

Fish Otoliths in Cetacean Stomachs and Their Importance in Interpreting Feeding Habits¹

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ABSTRACT

The stomachs of 17 cetaceans of seven species (3 Kogia simus, 5 Stenella longirostris, 3 S. graffmani, 2 Lagenorhynchus obliquidens, 2 Delphinus delphis, 1 Lissodelphis borealis, and 1 Phocoena sinus) yielded 18,164 fish otoliths representing over 51 species, 40 genera, and 22 families. Lanternfish (family Myctophidae) otoliths accounted for more than 89% of the total, and they had come from at least 19 species belonging to nine genera. Only two fish species could have been identified if we had not been able to utilize otoliths. To be useful in food studies involving otoliths, cetacean stomachs cannot be placed in formalin solutions, even for short periods.

The kinds and diversity of species preyed upon by several of these cetaceans indicate that they routinely forage in depths of 650-800 ft (200-250 m), and a few such as *Kogia simus* may descend to 1000 ft (300 m) or deeper.

INTRODUCTION

ALTHOUGH many references are available concerning the few entire fishes encountered in cetacean stomachs, or observed being fed upon, no publication presents a thorough or extensive discussion of the piscivorous activities of whales, porpoises, and dolphins. This paucity of information apparently reflects the failure of cetacean researchers to recognize fish otoliths per se, and to realize the usefulness of these objects in food habit studies. Scales, vertebrae, eye lenses, teeth, bits of smelly flesh, and other fish fragmentia making up the soupy, often worm-ridden mixture typically encountered in a cetacean stomach seldom can be identified to species, but teleost otoliths are slow to digest and can furnish accurate qualitative as well as quantitative data. Their ultimate identification, however, requires a fairly extensive comparative collection from the species most likely to be fed upon.

During the past several years, we have routinely examined stomachs of cetaceans that have been stranded, harpooned, or captured incidental to purse-seine and gillnet fisheries, and have saved otoliths, cephalopod beaks,

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and other identifiable remains that we have encountered. The stomachs of seven species (pygmy sperm whale, Kogia simus, Pacific spotted dolphin, Stenella graffmani, spinner dolphin, Stenella longirostris, white-sided dolphin, Lagenorhynchus obliquidens, common dolphin, Delphinus delphis, northern right whale dolphin, Lissodelphis borealis, and Gulf of California harbor porpoise, Phocoena sinus) have yielded otoliths, and all but Phocoena sinus have also contained cephalopod beaks. Although each individual bony fish has three pairs of otoliths (sagittae, asterisci, and lapilli), the asterisci and lapilli usually are extremely small, and even if found, they rarely are used in food studies involving fish ear stones. All otoliths referred to in this report are sagittae unless otherwise noted.

Because formalin will dissolve fish otoliths and render them unrecognizable in a matter of days, stomachs should be examined as soon as possible, or they should be frozen until they can be worked on. Preservation of stomachs in alcohol is satisfactory for a short period, but subsequent separation of otoliths and other identifiable remains is much more difficult and time consuming than when working with fresh material. Otoliths can be preserved dry or in alcohol, but first they should be rinsed in water to remove extraneous amorphic material. When making comparisons, a binocular microscope at 6–10 magnifications is almost a necessity.

Although otoliths are the most important tools available for identifying teleost fishes eaten by whales, porpoises, and dolphins, only 12 reports have noted their occurrence in cetacean stomachs since the first was published in 1903.

Thomas Scott (1903) opened the door more than 65 years ago for researchers to use teleost otoliths in determining food habits of fish-eating cetaceans. He identified and illustrated 280 gadid (Gadidae), sand lance (Ammodytes sp.), and other earstones found in the stomach of a common porpoise, Phocoena phocoena, captured off the coast of Scotland. In spite of Scott's pioneer work, we know of only 12 additional published reports of otolith occurrence in cetacean digestive tracts, and 20 years were to pass before the first of these appeared (Schmidt, 1923). In that year, Johannes Schmidt, in a letter to the editor of Nature, reported having sent to the British Museum of Natural History 15,191 sagittae that he had removed from the stomach of a "common long-nosed porpoise," Delphinus delphis, harpooned off southern Spain in the Mediterranean during a research cruise on the Thor in June 1910. G. A. Frost (1924), after seeing Schmidt's note, examined 4338 of these otoliths and assigned them to six species in three families (4324 Myctophidae, 10 Macrouridae, and 4 Scomberesocidae). His outline drawings are crude, but there is no question that he correctly identified to family the four kinds of lanternfishes and possibly the scomberesocid, but his "Macrurus" very likely is a barracudina, family Paralepididae.

Vladykov (1946) was the next to note fish otoliths in cetacean stomachs, reporting more than 1000 cod (Gadus and Microgadus), smelt (Mallotus), and other sagittae from the digestive tracts of white whales, Delphinapterus

leucas, taken in the Saint Lawrence River, Canada. In 1948, Scheffer and Slipp noted "otoliths and bones of fish" in the stomach of a pygmy sperm whale, Kogia breviceps, from the coast of Washington. They questionably identified a partially digested fish as Trichodon, but were unable to assign names to the 21 otoliths, none of which appears to have been saved (V. B. Scheffer, personal communication).

