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The acoustic predation hypothesis: linking underwater observations and recordings during odontocete predation and observing the effects of loud impulsive sounds on fish

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Abstract

Marten *et al*. (1988) analyzed killer whale (*Orcinus orca*) and bottlenose dolphin (*Tursiops truncatus*) high amplitude impulse sounds ('bangs') in feeding situations in the wild. Animals were observed from boats and only could be seen at the surface, so no underwater visual data were linked to the bangs. The purpose of this paper was to provide synchronous underwater visual and hydrophone data of individual cetaceans chasing fish, both in the wild and in captivity. We also simulated odontocete bangs with underwater air and water guns (used for underwater seismic oil exploration) and assessed the effects of their loud impulse emissions on northern anchovies (*Engraulis mordax*). Effects of multiple-impulse treatments ranged from flight to disorientation and death. The results are consistent with the Norris and Møhl (1983) acoustic predation hypothesis. We hope this information can serve as a useful background for other scientists who might encounter predation situations in the wild, or who might wish to do laboratory experiments on this interesting, but difficult to study hypothesis.

Key words: bang theory, acoustic predation hypothesis, spotted dolphins, bottlenose dolphin, killer whale, northern anchovy

Introduction

The hypothesis that dolphins and other toothed whales stun or kill their prey with high amplitude sound (i.e., The Big Bang Theory) was first proposed with a body of supporting evidence by Norris & Møhl (1983). Marten *et al*. (1988) explored the theory with field observations and laboratory experiments, finding that there were situations in which odontocetes feeding in the wild emit high amplitude, low-frequency impulse sounds. Although there are additional acoustic data consistent with the hypothesis (such as Smolker & Richards, 1988), a major gap in information is a lack of underwater observations on both predator and prey. A second gap in information, is the absence of any demonstration that dolphin-like sounds (as opposed to the explosions referred to in Norris and Møhl, 1983) can stun or kill fish. Herein, we emphasize underwater observational and acoustic data.

We defined a 'bang' to be a loud impulse sound, much greater in amplitude than the sonic portion of echolocation clicks and longer in duration than echolocation clicks, and typically tens to hundreds of msec, rather than <1 msec, like echolocation clicks. Bangs are also of much lower frequency than clicks, with almost all energy <5 kHz, and with substantial energy <1 kHz.

Zagaeski (1987) produced high-intensity sound waves from 10–26 kV sparks, which caused disorientation and abdominal hemorrhaging in guppies (*Lebistes reticulatus*). We present data here on the stunning and killing effects of a Bolt Technology Hydrogun on northern anchovies (*Engraulis mordax*). The similarities and differences between Hydrogun and toothed whale predation sounds are discussed. The information presented herein, when combined with information from the earlier report by Marten *et al*. (1998), continues to build an interesting case for the acoustic Big Bang Theory.

Materials and Methods

Each section below represents a separate study by different researchers. Together, they provide a coherent body of information relevant to the acoustic prey-stunning hypothesis:

Wild Atlantic spotted dolphins off the Bahamas
Since 1985, a resident group of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) has been observed under water for 5 months each year in the Bahamas. This study site provides a unique opportunity for close-up and regular underwater observations of dolphin behavior. Life history (Herzing, 1997), association patterns (Herzing & Brunnick, 1997), behaviors, sounds (Herzing, 1996), and interspecific interactions (Herzing & Johnson, 1997) have been documented for this group. Many (1587) underwater videotaping sessions (averaging 32 min/session), including sound recordings, were documented over a 14-year period. Underwater sessions were taped using a Hi8-mm video camera with simultaneous hydrophone input (Labcore 76, linear response to 22 kHz, sensitivity − 192 dB re 1 μPa). The frequency response of the camera-hydrophone system was thus limited by the video camera to approximately 19 kHz. Behavioral categories included foraging, resting, traveling, courtship, play, aggression, and affiliative behaviors. Sounds were processed using Spectral Innovation's 32-bit floating-point digital signal processor with a 125-kHz, 16-bit analog-to-digital card (maximum sample rate of 62.50 kHz). Sounds were measured using Canary 1.2 (Cornell University Acoustics Laboratory) software.

Table 1. Average peak frequencies and duration of loud impulse sounds for each feeding/experimental situation.

Species and Location	Average Peak Frequency (Hz)	Average Duration (msec)
Spotted Dolphins		
Bahamas	3,092	74.8
Killer Whales		
San Juan		
Single Sound	600	100.0
Doublet Sounds	4,500	100.0
Killer Whales		
Johnstone Strait		
Feeding Episode 1	490	100.0
Feeding Episode 2	547	56.0
Feeding Episode 4	600	107.0
Feeding Episode 5	318	87.0
Bottlenose Dolphins		
Alabama		
Single Sound	5,000	45.0
Doublet Sounds	500 & 4,500	45.0
Bottlenose Dolphins		
Sea Life Park		
Hawaii	1,000	22.5
Bolt Technology		
Model 10 Hydrogun	800	3.0

Wild killer whales feeding near Johnstone Strait
A camp was set-up on Craycroft Island in Johnstone Strait for observing killer whales (*Orcinus orca*) from a cliff and simultaneously recording their sounds using two Magnavox U.S. Navy sonobuoy hydrophones (frequency response linear to 30 kHz). Several episodes of killer whales chasing salmon were observed and notes taken with simultaneous recordings onto a Sony SD-153 cassette recorder (frequency response linear to 17.5 kHz). The whales were recorded whenever they came by the cliff. Whether or not the killer whales were feeding and behavioral notes were collected.

