

DUSKY DOLPHIN (*LAGENORHYNCHUS OBSCURUS*) FORAGING IN TWO DIFFERENT HABITATS: ACTIVE ACOUSTIC DETECTION OF DOLPHINS AND THEIR PREY

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ABSTRACT

Active-acoustic surveys were used to determine the distribution of dusky dolphins and potential prey in two different New Zealand locations. During seven survey days off Kaikoura Canyon, dusky dolphins were found within the Deep-Scattering Layer (DSL) at 2000 when it rose to within 125 m of the surface. As the DSL rose to 30 m at 0100, the observed depth of dolphins decreased, presumably as the dolphins followed the vertical migration of their prey. Acoustically identified subgroups of coordinated animals ranged from one to five dolphins. Time, depth of layer, and layer variance contributed significantly to predicting foraging dusky dolphin subgroup size. In the much shallower and more enclosed Admiralty Bay, dolphins noted at the surface as foraging were always detected with the sonar, but were never observed in coordinated subgroups during the brief (two-day) study there. In Admiralty Bay dolphin abundance was correlated with mean volume scattering from potential prey in the water column; and when volume scattering, an index of prey density, was low, dolphins were rarely present. Ecological differences between the deep waters of Kaikoura Canyon and the shallow nearshore waters of Admiralty Bay may result in differences in how, when, and in what social groupings dusky dolphins forage.

Key words: foraging strategy, scattering layer, behavior, acoustic survey, dusky dolphins, *Lagenorhynchus obscurus*, mesopelagic prey.

Foraging decisions may affect the fitness of individuals and the dynamics of the population because the amount of food an animal can obtain affects its growth, survival, and reproductive success (Beyer 1995). Top predators such as marine mammals consume significant quantities of prey and may affect the distribution

and abundance of their prey, thus an understanding of their foraging behavior is also necessary to better understand ecosystem functioning (Kenney *et al.* 1997). Despite the importance of foraging, the difficulties of working in pelagic marine environments have limited our knowledge of predator-prey interactions. In particular, the heterogeneous and dynamic nature of resource distribution so characteristic of the marine environment (Steele 1978), combined with the mobility of animals at higher trophic levels in the ocean and our inability to directly observe the interactions occurring beneath the surface, have limited our progress.

The dusky dolphin (*Lagenorhynchus obscurus*), a small delphinid common to the cold-temperate waters around New Zealand, western South Africa, and South America (Gaskin 1968, Van Waerebeek *et al.* 1995), provides a useful predator for studying the ecology of foraging in pelagic environments because of the flexibility of its feeding habits. Because experiments that manipulate prey resources are difficult to conduct in the pelagic environment, temporal, and spatial variation in prey and predator must be used to provide insights into their interactions. The habitats and resources utilized by dusky dolphins vary widely. In Golfo San José, Argentina, and Marlborough Sounds, New Zealand, shallow-water bays support numerous scattered groups of dolphins feeding during the day on small schooling fishes (Würsig and Würsig 1980 for Argentina, Markowitz *et al.* 2003 for Marlborough Sounds, New Zealand). This contrasts with the waters of Kaikoura Canyon, New Zealand where the Subtropical Convergence and the more than 1,000-m deep Kaikoura Canyon combine to create a productive region of upwelling. Here, mesopelagic fishes, squid, and other species associated with a vertically migrating deep-scattering layer can be found relatively close to shore. The head of Kaikoura Canyon lies within approximately 500 m of shore, and drops rapidly to depths of more than 1,000 m in just over one kilometer from shore. Large groups of dusky dolphins and other marine mammals, probably attracted to the area by its rich prey abundance and favorable water temperatures, are encountered in the area year-round (Gaskin 1968, Cipriano 1992). Dusky dolphins here move offshore during late afternoon and evening to feed on the rising scattering layer, which may rise to within 30 m of the surface at night (Cipriano 1992).

