

SOUNDS OF SEX AND DEATH IN THE SEA: BOTTLENOSE DOLPHIN WHISTLES SUPPRESS MATING CHORUSES OF SILVER PERCH

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ABSTRACT

Prey often exhibit avoidance behaviors when predators are present. We observed diminished loudness of mating choruses of male silver perch *Bairdiella chrysoura* in spawning areas when vocalizing bottlenose dolphins *Tursiops truncatus*, which hunt fish acoustically, were present. Experimental playback of bottlenose dolphin sounds revealed that male silver perch mating calls were reduced by an average of 9 dB. This “acoustical avoidance” behavior, demonstrated previously for interactions involving bats hunting insects and frogs, may also be a common phenomenon in acoustically mediated predator-prey interactions in the sea.

Keywords: Underwater acoustics, marine mammal vocalizations, soniferous fish signals, predator avoidance, playback experiment

INTRODUCTION

Successful avoidance of predators by prey often requires that prey reduce the conspicuousness of their visual, olfactory, or other cues. This signal reduction inhibits the predators from successfully locating their prey. In addition to visual and olfactory cues, prey often produce acoustical cues for the purpose of mating, including the periodic choruses produced by males advertising for mates in insects (Alexander 1975, Sismondo 1990, Hoy 1991, Greenfield 1994), anurans (Wells 1988, Schwartz 1994), and fishes (Fish and Mowbray 1970). “Acoustical avoidance” of predators, also known as prey adaptive silence (Curio 1976), has been shown to be one reason that chorusing insects and frogs cease sound production (Tuttle and Ryan 1982, Tuttle et al. 1982, Spangler 1984). Other hypothesized reasons for the

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cessation of sound production in insects and frogs include avoiding interference from sounds produced by other chorusers, female preference for males that periodically chorus, short-term muscle fatigue and long-term energy conservation (Zelick and Narins 1982, Schwartz 1991). However, it is not known why certain species of fish stop producing their male advertisement choruses.

Silver perch *Bairdiella chrysoura* (Pisces: Sciaenidae) are marine fish in which breeding males produce nocturnal advertisement calls (Mok and Gilmore 1983) in unison-bout choruses that are associated with spawning (Fish and Mowbray 1970, Luczkovich et al. 1999). Along the Atlantic Coast of North America, silver perch compose up to 32% of bottlenose dolphin *Tursiops truncatus* diets (Barros and Odell 1990). Barros and Myrberg (1987) hypothesized that soniferous fish mating choruses, which are the "sounds of sex", may also increase the choruser's risk of predation by the acoustically oriented bottlenose dolphin. Thus, these authors proposed that bottlenose dolphin may find prey by passive listening.

In this investigation, we test the hypothesis that silver perch respond to bottlenose dolphin vocalizations by exhibiting "acoustical avoidance". With recordings made in Pamlico Sound using custom-built autonomous sonobuoys, we detected the cessation of nocturnal advertisement choruses when bottlenose dolphin are vocalizing near silver perch spawning aggregations. Using playback experiments, we show that the bottlenose dolphin whistles cause this "acoustical avoidance" by chorusing male silver perch.

MATERIALS AND METHODS

Sonobuoy recordings

In order to document variations in the loudness of silver perch choruses and other soniferous organisms, we deployed eight autonomous recording sonobuoys daily during peak spawning season (18-21 May 1998) in water depths of 1-6 m at random positions within a 10 km × 10 km grid superimposed over Ocracoke Inlet, North Carolina, USA. The custom-built sonobuoys suspended a hydrophone (Goulton Industries, Inc. GLN-9190) below the water surface and enclosed a cassette tape recorder (Sony TCM-313) with a programmable timing circuit. Each sonobuoy was anchored and programmed to record for 90 s every 15 min from two hours before sunset (1800 local time EDT) until 0200 hours on the following morning. We sampled the sonobuoy recordings at 24,000 Hz using an analog to digital board (National Instruments NB-A2150F) with anti-aliasing filters connected to a Power Macintosh computer.