The remaining eight reports we were able to find that mentioned otoliths in cetacean stomachs have been published during the last 12 years. Three of these (Cadenat, 1959a, b; and Cadenat and Doutre, 1959) concern *Tursiops truncatus*, *Delphinus delphis*, and *Stenella longirostris* from off the west coast of Africa, whereas the other five publications (Brown and Norris, 1956; Norris and Prescott, 1961; Best, 1963; Daugherty, 1965; and Fiscus and Niggol, 1965) pertain to dolphins from the eastern north Pacific, primarily off California.

The African Tursiops stomach (Cadenat, 1959a) contained several partially digested snake mackerel, Gempylus serpens, and numerous otoliths from at least four kinds of deep-living macrourids and morids (Moridae), but the earstones noted in the stomachs of 10 of 25 D. delphis (Cadenat, 1959b) and 4 of 4 S. longirostris (Cadenat and Doutre, 1959) were neither enumerated nor identified, except for the notation that a large percentage of the otoliths in the Stenella stomachs appeared to be "a la famille des Scopelidae" [= Myctophidae].

The large, pointed, first stomach chamber of a Lagenorhynchus obliquidens from off California was "filled with partially digested anchovies, fish bones, otoliths, fish eye lenses and one blanched but otherwise undigested squid . . . " (Brown and Norris, 1956). Neither these otoliths nor the "unidentified fish otoliths" noted in the stomach of a Delphinus delphis (Fiscus and Niggol, 1965) are available for examination. A Tursiops gilli from southern California had eaten mostly shallow-water bottom-living forms as evidenced by 102 otoliths from 8 species (Norris and Prescott, 1961). On the other hand, the stomach of a Phocoenoides dalli reported by these same authors yielded 30 otoliths from two species (hake, Merluccius productus, and anchovies, Engraulis mordax) that it very likely had consumed more than 400 ft (120 m) beneath the surface. Finally, Best (1963) in discussing Merluccius productus, stated that "hake otoliths have been identified among the stomach contents of... Lagenorhynchus obliquidens and Phocoenoides dalli," and Daugherty (1965) reported that otoliths often are found in stomachs of eastern Pacific cetaceans mentioning particularly Stenella, Tursiops, Lagenorhynchus, and Phocoenoides.

FISHES EATEN BY KOGIA SIMUS

Brownell examined the stomachs of three pygmy sperm whales harpooned offshore from Taiji, Wakayama, Japan in July 1967, and found 153 otoliths that had come from a minimum of 92 fish representing 18 species in seven families (Table I, Fig. 1). Unfortunately we lack a good comparative collection of otoliths from Japanese fishes so we cannot identify many of these sagittae

TABLE I. Numbers and kinds of fish otoliths found in stomachs of three Kogia simus captured off Taiji, Japan, during July 1967.

	Whale identity and no. of otoliths						
Kind of fishes eaten	RLB 392*	RLB 397a	RLB 400a				
Argentinidae	enggarater an airminina an an airminina <u>filipa a ann airminina an airminina airmi</u>						
Glossanodon sp.	3	5	2				
Nansenia sp.		2	2				
Congridae		-	-				
Congrid		$\dot{2}$					
Gonostomatidae		~					
Gonostomatid			3				
Ichthyococcus sp.	10		7				
Macrouridae							
Coelorhynchus?			4				
Macrourid #1	3	1	7				
Macrourid #2		14	9				
Moridae							
Morid #1	3	14					
Morid #2		1					
Morid #3		3					
Myctophidae		•					
Diaphus #1			1				
Diaphus #2			2				
Hygophum?			1				
Lampadena #1	19	12	14				
Lampadena #2			2				
Symbolophorus sp.		1	3				
Sternoptychidae							
Polyipnus sp.		2	1				
Total .		57	58				

aR. L. Brownwell field numbers.

to genus and species. Cephalopod beaks and crustacean remains also were present in these stomachs.

The 38 otoliths (5 species) found in one stomach (RLB 392) were from at least 22 fish (10 Lampadena, 5 Ichthyococcus, 3 morids, 2 Glossanodon, and 2 macrourids), whereas the 57 and 58 otoliths in the other two stomachs represented a minimum of 37 (11 species) and 33 fish (14 species), respectively. Only 3 of the 18 species (Lampadena, Glossanodon, and a macrourid) had been eaten by all three Kogia, but these three species contributed 66 of the 153 otoliths. Most of the otoliths were in relatively good condition, but even those considerably eroded from digestive action were readily identified. A family-by-family discussion of the 153 otoliths in these three stomachs (Table I) follows.

Argentinidae. — Fourteen of the 153 otoliths were from two genera of argentines, Glossanodon and Nansenia, representing a minimum of eight fish. All of these otoliths were from large adults, but Glossanodon probably never exceeds 10 inches (250 mm) and 2 oz (60 g), whereas Nansenia is slightly smaller. Members of these two genera seldom approach within 650 ft (200 m) of the surface.

Congridae. — A pair of sagittae very similar to those of Ariosoma were found in one stomach. Congrids such as Ariosoma often inhabit the scattering layer and probably migrate toward the surface at night, possibly even reaching the surface. Although these sagittae were from an adult eel, it probably would have been only 10–12 inches (250–300 mm) long.

Gonostomatidae. — The 20 gonostomatid otoliths we found in these stomachs were from a minimum of 11 fish: 9 Ichthyococcus, and 2 unknown gonostomatids, possibly a close relative of Vinciguerria. Although all were from large adults, the unknown gonostomatids probably were less than 2 inches (50 mm) long, but several of the Ichthyococcus sagittae had come from very large individuals, probably exceeding 5 inches (125 mm). Gonostomatids usually are deeper than 1000 ft (300 m) during daylight hours, but move closer to the surface at night. Vinciguerria often reaches the surface at night, but Ichthyococcus usually remains 650-800 ft (200-250 m) down.

