Technical Reports of the Institute of Cetacean Research (2017) pp. 44–57

Technical Report (not peer reviewed)

Overview of stomach content analyses for sei, Bryde′s and common minke whales under the offshore component of JARPNII, and temporal changes in feeding habits

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ABSTRACT

This study presents an overview of the stomach content analyses for sei, Bryde′s and common minke whales off the Pacific coast of Japan based on data and samples collected by the offshore component of JARPNII during 2000–2016. The three species were highly dependent on small pelagic fish, in addition to planktonic crustaceans. The prey species composition in sei whales drastically changed from Japanese anchovy in the early 2000s to Japanese sardine in 2014 to 2016, while copepods (*Neocalanus* spp.) steadily occurred throughout the years in offshore waters. Bryde′s whale had a simple prey composition involving mainly Japanese anchovy, but a lesser amount of this prey species was observed during the last three years. Prey composition in common minke whales in offshore waters showed that Japanese anchovy and Pacific saury are the main prey species, while in the vicinity of northern Japan, Japanese anchovy and walleye pollock were the dominant prey species. These three whale species showed diversities in their feeding habits reflecting changes in prey species populations and availability through the years.

INTRODUCTION

The Japanese Whale Research Program in the western North Pacific, Phase II (JARPNII) started in 2000 with the primary purpose to study the interactions between fisheries and cetaceans through ecosystem modeling of the Pacific side of Japan, an area well known as a large fisheries ground (GOJ, 2002; 2004). The goal of JARPNII was to assist in the formulation of effective ecosystem-based fisheries management in this research area.

This paper focuses on the study of the feeding ecology of three baleen whale species, sei whale (*Balaenoptera borealis*), Bryde′s whale (*B.edeni*) and common minke whale (*B. acutorostrata*) based on surveys under the offshore component of JARPNII (whales sampled by the pelagic research vessels) . The baleen whales in offshore waters are highly dependent on abundant pelagic fishes and zooplankton which are important components of the food web in the subarctic region of the western North Pacific.

Eggs and larvae of pelagic fish, such as Japanese anchovy *Engraulis japonicus* and Japanese sardine *Sardinops melanostictus* are transported by the Kuroshio Current to offshore waters (Itoh *et al.*, 2009; 2011; Okunishi *et al.*, 2011), and these species are important prey items for baleen whales, in addition to crustaceans such as krill. In fact, the Japanese anchovy was found in the stomach of sei, Bryde′s and common minke whales sampled in the early half of the JARPNII (Konishi *et al.*, 2009), in addition to mackerel (genus *Scomber*). Acoustic and trawling surveys during JARPNII (Murase *et al.*, 2012) showed that Japanese anchovy was distributed widely in the survey area between 2004 and 2007. Because these pelagic fish species are also commercially important, there are many studies on the catch history (Yatsu *et al.*, 2005; Yonezaki *et al.*, 2015), optimal environment (Takasuka *et al.*, 2007) and transportation to offshore areas (Itoh and Kimura, 2007; Itoh *et al.*, 2009; 2011). These studies suggested synchronized exchange of favorable environmental conditions between Japanese sardine and Japanese anchovy caused by climate change, which can be defined by Pacific Decadal Oscillation (PDO) (Mantua and Hare, 2002).

In the early 2000s, when sampling of sei and Bryde′s whales started in the JARPNII, the sardine population had already collapsed and the anchovy catch had increased (Yatsu *et al.*, 2005; Takasuka *et al.*, 2008; Itoh *et al.*, 2009). Since PDO fluctuations occur in scale from 15–25 years and 50–70 years (Mantua and Hare, 2002), the continuous sampling under the JARPNII for more than a decade is useful to see changes in the feeding habits of sei, Bryde′s and common minke whales.

The main purpose of this study was to present an overview of the studies of feeding ecology of sei, Bryde′s and common minke whales based on stomach content analyses, and to examine decadal changes in the feeding habits of these three species.

MATERIALS AND METHODS

Study area

The JARPNII research area has a unique environment under the effect of both the cold Oyashio Current and the warm Kuroshio Current and this transition region covers most of this research area (see Favorite *et al.*, 1976). High productivity is an important factor related to spring blooming in the lower trophic level (Liu *et al.*, 2004). Copepods (*Neocalanus* spp.) are the dominant zooplankton in the Oyashio region during spring to summer in the surface layer, which depend on phytoplankton (see Kobari and Ikeda, 1999; Tsuda *et al.*, 2001).

The occurrence of subarctic gyres near the Kuroshio Current is also important to marine mammals (Springer *et al.*, 1999). Basic oceanic features of oceanic fronts, Kuroshio-current and eddies in July are illustrated as an example (Figure 1). To examine positions of oceanic fronts, Argo data were used for salinity and temperature profiles (http://www.argo.ucsd.edu, http://argo.jcommops.org). To draw the Kuroshio-current and eddies, sea surface height data were obtained from the AVISO webpage (http://www.aviso.altimetry.fr/duacs/). Another topographic feature associated with prey distribution in this area is the Emperor Seamounts and the Shatsky Rise which cause upwelling and changing current stream (Figure 2). The northward branch of the Kuroshio Extension Front near the Shatsky Rise is located around 160°E (Mizuno and White, 1983).

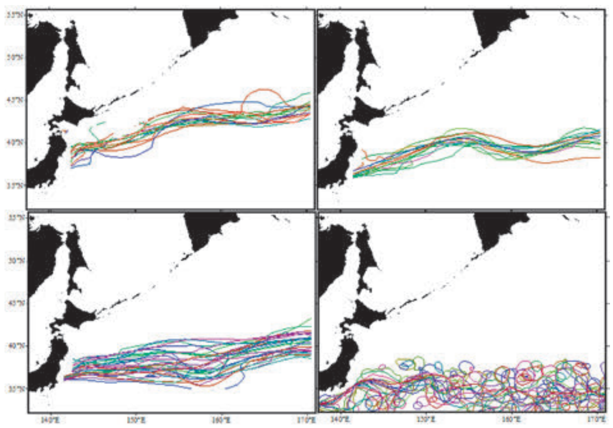

Figure 1. Geographical locations of oceanic fronts at western North Pacific in July during 2001–2013. Original data from Argo float (JAMSTEC). Upper left: Subarctic Front: 4°C isotherm at 100 m depth (Argo data from JAMSTEC). Upper right: Subarctic boundary. Salinity of 34 psu at near surface (Argo data from JAMSTEC). Bottom left: Kuroshio extension northern branch. Bottom right: Kuroshio extension from sea surface height (AVISO absolute dynamic topography derived from sea surface height measured by several satellites, AVISO, France, http://www.aviso.altimetry.fr); estimated current eddies area also drawn. Detail of oceanographic features in the JARPNII area during 2000 to 2013 is well described in Okazaki *et al.* (2016). Definition of boundary followed description in Kida *et al.* (2015).

Whale sampling

Data and samples used in this study were obtained by the JARPNII offshore component in the period 2002–2016 for sei whales; 2000–2016 for Bryde′s whales; and 2000–2013 for common minke whales. Sample sizes of the whales examined are shown in Table 1. Details of the survey procedure under JARPNII are available in Bando *et al.* (2016) and Tamura *et al.* (2016). During the sampling survey, information on catch date and location for each whale sampled as well surface temperature where the whales were first sighted, was recorded.

