Using active acoustics to compare lunar effects on predator–prey behavior in two marine mammal species

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ABSTRACT: Many delphinids feed on vertically migrating sound-scattering layers. The migration of micronektonic animals in these layers is strongly affected by light, both solar and lunar. Active acoustic approaches were used to observe lunar phase effects on the diel patterns of sound-scattering layers in 2 habitats and to simultaneously observe the behavior of foraging spinner dolphins *Stenella longirostris* in Hawaii and dusky dolphins *Lagenorhynchus obscurus* in New Zealand. Lunar phase was important in structuring the behavior of diurnally migrating animals in scattering layers off both New Zealand and Hawaii. While the responses of these scattering layers to lunar phase differed between locations, the layers were similar in continuing to migrate to surface waters during all moon phases, in contrast to results from other locations. In both dusky and spinner dolphins, dolphin relative abundance increased with increasing lunar illumination. The dolphin response to lunar phase is not clearly explained by the observed changes in prey. However, the results suggest that lunar phase is likely to be important in driving behavior of the many delphinid species that forage on vertically migrating prey. Active acoustics can be used to simultaneously study predator and prey, elucidating the foraging behavior of other dolphin species feeding on sound-scattering layers. Comparing the observed patterns to the phylogeny of these diverse species could provide insights into the evolution of behavior in delphinids.

KEY WORDS: Lunar cycle · Vertical migration · Marine mammal · Foraging · Sound-scattering layer · Diel

INTRODUCTION

Active acoustic techniques, i.e. those that use sounds that are both transmitted and received, have long been used to study fish and zooplankton. The first reported active acoustic detection of fish occurred in 1929 (Kimura 1929) and the first sonar echogram (time versus depth graph of echo intensity) of fish a few years later (Sund 1935). The first acoustic surveys for fish by what is now the US National Oceanic and Atmospheric Administration (NOAA) Fisheries Service began in 1976. Fish abundance surveys via active acoustics are presently a standard stock assessment tool (MacLennan 1990) used both by the US-based NOAA and

agencies of other governments worldwide. Active acoustic techniques are now used to obtain size estimates of individual animals (e.g. Holliday 1977), to observe behaviors at a variety of time and space scales (e.g. Torgersen & Kaartvedt 2001, Klevjer & Kaartvedt 2003), and to measure animal distribution and biomass (e.g. Benoit-Bird & Au 2006, Pieper 1979).

The first published account of the use of active acoustics to observe marine mammals was in a 1960 *Science* paper reporting the diving behavior of a group common dolphins detected using a US Navy sonar (Edwards & Livingstone 1960). These authors were the first to note the intense echoes from the dolphins, which permitted observations of their underwater

behavior. Excited about the possible application, Edwards & Livingstone (op. cit., p. 36) commented that 'Further observations with echosounders may add considerably to our knowledge of [marine mammals]'.

Marine mammals are strong sonar targets because of their size (Edwards & Livingstone 1960, Dunn 1969, Love 1973, Levenson 1974) and their air-filled lungs (Edwards & Livingstone 1960, Au 1996). Quantitative field measurements at relatively high frequencies (tens to hundreds of kHz) of dusky dolphins *Lagenorhynchus obscurus* (Benoit-Bird et al. 2004), spinner dolphins *Stenella longirostris* (Benoit-Bird & Au 2003a), sperm whales *Physeter macrocephalus* (Jochens et al. 2008) and pilot whales *Globicephala* sp. (K. Benoit-Bird unpubl. data) have found that a small number of extremely strong echoes, likely from the lungs and air-filled nasal passages (Benoit-Bird & Au 2003a, Benoit-Bird et al. 2004), are detected from each individual. However, the target strength of the remainder of an individual dolphin, while consistent within a species, is considerably lower than that of a fish of equivalent size (McClatchie et al. 1996, Bertrand et al. 1999, Benoit-Bird & Au 2003a, Benoit-Bird et al. 2004). The impedance match between blubber and the surrounding seawater may cause this low target strength (Fig. 1). Depending on the resolution of the sonar and the size of the animal, many of these echoes

can be recorded from 1 individual, but the number of echoes with a given instrument is quite consistent both vertically and horizontally within a species (Benoit-Bird & Au 2003a, Benoit-Bird et al. 2004, Jochens et al. 2008). The results of these field studies compare well with controlled measurements of a bottlenose dolphin *Tursiops truncatus*, which also showed relatively low target strength values, with the exception of strong echoes from the lungs (Au 1996). Similar echo returns have been noted from bottlenose dolphins (Ridoux et al. 1997), fin whales *Balaenoptera physalus* (Nøttestad et al. 2002a), and killer whales *Orcinus orca* (Similä & Ugarte 1993, Similä 1997, Nøttestad et al. 2002b) in qualitative field studies that analyzed the visual output of the sonar. Taken together, the echo characteristics of dolphins including their unusually low target strengths, the strong echoes from their lungs, and the specific number of echoes from a given species make dolphins unique and identifiable sonar targets.

Despite optimistic predictions of Edwards & Livingstone (1960) about active sonar research and the intense identifiable echoes from whales and dolphins, studies of marine mammals with active acoustics have been limited. While many studies have used active acoustics to study prey, and then related these data to visual or passive acoustic listening observations (e.g. Fiedler et al. 1998, Acevedo-Gutierrez & Parker 2000), only relatively recently has the tool been implemented to gather data on marine mammal swimming speed, distribution, overlap with prey, and feeding behaviors (Similä & Ugarte 1993, Ugarte 1993, Ridoux et al. 1997, Similä 1997, Nøttestad & Axelsen 1999, Nøttestad & Similä 2001, Nøttestad et al. 2002a,b, Benoit-Bird & Au 2003a, 2009a,b, Benoit-Bird et al. 2004, Jochens et al. 2008). In these studies, few, if any, effects have been observed on marine mammal behaviour from echosounder-type active acoustic equipment (Nøttestad et al. 2002a, Benoit-Bird & Au 2003a, 2009a) though there is always a concern about noise effects.

Overall, past studies clearly demonstrate the advantages of using active acoustics. Active acoustics allows scientists to 'see' below the surface over ranges of hundreds of meters, orders of magnitude greater than optical approaches, and is not affected by time of day, a distinct advantage over optical techniques. Typically, the entire depth range can be sampled simultaneously with resolution on the order of 10 cm, and surveys can be conducted relatively rapidly, allowing great coverage. Finally, the most significant advantage of active acoustics emerge when the developments of fisheries acoustics are applied to marine mammal studies. Using the analytical approaches developed by this vigorous field (fisheries acoustics), active acoustic techniques can provide simultaneous, coincident data on marine mammals, fish, and zooplankton, allowing compar-
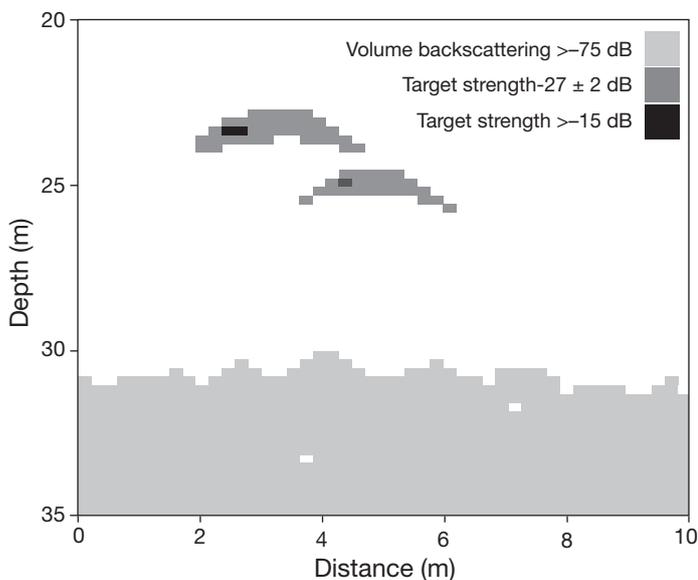

Fig. 1. Echoes from a 200 kHz echosounder of 2 spinner dolphins swimming just above a sound scattering layer, which is shown only in part. Volume backscatter (i.e. echoes from small animals that cannot be individually separated) is shown in light grey (the scattering layer). Single target detections in the narrow target strength range consistent with the body of spinner dolphins are shown in dark grey. Intense echoes likely from the dolphins' lungs are shown in black. These data show the spatial resolution at which dolphins can be observed with a typical split beam echosounder

isons between predator and prey to be made with identical resolution and coverage on the same temporal and spatial scales. This strength has been made use of in previous work to explore predator–prey dynamics in a variety of marine mammal species.