In 1986, 102 recordings were made from 29 June to 10 September. The whales were identified individually, or by pod affiliation. The majority of recordings were from whales in A pod, Dl pod, and Ill pod, all members of the northern resident community of Johnstone Strait (Ford & Fisher, 1983). The two sonobuoy hydrophones were submerged 1.5 to 3 m under water, approximately 10 m offshore, resting on the bottom. The hydrophones were attached to a 100-m cable connected to the Sony SD-153 cassette recorder. Oscillograms and power spectra were made on a Hewlett Packard 5451C sound spectrum analyzer.

Rise-times were obtained by examining oscillograms with an expanded time scale. A breach, which occurred within range of the hydrophone also was recorded and analyzed for comparison with the bangs recorded during chases of salmon.

Killer whales off the San Juan Islands
Killer whales were followed by a boat near the San Juan Islands. When whales were feeding on salmon, sound recordings were made through a Magnavox U.S. Navy sonobuoy hydrophone (response linear to 30 kHz) onto a Sony TCD5M stereo audio cassette recorder (response linear to 17.5 kHz). From the 3 h of audio recordings, ten of the loudest bangs (relative to clicks before and after the bang) were analyzed to obtain the average spectral parameters for this study site (Table 1, bangs in Figure 3), using Sound Designer on a Power Macintosh 7100AV.

Wild bottlenose dolphins off the Alabama coast
In August 1986, bottlenose dolphins (*Tursiops truncatus*) were studied in the shallow, nearshore waters of the Gulf of Mexico and Mobile Bay, Alabama, which surround the Ft. Morgan Peninsula. At 1737h (CDT) on 20 August 1986, nine bottlenose dolphins were found socializing and 'milling-feeding' in Gulf of Mexico waters approximately 150 m off Fort Morgan Peninsula, Alabama. A private fishing boat was anchored within 50 m of the school and the occupants of the boat were catching mullet. A second boat approached, turned

off its engine, and proceeded to fish. Recordings and observations were made from a 10-m inboard boat, and from a 4-m inflatable boat equipped with an outboard motor. Dolphin sounds were recorded with either a Magnavox U.S. Navy sonobuoy hydrophone (response linear to 30 kHz) or with a Yak-Yak hydrophone coupled to a Sony TC-D5M portable audiocassette recorder (system response linear to 17.5 kHz). Observations of surface behavior of dolphins were narrated onto one channel while the hydrophone was recorded simultaneously onto the other channel. Audio tapes were analyzed on a Multigon Uniscan II sonogram display (analysis range to 40 kHz), a Hewlett-Packard 5451C Fourier analyzer, and Sound Designer software on a Power Macintosh 7100AV. We defined a 'doublet' as two loud impulses in sequence, separated by a time interval that is the same order of magnitude as the duration of the pulses themselves.

Laboratory experiment with live fish and dolphins at Sea Life Park, Hawaii

Ten live fish (*Tilapia spp.*) were placed in the tank adjacent to the underwater viewing laboratory of Earthtrust at Sea Life Park, Hawaii. The 'Wolphin' (a hybrid between a bottlenose dolphin and a false killer whale) and three adult female bottlenose dolphins were present. Tracks of the fish and the dolphin predator were plotted from video footage taken through an underwater window in the tank, showing the locations where bangs occurred. Underwater sound recordings were made in stereo through two Magnavox U.S. Navy sonobuoy hydrophones (response linear to 30 kHz) spaced approximately 4 m apart. The position of the bangs also was checked, using amplitude differences in the stereo hydrophone data, to confirm a bang came from the pursuing dolphin.

Effects of loud impulse sounds on northern anchovies

Approximately 400 northern anchovies (*Engraulis mordax*), 13.5–16.5 cm in length, were confined in a 16 m × 8 m, 2–3 m deep area in the Santa Cruz Harbor, using a large 6-mil polyethylene bag. This arrangement was chosen to minimize the reflection and reverberation effects encountered in a tank, yet retain the ability to measure sound amplitude and provide an environment as similar as possible to the wild.

Anchovies were typically from 1 to 5 m from the Hydrogun. Average impulse sound pressure level of exposure ranged from 216.3 dB re 1 μPa at 1 m to 205.3 B re 1 μPa at 5 m. We measured sound pressure level with and without the polyethylene between the sound source and the hydrophone, and found the polyethylene to be transparent to sound. Therefore, sound experiments could be conducted confining the fish, without measurable sound reflection or reverberation. To allow the fish to adjust to the artificial environment, the anchovies were maintained in the bag for three days before the sound tests were conducted. Loud impulse sounds were given from a Bolt Technology Model 10 Hydrogun and the behavior of fish was video-tape. The Model 10 Hydrogun is an underwater sound projector, which employs cavitation to produce high intensity, broadband impulses. The watergun was set to give one impulse every 15 s and the anchovies were exposed to 693 pulses over a four-hour period.