Prey information

Prey information was obtained by examining stomach content of the whales sampled. Most of the stomachs were occupied by a single prey species. The methodology for stomach content analysis was described in previous

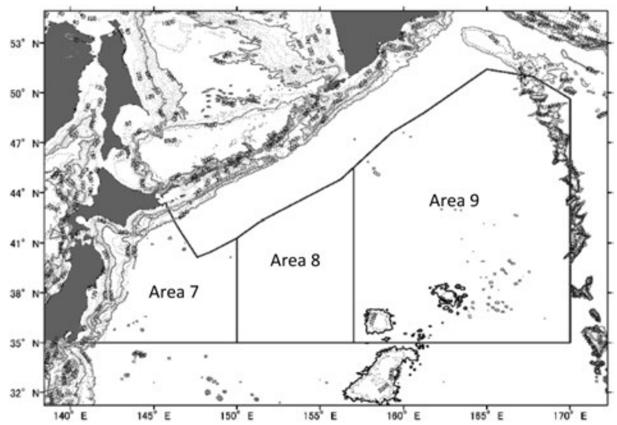

Figure 2. The locations of major geographic features at the JARPNII research area with isobath to 4000 m depth. The contours are from the GEBCO bathymetric atlas (Amante and Eakins, 2009). Survey Areas are shown with thick black line. Shatsky Rise and Emperor Seamounts are also drawn by 3000–4000 m isobath in depth in the eastern part of the research area at 155°E–160°E and around 170°E, respectively.

Table 1
Number of sei, Bryde's and common minke whales caught under the JARPNII, by area, month and year.

	Area 7					Area 8						Area 9						
Sei	May	Jun.	Jul.	Aug.	Sep.	May	Jun.	Jul.	Aug.	Sep.	Oct.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Total
2002								4		3				32				39
2003		1	4			3	16						11	12	3			50
2004							2						9	36	27	26		100
2005						12	3	16				5	41	17	6			100
2006		1	4				19	28					19	6	23			100
2007		2	4			16	2	6				22	23	16	9			100
2008							24	9					35	15	17			100
2009						11	1	19				18	38	13				100
2010		10					9	6					18	29	28			100
2011				1			5	11	13				26	11	28			95
2012							31	3					21	45				100
2013									11						35	54		100
2014						3	10	8				13	49	7				90
2015							7	10						44	29			90
2016	4					6	6	16				12	46					90
Bryde's	May	Jun.	Jul.	Aug.	Sep.	May	Jun.	Jul.	Aug.	Sep.	Oct.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Total
2000				24	19													43
2001	6	33	11															50
2002				13				7	23					7				50
2003	1	19	7				14							9				50
2004							13						26	5		6		50
2005		3	36				8						3					50
2006			5					11					16	5	13			50
2007		4	1	6				20	9					8	2			50
2008			26					9						15				50
2009							27						23					50
2010		1												49				50
2011			32	5				4					5		4			50
2012							3	14						17				34
2013								1	14		3			1	4	4	1	28
2014			13					10						2				25
2015		21					4											25
2016								9						16				25
Minke	May	Jun.	Jul.	Aug.	Sep.	May	Jun.	Jul.	Aug.	Sep.	Oct.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Total
2000				6	18										16			40
2001	28	22						22						23	5			100
2002				6	54			1	7	3				20	5	4		100
2003	22		2			19	18						11		28			100
2004					16									24	60			100
2005		14	18			10		4				10	3	3	38			100
2006	16	11	11				26	12					10	14				100
2007		79				1	14					1	5					100
2008							5						3	29	22			59
2009	4	11	4			1		16				3	4					43
2010														12	2			14
2011			47										1		1			49
2012	57	14					3											74
2013															3			3

reports (e.g. Tamura *et al.*, 1998; Konishi *et al.*, 2009), and it involves the steps shown in Figure 3. Prey length distributions for pelagic fish in the stomachs of the sampled whales are shown in the Appendix.

RESULTS

Sei whale

Figure 4 shows the geographical position (based on the first sighting) of sei whales sampled including information of the prey species found in the stomachs. Whales were widely distributed in the survey area, but mostly from east of 150°E and south of 46°N between north of the Kuroshio extension and just north of the Subarctic Front (see also Figure 1).

The main prey species were copepod (*Neocalanus spp.*), euphausiid (*Euphausia spp.*), Japanese anchovy, two mackerel species (*Scomber japonicus* and *S. australasicus*) and Japanese sardine. Pacific saury (*Cololabis saira*) was found in the eastern side of the research area in every year. Most of the copepods found in the stomachs were 5th copepodite stage of *Neocalanus cristatus* and *N. plumchrus* (also see Konishi *et al.*, 2009). Minimal armhook squid (*Berryteuthis anonychus*) was also found mainly in far eastern areas near the Emperor Seamounts. The locations of whales feeding on Japanese sardine was the most eastern in the survey area, overlapping with whales feeding on Japanese anchovy and copepods.

Prey composition in the stomach of sei whales sampled during 2002–2016 is shown for each Area in Figure 5. Copepod and Pacific saury were dominant preys in Area 9 than in western Area 8, while Japanese anchovy and euphausiid were found widely in both Areas 8 and 9. In the years 2002–2012, Japanese anchovy, copepod and

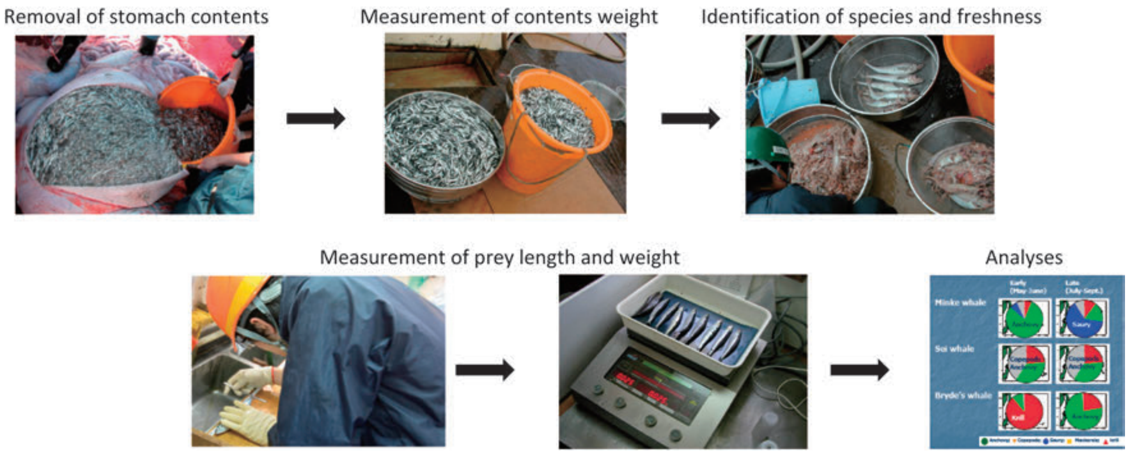

Figure 3. A schematic diagram of the steps in the analyses on stomach contents.