Although the exact responses of a predator to changes in prey may not be fully understood, the flexible resource use and foraging behavior of dusky dolphins provide us the opportunity to investigate how changing environmental forces affect predator behavior. Studies of dusky dolphin foraging, taken together with research on other scattering layer consumers (see Benoit-Bird and Au 2003), provide information on the range of responses pelagic predators can use to exploit this resource. The micronektonic animals in scattering layers serve as one of the most important food resources in the ocean worldwide (Rasmussen and Giske 1994). In New Zealand, the abundant and diverse members of this scattering layer, including the myctophid fish, and small squid that are important food resources for dusky dolphins (Cipriano 1992), are extensively distributed (Robertson *et al.* 1978). The mesopelagic animals in this New Zealand scattering layer also serve as an important food resource for deepwater fish such as roughy (*Hoplostethus* spp.) and hake (*Macruronus novaezelandidae*) (Kuo and Tanaka 1984, Rosecchi *et al.* 1988, Kerstan 1989), marine birds including Cook's petrel (*Pterodroma cookii*) (Imber 1996), and pelagic squid (Saito *et al.* 1974, Jackson *et al.* 1998).

Dusky dolphins serve as a good model for understanding foraging on New Zealand's scattering layer because of their relative accessibility and the ability to

describe their vertical and horizontal distributions, while simultaneously describing the volume scattering and distribution of the scattering layer using active sonar surveys (Benoit-Bird and Au 2003). Comparison of these results with those from dusky dolphins foraging on schooling prey may provide further insight into the factors that are most important for scattering layer consumers. We used active acoustic surveys combined with behavioral sampling to examine the nighttime foraging behavior of dusky dolphins in the scattering layer in the deep waters of Kaikoura Canyon and the daytime behavior of dusky dolphins pursuing schooling fish in the shallow, protected waters of Admiralty Bay, Marlborough Sounds, New Zealand. The objectives of the study were to (1) examine the vertical movements of the deep-scattering layer; (2) investigate dolphin foraging patterns and group size in relation to the volume scattering of the layer, its heterogeneity, depth, and the time of day; and (3) compare this to dusky dolphin foraging in the protected shallow-water environment of Admiralty Bay.

METHODS

Active-acoustic surveys were used to determine the distribution of dusky dolphins and potential prey in two different locations off the South Island of New Zealand in winter 2002. In the Admiralty Bay area ($40^{\circ}51'S$, $173^{\circ}55'E$ to $40^{\circ}60'S$, $173^{\circ}50'E$), where dusky dolphins feed on small fish, a total of 122 km of transects were surveyed on 7 and 8 August 2002. These surveys were conducted continuously between 0930 and 1800 local time along planned, parallel transects within Inner Admiralty Bay, which is oriented north-south, with its mouth opening north-northeast. The bay is about 7 km long and 4.5 km wide at its widest point. This relatively enclosed area, with little to no oceanic swell at the surface, is not deep enough to provide habitat for a mesopelagic scattering layer. Transect lines were oriented north-south along the length of the inner bay, 0.9 km apart, running to within approximately 500 m of shore.

In the Kaikoura Canyon area ($42^{\circ}27'S$, $173^{\circ}51'E$ to $42^{\circ}35'S$, $173^{\circ}33'E$), where dusky dolphins feed at night on a sound-scattering layer, surveys were conducted continuously between 1800 and 0530 local time, covering a total of 250 transect kilometers between 27 July and 2 August 2002. Kaikoura Canyon is 60 km long, up to 1,200 m deep and has a generally U-shaped profile. Its head is within 500 m of the shore; thus oceanic waters are found close to shore. These open-ocean waters support mesopelagic animals, such as myctophid fish and medium-sized squid, that are part of a sound-scattering layer and serve as potential prey for dusky dolphins. Because almost nothing is known about the scattering layer in Kaikoura Canyon, acoustic transects were conducted both along and across the canyon and were designed to cover as much of the area as possible.