Perhaps one of the most powerful outcomes of the combined strengths of active acoustic sampling (one that has not been fully explored) is the potential to perform comparative foraging studies on marine mammal species. This approach could provide substantial information on the evolution of behavior in marine mammals. Lanternfishes (Myctophidae) and mesopelagic cephalopods that often form sound-scattering layers are an important food resource in the ocean worldwide (Rasmussen & Giske 1994) and are the primary prey of many delphinid species across a range of genera. Dolphins living in the waters of Hawaii and New Zealand have similar foraging habits. The spinner dolphin *Stenella longirostris* is a pan-tropical pelagic species feeding almost exclusively at night on mesopelagic fishes and squid species found in sound-scattering layers throughout its range (Cadenet & Doutre 1959, Fitch & Brownell 1968, Perrin et al. 1973, Norris & Dohl 1980, Norris et al. 1994). The dusky dolphin *Lagenorhynchus obscurus* is a similarly sized species that resides in the cold-temperate waters around New Zealand, western South Africa, and South America (Gaskin 1968, Van Waerebeek et al. 1995). Dusky dolphins in shallow bays feed during the day on small schooling fish (Würsig & Würsig 1980, Markowitz et al. 2004), while in the waters of Kaikoura Canyon, New Zealand dusky dolphins feed at night on mesopelagic micronekton in a sound-scattering layer (Cipriano 1992, Würsig et al. 1997). Off both Hawaii and Kaikoura, the behavior of the mesopelagic animals combined with the local topography brings these prey layers unusually close to the shoreline (Robertson et al. 1978, Cipriano 1992, Benoit-Bird et al. 2004, Benoit-Bird & Au 2006). In both habitats, the mesopelagic micronekton layers undergo extensive diel migrations, moving from daytime depths of up to 600–1000 m, where they are inaccessible to dolphins, to within meters to a few tens of meters of the surface at night, where they are exploited by the dolphins (Cipriano 1992, Benoit-Bird et al. 2001, 2004, Benoit-Bird & Au 2003b). Both species of dolphins follow diel movements in their prey, resulting in substantially shallower dives near the middle of the night than near crepuscular periods (Benoit-Bird & Au 2003a, Benoit-Bird et al. 2004)

One of the most significant factors affecting the behavior of diel migrators is light, both solar and lunar (Blaxter 1974). The magnitude of diel migration, its timing, the number of animals undergoing migration, the condition of the migrating animals, and their spatial distribution have all been shown to correlate with features of the light field (Clarke 1970, Blaxter 1974, Helfman 1993, Ringelberg 1995). These changes in diel migration are likely to be important to any predator foraging on scattering layers, but for surface breathing marine mammals, changes in vertical distribution of prey, and thus potential foraging time, are likely to be particularly important. Changes in sunlight occur primarily seasonally, a pattern correlated with many other environmental changes. Dramatic changes in sunlight also occur during rare solar eclipses, changes that have been exploited to reveal a great deal about diel migration (Bright et al. 1972). In contrast, changes in moonlight occur regularly at relatively short time scales, approximately monthly, permitting repeated observations over the time scale of a single research project. The goals of this work were to apply active acoustic approaches to (1) observe changes in the diel patterns of distribution of mesopelagic micronekton over lunar cycles in 2 habitats, (2) observe changes in the distribution and behavior of foraging dolphins over the lunar phase in each habitat, and (3) compare responses in Hawaii and New Zealand to begin to provide insight into the evolution of delphinid foraging behavior.

MATERIALS AND METHODS

Along transects in both Hawaii and New Zealand, sampling of the micronekton scattering layers and subsurface dolphins was conducted using Simrad EK60 split-beam echosounders; in Hawaii, we used 38, 70, 120, and 200 kHz and in New Zealand 38, 120, and 200 kHz. Position data from a DGPS were saved with each echo. The 38 kHz system used a pulse length of 512 µs and a 12° conical beam. The 70, 120, and 200 kHz systems each had a conical beam with an angle of 7° and pulse lengths of 256 µs. Echosounders were calibrated using an indirect procedure incorporating a 38.1 mm diameter tungsten carbide reference sphere, as described by Foote et al. (1987). In addition, the characteristics of the outgoing signals from each transducer were measured using a calibrated, wideband, omni-direction hydrophone (BM8263 Biomon) and digitized with a Tektronix DPO4034 oscilloscope at a sampling rate of 10 MHz. The power settings for each instrument were selected to provide a source level of less than 180 dB re 1 µPa (rms), the current guideline for preventing temporary hearing impairment for marine mammals (National Marine Fisheries Service 2003). The bandwidth about the center frequency of each signal was also measured. The bandwidth was 3.5 kHz for the 38 kHz signal, 6.2 kHz for the 70 kHz signal, 9.0 kHz for the 120 kHz signal, and 10.7 kHz for the 200 kHz signal.

Visual observations. During all sampling, visual observers scanned for surfacing marine mammals for 5 min every 30 min. Animals close enough to the vessel to be seen clearly were identified to species. This was particularly effective during the quarter and full moon when conditions were calm and moonlight would reflect from the backs of surfacing animals. In Hawaii, that represented just over $\frac{2}{3}$ of the sampling time and in New Zealand, just over half. In Hawaii, spinner dolphins surface in relatively large groups (Benoit-Bird & Au 2009a), making them relatively easy to detect visually and often audibly. All dolphins observed during sampling in Hawaii were identified as spinner dolphins. In New Zealand, dusky dolphins were seen in small groups, making them more difficult to observe; however, all dolphins sighted were found to be dusky dolphins. Visual detections of dolphins were compared with active acoustic data in the minute prior to and the minute after the visual observation.

Lunar phase. Lunar phase information and sun rise and set times were obtained from the United States Naval Observatory (http://aa.usno.navy.mil/data/). These data are freely available for positions throughout the world. Direct measurements of nocturnal irradiance are extremely difficult to obtain because of the extremely low light levels (Kaul et al. 1994). At the time of this study, there were no commercially available sensors capable of these measurements. We estimated cloud cover in 5% increments every 30 min as a simple proxy of moonlight.

Hawaii. Sampling was conducted off the leeward coast of Oahu, Hawaii from the 10 m FV 'Alyce C'. The study area covered 2 sites: a southern site in the area of 21° 19.3′ N, 158° 8.3′ W known as Electric Beach, and a northern site in the area of 21° 30.5′ N, 158° 14.2′ W known as Makua Beach (Fig. 2). Both of these areas are known as daytime aggregation sites for spinner dolphins (Lammers 2004) and active nighttime feeding areas (Benoit-Bird & Au 2003b). Data used in this study were incidentally collected from studies sampling mesopelagic micronekton (see Benoit-Bird et al. 2008, McManus et al. 2008).

When sampling in Hawaii, the echosounder transducers were mounted 1 m below the surface on a rigid mount attached to the vessel's gunnel so that the centers of each transducer were no more than 35 cm apart, allowing maximum

spatial comparability of the data (Korneliussen et al. 2004). A high resolution profiler was used (in addition to the echosounders) during sampling off Hawaii to characterize micronekton at stations along the surveyed transects. The profiler was equipped with a SBE-25 CTD (temperature, salinity, pressure), a suite of instruments for measuring other physical and optical properties of the water column, and a low-light camera system for micronekton. The camera system using only infra-red lighting was used to identify micronekton and measure animal size as well as quantitatively estimate the numerical density of animals while causing no significant avoidance (see details in Benoit-Bird & Au 2006). At all stations, the profiling package was lowered from the surface to within 5 m of the seafloor or 150 m, whichever was shallower, at a rate of $10–15$ cm s^{-1}. The profiler was then raised to $3–5$ m above the minimum depth of the shallowest observed scattering layer as rapidly as possible and lowered at $10–15$ cm s^{-1} to $2–3$ m below the deepest observed layer. This was repeated again to provide 3 replicate casts in the video data.
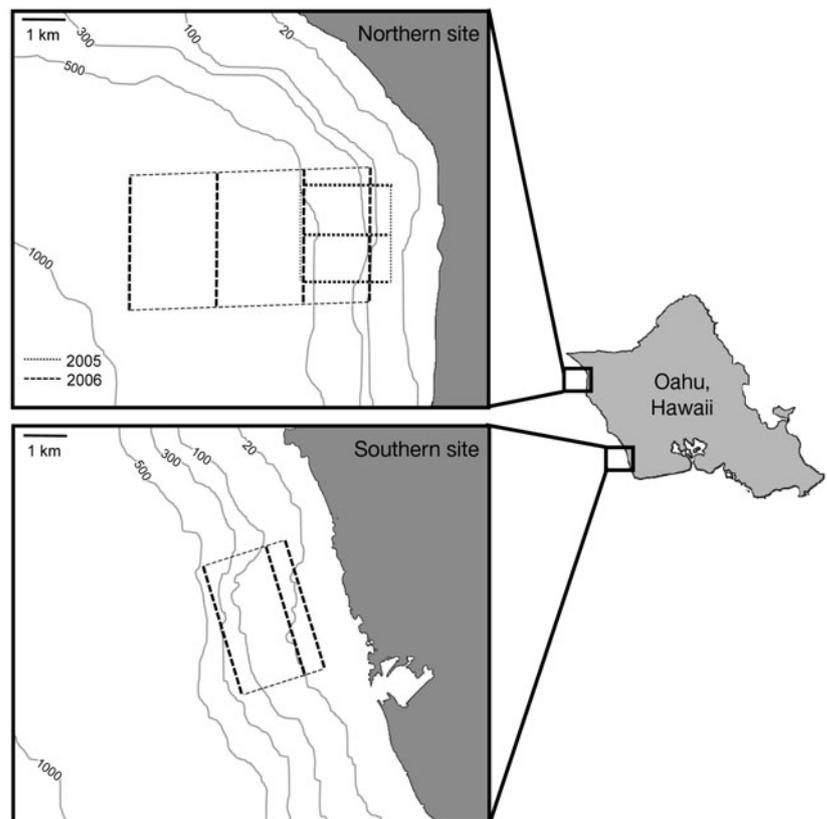