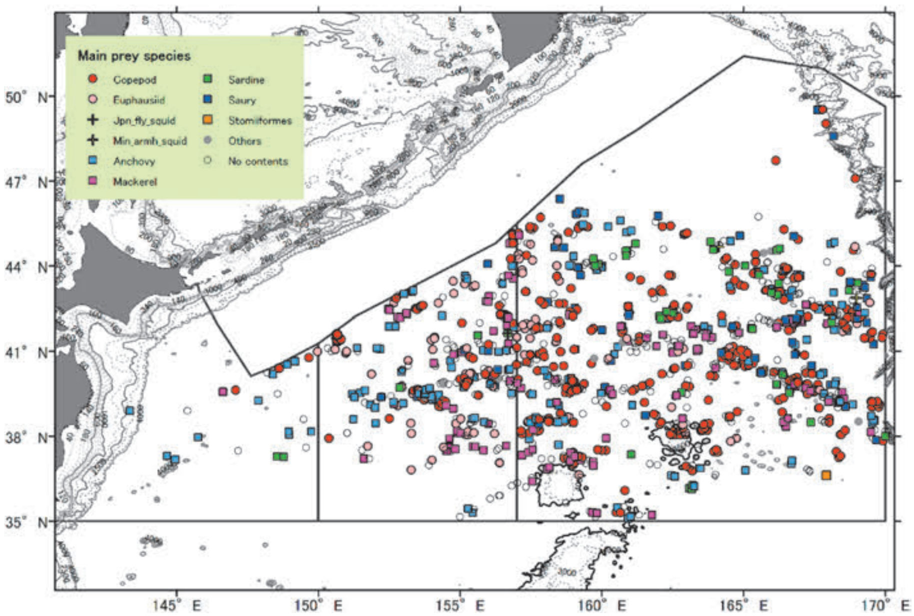

Figure 4. The distribution of sampled sei whales (based on first sighting), and information of prey species in their stomachs (period 2002–2016). The contours are from the GEBCO bathymetric atlas.

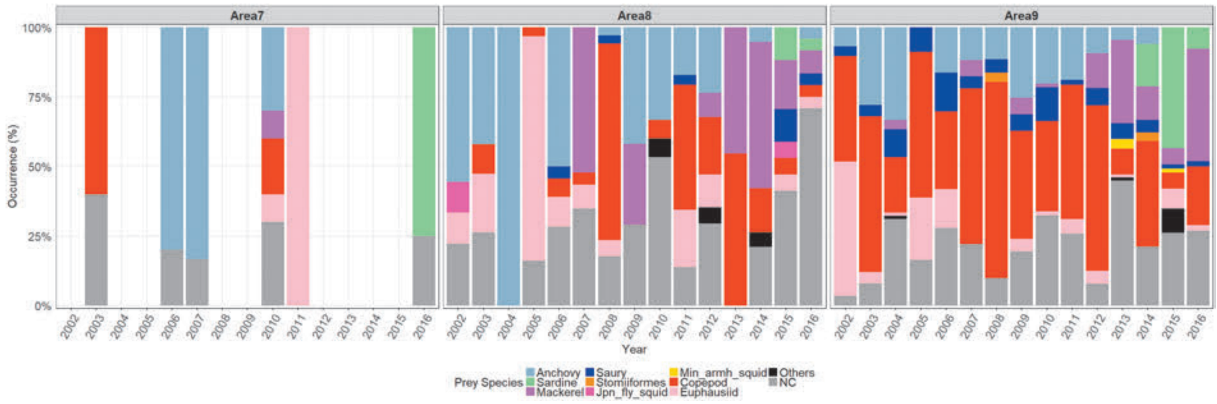

Figure 5. Prey composition in the stomach of sei whales sampled in the period 2002–2016, by Area and year.

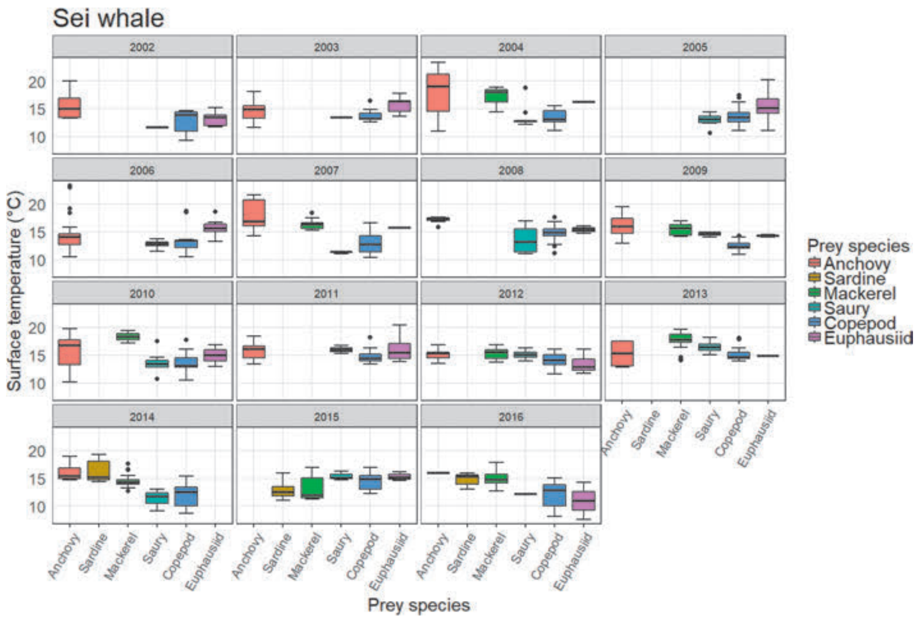

Figure 6. Surface temperature in which sei whales were sampled, and prey species in their stomachs (2002–2016).

euphausiid were major components with the exception of years 2005 and 2008. After 2007, mackerel became one of the major preys which coincided with a decreasing occurrence of anchovy and copepod. In the years 2014–2016, Japanese sardine was the dominant prey while some Japanese anchovy was found only in 2016. Stomachs with no contents (NC) were also found widely throughout the survey years. Japanese sardine was not the main prey species until recently.

Figure 6 shows the surface temperature in which sei whales were found, including information on prey species in their stomachs. Surface temperature in which sei whales were found varied according the prey species. Japanese anchovy was found in a wider range of surface temperatures. Copepods and Pacific saury tend to be found at lower temperatures (*c.a.* <15°C) than mackerel. Although a variation of surface temperature is observed within years, these are not consistent among years. Length distribution of main fish prey species in the stomachs of sei whales had different modes among years (see Appendix).

Bryde's whale

Figure 7 shows the geographical position (based on the first sighting) of Bryde's whale sampled including information of the prey species found in the stomach. Their distribution is mainly south and west of the distribution of sei whales sampled. They were concentrated around 145°E–150°E and 155°E–160°E, south of 41°N. Japanese anchovy and euphausiids were found in a wide longitudinal range. Mackerels and stomiiforms (*Vinciguerria nimbaria* and *Maurolicus muelleri*) occurred offshore.