A Computrol, Tournament Master Fishfinder NCC 5300, modified to read directly into a laptop computer, was used to collect acoustic data from dusky dolphins and their potential prey to 156 m in depth (Benoit-Bird *et al.* 2001). The echosounder used a 130 μ sec long, 200 kHz pulse that is probably well above the hearing range of these dolphins (Johnson 1967). The envelope of the echo was digitized at a sampling rate of 10 kHz using a Computer Board PC DAS16/12-AO. Data acquisition was triggered by the outgoing signal. The transducer's signal was a downward pointing, 10° cone (Benoit-Bird *et al.* 2001). The transducer was towed beside the vessel at 2.6 m/sec (5 kt) over the bottom off Kaikoura where the water was deep, and at up to 4.1 m/sec (8 kt) in Admiralty Bay where the water was

shallow. During these surveys, position data were collected with a GPS every 5 min off Kaikoura and every 2 min in Admiralty Bay, as well as at every change in course.

Dusky Dolphins

Target strengths of large individual targets were calculated using an indirect calibration procedure incorporating reference targets (Benoit-Bird and Au 2003). As was done with spinner dolphins by Benoit-Bird and Au (2003), dusky dolphins were observed swimming beneath the transducer to determine their scattering characteristics. Like spinner dolphins, dusky dolphins have a combination of unique scattering characteristics that makes it possible to separate them from animals other than dolphins. The overall target strength of the dolphins was consistent as a function of depth, within 2 dB of -28 dB. The regression relationship for dusky dolphin target strength shows this lack of significant change in target strength with depth (dolphin target strength = $-28 - 0.0003 \cdot \text{depth}$, $r^2 = 0.006$, $n = 2,169$, $P = 0.94$). The target strength of dusky dolphins is much less than a fish of equivalent length (Love 1970) and very similar to the target strength of spinner dolphins (Benoit-Bird and Au 2003). Stronger echoes, presumably from the lungs of the animal (Au 1996), were found near one end of the animal, which we designated the front. The approximate number of echoes obtained from dolphins was also consistent, both in the horizontal (~ 15 echoes) and vertical (~ 4 echoes) directions. Active-acoustic dolphin identification was confirmed by visual sightings of surfacing animals.

During acoustic surveys, observers noted the presence of dolphins, identified the species, and recorded surface behaviors. Dusky dolphins were observed visually off Kaikoura approximately 84% of the time that dolphins were detected acoustically, despite limited nighttime visibility, as at least one animal usually approached the boat during an acoustic detection. Even though our ability to visually identify the species of each animal detected acoustically was limited in Kaikoura Canyon, at no point during the surveys was any other cetacean species sighted, supporting our estimation of dusky dolphins as the sole cetacean target species. Dusky dolphins were observed visually 100% of the time that they were acoustically detected during daytime in Admiralty Bay. Bottlenose dolphins were visually detected on one occasion. These data were excluded from the analyses. In both locations, an estimate of the number of animals present was made when visibility permitted. The behavior of visible dolphins was categorized when possible as resting at the surface, milling, directional swimming, apparent foraging, or interacting with the boat. The presence of bird species was also noted. Because surveys followed a planned course, groups were not followed, and therefore our observations were short snapshots of the group's surface behavior. The behaviors that we collected were not substantial enough during these brief studies to include in the discussion of this paper except to compare behavior that was noted as apparent foraging from the surface in this and other studies (Markowitz *et al.* 2003, McFadden *et al.* 2003¹) with the underwater depth distribution of the dolphins and their prey.

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

¹ MCFADDEN, C. J., T. M. MARKOWITZ AND B. WÜRSIG. 2003. Dusky dolphin foraging in Admiralty Bay, New Zealand, 2002. Report to the Marlborough District Council, Blenheim, New Zealand. 37 pp.

located at a particular depth by the diameter of the beam at that depth (Benoit-Bird and Au 2003). The relative abundance (analogous to catch-per-unit-effort) of dusky dolphins was defined as the percent of sampling time that dolphins were observed. We considered individual dolphins detected acoustically within 15 sec of each other (about 40 m along a transect) to be part of the same group, and calculated the observation time 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 sec. Because abundance is not based on counting of animals but rather 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 calculated relative abundance.

The subgroup size of acoustically detected dolphins was defined by looking at 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 perpendicular 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 a few meters of each other, and at approximately the same angle were defined as a subgroup (Fig. 1).