Fig. 2. Transect sampling design at 2 sites off the leeward coast of Oahu, Hawaii. Bottom contours are shown in meters. Primary transects are shown in heavy dashed lines with connecting transects in light dashed lines. The northern site was sampled during 2 different years, indicated by differently dashed patterns. In all designs, the order of sampling was randomized each night. Geographic coordinates are in 'Materials and methods: Hawaii'

During 14 nights between February 9 and 28, 2005, sampling was conducted between 18:00 and 04:00 h local time. These nights coincided with new moon, first and last quarter, and full moon periods. At each site, one 3-km long transect was located at 1.5, 3.0, 5.0, and 7.0 km from the shoreline. This range covers nearly the entire nighttime range of the horizontally migrating mesopelagic layer (Benoit-Bird & Au 2006). Each transect was sampled once in the hour following 18:00, 21:00, 00:00, and 03:00 h local time. The order of sampling by site and the order of transects within a site were determined using a randomized complete block design. High resolution profiles were taken at the end of each transect and vertical net tows for zooplankton were conducted at the ends and midpoints of each transect.

Between April 20 and May 27, 2005, the southern site was sampled from 20:00 until 03:00 h local time during four 3-night series. The surveys coincided with full moon April 23–25, new moon May 7–9, first quarter May 15–17, and full moon May 22–24. Sampling in each 3-day survey was conducted continuously from 20:00 to 03:00 h local time. Three 3-km long transects were located 1.0, 1.5, and 3 km from the shoreline. Vertical casts with the profiling package and a zooplankton net were carried out at the ends and midpoint of each transect. The starting position along the survey grid was randomized each night, as was the order of the transects

Between April 9 and May 16, 2006, the northern site was sampled from 20:00 until 03:00 h local time during three 3-night series. The surveys coincided with full moon April 13–15, new moon April 26–28, and last quarter May 12–14. Three 2-km long transects were located across slope running from 1 to 3 km from shore. Vertical profiles and net tows were conducted 1.0, 1.5, 2.0, and 3.0 km from shore along the center transect. The position of the first cast along the center transect, direction of travel of the first transect (towards or away from shore), and whether the right or left flanking transect was sampled next were all randomly selected each night.

New Zealand. Sampling in New Zealand was conducted from the 16 m FV 'Bundi'. Echosounder transducers were mounted with their center points less than 35 cm apart on a 2 m long towfish that was towed directly alongside the vessel at a depth of 1 m. The study area over and surrounding Kaikoura Canyon (42° 27′ S, 173° 51′ E to 42° 35′ S, 173° 33′ E) was sampled from 20:00 to 06:00 h local time on 7 nights between February 6, 2006 and March 18,

2006, encompassing 2 nights with the moon in first quarter phase, 3 with a full moon, 1 with a new moon, and 1 night during the last quarter.

Sampling in New Zealand was centered on a 15 km long transect running perpendicularly to the shoreline over the head of the main body of Kaikoura Canyon where it meets Conway Trough. A series of 12 across-slope transects approximately 5 km in length zig-zagged across this center transect (Fig. 3). The order of sampling was randomized each night so that all zig-zagging transects were sampled once and the center transect twice.

Data analysis. *Dolphins:* Target strengths of large, individual targets were measured using SonarData's Echoview program with a target strength threshold of −40 dB and a pulse length determination level of 12 dB, normalized pulse lengths between 0.8 and 2.0, a maximum beam compensation of 12 dB and a maximum SD of both axes of 3°. During previous studies (Benoit-Bird & Au 2003a, Benoit-Bird et al. 2004) to determine their scattering characteristics, dolphins of each species were observed swimming beneath the transducer. Passive acoustic observations were used to identify dolphin species during these studies (Benoit-Bird & Au 2003a, Benoit-Bird et al. 2004), further validating the active acoustic detection criteria. The overall target strength of both species of dolphins was consistent as a function of depth, i.e. within 2 dB of −28 dB at 200 kHz for dusky dolphins and within 2 dB of −27 dB at 200 kHz for spinner dolphins. As in previous work, stronger echoes, presumably from the lungs of the animal (Au 1996), were found near one end of the animal, which was designated the front. The approximate number of echoes obtained from dolphins with
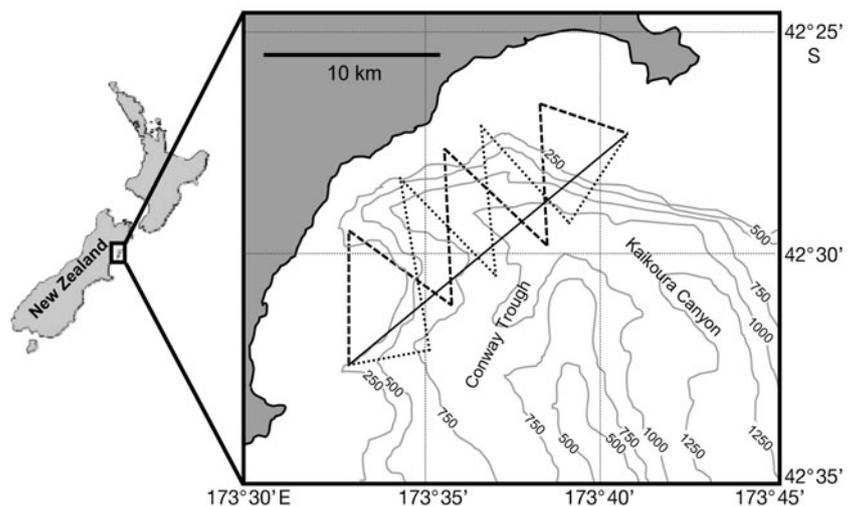

Fig. 3. Transect sampling design off Kaikoura, New Zealand. Bottom contours are shown in meters. Each zig-zag transect series (broken lines) was sampled once each night and the center, straight transect (solid line) was sampled twice. The order of sampling was randomized each night

the 200 kHz echosounder was also consistent in both the horizontal (~15 echoes) and vertical (~4 echoes) directions. Active-acoustic dolphin identification was confirmed by visual sightings of surfacing animals when visibility permitted.

To calculate the mean depth of dolphins, the number of dolphins was corrected for search area differences as a function of depth by dividing the number of animals located at a particular depth by the diameter of the beam at that depth (Benoit-Bird & Au 2003a). The relative abundance (analogous to catch-per-unit-effort) of dusky dolphins was defined as the percent of sampling time that dolphins were observed within a 1 h sample. Individual dolphins detected acoustically within 15 s of each other (about 40 m along a transect) were considered to be part of the same group, and the observation time was calculated as the total time from the first sighting in the group until the last. Sightings of a single animal were assigned an observation time of 5 s. Because relative abundance is not based on counting of animals but rather on the percentage of sampling time that dolphins were observed, multiple returns from the same animal within a short time of each other would have little effect on the relative abundance calculated in 250 m transect sections.

The subgroup size of acoustically detected dolphins was defined by observing the orientation of animals relative to the direction of the transect, the proximity of animals, and their swimming angle. The position of a strong lung echo nearer to one end of the series of echoes allowed determination of the orientation of dolphins swimming either with or against the transect. The direction of dolphins swimming perpendicularly to the transect was ambiguous because a lung echo would be roughly centered within the dolphin's echo. Echoes that indicated dolphins swimming in the same direction, within 5 m of each other, and at approximately the same angle were defined as a subgroup (see Benoit-Bird et al. 2004).

