In this paper we discuss an hypothesis. We marshall scattered supportive evidence, outline its problems, and explore its ramifications and suggest tests. We do not prove it.

The hypothesis is that some odontocete cetaceans may emit sounds so intense that their prey is debilitated and capture made easier. Collateral to this idea is the possibility that this capability may have had profound effects on the evolution of modern cetaceans, to be found especially in their behavior and anatomy.

At this point the idea seems to have appeared briefly three times. This is the first full-scale review. The first to mention it were Bel'kovich and Yablokov (1963). They calculate, using the very high frequency of 196 kHz, that a sound intensity of 10 watts/cm² (which corresponds to about 6.5 atmospheres pressure) might be developed and that it could be perceived as a powerful shock that could stun prey. They note that even a small dolphin might thus be able to stun prey. Next, Berzin (1971), after lengthy studies of the sperm whale (Physeter catodon), concluded that neither their teeth nor jaws were essential for food getting. He first noted that almost all food items in sperm whale stomachs are intact. Even very large squids and sharks measuring up to 3 m in length usually show no tooth marks. He continues:

Moreover our material included up to ten sperms with well-filled or at least normally filled stomachs in which the entire jaw was either turned aside already at the very base, or turned inside out with the tooth row outward, or else rolled up in a ring, arch, etc. . . . In such animals not a single tooth nor even the jaw could take any part in gripping the prey. Analysis of all these data leads one to a conclusion which at first glance appears preposterous: there is reduction not only of the function of the teeth but also that of the entire lower jaw in the digestive process of the sperm whale. Only thus can the facts, which contradict what is generally accepted be explained.

He proposes acoustic stunning as an hypothesis.

Finally, while we were preparing this paper we learned of the observations of Robert Hult (1982), who observed captive bottlenose dolphins disorient schooling fish, apparently by use of click trains. He too, concluded that acoustic prey disorientation was likely.
The odontocetes, or toothed whales, form a diverse group of about 68 species, ranging in weight from approximately 50 kg to 50 metric tons. Sound plays a vital role in the odontocete way of life, mediating communication and orientation.

Odontocetes are predators; the prey organisms are typically shrimps, fishes of diverse kinds and sizes, cephalopods, sea birds, and other marine mammals. Occasionally a few benthic invertebrates are eaten. This large spectrum of prey could be expected to be matched by a similar spectrum of food-getting specializations, but the match is hardly evident. Indeed, for many predator-prey combinations it is hard to envision how the cetacean succeeds at all without specialized feeding adaptations, or even in the face of what seem to be serious impediments to successful feeding. Anomalous combinations of predator and prey that come to mind are narwhal/pandalid shrimp, killer whale/herring, beaked whale/squid (especially for those whales whose teeth seem functionless in feeding, or even restrict the opening of the jaws), and especially the sperm whale that consumes prey of probably the largest size range among all mammals, ranging from 4-cm lantern fish to giant squids of 3-m mantle length (Berzin 1971; Gaskin and Cawthorn 1967; Okutani and Satake 1978).

The nearest parallels to our suggestion are fishing with explosives, and the poorly understood sonic prey capture by alphaeid crustaceans (pistol shrimps).

We assemble and assess the diverse evidence related to cetacean prey debilitation. Our discussion is organized into these topics: (1) the evolution of feeding structures of odontocetes; (2) the special case of the sperm whale; (3) the effects of shock waves on marine animals; (4) the maximum sound pressures of odontocete pulses; (5) the behavior of odontocetes during prey capture; (6) the aggressive use of intense sounds; (7) sonic prey capture by shrimps; (8) evolutionary perspectives; and (9) problems with the hypothesis.

**THE EVOLUTION OF FEEDING STRUCTURES OF ODONTOCETES**

Two important trends related to feeding are evident in the fossil history of odontocetes from their archaeocete origin to today. First, while nearly all ancient forms had long narrow beaks many modern forms are blunt beaked. Second, the teeth of ancient forms were typically numerous and prominent, while many modern genera show marked tooth reduction or outright loss. Some species are even functionally edentulous.

The oldest archaeocetes (Protocetidae) from the lower middle Eocene possessed the normal eutherian tooth row, including incisors, canines, three-rooted premolars and molars typical of carnivores. Most of these teeth show some lateral flattening (Kellogg 1936). In later archaeocetes the eutherian pattern becomes less and less evident as the teeth mostly become prominent leaflike serrated pyramids that interlock as the jaw closes. They are strikingly reminiscent of the teeth of the modern crab-eater seal (Lobodon) and though most literature on archaeocete teeth describes them as shearing or cutting teeth, their major use was probably similar to that of the seal, which eats small crustacean prey (krill). That is, when an aquatic animal closes its mouth prey will be forced out of the mouth by excurrent water unless the teeth are so constructed and arranged that they
produce a basket or cage before the jaws are completely closed. The size of prey
may be reflected hardly at all by tooth size. The flattened, serrated and interlocking
pyramids of archaeocetes, and their descendants the squalodont odontocetes,
allow water to escape as the jaw closes, through the serrations and interspaces.
The pyramidal shape produces a cage that becomes more and more complete as
the jaws close. The thinness of the teeth allows them to slice through the water
without producing major excurrent streams. The narrow rostra of these ancient
animals also reduced excurrent water flow to a minimum as the jaws closed.
Overall, the configuration of both archaeocete and squalodont teeth can be per-
ceived as modifications on terrestrial dentition to allow trapping of prey under
water.