Spectrographic analyses

We analyzed the frequency content of recorded sounds using power spectra, average power spectra and spectrographs. Power spectra are plots of the acoustic power in the signal as a function of frequency. The power spectral density is defined as the acoustic power in individual frequency components of a power spectrum. For example, a 1-Hz wide component of a power spectrum with a power spectral density of 95 dB represents the same acoustic power as a 95-dB sine wave. We produced all power spectra using 1024-point Hanning-windowed Fast Fourier Transforms (FFT's) of the sampled recordings.

An average power spectrum has frequency components that are the averages of frequency components from individual power spectra in successive time windows. This calculation averages out the contributions of transient sounds and emphasizes frequencies present throughout the signal. We used average power spectra to emphasize the average frequency components in a signal over short periods of time (< 1 min).

Changes in the frequency content of successive power spectra were visualized using spectrographs, which are three-dimensional plots of time on the horizontal (x) axis, frequency on the vertical (y) axis and power spectral density shown as varying shades of gray representing the third (z) axis. Thus, a vertical (y - z) slice of a spectrograph is a power spectrum. We analyzed sounds using two types of spectrographs, continuous spectrographs and composite spectrographs.

Continuous spectrographs have no time gaps between the successive power spectra. As a smoothing technique in continuous spectrographs, we chose overlapping time windows for successive power spectra, which causes the spectrograph to appear less "grainy" along the time axis. Continuous spectrographs are useful for analyzing frequency components during short time intervals (< 1 min) within a recording. However, producing continuous spectrographs of longer recordings requires large amounts of computation time and computer memory, so we chose a sampling technique to produce composite spectrographs for long recordings.

Composite spectrographs have a time interval (gap) between the windows used for power spectra. For example, our sonobuoys make a 90-s recording every 15 min producing a data tape during a single night with 33 segments that last a total of 49.5 minutes. However, this tape actually represents the sound recordings from a time period of 8.3 hours. A composite spectrograph of one night's sonobuoy data consists of one average power spectrum for every 5 s on the data tape plotted as a function of time. Each 90-s sample on the tape is represented by 18 successive average power spectra in the spectrograph. Although there is 13.5 min in between each 90-s sample, power spectra from each sample are shown next to each other in the composite

spectrograph. Thus, each 90-s sample is taken as being representative of an entire 15-min time interval. Composite spectrographs emphasize long duration sounds such as those of fish choruses lasting for hours and de-emphasize short duration sounds such as dolphin vocalizations lasting less than 10 s.

Playback experiments

To test our hypothesis that chorusing male silver perch were acoustically avoiding bottlenose dolphin, we conducted playback experiments at the docks of the National Marine Fisheries Service, Beaufort Laboratory, Beaufort, NC, in the Newport River. In the playback experiment, we played the test sounds through an underwater speaker (Model DRS-8, Ocean Engineering Enterprises, North Canton, OH) 2 m below the water surface. We recorded all sounds using a digital audio tape (DAT) recorder (Sony model TCD-D8 recorder, frequency range: 20-22,000 Hz \pm 1 dB, sampling frequency: 48,000 Hz), an InterOcean Model 902 Acoustic Listening and Calibration System, (frequency range: 20-10,000 Hz) consisting of an InterOcean Model T-902 hydrophone (omnidirectional with sensitivity -195 dB Nominal re 1 V/ μ Pa) connected to an amplifier (gain adjustable from 15 dB to 95 dB in 10 dB increments plus vernier adjustment) with a rectifier-type AC meter (peak deflection within 3 dB of continuous signal for 100 ms pulse) calibrated in dB re 1 μ Pa. The hydrophone was placed 2 m below the water surface and 2 m from the speaker. To reduce size of the data set and computation time, we subsampled digital recordings from 48,000 Hz to 24,000 Hz using anti-aliasing filters.