Macrouridae. — Macrourids usually inhabit muddy bottom areas at depths of 1500-5000 ft (450-1500 m), but some may be found as shallow as 650 ft (200 m) and others deeper than 10,000 (3000 m). Most species never leave the bottom except to move a few feet off during feeding activities. The 38 macrourid otoliths were from three species, and represented at least 22 individuals. All three Kogia had fed on these bottom-dwelling forms. Our use of the name Coelorhynchus for four of the macrourid otoliths is questionable because of the state of digestion. Most of the macrourid otoliths probably came from 10-14-inch (250-350 mm) long fish weighing as much as $\frac{1}{4}$ 1b (100-225 g) each.

Moridae. — The 21 morid otoliths from at least 16 individuals also represented three species of bottom-dwelling fish. These likely were captured at depths exceeding 650 ft (200 m) but shallower than 1500 (450 m). They probably were slightly smaller than the macrourids.

Myctophidae. — Lanternfish otoliths comprised the greatest number (55) and kinds (6) found in these stomachs, but only one kind (45 sagittae from an undescribed species of Lampadena) was of major importance. These 45 otoliths represented a minimum of 25 lanternfish, and their sizes suggested that they had come from individuals that were 8–10 inches (200–250 mm) long. Differences between these otoliths and those of the known species of Lampadena were pointed out by Nafpaktitis and Paxton (1968) in a recent review of the genus. The other 10 lanternfish otoliths represented five species apparently belonging to four genera (Table I, Fig. 1). All but one of these were in the same stomach. During daylight hours members of these four genera

(Lampadena, Symbolophorus, Diaphus, and Hygophum) are found at a depth of about 1000 ft (300 m), but at night all are known to migrate into surface waters. A 4-inch (100-mm) fish would be large for an adult of most of these.

Sternoptychidae. — Three Polyipnus otoliths were the only representatives of this family found in these stomachs. Polyipnus seldom exceeds 2 inches (50 mm) when full grown, and usually remains 650-800 ft (200-250 m) beneath the surface.

FISHES EATEN BY STENELLA GRAFFMANI AND S. LONGIROSTRIS

Stenella longirostris and S. graffmani occur sympatrically in the eastern tropical Pacific, and frequently school together, often in the company of yellowfin tuna, Thunnus albacares. During 1967 and 1968, we found otoliths in the stomachs of five S. longirostris and one S. graffmani that had been netted with tuna during daylight hours in the eastern Pacific between about 12° and 20°N lat. Previous to 1967, Fitch had identified several thousand otoliths from the stomachs of two S. graffmani netted in the same general area during 1959 and 1963 (Table II, Fig. 2). The stomachs of these eight dolphins also contained cephalopod beaks, so there is a slight possibility that some of the otoliths had been transferred from the squid and/or octopus stomachs, particularly those of such tiny fishes as Vinciguerria, Diogenichthys, and Bregmaceros.

Although the five S. longirostris had fed upon 6-15 kinds of fish, two kinds of myctophids, Benthosema panamense and Lampanyctus parvicauda, comprised over 50% of their piscivorous diet, both individually and as a group. Benthosema panamense was also important to S. graffmani, being the only species noted in one of the three stomachs and contributing all but 3 of the 1238 otoliths found in a second. This tropical lanternfish normally undertakes a diurnal migration, but sometimes dense "balls" (schools) of Benthosema remain at the surface during daylight hours, where they have been observed under attack by birds, fish, and dolphins. Even though both dolphins had fed heavily upon Benthosema, we believe that S. longirostris had captured its prey several hundred feet down, whereas S. graffmani had fed at or near the surface.

A family-by-family discussion of the several thousand otoliths found in Stenella stomachs (Table II) follows.

Bathylagidae. — The Bathylagus otoliths in the stomachs of Stenella longirostris may have been those of B. pacificus, a species that lives more than 650 ft (200 m) beneath the surface and does not undertake a diurnal migration. They were not from B. stilbius, one of the commonest blacksmelt in that area and a known vertical migrator. None of the 15 otoliths in the three stomachs was from a large fish, perhaps 4 or 5 inches (100–125 mm) being about maximum.

Bregmacerotidae. — Only the stomachs of S. longirostris contained otoliths of Bregmaceros bathymaster, even though the species is known to migrate from