As odontocetes differentiated in the lower Miocene the large serrated teeth gave
way to homodont tooth rows composed of very numerous slim conical single-
rooted teeth, for the most part still positioned on slim rostra. These teeth, as in
many modern species, tended to be tilted or splayed outward from the narrow
rostrum. The teeth interlocked before the jaw closed, once again minimizing the
effect of excurrent turbulence. This was the pincers jaw, and it must have served
then as it does long-snouted odontocetes today. It allowed the animal to pluck
small prey from the water with a quick snap of the jaws. Prey were pierced by the
teeth, or merely entrapped and held. Then, as the cetacean swam forward a slight
opening of its jaws allowed the prey to sweep backward in the water current
toward the gape. Such pincers jaws became remarkably elongate in many early
Miocene forms, especially in the families Platanistidae and Eurhinodelphidae, for
which very narrow jaws in excess of 2 m in length have been described (Kellogg
1924, 1925). Forms with quite elongate jaws, albeit of less extreme length, survive
today in the modern platanistid genera *Platanista, Inia, Pontoporia*, and *Lipotes*,
and in a number of odontocete genera, primarily oceanic, such as *Stenella* and
*Delphinus*.

Probably in all odontocetes, once prey reaches the gape a rapid retraction of the
lingual apparatus (especially the tongue which acts as a piston in drawing in water)
causes a transitory current of water into the mouth, allowing prey to be engulfed.
With the development of modern delphinid, phocoenid, and monodontid genera
the pincers beak has frequently either been reduced or lost. We can enumerate
*Grampus, Globicephala, Delphinapterus, Monodon, Orcaella, Peponocephala,
Feresa, Pseudorca, Orcinus, Cephalorhynchus, Phocoena, Phocoenoides*, and
*Neophocaena* as genera in which the elongate rostrum is markedly reduced or
even lost altogether and is dominated by its lingual portion. The mandibular
symphysis, which is a very elongate fusion in ancient forms, becomes a mere
joining of the apex of a V-shaped jaw (fig. 1). The food capture event in these
forms tends to become a single grasp of prey followed by a drawing of prey into
the gape. In the case of dead prey (the usual food source in marine exhibits where
these animals are sometimes held) food may be simply engulfed without being
grasped by the tooth rows. The need to surprise prey far in advance of the main
bulk of the animal and to entrap it swiftly seems to have been avoided. How, then,
do these animals manage to deal with their swift usually elusive prey? A potential
explanation lies in the evolution of echolocation, and prey debilitation.
Fig. 1.—Examples of the evolutionary trend in cetacea toward short snouts and short mandibular symphyses. a, *Proteus gludon* iitis (after Kellogg 1926), an Eocene archaecoce, showing the nearly terrestrial mammalian snout. The mandibular symphysis is described as long; b, *Squalodon calvertensis* (after Kellogg 1925), *Eurhadinus bossi*, a Miocene eurhadinodelphid, with a very elongate symphysis; c, *Squalodon longirostris*, the spinner dolphin, a modern long-snouted delphinid with a short symphysis; d, *Ziphius cavirostris*, a modern but relicsist platistid, with an elongate symphysis; e, *Squalodon elongatus*, the northern pilot whale, a short-snouted delphinid with a short symphysis; f, *Globicetophila medusa*, the modern long-snouted delphinid with a short symphysis.
During the development of echolocation in odontocetes there is an apparent trend toward the development of a narrow intense sound beam. The most archaic living forms are the platanistid river dolphins. Measurements of their emitted sound fields show them to be relatively broad cones of sound (Pilleri et al. 1979) while that of the more modern *Tursiops truncatus* is an intense and very narrow beam (Au et al. 1978). This trend toward a narrow beam enhances long-range detection, a feature of much competitive importance, and at the same time concentrates sound energy. At some point in this process prey debilitation may well have appeared as a by-product.

The trend toward loss of functional teeth is also marked in Neogene odontocete history. Nearly the entire beaked whale family Ziphiidae has lost functional teeth. Only the most archaic forms, such as *Tasmacetus* and *Berardius*, maintain numbers of functional teeth. The teeth that remain in the genera *Hyperoodon*, *Mesoplodon*, and *Ziphius* are probably not used in food getting. They are unerupted in females. Certainly in the case of a large male *Mesoplodon densirostris* (observed by Norris off the island of Hawaii) the enlarged teeth seemed not to have been used in feeding since they were both tassled with numbers of elongate soft-bodied barnacles (probably *Conchoderma*). These surely would have been crushed had the teeth been used to grasp prey (see Clarke [1966] for other examples). The two flattened teeth of the strap-toothed whale, *Mesoplodon layardi*, erupt just posterior to the mandibular symphysis, and in old males may partially encircle the upper jaw, markedly restricting the gape (Turner 1879).

The teeth of the sperm whale, *Physeter catodon*, are usually restricted to the lower jaw (an unerupted upper tooth row has sometimes been reported) and do not erupt before puberty (Caldwell et al. 1966). As noted earlier by Berzin (1971) none of these teeth is essential for feeding.

The evident dentition of the narwhal (*Monodon monoceros*) usually consists of a single erupted tusk, nearly always on the left. Buried in the tissue of the snout are an additional unerupted tusk (neither erupts in females) and a second pair of very small vestigial teeth (Fraser 1938). The erupted tusk of males can be long, often attaining 2.5 m in length, or two thirds the body length (Nishiwaki 1972). Though many speculations have been put forth about how this tusk is used, the only direct evidence links it to intraspecific “fencing” between males (Silverman and Dunbar 1980). Embedded or broken tusks have been found. Just how a male narwhal manages to capture swift and rather small prey with such a hydrodynamic and inertial nuisance protruding from its head is a continuing mystery. Especially the long and heavy tusk would seem to make impossible rapid movements of the head such as one assumes might be connected with prey capture.

