

ミナミハンドウイルカ(*Tursiops aduncus*)の前胃内における 摂食物の消化過程

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Digestion Process of Ingesta in Forestomach of Indo-Pacific Bottlenose Dolphin (*Tursiops aduncus*)

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Abstract

We investigated the relationship between elapsed time and the process of food digestion in the forestomach and the estimated time for stomach evacuation in an Indo-Pacific bottlenose dolphin. The digestion process was observed with a gastroscope to reveal the characteristic progress of digestion of different prey species. Single flying fish (approximately 100 g) and mackerel (approximately 200 g) were similarly digested, despite the difference in their size. Single squid (approximately 100 g) was digested faster than similar sized flying fish. The weight of stomach contents and the digestion time to evacuation showed an apparent positive relationship, and a full stomach content of flying fish was digested to the point of evacuation within approximately 10 hours of ingestion. Since it is an experimental result using only one dolphin, it cannot be immediately applied to the stomach content analysis of wild individuals, but it is considered that the difference in digestion time among prey species can be compared.

Key Words: digestion stages, digestion time, forestomach contents, gastroscope, Indo-Pacific bottlenose dolphin

Introduction

The feeding habits of cetaceans have been studied by many researchers using various analytical methods such as analysis of stomach content (Ohizumi et al., 2003; Konishi et al., 2009; Romero et al., 2012), stable isotope ratios (Abend and Smith, 1997; Hoekstra et al., 2002; Ohizumi and Miyazaki, 2010), and levels of fatty acids (Grahle-Nielsen et al., 2010; Waugh et al., 2012), and even direct observation of feeding activities (Similä and Ugarte, 1993). These studies were qualitative in nature, and only a few studies have attempted to estimate the feeding rate from stomach content analysis (Yasui and Gaskin, 1986; Ohizumi and Miyazaki, 1998). However, the data used for estimation was unclear, particularly those concerning the number of feeding bouts, the digestion time for each prey species, and the residence time of hard digestion-resistant parts in the stomach.

Stomach content analysis is a classic method, but it

has an advantage over newer analytical techniques such as analysis of stable isotope ratios and fatty acid levels in clarifying prey species, the number of prey ingested, and the prey size. Therefore, stomach contents can also provide an estimate of the mass of food ingested. However, this does not mean that daily ration or consumption per unit of time can be estimated by stomach content analysis because stomach contents provide a “snapshot” of information related to the feeding of each animal (Desportes and Mouritsen, 1993). Consequently, this method does not provide temporal information.

Daily ration or required energy has been estimated from a metabolic base (Kenney et al., 1997; Sigurjónsson and Víkingsson, 1998) rather than by stomach content analysis. Metabolic studies on marine mammals, particularly cetaceans, are still limited and data interpretation is convoluted and difficult. Early studies estimated a higher metabolic rate compared to studies of terrestrial mammals of similar size (Kanwisher and Sundnes, 1965; Hampton et al., 1971), but some studies argued that the resting metabolic rate or required food mass were not significantly higher than those of terrestrial mammals (Lavigne et al.,

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1986; Innes et al., 1987). Recent studies reported that bottlenose dolphin (*Tursiops truncatus*) has 1.6 times higher resting metabolic rate than terrestrial mammals, but that the dynamic metabolic scope from resting to exercising is low (Williams et al., 1993) due to the lower metabolic cost of swimming (Williams et al., 1992, 1993), which in turn implies a similar total metabolic rate.

Meanwhile, ocean wide food consumption by cetaceans has been estimated for evaluating their ecological importance (Markussen et al., 1992; Kenney et al., 1997; Sigurjónsson and Víkingsson, 1998; Tamura et al., 1999; Hunt et al., 2000). Most of these were based on estimates of a metabolic base; however, such estimations are difficult to validate because the method of verifying estimated requirements is poor. A different technique, independent of metabolic bases is required to verify food consumption or energy requirement by cetaceans.