Prey: Foraging dive depths for both dolphin species have been observed to be limited to about 150 m (Benoit-Bird & Au 2003a, Benoit-Bird et al. 2004). All prey analyses presented are thus limited to this depth, or the bottom in shallow water in both locations. For comparison with previous work, analyses were focused on the 200 kHz data. The total calibrated scattering intensity of prey (σ) was calculated for each 1 m^3 sampled. This is analogous to the more commonly reported s_v, or volume backscattering, but on a linear rather than a logarithmic scale. Because the identity of animals causing the scattering could not be determined in New Zealand, even though extensive data were available for the Hawaii samples, prey abundance and numerical density estimates were not made for either location. The mean, maximum, and statistical

variance in σ at depths shallower than 150 m were calculated in 250 m horizontal sections of survey transects.

Because prey depth is an important constraint for dolphin feeding, the minimum depth reached by the scattering layer each sampling night was measured. This feature was not determined to be spatially correlated in previous studies in New Zealand, so no space effects were taken into account (Benoit-Bird et al. 2004). However, in Hawaii, distance from the shoreline is a critical parameter in determining scattering layer depth (Benoit-Bird et al. 2001), so a minimum depth was calculated for each distance from the shoreline. For both locations, the time relative to sunset at which the scattering layer passed 150 m on its upward migration and the time relative to sunrise that 150 m was passed on its downward migration were measured, taking distance from shore into account in only the Hawaii data.

Statistical analyses. Data were categorized into 3 lunar phases, with first and third quarters pooled to increase the sample sizes during these similar light periods. To analyze temporal effects, time was categorized into hourly increments. Recent studies have shown that lunar phase can have significant effects on the biomass of diel migrators that is independent of actual light (Hernandez-Leon et al. 2001, 2002), so cloud cover, a proxy for moonlight reaching the surface, was also tested using the estimated cloud cover for each hour of data in the New Zealand data. Cloud cover in New Zealand ranged from 0 to 100%, however cloud cover in Hawaii varied only between 0 and 15%, with very few values greater than 5%, so this factor was not tested in the Hawaii data set. ANOVAs followed by post hoc tests with Bonferroni corrections for multiple comparisons were used to assess the effects of lunar phase, time, and, for Hawaii, distance from the shoreline on features of prey and dolphins measured using the 200 kHz echosounder. Mean prey volume scattering was log-transformed to meet the ANOVA assumption of a normal distribution with equal variance. To investigate any potential changes in the frequency response of the scattering layer, an ANOVA was used to assess the effects of lunar phase and acoustic frequency on the log transformed mean volume backscatter.

RESULTS

Prey acoustic scattering characteristics at 200 kHz in the upper 150 m of the water column were analyzed as function of lunar phase in each habitat (Fig. 4). A series of ANOVAs was used to determine the effects of lunar phase, cloud cover, and time of night on each volume
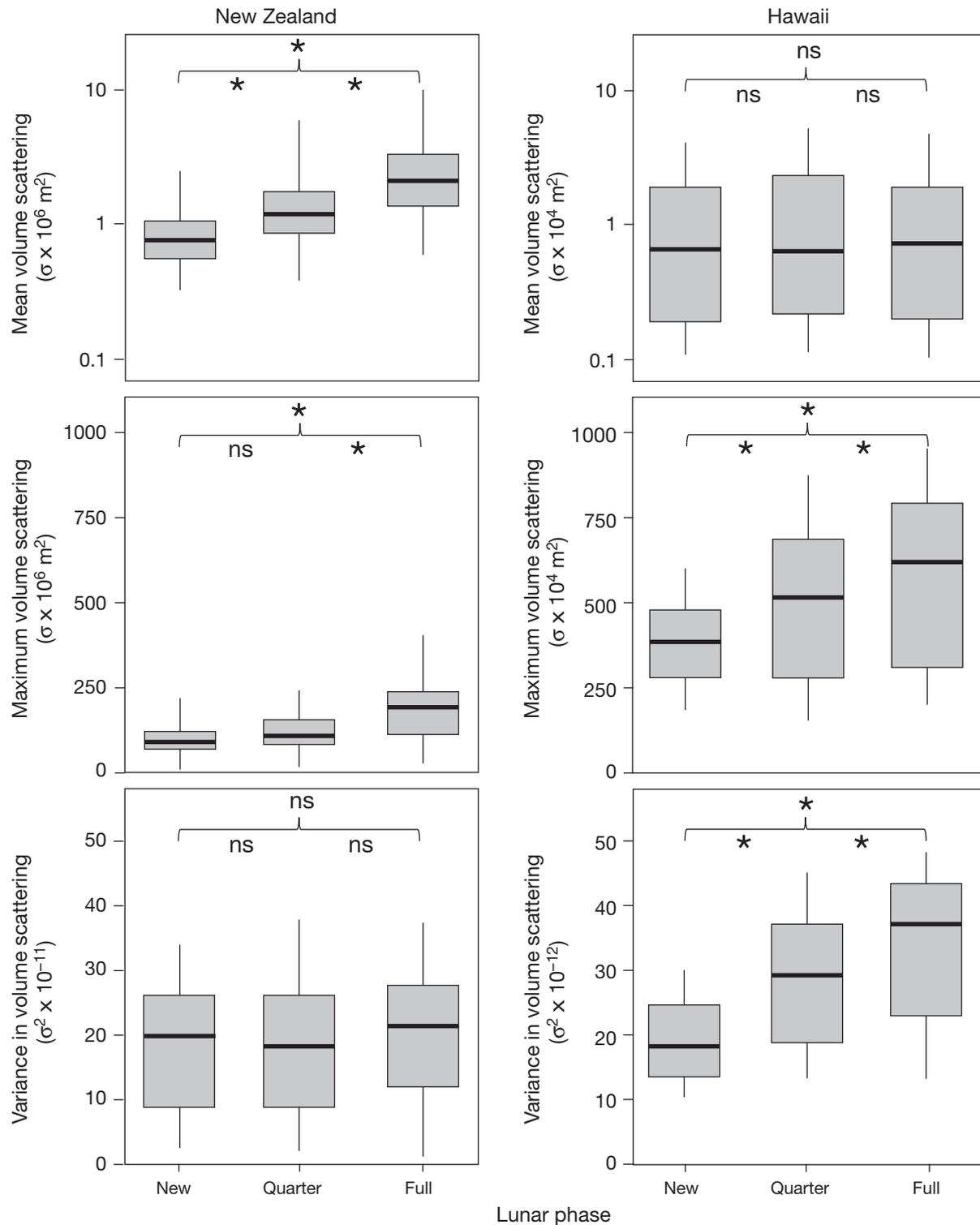
Fig. 4. Prey acoustic scattering characteristics at 200 kHz in the upper 150 m of the water column as function of lunar phase in each habitat. For all plots, dark bars show the median, the box shows one interquartile range, and the error bars indicate the 95% confidence interval. Results of post hoc analyses are indicated at the top of each graph, with significant differences indicated (*), and tests with p-values > 0.05 labeled 'ns' (not significant). The raised center symbol in each graph shows the comparison of new and full phases while the lower symbols indicate comparisons between quarter phase and the adjacent phase. Mean volume scattering, shown in the top panels, is plotted on a log scale. Note that the vertical scales of mean volume scattering between habitats are different by 2 orders of magnitude. Maximum volume scattering is shown in the middle panels. Again, note the difference of 2 orders of magnitude on the vertical scale. In the lower panels, variance in volume scattering is shown. Here, the difference in vertical scales is 1 order of magnitude

Table 1. Summary of ANOVA results for prey characteristics and dolphin abundance and depth. Values are probabilities; ns: $p > 0.05$

	New Zealand					Hawaii					
	Lunar phase	Cloud cover	Time	Phase × Clouds	Phase × Time	Lunar phase	Time	Distance from shore	Phase × Time	Time × Distance	Phase × Distance
Mean volume scattering	<0.01	ns	<0.001	ns	ns	ns	<0.001	<0.001	ns	<0.001	ns
Maximum volume scattering	<0.05	ns	<0.01	ns	ns	<0.005	<0.001	<0.001	ns	<0.001	ns
Variance in volume scattering	ns	ns	<0.005	ns	ns	<0.01	<0.01	<0.005	ns	<0.05	ns
Dolphin relative abundance	<0.005	ns	<0.05	ns	ns	<0.001	<0.001	<0.005	ns	<0.001	ns
Minimum layer depth	ns	ns	–	ns	–	<0.005	–	<0.001	–	–	ns
Dolphin mean depth	ns	ns	<0.005	ns	ns	<0.05	<0.001	<0.001	ns	<0.005	ns
Upward migration timing	<0.01	ns	–	ns	–	ns	–	<0.001	–	–	ns
Downward migration timing	<0.05	ns	–	ns	–	ns	–	<0.001	–	–	ns
Total accessible time	<0.005	ns	–	ns	–	ns	–	<0.001	–	–	ns

scattering characteristic (Table 1). Cloud cover showed no significant main effect on any variable measured and had no significant interactions with other terms. Time and lunar phase did have significant main effects, but did not have a significant interaction effect. The results of post hoc analyses for lunar phase are shown in Fig. 4. These graphs do not separate data by time or distance from the shoreline, and so show only the effect attributable to lunar phase. Because there was no significant interaction between lunar phase and time or distance from the shoreline, the lunar phase effect overlies these other significant factors. However, taking these other significant factors into

account would substantially reduce the range of observed values and the 95% confidence intervals, allowing greater predictive capabilities.