The genus *Grampus*, a moderate-sized dolphin frequenting the continental margins and feeding extensively on squid, has undergone marked tooth loss. The upper jaw is edentulous while 2–14 teeth are found in the lower jaw (Nishiwaki 1972; True 1889).

The entire family of small blunt-nosed coastal species, the Phocoenidae, shows either reduction of functional teeth to small size (*Phocoena, Neophocaena*) or their burial in the gums along with extreme reduction in size (*Phocoenoides*).

It is striking that those forms showing tooth reduction or loss, with the excep-
tion of the beaked whales, are also short-snouted forms. Not all short-snouted forms show tooth loss, however. The group of cetaceans that are known or are suspected to feed on large prey, including other mammals, are also short snouted (Feresa, Pseudorca, Orcinus). All have very stout, deeply rooted, interlocking teeth capable of biting mouthfuls of tissue from even very large prey (e.g., a killer whale attack on an adult blue whale has been photographed and described; Tarpy 1979). But these predators represent a very different adaptive trend from genera showing tooth loss, which typically feed on small to moderate-sized prey, often squid, and eat them whole.

Whatever the feeding adaptation of these forms with tooth loss may be, it must allow them to approach and capture small, fast-moving, maneuverable prey. Capture must be accomplished in spite of the relative inflexibility of their bodies. We list tooth reduction or loss in 27 of 67 modern odontocete species, or 43%.

THE SPECIAL CASE OF THE SPERM WHALE

This whale requires independent consideration for two reasons. First, the size range of food items it consumes, and their ecological types, are probably the greatest among all living mammals. Second, the massive structures of its forehead, which may involve 30% or more of its length (Matthews 1938) are now implicated in sound emission (Norris and Harvey 1972), and some structures (the "junk" and the air sacs) are thought to be widely homologous throughout the odontocetes. The junk, for example, is a stout connective tissue and fatty mass lying on top the rostrum and is thought by Schenkkan and Purves (1973) to be homologous with the melon of other odontocetes.

While sperm whales are primarily cephalopod eaters (of at least 31 species) they also consume a wide variety of fishes (at least 50 species) ranging through bottom or deep water forms such as skates, grenadiers, cottids, sablefish, agonids, bathypelagic angler fishes, to surface forms such as puffers, and swift pelagic forms such as mackerels, barracuda, tuna, and salmon (Berzin 1971). Most remarkable of all is the size range involved which varies from squids with mantle lengths of 3 m (Clarke 1955) to lantern fish only a few cm long. How indeed, or why, a giant sperm whale should catch tiny lantern fish is not immediately apparent.

The sperm whale lower jaw consists of a slender rod of bone, fused along a very long mandibular symphysis, surmounted by two rows of widely spaced, blunt teeth that do not erupt until sexual maturity (Caldwell et al. 1966). In adults, the tip of the jaw begins a meter or more behind the tip of the broad snout, a position unsuitable for surprise attacks. And, as Berzin (1971) noted, any explanation of the food-gathering strategy of sperm whales should ascribe only a secondary role to the lower jaw. If it is used at all, the prey seldom show it. Caldwell et al. (1966) have examined many large fresh squid taken from sperm whale stomachs and only rarely noted any tooth marks on them; usually they were completely undamaged. Berzin (1971) cites similar observations. Spanish hand whalers have observed that live squid may sometimes swim out of the stomachs of freshly harpooned sperm whales (B. Möhl, personal communication from harpooner Carmona, at La Coruna, Spain, 1977).
Squids are among the fastest moving marine creatures; burst speeds of 55 km per hour have been reported (Akimushkin 1965). Commercial fishing is mainly done with seines at places where high-density schools are found; trawling is inefficient because of its low speed. The sperm whale, however, is not a particularly fast or maneuverable odontocete. Undisturbed, the animal moves at 2–3 knots (3.6–5.4 km per h); according to Berzin (1971) pursued or wounded sperms can develop speeds of 7–12 knots (12.7–21.7 km per h). Lockyer (1977) reports a maximum of 23 knots (41.6 km per h) based on sonar recordings. Measured by passive acoustic tracking Watkins and Schevill (1977a) reported speeds of a few knots in undisturbed animals. So the sperm whale does not seem capable of matching the speed required to catch up with the prey species mentioned above, much less outmaneuvering them. The large weight ratio of roughly 10,000:1 between the predator and its average prey should be borne in mind when evaluating the possibility of active pursuit. To accelerate a 30 ton sperm whale from 2 to 25 knots requires some 600 kcal. Assuming a propulsive efficiency of 0.85 (Lang 1966) and an energy conversion efficiency of 0.25, the caloric value of a squid weighing 3.5 kg—caught by pursuit by the whale—would not pay the costs of acceleration, let alone offset the cost of drag resistance. None of this explains how the huge, relatively inflexible whale can maneuver sufficiently well to catch the squid.