Prey

The total calibrated scattering intensity of prey (σ) was calculated for each cubic meter sampled. Because the identity of animals causing the scattering could not be determined in either location, prey abundance and numerical density estimates could not be made. Variance in the acoustic scattering of prey off Kaikoura was calculated on the integrated scattering strength over the entire layer within each 1-m interval for 25 m around each acoustic detection of dolphins. The position, depth, and scattering strength data from the echosounder were mapped in ArcView's Geographic Information System with 3-D Analyst to determine the horizontal and vertical distribution of prey animals and dusky dolphins. The Webster method (Webster 1973), a technique used to find significant differences in a variable over space, was used to determine the edges of the scattering layer off Kaikoura. Using a 2×2 -m window, a *t*-statistic was calculated by subtracting the mean volume scattering in one window from the mean volume scattering in the other and dividing by the standard deviation of the volume scattering of the entire transect (Legendre and Legendre 1998). The depths of a significant change in volume scattering ($\alpha = 0.05$), determined by a series of one-tailed *t*-statistics with progressive Bonferroni corrections (Legendre and Legendre 1998), were defined as the top and bottom of the layer. Significant differences, either alongshore or with depth within these outermost boundaries determined internal boundaries of volume scattering.

Data Analysis

To investigate the relationship between dolphin relative abundance and the volume scattering of prey, the average volume scattering of prey in 0.25-, 0.5-, and 1-km intervals of the entire survey was compared to the relative abundance of dusky dolphins in these same intervals using regression analysis. For the Kaikoura data the

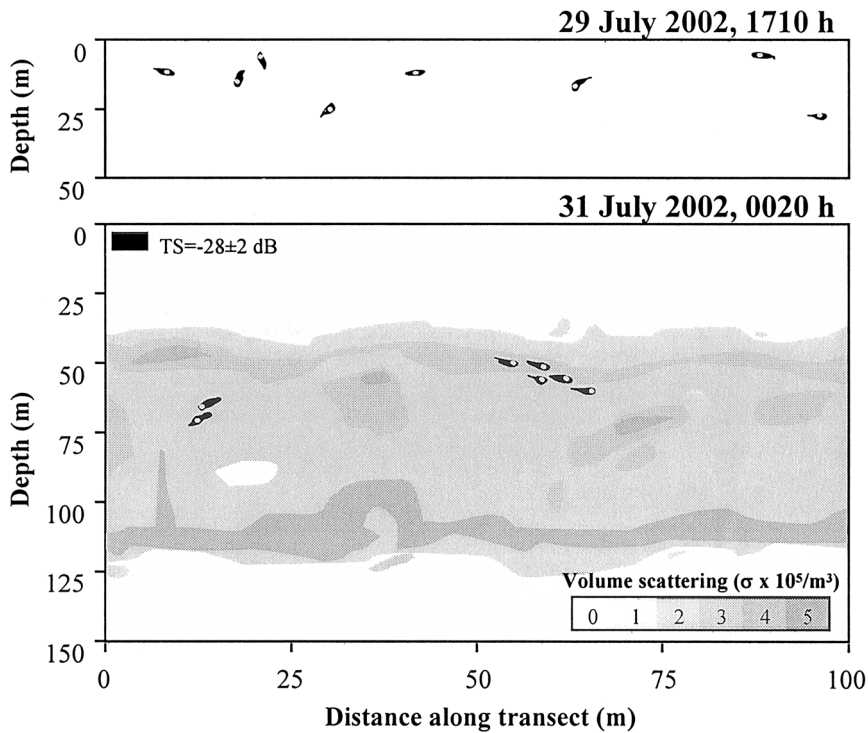


Figure 1. Examples of dusky dolphin acoustic detections off Kaikoura, New Zealand. The black areas show echoes that have target strengths consistent with dusky dolphins. The gray point in each dolphin signal represents the strong echo presumably from the lungs of the animal. The top panel shows animals before a scattering layer was present in the upper 150 m of the water column. Dolphins detected were not in organized subgroups. The bottom panel shows dolphins foraging within the layer at its shallowest depth. The gray scale is directly related to the volume scattering of the mesopelagic layer. The dolphins in this example were in two clear subgroups. The dolphins in each group were in close proximity to each other, were swimming at approximately the same angle, and were oriented in the same direction.