Of 211 visual sightings of spinner dolphins during the Hawaii sampling, dolphins were detected on the echosounder within 1 min of the sighting 209 times. Of the 84 visual sightings of dusky dolphins during the New Zealand sampling, dolphins were detected with the echosounders within 1 min of the observation 79 times, strongly supporting the ability to detect and recognize dolphins in the echosounder data. The relative abundance of dolphins detected with the 200 kHz echosounder is shown as a function of lunar phase in
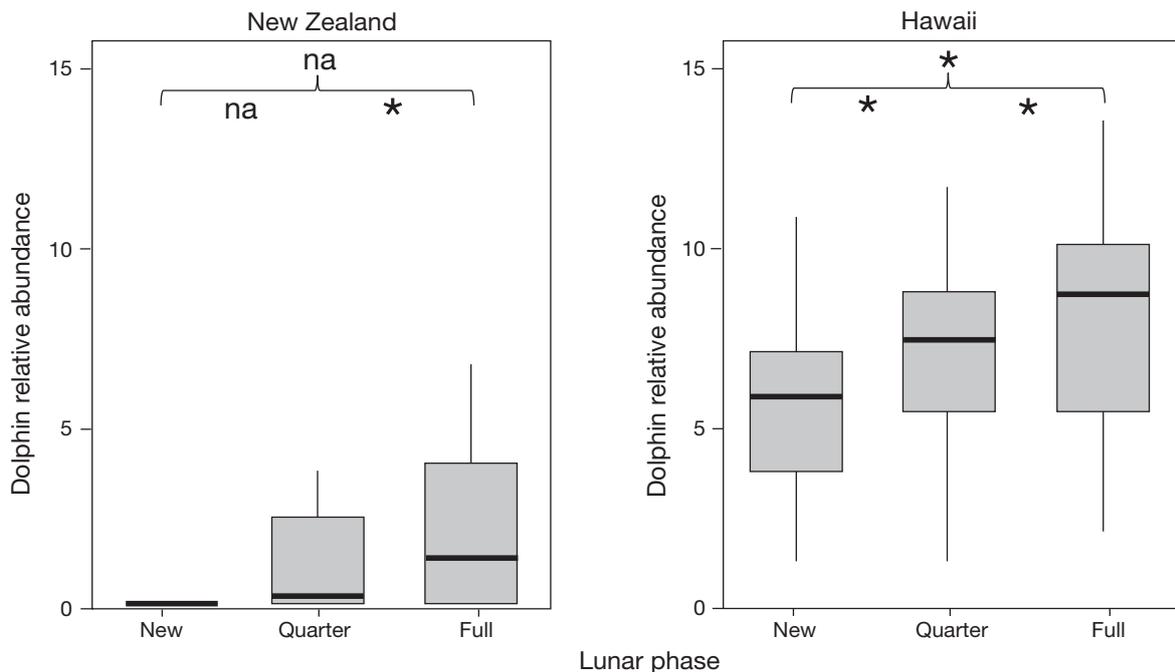

Fig. 5. Dolphin relative abundance in 1 h increments as a function of lunar phase for each habitat. Dark bars show the median for each phase, the box shows one interquartile range, and the error bars show the 95% confidence interval. Results of post hoc analyses are given at the top of each graph, with significant differences indicated (*). Because no dolphins were detected during the new moon in New Zealand, post hoc analyses were not conducted (na: not applicable). The raised symbol in each graph shows the comparison of new and full phases while the lower symbols indicate comparison between quarter phase and the adjacent phase

Fig. 5. The ANOVA results are summarized in Table 1, with post hoc test results indicated in the figure. These show that there is a significant effect of lunar phase on dolphin behavior. Because of the limited depth range of dolphins, all echosounder frequencies used were able to detect dolphins to their full diving range. Each dolphin detection was made simultaneously at all frequencies, and thus the relative abundance of dolphins at all frequencies was identical. Slight differences in dolphin target strength (TS) by frequency were observed: dusky dolphins $\overline{TS}_{38\ kHz} = -26.6$ dB, $\overline{TS}_{120\ kHz} = -28.4$, $\overline{TS}_{200\ kHz} = -28.1$ dB; spinner dolphins $\overline{TS}_{38\ kHz} = -25.4$, $\overline{TS}_{70\ kHz} = -26.2$, $\overline{TS}_{120\ kHz} = -27.1$, $\overline{TS}_{200\ kHz} = -26.8$ dB.

The minimum depth of the scattering layer reached during each night sampled is shown in Fig. 6 as a function of lunar phase. Extreme differences in depth as a function of distance from the shoreline necessitated separating the Hawaii data by this factor. Off New Zealand, there was no significant change in minimum layer depth as a function of lunar phase, while in Hawaii there was a significant lunar phase effect (Table 1). Post hoc analyses on the Hawaii data by dis-

tance from shore (summarized in Fig. 6) showed that lunar phase only had a significant effect in the samples within 3 km of the shoreline, with the scattering layer found deeper during a full moon than during a new moon, at an average of 4.3, 5.4, and 9.2 m at 1.0, 1.5, and 3.0 km from the shoreline, respectively. The mean depth of dolphins showed a similar pattern (Table 1). In New Zealand, no effect of lunar phase on mean dolphin depth was detected. Off Hawaii, a significant effect was observed by lunar phase, time, and distance from the shoreline, but lunar phase did not significantly interact with these other factors, simplifying post hoc comparisons. Post hoc tests showed a significant effect (p < 0.05) of lunar phase on spinner dolphin mean depth at only 1.0, 1.5, and 3.0 km from the shoreline, with mean increases in dolphin depth between new and full moons of 3.3, 6.1, and 10.4 m, respectively.

Effects of lunar phase on the timing of vertical migration were assessed by measuring the time each night that the top edge of the scattering layer passed 150 m on both its upward and downward migration (Fig. 7). The depth of 150 m is an estimate of the depth limit of
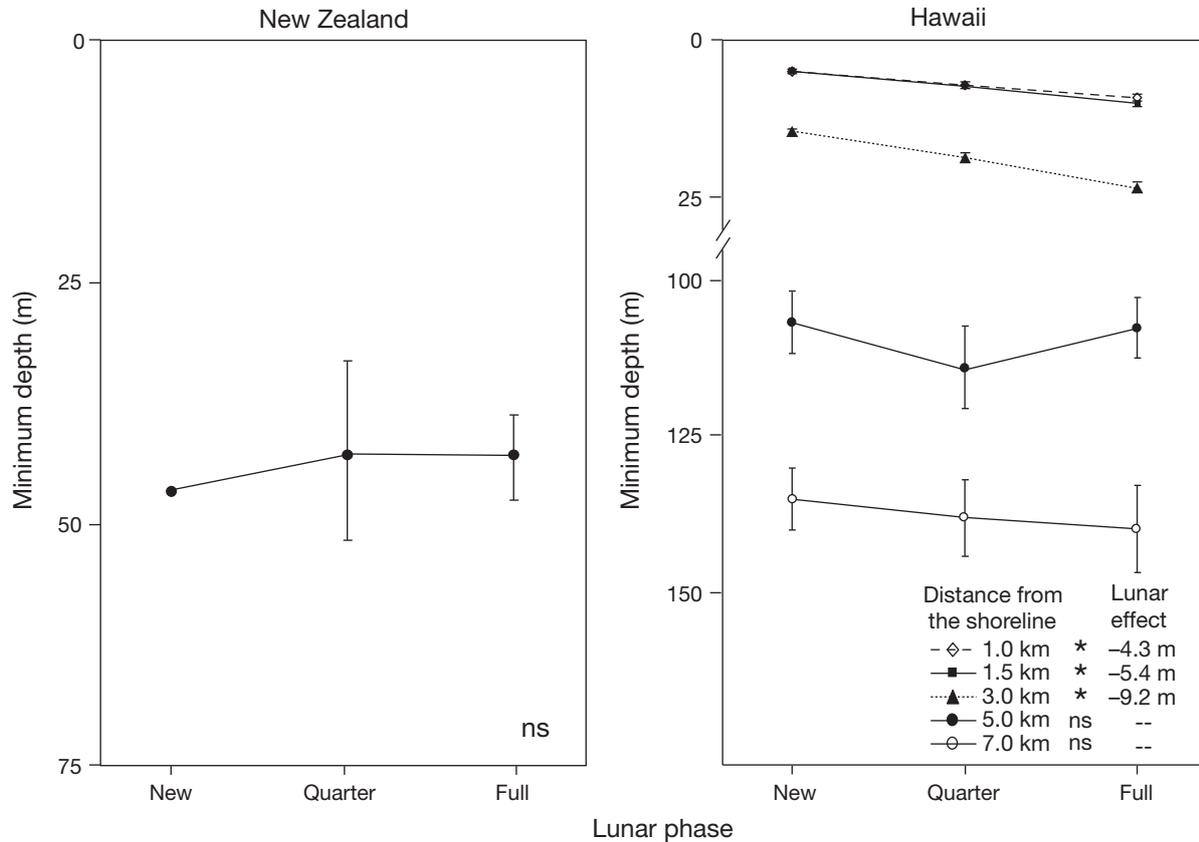

