Dietary studies of toothed whales: A review of technical issues and new topics

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SUMMARY: Understanding the feeding habits of toothed whales is important in studies of cetacean ecology. The techniques of stomach content analysis have become more refined, and it is now possible to identify a lots of fishes and cephalopods using hard parts such as otoliths and beaks. These hard parts can also provide estimations of the body sizes of several hundred prey species. The prey selectivity of toothed whales has been summarily dismissed as being "opportunistic" and there has been little discussion about the mechanisms of prey switching. Recent detailed information on prey items has enabled researchers to consider prey selectivity when data of prey abundance are available. The detection of selection criteria may be an interesting topic in future studies concerning behavioral ecology. The ecological importance of cetaceans has been considered recently, and their prey consumption has been discussed as a matter of concern about competition with fisheries. Some toothed whales in coastal areas consume many prey species that are commercially caught. However, the competitive status may not only depend on the overlapping of prey, but also on the prey abundance and the ecological response of prey to predation and harvesting pressures.

KEYWORDS: beak, food consumption, otolith, prey selection, stomach contents, toothed whale

INTRODUCTION

Understanding the feeding habits of toothed whales is important in studies of cetacean ecology. Researchers can obtain detailed information about food and feeding habits by analyzing stomach contents. Recently, the trophic importance of cetaceans in the marine ecosystem has been regarded. Information on the diet and prey consumption of cetaceans has sparked interest not only from a purely academic viewpoint but also as a concern to fisheries management. This paper reviews some technical issues in stomach content analyses, as well as several new topics, and considers the current status of dietary studies of toothed whales and problems in those studies.

PREY SPECIES IDENTIFICATION AND SIZE ESTIMATION

Hard parts of prey, such as fish otoliths and squid beaks, are resistant to digestion. The morphology of these hard parts was first systematically used for identification of prey species in the stomach contents of toothed whales during the 1960s. Scientists were able to identify even digested prey and could estimate the number of prey items ingested. This method for identification requires many reference samples covering a variety of potential prey species. The key characteristics in the otoliths and beaks of each species must be identified prior to the analysis. These two points are potential barriers to stomach content analysis, but published information is

becoming increasingly available (Table 1). In addition to otoliths, some other bones are also useful for fish identification. Otoliths have a heavier specific gravity and are easier to collect than other bones from a mixture of stomach contents. Additional bones are useful, however, for species whose otoliths are very small.

The number of prey items found in stomach contents may be overestimated when the estimate is based on the number of hard parts detected. This may be a result of the accumulation of hard parts over time, and it may be a result of misidentifying "prey of prey". A typical expected case of "prey of prey" would occur in species that feed on ommastrephid squids, which in turn prey heavily on myctophids. However, myctophid otoliths comprised <1% of prey items found in the stomach contents of northern form short-finned pilot whales (*Globicephala macrorhynchus*) that feed mainly on ommastrephid squids (Ohizumi H. & Isoda T., unpubl. data). Thus, "prey of prey" may not have a substantial impact on estimates of stomach contents. Japanese common squids (*Todarodes pacificus*) often discard the heads of fishes. This reduces the number of "prey of prey" otoliths. On the other hand, accumulation may cause errors in estimates of the daily ration, or feeding rate.

For some species, prey sizes can be allometrically estimated from the sizes of otoliths or beaks (Table 1). However, Tollit *et al.*¹⁾ noted that otoliths in the feces of pinnipeds were up to 30% smaller than their original sizes. This problem may be avoided in the analyses of

Table 1. Published references of otolith and beak.