We recorded mating calls of free-ranging male silver perch before and after playing the whistle of bottlenose dolphin for 10 s through the underwater speaker. Figure 1 is a continuous spectrograph of the bottlenose dolphin whistles used for the dolphin sound playback. These whistles were recorded in October 1998 in Pamlico Sound, NC. In addition to the bottlenose dolphin sounds, the recording has background noise associated with an estuarine environment, which had no effect on the silver perch behavior. We played back the dolphin sounds at 145 dB re 1 μ Pa measured by the meter connected to our hydrophone. This level is within the range of sound levels produced by bottlenose dolphin (Tyack 1985).

We separated silver perch contributions to the recorded sounds by measuring the peak of the power spectrum in the silver perch range of frequencies, 950-1200 Hz (Luczkovich et al. 1999). As an indicator of the silver perch contribution to the overall sound level (silver perch loudness), we calculated the average power spectrum for a 10-s interval (234 successive power spectra) and used the peak power

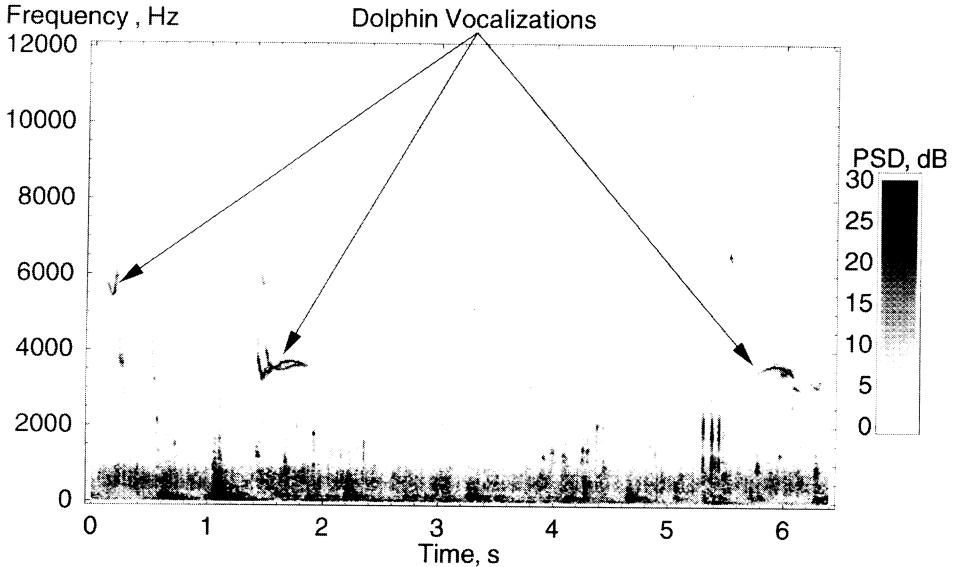


Figure 1. A continuous spectrograph of the recording of bottlenose dolphin sounds used for the playback experiment. The arrows indicate the bottlenose dolphin sounds. The recording was sampled at 24,000 Hz, and Fast Fourier transforms were taken on 1024-point Hanning windows with 256 samples between the beginning of each successive Fast Fourier Transform. The power spectral density is shown on a relative scale with 0 dB representing the background level.

spectral density (PSD in dB) in those frequencies. We measured the silver perch loudness averaged over 10-s intervals immediately before and from 20–30 s after the sound playback began.

As silver perch choruses fluctuate in sound pressure level naturally due to the behavior of the fish, the mean loudness of their mating calls following dolphin whistle playbacks was compared with two control treatments using an Analysis of Covariance (ANCOVA). The loudness of the silver perch mating chorus during the 10-s interval immediately prior to the dolphin whistle or the control treatments was used as a covariate. Two types of control treatments were performed on the same night and at the same place as the dolphin whistle playback treatment: 1) to determine changes in loudness that may occur at random or due to other unexplained factors, we measured mean silver perch loudness immediately before and 20–30 s after an *ad-hoc* selected point during a 120-s recording of a silver perch chorus (the “no sound” treatment) and 2) to control for the startle effect of playing any sound, we measured the silver perch loudness immediately before and 20–30 s after playing a 700-Hz tone through the speaker (the “tone” treatment). No biologically produced

sounds we have measured thus far in the underwater environment of North Carolina are similar to that particular frequency.