Fig. 6. Minimum observed depth of the scattering layer as function of lunar phase. Values are means ± 95% CI. No significant effect was observed off New Zealand. In Hawaii, because of the horizontal component of diel migration of the scattering layer, data are broken up as a function of distance from the shoreline. Note the break in the *y*-axis here because of the large differences in layer depth observed, and the 1.0 and 1.5 km samples almost overlap near the top of the graph. *: distances showing a significant effect (p < 0.05) of lunar phase on minimum layer depth; ns: p > 0.05. The change in minimum layer depth for those distances where lunar phase was significant is also shown
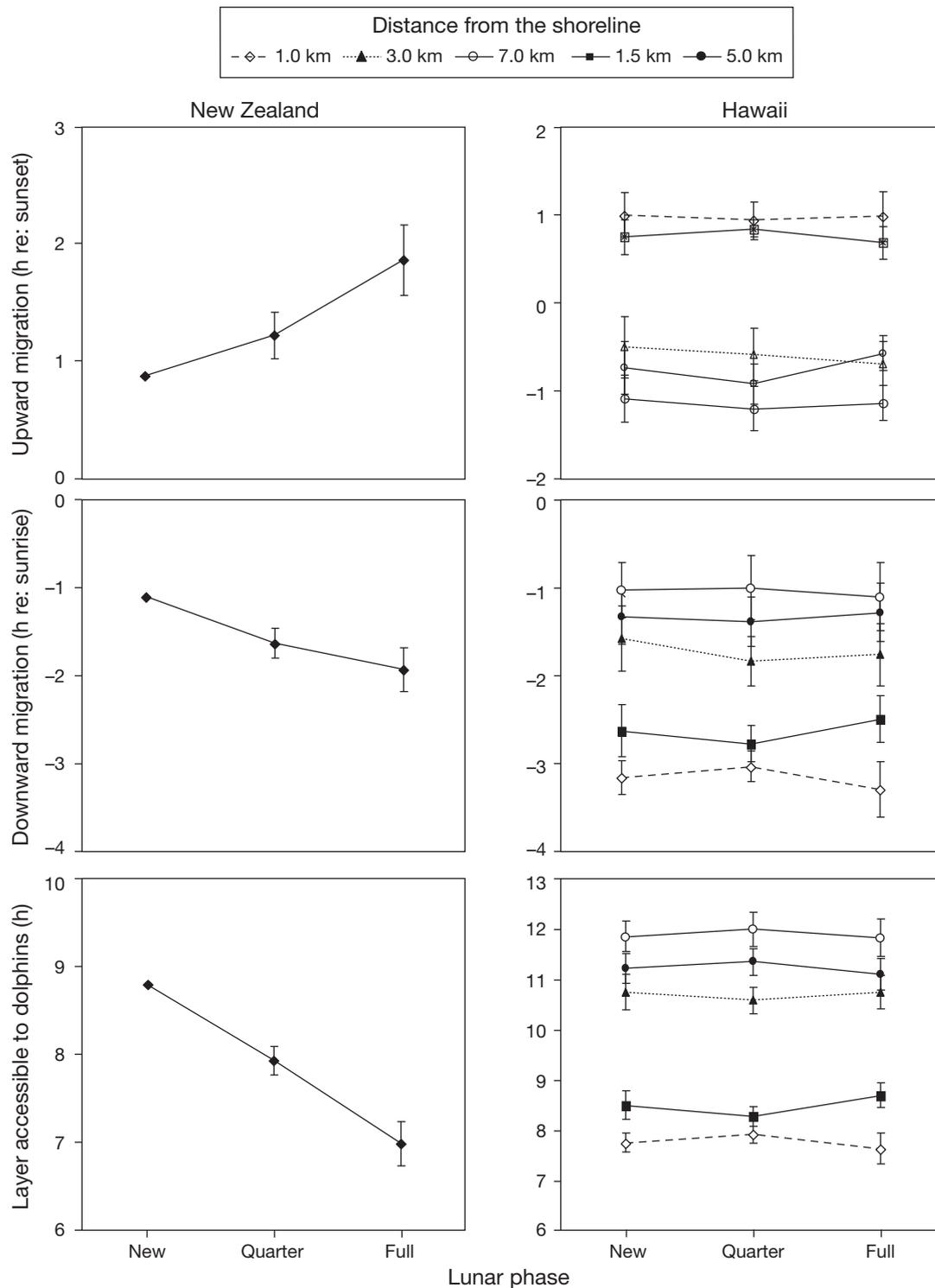
Fig. 7. Time that the scattering layer passed 150 m, i.e. the maximum diving depth for dusky and spinner dolphins. On the layer's upward migration, time is presented relative to sunset (h re: sunset) to account for seasonal variation in migration timing. A positive value represents time after sunset (0), while a negative value represents time before sunset. On the layer's downward migration, time is presented relative to sunrise (0) with negative values represented hours before sunrise (h re: sunrise). In the lower panels, the total time each night the scattering layer was above 150 m, i.e. the total time the layer was accessible to dolphins, is shown. Values are means ± 95% CI. Off New Zealand, all 3 measures showed a significant effect of lunar phase; however, limited sample sizes precluded post hoc analyses. No significant effect of lunar phase was observed for any distance from the shoreline for the Hawaii data

foraging of these 2 dolphin species. The time the layer passed 150 m was referenced to sunset for the upward migration and sunrise for the downward migration in order to remove any effects of changes in day length over the 2 mo sampling off New Zealand and the 4 mo sampled off Hawaii. The total time each night that the scattering layer was above 150 m, or the total time the scattering layer was accessible to dolphins on a given night, was also analyzed. ANOVA results are summarized in Table 1. Because of the small sample size off New Zealand for migration timing measurements and the lack of a lunar phase effect off Hawaii, no post hoc analyses were conducted.

While it was not possible to sea-truth the New Zealand data, the frequency response of scattering, (i.e. the relative frequency of volume backscatter) can tell us something about changes in the composition or sizes of animals in the scattering layer. An ANOVA on the mean scattering strength at each frequency showed significant effects of lunar phase and frequency and a significant interaction between the 2 variables ($p < 0.05$ for all comparisons) for the New Zealand samples. This significant interaction term indicates a change in the frequency response as a function of lunar phase (Fig. 8). The Hawaii samples showed a significant frequency effect, but no effect of lunar phase or the interaction between the two, showing no changes in the frequency response as a function of lunar phase. An ANOVA on the proportion of myctophid fishes in the layer and the length of myctophids identified with the low-light camera system showed no significant effect of lunar phase and no lunar phase interactions ($p \gg 0.05$ for all comparisons).

No distinct subgroups (e.g. individuals oriented in the same direction within 5 m of each other and at approximately the same angle) were observed in New Zealand dusky dolphins. Distance to nearest neighbor methods were used, with positions of individual dolphins as the unit to analyze the distribution patterns of dolphins. Because acoustic sampling occurred beyond transects, a boundary strip of at least the expected distance to the first nearest neighbor for a random distribution was included to limit bias. The Clark & Evans (1954) index of aggregation was calculated and the distribution was tested with Thompson's test (Thompson 1956), a modified chi-squared test, at $\alpha = 0.05$. This test allows the following distributions of patches to be tested: significantly greater than random, uniform pattern, and significantly less than random, a clumped pattern. Dusky dolphins were observed in a significantly less than random distribution. Spinner dolphins off Hawaii were always observed in distinct subgroups of 2 individuals. These subgroups were found in larger groups, as indicated by the highly significant clumped distribution. However, the sizes of these larger groups could not be adequately described using downward looking echosounders (Benoit-Bird & Au 2003a). To determine the distribution of spinner dolphin groups, the mean position of the entire group was then used to test the distribution of animals. The results show that spinner dolphin groups were distributed in significantly greater than random, or uniform patterns.