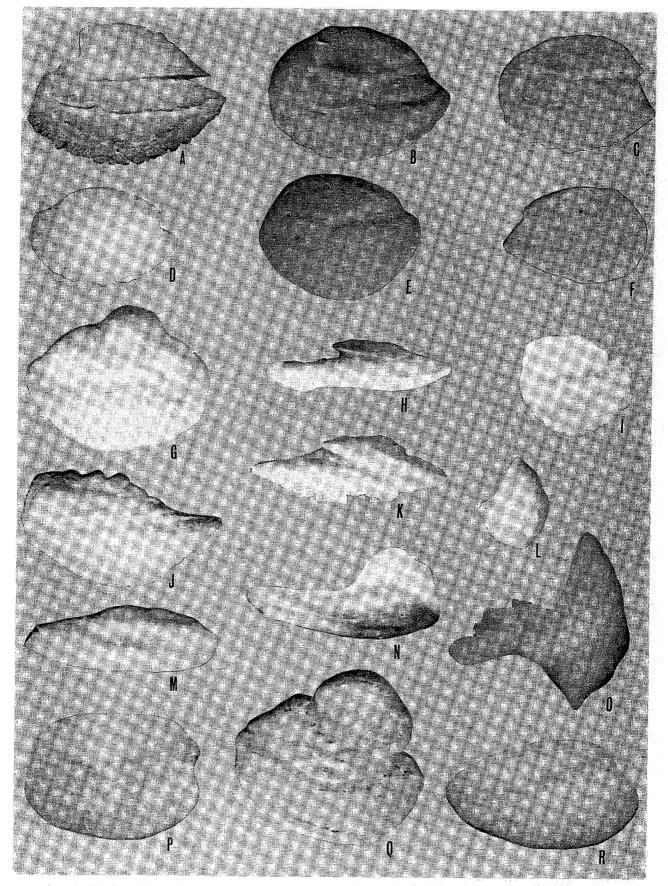


Fig. 1. Sagittae (inner faces) of 18 species of fish found in stomachs of Kogia simus. For each illustrated otolith, information on whether it is left (l) or right (r), length (mm), and notations, if it is atypical are: (A) Lampadena #1, l, 9.2; (B) Symbolophorus sp., l, 4.2; (C) Diaphus #1, l, 2.6; (D) Lampadena #2, l, 3.2; (E) Hygophum?, l, 2.7, badly digested; (F) Diaphus #2, r, 2.4, badly digested; (G) congrid, r, 5.6; (H) morid #1, r, 7.3; (I) gonostomatid, l, 1.0; (J) Glossanodon sp., l, 7.4; (K) morid #2, r, 6.7; (L) Polyipnus sp., r, 1.8, rostrum missing; (M) Nansenia sp., r, 5.2, badly digested, rostrum tip missing; (N) morid #3, r, 7.2, badly digested; (O) Ichthyococcus sp., r, 5.7; (P) macrourid #1, l, 4.0; (Q) macrourid #2, l, 5.0; (R) Coelorhynchus?, l, 4.5, badly digested.

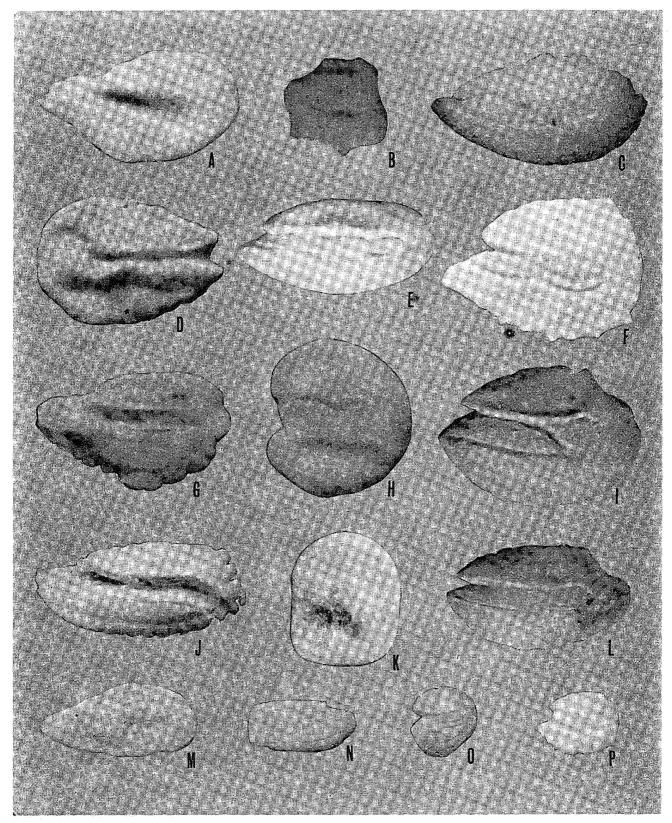


Fig. 2. Sagittae (all inner faces except Benthalbella) of 16 species of fish found in stomachs of Stenella longirostris and S. graffmani. For each illustrated otolith, information on whether it is left (l) or right (r), length (mm), and notations if it is atypical are: (A) Bathylagus sp., r, 1.7, rostrum tip missing; (B) Bregmaceros bathymaster, l, 1.5; (C) Oxyporhamphus micropterus, r, 5.4; (D) gonostomatid, l, 1.4; (E) Lampanyctus parvicauda, r, 4.1; (F) Diaphus sp., r, 3.0; (G) Vinciguerria lucetia, r, 1.5; (H) Diogenichthys laternatum, r, 1.1; (I) Symbolophorus evermanni, r, 4.1; (J) centrolophid?, r, 4.6; (K) Lampanyctus idostigma, r, 0.9; (L) Myctophum aurolaternatum, r, 4.0; (M) unidentified from S. longirostris M-33-67, r, 2.4; (N) Benthalbella sp., r, 2.6, outer face; (O) Hygophum sp., r, 1.7; (P) Benthosema panamense, r, 2.0.

