MESOPELAGIC FISHES EATEN BY FRASER'S DOLPHIN, *LAGENODELPHIS HOSEI*[1]

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ABSTRACT

Examination of the stomach contents of three specimens of the rare pantropical dolphin, *Lagenodelphis hosei*, showed them to have been feeding on a mixed diet of mesopelagic fishes, shrimps, and squids, with fishes by far the most important component. Ecologically and morphologically the prey fishes comprised three types: A group of elongate, solitary, vertically mobile species; deep-bodied, aggregative, nonmigratory fishes; and thick-bodied, dark colored nonmigrators. Based on the known vertical distribution patterns of the prey species, the three dolphins had been feeding at depths near 250 and 500 m. The large sizes and species composition of the prey fauna indicate that the dolphins were feeding selectively, ignoring the smaller, more abundant vertically migratory species that dominate the upper mesopelagic midwater fish fauna of the eastern tropical Pacific. The estimated nutritional value of the ingested prey is similar to the values reported for related cetaceans maintained in captivity.

Until recently Fraser's dolphin, *Lagenodelphis hosei*, was known only as a skeleton, collected before 1895 from a beach in Sarawak, Borneo, and deposited in the British Museum of Natural History. From these bones, F. C. Fraser described the species in 1956, but it was not until 1971 that living specimens were observed and recognized as *L. hosei* (Perrin et al. 1973a). Subsequent reports have appeared which suggest a pantropical distribution (Tobayama et al. 1973; Caldwell et al. 1976; Miyazaki and Wada 1978). Most of the accumulating information on this rare and little-known dolphin is concerned with its distribution and anatomical distinctions, although Tobayama and his colleagues briefly described the stomach contents of a specimen found at Kamogawa, Japan.

Fitch and Brownell (1968, 1971) have demonstrated the usefulness of fish otoliths found in cetacean stomachs as reliable indicators of prey identity and, in some cases, of feeding depths. The shape of these characteristic structures is often species-specific, and they are relatively resistant to digestion. Other bones, such as dentaries, urohyals, and opercular, can also be helpful as indicators if digestion has not progressed too far (Miyazaki et al. 1973). There is a nearly direct relationship between otolith dimensions and standard length for adult fishes (Fitch and Brownell 1968); thus the sizes of the ingested fish can be quantified by comparing otolith measurements with otolith and standard length data from fish collected by trawling. These size data can in turn be used to estimate the nutritional value of the ingested fish by referring to data on their chemical composition (e.g., Childress and Nygaard 1973).

In addition to the information they provide about a predator's feeding habits (Perrin et al. 1973b), stomach content analyses are also valuable for estimating predation pressure on the prey fauna. With regard to predation by nekton on micronekton, such data may be of particular value because this major trophic link is one of the most poorly understood aspects of oceanic community dynamics.

MATERIAL AND METHODS

We examined the stomach contents of three female specimens of *Lagenodelphis hosei* that were captured by purse seine in the eastern tropical Pacific (lat. 5°N, long. 122°22'W) in May 1972 and acquired by Harvard University's Museum of Comparative Zoology. The first specimen (MCZ 52979) was about 230 cm long and carried a well-developed fetus. The sizes of the second and third individuals (MCZ 54379, MCZ 56572) were about 215 and 210 cm. The stomachs were removed intact from the specimens, which had been frozen since capture. The stomachs were thawed and opened, and their contents were gently washed through a graded series of screens to

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separate the soft tissue. After drying, the otoliths (sagittae) and other distinctive bones were picked out by hand. The bones were identified by comparison with material from fish specimens collected from both the Atlantic and Pacific Oceans by midwater trawling.

RESULTS

The first stomach contained about 1 l of material, nearly half of which was partially digested squid flesh; a roughly comparable portion was composed of fish bones. Fish muscle, squid beaks, and shrimp remains made up the small remainder. The second stomach's 2 l volume was roughly 90% fish bones, with small amounts of squid and fish flesh, shrimp carapaces, and squid beaks. No soft tissue remained in the third stomach; the volume of its contents was only about 0.125 l, and 90% of this was composed of shrimp exoskeletons. The remaining volume was due to fish bones, squid beaks, and eye lenses. Fish had clearly been the dominant component of the diets of all three Fraser's dolphins.