A calibrated sound system was used to record and analyze sounds measured at 0.5-m intervals from the sound source. Recording was done with a Bruel and Kjaer (B & K) 8103 hydrophone, through a B & K 2634 charge amplifier, onto a Racal Store 4DS tape recorder (FM channel), using Ampex 797 tape, and recording at 38.1 cm/sec. The hydrophone was calibrated with a B & K 4223 hydrophone calibrator. Sound pressure levels were measured with a B & K 2230 precision integrating sound level meter using its 'fast' and 'peak' settings. Spectral analysis was done on a Hewlett Packard 5451-C Fourier analyzer. Rise-times were obtained by examining oscillograms with an expanded time scale. Additional details on the sound tests conducted on northern anchovies with the Bolt Hydrogun and Bolt Airgun can be found in Schilt (1991).

Results

We found two apparent strategies by dolphins employing potentially debilitating sounds during predation. In wild Atlantic spotted dolphins, the sound was not a big 'bang,' but was spread out through time as a continuous, loud buzz. In killer whales and bottlenose dolphins (*Tursiops truncates*), it was packaged into loud impulsive sounds. Observations from the wild include apparently stunned or dead fish, and the acoustic strategy involved in these situations we call the 'buzz' strategy. The 'bang' strategy occured during fish chases by captive bottlenose dolphins, and therefore possibly also is used in feeding situations in the wild by bottlenose dolphins or by killer whales. More detailed analysis of sound recordings and observations of the wild killer whales chasing and eating salmon, can be found in Newman (1988).

Table 1 is a tabulation of average peak frequency and duration of 'bangs' observed during predation, under all study situations, summarized below:

Wild Atlantic spotted dolphins off the Bahamas

Since 1985, 315 incidences of foraging were observed. Foraging included surface feeding, bottom foraging, digging in the sand, and nocturnal foraging. The most frequent type of foraging

Figure 1. In two instances in 1991 Atlantic spotted dolphins were observed in apparently dense areas of prey. Over 20 spotted dolphins (*Stenella frontalis*) were observed foraging within a 20 m area of sand. Various prey species, including wrasse (*F. Labridae*), blenny (*F. Tripterygiidae*), and clinids (F. Clinidae) were observed. During these dense foraging events, small fish often came to the surface apparently stunned. During this period, researchers grabbed the fish, without resistance, and collected them as samples of prey items. Even some fish not taken out of the water did recover.

observed was searching and locating prey on the sandy bottom at a depth of 5–15 m (Figure 1). Many species of prey were observed taken by the spotted dolphins (Herzing, 1996). In all incidences, a 'bang', as described previously by Marten *et al.* (1988), was never heard or recorded. Instead, spotted dolphins used continuous buzzes when observed capturing fish. Although not a 'bang' by definition, foraging buzzes consisted of extended click trains, usually with a repetition rate of 200 Hz, followed by a terminal phase of buzzing (up to 500 Hz) as the prey was retrieved from under the sand.

The average size of prey items was 8–10 cm. Duration of continuous buzzes ranged from 2 s to 2 min. Peak frequencies and durations for four sample singles of pulses within buzzes were: (a) 1.72 kHz/141.9 ms, (b) 1.63k Hz/57.3 ms, (c) 4.64 kHz/32.3 ms, and (d) 4.38 kHz/67.6 ms (Figure 2). Although absolute source levels were not measured during these encounters, sound pressure levels and high frequency information has been recorded in other circumstances for this group of dolphins with peaks at 40–50 kHz, and 130–140 kHz and source levels of 210 dB re 1 μPa. Like the two phases described for bats (i.e., the search phase, and the terminal phase; Altringham, 1996) the dolphin buzz could have two different phases. During searching, the low repetition rate (200 Hz) is employed, and upon finding a prey item, an increase in repetition rate (500 Hz) is used while the prey is retrieved and possibly debilitated.

Wild feeding killer whales

Bangs recorded from the Johnstone Strait site had a relatively high amplitude compared to the echolocation clicks preceding them (Figure 3-A). Most bangs were low frequency, with energy concentrated <1 kHz (and often <500 Hz). We recorded both single bangs and sequences of bangs. Figure 3-B shows the oscillogram and power spectrum of two impulsive sounds emitted in close succession during a suspected feed on salmon in the San Juan Islands. The oscillograms and power spectra from the cliff site resembled the San Juan Island results, but with some variation (Figures 3-A,B). Rise-times from both sites were positive in pressure and averaged 1.0 ms.

In the Johnstone Strait cliff site, bang sounds were present in 16% of the total 102 recordings. We report here only the clearest cases in which both killer whales and salmon were seen. Bangs were present in each episode (100%). The average duration of 14 bangs was 113 ms. The average peak frequency of 9 bangs was 395 Hz. The average frequency range of nine bangs was 93 to 1422 Hz (n=9).