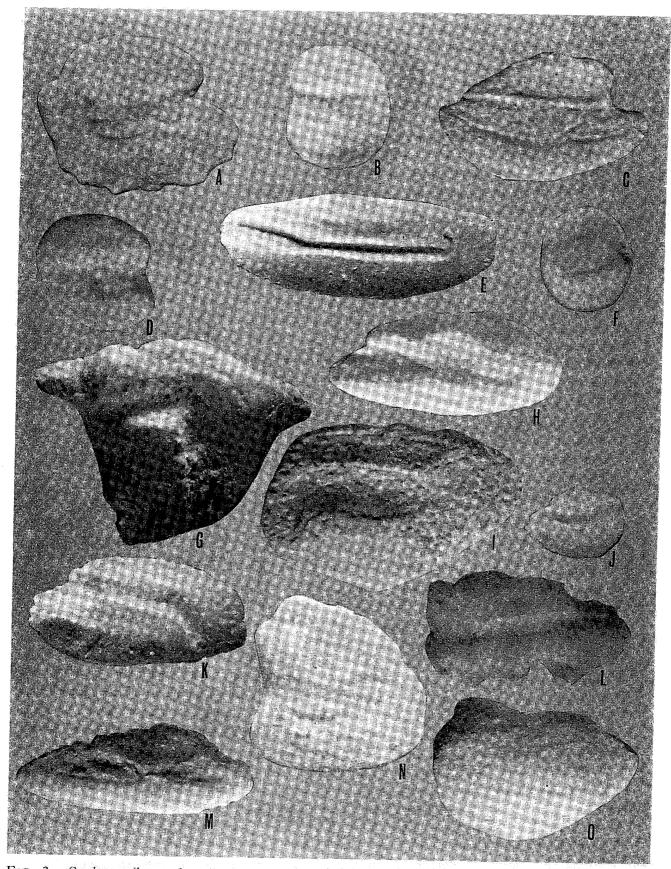


FIG. 3. Sagittae (inner faces) of 15 species of fish found in stomachs of Lissodelphis borealis (A through F), Phocoena sinus (G and K), Lagenorhynchus obliquidens (H and I), and Delphinus delphis (J, I, M, and O). For each illustrated otolith, information on whether it is left (l) or right (r), length (mm), and notations if it is atypical are: (A) Diaphus sp. near theta, l, 2.1; (B) Lampanyctus sp. near ritteri, r, 1.1; (C) Lampadena urophaos, r, 6.4; (D) Triphoturus mexicanus, l, 1.3, badly digested; (E) Icichthys lockingtoni, r, 9.1; (F) Scopelogadus bispinosus, l, 1.0; (G) Bairdiella icistius, r, 8.7; (H) Engraulis mordax, r, 3.5, badly digested; (I) Seriphus politus, l, 7.5, lumpy from formalin preservation; (J) Bathylagus sp., r, 1.1, rostrum tip missing; (K) Orthopristis reddingi, r, 6.7; (L) Argentina sialis, l, 2.7, ventral margin broken; (M) Merluccius productus, l, 7.2; (N) Porichthys notatus, r, 2.9; (O) Otophidium taylori, r, 4.4.

TABLE II. Numbers and kinds of fish otoliths found in the stomachs of two species of Stenella from the eastern tropical Pacific.^a

Kinds of fishes eaten	No. of otoliths							
	Stenella longirostris				Sten	Stenella graffmani		
	1	2	3	4	5	1	2	3
Bathylagidae	Militaria de des Grando							*
Bathylagus sp.	1	12			2			* .
Bregmacerotidae								an in the second
Bregmaceros bathymaster	11	76	6	89	61			
Centrolophidae?								
Centrolophid?	2	16			5	45		
Exocoetidae								nagata gara
Oxyporhamphus micropterus						29		
Gonostomatidae				•				. 1929 770
Gonostomatid		7						
Vinciguerria lucetia	256	126	3	435	497		3	
Myctophidae								
Benthosema panamense	1	241	234	6147	983	4	1235	2357
Diaphus sp.	1							
Diogenichthys laternatus	949	97	60	302	15	4		
Hygophum sp.	1	35		4	1			
Lampanyctus idostigma	13	1			12			
Lampanyctus parvicauda	1916	465	30	27	282			
Myctophum aurolaternatum	2	107		7	106	8		
Symbolophorus evermanni	3	13						
Unidentifiable myctophids	78	54	13					
Paralepididae								
Stemonosudis?					30			
Scopelarchidae					e de la companya de La companya de la co			
Benthalbella sp.		1						
Unidentified		2			1	1		
Total	3234	1253	346	7011	1995	91	1238	2357

*Capture data (all specimens netted with tuna; M-numbers are accession numbers of Cetacean Research Laboratory, Little Company of Mary Hospital, Torrance, Calif.). Stenella longirostris: (1) M-57-66, about 350 miles (>550 km) SW of Manzanillo, Mex., in early 1966; (2) M-33-67, same general area as (1), but March 1967; (3) M-20-68, 12°N lat, 92°W long, February 21, 1968; (4) M-60-68, 13°N lat, 99°22′W long, April 16, 1968; (5) M-70-68, ca. 350 miles (±550 km) SW of Acapulco, Mex., April 1968. Stenella graffmani: (1) M-32-67, ca. 350 miles (>550 km) SW of Manzanillo, Mex., March 1967; (2) 150 miles off Acapulco, Mex., November 1959; (3) off Costa Rica, January 1963, Jules Crane data.

the depths into surface waters at night. A full-grown B. bathymaster would hardly exceed 3 inches (75 mm) and 1 g.