The three stomachs yielded 2,918 otoliths plus several hundred identifiable dentary, opercular, and cleithral bones. Table 1 presents the otolith data and the identities of the fishes they represent. An account of the most abundant fishes follows. Stomiatoid genera are classified according to Weitzman (1974).

Gonostomatidae

Otoliths of the genus *Gonostoma* are highly distinctive and easily discerned among stomach contents. The *Gonostoma* otoliths and dentary bones from the *L. hosei* stomachs are probably all from *G. elongatum*. We estimated the size of the fishes by comparing their dentary bones with those from specimens of *G. elongatum* which were collected by midwater trawling gear, albeit from Atlantic populations. The range of estimated standard lengths, 83 to 225 mm, shows that many of those ingested by the dolphins were quite large by trawl-sample standards (see Backus et al. 1965, 1969; Clarke 1974).

Sternoptychidae

Two sternoptychid genera were present in all three stomachs. Most of the *Argyropelecus* otoliths can be assigned with confidence to *A. lychnus*, while the remainder are probably from *A. affinis*. These hatchetfish occupy limited depth horizons both day and night and are common forage of large pelagic animals. Our size estimates are based on the length of cleithra from the dolphin stomachs compared with those from specimens of *A. lychnus* trawled in the eastern South Pacific and on comparisons of otoliths with trawl-caught *A. lychnus* from the eastern North Pacific. Both methods indicated that the dolphins had been feeding on a size range of about 40 to 70 mm. Here again the larger specimens ingested by *L. hosei* exceed the size of those commonly collected by trawling (Baird 1971).

Among the sternoptychid otoliths found in the dolphin stomachs, we are least certain of those tentatively designated *¿Maurolicus muelleri?* in Table 1. While this species is worldwide in distribution, and the sagittae resemble slightly digested versions of those from trawled Atlantic specimens, some uncertainty remains.

Photichthyidae

The examples of *Ichthyococcus* reported here are most likely from *I. irregularis*, which inhabits the eastern Pacific region where the three Fraser's dolphins were captured (Rechnitzer and Böhlke 1958). The peculiar configuration of *Ichthyococcus* otoliths is such that their fragile anterior projections are easily broken or dissolved, thus precluding accurate otolith length measurements. In this case we have used otolith heights for our estimates of fish size. When plotted on an otolith height vs. standard length curve for *I. irregularis* from the eastern Pacific, the otolith heights of these specimens suggest that the individuals caught by the dolphins ranged from 40 to 69 mm (Fig. 1). The largest otoliths from the dolphin stomachs are at the upper size limit of those available for comparison from trawl collections.

Chauliodontidae

Chauliodus otoliths and dentary bones were present in all three dolphin stomachs. We estimate the average standard length at about 180 mm, based on dentary length. These fishes have wide vertical ranges and exhibit irregular patterns of diel migration. Their movements appear to be related to their role as predator of vertically mobile gonostomatids, sternoptychids, and myctophids. Among the species which inhabit the eastern Pacific, it is most likely that the abundant remains attributable to this genus are from *C. barbatus*.

Paralepididae

Adult barracudina otoliths were present in all three

TABLE 1.—Otoliths and other fish bones identified from the stomach contents of three specimens of *Lagenodelphis hosei* from the eastern tropical Pacific.