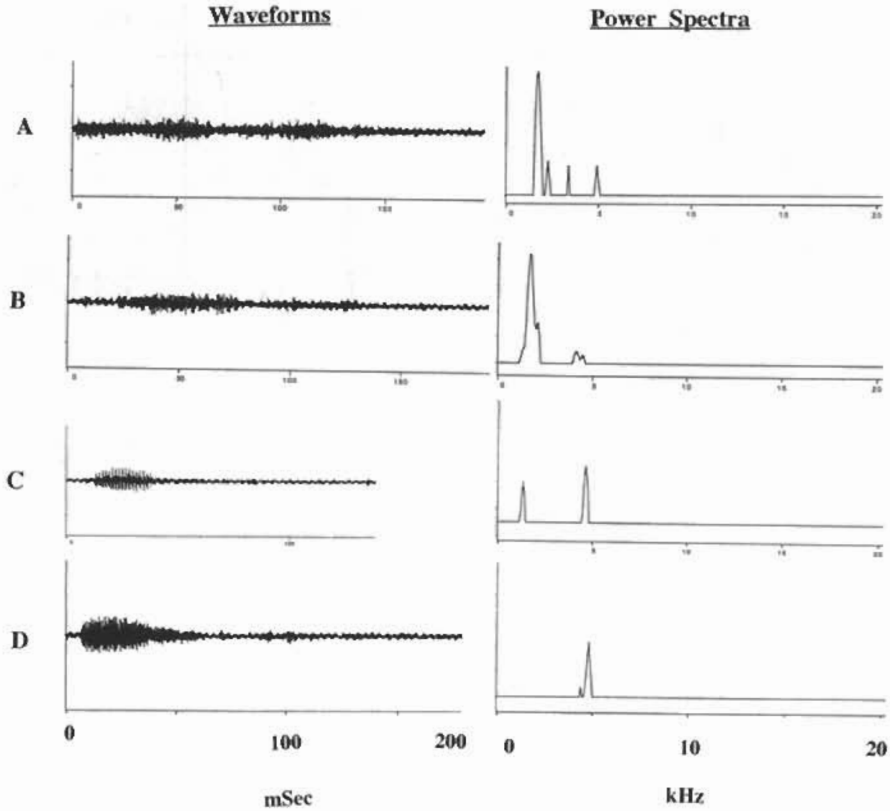

Figure 2. Peak frequencies and durations for four single pulses from Atlantic spotted dolphin buzzes: (A) 1.72 kHz/141.9 ms, (B) 1.63 kHz/57.3 ms, (C) 4.64 kHz/32.3 ms, and (D) 4.38 kHz/67.6 ms.

Feeding episode 1—One whale of A1 pod paralleled a fish at high speed and then engulfed it. There were three sets of sounds during this encounter: first a series of clicks followed by a bang, then 3 sounds that could be bangs, followed by a 'moan' and a final sound, followed by two louder clicks, and an intense scream.

Feeding episode 2—Many whales were feeding at night, and the water was bioluminescent, which allowed a clear view of the movement of whales and fish. A specific whale was observed chasing a fish, with the whale leaving a large bioluminescent trajectory and the fish a smaller trajectory. We could see the pursuit prior to the whale capturing the fish. The whale's head was pointed directly at the fish before eating it. Between the time the whale closed-in one the fish and ate it, five closely spaced bangs were heard. The bangs were greater in amplitude than the accompanying sounds and clicks, and the inter-bang intervals were uniform, averaging 800 ms. Later there were two bangs, preceded and followed by clicks.

Feeding episode 3—A pod was directly under the cliff and a salmon jumped. It appeared that the whales were after the salmon. Then a whale jumped out of the water, made a splash, and submerged. While the whale was under water there were three bangs. We do not know if they occurred before or after the capture.

Feeding episode 4—We saw splashing and quick movements, and old female (A2) suddenly appeared at the kelp edge with A50 (suspected to be a second-generation, direct matrilineal descendant of A2.) With the second surfacing, after some head-first, tail-up dives, A2 had a fish in her mouth. A50 surfaced next to A2 and they dove together. A2 then passed the fish to A50 under water. Young bull, A38, was seen at the same spot at the next surfacing. A38 is suspected to be a sibling of A50. A50 had nothing in its mouth, nor did A2. A gull picked up what looked like a fish scrap. Then, some other killer whales in pod A30 arrived as A2, A50, and A38 swam away. A30 was behind A38 by 20–30 m. There were four sets of bangs. Set 1 was

