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To Whistle or Not to Whistle? Geographic Variation in the Whistling Behavior of Small Odontocetes

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Abstract

Whistles are used by odontocetes to varying degrees. During a visual and acoustic survey of dolphin abundance in the eastern tropical Pacific Ocean (ETP), whistles were heard from 66% of single species schools and from 98% of mixed species schools. In contrast, whistles were heard from only 24% of single species schools and 23% of mixed species schools during a survey of temperate waters off the western United States. The most common species encountered in the ETP were *Stenella coeruleoalba*, *S. attenuata*, and *Tursiops truncatus*, all of which whistled frequently. The most common species encountered in the temperate study area were *Delphinus delphis*, *Phocoenoides dalli*, *Lissodelphis borealis*, and *Phocoena phocoena*, only one of which whistled (*D. delphis*). Why do small odontocete species living in the ETP whistle more frequently than those living in colder waters farther north? Six hypotheses are explored: (1) predator avoidance, (2) group size, (3) school composition, (4) behavior state, (5) temporal variation, and (6) anatomical differences. Multivariate logistic regression with whistling as the dependent variable and group size, school composition, time of day, presence of a beak, and study area as independent variables showed that all variables were significant ($p < 0.001$). An explanation of the aggregation of whistling species in the tropical study area and nonwhistling species in the temperate study area is likely found in some combination of the hypotheses discussed.

Key Words: whistling behavior, odontocete, hydrophone array, passive acoustic monitoring, delphinid, phocoenid

Introduction

Odontocete cetaceans produce a considerable diversity of acoustic signals, which have generally been placed into three distinct categories: (1) echolocation clicks, (2) burst pulse sounds, and (3) whistles. Echolocation clicks are short, broadband pulses with peak frequencies that vary from tens of kilohertz (e.g., rough-toothed dolphins, *Steno bredanensis*, Norris & Evans, 1966) to well over 100 kHz (e.g., bottlenose dolphins, *Tursiops truncatus*, Au, 1980; Dall's porpoises, *Phocoenoides dalli*, Hatakeyama & Soeda, 1990). These clicks have a rapid rise time and short duration, ranging from approximately 50 µs (e.g., *T. truncatus*, Au, 1980) to 400 µs (e.g., *P. dalli*, Hatakeyama & Soeda, 1990). Echolocation clicks generally occur in trains containing few to hundreds of clicks and are used for navigation and object detection and discrimination (Au, 1993). Burst pulse signals are broadband click trains with very short inter-click intervals. These sounds take on a tonal quality to human ears because the clicks are repeated at such high rates that the rate itself, rather than the individual clicks, is audible (Watkins, 1967; Herzing, 2000). Burst pulses have been qualitatively described using many terms such as buzzes, creaks, pops, and squeals (Caldwell & Caldwell, 1967; dos Santos et al., 1990; Herzing, 1996). It is thought that these signals play a role in social interactions, although they may also function in echolocation tasks (Overstrom, 1983; Herzing, 1996). Whistles are continuous, narrowband, frequency-modulated signals that often have harmonic components. They range in duration from several tenths of a second to several seconds (Tyack & Clark, 2000). The fundamental frequency of most whistles ranges from 2 to 20 kHz, although whistles with fundamentals extending to almost 35 kHz have been reported for several species (Lammers et al., 2003; Oswald et al., 2004). Whistles are believed to function as social signals (Janik & Slater, 1998; Herzing, 2000; Lammers et al., 2003).

Since many whistles have fundamental frequencies below 20 kHz and can be recorded using standard audio equipment, studies examining social communication have focused on these signals rather than higher frequency burst pulses. This emphasis has led to the assumption that whistles are the primary social signals for odontocetes. However, several species, including members of the families Kogiidae, Physeteridae, and Phocoenidae and of the subfamily Cephalorhynchinae do not produce whistles (Schevill et al., 1969; Watkins et al., 1977; Herman & Tavolga, 1980; Watkins & Wartzok, 1985; Tyack, 1986; Dziedzic & De Buffrenil, 1989; Dawson, 1991; Ridgway & Carder, 2001; Madsen et al., 2005; Morisaka & Connor, 2007). These species are thought to communicate exclusively through pulsed sounds (Herman & Tavolga, 1980; Dawson, 1991).

May-Collado et al. (2007) examined relationships among species that whistle frequently and those that whistle infrequently or not at all by summarizing data from over 300 studies on cetacean tonal sounds and social structure and phylogenetically testing existing hypotheses on their co-evolution. Their phylogeny of 66 cetacean taxa was based on Cytochrome b sequences and provided a detailed phylogenetic hypothesis representing 63 species and 24 outgroups (May-Collado & Agnarsson, 2006). Based on their results, two possible scenarios emerge: (1) whistles may have evolved independently twice—once in Baird's beaked whales (*Berardius bairdii*) and once in the node leading to delphinoids plus river dolphins and Platanista, with secondary losses in Phocoenidea and within Delphinidae (*Cephalorhynchus* spp. and *Lissodelphis* spp.), and (2) whistles may have evolved once in the common ancestor of the ziphiids, river dolphins and Platanista, and delphinoids, with secondary losses in Hyperoodon, Phocoenidae, and within delphinids.

What pressures drove the evolution and secondary losses of whistling behavior? Answers might be found by examining the geographic distribution of whistling vs nonwhistling species. Here, we present data that suggest that whistle use by odontocetes varies geographically. We will also discuss six hypotheses that might explain why species in the eastern tropical Pacific Ocean (ETP) whistle more frequently than species in the eastern North Pacific Ocean.

Materials and Methods

Acoustic recordings were made during two shipboard line-transect surveys conducted by the Southwest Fisheries Science Center (NOAA, NMFS). The Stenella Abundance Research (STAR) survey took place in the ETP from 28 July to 9 December 2000. The study area extended from the United States/Mexico border southward to the territorial waters of Peru, and from the continental shores of the Americas west to the longitude of Hawaii (Figure 1). This area will be referred to as the tropical study area.