DISCUSSION

Dolphins

Here, we present the first published multi-frequency field measurements of dolphin echoes. Over the frequency range used (38 to 200 kHz), a very weak frequency response was observed in dolphin target strength. This response was consistent between the 2 species measured, with a very slight increase in target strength at 38 kHz relative to the higher frequencies. Spinner dolphins had 1.2 to 1.3 dB higher target strengths than dusky dolphins at all frequencies. Dolphins in the upper 150 m were equally detectable at all frequencies used because of their intense target strengths and their unique combination of scattering characteristics. Increasing attenuation at higher acoustic frequencies occurs in the ocean, however, so deeper diving species would only be detected at the lower frequencies. Typical effective depth ranges for the echosounders used are 200, 350, 600, and 1200 m at 200, 120, 70, and 38 kHz, respectively. The maxi-
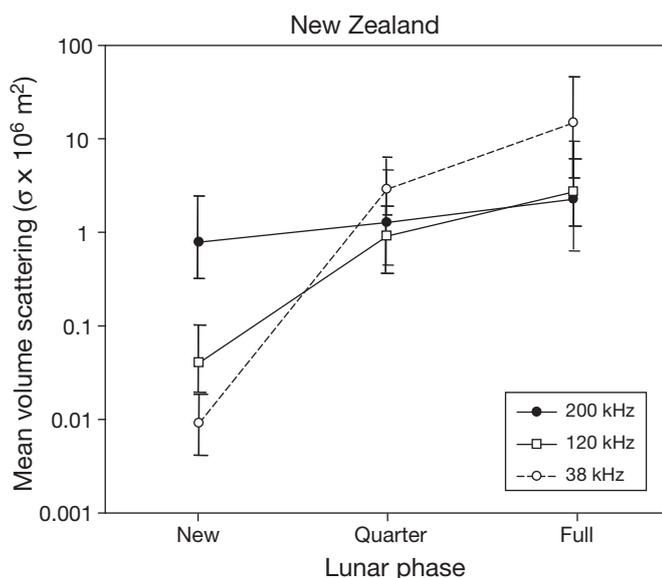

Fig. 8. Mean volume scattering on a log scale as a function of lunar phase for all 3 frequencies used off New Zealand. Values are means ± 95% CI. All 3 frequencies showed a significant lunar phase effect. There was also a significant interaction between lunar phase and acoustic frequency

mum vertical resolution of the echosounders is also a function of acoustic frequency, with higher frequencies having higher resolution. The equivalent dolphin detection capabilities support the selection of echosounder frequency based on the depth coverage required, vertical resolution needed, the scattering characteristics of other targets of interest (prey for example) and the hearing capabilities of the focal species in question.

One concern in the use of active acoustics in studying marine mammals is the risk of sound exposure. The source levels of all signals used in this study were lower than the maximum limit prescribed by NMFS for prevention of temporary auditory impairment (National Marine Fisheries Service 2003). Of course, the risk of sound exposure for a marine mammal is related not only to the intensity of the absolute signal, but also to the sound's duration, its duty cycle, and its degree of directionality. The mammalian ear functions as an energy detector (see a review in Green 1985), so we must consider the amount of energy present within the ~200 ms integration window of the mammalian ear. In the present study, signals were generated by the echosounders at a rate of 3 Hz or less, meaning that only 1 signal would be in each auditory integration window. Given the characteristics of the echosounder's signals, the energy flux density calculated using the 90% energy approach prescribed by Madsen (2005) was 145 dB re μPa^2s for the 38 kHz signal, the longest signal used in this study, while the other, higher frequency signals that had half the duration, also had half the intensity at 142 dB re 1 μPa^2s. While no criteria for energy flux density exposures for marine mammals currently exist, comparisons show that these signals represent relatively low energies. For example, the echosounder signals used in the present study have approximately 100 times less energy than a *Stenella* species' echolocation click (K. Benoit-Bird & W. Au, unpubl. data), 1000 times less energy than a tactical mid-frequency sonar (Madsen 2005) or a sperm whale click (Mohl 2002), and 10 000 times less energy than a seismic watergun (Finneran et al. 2002). The echosounders used in the present study were also highly directional, so only animals swimming nearly directly beneath the transducer would be able to hear the sound source, further limiting the exposure. Given the large numbers of echolocation clicks produced by dusky dolphins (Au & Würsig 2004) and spinner dolphins while feeding (Benoit-Bird & Au 2009b) and the narrow beams of the echosounders, dolphins are likely exposed to much more energy from their own signaling than from the echosounders used in our study.

While the echosounders used in the present study are highly unlikely to cause direct harm to dolphins, it is much more difficult to determine whether the echosounders could change the behavior of the dolphins being studied. While several field studies have noted very few effects of echosounder-type active acoustic studies on the behavior of marine mammals (Benoit-Bird & Au 2003a, 2009a, Nøttestad et al. 2002a), no experimental studies have been conducted to observe potential behavioral responses. Recent work in fish has shown significant vessel avoidance, affecting absolute estimates of fish biomass (e.g. Freon et al. 1993, Soria et al. 1996, Vaboe et al. 2002). These studies have found that the vessel itself, rather than the acoustic instruments likely caused the changes in fish behavior because the highly directional nature of the echosounders used means that animals are unlikely to be able to hear the signals until the vessel is nearly directly over them and, thus, they have already been sampled (Soria et al. 1996, Vaboe et al. 2002). However, the avoidance of the vessel did not affect the relative abundance measures made using the same vessel (Freon et al. 1993), as is the case for the lunar phase comparisons made within each site here.

Scattering layers

The features of the scattering layer measured off Kaikoura, New Zealand in the present study during the late austral summer/early fall were similar to those measured at the same location in the austral winter of 2002 (Benoit-Bird et al. 2004). The ranges of mean volume scattering values and variance in volume scattering were quite similar between the 2 studies. When measured using the time of sunset and sunrise, the timing of migration was also similar between the 2 time periods studied. However, when layer migration is measured instead as the total time the layer is above 150 m and thus accessible to dusky dolphins, a drastic difference was observed. Instead of the 7 to 9 h of prey accessibility to dusky dolphins in the data presented here from austral summer/fall, the measurements from the austral winter of 2002 showed prey above 150 m for 12 to 13 h each night. These changes in duration of prey availability might account for the differences in dusky dolphin foraging behavior observed. In the austral winter study, dusky dolphins were observed as solitary individuals, as they were in all samples in this study, but they were also observed in groups of up to 5 individuals. These distinct subgroups were not observed in the present study. This variation highlights the flexibility of dusky dolphin foraging behavior.

The measurements of the scattering layer off Hawaii in the present study were also quite similar to those taken at the same locations in previous work (Benoit-Bird & Au 2003a). Mean scattering, maximum scattering, and variance in scattering were all similar in their

distribution to those measured previously at various times of the year encompassing all 'seasons' (Benoit-Bird & Au 2003a,b, 2004a, 2006). While migration timing is similar relative to sunset and sunrise in all studies (as in the New Zealand data) unlike off New Zealand, the duration of scattering layer presence also changed little throughout the year off Hawaii. This difference is likely due to the position of the sites relative to the equator. Throughout the year, day length varies by >6.5 h at New Zealand's latitude, while near Hawaii, day length varies by less than 2.5 h. Given the observation that the timing of the layer's migration is tightly coupled to sunset and sunrise at both sites, changes in the duration of layer availability to dolphins should match the duration of night length. Spinner dolphins in the present study exhibited behaviors consistent with those observed previously with pairs of dolphins foraging as parts of larger groups.

Sound-scattering layers of micronekton detected off Hawaii and New Zealand both serve as prey for dolphins. Strong similarities in layer composition between the 2 areas have been recorded in published studies (Robertson et al. 1978, Reid et al. 1991, Benoit-Bird & Au 2006). At both sites, scattering layers observed were easily separated from the background and were discretely bounded. In both New Zealand and Hawaii, the scattering layers underwent strong diel migrations, moving from deep waters to areas accessible to foraging dolphins only at night. In New Zealand, this migration was consistent across all transects surveyed. The scattering layer off New Zealand remained at least 30 m from the surface in all samples. In Hawaii, horizontal migration of micronekton meant that vertical movement was constrained by the seafloor as the layer approached the island (Benoit-Bird et al. 2001, Benoit-Bird & Au 2006). This horizontal migration also resulted in differential depth movement, with layers closer to the shoreline also found closer to the surface than those that made less extensive horizontal migrations. As a result, off Hawaii, parts of the scattering layer could be found within a few meters of the surface but not at all locations.

Substantial differences were observed in the scattering characteristics of the layers in New Zealand and Hawaii. The mean volume scattering and maximum volume scattering measured off Hawaii were 2 orders of magnitude higher than measured off New Zealand. The differences could be due to differences in the composition of layers, the scattering characteristics of the individual organisms in the layers, or the numerical density of animals in these layers. These possibilities are not mutually exclusive; however, numerical density has the strongest impact on volume scattering given that individual animals in both layers are in the same size range (MacLennan & Simmonds 1992). This suggests that the density of prey is much higher in Hawaii than in New Zealand, which is not unexpected given the remarkably high densities measured off Hawaii (up to 1800 ind. m^{-3}, Benoit-Bird & Au 2006). In addition to strong differences in the strength of scattering, the 2 sites showed large differences in the variance of volume scattering, a measure of the heterogeneity in the scattering layers. Volume scattering off New Zealand was fairly uniform while the variance in volume scattering off Hawaii was at least one order of magnitude higher, indicating a much patchier prey distribution.

