB separate east of 150°E, this area between SAF (OyF) and SAB is referred to as the Transition Domain. Northern part of Transition Zone (NTZ); area of between the Subarctic Boundary and 6°C isotherm at 300m, which is index of the Kuroshio Bifurcation Front (KBF); the northward branch form the Kuroshio Extension Front near the Shatsky Rise located around 160°E (Mizuno and White 1983), however in this study, south of 6°C isotherm at 300m in the Transition Zone was assume to strong influence area from the Kuroshio. Southern part of Transition Zone (STZ); area of between 6°C isotherm at 300m and the Kuroshio Extension Front (KEF). Kuroshio Zone (KZ); south of the Kuroshio Extension Front which is defined as a 14°C isotherm at 200m depth.

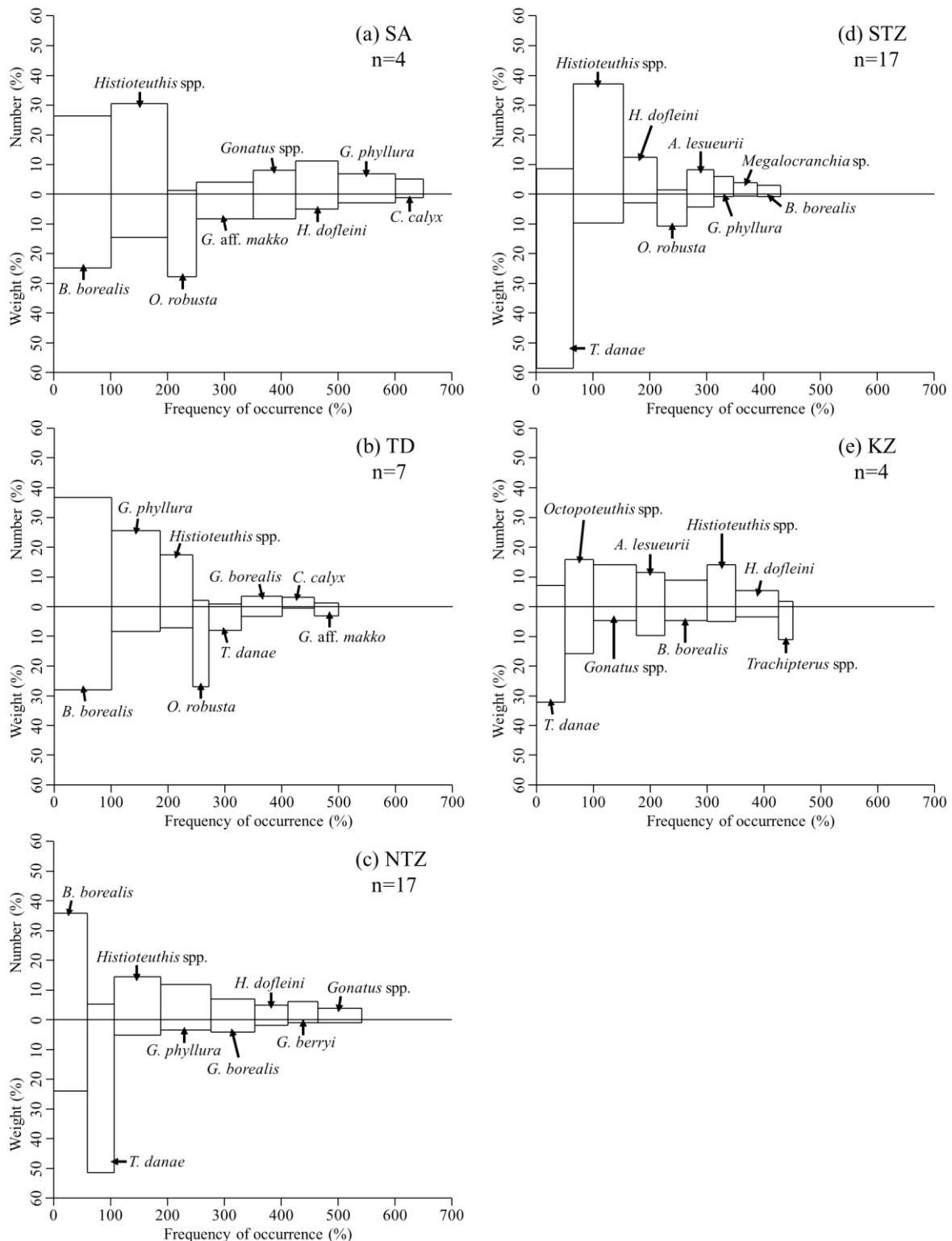


Figure 2. Percentage composition of eight major prey items found in stomachs of sperm whales in five water masses. The each rectangle indicates an Index of Relative Importance for each food item.

(a) SA: Subarctic Region, (b) TD: Transitional Domain, (c) NTZ: Northern part of Transition Zone, (d) STZ: Southern part of Transition Zone, (e) KZ: Kuroshio Zone; n is the number of whales.