We have found four proposals in the literature describing how the sperm whale might manage to catch its food. Beale (in Berzin 1971) suggests that prey are lured into the gape by the attractive light coloration of the mouth. This explanation leaves unexplained how such color manifests itself in abyssal darkness where the whale often feeds, but it might explain the uninjured stomach contents and the lack of function of the lower jaw. Clarke (1979) suggests that the whale waits motionless and neutrally buoyant until dense schools of prey are within reach of its jaws. This leaves the observation of uninjured stomach contents, the unimportance of the lower jaw and the overall morphology of the mouth apparatus unexplained, but is consistent with the requirement of low speed. Also, a required daily catch of 1,000–2,000 kg of food, either fish or squid, would seem to require an efficient system and abundant schools of prey. Caldwell et al. (1966) speculate that food may be ingested by a sucking motion of the tongue. While we believe this action does happen to draw prey into the mouth, the explanation is incomplete and fails to explain how prey are brought close enough to allow the tongue to act. It does not project a use for the jaw, but is otherwise consistent with observations.

All these questions seem to be resolved if the sperm whale is able to immobilize its prey before engulfing it. The wide range of food sizes is then explained because a stunning sound beam would be at least relatively nonselective about either size or species of prey in its path. Even temporarily immobilized prey could be taken at will, and the jaw would not have to be used to catch and kill them.

The range of sound intensity a sperm whale can emit remains unknown, but it is fair to say sperm whales possess remarkably large and complex phonation systems in their forehead anatomy.

It is a rare event when biologists may examine a living sperm whale, and even
though they have long been known to produce loud clicks, only recently has direct evidence been obtained that these sounds emanate from their foreheads. A juvenile sperm whale was recently held in a New York yacht basin. Two independent observers under instructions from the senior author were able to define the area where clicks issued from the animal by the simple expedient of feeling them with their hands. Only in a circular region over the forehead above the upper jaw could sounds be felt, and there they produced impacts described as so strong that the hand was hit and forced away from the animal’s head. These sounds could be heard in air across the entire yacht basin, an indication of their high intensity (William Rossiter, personal communication; for a popular account, see Ellis 1981).

The soft tissue of the sperm whale forehead is structurally complex. A huge curving chamber filled with liquid wax (the spermaceti organ) forms the upper forehead. It is encased in thick muscle and a tendinous case. At either end and below it are large air sacs that are diverticula of the right nasal passage. To its left runs the large hoselike left nasal passage ending in an anterior blowhole. Below the spermaceti organ and continuous with it posteriorly is a larger mass of tissue, the junk, composed of wax-invested connective tissue wedges alternating with spermaceti-filled spaces that resemble a series of stacked lenses. These terminate beneath the anterior snout just above the rostrum, approximately where the sounds were found to emanate.

This unusual anatomy has been implicated by Norris and Harvey (1972) in the production of the unique burst-pulsed sound packets of the sperm whale. Their theory of a reverberating and focusing mechanism has received substantial support by allowing predictions of whale length from sound packet analysis based on the geometry of reflecting sound mirrors as related to known allometric growth curves (Møhl et al. 1976), and by allowing calculation of size distributions of schools of whales by sound analysis (Adler-Fenchel 1980).

These predictions immediately lead to the next question: Since the spermaceti organ (or complex of organs) emits sounds, what is the survival value of investing so much of the whale’s developmental resources in performing this function? Part of the explanation for the large size could be to achieve directionality with the low frequency sounds produced by the whale. Backus and Schevill (1966) have shown that the clicks emphasize such frequencies, peaking in the 1–5 kHz range. Frequencies below 10 kHz are most suitable for long-range sonar, and directionality is an important property of a sonar system since range, efficiency, and susceptibility to noise are all directly affected. It is at present conjectural that sperm whales use their clicks for sonar, but it would be rather surprising if they did not. Increased size can allow directionality to be maintained at lower frequencies. Assuming the acoustic aperture of sperm whale “nose” to be 1 m, and applying the equation for a plane piston radiator (as was done by Au et al. [1978] for Tursiops), the 3 dB beam width at 5 kHz to be expected is 18 degrees. This is about twice the width observed for Tursiops at 120 kHz. The rather broad lobe of radiation to be inferred from the spectral content of the clicks and the cross section of the head might conceivably be improved upon by the length of the organ providing a collimating effect. The lens-shaped spermaceti bodies of the junk may
be important in producing this effect. We have found no direct measurements of
directionality of sperm whale clicks in the literature. The successful passive range
and bearing estimation of sperm whales reported by Watkins (1980) indicates a
rather low directionality of the usual clicks. The only safe observation that can
now be made is that the required dimensions for achieving directionality, and
possibly even focusing, are present. By such means, high energy sound pulses
might be concentrated in a limited volume of water.

A conspicuous feature of the spermaceti organ complex is its massive muscular-
tendinous layer, stretching from the top of the skull to the anterior part of the
spermaceti case. The cross section of this layer is about 0.5 square m. Assuming
50% to be muscular, and the force during contraction to be 4 kg per square cm
(Karpovich 1965, p. 10), the sperm whale should be able to pull its spermaceti
organ backward with a force of 10 metric tons. This force would build up pressure
in the frontal sac airspace and could drive a high-intensity pneumatically actuated
sound generator. The point is that ample power is available.

In summary, we find the dimensions and structure of the spermaceti organ
complex not to be in conflict with the functions of a high-power sound generator,
possible with focusing abilities. From simplistic scaling, based on the data for
Tursiops maximum sound pressure, a maximum source level of the sperm whale
pulse on the order of 265 dB // 1 μPa, dependent on the directionality assumption,
could be possible. Such pressures are above known lethal thresholds for prey
species by a handsome margin. That such pressures are also very much above
those thus far reported for sperm whales (Levenson 1974) is not surprising, as
argued below.