Family-species	Stomach #1	Stomach #2	Stomach #3	Total	Rank	Other bones	Calculated length (mm)
Serrivomeridae							
Serrivomer sp.	4	1	3	8			
Argentinidae							
Nansenia sp.	7	6	5	18			
Bathylagidae							
Bathylagus sp.	11	9	16	36			
Opisthoproctidae							
Dolichopteryx spp.	14	9	5	28			
Gonostomatidae							
Gonostoma ¿elongatum?	66	81	37	184	5	dent.	83-225
Sternoptychidae							
Argyropelecus lychnus	68	59	50	177	6	cleith.	40-70
Argyropelecus affinis	61	16	35	112	11		25-35
¿Maurolicus muelleri?							
Photichthyidae							
Ichthyococcus ¿irregularis?	69	49	2	120	9		40-69
Vinciguerria ¿lucetia?	3	1	2	6			
Chauliodontidae							
Chauliodus ¿barbatus?	103	80	55	238	3	dent.	85-200
Unidentified stomiatoids	37	7	0	44			
Unidentified alepocephalids	2	7	5	14			
Paralepididae					13		200-300
Paralepis sp.	1	13	0	14			
Notolepis sp.	8	15	0	23			
Sudis sp.	8	7	26	41			
Unidentified paralepidids	0	4	5	9			
Evermannellidae							
Evermannella ¿ahlstromi?	49	39	31	119	10		35-90
Scopelarchidae							
Scopelarchus guentheri	51	45	31	127	8		80-160+
¿Scopelarchoides nicholsi?	29	29	9	67	15		65-140
¿Rosenblattichthys volucris?							
Scopelosauridae							
Scopelosaurus sp.	0	0	2	2			
Myctophidae							
Benthosema panamense	0	10	0	10			
Bolinichthys ¿longipes?	8	7	10	25			
Diaphus spp.	10	21	12	43			
Diogenichthys laternatus	2	6	4	12			
Hygophum spp.	8	11	5	24			
Lampadena luminosa	80	153	22	255	2		75-105
Lampadena urophaos	2	7	0	9			60-70
Lampadena sp.							
Lampanyctus ¿nobilis?	68	33	2	103	12		70-120
Lampanyctus ¿idostigma?	67	80	61	208	4		60-95
Lampanyctus ¿parvicauda?	6	12	0	18			
Myctophum spp.	12	10	3	25			
Protomyctophum spp.	12	5	38	55			
Symbolophorus ¿evermanni?	5	0	0	5			
Unidentified myctophids	0	29	29	58			
Neoscopelidae							
Scopelengys sp.	0	1	0	1			
Bregmacerotidae							
Bregmaceros sp.	8	8	6	22			
Melanonidae							
Melanonus sp.	45	12	14	71	14		120-220
Melamphaidae							
Melamphaes sp.	14	26	6	46			
Poromitra sp.	0	2	0	2			
Scopelogadus m. bispinosus	23	59	61	143	7		30-65
Diretmidae							
Diretmus argenteus	55	187	121	363	1	operc.	60-285
Anoplogasteridae							
Anoplogaster cornuta	2	6	2	9			
Chiasmodontidae							
Pseudoscopelus sp.	2	9	3	14			
Nomeidae							
Cubiceps cressa	8	2	0	10			
Totals	1,028	1,172	718	2,918			

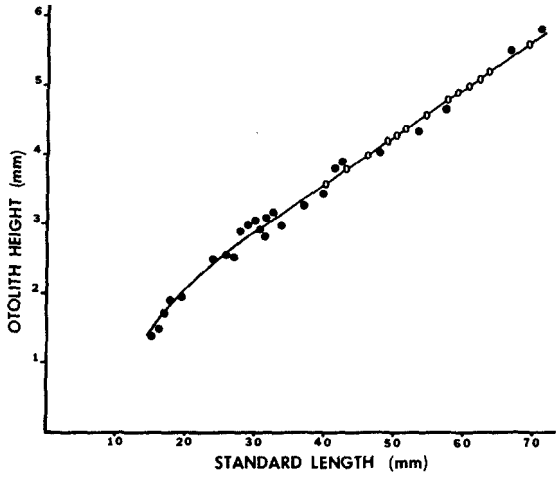

FIGURE 1.—Otolith height vs. standard length curve for *Ichthyococcus irregularis*. Solid circles represent specimens collected by midwater trawls, from which the curve was drawn. Open circles represent otoliths found in the dolphin stomachs, from which the fish sizes were estimated.

dolphin stomachs, and at least three genera are represented. Comparative material of these little-known fishes is rare, since adults are seldom captured (Rofen 1966) but the abundance of their larvae (Ahlstrom 971, 1972) and juveniles suggests that they are quite numerous. These fishes are inadequately sampled by current trawling gear and our knowledge about their ecological relationships is meager. The sizes of the otoliths that we found in the dolphin stomachs indicate that they were feeding on barracudinas of a size range uncommon in trawling collections, but because little comparative material is available, we cannot reliably estimate their lengths except to say that the majority of individuals were probably between 200 and 300 mm long.