Reference	Parts	No. of species	No. of family	No. of regression (sp.)		Area
				Body length	Body weight	
Fish						
Ohe 15)	Otolith	415	124	-	-	Japan
Smale <i>et. al.</i> 16)	Otolith	972	181	203	193	South Africa
Rivaton and Bourret 17)	Otolith	998	162	-	-	Western South Pacific-Indo Ocean
Harvey <i>et. al.</i> 18)	Otolith	76	24	62 (46)*	60	Eastern North Pacific
Ohizumi <i>et. al.</i> 19)	Otolith	36	1	17	18	Western North Pacific
Hotta 20)	Skull, Vertebrae	266	106	-	-	Japan
Takahashi 21)	Skull, Vertebrae	256	100	-	-	Inland Sea, Japan
Tatara <i>et. al.</i> 22)	Vertebrae	-	-	74	74	Inland Sea, Japan
Watt <i>et. al.</i> 23)	Premaxillae, Vertebrae	51	16	31	-	North Sea
Cephalopod						
Hotta 24)	Lower beak	21	9	-	-	Japan
Wolff 25)	Lower, upper beak	19	8	18	18	Pacific Ocean
Clarke 26)	Lower beak	ca. 207	40	60**	68**	World ocean
Kubodera <i>et. al.</i> 27)	Lower beak	50	19	-	-	Western North Pacific

* 62 original and 46 cited regressions are listed. ** including some families and genera.

stomach contents by selecting fresh otolith samples for measurements (Fig. 1).

Fig. 1 Otolith length of *Coryphaenoides longifilis*, in the stomach contents of Baird's beaked whales in the western North Pacific. The mean of two groups are not significantly different (*t*-test, $p=0.93$). (Ohizumi *et. al.* unpubl.)

ENERGY DENSITY OF PREY

Accurate energy density is an essential factor for conversions between mass of food ingested and energy intake. The energy conversion factor is essential in estimating food consumption from the metabolic energy requirement. Some prey species show seasonal variations in fat content, which causes considerable differences in their calorie contents. Ontogenetic variation in fat and calorie content should also be considered. Mårtensson *et. al.*²⁾ investigated caloric variability in 7 Atlantic fishes. This study found that the average energy density of capelin increased about 1.5 times from spring to summer. The variation of the

energy density seemed to result in minor adjustments; however, an adjustment in the energy density of approximately -10 % raises the estimate of food consumption by Atlantic minke whales by about 300,000 t³⁾.

PREY SELECTIVITY

Prey selectivity is a central concept in the feeding ecology of animals. Prey species in the stomach contents are often seasonally and locally different even in the same species of dolphin. This results in the common interpretation that dolphins are "opportunists", feeding on any potential prey, and that the prey item found most often in the stomach contents is also the most abundant prey^{3),4)}. The designation "opportunistic feeders" suggests that dolphins are not "specialists", but it does not explain whether dolphins show some selectivity or not. To detect prey selectivity, both the relative abundance of potential prey in the habitat as well as the relative contributions of prey in the stomach contents must be analyzed.

Dall's porpoises in the northern Sea of Japan, feed mainly on Japanese pilchard (*Sardinops melanostictus*) when the pilchard is abundant⁵⁾. After a drastic population decline of the pilchard, Dall's porpoises switched prey to benthic walleye pollock (*Theragra chalcogramma*)⁵⁾. In this case, the biomass of walleye pollock does not relate to the selection, but the availability of the epipelagic pilchard relates to the selection for walleye pollock. Dall's porpoises most likely prefer epipelagic prey, and this may be correlated to foraging efficiency in habitats where there is some spatial structure in the distribution of potential prey⁵⁾. This example implies prey selection among toothed whales, and it is an interesting issue to consider, in light

of behavioral ecology, the question of how whales distinguish prey species, and what is the selection criterion?

Once we understand the mechanism of prey selection, we will be able to predict how prey switching is correlated to variations in the prey population. Fisheries management based on a single-species model has many limitations; a multi-species management model is needed in the future. Such an ecosystem-based model would require information on prey selection to construct a more realistic model.