EFFECTS OF SHOCK WAVES ON MARINE ORGANISMS

While fishing by explosives is a well-known method, understanding of the
biological effects of the active component, the high-intensity pressure pulse, has
not advanced much beyond establishing the relationship between peak pressure
and rapid lethality for a number of fish species. For explosives with fast onset
(short rise time), such as dynamite and TNT, lethal thresholds are between 40 and
70 psi (229 and 234 dB // 1 μPa), while for slow rise time explosives like black
powder, 5 to 10 dB higher pressures are required. The observed signs of damage
are hemorrhage and a rupture of viscera, swimbladders, kidneys, or gonads
(Hubbs and Rechnitzer 1952). Of sublethal effects, transient stunning is known to
occur, but neither the actual physiological mechanism, nor threshold values are
known.

With cephalopods, our own preliminary observations (B. Møhl, K. S. Norris, P.
Norris and K. J. Staehr, MS) indicate short-term tolerance to high rise-time
shocks of up to 260 dB // 1 μPa for the small Alloteuthis subulata (mantle length 4
cm, 17 trials), while the larger Loligo vulgaris (mantle length 18–27 cm, 5 trials)
were fatally injured by peak pressures of 246–252 dB // 1 μPa, and died within 3–
11 min. The lowest pressure that will debilitate the larger squid remains unknown.
The effects of high-intensity sound on crustaceans remain unknown.
According to the most widely accepted ideas on odontocete impulsive sound production, generation takes place in the soft tissues of the forehead, close to the distal openings of the bony nares, in specialized structures with suggested homologies to muzzle structures in terrestrial mammals. The sound is transmitted to the water through the melon, a fat and connective tissue complex, and perhaps also through the bony rostral tip.

Obtaining a meaningful measure of sound intensity requires knowledge of the position and orientation of the animal in relation to the recording hydrophone, a suitable acoustic environment, and calibrated recording and analyzing instrumentation with adequate bandwidth and dynamic range. When, further, a measure of maximum intensity is asked for, the animal must agree to do its best and direct sonic output toward the hydrophone. It is hardly surprising that all these conditions have only rarely been met. In captivity most odontocetes produce relatively low-level sounds in the 140–180 dB re 1 μPa range (Diercks 1972). Recordings of clicks in nature have tended to be of about the same levels (Fish and Turl 1976; Watkins 1980).

In an experimental situation, however, approaching open water conditions, Murchison (1980) trained two Tursiops to perform a sonar detection task against high background noise at distances up to 73 m, using 2.54- and 7.6-cm spheres as targets. Under such conditions average source levels for single click series as high as 228.6 dB re 1 μPa / 1 yd were measured (Au et al. 1974). This is five orders of magnitude above the generally quoted levels. The peak power requirements of the transmitting organ for such pulses is on the order of 1 kw, assuming a peak to peak source level of 230 dB re 1 μPa and a directivity index of 24 dB. In another related experiment (Au et al. 1978) mean source levels of 218 dB re 1 μPa / 1 yd were registered; peak energy was in the 120 kHz region. Later, by avoiding a reverberant bottom ridge encountered in the Murchison test, detection range was extended to a remarkable 113 m (Au and Snyder 1980).

These findings are relevant to the present problem for three reasons. First, peak levels equal to established lethal thresholds of fish can be produced by Tursiops; second, such levels are apparently not harmful to their producer, and third, odontocete source levels measured in captivity or at sea generally are not indicative of maximum levels. Only specially designed experiments have allowed such measurements to be made, and even then no assurance can be given that an absolute maximum has been reached. The obvious experiment of training a dolphin to ensonify a fish with high intensity sound still remains to be done.

Captive observations have shown that very loud impulsive sounds may be used by dolphins in social contexts other than feeding, including aggressive sequences and startle responses. A threat signal, the jaw clap, is a common emission of the bottlenose dolphin, and is sometimes so intense that it can be heard through tank walls (Tavolga and Essapian 1957; Lilly 1962). Loud cracks, without jaw movement are reported by Caldwell et al. (1962) when a light was suddenly shown in a dolphin’s eyes at night. An aggressive response signal was elicited by the senior author from a captive male spinner dolphin by directing sharp sounds at it. The
elicited sound was intense enough to cause ringing in the ears of earphone-equipped listeners. In no case have source levels been derived for these social signals.

**BEHAVIOR OF ODONTOCETES DURING PREY CAPTURE**

A number of anecdotes derived from incomplete field observations of dolphin feeding can be explained if odontocetes possess acoustic prey debilitation capability. But none rule out other possible causal features such as fatigue effects. Nonetheless they support the possibility of acoustic debilitation and are presented in Appendix 1.