Most of the cetaceans, particularly toothed whales, feed on fish and/or squids. These prey items are digested in the stomach from “fresh” stage to fragments of bone or otoliths for fish and beaks for squid before the stomach is evacuated. There are several digestion stages between the fresh to the final stage, but few studies described the progress of digestion. If a relationship between digestion time and its stages is known, the elapsed time after ingestion can be inferred. This means an axis of time can be set for stomach content analysis, which can be a base for estimating consumption per unit of time. Digestion or evacuation time of the stomach contents has been used to estimate the required daily food mass from stomach content analysis in fish studies (Pennington, 1985; Andersen, 2001; Darbyson et al., 2003; Butler et al., 2010; Nakatsuka et al., 2010).

Some researchers attempted to estimate the time taken for digestion in the cetacean stomach. Sekiguchi and Best (1997) found >10 hours for digestion of a single prey item for some prey species in experiments using artificial digestive solutions *in vitro*, but such experiments apparently failed to simulate vermiculation even if the sample was agitated. A few studies observed stomach contents of culled dolphins and seals at several hours after feeding (Tobayama, 1974; Murie and Lavigne, 1986), but such methodology is very difficult to repeat with current ethical standards.

The purpose of the present study is to observe the various stages of digestion in relation to elapsed time after feeding with a gastroscope in the forestomach of an Indo-Pacific bottlenose dolphin. Observation using a gastroscope can be performed with minimum invasive

stress after sufficient training. Gastroscope observation *in vivo* not only provides an accurate status of the stage of digestion, but also enables observation of the functioning stomach, which allows us to consider any effect of physical digestion for evaluating the relationship between the progress of digestion and elapsed time. Further, information on the digestibility of a prey species is an important consideration in the absorption of ingesta and/or medicine in the context of veterinary science.

Materials and Methods

All experiments were conducted in the Okinawa Churaumi Aquarium (Motobu, Okinawa, Japan). Two types of experiments were conducted to observe the digestion process of a single prey item, and the digestion time of a food mass. A gastroscope system (VQ-1223A with 2 m and 3 m fibers, CLV-U40D light source and VO-2A video system sensor, OLYMPUS) was used to observe the forestomach contents of a dolphin fed on experimental food. The scope operator and observers used a goggle-type display (Eyetrekk, OLYMPUS) and an LCD monitor (LMD-2020, SONY), respectively. The observations were recorded on a digital video tape recorder (GV-D1000, SONY). The animal was fed small amounts of capelins for the last meal of the day before the experiment, and was then fasted for at least 12 hours. The dolphin was fed experimental prey, and called to the poolside at scheduled times. The dolphin kept tail beating to stay positioning at the poolside with the head out of the water and mouth open. The gastroscope was inserted into the forestomach with the dolphin's compliance. We used a healthy Indo-Pacific bottlenose dolphin (an approximately 40 years old male of 259 cm body length and 189 kg body weight) that was sufficiently trained to voluntarily accept the gastroscope. At the observation time, fluid in the forestomach was pumped out using an aspirator (MMC-1400 WDX, Shin-ei Kogyo) to obtain a clear vision and the forestomach was then inflated with air. Sometimes the lens of the scope was rinsed with a little water from a nozzle at the tip because the lens was smeared with gastric fluid. The fiber of the scope was directed to observe the entire inside of the forestomach. Observation was limited to one daily scheduled time to avoid the effects of scope insertion and the pumping out of gastric fluids. The volume and pH of collected fluids were measured immediately after observation.

For the observation of single prey species digestion, the dolphin was fed an experimental prey in the morning.

Observation was scheduled at 30, 60, 90, and 120 minutes after feeding, and the gastroscope observations were all completed before noon. Flying fish (*Cypselurus poecilopterus*), mackerel (*Scomber japonicus*), and squid (*Todarodes pacificus*) were the experimental prey. These prey items were selected based on their body weight of 100–109 g for flying fish and squid, and 190–199 g for mackerel from a frozen block of daily food. The observation process was ended within approximately 10–15 minutes except for the squid that took about 20 minutes because of some difficulties in observation. Therefore, the scope was inserted successively at 30 and 60 minutes and at 90 and 120 minutes on the same day, respectively, in the case of squid.

