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FEEDING RATE AND DAILY ENERGY INTAKE OF DALL'S PORPOISE IN THE NORTHEASTERN SEA OF JAPAN

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Abstract: We examined thirty stomachs of Dall's porpoises (*Phocoenoides dalli*) collected on board a hand harpoon fishery vessel in the Sea of Japan off Hokkaido in May 1995 Maximum ratio of stomach content weight to body weight of the sated animals (MRSCW, 1 68%) was recorded early in the morning, and average of the ratio decreased in the daytime T TOBAYAMA (Studies on the feeding habits of the little toothed whales. Ph. D. thesis, Univ Tokyo, 1974) reported that digestion time was eight hours from full stomach to empty on captive *Tursiops gilli* and *Delphinus delphis* The eight hour digestion profile was almost middle of the possible digestion time range found in this study. Assuming that the digestion time was eight hours, maximum daily digestible food intake was estimated at 5.04% (MRSCW × 24/8) of body weight. This value is between the feeding rate indirectly obtained from the biological concentration rate of mercury in the wild Dall's porpoise (2–3%), and that directly measured from a captive porpoise (12 5%) Daily intake of energy was calculated as 27 2 MJ for a 108 kg Dall's porpoise from prey energy density, weight contribution rate of prey and 5% feeding rate. This is close to 25 5 MJ of the daily energy requirement calculated by the allometric method using body weight.

key words: Dall's porpoise, *Phocoenoides dalli*, feeding rate, energy intake, stomach contents

Introduction

Feeding rate is an index of daily ration expressed as percent of body weight (SERGEANT, 1969). Feeding rate is not only basic information for study of animal energetics, but is also important for studies of energy flow through the food web in the ecosystem.

Although there have been some studies on feeding rates of small cetaceans, most of them utilized animals in captivity (*e.g.* SERGEANT, 1969; TOBAYAMA, 1974; RIDGWAY, 1966; KASTELEIN *et al.*, 1993). Feeding rates estimated from captive animals have been criticized as overestimates, because they tend to eat too much (YASUI and GASKIN, 1986). YASUI and GASKIN (1986) estimated the feeding rate of the wild harbor porpoise *Phocoena phocoena* in the Bay of Fundy. They figured out the energy expenditure consistent with the daily energy intake. This supported the validity of their estimate of feeding rate. MIYAZAKI and KIMOTO (1987) estimated the feeding rate of wild Dall's porpoise *Phocoenoides dalli* in the Pacific Ocean, but they did not verify the value by an independent method. Many researches have revealed feeding habits of wild small cetaceans, but most of them reported only prey species or estimated original weights of prey in the stomach. It is difficult to estimate feeding rate because undigested fresh foods are rare in the stomach, and the number of feeding bouts in a day is difficult to know. YASUI and GASKIN (1986) and MIYAZAKI and KIMOTO (1987) were rare examples of studying feeding rates of wild small cetaceans. Feeding rates of wild small cetaceans are still poorly known.

Dall's porpoise is widely distributed from the subarctic to the boreal zone of the North Pacific and adjacent waters. They are one of the most numerous species of odontocetes in the area. Since it is expected that they play a major role as a higher trophic level predator in the northern North Pacific, it is important to clarify the feeding rate of Dall's porpoise as well as prey items.

Materials and Methods

Thirty Dall's porpoises were killed and stomach samples of all porpoises were collected on board a hand harpoon fishery vessel (19 gross tons) from 16 to 26 May 1995 in the Sea of Japan off southwestern Hokkaido. Searching efforts were made from dawn to dusk but efforts in afternoon were tend to be omitted due to the rough sea state. Body length and girth at the anterior insertion of the dorsal fin were measured. Body weights of porpoises were estimated by the equation,

$$y = 37.657x + 4.755,$$

where y is the body weight of a porpoise (kg), and x is the body length multiplied by squared girth (m^3). This relationship was obtained from North Pacific Dall's porpoises ($r^2 = 0.965$, $n = 106$; OHIZUMI and YOSHIOKA unpublished data).