Centrolophidae? — The most abundant otoliths in the stomach of S. graffmani M-32-67 were those of an unknown stromateoid. These otoliths (Fig. 2J) compare favorably with those of Seriolella, but according to Haedrich (1967), Seriolella "is restricted to cool temperate waters of the Southern

Hemisphere." We believe that they represent a species of centrolophid, but to our knowledge no member of the Centrolophidae is known from waters off tropical west Mexico. In any event, stromateoids (including Centrolophidae) are noted for their association as juveniles with floating debris, jellyfishes, and similar items, so the fishes these came from probably were eaten at or near the surface. Three of the *S. longirostris* stomachs we examined also contained otoliths of these stromateoids, but in much smaller numbers (Table II).

Exocoetidae. — Twenty-nine otoliths in the stomach of S. graffmani M-32-67 were from the shortwing flyingfish, Oxyporhamphus micropterus. This tropical species is strictly an inhabitant of surface waters. A really large individual might attain a length of 8 inches (200 mm) and a weight of 2 ounces (55 g).

Gonostomatidae. — Otoliths of Vinciguerria lucetia were relatively abundant in four of the five stomachs of Stenella longirostris, but only three were present in the S. graffmani stomachs. Vinciguerria lucetia inhabits depths of 650 to 1000 ft (200–300 m) during daytime, but migrates toward the surface at night and often can be dipnetted from under a bright light suspended above the surface. At maximum size they are just over 2 inches (50 mm) long and weigh but a few grams. Seven otoliths in one S. longirostris stomach (M-33-67, Fig. 2D) appear to be those of a gonostomatid but our comparative collection of gonostomatid otoliths was small, so we were unable to make a positive identification.

Myctophidae. — At least eight species of lanternfish had been fed upon by S. longirostris and three by S. graffmani. Six of these, Symbolophorus evermanni, Myctophum aurolaternatum, Diogenichthys laternatus, Benthosema panamense, Diaphus, and Hygophum, are found in surface waters at night, but the two species of Lampanyctus identified from the S. longirostris stomachs are deep (± 400 m) during daylight hours and usually remain fairly deep (± 200 m) at night. Three to 5 inches (75–125 mm) would be about maximum length for all of the myctophids except Diogenichthys, which seldom attains 2 inches when full grown.

Paralepididae. — The 30 barracudina otoliths in the stomach of S. longirostris M-71-68 are difficult to assign to a genus because of a shortage of comparative material. They are not from Paralepis, Notolepis, Sudis, or Lestidium, and several other genera are unknown in the eastern Pacific. Barracudinas are most abundant at depths of 1000-2500 ft (300-800 m), but range both above and below these depths. Adults of Stemonosudis are unknown in collections, but the otoliths in this dolphin stomach unquestionably were from adults. Based upon otoliths from other family members, these fish could have been 10-12 inches long (25-30 mm).

Scopelarchidae. — One otolith (from S. longirostris) was from a 4- to 5-inch (100-125 mm) Benthalbella, a fish that usually lives 800-1000 ft (250-300 m) down during daylight hours. Young individuals migrate into surface waters at night, but the habits of adults are unknown.

FISHES EATEN BY LAGENORHYNCHUS OBLIQUIDENS

We examined the stomachs of only two *L. obliquidens* that contained otoliths. One, a 5-ft 11-inch (179.5-cm) long female weighing 121 lb (55 kg), was found stranded at Long Beach, California, on August 21, 1967. Its stomach was gorged with partially digested fish (Pacific hake) and cephalopod remains (William Walker, personal communication), and yielded 57 otoliths (Table III, Fig. 3). Of the 43 hake otoliths, 29 were from fish that would have been

Table III. Numbers and kinds of otoliths found in the stomachs of Lagenorhynchus obliquidens, Delphinus delphis, and Lissodelphis borealis from southern California.

Kinds of fishes eaten	No. of otoliths							
	Lagenor obliqı	hynchus uidens	Delphinus delphis					
	M-31-63ª	M-26-67ª	M-02-68ª	RLB 69b	Lissodelphis borealis			
Argentinidae								
Argentina sialis				3				
Bathylagidae								
Bathylagus sp.				1	•			
Batrachoididae								
Porichthys notatus				3				
Centrolophidae								
Icichthys lockingtoni					2			
Engraulidae								
Engraulis mordax	4	12	127	14				
Melamphaidae								
Scopelogadus bispinosus					1			
Merlucciidae								
Merluccius productus	3	43		97	2			
Myctophidae								
Diaphus cf. theta			1		23			
Lampadena urophaos					7			
Lampanyctus cf. ritteri					5			
Stenobrachius leucopsarus			3					
Triphoturus mexicanus					5			
Unidentifiable myctophids					107			
Ophidiidae								
Otophidium taylori				1				
Sciaenidae								
Seriphus politus		2						
Scomberesocidae								
Cololabis saira			2					
Total	7	57	133	119	152			

^aAccession number of Cetacean Research Laboratory, Little Company of Mary Hospital, Torrance, Calif.

bR. L. Brownell field number.

16-20 inches (400-500 mm) long, but the other 14 had come from smaller individuals (±8 inches or 200 mm long). These hake almost certainly had to be caught at a depth greater than 400 ft (120 m), and the anchovies may have been also, since all 12 otoliths represented large *Engraulis* (±7 inches or 180 mm), a size that typically inhabits depths of 400-650 ft (120-200 m). *Seriphus* is known only from relatively shallow (±30 m) inshore waters.

The other L. obliquidens (M-31-63) had stranded itself alive near the Santa Monica pier on August 29, 1963. In addition to the three Merluccius and four Engraulis otoliths, its stomach contained some cephalopod beaks and the fused pharyngeal tooth patch from a white seaperch, Phanerodon furcatus. Phanerodon is known only from relatively shallow (± 30 m) inshore waters, but the hake and anchovies probably had been caught at a depth greater than 120 m.