Lunar phase effects

Scattering layer features off both New Zealand and Hawaii were affected by lunar phase, potentially because of light, though the mechanism cannot be directly examined with our data. In New Zealand, samples during the new moon were limited due to weather. However, for all analyses, the new moon fit the trends from the quarter and full moon samples that had larger sample sizes, so while the power to detect changes is affected by this limitation, the consistency permits interpretation of the observed lunar patterns. The mean and maximum volume scattering off New Zealand both increased with increasing lunar illumination. Variance in volume scattering, a measure of patchiness, and the depth of the scattering layer, however, were not affected by lunar phase. The most dramatic change observed off New Zealand with lunar phase was the timing of migration. Upward migration occurred later with increasing lunar illumination, while downward migration occurred earlier. The result was that the scattering layer was within the diving range of dolphins for about 2 h less during a full moon than a new moon. This represents a loss of more than 20% of potential foraging time for dusky dolphins during full moon phase. Effects of lunar phase on the subtleties of diel migration timing have not been reported for other scattering layers. Another significant change observed off New Zealand is highlighted by the change in the frequency response of volume backscatter, with lower frequencies increasing their scattering strength relative to high frequencies with increasing lunar illumination. This suggests a change in the composition of the size of animals in the scattering layer. The increase in scattering at 38 kHz is consistent with larger animals becoming more abundant. However, because sea-truthing could not be conducted, this hypothesis could not be tested.

Off Hawaii, a significant lunar phase effect was observed for maximum volume scattering and the variance in volume scattering (i.e. the patchiness of layers)

but not for the mean volume scattering. Unlike off New Zealand, the timing of migration was not affected by lunar phase. However, the depth of the scattering layer was affected, at least along the nearshore transects. As a result, the scattering layer was found nearly 10 m deeper during a full moon relative to a new moon. This likely represents a relatively small increase in energetic costs for spinner dolphins to dive to the prey, but may also slightly decrease the time the dolphins can remain at depth (Williams et al. 1999). No significant change in the frequency response of volume backscatter was observed off Hawaii as a function of lunar phase. This suggests that the size of individual animals in the scattering layer and the layer's taxonomic composition is not affected by lunar phase. This was confirmed with the low-light video system data, which showed no effect of lunar phase on measures of layer composition or individual animal size.

The lunar phase effects observed at both sites were different from those observed in previous studies. Several previous studies found that vertical migrants avoid the surface during full moon periods, often remaining deeper than 200 m during periods of high lunar illumination (Clarke 1973, Blaxter 1974, Roger 1974, Pinot & Jansa 2001). This is hypothesized to result from animals following specific light isolumes (Boden & Kampa 1967). During a full moon, lunar illumination can place an isolume hundreds of meters deeper than during a new moon; in fact, in subtropical waters, the light level at 150 m during a full moon can be the same as at 500 m during the middle of the day (Clarke & Denton 1962). In New Zealand, no change in layer minimum depth was observed, with the scattering layer still moving within 35 m of the surface during a full moon. In Hawaii, while changes in layer depth were observed, the change was <10 m, not the hundreds of meters observed in previous studies, and the scattering layer still came within 10 m of the surface nearshore. While lunar phase was observed to modify vertical migration, it did not cause dramatic alterations in vertical distribution or cause migration to stop entirely. Micronektonic animals in both New Zealand and Hawaii moved much closer to the surface during full moon nights than predicted by the light isolume hypothesis (Boden & Kampa 1967). It is not clear why the extent of vertical migration in both of these habitats is less affected by moon phase than previously observed, particularly in Hawaii where attenuation by clouds cannot be invoked.

The increase in either the mean or maximum scattering observed in surface waters with increasing lunar illumination observed in New Zealand and Hawaii is also in contrast with results of previous studies. Off Hawaii, the combination of (1) increasing depth of the upper edge of the scattering layer during the full moon along with (2) the bottom edge of the layer remaining at the same depth and (3) a constant mean volume scattering strength resulted in an increase in maximum volume scattering because the animals were more tightly packed vertically. Off New Zealand, the increase in mean volume scattering was accompanied by an increase in maximum volume scattering and no accompanying change in vertical distribution, so the increase likely represents an increase in total abundance of animals above 150 m. Increases in zooplankton abundance during full moons have been observed as zooplankton are released from grazing pressure from vertical migrators (Hernandez-Leon et al. 2002). However, these increases are restricted to small animals that are not vertical migrators, quite different from the relatively large (2–10 cm length off Hawaii), vertically migrating animals studied here. Other studies of diurnally migrating micronekton have found decreases in their abundance tied to deepening of scattering layers during full moons. (Clarke 1973, Blaxter 1974, Roger 1974, Pinot & Jansa 2001). Despite the subtle differences observed between New Zealand and Hawaii, the responses to lunar phase of these 2 systems were far more similar to each other than to previously studied sound-scattering layers.

Differences in dolphin detection rates and behaviors were also observed between New Zealand and Hawaii. The relative abundance of dolphins off New Zealand was lower than that off Hawaii. In addition, dusky dolphins in the present study were not found in distinct subgroups while spinner dolphins were found in pairs that were part of larger groups, which have been shown to herd prey (Benoit-Bird & Au 2003a, 2009a). However, in both locations, dolphin relative abundance was significantly affected by lunar phase, with more dolphins detected during a full moon than during a new moon. In New Zealand, no dusky dolphins were detected during the single new moon night sampled. This fit the general trend observed in the remaining data, though it should be interpreted with caution. It raises the question of what both dusky and spinner dolphins are doing during these nights with lower illumination and why. Dolphins might be changing their behavior or feeding habitat in a way that reduces their detectability, perhaps moving outside the study area. Dusky dolphins, because of their varied diet, could be switching to prey in a different location or prey accessible at a different time. Spinner dolphins, however, cannot be feeding during the day because of their prey specificity. Transects in Hawaii covered the full extent of the scattering layer's distribution onshore to offshore, so any changes in dolphin habitat use would have to be alongshore to account for the observed pattern. In both habitats, some features of the prey field would suggest more favorable foraging dur-

ing the new moon, with an increased duration of prey availability off New Zealand and shallower prey off Hawaii. While prey off New Zealand are likely smaller during a new moon, no change in prey composition was observed in Hawaii. The differences in the volume scattering characteristics with lunar illumination were relatively small at both sites yet dolphins in both locations showed this pattern of decreased relative abundance with lower lunar illumination. The light from the moon itself provides possible explanations. Visual predators might be expected to forage more effectively during a full moon than in other stages because of the moonlight available for vision. Dolphins might augment acoustic sensing with vision when enough light is available. Alternatively, prey might be more effective at predator avoidance during better lit nights. Perhaps dolphins are more efficient at foraging on dark nights during a new moon and are satiated earlier in the night, switching to other behaviors earlier during a new moon and thus being detected less often.

CONCLUSIONS

Lunar phase was observed to be important in structuring the behavior of diurnally migrating animals in scattering layers off both New Zealand and Hawaii. While the responses of these scattering layers to lunar phase differed, the layers were similar in continuing to migrate to surface waters during all moon phases. Neither layer fit the light isolume hypothesis that other sound-scattering layers have been observed to follow. Lunar phase was also important in structuring the behavior of the dolphins that forage on these migrating layers. Both dusky and spinner dolphins were detected more often with increasing lunar illumination. This response to lunar phase is not clearly explained by the observed changes in prey with lunar phase. Comparing these 2 species of dolphins, dusky dolphins are relatively generalist foragers with flexible foraging strategies and a moderate blubber store. Dusky dolphin prey is relatively low in density but the variability in prey layers is also low, leading to high prey predictability. Spinner dolphins are foraging specialists with a narrow range of observed foraging behaviors and very limited blubber stores. The prey of spinner dolphins occurs at very high densities but density is highly variable and thus is less predictable at small scales. These differences in dolphin biology and prey distribution and behavior likely present significantly different pressures on foraging in these 2 species. Despite the differences between dusky and spinner dolphins, lunar phase was important to the foraging of both species. This suggests that lunar phase is likely to be important in driving behavior of the many delphinid species that forage on vertically migrating prey that form sound-scattering layers. The large differences in vertical migration behavior observed in this study compared to previous ones suggest stronger responses by dolphins to lunar phase are likely. Using techniques like active acoustics to study the behavior of prey and predators simultaneously, the foraging behavior of other dolphin species feeding on sound-scattering layers could be investigated. Comparing the observed patterns to the phylogeny of these diverse species would provide insights into the evolution of behavior in delphinids.

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