RESULTS

Sonobuoy recordings

Bottlenose dolphin vocalizations were associated with diminished loudness of the mating chorus of male silver perch. Figure 2 is a composite spectrograph made from a typical sequence of recordings of silver perch chorusing on 19-20 May 1998 in Ocracoke Inlet prior to, during, and after bottlenose dolphin vocalizations. Bottlenose dolphin vocalizations are not visible on this composite spectrograph because the duration of the vocalizations is too short to be resolved on the long time scale. From 1807 EDT until midnight, most of the sound energy in the spectrograph is between 1000 and 2000 Hz, which is characteristic of silver perch choruses (Fish and Mowbray 1970, Mok and Gilmore 1983, Luczkovich et al. 1999). However, at 0024 EDT, bottlenose dolphin whistles were recorded and are clearly visible in the continuous spectrograph of that tape sequence (Figure 3). In addition

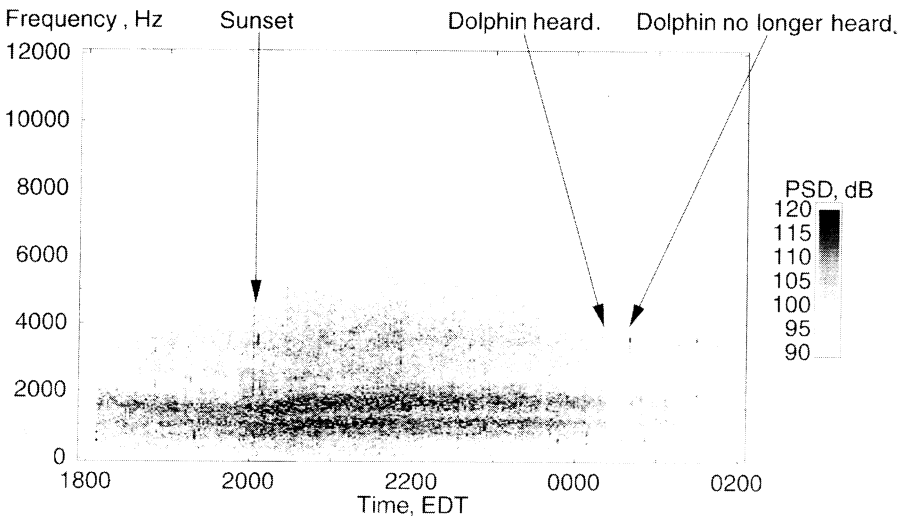


Figure 2. A composite spectrograph of a sonobuoy recording made May 19-May 20, 1998 in Pamlico Sound (North Carolina, USA). The recording was sampled at 24,000 Hz, and Fast Fourier Transforms were taken on 1024-point Hanning windows spaced every 5 s on the recording. There is a time gap of 13.5 min between each set of 18 power spectra in this spectrograph. All sounds are measured re 1 μ Pa.

to the bottlenose dolphin sounds indicated by the arrows, the spectrograph also contains noise produced by the sonobuoy bobbing in the waves. This wave noise appears as broadband vertical lines in the spectrograph. There was a decrease in loudness of the silver perch chorus from 103.9 dB to 94.9 dB during 10-s intervals at 0009 EDT and 0025 EDT, respectively. This 9 dB attenuation represents an approximate 8-fold drop in sound intensity. After 0100, bottlenose dolphin whistles were no longer heard and silver perch chorusing resumed (Figure 2). This sequence of events was repeated on 7 separate sonobuoy recordings made in May 1998.