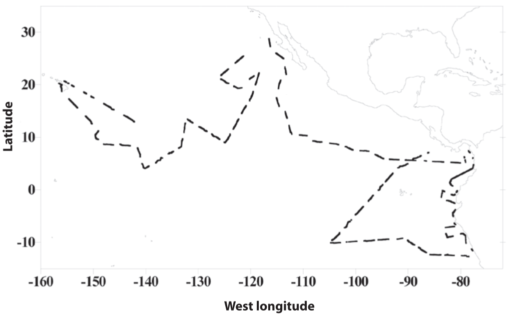

Figure 1. ETP study area and trackline of acoustic effort for the STAR 2000 marine mammal abundance survey

The Oregon, California, and Washington marine mammal survey (ORCAWALE) took place in the eastern north Pacific from 30 July to 8 December 2001. The study area extended from the coast of Washington, Oregon, and California, out to a distance of approximately 300 nmi (Figure 2). This area will be referred to as the temperate study area.

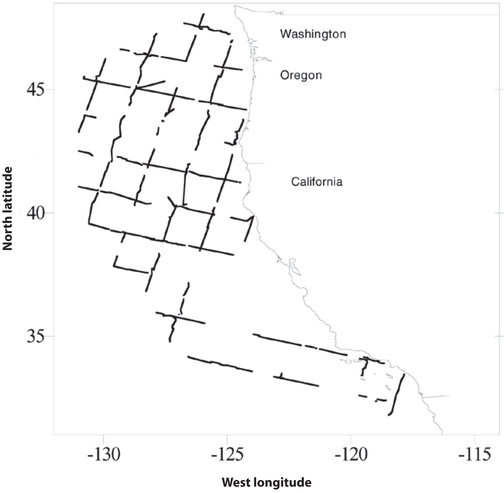

Figure 2. Temperate study area and trackline of acoustic effort for the ORCAWALE 2001 marine mammal abundance survey

During both surveys, a team of three experienced biologists actively searched for marine mammals using two sets of 25 × 150 binoculars and by naked eye in Beaufort sea states of 5 or below. When cetaceans were sighted, the visual observers went *off-effort* and approached the sighting for species identification and group size estimation. Sightings made while observers were off-effort were not approached. Group size was estimated independently by each observer. Group sizes reported here are simple arithmetic averages of the observers' best estimate for each group. Groups were generally widely separated during these open ocean surveys. In the uncommon situation in which there was confusion regarding group boundaries, a consensus decision was made among observers. Time spent with each group ranged from minutes to hours.

Cetacean vocalizations were monitored and recorded using a towed hydrophone array. The array was towed 300 m behind the research vessel at a depth of approximately 4 to 6 m during daylight hours and when Beaufort sea state was less than 6. Two arrays built by Sonatech Inc. (Santa Barbara, California), were used during both surveys: a five-element array (flat frequency response +4 dB from 2 kHz to 45 kHz at -132 dB re: 1 v/µPa after internal amplification) and a three-element array (flat frequency response +3 dB from 2 kHz to 120 kHz at -164 dB re: 1 v/µPa after internal amplification). Signals from both arrays were sent through a Mackie CR1604-VLZ mixer for equalization and were recorded using a Tascam DA-38 eight-channel digital recorder (48 kHz sampling rate). Recordings were also made directly to the computer hard drive via an analog-to-digital conversion card (National Instruments DAQCard-6062E) using a 200-kHz sampling rate.

An acoustic technician monitored signals from two hydrophones in the array using a stereo headset and real-time scrolling spectrographic software (*Ishmael*, Version 1.0) (Mellinger, 2001). *Whaltrak*, a custom-written mapping software by J. Barlow with a GPS-interface, automatically logged time and position every 5 min while the array was being monitored. A time-stamped comment noting acoustic activity was entered into *Whaltrak* at 5-min intervals. The acoustic technician was *on-effort* whenever the towed array was in the water and went off-effort when the visual observers went off-effort to approach a sighting.

Confirmation that the dolphin schools sighted produced the vocalizations detected was obtained by comparing the angle and distance of acoustic detections with the location of the sighting. Bearing angles to vocalizations were determined using phone-pair cross-correlation algorithms in *Ishmael*, and distance was determined by examining the convergence of bearing angles plotted on *Whaltrak*. The convergence of bearing angles was continually examined to determine the location and cohesiveness of dolphin schools. In the open ocean, most schools are distinct groups that are easily distinguished using this method. Periods of high density require finer detail examination of the convergences of bearing angles, and school boundaries were determined based on visual observations and knowledge of the behavior of the species in question. This analysis was done in real time and reconfirmed by post-processing back on land.

When a group was detected acoustically before it was seen, localization continued until the group was sighted. If the acoustic location matched the location of the sighting, it was considered to be the same group. Acoustic detection distance was defined as the greatest distance at which the vocalizing dolphins could be successfully localized. Angle and distance to visual sightings were determined using angles and reticles marked on 25 × 150 "big-eye" binoculars.

Results

During the tropical survey, 17,337 km of trackline were surveyed visually, and 9,274 km were surveyed acoustically (Figure 1). There were 420 sightings of delphinid schools during this survey. A total of 224 of these schools were encountered while the acoustics team was on effort. Out of these 224 schools, 158 were detected both visually and acoustically, and 66 were only detected visually. *Detected acoustically* refers to the detection of any or all of the three vocalization types (whistles, clicks, and burst pulses).

Visual effort during the temperate survey covered 7,432 km of trackline, and acoustic effort covered 8,132 km of trackline (Figure 2). There were 337 sightings of delphinid and phocoenid species during this survey, with 219 of those encountered while the acoustic team was on effort. Out of these 219 schools, 88 were detected both acoustically and visually, and 131 were only detected visually. Only sightings detected while the acoustic team was on effort were included in further analyses.

Tropical Visual Results

The most commonly sighted species during the tropical survey were striped dolphins (*Stenella coeruleoalba*), spotted dolphins (*S. attenuata*), and bottlenose dolphins (Table 1). Most species encountered during this survey were found in mixed species schools at least some of the time, and 28% of sighted schools were mixed species schools.