A direct test was carried out at the Oceanic Institute, Oahu, Hawaii, with three captive Hawaiian spinner dolphins (*Stenella longirostris*). Its results were also inconclusive from the standpoint of proving acoustic prey debilitation, but they do provide new data regarding ensonification of prey by dolphins. The test, performed on September 10–11, 1980, utilized an underwater viewing room equipped with listening gear, but no means of determining source levels. The spinner dolphin is a moderate-sized animal that forms large schools and feeds on small mesopelagic fishes, squids, and shrimps, mostly the deep scattering layer (Norris and Dohl 1980). Its prey items are typically small, including postjuvenile forms; the largest is about 10 cm in length. The akule used in this test were about twice this length and therefore not normal food. Another 12 akule from the same collection were placed in a nearby oceanarium tank, serving as a control group. Shortly after introduction of the fish, first one dolphin and then two, began to make click train runs on the fish school. They did so in a quite stereotyped manner; they always approached the school from its side, racing at it while emitting a whining crescendo of clicks. The fish school typically parted in front of the onrushing dolphins, both parts turning tightly toward the passing dolphin’s tail (fig. 2). The mammal was unable to turn so tightly and had to make a broad circle before coming in for another run on the now re-formed fish school. Such runs continued for approximately an hour without noticeable effect on the fish. After 2 h, involving perhaps two dozen runs by the dolphins a noticeable depolarization of the fish school began to appear. All the fish no longer pointed in the same direction. They began to wander from the school. A wandering fish usually drew the attention of a dolphin, who pursued it relentlessly, emitting train after train of rapid clicks. The fish was typically placed within a few cm, often 1 or 2, of the rostral tip, or well within the expected near field. During such pursuit the dolphin scanned with its rostrum, in small rapid excursions, presumably playing the sound field across the fleeing fish. By this time the fish were unable to avoid the dolphins, either in their main school, or as separated individuals. One such wandering fish was noted to change from a silvery color to a pale lemon yellow.

The fish school traversed the central drain box, which was drawing a modest vortex. The fish struggled and dipped down as they passed over the drain; behavior that would not be expected in a normal school. One fish was spun down and sucked from the tank.

No fish were eaten, and the dolphins continued to take their normal ration of
fresh frozen fish. In this entire sequence the stereotyped insistent click trains directed at fish were suggestive of a familiar pattern. Control fish though severely harassed by predatory jacks (Caranx) retained coherent polarized schooling.

POSSIBLE SONIC PREY CAPTURE BY SHRIMPS

The snapping or pistol shrimps, family Alphaeidae, produce sharp metallic clicks. The crackling of their clicks is well known to all who try to listen underwater where they are common. The click is produced by the chelate leg that may be about half the size of the body. The claw is cocked and held open by two microscopically smooth adherent plates between which a film of water is held. The muscles of the claw overcome the tensile strength of this film and when a force of about $2 \times 10^3$ dynes is built up the claw snaps shut and both a jet of water, directed ahead of the claw, and a sharp snap are produced. MacGinitie and MacGinitie (1968) report that the clicks of Alphaeus californiensis are used both defensively and offensively. When small gobies (genera Clevelandia and Gillichthys) were introduced into an aquarium battery jar with the shrimp, the shrimp often emerged from its burrow, stalked the fish with snapping claw outstretched, and when a short distance away snapped the claw shut, stunning the fish, which
was usually retrieved and eaten. This behavior was a common exhibit for visitors to the Kerckhoff Marine Laboratory, Newport, California, where for many years the MacGinitie’s were directors.

Though the mechanism of click production has been investigated in some detail (see Morris et al. [1980] for references) no records of the intensity or wave form of individual clicks seem to have been made. The clicks are certainly intense. The MacGinitie’s reported that if the battery jar in which the shrimps were held had been scratched it would sometimes shatter when the shrimp clicked.

For our discussion here the observations are important because they show that sharp pulses of sound might be used by other aquatic animals, without damage to themselves, to capture prey. The impedance relations of animals immersed in water mean that much more sound energy from a click will enter prey than for a click in air. Nearly all of the energy of a bat click, for example, is reflected from its prey.

**EVOLUTIONARY PERSPECTIVES**

For any biological hypothesis to be interesting, it should be plausible in an evolutionary sense. This implies that each step in an evolutionary sequence must have an adaptive value of its own. Acoustic stunning in odontocetes appears to present few problems in this context. Specialized sound-generating organs originally developed in response to communicational needs, then became part of a sonar system. This is a switch in function that initially did not require morphological changes. Any increase in output power will improve the range or performance of a sonar system. Thus, a selection pressure for high output sound-generating organs is easy to imagine. Eventually, the intensity could become high enough to cause a completely new effect: The prey, ensonified for orientational purposes, become debilitated by sound. This new function can again serve as a base for further modifications. This evolutionary pattern is conceptionally identical to, and inspired by the one proposed by Lissman (1958) for evolution of strongly electric fishes. Darwin (1872) regarded the strongly electric fish as a serious problem for his theory of evolution. At that time electrolocation, which is the key for understanding the adaptive value of weakly electrical fishes, was unknown. Darwin postulated an explanation basically along the missing link theme. If indeed acoustic stunning is performed by odontocetes, no major functional links are missing. Furthermore, some puzzling aspects of the evolution of modern odontocetes become explainable, such as loss of the pincers jaw and loss of functional teeth, as outlined above.

**PROBLEMS FOR THE HYPOTHESIS**

While the hypothesis of acoustic stunning of prey by odontocetes (not necessarily by all of them and at all times) would seem to explain some enigmas, such as how the sperm whale catches his food, the absence of weapons and so on, there are indeed a number of observations that are not supportive. One is the absence of reports of high-intensity pulses from animals in nature. To be sure, a number of
very hard-to-meet conditions are required for their recording, as was outlined in a previous section. If not specifically listened for, high-intensity clicks in conjunction with series of normal-intensity clicks usually saturate electronics, leaving little possibility for assessment of intensity. Another reason for the lack of reports on high-intensity sound pulses are the effects of directionality and focusing. Such effects require the hydrophone to be close to the ensonified target to record the level properly. Finally, pulses of high intensities form shock waves that suffer from excessive, nonlinear attenuation (e.g., Shooter et al. 1974). Source levels, computed from assumptions of spherical attenuation, are then too low. Notwithstanding such explanations, it still seems unusual that if a number of odontocete species obtain their daily food by acoustic shocking, they have gone unnoticed by marine acousticians.