Playback experiments

A similar response was observed during our bottlenose dolphin whistle playback experiments at the Newport River. Figure 4 shows an example of the silver perch response to the “whistle” playback (a series of bottlenose dolphin whistles shown as a spectrograph in Figure 1) and “tone” (700-Hz control tone) playback. The “no sound” measurements were taken during the 120-s segment preceding each trial when no sounds were being played. There was significant decrease in loudness of the silver perch mating chorus after playing

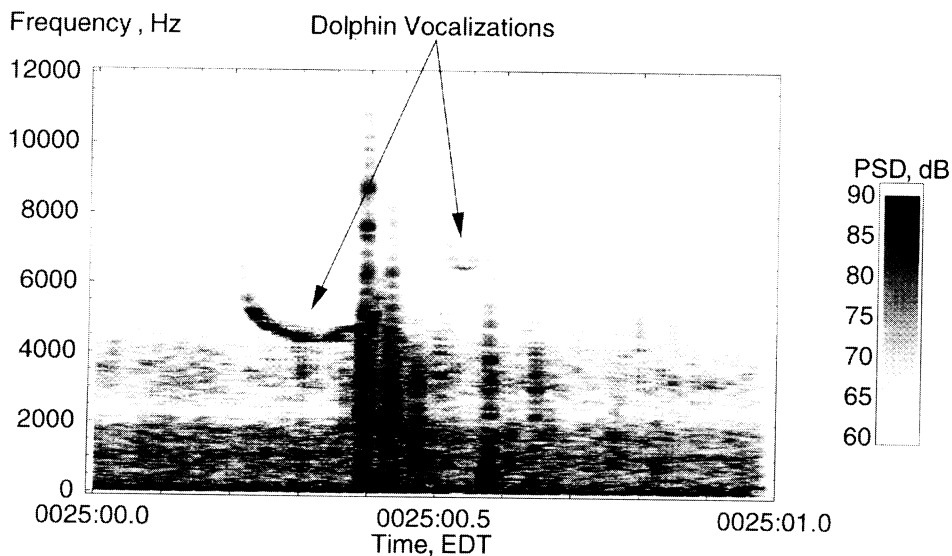


Figure 3. A continuous spectrograph of a segment of the same sonobuoy recording shown in Figure 2. The recording was sampled at 24,000 Hz, and Fast Fourier Transforms were taken on 1024-point Hanning windows with 64 samples between the beginning of each successive Fast Fourier Transform. All sounds are measured re 1 μ Pa.

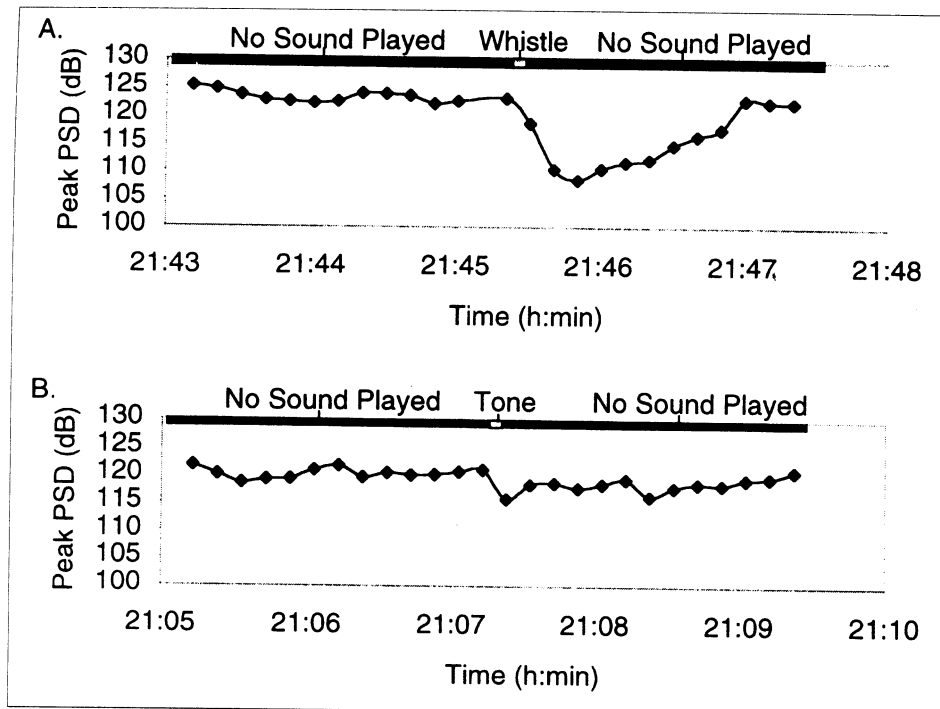


Figure 4. Time variation of silver perch loudness during the playback experiment. The sound was sampled at 24,000 Hz, and the average power spectrum is calculated over a 10-s interval using successive 1024-point Hanning windows. The peak value in the silver perch range (950 - 1200 Hz) is plotted vs. time. All sounds are measured re 1 μ Pa. A. An example of the silver perch response to whistle playback. B. An example of the silver perch response to the tone playback.