Large group sizes (Table 1) were common in the tropical study area (mean = 91.4 individuals, SD = 178.8). Species with the largest mean group sizes were long-beaked common, short-beaked common, spinner, and spotted dolphins. Dusky dolphins (*Lagenorhynchus obscurus*) also had a large mean group size, but this result was skewed by one very large mixed-species school (group size = 1,167 individuals). Without this sighting, the mean group size for dusky dolphins was 39.9 individuals (SD = 35.7). Species with the smallest group sizes included pygmy killer whales (*Feresa attenuata*), rough-toothed dolphins, and Risso's dolphins (*Grampus griseus*).

Table 1. Summary of small odontocete species sighted during marine mammal abundance surveys in a tropical study area and a temperate study area; number of single species and mixed species schools as well as mean school sizes (with SD italicized and in parentheses) are given for each species. Final column for each survey gives the percent of the total number of small odontocete sightings accounted for by each species. Last row gives the overall number of sightings and overall mean group sizes (with SD in parentheses) for each survey. "Unidentified" refers to schools that could not be identified or could only be identified to the genus level.

	Tropical						Temperate					
Species	# single species schools	# mixed species schools	Single species school size	Mixed species school size	Overall school size	% total sightings	# single species schools	# mixed species schools	Single species school size	Mixed species school size	Overall school size	% total sightings
Long-beaked common dolphin	8	1	517.4 *(492.9)*	1,167.0	589.5 *(509.3)*	2.1	1	1	825.0	77.0	452.0 *(528.9)*	0.6
Short-beaked common dolphin	36	3	288.5 *(297.1)*	284.0 *(103.5)*	288.2 *(286.1)*	9.3	80	5	97.2 *(170.9)*	671.6 *(732.3)*	137.3 *(283.4)*	25.2
Unidentified common dolphin	1	0	80.0	n/a	80.0	0.2	4	0	20.2 *(14.0)*	n/a	20.2 *(14.0)*	1.2
Risso's dolphin	21	7	15.4 *(26.5)*	67.7 *(24.4)*	28.5 *(34.4)*	6.7	20	8	13.4 *(8.4)*	36.1 *(29.2)*	19.8 *(19.5)*	8.3
Unidentified pilot whale	4	6	10.6 *(4.9)*	64.3 *(65.4)*	42.8 *(56.2)*	2.4	1	0	3.0	n/a	n/a	0.3
Short-finned pilot whale	18	10	20.2 *(13.1)*	58.4 *(32.8)*	33.8 *(28.5)*	6.7	0	0	n/a	n/a	n/a	0.0
Killer whale	4	3	6.8 *(6.8)*	64.4 *(58.6)*	31.5 *(46.0)*	1.7	7	0	5.9 *(2.6)*	n/a	5.9 *(2.6)*	2.1
Striped dolphin	77	7	44.8 *(39.5)*	170.7 *(123.2)*	55.3 *(61.3)*	20.0	1	5	29.0	389.9 *(274.1)*	329.8 *(286.0)*	1.8
Bottlenose dolphin	29	27	29.2 *(70.3)*	61.7 *(38.6)*	44.9 *(59.1)*	13.3	5	6	14.8 *(7.1)*	28.9 *(28.7)*	22.5 *(22.1)*	3.2
Unidentified dolphin species	94	6	11.9 *(17.1)*	52.1 *(40.4)*	14.3 *(21.2)*	23.8	19	0	6.6 *(4.8)*	n/a	6.6 *(4.8)*	5.6
Dusky dolphin	4	1	39.9 *(35.7)*	1,167.0	265.3 *(504.8)*	1.2	0	0	n/a	n/a	n/a	0.0
Pygmy killer whale	2	0	14.7 *(17.9)*	n/a	14.7 *(17.9)*	0.5	0	0	n/a	n/a	n/a	0.0
False killer whale	3	2	30.1 *(17.2)*	60.5 *(20.5)*	42.3 *(23.0)*	1.2	0	0	n/a	n/a	n/a	0.0
Pantropical spotted dolphin	35	31	105.9 *(117.8)*	261.9 *(207.0)*	180.3 *(182.8)*	15.7	0	0	n/a	n/a	n/a	0.0
Rough-toothed dolphin	6	2	12.2 *(10.8)*	49.9 *(54.3)*	21.6 *(28.4)*	1.9	0	0	n/a	n/a	n/a	0.0
Spinner dolphin	11	30	123.0 *(131.8)*	267.9 *(207.5)*	229.0 *(199.5)*	9.8	0	0	n/a	n/a	n/a	0.0
Pacific white-sided dolphin	0	0	n/a	n/a	n/a	0.0	16	7	8.7 *(10.4)*	85.3 *(46.1)*	31.7 *(43.9)*	6.8
Northern right-whale dolphin	0	0	n/a	n/a	n/a	0.0	28	8	14.9 *(16.0)*	78.8 *(45.5)*	27.7 *(35.2)*	10.7
Dall's porpoise	0	0	n/a	n/a	n/a	0.0	101	0	3.2 *(2.3)*	n/a	3.2 *(2.3)*	30.0
Harbor porpoise	0	0	n/a	n/a	n/a	0.0	31	0	2.0 *(1.0)*	n/a	2.0 *(1.0)*	9.2
Totals	353	136	74.6 *(166.2)*	182.0 *(215.2)*	91.4 *(178.8)*		314	40	38.6 *(155.3)*	116.9 *(191.9)*	43.9 *(159.0)*	

Temperate Visual Results

The most commonly sighted species during the temperate survey were Dall's porpoises, short-beaked common dolphins, harbor porpoises (*Phocoena phocoena*), and northern right-whale dolphins (*Lissodelphis borealis*) (Table 1). Mixed species schools were less common in the northern study area compared to the ETP, with mixed species schools comprising only 11% of sightings.

Although not as common as in the tropics, large schools were encountered in the temperate study area. These included long-beaked common, short-beaked common, and striped dolphins. Harbor and Dall's porpoises had the smallest mean group sizes.

Pooled Visual Results

When results from both surveys were pooled, mixed species schools were significantly larger than single species schools (mixed species: n = 90, mean = 165.1 individuals, SD = 210.3; single species: n = 667, mean = 57.6 individuals, SD = 162.0; t-test, $p < 0.001$). Mixed species schools also were significantly larger than single species schools for each survey individually (t-tests, tropical $p < 0.001$, temperate $p = 0.02$) (Table 1). Overall mean school size (including both single and mixed species schools) was significantly greater in the ETP study area than in the northern study area (t-test, $p < 0.001$) (Table 1).