It may be advantageous for a dolphin merely to incapacitate prey when the dolphin is close enough to take it immediately. An indiscriminately used killing beam would certainly attract other predators to share in prey thus debilitated. This effect would be greatest if the dolphins used sounds that were immediately lethal at some distance ahead of it. A more efficient system might be to approach the prey closely, holding it close to forehead sound generators, and then take the prey when it had lost a modest degree of escape ability. Even in this case some prey would be likely to escape, and it may well be that the reason dolphins are often accompanied by predators such as tunas is that easily caught food accompanies the passage of a feeding dolphin school. Final possibilities are that the production of intense sounds capable of killing prey at distance may be dangerous to circling dolphins, or that it may be physiologically expensive to produce such sounds.

If odontocetes are indeed producing damaging, high-intensity pulses, how can they protect themselves from tissue damage? Since the energy is directed away from the animal and possibly even focused at a point outside the animal by interference, this would seem to present less of a problem than, for example, an electric pulse in strongly electric fishes. The problem of self-inflicted ear damage also appears to be minor, partly because the ears are well shielded by air barriers, and partly because the animal may be able to utilize the middle ear reflex (McCormick et al. 1970). Whatever the detailed mechanism may be, the demonstration of high intensity pulse production in *Tursiops* by Au and co-workers is a good indication that this problem has been solved.

Captive animals present different problems. Apparently, the bottlenose dolphin as a rule emits at sound power levels about 5 orders of magnitude or more below its capacity (Au et al. 1974). This could be an understandable response to confinement in the usually highly reverberant tanks, or it may be that to produce the loudest sounds is a taxing event. The aggressive, high-intensity "jaw clap" sound is a repeatedly reported exception, as is the aggressive use of sound, reported here.

Perhaps the most intriguing of all are the questions about behavioral relations posed by having such a weapon available to all or nearly all members of a school. Despite differences of physical strength that might exist between sexes and age classes, such a capability might produce a remarkable degree of social symmetry.
Another potential objection arises from the observation that pinnipeds are able to catch most of the same food species as odontocetes do. Squids, which present problems to commercial trawling because of their speed and maneuverability, have been reported found in the stomach contents of elephant seals, fur seals, and sea lions (King 1964). However, the pinniped solution to the final phase of catching (the long movable neck, the broad, terminal mouth, and visual guidance) differs considerably from that available to odontocetes. The latter may be capable of higher speed, but are probably inferior in close tracking of objects with erratic courses, such as shrimps and squids. In most delphinids, the mouth is terminal, but beaklike and the neck highly condensed. In the sperm whale, the mouth is meters behind the tip of the snout, and in the male narwhal the long, forward projecting tusk would seem to cause a low probability in successful prey stalking or rapid head movements during close range hunting; e.g., for shrimps. Also, in odontocetes the lateral position of the eyes suggests visual guidance to be of less importance than in pinnipeds. For the deep-diving species at depth, eyes are useful only in situations involving bioluminescence. However, echolocation can hardly qualify as full substitute for vision, partly because of its directionality, partly because of its low information rate, and partly because of poor coverage of the area below the head. It seems, therefore, that for the pinniped argument to negate the theory requires a demonstration of essentially the same strategies for orientation and hunting being used in both groups of marine mammals, which is not the case.

In summary, the major objection against the hypothesis of acoustic debilitation appears to be the absence of direct and unequivocal observation on catching behavior that can be assigned to acoustic debilitation, and the lack of reports of measured high-level pulse emission in nature.

POSSIBLE EXPERIMENTS

The central need is for a direct observational test of prey debilitation by a dolphin in a captive environment, acoustically monitored in a quantitative fashion. If such a test succeeds, the cause of prey death needs to be investigated, as does the feature in the debilitating sound that produces the effect. It could be, for example, that the negative pressure deflection of a high-intensity pulse causes cavitation effects in prey tissues.

At-sea listeners need to listen with equipment that will allow routine assessment of the ranges of sound pressure in the signals of wild animals, especially during feeding episodes.

SUMMARY

1. The hypothesis is presented that some odontocetes may debilitate prey by use of brief intense sounds.

2. In several cases, considering the feeding structures of a given odontocete species, it is not apparent how they capture the prey species on which they feed.
Especially in these cases, prey should be able to outdistance the odontocete in question or outmaneuver it.

3. Some field observations are strongly suggestive of prey debilitation by odontocetes. Fish have been seen to lose orientation capability in the presence of ensonifying dolphins, and wild fish schools being fed upon by dolphins were found to be so lethargic they could be removed from the water by hand.

4. In the evolutionary development of modern odontocetes, feeding mechanisms have shifted from a modified terrestrial tooth row capable of entrapping prey (the cage jaw), to very elongate jaws (pincers jaws) capable of snapping prey from the water, in early Miocene dolphins, to the loss of such beaks and teeth in many modern forms which made their appearance in middle and late Miocene. The major means of ingestion has become suction, activated by a piston tongue. These trends seem associated with a narrowing of the emitted sound field, probably as an evolutionary response toward the development of increased range by their echolocation pulses. It is hypothesized that as the beam narrowed and intensified it began to disorient prey. These trends are tied to the telescoping and asymmetry of the dolphin skull.