the "whistle" sound relative to the loudness after the "tone" and "no sound" control treatments (Figure 5). The silver perch chorus loudness, adjusted for the covariate, averaged $110.4 (\pm 1.01)$ and $110.8 (\pm 1.13)$ dB for the "no sound" control and the 700-Hz "tone", respectively. The power spectral density for silver perch mating calls fell to an average of $101.8 (\pm 1.01)$ dB after a dolphin whistle was played, a significant decrease of 9 dB [ANCOVA, $P = 0.000001$ (among playback treatment adjusted means), $P = 0.13$ (among slopes of regression lines for each treatment), $R^2 = 0.81$, $n = 54$].

DISCUSSION

Our observations indicate that acoustic signaling by silver perch may not only increase the possibility of attracting a mate (Mok and Gilmore

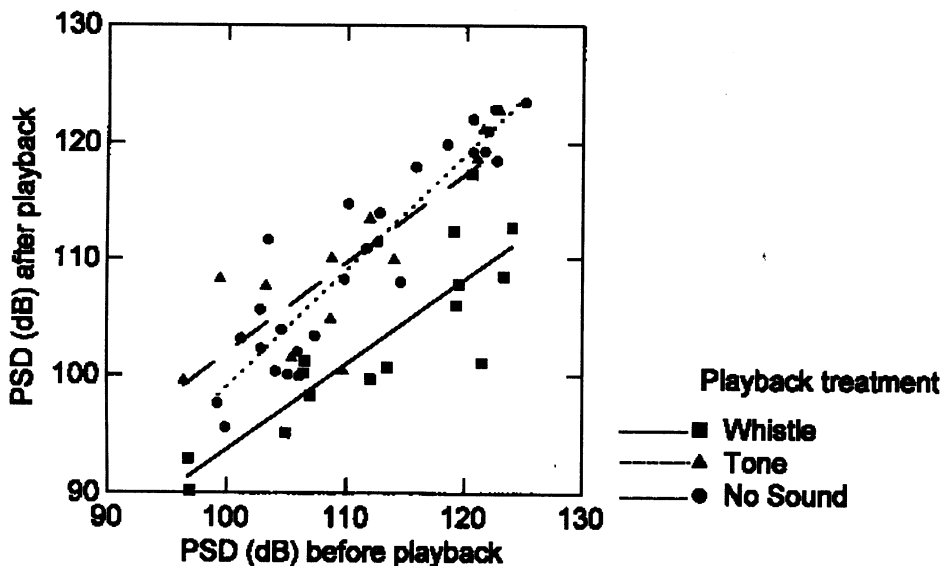


Figure 5. Loudness (dB re 1 μ Pa) of silver perch *Bairdiella chrysoura* mating chorus during a 10-s interval immediately before playback of the experimental sound source plotted against the loudness of the chorus 20-30 s after a playback. Experimental sound sources were: a 10-s recording of bottlenose dolphin *Tursiops truncatus* whistles; a 10-s recording of a 700-Hz tone. Also shown is the loudness (dB re 1 μ Pa) of silver perch mating calls before and after an *ad-hoc* point in a 120-s recording of mating calls (“no sound” treatment). The before playback loudness was used as the covariate in an ANCOVA.