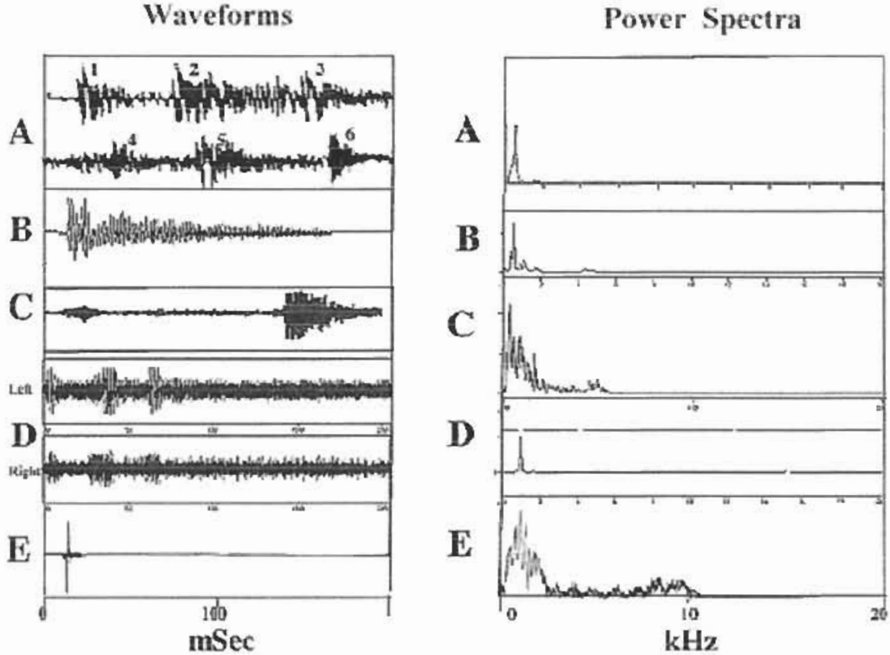

Figure 3. Representative waveforms and power spectra of high amplitude impulse sounds emitted during close pursuit of prey fish, from killer whale (*Orcinus orca*) and bottlenose dolphin (*Tursiops truncatus*) study sites and northern anchovy experiments. Waveforms 0-200 ms, power spectra 0–20 kHz, and an arbitrary y-scale, since absolute amplitudes were unknown. **A.** Killer whales observed under water chasing salmon from a cliff in Johnstone Strait, British Columbia. 1–5: The culminating bang sequence of Feeding Episode 4: five 'bangs' in quick succession, ranging from 40–90 ms, with a frequency range of 200–700 Hz, and an average peak frequency of 306 Hz. 6: Typical single short-duration bang recorded from the cliff while a salmon was chased and eaten by a killer whale. The power spectrum is the average power spectrum of 1–5. **B.** Bangs from Killer whales that appear to be feeding on salmon in the San Juan Islands. Oscillogram and power spectrum. Two 'bangs' in quick succession: peak frequency=600 Hz, durations approx. 100 ms. **C.** Pulses from Atlantic bottlenose dolphins feeding on mullet off the coast of Gulfshores, Alabama. Oscillogram and power spectrum. Peak frequency 400 Hz, duration 70 ms. **D.** Two bangs from a bottlenose dolphin in quick succession from underwater video recordings at Sea Life Park Hawaii during close, fast chase of live fish. Oscillogram and power spectrum. Peak frequency 1 kHz, durations 20–25 ms. The greater amplitude in the left channel indicated that sounds were emitted by a dolphin in the left half of the 2-hydrophone array field, which was the dolphin chasing the fish (trajectories in Figure 4). **E.** Sample oscillogram and power spectrum of the Bolt Model 10 Hydrogun. Peak frequency 800 Hz, duration 3 ms. Average sound pressure level at 1 m was 216.3 dB re 1 μPa. These sounds stunned and even killed northern anchovies (*Engraulis mordax*).

clicks, then 2 bangs, followed by possible crunches, grunts, and some highly pulsed sounds, then 3 screams. Set 2 had whistles, then 4 bangs. Shortly after, there were clicks, then a bang, a pause, and then 5 bangs (Figure 3-A, 1–5).

Bangs from the Johnstone Strait site fell into four categories of waveforms: (1) rapid onset and rapid decay (as in Figure 3A.6), (2) rapid onset and slow decay, sometimes having additional amplitude peaks after the first amplitude peak (as in Figure 3A.2 and possibly 3A.2–.3, together), (3) slow onset and slow decay, and (4) slow onset and slow decay, and low amplitude.

Bangs occurred either singly or in a rapid sequence. At the Johnstone Strait site, single bangs were most common (28 recorded), followed by 5 in sequence (12 sequences recorded), 4 in sequence (3 sequences recorded), 2 in sequence (2 'doublet' sequences recorded), and 3 in sequence (1 sequence recorded). Singles and doublets were most common at the San Juan Island study site.

Two other observations from the Johnstone Strait site are relevant to killer whale natural history: (1) food sharing between related individuals in feeding episode 4; and (2) a suggestion in the sound recordings that the whales repeat some calls back and forth during heightened levels of feeding.

Wild bottlenose dolphins off Alabama coast
Between 1740–1743h the bottlenose dolphin group produced 7 loud impulse sounds; four were single pulses, and three were doublets consisting of two clear and separate pulses. A sample waveform and power spectrum of one of the loud impulse sounds is shown in Figure 3C. At 1746h, the dolphins were joined by a second group of four dolphins. A third group (number of individuals unknown) arrived and rendezvoused with the other dolphins at 1747h, and a fourth group (number of individuals unknown) arrived at 1752h, thus forming one large, loosely organized school comprising of several sub-groups, all of which were engaged in milling or feeding. Between 1750–1807h, 42 separate loud impulse sound emissions were recorded. Twenty-seven were single impulses, 6 were composed of two nearly synchronous pulses, and 9 were doublets.