Tropical Acoustic Results

Based on single species recordings, vocalizations were detected from every dolphin species that was sighted during the tropical survey, with the exception of dusky dolphins and pygmy killer whales. The species most commonly detected acoustically included striped, short-beaked common, bottlenose, spotted, and spinner dolphins. Whistles were heard during 36% of the 627 h spent monitoring the array, including 70% of the 224 schools that were encountered while the hydrophone array was in the water. Whistles were detected from a greater proportion of mixed species schools vs single species schools (Table 2).

Temperate Acoustic Results

With the exception of Dall's and harbor porpoises, vocalizations were detected from every small cetacean species that was encountered during the temperate study area. Most clicks from the two porpoise species that were encountered are too high in frequency to be detected by our monitoring equipment. Short-beaked common, Risso's, Pacific white-sided (*L. obliquidens*), and northern right-whale dolphins were the species most commonly detected acoustically. Whistles were not heard from northern right-whale dolphins. They also were not heard from single species schools of bottlenose or Risso's dolphins, but they were heard when these two species were encountered together (Table 3). It cannot be determined with certainty which species produced those whistles. Whistles were heard during only 13% of the 376 h spent monitoring the array, and they were detected from 23% of the 219 schools that were encountered while the hydrophone array was in the water. Ninety of the schools that were encountered while the array was in the water were porpoise species. If these schools are omitted, whistles were detected from 46% of the 129 delphinid schools that were encountered. Whistles were detected from a greater proportion of single species schools vs mixed species schools when only dolphins were included in the analysis. There was little difference between mixed and single species schools when both dolphins and porpoises were included in the analysis (Table 2).

Pooled Acoustic Results

The two study areas were pooled, and schools of small odontocetes that were encountered while the hydrophone array was being monitored (n = 443) were examined. Mean group size for whistling species (mean = 105.4 individuals, SD = 205.9, n = 318) was significantly greater than mean group size for nonwhistling species (mean = 4.9 individuals, SD = 8.4, n = 125; t-test, $p <$ 0.001). Table 3 shows the total number of schools of whistling species that were encountered and

Table 2. Number of mixed and single species schools that were encountered while the towed hydrophone array was being monitored, and percent of each for which whistles were detected in the tropical study area, in the temperate study area, and for both study areas combined

	Mixed species		Single species	
Study area	n	% whistling	n	% whistling
Tropical	55	98	169	66
Temperate (including dolphins and porpoises)	15	23	204	24
Temperate (dolphins only)	13	38	116	47
Both (including dolphins and porpoises)	70	81	373	42
Both (dolphins only)	68	84	285	57

Table 3. Number of schools of whistling species encountered while the towed hydrophone array was being monitored, and the percentage of schools for which whistles were detected in the tropical and temperate study areas

	Tropical		Temperate	
Species	*n*	% whistling	*n*	% whistling
Single species schools				
Long-beaked common dolphin	2	100	1	100
Short-beaked common dolphin	24	92	51	84
Risso's dolphin	13	23	15	0
Short-finned pilot whale	11	45	0	n/a
Pacific white-sided dolphin	0	n/a	7	14
Dusky dolphin	2	0	0	n/a
Pantropical spotted dolphin	8	62	0	n/a
Spinner dolphin	6	83	0	n/a
Striped dolphin	45	75	0	n/a
Rough-toothed dolphin	4	50	0	n/a
Bottlenose dolphin	14	78	4	0
Northern right-whale dolphin	0	n/a	20	0
Mixed species schools				
Long-beaked common and dusky dolphins	1	100	0	n/a
Short-beaked common and striped dolphins	3	100	2	100
Bottlenose and Risso's dolphins	4	100	2	50
Bottlenose dolphin and short-finned pilot whale	6	100	0	n/a
Bottlenose and rough-toothed dolphins	1	100	0	n/a
Bottlenose and striped dolphins	1	100	0	n/a
Pantropical spotted and spinner dolphins	18	100	0	n/a
Striped and Risso's dolphins	1	100	0	n/a
Striped and spinner dolphins	1	100	0	n/a
Pacific white-sided and northern right-whale dolphins	0	n/a	5	0
Risso's and northern right-whale dolphins	0	n/a	2	0

the percentage of schools for which whistles were detected for both surveys. Eighteen percent of whistling species and 4% of nonwhistling species schools encountered were mixed species schools.

Schools that did not produce whistles while in range of the array were generally small ($n = 229$, mean group size = 14.0 individuals, SD = 28.3). Seventy-one percent of these schools contained 10 or fewer individuals, and 91% included 30 or fewer individuals (Figure 3). Schools that did whistle were significantly larger ($n = 194$, mean group size = 162.5 individuals, SD = 257.4; *t*-test, $p < 0.001$) than those that did not. Only 14% of whistling schools were made up of 10 or fewer individuals, and 31% contained 30 or fewer individuals. Sixty percent of the whistling species schools contained more than 40 individuals, and every group containing more than 150 individuals whistled ($n = 50$).

Logistic Regressions

Univariate logistic regression with whistling as the dependent variable and time of day (morning = sunrise to 1000 h, midday = 1000 to 1400 h, and afternoon = 1400 h to sunset) as the independent variable showed that time of day was significant for both study areas combined ($p = 0.004$). Overall, the number of whistling species schools encountered decreased from midday to afternoon, and the number of nonwhistling species schools increased from morning to afternoon (Figure 4). Temporal patterns in whistling varied among species (Figure 5). For short-beaked common dolphins, the number of whistling species schools that were encountered decreased with time of day, and the number of nonwhistling species schools encountered increased with time of day. For striped dolphins, the number of whistling species schools encountered remained relatively constant throughout the day, but no nonwhistling species schools were encountered in the morning. Whistling activity did not vary with time of day for either spotted or bottlenose dolphins. Sample sizes for other whistling species were too small to be included in this analysis. A Generalized Additive Model (logit link function) with whistling as the dependent variable and decimal time as a continuous independent variable showed that time of day was significant ($p = 0.001$), with whistling being most common in the morning and relatively constant from noon onward (Figure 6).