Prey composition in the stomachs of Bryde's whales sampled during 2000–2016 is shown for each Area in Figure 8. Japanese anchovy, stomiiforms and euphausiid were the dominant prey species. Mackerels were occasionally found in some years. The composition of main

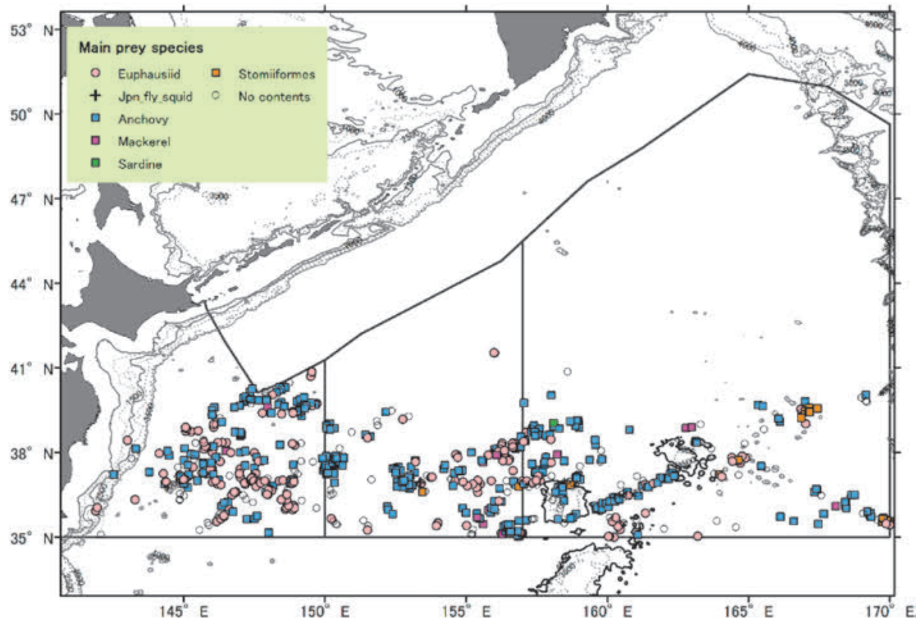

Figure 7. The distribution of sampled Bryde's whales (based on first sighting), and information of prey species in their stomachs (period 2000–2016). The contours are from the GEBCO bathymetric atlas.

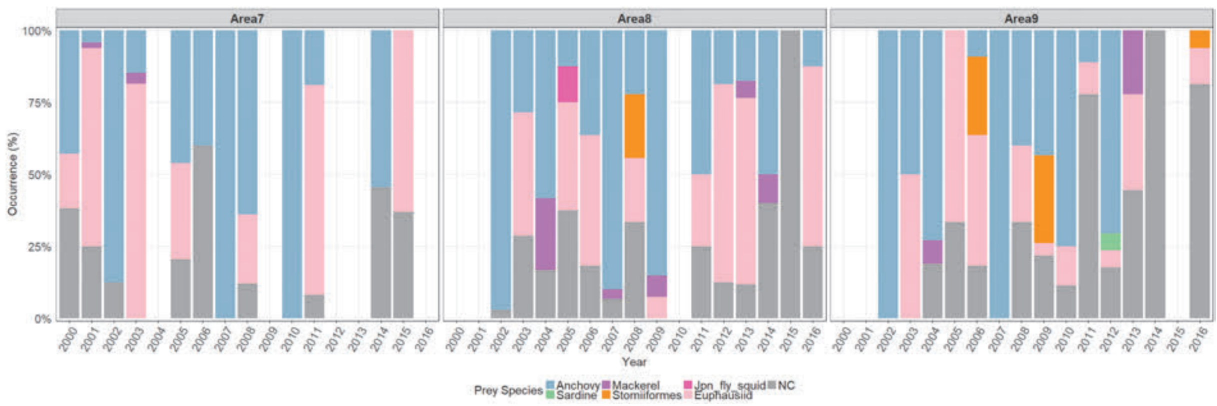

Figure 8. Prey composition in the stomach of Bryde's whales sampled in the period 2000–2016, by Area and year.

prey species is highly variable among years, however there was no obvious variation among Areas and decadal change in the prey composition. However, it should be noted that lower occurrence of anchovy and high occurrence of 'NC' stomachs were observed in the last two years (2015–2016). Japanese sardine was not a main prey species and was just found occasionally.

Figure 9 shows the surface temperature in which Bryde's whales were found, including information on prey species in their stomachs. Bryde's whales fed on prey in warmer surface temperature areas compared to sei and common minke whales in JARPNII. No obvious variation of surface temperature among the prey species was observed. Length distribution of pelagic fish prey species showed variation of mode among years (see Appendix).

Common minke whale

Figure 10 shows the geographical position (based on the first sighting) of common minke whales sampled including information of the prey species found in the stomach. Figure 11 shows details of the coastal area in the western side of the research area.

Pacific saury is the key prey species in offshore waters and common minke whales occurred mainly north compared to the sei whales sampled. Japanese anchovy was found widely through longitudinal sectors, and also was intensively fed on by common minke whales in the coastal area (Figure 11). Minimal armhook squid and Pacific pomfret (*Brama japonica*) were found in the far northeastern regions near and above the Emperor Seamounts (Figure 10). In coastal waters, walleye pollock (*Theragra chalcogramma*), which occurs at bottom or midwater depth, was commonly found above shelf edge and slope off eastern

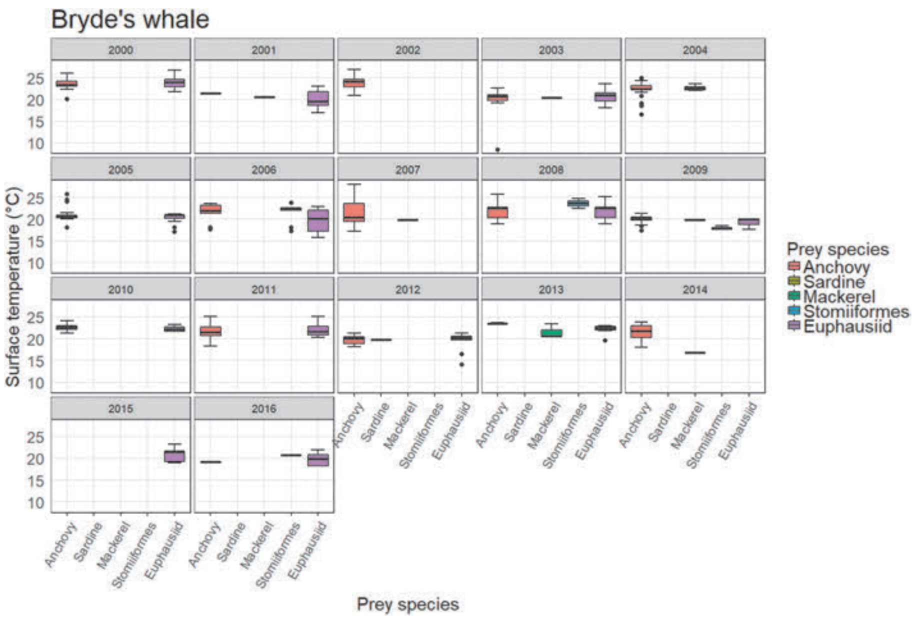

Figure 9. Surface temperature in which Bryde's whales were sampled, and prey species in their stomachs (2000–2016).