Laboratory experiment with live fish and dolphins at Sea Life Park, Hawaii
The dolphins showed intense interest and produced intense pulse sounds once live fish were introduced to the tank. The dolphins often chased the fish and emitted loud pulsed sounds. One of these chases is shown in detail in Figure 4. It was a quick chase with two click trains followed by two much louder 'bangs' (Figure 3D). The effects of the sound on the fish are unknown, because the fish disappeared out-of-view.

We know of no reports of bottlenose dolphin 'bangs' accompanied by underwater observations of the dolphin or the fish, let alone both. This observation was the first concrete, videotaped instance of a dolphin emitting bangs while closely chasing a fish. Although bangs have been recorded in wild situations showing all the signs of feeding (diving birds, and floating dead fish), this is the first documented case of the emission of bangs by a dolphin closely chasing a fish.

Effects of loud impulse sounds on northern anchovies
The anchovies lived in the vinyl bag for three days before the sound treatment, with only an occasional mortality, and only suffered debilitation and increased mortality on the day of the sound treatment, ruling out non-acoustic causes of death.

Figure 3E shows a sample waveform and power spectrum of the Bolt Hydrogun at a distance of 1 m. Rise-time of the waveform was negative pressure and averaged 0.75 s. The anchovies exposed to the Bolt Hydrogun initially had a startle and flight reaction, and then tended to swim in circular patterns, aggregating in the deepest area of the underwater enclosure, about 2–3 m from the sound source. In the latter half of the four hours of exposure to 693 pulses, the fish displayed ill effects from the sounds. Eventually, many of the fish jerked with each Hydrogun bang, and some swam rapidly and somewhat erratically in a corkscrew pattern. Ten of the anchovies were killed by the experiment. The dead individuals had dark patches of discoloration on the ventral surface.

Discussion

Wild Atlantic spotted dolphins off the Bahamas
In over 14 years, 315 observations of foraging, and 800 h of close-up underwater observations in the Bahamas not a single 'bang' was recorded. There could be many factors that explain the difference in strategy in sound debilitation. Atlantic spotted dolphins are small compared to bottlenose dolphins and killer whales. Sound production capabilities and uses could differ significantly by species. Also, prey species of Atlantic spotted dolphins in these observations were: (1) under the sand - providing a potentially acoustically 'cluttered' environment, requiring modified or different sound strategies or (2) small and perhaps stationary, compared to larger prey items moving freely in the water column. Both factors could significantly affect the sound strategy of the predator. In addition, the strategy of the prey to avoid or escape a predator, in this case dolphins, is unknown. In bats, the behavior, such as loss of equilibrium, 'freezing', or the 'evasion' strategy of the moth prey such as escape, determine subtle differences in the use of search and targeting strategies during the attempted capture by bats (Altringham, 1996). It could be that spotted dolphins and other odontocetes use 'bangs' when chasing larger prey in the water column, and a 'buzzing' strategy when retrieving buried prey.

Wild feeding killer whales
Killer whales made loud impulse sounds while chasing salmon. The chase could not be seen well enough to determine if something happened to the salmon at the time that the sound was emitted. The time-course and power spectrum of sounds (Fig. 1A, B) appeared to be similar to those collected from killer whales suspected to feed on salmon in Prince William Sound, Alaska (Marten *et al.*, 1988).

Recordings of *O. orca* have been made for a number of years in Johnstone Strait, but bangs have rarely, if ever, been detected (David Bain and John Ford, pers. comm.) Perhaps the killer whale feeding strategy is different in the water below the cliff in Johstone Strait, with the presence of a rock barrier,