1983), but also may increase the risk of predation by bottlenose dolphins. In an evolutionary response to this threat, silver perch exhibit “acoustical avoidance”. Whistles produced by bottlenose dolphins indicated their presence in the vicinity of the sonobuoys and were associated with the interruption of silver perch chorusing on seven occasions. Human disturbance is not likely to have caused the interruptions, as the sonobuoy recorders were triggered electronically and no boat noise was recorded in the vicinity of the sonobuoys. Our playback experiments demonstrated that the silver perch responded to bottlenose dolphin whistles by ceasing their chorusing, which lowers the measured sound pressure levels. This diminished sound pressure level is most likely due to the cessation of sound production by individual silver perch close to the sound source, with the continued chorusing of distant male silver perch and other biological and non-biological noises in the background (background levels are typically around 100 dB). An alternate explanation is that fish in the vicinity of the sound source and hydrophone responded to the dolphin whistle

playback by swimming away from that location, causing a decrease in the loudness of the chorusing.

The duration of the lowered sound pressure levels was relatively short (~ 60 s) in the playback experiment, but longer in the field sonobuoy recordings (> 90 s, the length of a sonobuoy recording). This difference in duration of the lowered chorusing could be explained by the continued presence of bottlenose dolphins near the sonobuoy during the recording and other stimuli associated with their foraging (echolocation vocalizations, visual cues, chemical cues and water disturbances). In the playback experiment, no significant difference was detected in the silver perch chorus loudness when no sound was being played or when a continuous 700-Hz tone, a sound frequency not associated with any particular species of fish or mammal, was played for 10 s. Thus, the silver perch in the area where we conducted the experiment were not responding to novel sounds in the environment that might have evoked an avoidance response. We found no evidence that any of the male silver perch produced an alarm call to alert others in the chorusing group to cease calling, although this type of signaling cannot be ruled out.

As a large proportion of the bottlenose dolphin diet is composed of soniferous fishes, dolphins may detect aggregations of prey by passive listening (Barros and Odell 1990) as well as by ultrasonic echolocation. Our studies support this suggestion. The detection of simulated ultrasonic bottlenose dolphin sounds by American shad *Alosa sapidissima* has recently been verified in the laboratory (Mann and Popper 1997). However, American shad are sensitive in the ultrasonic range (80-100 kHz) as well as frequencies lower than 10 kHz (Mann et al. 1998). As bottlenose dolphin ultrasonic echolocation clicks would not be detected by our recording sonobuoy system, we do not know if the dolphins were producing ultrasonic sounds in the vicinity of the silver perch chorusing. To our knowledge, there are no audiograms of silver perch, so we do not know if the silver perch would respond to ultrasound by ceasing unison-bout chorusing. Nonetheless, based on our playback experiment, it is clear that free-ranging silver perch were induced into reducing their chorusing intensity by dolphin whistles in the 3000-8000 Hz range. Such whistles are thought to function as signals within dolphin groups and are not used for echolocation (Caldwell et al. 1990). Thus, it appears that silver perch responded to the signature whistles of bottlenose dolphins by exhibiting "acoustical avoidance".

Silver perch individuals that ceased to make sounds when acoustically sensitive predators were nearby would be favored by natural selection. The most parsimonious explanation for the silver perch response to the bottlenose dolphin whistles is that the fish have evolved prey adaptive silence behavior and thus stop producing sounds that give away their location to the acoustically sensitive predator. In

a dark, turbid environment such as Pamlico Sound, such an evolved response would provide a reliable way of avoiding the predatory dolphin, thus the whistle being a "sound of death".

Our findings provide further support for the predation hypothesis for explaining why chorusing animals cease calling, although the long-term energetic costs of continued calling may also contribute to the observed periodicity in chorusing. Thus, Winston Bailey's axiom (Bailey 1991) "As a general rule it is better to mate tomorrow than be eaten today" appears to hold true for silver perch as well as insects and frogs.

ACKNOWLEDGEMENTS

We would like to thank Arthur Popper for reviewing an earlier version of this manuscript and suggesting improvements. We would also like to thank the North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries and the U.S. Fish and Wildlife Service for making funding possible to do this project under the Sportfish Restoration Program (Contract F-62). Finally, we are grateful to the Beaufort, North Carolina laboratory of the National Marine Fisheries Service for allowing us to use their docks for the playback experiments.

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Received 26 August 1999, revised 23 November 1999 and accepted 1 December 1999.