5. The sperm whale may catch its swift squid prey leaving no evident tooth marks, and such prey may be alive in sperm whale stomachs. The disparity between the speeds of the sperm whale and squid and the costs of sperm whale acceleration are discussed. Sperm whales eat a very wide-sized range of prey, and small items will not repay the costs of the whale’s locomotion. The forehead sound-beaming anatomy is postulated to allow prey debilitation.

6. Bottlenose dolphins are known to emit sounds intense enough to kill fish, and probably also squid.

7. Some evidence implicates snapping shrimp in sonic prey stunning.

8. The major problem for the hypothesis is the lack of recordings of such very intense odontocete sounds at sea.

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APPENDIX A

FIELD OBSERVATIONS OF ODONTOCETE FEEDING

Scattered observations suggest that the prey of odontocete cetaceans may sometimes be immobilized, slowed, or disoriented prior to being eaten. While none of these examples offer proof, most require explanations that are not immediately apparent unless prey debilitation is correct. Species of the genus *Lagenorhynchus* form large schools typically living on the continental shelves of both hemispheres. Common food items are surface
schooling fishes and squids. Two observations, one from Argentina (L. obscursus) and one reported to Norris by a fisherman from the San Benito Islands off Baja California, Mexico (L. obliquidens), concern schools feeding on anchovies (Engraulis sp.). In both observations the small fish were “balled up” at the surface and surrounded by a school of dolphins whose members individually cut through the school taking mouthfuls of fish at each pass. In both cases the observers noted that the fish were lethargic and did not successfully evade the dolphins. In both cases the fish were easily scooped from the water with a hand net, or even picked up by hand. In the Argentine example Wursig and Wursig (1980) noted that the dolphins dove and brought up a milling ball of fish, holding it against the surface where larger fish and birds also fed. They noted the dolphins swimming one at a time through the fish, taking from one to five at a pass. No correlated sounds were heard, or listened for.

In these cases the fish were clearly lethargic, but it is not possible to define a cause for this debility from these observations. Lethargy could have been a direct result of ensonification by the dolphins, or it could have been an effect of accumulated lactic acid debt in the fish due to pursuit by the dolphins, or it might have been the result of crowding which could have reduced oxygen tensions or increased CO₂ in the seawater to debilitating levels (Moss and McFarland 1970).

Two somewhat similar observations have been obtained by Norris. One was made in 1963 and the other in 1980. These observations, involving much larger prey and whales, were made on board oceanarium dolphin capture vessels in Hawaii. The dolphins were false killer whales (Pseudorca crassidens), a large, swift oceanic species found throughout the warm waters of the world. The species reaches about 540 cm total length in males, and 460 cm in females. In both cases small schools (8–15 animals) were found feeding on mahimahi (Coryphaena hippurus), a swift predatory surface fish that reaches about 30 kg in weight.

In the 1980 encounter the boat approached a group of three whales engaged in feeding. A whale had captured one of these fish weighing an estimated 15 kg, and the three whales were tearing it apart while another fish of similar size lay floating at the surface on its side, apparently unbitten (no blood was evident) but immobile. Rainbow colors were described as playing across its body, as usually happens when these fish are brought aboard a fishing vessel. The earlier account also mentions an immobilized and apparently unblemished fish. While one cannot be sure why the fish were immobile, their small numbers rule out chemical change in seawater as a cause, since many fish in a restricted volume of water are required to produce the effect. Fatigue, however, cannot be ruled out.

An instance of feeding by a wild killer whale (Orcinus orca) that is suggestive of a means of prey immobilization has been reported to us. In the summer of 1973 Donald White, a behavioral biologist, observed a small pod of female and juvenile whales, apparently in the act of foraging in Johnstone Strait, off Northern Vancouver Island, British Columbia, Canada. As the whales approached the stern of his boat he noticed a swirl at the surface near the rail of his ship. He looked down to see a medium-sized salmon (ca. 2.5–3.5 kg) swimming very rapidly away from the whales just below the surface. As he watched, the salmon suddenly dove to a depth of about 1 m, abruptly stopped, and lay motionless. The whales, which had been traveling at a moderate speed, 3–6 m behind the fish, did not change speed but approached the fish and a cow took it as they passed the vessel. White wondered at the time if the whales might be able to stun prey acoustically. He was not monitoring sound and heard nothing above the surface.

While this paper was in preparation we learned of a quite similar series of observations of captive bottlenose dolphins herding fish back and forth between two rocks in a Florida marine exhibit (Hult 1982). The dolphins insistently directed click trains at the fish which sometimes became separated from their school. In one such instance a dolphin struck the wandering fish with its flukes and ate it. In other instances the fish were observed to “corkscrew” as they were being ensonified. The fish school gradually decreased in numbers over a month’s observation, from about 40 to 9 at the end, but one cannot be sure the dolphins were responsible since other predators were in the tank.

Another incident was reported by Hardy Jones, a photographer and writer of the Living
Ocean Society of Sausalito, California. Jones states that he was diving over an offshore bank near the Bahamas Islands, observing a school of spotted dolphins (Stenella sp.) that allowed him to swim in close proximity with them. He noted one dolphin accompanied by some mackerellike fishes slowly approach a small, pearly knife fish while emitting a loud click train. When the dolphin was about a meter from the fish Jones reported that the fish fluttered up from the bottom. One of the accompanying fish rushed forward and took the fish. The dolphin made no move toward the fish. While suggestive of acoustic stunning one still cannot be sure that the sounds emitted by the dolphin were causative in the apparent debilitation of the fish.

LITERATURE CITED