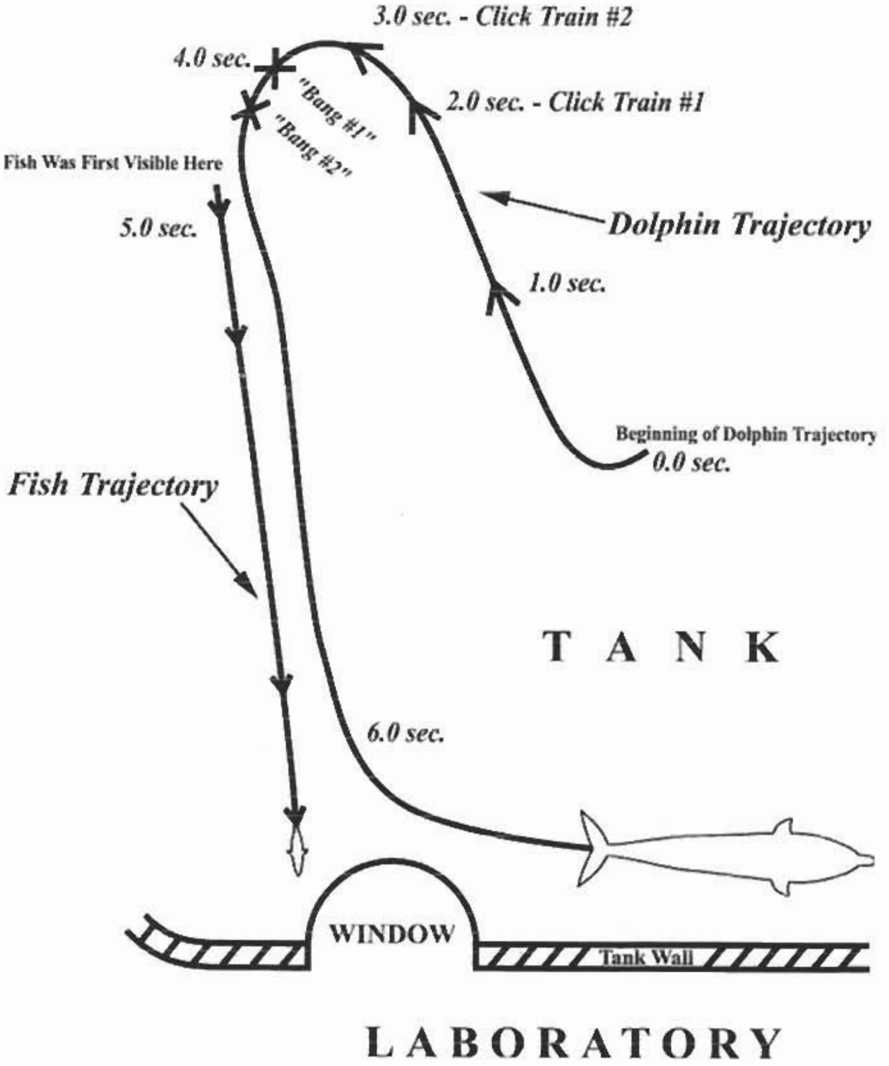

Figure 4. Top view of the track of the dolphin predator in a live fish experiment video-taped through an underwater window into the tank, showing where the two bangs were emitted, and where the fish went out of view. The dolphin followed 10–100 cm behind the fish at high speed for 7 s. The 20-m trajectory of fish and pursuing dolphin made a very strong 'hairpin' turn in it, where the fish rapidly turned to escape from the dolphin, and where the dolphin emitted the two bangs.

compared to waters further offshore, where there are no such barriers. The average peak frequency of cliff recordings of killer whale bangs was 395 Hz; close to the low frequency zone of best hearing in Atlantic salmon (*Salmo salar*), Hawkins & Johnstone, (1978).

We analyzed echolocation clicks and found them to have a positive pressure front. The bangs associated with the clicks also had a positive initial rise, which is consistent with being produced by the same source or mechanism. There could be an acoustic continuum between echolocation clicks and bangs, in which long, loud clicks grade into short, low amplitude bangs. By comparison, cavitation such as the Bolt Hydrogun, or possible cavitation from the flukes during breaching, has a negative pressure front. From the literature, however, some clicks seem to have a negative pressure rises (Purves 1983). It should be noted that a potential confounding source of sound, which could be recorded during predation, is the physical impact between the killer whale and salmon. The crunch-like sounds of salmon ingestion after bangs, on the other hand, were distinguishable from the bangs during the chase.

Bangs with slow onsets and long duration, both high and low amplitude, were not as closely associated with fish chasing, and could be sounds not produced at the animal's head. Loud impulse sounds during a breach were longer in duration (750 ms) and higher in peak frequencies (range 500–4500 Hz) than bangs during salmon chasing and capture.

Finally, the cliff site observation of food sharing between matrilineal direct descendants in feeding episode 4, at Johnstone Strait, is similar to the food sharing and hypothesized patrilineal kin selection of terrestrial social carnivores, such as African wild dogs, *Lycaon pictus* (Malcolm & Marten, 1982).

Wild bottlenose dolphin predation off Alabama coast

Bottlenose dolphins were recorded while feeding on mullet. The dolphins produced a wide variety of sounds, ranging from sounds similar to those of gibbons, to many pulsed sounds, and some single 'bangs'. Fishermen in two boats caught fish next to the dolphin school. Three separate schools of dolphins approached and joined the activity of the first school. This multi-group rendezvous and feeding aggregation was similar to the activities of dusky dolphins (*Lagenorhynchus obscurus*) reported by Würsig & Würsig (1980) during which one feeding school was joined by other schools, all of which participated in the fracas. The principal observer (M. Poole) entered the water with mask, fins, and snorkel, and the loud impulse sounds were clearly audible to him. He could not see the dolphins under water, but the strength and clarity of the 'bangs' suggested that they were, indeed, powerful.

Laboratory experiments with live fish and dolphins at Sea Life Park, Hawaii

The most interesting result of the live fish experiment was the video recording of the chase where the dolphin emitted a click train followed by two loud pulsed sounds. In this way, sounds were similar to those recorded previously from bottlenose dolphins in the wild suspected of feeding on fish (Marten *et al.*, 1988), and similar to the bangs in the Alabama case above. This is the only time such a chase and bangs have both been recorded simultaneously under water. Our sound recordings from suspected feeding situations in the wild in bottlenose dolphins (Marten *et al.* 1988) made us hypothesize that this kind of chase with sonar click trains followed by bangs occurred. It is interesting to have a first corroborating case of this from the easier-to-observe captive case; it provided at least a first link in interpreting the earlier sound-only data from boats.