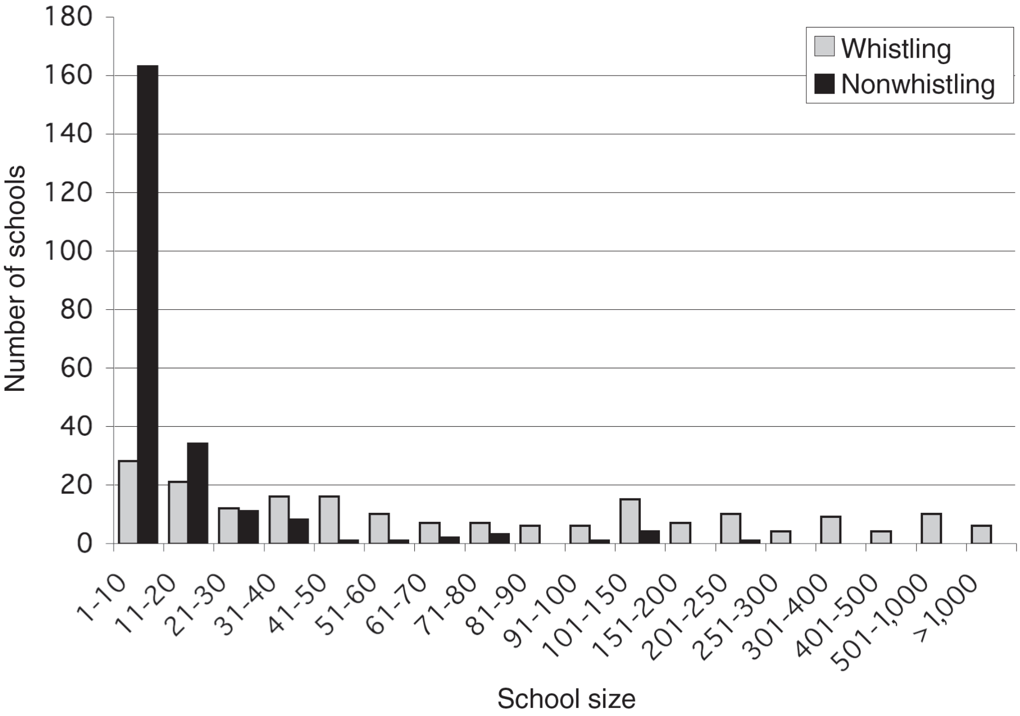

Figure 3. Number of whistling and nonwhistling schools in different school size categories encountered while the array was being monitored during the STAR and ORCAWALE surveys

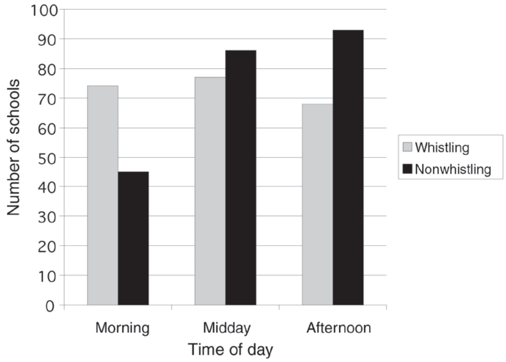

Figure 4. Number of whistling and nonwhistling species schools encountered while the array was being monitored during the STAR and ORCAWALE surveys; morning = sunrise to 1000 h, midday = 1000 h to 1400 h, and afternoon = 1400 h to sunset.

Additional univariate logistic regressions were performed with whistling as the dependent variable and group size, school composition (mixed vs single species), presence of a pronounced beak (the external projection of the rostrum forward of the melon), and study area as the independent variables. All variables were found to be significant ($p < 0.001$ for all variables).

Multivariate logistic regression with whistling as the dependant variable and group size (log transformed), school composition, time of day (morning, midday, afternoon), presence of a pronounced beak, and study area as the independent variables showed that all five independent variables were significant when considered together ($p < 0.001$ for all variables).

Discussion

Nearly every delphinid species encountered in the tropical study area produced whistles. The only exceptions were pygmy killer whales and dusky dolphins. Pygmy killer whales were encountered on only one occasion while the array was in the water, and this school was composed of only two animals. Four dusky dolphin schools were encountered during the tropical survey; however, they were all encountered within a 2-h period. Little time was spent with any of the groups, and it is possible that vocalizations were not detected due to the small window of opportunity available. Both of these species have been observed to produce whistles in other areas (pygmy killer whales

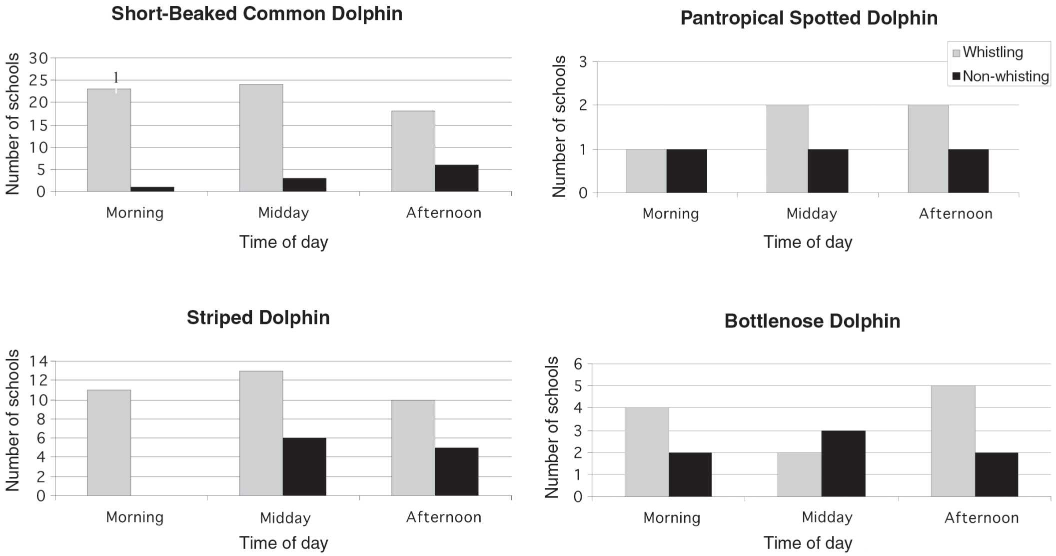

Figure 5. Number of whistling and nonwhistling schools encountered in the tropical and temperate study areas by species and time of day; morning = sunrise to 1000 h, midday = 1000 h to 1400 h, and afternoon = 1400 h to sunset. Grey bars represent whistling species schools, and black bars represent nonwhistling species schools.