Evermannellidae

Evermannellids are also midwater predators whose adult stages and ecology are poorly understood because of a scarcity of material. In contrast to the paralepidids, their larvae are less common in the eastern tropical Pacific (Ahlstrom 1971, 1972), yet they outnumbered barracudinas in the dolphin stomachs. Evermannellids are known to consume vertically migrating micronektonic fishes and squids, but apparently they do not migrate regularly themselves. Their sagittae are quite distinctive, and based on comparative material from the western Pacific, we estimate the sizes of the ingested fish to range from 35 to 90 mm long.

Scopelarchidae

Like the two preceding families, the "pearl-eyes" are mesopelagic predators, adept at eluding trawling gear. Based on the size range of the otoliths, *L. hosei* had been feeding upon large, adult specimens. At least three kinds of scopelarchid otoliths are present in the material; the most numerous are most likely to be from *Scopelarchus guentheri*. We estimate the size range of these individuals to be from 80 to >160 mm, based on an extrapolation from trawl-caught specimens from the western Pacific. This greatly exceeds the known size range of *S. guentheri* (Johnson 1974).

Myctophidae

Lanternfishes of the family Myctophidae are found throughout the world ocean as more than 225 species in a wide variety of niches and depth ranges. Myctophids commonly provide the bulk of the vertically migrating fish fauna which contribute to sound scattering layers. At least 10 genera are represented by the otoliths we found in the dolphin stomachs, but the majority are from *Lampadena* and *Lampanyctus*. In addition to being the most numerous, the otoliths from these two genera were obviously from much larger individuals than those of the less abundant myctophids. We believe that most of the smaller otoliths, many of which are heavily eroded, may have entered the dolphin stomachs secondarily as stomach contents of predatory fishes or squids. Among these smaller myctophids are several vertically migrating types and surface-oriented species (e.g., *Diogenichthys laternatus, Benthosema panamense, Symbolophorus evermanni).*

The *Lampadena* otoliths represent three species: *L. luminosa*, which is by far the most abundant; *L. urophaos*; and a form which has not yet been described (Fitch and Brownell 1968; Nafpaktitis and Paxton 1968). We estimate the size range of the ingested individuals of *L. luminosa* to be 75 to 105 mm and that of *L. urophaos* to be 60 to 70 mm. *Lampanyctus* otoliths are also divisible among three species: *L. nobilis, L. idostigma,* and *L. parvicauda.* Large individuals of these two genera often live as deep as 1,000 m, and either forego the vertical migration patterns typical of other myctophids or are easily able to avoid trawling gear near the surface.

Melamphaidae

Adult melamphaids are generally robust fishes found at mesopelagic depths in all oceans. They are

not generally known to be regular diel vertical migrators, although smaller individuals are usually found at shoaler depths, and there is evidence that the juveniles of at least one species do migrate vertically (Keene 1973). *Scopelogadus mizolepis bispinosus* is the only member of its genus known to inhabit the area where the Fraser's dolphins were captured. Adults are usually found below 400 to 500 m (Ebeling and Weed 1963). Based on the otolith height vs. standard length relationships of *S. beani* and *S. m. mizolepis* from the Atlantic and *S. m. bispinosus* from the eastern Pacific, more than half of the ingested *Scopelogadus* were between 40 and 65 mm long.