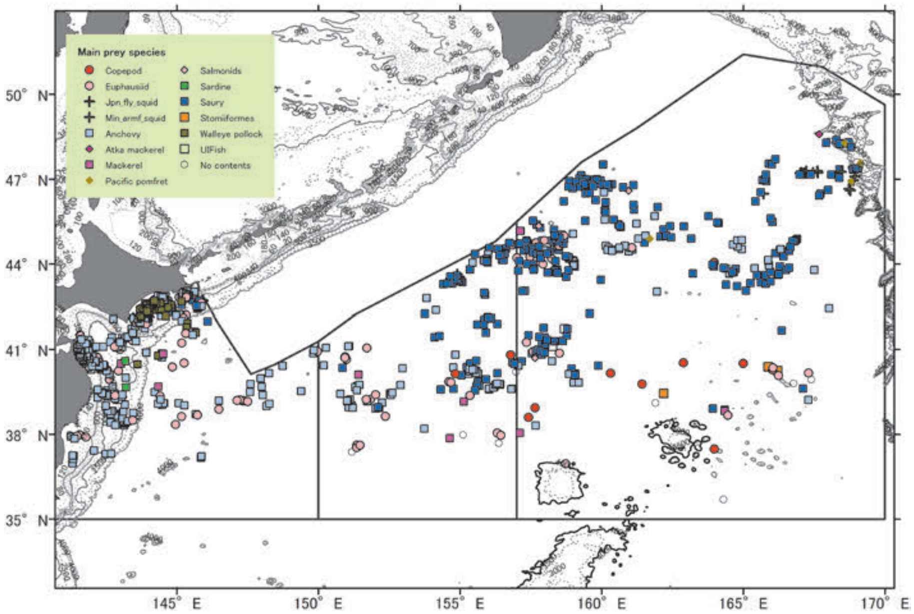

Figure 10. The distribution of sampled common minke whales (based on first sighting), and information of prey species in their stomachs (period 2000–2013). The contours are from the GEBCO bathymetric atlas.

Hokkaido (Figure 11). Japanese anchovy, Pacific saury and euphausiids were also common prey species in this area. The Japanese flying squid (*Todarodes pacificus*) was also found just on the continental slope but only in early years of JARPNII (Figures 10 and 11). Feeding on Japanese anchovy and euphausiid by common minke whales was also found above the continental shelf off Hachinohe (Figure 11).

Prey composition in common minke whales differs among years, but not to the extent as in the case of the sei whale. Recent transition of pelagic fish species was not found probably due to the absence of common minke whale samples during 2014–2016 (see Table 1 and Figure 12).

Surface temperature varied in the range of 10°C–20°C, and the range was small in the offshore area (Figure 13). Length distribution of Japanese anchovy, mackerel and Pacific saury in the stomach of common minke whales differs within and among years (see Appendix).

DISCUSSION

This study showed a general overview of stomach content analyses and decadal changes in feeding habits for sei, Bryde's and common minke whales in the western

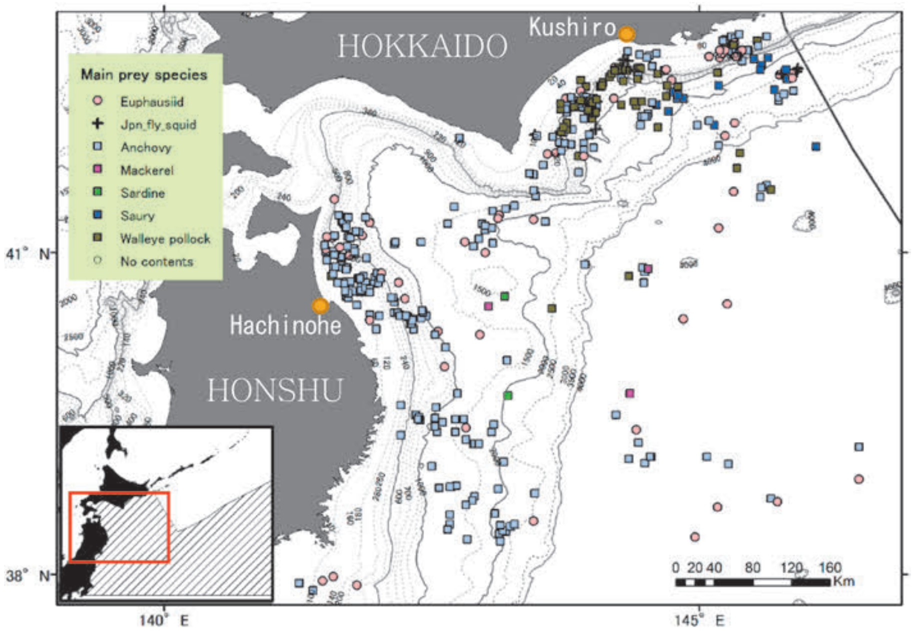

Figure 11. Amplified plots of Figure 10 to show details of the situation in areas near to the coast of the Pacific side of Japan and northern Honshu and Hokkaido.

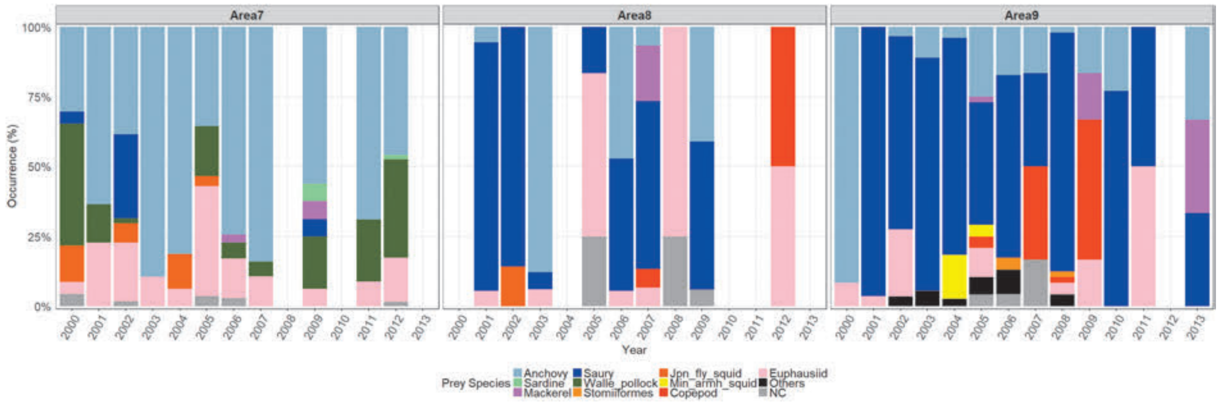

Figure 12. Prey composition in the stomachs of common minke whales sampled in the period 2000–2013, by Area and year.