The dolphin was usually fed a total of approximately 10 kg of food per day, and we assumed that 5 kg approximated a full stomach, which corresponds to approximately 2.65% of the dolphin's body weight. Flying fish weighing 5.0, 2.5, and 1.25 kg were used for the measurement of the relationship between digestion time and food mass. Individual flying fish were of the same size as that in the single prey experiment. The dolphin was opted out from the daily dolphin attraction show schedule, and experimental prey was fed between 7:00 and 8:00 am. Schedules of observation were set at 8, 10, and 12 hours for 5 kg, 5, 6, 7, and 8 hours for 2.5 kg, and 3, 4, 5, and 6 hours for 1.25 kg.

Results

Observation in the forestomach

Gastrosopic observation identified active vermiculation of the forestomach wall. The squeezing of the stomach wall often blocked the scope from exploring the bottom of the forestomach; therefore, we had to inflate it with air and insert the scope forward when the stomach wall relaxed. The contents of the stomach were soaked in gastric fluid. The mean volume of fluid pumped out was 472 ± 266 ml (100–600 ml), and the pH was 1.69 ± 0.44 (0.8–2.8) in the individual prey digestion experiment. However, these measurements also contained some water used for scope lens cleaning. The fluid apparently ran from the fundic chamber, which was suggested by the stream observed to be falling into the forestomach.

Digestion of single prey items

The processes of digestion for single prey items of flying fish, mackerel, and squid are summarized in Table 1. The body of flying fish was partially digested 30 minutes

Table 1. General description on progress of prey digestion along elapsed time.

A: Flying fish				
Parts	30 min. (4 obs.)	60 min. (5 obs.)	90 min. (7 obs.)	120 min. (6 obs.)
Skin	disappeared	disappeared	disappeared	disappeared
Fin	disappeared membrane disappeared, ray remain	partially digested, or disappeared	disappeared	disappeared
Muscle	apparently intact	partially digested, or disappeared	partially digested, or disappeared	disappeared
Vertebra	intact (inside of body)	fractured	fractured, or fragments	fragments, or fractured
Empty	no	no	2/7 obs.	3/6 obs.
B: Mackerel				
Parts	30 min. (5 obs.)	60 min. (8 obs.)	90 min. (8 obs.)	120 min. (5 obs.)
Skin	disappeared	disappeared	disappeared	disappeared
Fin	disappeared	disappeared	disappeared	disappeared
Muscle	apparently intact or partially digested	partially digested or apparently intact	most digested	disappeared, or most digested
Vertebra	intact or fractured?	intact or fractured	fractured, or fragments	fragments
Empty	no	no	2/8 obs.	2/5 obs.
C: Squid				
Parts	30 min. (4 obs.)	60 min. (4 obs.)	90 min. (4 obs.)	120 min. (4 obs.)
Skin	disappeared	disappeared	disappeared	disappeared
Mantle	partially digested fin	partially digested, very thin	disappeared	disappeared
Head	separate from mantle?, eyelid open	separate from mantle	disappeared	disappeared
Gladius	front tip exposed, or most exposed	almost exposed	not confirmed	separated
*Empty	no	1/4 obs.	4/4 obs.	4/4 obs.

*including separated eye lens, beaks, gladius, and slimy remnants

after ingestion, the skin and the pectoral fin membrane had disappeared (Fig.1 A1~2). The eye lens had also dropped out, and the abdomen was open along the median line (Fig.1 A3). At 60 minutes, the muscles of the body axis were partially digested. The vertebra was exposed in between digested muscle, and the axis fractured into several pieces (Fig.1 B1~2). In one observation, a vertebral column free from muscle was observed (Fig.1 B3). Ingesta of similar digestion status, with empty or almost empty stomachs containing fragments of bone, were also observed at 90 minutes (Fig.1 C). Only empty stomachs or fragments of bone were observed after 120 minutes (Fig.1 D). A logistic regression estimated 87 minutes (95% confidence limit was 50.9–118.0 min., $p = 0.0002$, $n = 22$) as the required time for the complete digestion of flesh at 50% probability.