Diretmidae

Diretmus argenteus, the most abundant fish in the dolphin stomachs, is another poorly understood mesopelagic species. The sketchily known details of its natural history suggest that it is a deep-dwelling (ca. 400 to 800 m), nonmigrating fish which inhabits broad temperate and tropical areas of the Atlantic, Pacific, and Indian Oceans (Woods and Sonoda 1973). We have found euphausiid shrimp and lanternfish remains in the few *Diretmus* stomachs we have examined. Except for the absence of bioluminescent organs, they resemble the hatchetfishes in external appearance. While many smaller individuals were also present, the characteristic opercular bones and otoliths indicate that the majority of the ingested fishes were between 180 and 285 mm SL.

Crustaceans

In contrast to the relatively large size of many of the ingested fishes, the crustacean remains (Table 2) in the three dolphin stomachs were generally at the upper limit of the size range, which is collected by trawling gear. This suggests that midwater trawls are capable of sampling the full size range of the crustacean species involved but probably not that of the fishes. Like the fishes, however, these shrimps are relatively deep-living species, occupying depths of at least 200 m at night and 400 to 700 m by day.

TABLE 2.—Crustaceans identified from the stomach contents of three specimens of *Lagenodelphis hosei* captured in the eastern tropical Pacific.

Family-Species	Stomach #1	#2	#3	Total
Oplophoridae				
Acanthephyra smithi	10	25	7	42
Acanthephyra curtirostris	0	2	0	2
Notostomus sp. (P) ¿*longirostris*? ¿*pattentissimus*?	2	1	1	4
Systellaspis braveri	0	1	0	1
Systellaspis debilis	0	1	0	1
Pasiphaeidae				
Pasiphaea truncata	3	6	3	12
Sergestidae				
Sergestes (sergia) *inequalis*	0	0	7	7
Sergestes (sergia) sp.	0	1	0	1
Totals	15	37	18	70

Nutrition

In order to estimate the approximate nutritional value of the fish portion of the stomach contents we relied upon caloric values calculated for midwater fishes reported by Childress and Nygaard (1973). They found a range of 57.7 to 165.8 kcal/100 g wet weight for fishes which were morphologically and ecologically similar to the ones eaten by the dolphins. We multiplied these figures by length/weight relationships of from 0.067 to 0.189 g/mm (our data from the same kinds of fishes), the estimated length ranges of the species (based on otolith length vs. standard length relationships), and half the number of otoliths in each stomach. The rough estimates of nutritional value were not less than 5×10^4 cal for the first stomach, 6×10^4 cal for the second, and 4×10^4 cal for the third. We do not know if the otoliths we found are the result of a single day's feeding or that of some other time interval. However, the lack of large numbers of heavily eroded otoliths in the stomachs suggests that their residence time was relatively short.

Similar logic and calculations based on Childress and Nygaard (1974) lead to estimated values of 6×10^3 cal, 2×10^4 cal, and 8×10^2 cal for the crustacean portions of the stomach contents of the three Fraser's dolphins.

The total estimated caloric values for fish and crustaceans ingested by *L. hosei* are within the same order of magnitude as the value that can be calculated from the daily feeding rates of similar cetaceans which have been kept in captivity (Sergeant 1969). While we have not included the nutritional value of the ingested squids in these estimates, the very small proportion of the diet represented by squids suggests that their contribution was negligible.

DISCUSSION

The presence of otoliths in the stomach of a pelagic top carnivore does not necessarily mean that their original owners were ingested directly. Rather it is quite likely that some of these persistent remnants were first consumed by predatory fishes or squids and transferred via their stomachs as they, in turn,

were eaten by *L. hosei.* We take the presence of dentary, cleithral, and opercular bones, however, as evidence of direct ingestion, since these structures are more subject to dissolution by digestive action than are otoliths. The absence of remains from intermediate predators (e.g., scombroids, trichiuroids) suggests that no further trophic-level steps were involved.

The fishes which are most abundantly represented in the three dolphin stomachs can be separated into three groups based on morphological and ecological similarities. *Diretmus, Argyropelecus,* and *Ichthyococcus* are all silvery, deep-bodied, large-eyed forms which inhabit upper mesopelagic depths between 250 and 450 m in the eastern tropical Pacific (Robison 1973) and commonly occur in loose aggregations. They possess gas-filled swim bladders which undoubtedly make excellent echolocation targets. These fishes do not undertake regular, extensive, diel vertical migrations. They eat copepods, euphausiids, and small fishes which are associated with vertically mobile sound scattering layers (SSL).