mean volume scattering in the 25 m surrounding dolphins (dolphin-present) was compared with the mean volume scattering in the 25-m intervals surrounding these areas (dolphin-absent), using a split-plot analysis of variance (ANOVA) that also incorporated time of day and night. This effectively deals with the issue of autocorrelation along transects as it uses a repeated measures statistic to eliminate the effects of autocorrelation within the dolphin presence/absence comparison.

For the Kaikoura data the effects of time of day, layer minimum depth, variance in prey volume scattering, and sampling night on dolphin subgroup size were investigated with individual and multiple regression. Bartlett's tests for homogeneity of variance for each variable proved insignificant, so no transformation of the data was required (time $B_c = 2.33$, $P = 0.68$; minimum depth $B_c = 0.59$, $P = 0.95$; prey variance $B_c = 3.93$, $P = 0.44$). Successive addition of each variable allowed the separate effects of multiple factors to be investigated by testing for significant changes in r^2 values.

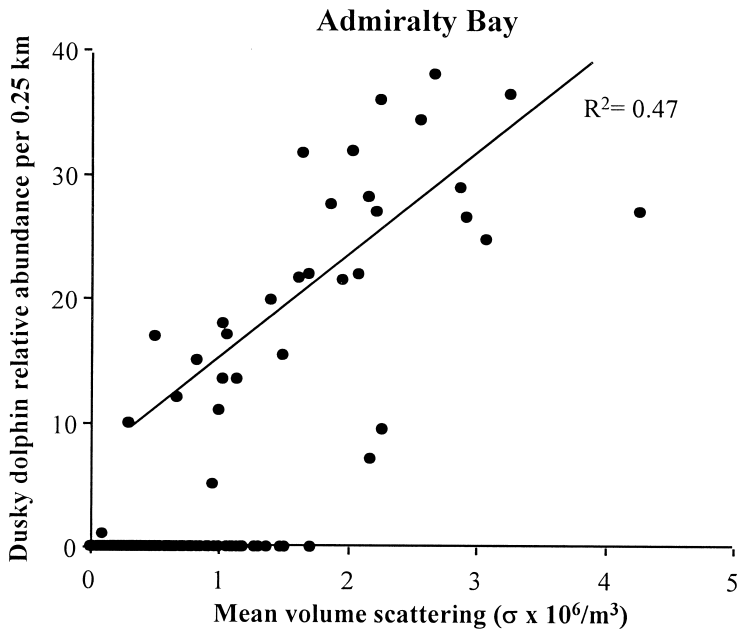


Figure 2. Volume scattering and the relative abundance of dusky dolphins in each 0.25 km surveyed in the Admiralty Bay area. The regression is fitted only to areas that contained dolphins.

RESULTS

Admiralty Bay

During the two days of our surveys in winter 2002, there were an unusually low number of dusky dolphins inside Admiralty Bay and, therefore, the results presented should be regarded as preliminary. During our observations, dusky dolphins in Admiralty Bay were always visually sighted when dolphins were detected with the sonar. Dolphins noted at the surface to be milling or traveling were never detected with the sonar, indicating that they were not diving below the boat to be picked up by the sonar. Dolphins noted at the surface as foraging were always detected with the sonar. Dusky dolphins were visually sighted and acoustically detected as part of groups ranging in size from 2 to 12 animals. All acoustic detections were of solitary dolphins swimming ≥ 4 m from other dolphins and not oriented similarly to other dolphins in the group.