FOOD CONSUMPTION AND COMPETITION BETWEEN WHALES AND FISHERIES

The daily energy requirement (D) can be estimated from a model based on the basal metabolic rate, BMR⁶⁾:

$$D = a b 70 W^{0.75} \text{ (kcal)} \quad \text{Eq. 1,}$$

where *a* and *b* represent assimilation efficiency and active metabolism, respectively. *W* denotes the body weight in kilograms. The assimilation efficiency is estimated to be about 80%⁸⁾. Active metabolism has been estimated at approximately 1.5–10 times BMR^{7,8)}. This wide variation is a result of different activity levels, and this factor can greatly change the results. At present, it is difficult to estimate activity levels of free-ranging animals, but about 3 times of BMR is estimated from captive odontocetes⁹⁾.

Considerable consumption by cetaceans suggests potential competition between marine mammals and

Table 2. Parameters for the estimation of consumption of walleye pollock by Dall's porpoises in the northeastern Sea of Japan.

Parameters		Source
Average body weight	100 kg	†
Population size	226000	Miyashita 28)
Calorific contribution of walleye pollock before population decline of pilchards	22% (in 1989)	Ohizumi <i>et al.</i> 5)
Calorific contribution of walleye pollock after population decline of pilchards	63% (in 1995)	Ohizumi <i>et al.</i> 5)
Energy density in walleye pollock	1.11 kcal/g	Perez 29)
Assimilation factor (<i>a</i> in Eq. 1)	1.25	††
Active metabolism factor (<i>b</i> in Eq. 1)	2	†††

†This value is based on the observed data, 104.6 ± 23.2 kg, *n* = 106, in the North Pacific (Ohizumi H. *et al.* unpubl. data). †† 80 % assimilation efficiency. †††This value provides identical (about 96%) result of the energy requirement estimation by the regression obtained from terrestrial carnivorous mammals (Farlow³⁰⁾ eq.4), and also provides relatively lower (about 81%) energy requirement of captive odontocetes (Innes *et al.* 31) eq.22) with energy conversion factor 1.11 kcal/g.

Fig. 2 Estimated consumption of walleye pollock by Dall's porpoises in the Sea of Japan and the average yield by fisheries along the coast of Sea of Japan, Hokkaido. The error bar shows standard deviation. Drastic increase of consumption by porpoises reflects the prey switching after population decline of Japanese pilchard.

fisheries¹⁰⁾, but few examples have been documented for toothed whales. In Japanese waters, direct competition with odontocetes may occur in coastal areas.

Dall's porpoises migrate from the southern Sea of Japan to western Hokkaido in early summer, then spread out around Hokkaido. Assuming the parameters listed in Table 2, the estimated 30-day consumption of walleye pollock by Dall's porpoises in the Sea of Japan off Hokkaido ranges from 7436 t to 21295 t before and after the population decline of Japanese pilchards. Although this is a rough estimate based on a limited migration period and assuming all the porpoises migrate to the area, estimated consumption is comparable to the average catch of walleye pollock in Hokkaido in a month (Fig. 2). Walleye pollock is an important commercial fish around Hokkaido, but catches have been declining. This decrease is probably due to a regime shift to warmer waters¹¹⁾, but the foraging pressure on pollock by Dall's porpoises, especially after the decline of Japanese pilchards, may assist this decrease.

However, even if a prey species overlaps commercial fish, we should consider whether it suggests competition or sharing in each case. If the target fish is robust enough to withstand fishing and predation by whales, there may not be competition. Japanese pilchard in the western North Pacific was an important prey item to many predators, including fisheries, when the population was abundant^{6,12,13)}. The population declined after the end of the 1980s, but likely not because of overharvesting or predation; rather, the increased mortality of yearling fishes attributed to the regime shift to warmer waters¹⁴⁾. This suggests that abundant Japanese pilchards were robust, and that all predators, including humans, could share the food.

These two examples, the suspected competition for walleye pollock and the absence of competition for Japanese pilchard, suggest that the problem of competition in the present instance depends not only

on the whales and fisheries, but also on the abundance and ecological responses of targets to foraging and fishing pressures.

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