For mackerel, skin and fins disappeared within 30 minutes (Fig.2 A1~2). Muscle was mostly almost intact at 30 minutes, but was partially digested in some cases and the body was broken into several pieces (Fig.2 A3). Partial digestion of muscle and collapse of the prey body was more evident at 60 minutes (Fig.2 B). At 90 minutes, most of the muscle was digested and fractured or fragmented vertebra was observed (Fig.2 C). Only bones, or an empty stomach was the common observation after 120 minutes (Fig.2 D), except for one observation where some partially digested

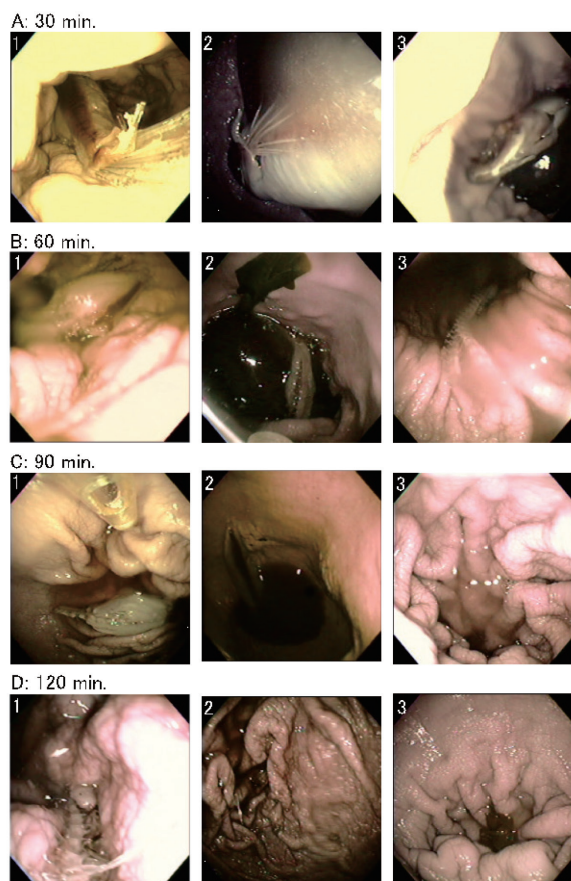


Fig.1 Digestion processes of single flying fish.

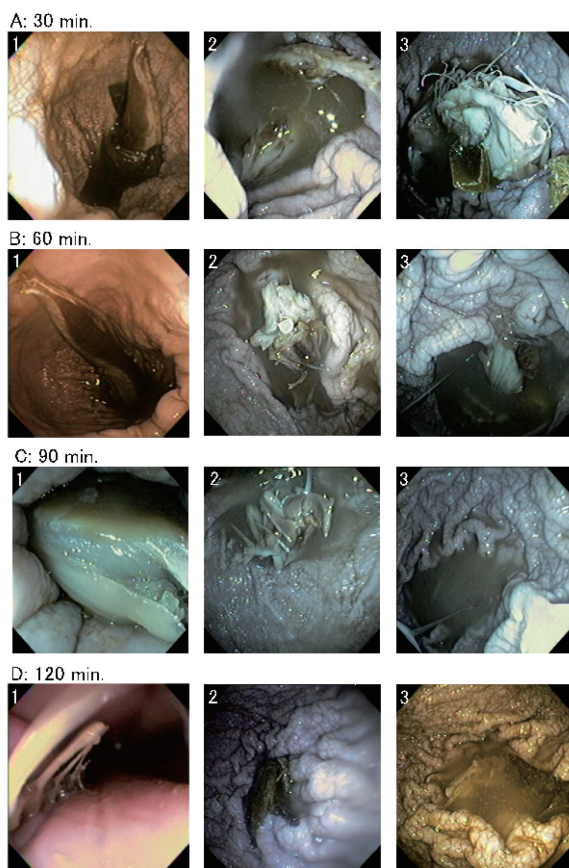


Fig.2 Digestion processes of single mackerel.

muscle was found. A logistic regression estimated 92 minutes (95% confidence limit was 70.0–139.2 min., $p = 0.0009$, $n = 26$) as the required time for complete digestion of flesh at 50% probability.