Dusky dolphin relative abundance in 0.25-km sections of the transects was correlated with the mean volume scattering of potential prey in the water column in Admiralty Bay (Fig. 2). There were relatively few dolphins in the bay area and there was a low level of acoustic scattering. We compared the mean volume scattering in σ/m^3 , a measure of the density of scatterers in linear form (rather than logarithmic form as in decibels), to the abundance of dolphins. Interestingly, in all of the 17 0.25-km intervals where volume scattering reached or exceeded $2 \times 10^{-6} \sigma/\text{m}^3$, dolphins were found. Where volume scattering was lower than this, dolphins were found only 15 times out of 474 incidences. We do not know the identity of

Table 1. Summary of a split-plot ANOVA comparing mean volume scattering in the 25 m immediately around dolphins with the 25 m on either side of the dolphin-present area off Kaikoura.

Source	SS	df	MS	F	P
Dolphins	53	1	53	0.91	0.84
Time	1,071	8	134	2.31	0.03
Night	92	3	31	0.53	0.77
Split-plot error	38,136	657	58		

the scatterers we measured in this area so we cannot directly compute numerical density from volume scattering. However, if this volume scattering value was measured in the scattering layer around Hawaii, it would equate to a density of 0.2 animals/m³. If we instead assume that the scatterers were the average 20 cm long fish, closer to the schooling fish typically consumed by dusky dolphins, the density creating this level of scattering would be closer to 0.06 fish/m³.

Kaikoura Canyon

Unlike Admiralty Bay, in Kaikoura Canyon where acoustic scattering was on average an order of magnitude or two higher than Admiralty Bay, there was no relationship between volume scattering and dusky dolphin relative abundance. The relationship was not changed by varying the length of transect utilized for the relationship (0.25, 0.5, and 1 km). This was confirmed by a split-plot ANOVA on mean volume scattering comparing the 25-m surrounding dolphin acoustic detections and 25-m surrounding dolphin-present areas (Table 1). No effect of dolphin presence or sampling night was detected. However, there was an effect of time of day on the mean volume scattering.

The effect of time of day on volume scattering was related to the vertical migration of the sound-scattering layer in Kaikoura Canyon (Fig. 3). The layer first appeared above the 150 m sampling depth at 1900 each night and reached a minimum depth of between 29 and 49 m between 2300 and 0100 local time. The layer's complete descent below 150 m was not observed by sampling that ended at 0530. Two discrete areas of higher volume scattering were observed within the overall scattering layer. One of these areas was consistently within a few meters of the bottom of the layer when the entire range of the layer was within the upper 150 m of the water column. The second strong scattering region appeared to migrate at a slightly different rate than the remainder of the layer. When observed, this strong scattering region was found within 35 m of the top of the scattering layer (Fig. 3). These changes in the position of the high volume scattering regions throughout the layer's migration cause a change in mean volume scattering as a function of time.

As the depth of the layer changed, the depth of detected dusky dolphins also changed (Fig. 3). The observed vertical distribution of acoustically detected dusky dolphins from 1700 to 1900 did not overlap with the scattering layer, suggesting that dusky dolphins were not foraging at these times, despite presumed foraging activities noted from surface behaviors. During this early part of the layer's migration, the layer was deeper than 140 m and was often outside our sampling range. As the scattering layer became shallower, the vertical distribution of dusky