North Pacific in terms of rather qualitative information based on data collected by JARPNII in the period 2000–2016. The Japanese anchovy was an important prey for the three whale species across the entire survey area, and it was also important in the coastal area for common minke whales. The results showed a remarkable shift in prey species in the case of the sei whales late in the JARPNII period (2015–2016), *i.e.* a limited occurrence of Japanese anchovy and higher incidence of Japanese sardine as main prey in the last three years (2014–2016). A similar decrease of Japanese anchovy as prey species of Bryde's whales also supported the prey shift.

There is no doubt that prey composition in the baleen whales reflected a pelagic fish shift from Japanese anchovy to Japanese sardine and mackerel in the western North Pacific. Mechanisms of these decadal scale shifts of pelagic fish composition in the western North Pacific were influenced by large-scale SST variability by the Aleutian Low (Miller *et al.*, 2004; Sasaki *et al.*, 2012). The responses to the SST in terms of growth rate in sardine, saury and anchovy differ. For example, the patterns of spawning temperature clearly show 'warm' and 'eurythermal' Japanese anchovy and 'cool' and 'stenothermal' Japanese sardine in the western North Pacific (e.g. Takasuka *et al.*, 2007; 2008; Oozeki *et al.*, 2009; Watanabe, 2009; Itoh *et al.*, 2011).

Locations where whales were found in JARPNII elucidated the site-specific feeding behaviors of the whales. Sei whales occurred where both pelagic fish and copepod were available which covers the offshore research area to mainly feed on copepod and small pelagic fish. Bryde's whales occurred from the near coastal area in sub-area 7 to around the Shatsky Rise in sub-area 9, where both

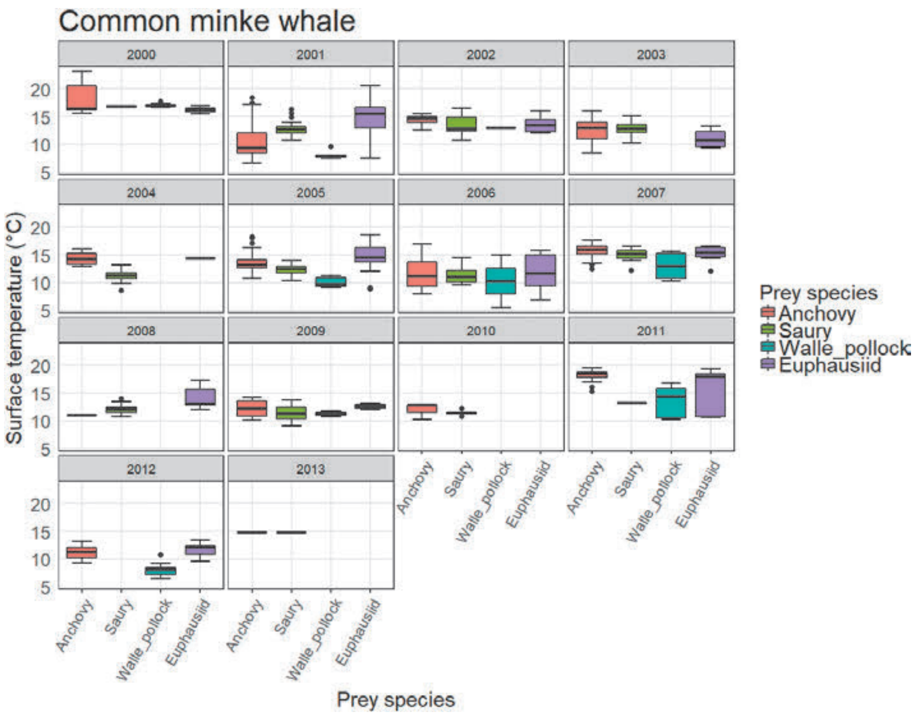

Figure 13. Surface temperature in which common minke whales were sampled, and prey species in their stomachs (2000–2013).

pelagic fish from the Kuroshio Current and euphausiid are both common. They possibly can feed on euphausiids even if pelagic fish is not available. Common minke whales showed unique feeding habits with occurrences at higher latitude to *ca.* 48°N and high dependency on Pacific saury in the offshore area and prey related to the continental shelf in coastal areas. They feed on minimal armhook squid near the Emperor Seamounts where the mature minimal armhook squid occurs in summer (Konishi and Tamura, 2007). Minke whales also feed on larger prey, such as walleye pollock, Pacific pomfret and salmonids.

This study highlighted the fact that feeding ecology studies of sei, Bryde's and common minke whales in the western North Pacific are benefited by long-term systematic surveys, which allow decadal-level variability be studied.

ACKNOWLEDGEMENTS

We would like to thank all researchers and crews involved in the JARPNII surveys, who supported feeding habits studies on board of *Nisshin-Maru* fleet. Thanks are also due to the members of the Institute of Cetacean Research for useful suggestions and helping to conduct stomach contents treatment. We finally thank the Fisheries Agency of Japan for supporting the JARPNII program.

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Appendix

Length distribution of main pelagic fish in the stomachs of sei, Bryde's and common minke whales during JARPNII period (2000–2016)

Length distributions of pelagic fishes in the stomach of sei, Bryde's and common minke whales are shown in Figs. A1–A4. Mackerels include both *Scomber japonicus* and *S. australasicus* because these species were sometimes found mingled in half digested stomach contents. The length distributions differ among years and whale species, suggesting that prey length, as also defined as age class, reflects the relative abundance and availability in the feeding area for the baleen whales.