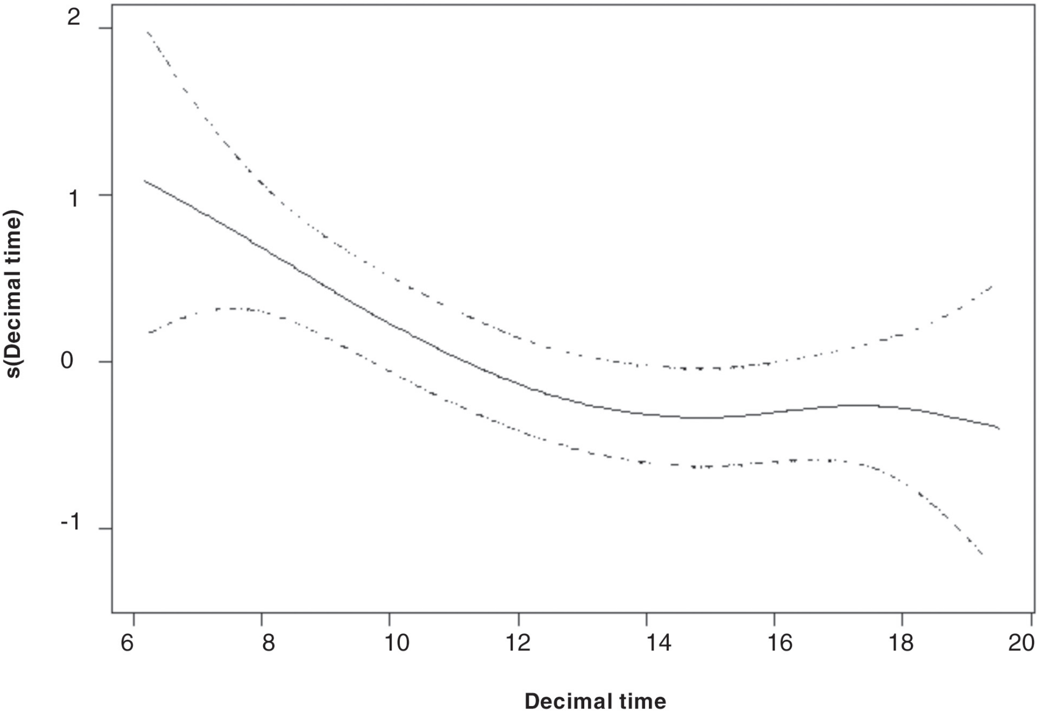

Figure 6. Response plot for Generalized Additive Model (logit link function, smoothing spline, three degrees of freedom) with whistling as the dependent variable and decimal time as the continuous independent variable; the solid line is the mean response curve and the dashed lines are the confidence intervals around the mean response. Greater values on the y-axis of this plot represent a greater probability that a group will have been whistling at that time of day. The probability of whistling was significantly higher ($p = 0.001$) in the morning and relatively constant from noon onward.

in Ecuador: Castro, 2004; dusky dolphins in New Zealand: Ding et al., 1995; Yin, 1999; Yin et al., 2001).

In contrast, three of the four species most commonly encountered in the temperate study area (harbor and Dall's porpoises, and northern right-whale dolphins) did not produce whistles. No vocalizations were detected from either harbor or Dall's porpoises. Most clicks produced by these species would have been too high in frequency to be detected by our monitoring equipment, and neither of these species are known to produce whistles (Tyack & Clark, 2000). Only burst pulses and clicks were heard from northern right-whale dolphins. Whistles recorded in the presence of northern right-whale dolphins have been reported in the literature only once (Leatherwood & Walker, 1979). If this species does whistle, it seems to be a rare occurrence (Rankin et al., 2007). Nonwhistling species accounted for approximately 50% of the schools encountered during this survey. The only whistling species that was frequently encountered was the short-beaked common dolphin. Other whistling species, such as bottlenose and striped dolphins, were found in the study area but accounted for only 5% of the total schools encountered.

The results of these two surveys suggest that whistling species are more common in the ETP, while nonwhistling species are more common in the cold-temperate waters of the eastern north Pacific. In the following sections, the authors explore six hypotheses that may explain this difference: (1) predator avoidance, (2) group size, (3) school composition, (4) behavior state, (5) temporal variation, and (6) anatomical differences.

Predator Avoidance

A major predator of small odontocetes is the killer whale (*Orcinus orca*) (Ford et al., 1998). In a 14-y study of the diet and feeding habits of killer whales in Prince William Sound, Alaska, transient killer whales were observed to prey only on marine mammals (Saulitis et al., 2000). While killer whales have been reported in both tropical and offshore waters, they are more common at higher latitudes and are found in greatest abundance within 800 km of major continents (Angliss & Lodge, 2004; Forney & Wade, 2007). As a result, small odontocetes in the temperate study area are more at risk of killer whale predation than those in the tropical study area.

The range of most sensitive hearing for killer whales is 18 to 42 kHz (Szymanski et al., 1999). Whistles produced by odontocetes range from 5 to 35 kHz (Rasmussen & Miller, 2002; Lammers et al., 2003; Oswald et al., 2004), are relatively omnidirectional at lower frequencies (Miller, 2002; Lammers & Au, 2003), and propagate well under water. Signals such as these likely serve as acoustic beacons for predators. Therefore, to avoid detection, it would be advantageous for dolphins to produce sounds that attenuate quickly such as directional, high-frequency clicks. This strategy of acoustic avoidance of predators is used by many animal species, including insects, frogs, fish, and birds (Curio, 1976; Klump et al., 1986; Haskell, 1999; Luczkovich et al., 2000).