In this study, we used only forestomach contents for analysis and the word "stomach contents" means forestomach contents. Stomach contents were weighed and sorted into three categories; undigested, half digested, and digested food remaining. For fish, "undigested" means specimens almost intact or only skin, fins and tip of mouth were missing. "Half digested" means that most of the muscle attached to bones, but the head was collapsed to expose the skull which still contained otoliths; sometimes the skull was detached from vertebra, and nearly half or most of the viscera were lost. For squids, "undigested" means almost intact, or the body was separated into mantle and head but dorsal mantle length was measurable. All squid samples used to estimate their weight belonged to this category. The term "digested food" means all other stomach contents including otoliths and beaks. Undigested and half digested foods were identified into species by their external morph if possible, otherwise otoliths or beaks were used for identification.

The number of each type of prey except for digested food was counted. Undigested fishes and squids whose mantle and head were not separated were weighed, and their standard length or dorsal mantle length measured. Length of fish vertebrae fragments with half digested muscle was also measured. The number of individuals that were digested into these fragments was estimated by dividing total fragment length by average standard length for each species. This value was added to the number of half digested fish. Weights of half digested food and undigested squid whose mantles were removed

Table 1 Weight and energy contribution rates of prey species for diunal feeding.

Species	Contribution rate for diunal feeding (%)		Energy density of prey	
	Weight	Energy	kJ/g	References
Japanese anchovy	7.44	12 22	8 28	RESOURCES COUNCIL (1987) partly corrected
Walleye pollock	37 19	34.25	4 64	PEREZ (1994)
Atka mackerel (muscle)	17 02	22.31	6 60	PEREZ and BIGG (1986)
Japanese sand lance	8 17	7.19	4.43	RESOURCES COUNCIL (1987)
Todarodes sp squid	30 18	24.03	4 01	CLARKE *et al.* (1985)

Weight contribution rates were obtaind from undigested and half digested preys found in all of the forestomachs

were estimated by their number and average weights of undigested food of each species.

All walleye pollocks (*Theragra chalcogramma*) were at least half digested and their bodies were broken into two or three pieces, probably because they were large and folded in the stomach. Therefore, only for walleye pollocks, the procedures mentioned above were not applied but otoliths (sagitta) taken out from skulls were used to estimate their body weight according to FROST and LOWRY (1981). The half number of these otoliths was recorded as the number of walleye pollocks.

Undigested food weights and estimated weights of half digested food for each species including estimated body weights of walleye pollock were summed up and regarded as the prey weights for recent feeding. Weight and relative calorific contributions of each species were calculated from prey samples of recent feeding (Table 1).

Results and Discussion

RSCW distribution

Porpoises were caught during the time of day 0456 to 1346. The ratio of stomach content weight to body weight (RSCW) before 0930 was significantly larger than that after 0930 ($\bar{x}=0.85\%$ and 0.46% respectively, U-test, $p=0.03$; Fig. 1). Many porpoises which had almost empty stomachs were caught after 0930. The maximum of RSCW was 1.68% recorded at 0516. This stomach was observed to be almost full, and contained undigested and half digested fishes. This animal was considered to be sated. The 1.68% of the RSCW would be almost the upper limit of stomach content under a natural environment (MRSCW). The decline of mean RSCW during the daytime indicates that Dall's porpoises mostly fed early in the morning and night, and feeding activity was reduced in the daytime, although there were some porpoises that fed in the daytime. This decrease of RSCW in the daytime might be caused by the digestion.