Lampanyctus, Lampadena, and *Scopelogadus* are dark, thick-bodied fishes with medium-sized eyes and regressed or fat-filled swim bladders as adults. They occupy lower mesopelagic depths between 500 and 750 m (Robison 1973), and while smaller individuals may be significant components of SSL's, specimens of the size range ingested by *Lagenodelphis hosei* are not known to be regular vertical migrators. Their food consists primarily of SSL crustaceans and fishes.

Chauliodus, Gonostoma, Scopelarchus, the evermannellids, and paralepidids are solitary, slender, fast-swimming predators which prey upon micronektonic (ca. 10-60 mm) fishes and crustaceans. These fishes exhibit wide mesopelagic depth ranges between 305 and 1,250 m (Robison 1973), they do not have swim bladders, and they undertake varying degrees of vertical migration which are probably related to the movements of their prey.

Tobayama et al. (1973) found otoliths from *Ichthyococcus elongatus, Polyipnus asteroides* (Sternoptychidae), and *Diaphus elucens*? to be most numerous in the stomach of a specimen of *L. hosei* collected off Japan. These authors concluded that the fishes were eaten at a relatively shallow depth at night. However, it is likely that only *Polyipnus* could have been taken near the surface. The two other species were probably taken no shallower than 300 m, day or night.

Furthermore, the inclusion of Coryphaenoididae in their listing of prey means that deep feeding must have occurred, although the use of this name is misapplied. Coryphaenoididae is an obsolete name for the deep-living fishes of the family Macrouridae (it is unlikely that they meant Coryphaenidae, since the latter fishes do not possess otoliths). It is also possible that the otoliths in question are from *Melanonus*, since the sagittae of these fishes are easily mistaken for those of macrourids. The report of *P. asteroides* by these authors may also be in error, since Baird (1971) stated that this species is known only from the western North Atlantic.

As a collector of midwater fishes, *L. hosei* provides a distinctly different perspective on the composition of the mesopelagic fauna than that obtained by conventional sampling methods. Many of the ingested fishes were as large or larger than the maximum size of specimens that have been collected by nets. In addition, fishes such as *Diretmus,* which are rare in trawl collections, were shown to be surprisingly abundant.

The relative abundances of the fish species found as dolphin food do not reflect the relative abundances of midwater fish species in the eastern tropical Pacific as determined by trawling or larval surveys (Ahlstrom and Counts 1958; Ahlstrom 1971, 1972; Robison 1973). *Vinciguerria lucetia,* which is one of the most common fishes in trawl hauls, is represented in the stomachs by only six otoliths. Only 12 otoliths were found from *Diogenichthys laternatus*, which is the most abundant species in larval surveys.

These small, vertically migratory species have been shown to be important in the diet of the spinner porpoise, *Stenella longirostris*, in the eastern tropical Pacific (Perrin et al. 1973b). The spotted porpoise, *S. attenuata,* which cooccurs with the spinner, was shown to feed primarily on epipelagic fish and squid in the same study. While the number of *L. hosei* stomachs we examined was too small for a valid comparison of feeding with *S. longirostris* and *S. attenuata,* the low degree of similarity between prey fish types suggests that each of the three cetacean species has a different feeding strategy. Additional support for this conclusion comes from the evidence that only *L. hosei* consumes crustaceans (Perrin et al. 1973b).

Based on our understanding of the fishes whose remains we examined, we conclude that the Fraser's dolphins had been feeding selectively, by depth and by prey size. Location and ingestion took place in near or total darkness, regardless of time. Two depth horizons were hunted, each containing a different variety of mesopelagic fishes. The shallowest level was not less than 250 m, and the deepest was not less than about 500 m. The Fraser's dolphins fed with similar success at each depth.

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