The observation of squid digestion was sometimes impaired by mucus-like digested contents smearing the scope lens. Because pigments on the squid surface were not found, the squid skin was probably digested within 30 minutes (Fig.3 A). At this stage the head may have been separated from the mantle, but it was not confirmed. The anterior end of the mantle was opened, and the gladius was exposed (Fig.3 A1). The peripheral tissue of eye was also digested to expose the irises, but the eye lenses were still inside (Fig.3 A3). At 60 minutes, the mantle was digested to a thin posterior fringe (Fig.3 B1~2). The head was separated from the mantle (Fig.3 B1). Empty and slimy remnants were observed in an observation (Fig.3 B3). After 90 minutes, no recognizable squid shape was observed (Fig.3 C, D), but some remaining hard parts such as beaks (Fig.3 C2), eye lenses (Fig.3 C3), and the gladius (Fig.3 D1) were observed, suggesting the empty state of the stomach.

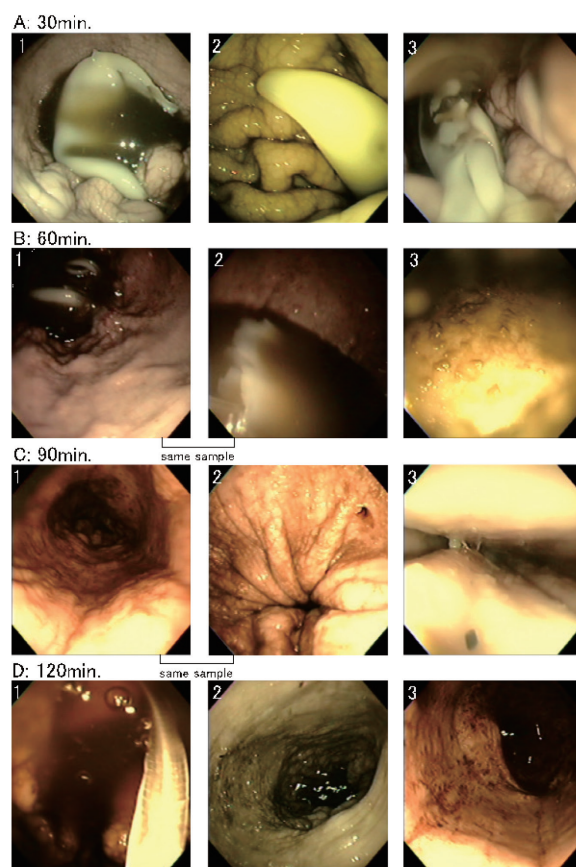


Fig.3 Digestion processes of single squid.

Digestion of food mass

Stomach contents of 1.25 kg, 2.5 kg, and 5 kg of flying

fish were found to be emptied 6, 8, and 12 hours, respectively (Fig.4). These observations could not obtain accurate information about the remaining volume of food in the forestomach; therefore, we had to evaluate the progress of digestion from the qualitative status of digestion based on the remaining flesh, or a confirmation of emptiness. The mass ingested and the scheduled elapsed time of confirmation of an empty stomach showed an apparent positive relationship (Fig.5).

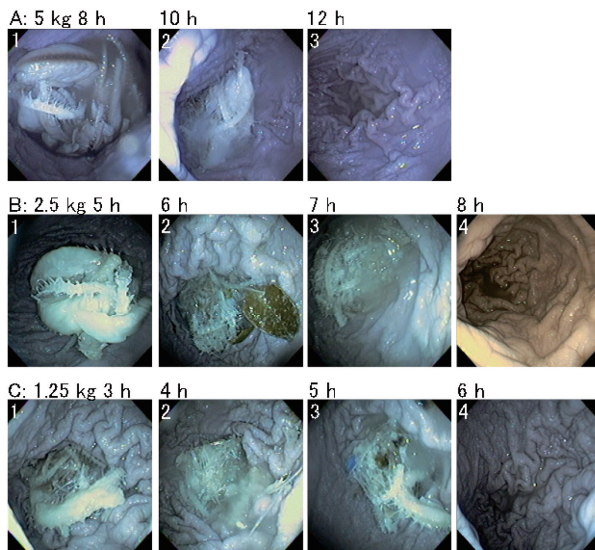


Fig. 4 Digestion processes of some masses of flying fishes.