Range of possible digestion time

Although the decrease of RSCW might be caused by the digestion process, stomach content after 0930 included undigested and half digested food originating from recent feeding; this seems to make the digestion profile unclear. Therefore, we subtracted prey

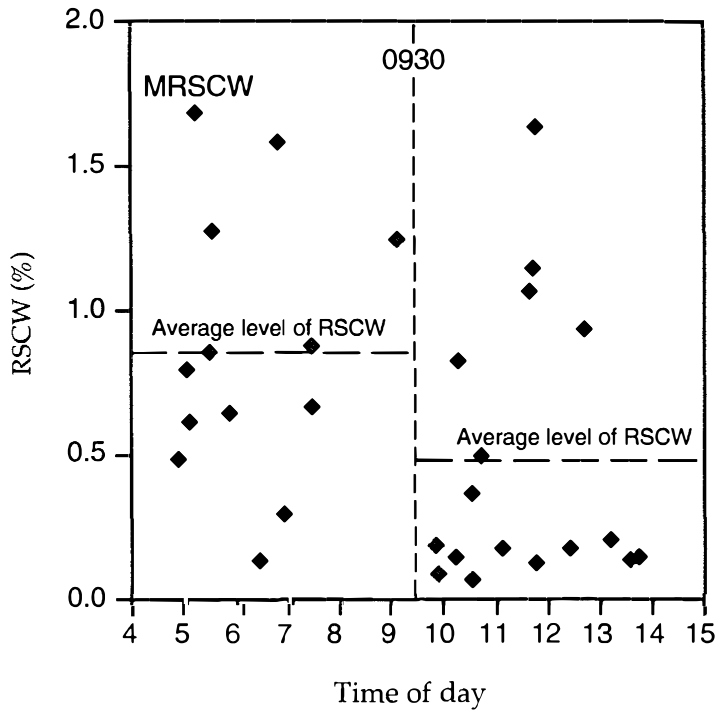

Fig. 1. Distribution of ratio of stomach content weight to body weight (RSCW) at catch time of day. Maximum RSCW (MRSCW) was 1.68%.

weights of recent feeding from whole stomach content weights of samples after 0930, and presumed that the weights of digested food remaining after 0930 originated from the foods taken early in the morning (Fig. 2). We considered that the decreasing profile from higher RSCW before 0930 to lower RSCW of digested food remaining after 0930 represents the digestion process. In this case, assuming that stomach contents of MRSCW at 0516 would be digested after 0930 and might be any point in the distribution range of RSCW after 0930. Possible digestion time from the MRSCW to empty was estimated to be at least five hours, and twelve hours at the most (Fig. 2).

TOBAYAMA (1974) reported that sated captive *Tursiops gilli* and *Delphinus delphis* ate the same quantity again eight hours later. Additionally he dissected fourteen stomachs of captive *Tursiops gilli*, *Delphinus delphis*, *Stenella coeruleoalba*, *Lagenorhynchus obliquidens*, and *Pseudorca crassidens* at various hours after feeding to observe the state of stomach contents. He concluded that stomachs became empty eight hours after active feeding. The eight hour digestion profile is almost in the middle of the possible digestion time range of this study (Fig. 2).

Estimation of feeding rate

Although true digestion time was unclear because accurate foraging time was unknown, assuming that digestion time of the porpoises is eight hours, maximum digestible food intake in twenty-four hours is calculated as MRSCW $\times$ (24/digestion time) $= 1.68 \times (24/8) = 5.04\%$ of body weight. This gives the maximum limit of feeding rate. However, this value is between feeding rates indirectly obtained from the biological concentration rate of mercury in wild Dall's porpoise (2–3%: MIYAZAKI and KIMOTO,