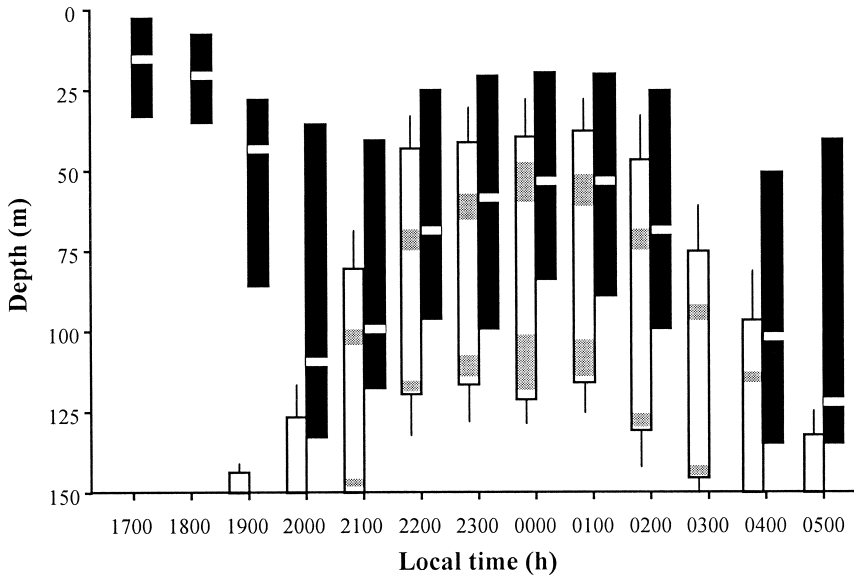


Figure 3. Depth distribution of the sound scattering layer and dusky dolphins off Kaikoura, New Zealand as a function of time. The open bars show the mean vertical range of the scattering layer. Error bars show the full range of the depth of the layer's edge. Gray areas within the prey distribution show areas of stronger scattering intensity. The filled bars show the entire depth range of dusky dolphin detections. The white line represents the mean depth of dusky dolphin detections corrected for beam effects. No dolphins were detected during the 0300 hour.

dolphins also became less deep. However, dolphins were never detected below 130 m, even though part of the scattering layer was at least this deep all but one hour each night. The mean acoustically observed depth of dusky dolphins was strongly correlated with the depth of the shallow high volume scattering region ($r^2 = 0.87$, $n = 2169$, $P < 0.001$). There was a systematic discrepancy in the correlation; dolphins were observed an average of about 1 m shallower than the minimum depth of the high scattering region (dolphin depth = high scattering depth - 1.1, $r^2 = 0.83$). Dusky dolphins were never observed in the deeper of the two higher volume scattering regions during the 7 h each night when this second intense layer was present.

The number of dusky dolphins within coordinated subgroups in Kaikoura Canyon varied from one to five (Fig. 4). When dolphins were not found within the scattering layer, dolphins were most often found individually (Fig. 1, top panel). Regression analysis was used to examine the effects of time, scattering layer minimum depth, variance in prey scattering, and night on subgroup size. Bartlett's tests for homogeneity of variance for each variable proved insignificant so no transformation of the data was required for regression analysis. Any apparent differences in variance in the figures appear to be caused by the use of cutoffs in the boxplots rather than real differences. Scatterplots of the data show this but make it more difficult to see the overall pattern in the data. The subgroup size of actively foraging dusky dolphins varied significantly with time. The most significant fit was a quadratic equation (Fig. 5, dolphin group size = $-0.08 * \text{time}^2 + 4.01 * \text{time} -$

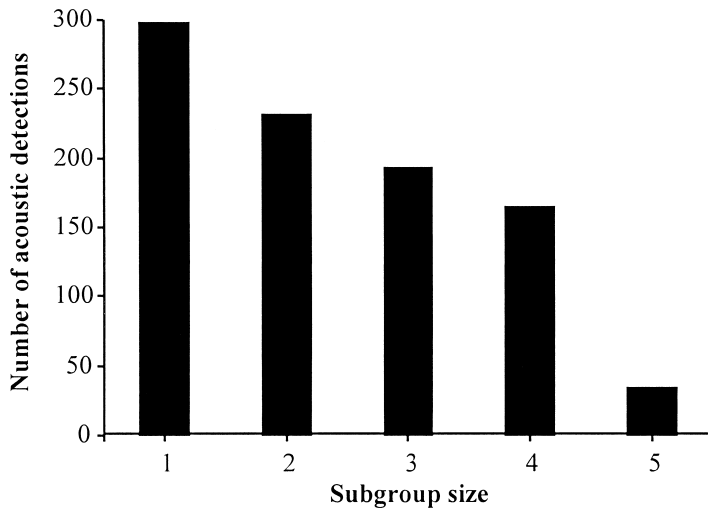


Figure 4. Histogram of the number acoustic detections of each subgroup size of dusky dolphins in the Kaikoura Canyon area. This histogram includes all detections, not just foraging animals.