FISHES EATEN BY DELPHINUS DELPHIS

Only two *D. delphis* stomachs (RLB 69, which was captured 4 miles off the San Pedro lighthouse between January and April 1964, and M-02-68, which was stranded alive at Zuma Beach on January 28, 1968) of many that Brownell examined contained otoliths. The 119 sagittae in the stomach of the 1964 dolphin represented a minimum of 63 fish belonging to six species in six families (Table III, Fig. 3). All of these fish could have been caught at or near the bottom in 650-800 ft (200-250 m) of water. None, including the hake, was very large, possibly 10 inches (250 mm) long, and weighing an ounce or so (±30 g). Five of these (*Argentina*, *Bathylagus*, *Merluccius*, *Otophidium*, and *Porichthys*) had not been reported among *D. delphis* food items previously.

The stomach of the Zuma Beach *Delphinus* contained 133 otoliths representing a minimum of 72 fish belonging to four species in three families and four genera. The Pacific saury, *Cololabis saira*, had to be taken at the surface, but the two lanternfishes and the anchovies probably were captured at least 600 ft (200 m) beneath the surface.

FISHES EATEN BY LISSODELPHIS BOREALIS

On November 8, 1967, an adult *L. borealis* was stranded near Imperial Beach, California, and Carl L. Hubbs, Scripps Institution of Oceanography, who examined the specimen, sent us 152 otoliths he washed out of the folds of its stomach along with "a multitude of squid beaks and lenses" (Carl L. Hubbs, personal communication). Most of these otoliths were digested considerably, but this did not preclude their identification to family, and in many cases to genus and species. Lanternfish otoliths representing at least four species (Table III, Fig. 3) comprised nearly 97% of the 152 sagittae. Less than a dozen of the 107 badly eroded otoliths that we identified only as myctophids (Table III) were of a type peculiar to *Lampanyctus*, whereas the others resembled *Diaphus* in size and configuration, but their state of digestion did not permit positive generic determinations. Possibly all seven species

known to be represented had been captured and eaten at least 650 ft (200 m) beneath the surface, although $5\frac{1}{2}$ -inch (135 mm) *Icichthys lockingtoni* are most abundant in the uppermost 150 ft (45 m).

FISHES EATEN BY PHOCOENA SINUS

The Gulf of California harbor porpoise was first described by Norris and McFarland in 1958, and to date only two entire specimens appear to have been collected (R. L. Brownell, unpublished data). Nothing has been reported in the literature on their food habits or other aspects of biology, and little is known of their behavior and distribution (Norris and Prescott, 1961). The stomach of one of the two complete specimens, an adult female (RLB 338), was examined on the beach about 20 km north of San Felipe, Baja California Norte, Mexico, on April 2, 1967. It contained 18 otoliths in rather poor condition, yet sufficient characteristics remained that the otoliths could be identified as having come from two species of shallow-water bottom-dwelling fishes. Thirteen of the otoliths (seven left and six right) were from the grunt Orthopristis reddingi, and five (three right and two left) were from the croaker Bairdiella icistius (Fig. 3). Both of these fishes are abundant throughout the upper Gulf of California; neither attains any great size, Orthopristis reaching perhaps 8 inches (200 mm), and Bairdiella possibly 10 (250 mm).

GENERAL DISCUSSION

From 18,164 otoliths found in the stomachs of 17 cetaceans, we determined that 18 kinds of fish had been eaten by Kogia simus, 16 kinds by Stenella longirostris, 9 by Delphinus delphis, 7 by Stenella graffmani, 7 by Lissodelphis borealis, 3 by Lagenorhynchus obliquidens, and 2 by Phocoena sinus. In addition we speculated on the sizes of fishes preyed upon as well as probable depth of feeding. On the basis of conventional recognition characters, only two fish species could have been identified: Oxyporhamphus micropterus in Stenella graffmani M-32-67, and Merluccius productus in Lagenorhynchus M-26-67.

Numerous well-documented accounts show that there is a direct relationship between otolith length and fish length for each species (Sastry, 1936; Fairbridge, 1951; Southward, 1962; Southward and Chapman, 1965; and many others). Thus, if one has accumulated this information for a given prey species, and undigested otoliths of that species have been found in the stomach of a predator, the lengths of the fishes eaten can be estimated reliably. Similarly, a reliable estimate can be obtained of the poundages ingested by utilizing a weight-length curve for the species in question.

There has been much speculation on whether the otoliths found in the folds of cetacean stomachs represent the remains of a single meal, or are an accumulation from several days of feeding. In our opinion, not even the 15,191 otoliths (representing more than 7596 fishes) reported by Schmidt (1923) represented a "full" meal for the *Delphinus* that they came from. We base this conclusion on the fact that it takes from 7000 to 10,000 adult *Benthosema*

panamense to fill a gallon jar, which is a much smaller volume than a distended dolphin stomach. Thousands of *B. panamense* otoliths were found in the *Stenella* stomachs we investigated, and these lanternfishes are similar in size to the myctophids eaten by Schmidt's *Delphinus*.

In these days of extensive porpoise research, it would be a simple matter to design experiments that would produce answers as to how long cetaceans retain fish otoliths in their stomachs. Once a rate of digestion has been determined, details regarding periodicity of feeding could be worked out with a high degree of accuracy.