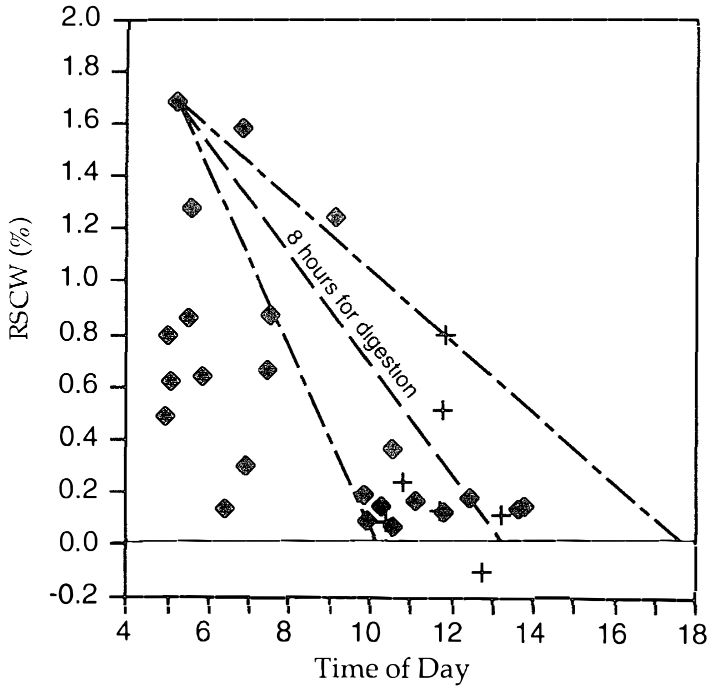

Fig. 2. Distribution of RSCW before 0930 and that of digested food remain after 0930. Range of probable digestion profile and eight hour digestion profile are shown by dotted and broken lines, respectively. Square dots indicate RSCW, crosses RSCW of digested food remain after 0930. A point of RSCW under zero would be an underestimate because fresh body weights of walleye pollock estimated from otolith length, instead of half digested walleye pollock weights, were subtracted from the stomach contents. In this case, the real RSCW of the digested food remaining at the true time of feeding on walleye pollocks would be located at the point of heavier RSCW.

1987), and directly measured from a captive porpoise (12.5%: RIDGWAY, 1966).

The stomach that gave MRSCW did not seem to be completely full from observation of the stomach condition. RIDGWAY (1966) showed that Dall's porpoise could eat a considerable quantity of food if available. CRAWFORD (1981) reported that maximum stomach content was 2505 m*l* from a 94 kg Dall's porpoise near the Aleutian Islands. This is roughly equal to 2.66% of body weight. The MRSCW may reflect availability of foods, and may be different among habitats of Dall's porpoises. The feeding time of the porpoises in this study was estimated early in the morning and at night. We have no data on feeding activities at night and we can not reject the possibility that MRSCW of more than 1.68% might be found at night. There have not been any studies that investigated stomach contents of Dall's porpoise at night with reference to catch time. The active time of feeding at night was unclear and we could not determine whether Dall's porpoises fed actively at night or early in the morning. The 1.68% MRSCW in this study was based on observation of almost full stomachs, but further study should be conducted to clarify the relation between food availability and MRSCW as well as for finding out MRSCW at night.

The estimated number of times of sating in a day (3 = 24/8) was derived theoretically; and this does not mean the actual number of feeding bouts in a day. There was no quantitative relation between undigested foods and other stomach contents (Fig. 3).