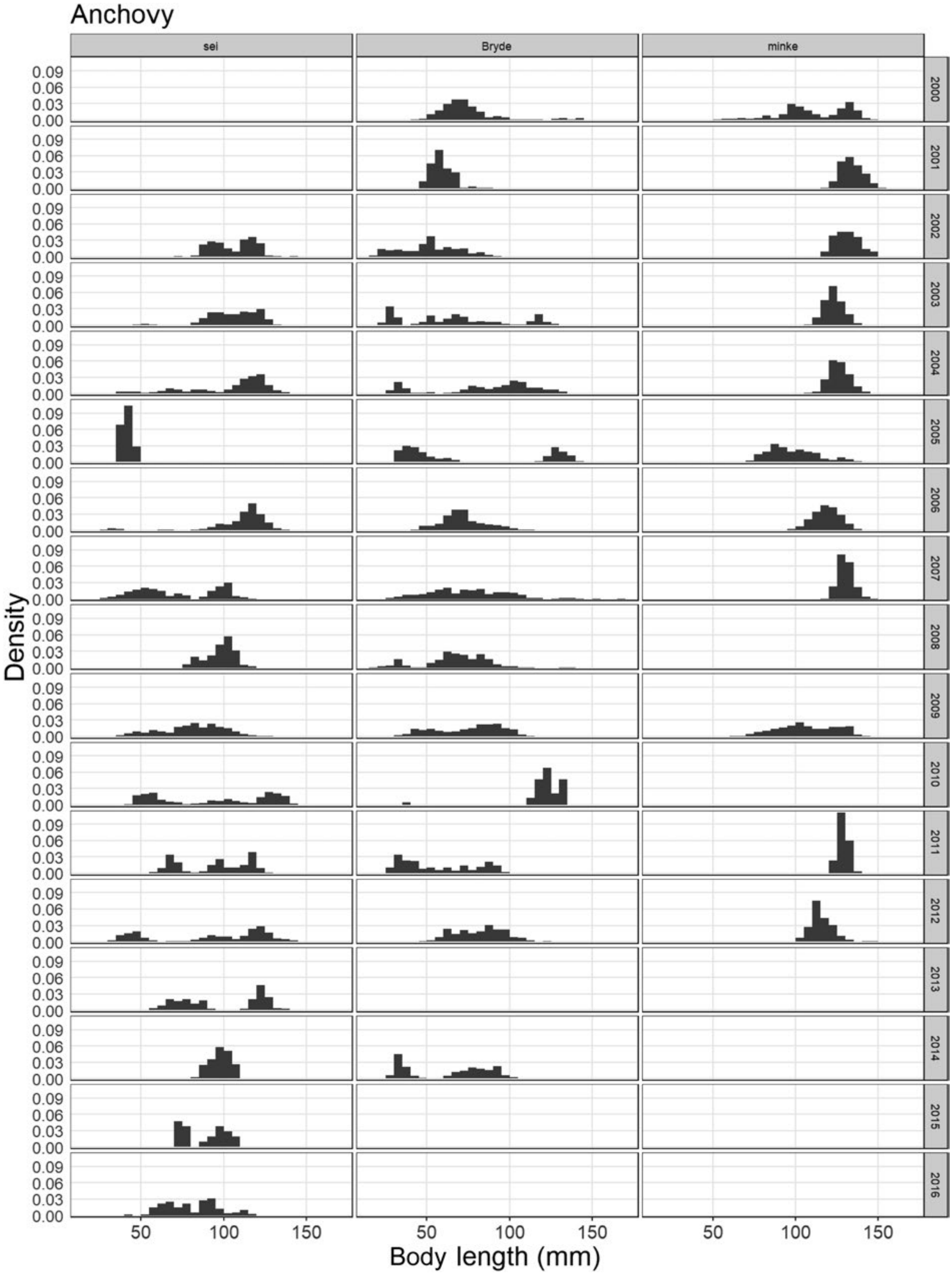

Figure A1. Length distribution of Japanese anchovy in the stomach of sei, Bryde's and common minke whales during JARPNII (2000–2016).

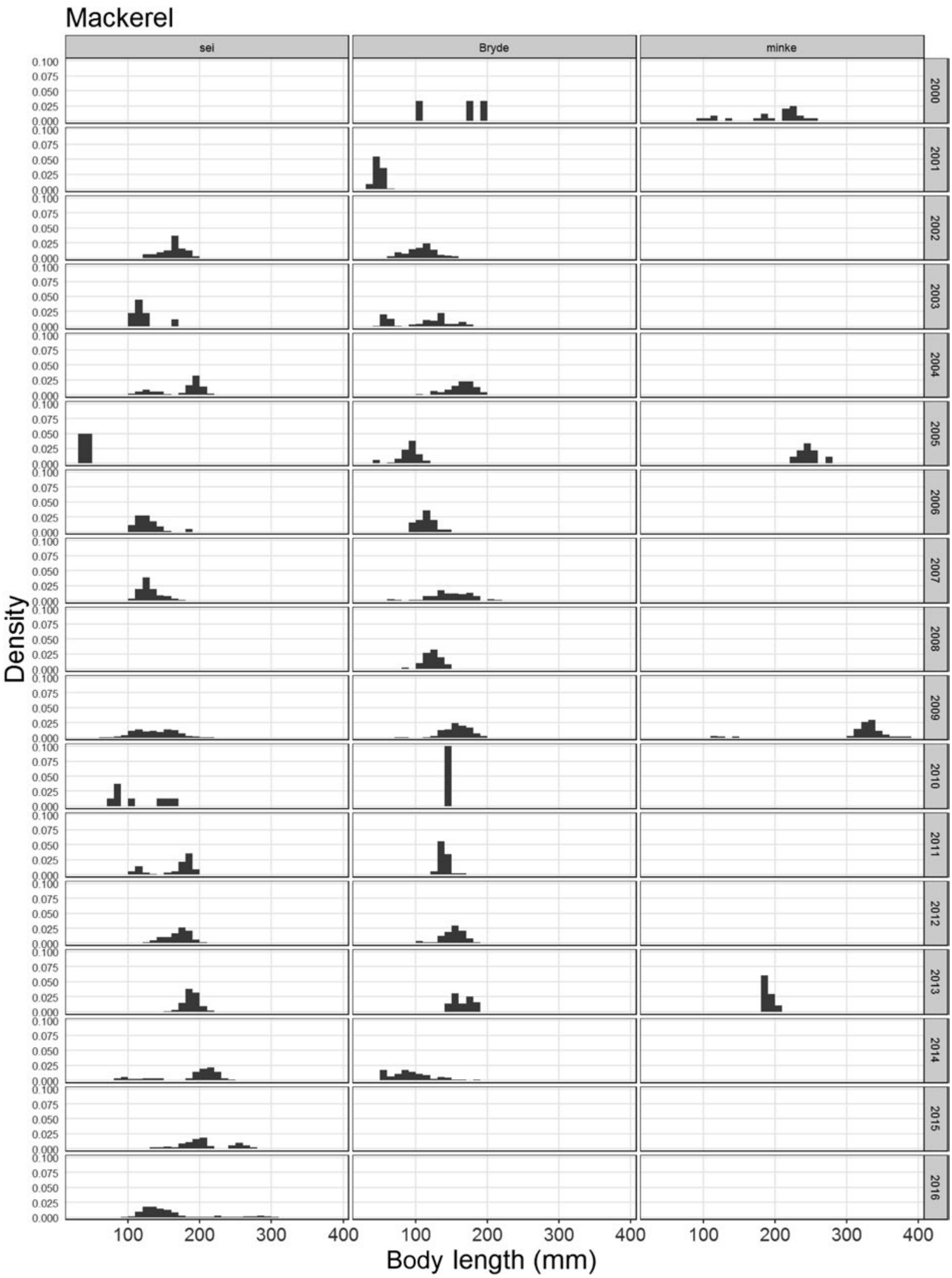

Figure A2. Fork length distribution of mackerels (including *Scomber japonicus* and *S. australasicus*) in the stomach of sei, Bryde′s and common minke whales during JARPNII (2000–2016).