Most small odontocete species in the temperate study area do not whistle but produce broadband, pulsed sounds with much of the acoustic energy well above 42 kHz. For example, Dall's porpoises produce clicks with a peak frequency of 135 to 149 kHz (Hatakeyama & Soeda, 1990), and harbor porpoises produce clicks with peak frequencies at 1.4 to 2.5 kHz and 110 to 140 kHz (both outside the range of best hearing for killer whales; Kamminga & Wiersma, 1981; Hatakeyama & Soeda, 1990; Verboom & Kastelein, 1995). High-frequency clicks are more directional and attenuate more quickly than the whistles produced more commonly by species in the tropical study area. The use of high-frequency sounds may therefore allow animals to communicate at close range while avoiding detection by predators (Andersen & Amundin, 1976; Tyack & Clark, 2000).

The idea that the high-frequency clicks produced by harbor porpoises might be an adaptation to avoid acoustic detection by killer whales was first proposed by Andersen & Amundin (1976). This hypothesis was supported by the work of Madsen et al. (2005) and Morisaka & Connor (2007), who linked the convergent evolution of whistle loss and high-frequency click production to the avoidance of acoustic detection by killer whales for *Cephalorhynchus* spp., phocoenids, *Kogia breviceps*, and likely *Pontoporia blainvillei*. This hypothesis also requires that killer whales use passive listening to locate prey. The use of passive listening is supported by the fact that mammal-eating killer whales produce fewer clicks than fish-eating killer whales (Barrett-Lennard et al., 1996). In addition, transient killer whales did not echolocate before attacking Dall's porpoises and vocalized only after a kill or when not hunting (Barrett-Lennard et al., 1996; Deecke et al., 2005). Other marine mammals have been observed to become silent and motionless in response to the presence of killer whales, which also supports the use of passive listening by these predators (Jefferson et al., 1991).

Some whistling species are found in the temperate study area, but they are more common in the southern portion of the study area, where killer whales are less common (Barlow, 2003; Forney & Wade, 2007). These whistling species are also found in larger schools than nonwhistling species, which may offer them more protection against predators (Norris & Schilt, 1988).

Group Size

Whistles may have many functions within schools of dolphins, including identification of family members or familiar associates; assembly of dispersed animals; and group coordination during foraging, flight, and travel. Whistles are relatively omnidirectional and propagate over greater distances than echolocation clicks or burst pulses. They may also have frequency-dependent directional qualities that could provide cues as to the location and direction of movement of whistling animals (Lammers & Au, 2003). This set of characteristics suggests that whistles are well suited to function as long distance communicative signals and may be used more frequently by species that travel in large schools.

Lammers et al. (2006) found that in schools of free-ranging Hawaiian spinner dolphins, whistles were typically produced by dolphins spaced widely apart, suggesting that whistles play a role in maintaining contact between animals in a dispersed group. Herman & Tavolga (1980) reported a general trend that large-school, communal foraging cetacean species whistle, while more solitary species do not. For example, harbor porpoises and Heaviside's dolphins (*Cephalorhynchus heavisidii*) do not whistle and are found alone or in small groups of a few animals. Whistling species such as *Stenella* spp. and bottlenose dolphins are often found in large groups. This is an imperfect relationship as both *Stenella* spp. and bottlenose dolphins are also found in small groups and northern right-whale dolphins can be found in very large groups, but it does seem to be a general trend worth investigating. In a phylogenetic examination of tonal sound production in relation to sociality, May-Collado et al. (2007) found a significant relationship between group size and the complexity of tonal sounds, with species living in larger groups producing more complex tonal signals. Similar trends have been found in other groups of animals such as the canid species. Kleiman (1967) reported that communal living and hunting canids have more complex communication systems than more solitary species.

In the tropical and temperate study areas, the mean group size of whistling species was significantly larger than nonwhistling species (*t*-test, $p < 0.001$). Groups that did not produce whistles while in range of the array were generally small, with most containing 30 or fewer individuals. In contrast, groups that did whistle tended to be large, containing more than 40 individuals (Figure 3). In addition, overall mean group size was significantly greater in the tropical than in the temperate study area (*t*-test, $p < 0.001$). The larger group sizes in the tropics may explain why whistles were heard more often in that study area. The observed trends support the hypothesis that whistling behavior is related to group size.

It is important to note, however, that the hydrophone array may have detected whistles from larger groups more frequently than from smaller groups simply because of the number of animals present. If each dolphin whistles even only occasionally, the number of whistles produced should increase with group size, thus increasing the probability of a whistle being detected while the array is in acoustic range of the school. Also, there is a greater probability that at least some of the individuals in a larger group will be in a whistling behavior state when encountered. Finally, a larger group may be dispersed over a larger area. If this is the case, the hydrophones may be in acoustic range of the group for a longer period of time, thereby increasing the probability of detecting a whistle (Stienessen, 1998).

School Composition

Whistles have been shown to contain species-specific information (Steiner, 1981; Ding et al., 1995; Oswald et al., 2003) and, therefore, may be important for recognition of conspecifics in mixed species schools. If this is the case, it can be expected that whistling species would be found in mixed species schools more often than nonwhistling species. For the two study areas combined, whistling species were more than four times as likely to be found in mixed species schools as were nonwhistling species. However, only 18% of whistling species schools were mixed. If school composition has influenced the development of whistling behavior, the authors would expect a greater proportion of whistling species schools to be mixed species schools. In addition, while whistles were detected slightly more often from mixed species schools than single species schools in the tropical study area (Tables 2 & 3), this difference was not large enough to provide strong support for the hypothesis that whistles are used more often in mixed species schools. In addition, the opposite trend was observed in the temperate study area: whistles were detected from a greater proportion of single species schools vs mixed species schools when only dolphins were included in the analysis. There was virtually no difference when both dolphins and porpoises were included in the analysis. Finally, mixed species schools were significantly larger than single species schools (*t*-test, $p < 0.001$). It is possible that whistles were heard from mixed species schools more often because of the school size effects discussed above. Further research into whistling rates within schools may help to elucidate the effect of school composition on whistling behavior.