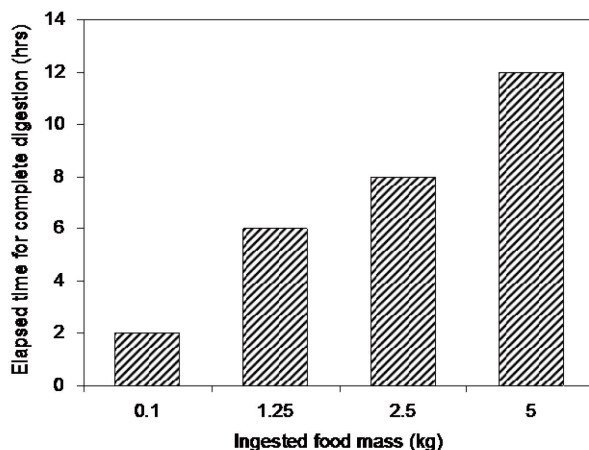


Fig. 5 Scheduled elapsed time at which complete digestion of food was observed. The plot for 0.1 kg food is from the result of single prey digestion. Only single observation was made for each mass except for 0.1 kg.

Discussion

Bias and Limitations

We observed digestion process of a single animal of dolphin. Health condition of the dolphin at the

experiments was good, but it is not clear he was “standard” individual. It is necessary to experiment by increasing the number of individuals and dolphin species to determine whether others will have the same digestion status over the same time. Therefore, present results cannot be immediately applied to the analysis of stomach contents of wild individuals. However, since multiple prey species were repeatedly tested with the same individual, it can be considered that the digestion speeds among prey species can be compared.

In the present study, we made intermittent observations of the forestomach digestion of a bottlenose dolphin; the gastroscope did not allow us continuous observation of the digested food items. The “stomach” of cetaceans, particularly dolphins, has three compartments including the forestomach, fundus, and pyloric chambers, followed by the duodenal ampulla. The present observations confirmed that digestive fluid ran into the forestomach from the fundus, but some half digested contents could be carried back and forth between the two. Limited gastroscopic observation may have missed the movement of contents between the chambers. This may explain some of the variation in stage of digestion at the same elapsed time.

Gastroscopic observations for single squid digestion were carried out successively from 30 to 60 minutes and from 90 to 120 minutes, whereas single observations were carried out daily for other fishes. Slimy remnants of digested squid required a longer observation time due to the need to rinse the lens; therefore, it became difficult to maintain a definite observation schedule in order to compare digestion stage of an ingested species at a particular elapsed time. It is possible that the pumping out of the digestive solution and the gastroscopic observation itself affected the progress of digestion; therefore, differences of digestion stage between 30 and 60 minutes could be ambiguous, but not for 90 and 120 minutes because digestion was already almost completed at 90 minutes.

General Digestion Process

The forestomach is lined with stratified squamous epithelium with no digestive glands (Slijper and Harrison, 1979; Olsen et al., 1994; Mead, 2002). It was considered to be a temporal space for the storage of ingested un-masticated food and an extensive muscularis externa indicates grinding of contents (Olsen et al., 1994). The connection between the forestomach and the fundic chamber is wide open; therefore, there is a reflux

of digestive fluids from the fundic chamber and some digestion takes place in the forestomach (Mead, 2002). Olsen et al. (1994) also pointed out that digestion is initiated in the forestomach because it usually contains various stages of digested or undigested foods. Christiansen et al. (2005) reported that whole capelin (*Mallotus villosus*) of approximately 100–120 mm was digested to a pulp-like substance following 10 hours of soaking (without agitation) in an artificial digestive solution to simulate the seal stomach. Sekiguchi and Best (1997) found that several species of fish and squid of approximately 100–200 mm in total length required 10 hours or more to be digested to 20% of their original weight in a similar experiment (this time including agitation) to simulate the dolphin forestomach. The present study is the first to directly confirm reflux from the fundic chamber and a strong vermiculation of the forestomach. This observation can apparently explain the strikingly fast digestion of a single item of food compared with artificial digestion experiments.

Digestion Stage and Required Time

The required time for digestion was similar among prey species, although mackerel were up to twice the size of flying fish. The progress of the digestion stages were similar between the two fish species, except at 30 minutes where the digestion was slightly more advanced in mackerel (up to half digested muscle) than in the flying fish (only the skin was digested). At 60 minutes, the muscle of the flying fish was half or completely digested; however, that of the mackerel had made little advancement on the digestion stage observed at 30 minutes. This slow initial digestion of flying fish is probably due to the large and hard pectoral fins that cover most of the both sides of the body. The relatively slower estimated digestion speed of muscle for mackerel may be caused by its larger size.