Effects of loud impulse sounds on northern anchovies

Loud impulse sounds can debilitate and even kill northern anchovies. The Bolt Hydrogun sound pulse resembles wild odontocete bangs recorded during feeding in that it is a loud pulse of relatively low frequency (broadband, peaking at about 800 Hz). One of the most important acoustic variables harmful to fish is rapid rise-time. The quicker the rise-time, the more debilitating a sound is to fish (Hubbs & Rechnitzer, 1952). The rise-time of the anchovy-lethal Hydrogun is much faster than the slower, more innocuous Airgun.

We conducted an identical experiment with the Airgun, which did not kill as many anchovies as quickly as the Hydrogun. The Bolt Technology PAR-AIR© guns Environmental Impact Report (Chelminski, 1987) stated that slow rise-times of 2–5 ms is non-lethal to fish, while a few (sec is lethal. Analysis of the rise-times of the Bolt Hyrogun pulses showed them to average 0.75 ms; the killer whale bangs recorded in this study, from the Johnstone Straits and the San Juan Islands, had an average rise-time of 1.0 ms, which is only slightly slower than the Bolt Hydrogun. Another way in which the odontocete bangs differed from the Hydrogun was that their initial rise was positive, whereas the Hydrogun, with its cavitation mechanism, was negative.

Salmonids are affected by low frequency sounds. Vanderwalker (1967) played sounds to juvenile Chinook salmon (*Oncorhynchus tshawytscha*), rainbow trout (*Salmo gafrded)*, and brown trout (*Salmo trutta*). When the fish received the sounds while in a tank, they exhibited a loss of equilibrium, interrupted by short periods of erratic swimming, and attempted rapid escape by swimming until exhausted. When the sounds were played to the fish in an open channel with flowing water, the fish also showed an effect, although not as severe. They swam away from the sound, and habituated to it with repeated exposure.

In the experiment presented herein, repeated sounds of the Hydrogun debilitated and even kill northern anchovies. The effects probably derive from confining the anchovies close to the sound source and exposing them to repeated sound emissions. The Hydrogun waveform differs from odontocete bangs mainly in duration, only 3 ms compared to tens of ms in killer whale and bottlenose dolphin bangs. It is conceivable (but certainly not proved in this experiment) that longer duration odontocete bangs, with the ongoing repetition of the pressure wave, achieve a similar effect to the repeated exposure to the Hydrogun pulses. If true, the rapid onset, long duration bangs from the killer whales at the Johnstone Strait site, particularly those with multiple amplitude peaks, and bang sequences, represent active efforts by the killer whale to prolong the bangs and their effects. (Note that bangs with multiple amplitude peaks are probably the same as bang sequences occurring so fast that the previous bang has not yet decayed when the next is emitted.) Alternatively, bang sequences could represent sounds generated during locomotion. (The somewhat rhythmic, uniform 800 ms inter-bang intervals in feeding episode 2 are a possible case in point.)

The cause of the dark areas on the ventral surface of the dead anchovies could be abdominal hemorrhaging of the kind observed by Zagaeski (1987) when he subjected guppies to sounds of 250 dB re 1 μPa at 15 cm, with rise-times of less than 10 μs. The Bolt Model 10 Hydrogun also has been observed to kill blueback herring in a 4 m × 4 m confined space, and has been used with some success to exclude American eels from a reservoir intake structure (Paul Chelminski, pers. comm.). Some northern anchovies died in similar experiments we conducted, in which the fish were confined and exposed repeatedly to long-term output from the Bolt Technology Model 600 Airgun, which had a broadband low-frequency spectrum, which peaks at 200 Hz, and whose pulses lasted about 50 ms. Further investigations are needed to determine the effects of less exposure, as well as the effects of odontocete bangs.

Conclusions and future research

Data presented herein represent another step in understanding odontocete predation in the wild. If true, the acoustic predation hypothesis is an interesting evolutionary story in which two strategies evolved: (1) continuous buzzing by the Atlantic spotted dolphins, and (2) packaging the pulses into discrete loud buzzes by killer whales and bottlenose dolphins. 'Bangs' have been recorded previously, but the combined audio-visual information presented here ties the loud impulse sounds recorded during predation to chasing a particular fish. Bangs are louder than the sounds before and after them, hundreds of times longer in duration than echolocation clicks, and quite low in frequency (often 1 kHz) for odontocete sounds. Our data are consistent with the acoustic predation hypothesis, and consistent with the debilitation mechanism proposed by Marten *et al.* (1988) for exploiting and overloading the hearing apparatus of fish to cause deafness, disorientation, and/or damage. Further experiments with artificial impulse sounds could shed light on the kinds of acoustic characteristics, such as rise-time and amplitude, needed to debilitate fish. The next step is to evaluate the effects of loud impulse sounds on fish recorded from wild odontocete predation events, vary acoustic parameters, and assess the effects of this variation on fish debilitation. More data are needed from the wild to prove or disprove the debilitation hypothesis. The next step in collecting data from wild odontocetes is to extend simultaneous audio-visual data even further, to determine the effects of loud impulse sounds on fish and during capture.

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