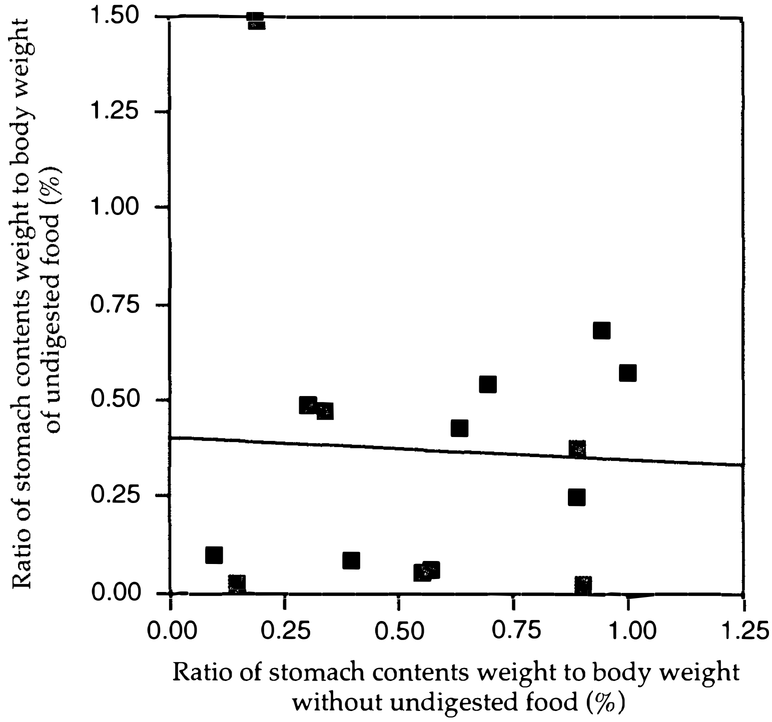

Fig. 3. Relationship between RSCW of undigested food and RSCW of other stomach contents. The RSCW originating from a previous feeding did not affect the food intake of next feeding bout ($y = 0.405 - 0.58x$, $r^2 = 0.002$, $p = 0.87$).

Probably this indicates that Dall's porpoises fed little by little. Actual number of feeding bouts in a day will vary.

SERGEANT (1969) showed another method for estimation of daily food intake mass as ten times the heart weight. INNES *et al.* (1986) stated that it was inappropriate to use ten times the heart weight to estimate daily intake mass or feeding rate, because the ratio of heart weight to body weight was not dimensionally consistent with the ratio of daily food intake mass to body weight. Moreover, SERGEANT (1969) used only captive dolphins to derive the method; therefore, estimates may be too large for wild dolphins. According to this method, the 108 kg Dall's porpoise, which gave MRSCW, had a 990 g heart; and it was estimated to feed on 9900 g/day, 9.2% of its body weight. This is about twice 5.04%.

Daily energy intake for a 108 kg porpoise

Daily intake of energy was calculated to be 27.2 MJ/day using the contribution rates of prey, energy density of each prey species (Table 1) and 5% of the feeding rate for the 108 kg Dall's porpoise which recorded MRSCW. This was similar to 25.5 MJ/day estimated by the allometric method for carnivorous mammals (FARLOW, 1976).

It has been generally accepted that marine mammals have prodigious appetites, and this is consistent with having higher metabolic rates than terrestrial mammals. However, recent studies have shown that higher metabolic rates were caused by using restrained, immature, or presumably growing animals, and rates of food consumption in marine mammals are not significantly different from those of terrestrial mammals

(LAVIGNE *et al.*, 1982; GASKIN, 1982; YASUI and GASKIN, 1986; WORTHY, 1990; INNES *et al.*, 1987). Therefore, the allometric method derived from terrestrial mammals is considered to be useful to estimate basal metabolic rates and daily energy requirements of marine mammals. RIDGWAY (1966) reported that a captive Dall's porpoise fed on mackerel up to 12.5% of its body weight. The calorific value calculated using this rate and energy density (5.60–7.98 kJ/g: WORTHY, 1990) for a 108 kg porpoise is between 75.6 to 107.7 MJ/day. This value is clearly large compared to the 27.2 or 25.5 MJ/day of this study. It might be an overestimate to apply the 12.5% feeding rate for a wild porpoise. Daily intake of energy for Dall's porpoises in the Pacific, which mainly feed on myctophids, is estimated as 18.0 MJ/day for a 108 kg porpoise (2.5% feeding rate: MIYAZAKI and KIMOTO, 1987; 2.7 kg Myctophiformes fishes with 6.60 kJ/g energy density: PEREZ and BIGG, 1986). This is low compared to the 27.2 or 25.5 MJ found in this study. CRAWFORD (1981) reported that a feeding rate of 21% is not unreasonable for Dall's porpoises which mainly feed on gonatid squids and myctophid fishes around the Aleutian Islands, but he assumed that all otoliths found in stomachs were ingested within a day. This assumption would lead to an overestimate, because, sometimes, thousands of otoliths of myctophid fishes were found from a stomach (CRAWFORD, 1981; OHIZUMI unpublished data), and digested food remains such as otoliths and beaks of squids tended to accumulate (SEKIGUCHI, 1994). The 5% feeding rate which gave an energy intake close to that estimated by the allometric method might be the most realistic value for a wild Dall's porpoise. However, as it is expected that seasonal and geographical change of prey energy density as well as physical and sexual conditions of porpoises will affect the feeding rate, further study is necessary.

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