Squid was digested faster than flying fish of the same size. Squid has an open mantle so digestive solutions can flow inside to digest both sides of the mantle and the viscera concurrently. The squid head connects to the mantle with only soft tissue; thus, it easily separates; the tentacles are slender and elongated. All these features provide a larger surface area exposure to digestive solutions, which may be a reason for the observed faster digestion.

These differences among prey species suggest some factors concerning the speed of digestion. Hard surface parts such as large fins and scales can be a hindrance to

the digestion of soft body parts. The relative surface area to body mass is probably an important factor, which is evident in the case of the squid. The relatively slower digestion of mackerel also suggests such factors. In addition to these structural and scaling factors, biochemical factors such as the water and lipid content of the prey may affect the speed of digestion. In the case of mackerel, a large mass of lipid viscera was observed at the last stage of digestion. Lipids can be digested in the pancreatic juice, which includes lipase secreted in the duodenal ampulla.

Digestion Period of a Full of Stomach

Observations were made at scheduled times; thus, the elapsed time at which the stomach was found empty did not always relate directly to the complete digestion time. Observations for 5 kg of food digestion should be suspected in this regard because these were made at 2 hours-differences, whereas the others were at 1-hour differences. Based on the progress of flesh digestion, the status of 5 kg of ingesta at 8 hours appeared to be earlier than that of 2.5 kg at 5 hours. Flying fish of 2.5 kg was completely digested after 3 hours, i.e., at 8 hours. Half digested contents of 5 kg at 8 hours may require 3 more hours, and an empty stomach at 12 hours (for 5 kg of flying fish) suggests it takes 11–12 hours to be completely digested. The digestion time experiment could make only one observation for each time and mass. Therefore, the apparent positive relationship between ingested food mass and elapsed time for complete digestion (Fig. 5) contains no information on error. At least an hour of potential variation should be considered because of the difference of observation schedule.

Tobayama (1974) reported that sated captive bottlenose dolphins (*Tursiops gilli*) and a common dolphin (*Delphinus delphis*) fed again to a sated level at intervals of approximately 8 hours. Further, Tobayama (1974) observed the stomach contents of captive bottlenose dolphins, a common dolphin, striped dolphins (*Stenella coeruleoalba*), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), and a false killer whale (*Pseudorca crassidens*) at various time of after feeding on mackerel and found that almost no prey items of original shape remained after 4 hours. In addition, the stomachs were near empty at approximately 8 hours. Ohizumi et al. (2003) observed stomach contents of Dall's porpoises (*Phocoenoides dalli*) in the north Pacific and found nocturnal feeding. The stomach content weight peaked early in the morning and reduced to be near empty approximately 8 hours after dawn. Murie and Lavigne

(1986) observed the stomach contents of some seals and found fish skulls still containing multiple otoliths until 8 hours after feeding and 13 hours for isolated otoliths. These previous studies and the present study suggest that 8–12 hours are the required time for digestion of the full stomach content after feeding. Differences in experimental design and limited data make statistical analysis difficult, but approximately 10 hours is considered to be the possible standard time required for the digestion of complete stomach contents.

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要 旨

ミナミハンドウイルカの食道胃における摂食物の消化過程と排出にかかる時間について調べた。消化プロセスを観察するために内視鏡を用い、餌種による消化過程の違いを明らかにした。一尾のトビウオ（約 100g）とサバ（約 200g）は、そのサイズの差にもかかわらず同じように消化された。一尾のイカ（約 100g）は、ほぼ同じサイズのトビウオより速く消化された。胃内容物の重量と空胃に至るまでの消化時間には正の関係性が見られ、満胃のトビウオは摂取の約 10 時間後に空胃に至るまで消化された。本実験は 1 頭のイルカのみを使って行われたので、これらの結果を直ちに野生個体の胃内容分析にあてはめて考えることはできないが、餌種間の消化過程の違いは比較可能と考えられる。

キーワード：消化段階、消化時間、前胃内容物、胃内視鏡、ミナミハンドウイルカ