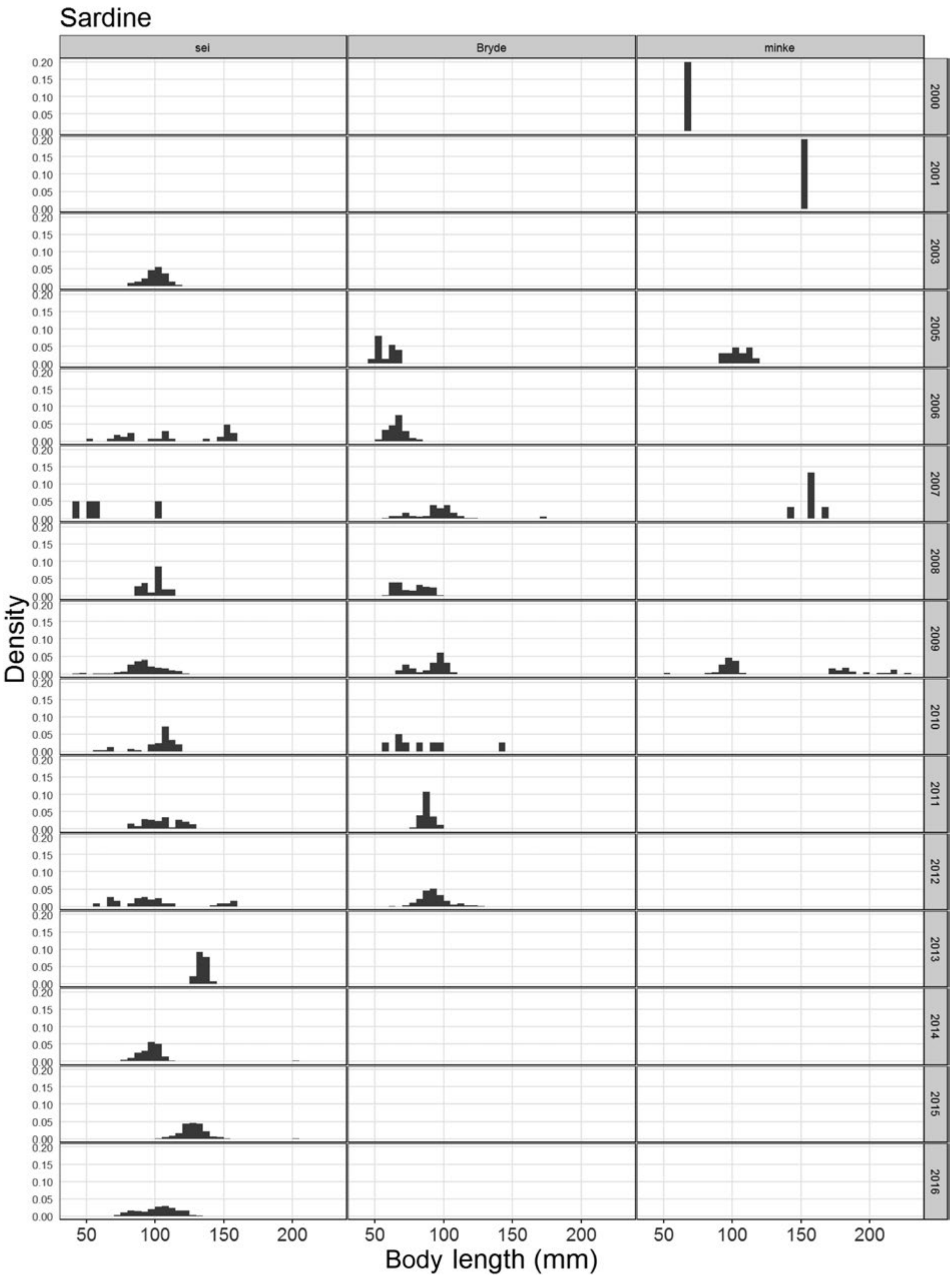

Figure A3. Length distribution of Japanese sardine in the stomach of sei, Bryde's and common minke whales during JARPNII (2000–2016).

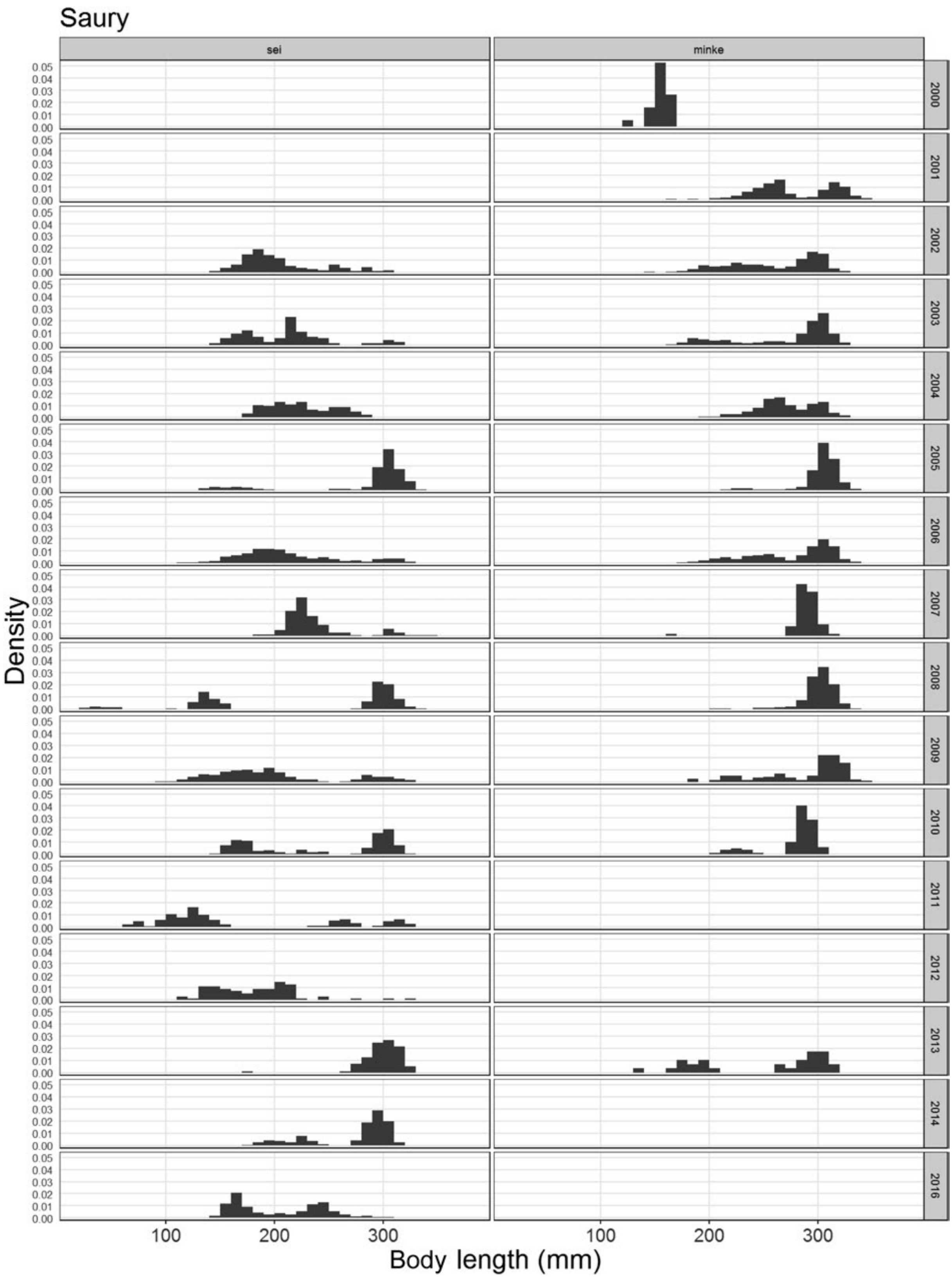

Figure A4. Knob length distribution of Pacific saury in the stomach of sei, and common minke whales during JARPNII (2000–2016).