We feel certain that three of the cetaceans we investigated (Kogia simus, Stenella longirostris, and Lissodelphis borealis) had been feeding 800 ft (250 m) or more beneath the surface, and that two others (Lagenorhynchus obliquidens and Delphinus delphis) had descended to depths exceeding 400 ft (120 m). On the other hand, Stenella graffmani and Phocoena sinus appear to have fed within 100 ft (30 m) of the surface, and probably even shallower.

At least 8 of the 16 species fed upon by Stenella longirostris are known to ascend into (or nearly into) surface waters at night, but we doubt if the spinner dolphin did much foraging for food in these upper water layers. Trawl nets towed in these surface waters at night usually yield rather poor catches of myctophids and other mesopelagic vertical migrators, an indication that population densities are too sparse to supply either the diversity of species or numbers of individuals that made up the spinner's food. Similar logic applies to Lissodelphis, and the bottom-dwelling morid and macrourid remains found in the Kogia simus stomachs are proof of its deep-diving ability.

We have been impressed with the apparent dependency of the smaller cetaceans on mesopelagic fishes, especially myctophids, which are generally conceded as being one of the most widespread and abundant, yet least utilized, fish families in the world oceans. If the day ever arrives that man finds it economically feasible to harvest fishes from the scattering layers, uncontrolled exploitation could have a disastrous effect on our dolphin, porpoise, and whale populations.

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REFERENCES

- Best, E. A. 1963. Contribution to the biology of the Pacific hake, Merluccius productus (Ayres). Cal. Coop. Ocean. Fish. Invest. Rept., 9: 51-56.
- Brown, David H., and Kenneth S. Norris. 1956. Observations of captive and wild cetaceans. J. Mammal., 37(3): 311-326.
- CADENAT, J. 1959a. Notes sur les Delphinidés ouest-africains. VI. Le gros Dauphin gris (Tursiops truncatus), est-il capable de faire des plongées profondes? Bull. Inst. Franc. Afrique Noire, Ser. A, 21(3): 1137-1141.

 1959b. Rapport sur les petits Cétacés ouest-africains. Résultats des recherches entreprises sur ces animaux jusqu'au mois de mars 1959. Ibid., 21(4): 1367-1440.
- CADENAT, J., AND M. DOUTRE. 1959. Notes sur les Delphinidés ouest-africains. V. Sur un *Prodelphinus* à long bec capturé au large des côtes du Sénégal, *Prodelphinus longirostris* (Gray) 1828 Ibid., 21(2): 777-798.
- DAUGHERTY, ANITA E. 1965. Marine mammals of California. Calif. Dept. Fish. Game Sacramento, Calif. 87 p.
- FAIRBRIDGE, W. S. 1951. The New South Wales tiger flathead, Neoplatycephalus macrodon (Ogilby). I. Biology and age determinations. Australian J. Marine Freshwater Res., 2(2): 117-178.
- Fiscus, Clifford H., and Karl Niggol. 1965. Observation of cetaceans off California, Oregon, and Washington. U.S. Fish Wildlife Serv., Spec. Sci. Rept. Fish., 498: 27 p.
- Frost, G. A. 1924. Fish otoliths from the stomach of a porpoise. Nature, 113(2835): 310.
- HAEDRICH, RICHARD L. 1967. The stromateoid fishes: systematics and a classification. Bull. Museum Comp. Zool., 135(2): 31-139.
- NAFPAKTITIS, BASIL, AND JOHN PAXTON. 1968. Review of the lanternfish genus Lampadena with a description of a new species. Los Angeles Co. Museum, Contrib. Sci., 139: 29 p.
- NORRIS, KENNETH S., AND W. N. McFarland. 1958. A new harbor porpoise of the genus *Phocoena* from the Gulf of California. J. Mammal., 39(1): 22-39.
- Norris, Kenneth S., and John H. Prescott. 1961. Observations on Pacific cetaceans of California and Mexican waters. Univ. Calif. Publ. Zool., 63(4): 291-402.
- Sastry, N.S. 1936. The relation of the age to the length of a fish and the length of its otoliths. J. Madras Univ., 8: 200-207.
- Scheffer, Victor B., and John W. Slipp. 1948. The whales and dolphins of Washington State with a key to the cetaceans of the west coast of North America. Am. Midland Naturalist, 39(2): 257-337.
- SCHMIDT, JOHANNES. 1923. Consumption of fish by porpoises. Nature, 112(2825): 902.
- Scott, Thomas. 1903. Some further observations on the food of fishes, with a note on the food observed in the stomach of a common porpoise. Twenty-first Ann. Rept. (1902) Fish. Bd. Scotland, Pt. III, Sci. Invest. p. 218–227.

- Southward, G. Morris. 1962. A method of calculating body lengths from otolith measurements for Pacific halibut and its application to Portlock-Albatross grounds data between 1935 and 1957. J. Fish. Res. Bd. Canada, 19(2): 339-362.
- Southward, G. Morris, and D. G. Chapman. 1965. Utilization of Pacific halibut stocks: study of Bertalanffy's growth equation. Rept. Intern. Pacific Halibut Comm., 39: 1-33.
- VLADYKOV, VADIM D. 1946. Etudes sur les mammifères aquatiques. IV. Nourriture de Marsouin Blanc ou Béluga (*Delphinapterus leucas*) du fleuve Saint-Laurent. Contrib. Québec Dépt. Pèch., 17: 157 p.