Behavior State

Certain behavior states, such as allomaternal behavior, defense from predators, and cooperative feeding require the maintenance of associations among individuals. Whistles may provide the vehicle for maintaining such associations and may be less important during other behavior states. Rasmussen & Miller (2002) report that whistles were heard from white-beaked dolphins (*Lagenorhynchus albirostris*) when they were socially active but never when they were feeding, traveling, or resting. Spinner dolphins are nearly silent when resting and become very vocal when traveling or feeding (Norris et al., 1994). Increased whistling rates during feeding have been observed for both pilot whales and common dolphins (Dreher & Evans, 1964; Busnel & Dziedzic, 1966). It is possible that the dolphins in the tropical study area spend more time in and/or were encountered more often while in vocally active behavior states. It was not possible to explore this hypothesis as behavioral data were not available for the temperate survey, and the sample size available for the tropical survey was not sufficient for statistical analysis. Further behavioral data collection would be a valuable addition to future surveys.

Temporal Variation

Whistle production may be affected by seasonality. Jacobs et al. (1993) found that bottlenose dolphins in the Newport River Estuary, North Carolina, produced more vocalizations per unit time during the fall than during the summer. Behavioral analyses showed that these dolphins spent the greatest proportion of their time feeding in the fall and socializing in the summer. Both the tropical and temperate surveys discussed here occurred between July and December. It is possible that species in the northern study area whistle more often during certain times of the year, such as mating or calving seasons, and that those seasons did not overlap with our surveys.

Whistle production may also be a function of time of day. Norris et al. (1994) report that Hawaiian spinner dolphins are quiet during the day when resting in protected bays, and whistling increases as the dolphins travel to deeper waters to forage late in the day. Whistles are abundant when the dolphins are feeding offshore at night. Stienessen (1998) found that dolphins in the Gulf of Mexico were more vocal at night than during the day and that the type of vocalization produced varied with time of day. For example, Atlantic spotted dolphins (*Stenella frontalis*) produced a higher proportion of whistles during the day and a higher proportion of pulsed sounds at night. The opposite was found to be true for Clymene dolphins (*S. clymene*). Evans & Awbrey (1988) reported diurnal differences in vocalizations recorded from common dolphins. During the day, whistles, click trains, and squeals were heard; whereas, click trains predominated at night.

Nighttime recordings were not made during the tropical or temperate surveys, but it was possible to examine vocal activity as a function of time of day for daylight hours. Overall, the number of whistling schools encountered decreased significantly from morning to afternoon (univariate logistic regression, $p = 0.004$; GAM, $p = 0.001$; Figures 4 & 6). Although sample sizes were small, whistling behavior patterns seemed to vary by species (Figure 5). These results suggest that, for at least some species, time of day did influence whether or not whistles were heard during these surveys.

Anatomical Differences

It is generally accepted that odontocetes produce sounds in the nasal passages of their foreheads (Ridgway et al., 1980; Amundin & Andersen, 1983; Cranford et al., 1997; Cranford, 2000). Although sound production has been shown to occur at the *phonic lips* or *monkey lips* in the nasal passages, the exact mechanism of sound production is not completely understood (Cranford, 2000). Several odontocete species have been reported to whistle and click simultaneously, which may indicate different generation mechanisms for these two types of sounds (Cranford, 2000). Whistle production appears to require greater nasal air pressure compared to click generation and may therefore require a different mechanism (Ridgway & Carder, 1988; Cranford, 2000). These observations suggest that whether or not a species whistles may be a function of anatomical differences such as the degree of symmetry in the head and the presence or absence of a pronounced beak.

Skull geometry and the structure of the air sac system and melon are distinctive between whistling delphinids and nonwhistling phocoenids (Cranford, 1988; Amundin & Cranford, 1990; Cranford et al., 1996). Delphinid skulls and soft anatomy are highly asymmetric, whereas phocoenid heads are relatively symmetrical. In addition, CT scans showed that there is less skull asymmetry in Pacific white-sided dolphins compared to bottlenose dolphins (Rasmussen & Miller, 2002). Pacific white-sided dolphins do not whistle often, while bottlenose dolphins whistle frequently. This trend does not hold true for all species, however. For example, *Kogia* spp. have markedly asymmetrical skulls (McAlpine, 2002) and have not been reported to whistle.

A noticeable anatomical difference between many whistling and nonwhistling species is the presence of a pronounced beak. Whistling species generally have pronounced beaks, while most nonwhistling species do not. This trend was evident in the tropical and temperate study areas. Species commonly seen in the tropics and not in the temperate study area included spotted, spinner, and rough-toothed dolphins, all of which have distinct beaks and whistle often. Dall's porpoises, harbor porpoises, and northern right whale dolphins were commonly observed in the temperate study area but not the tropical study area; all three of these species lack a definite beak and do not whistle. Perhaps head morphology affects the ability to produce or the energetic cost-effectiveness of producing whistles. Conversely, the tendency to whistle may be a phylogenetic trait that is just casually correlated with the presence of a beak. Again, there are exceptions to this observed trend. Beluga whales (*Delphinapterus leucas*) lack a definite beak and whistle prolifically.

Conclusions

The aggregation of whistling species in the tropical study area and nonwhistling species in the temperate study area does not appear to have a simple, univariate explanation. It is likely due to some combination of the hypotheses presented here and, perhaps, others that have not yet been explored. Multivariate logistic regression with whistling as the dependent variable showed that group size, school composition, presence of a pronounced beak, time of day, and study area were all significant ($p < 0.001$, all variables). Larger groups have a greater need for communication among individuals for coordination of activities. However, while group size does seem to have a strong effect on whistle production, it is likely correlated with other factors such as school composition and predator avoidance. Mixed species schools tend to be larger than single species schools, and individuals within these schools may have a greater need to communicate with conspecifics spread over larger areas. Whistles may be more effective than clicks for communication over these larger areas. Whistles may serve as "acoustic beacons" for predators, making whistling a disadvantage in areas where predators are common. The reduction or loss of whistling behavior to avoid detection by predators may also have led to smaller school sizes to compensate for the resulting restriction in communication distance. Further study into these interactions could shed more light onto the question of why some species whistle while others do not and ultimately lead to a deeper understanding of the functions of whistles in the lives of dolphins. It may also help in understanding why Phocoenids and *Cephalorhynchus* spp. lost the ability to whistle in their evolutionary history.

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