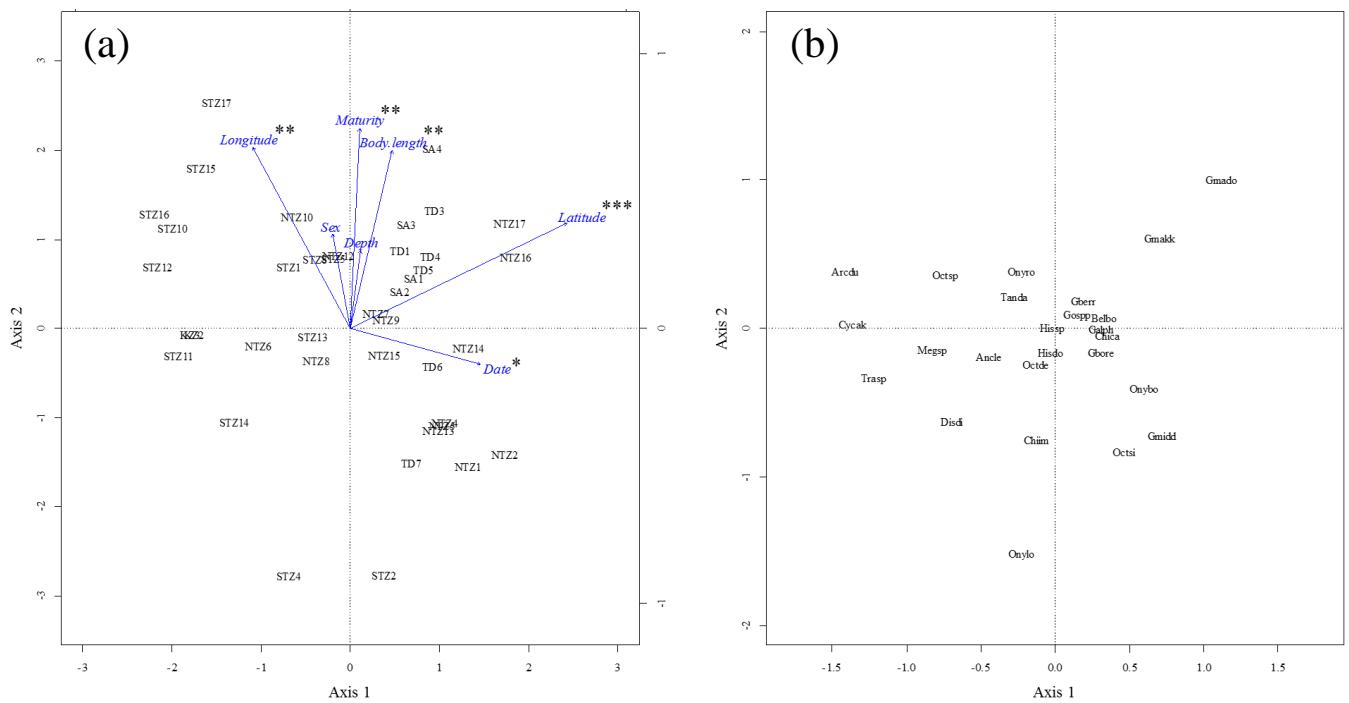


Figure 3. Canonical correspondence analysis ordination biplots, showing important prey items of sperm whales sampled in the western North Pacific, relation to the environmental and the variables (body length, sex, sexual maturity, longitude, sampled date, depth of sampled sites). (a) Biplot of sperm whales (sampling sites) and the environmental and the biological variables. (b) Biplot of important prey items and the environmental and the biological variables. Superscripts on environmental and biological factors represents p-values (**<0.001, **<0.01, *<0.05). The length and direction of arrow represents the strength and direction of the effect of the variables on the ordination. Codes for whales are the same as in Table 1. Species are identified by epithets formed from initial letters in genus and species names, see Table 2. Weight of prey species are used this analysis.

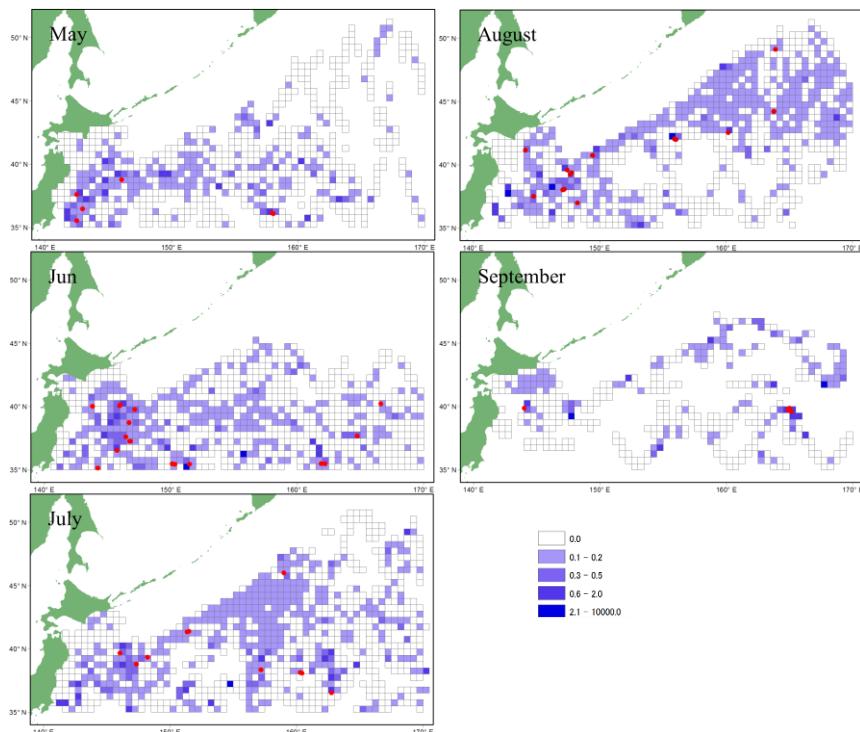


Figure 4. Density Index of sperm whales by 0.5 degree mesh (number of whales found per n.mile) based on sighting surveys under the JARPNI from 2000 to 2013. Red symbols indicate sighting position of sperm whales.