44.50, $r^2 = 0.46$, $P < 0.001$) where each term added significantly to the relationship. Subgroup size of foraging dusky dolphins was linearly related to the scattering layer's minimum depth (Fig. 6, dolphin group size = $-24.8 * \text{min depth} + 157.2$, $r^2 = 0.44$, $P < 0.001$). Variance in prey scattering volume was also related to group size with a cubic function providing the best fit with each term in the equation adding significantly to the fit (Fig. 7, dolphin group size = $0.0000005 * \text{variance}^3 - 0.0002 * \text{variance}^2 + 0.038 * \text{variance} + 1.46$, $r^2 = 0.51$, $P < 0.001$). To test the interrelationships of these factors, they were tested together in a multiple regression. Terms in the multiple regression were added from most to least significant to ensure that additional significance was not related to colinearity (Table 2). The partial regression coefficients for variance, time, and minimum depth were each significantly different from zero ($P < 0.001$ for each) and each added significantly to the prediction of dolphin subgroup size. However, sampling night did not significantly affect observed subgroup size. The largest subgroups occurred when the scattering layer was closest to the surface and when the volume scattering of the layer was most heterogeneous.

DISCUSSION

The use of quantitative data from active sonar to simultaneously assess dolphins and their prey is a powerful technique to study prey densities, vertical and horizontal movements of the prey community, and the depths and numbers of dolphins foraging on these prey (for example, Benoit-Bird *et al.* 2001, Benoit-Bird and Au 2003). We utilized this technique in two different locations, representing two distinct habitat types in which dusky dolphins can be found: shallow bays, where dusky dolphins may feed in a coordinated fashion on schooling fish, and waters where a deep-scattering layer can be supported and dusky dolphins feed on

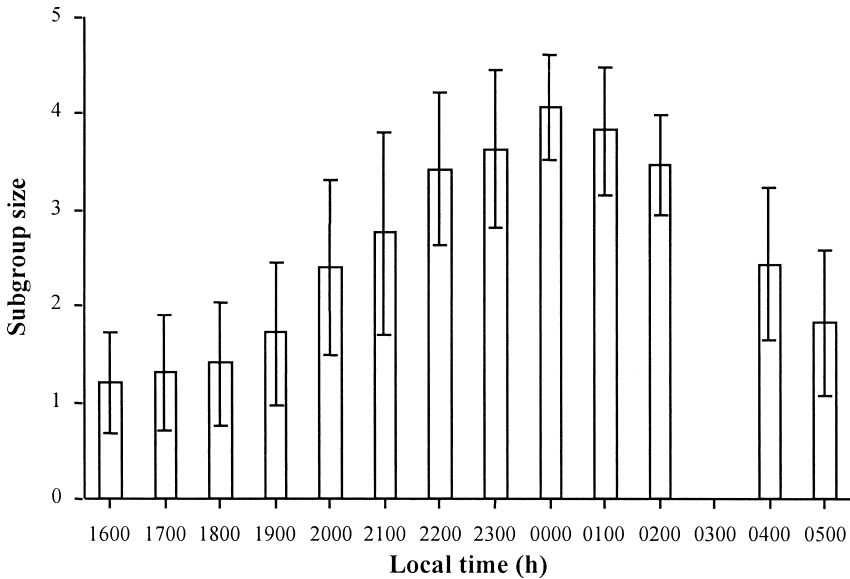


Figure 5. Dusky dolphin subgroup size off Kaikoura as a function of time. Error bars show standard deviation. No dolphins were detected at 0300.

mesopelagic fish and squid. In New Zealand some of the same photo-identified dolphins that feed at night on the scattering layer in Kaikoura Canyon move to the shallower inshore waters of the Marlborough Sounds, several hundred kilometers northwest of Kaikoura in the winter (June–August). There, these dolphins feed during the day on schooling fish (Markowitz *et al.* 2003, McFadden *et al.* 2003¹). Much, but not all, of this feeding involves dolphins herding schooling fishes (“bait balls”) to or near the surface (Markowitz *et al.* 2003), as has been described for duskiies feeding on anchovy in the shallow nearshore waters of southern Argentina (Würsig and Würsig 1980, Würsig 1986).

The two days of sonar transects conducted in Admiralty Bay of the Marlborough Sounds did not coincide with intensive bouts of dolphins feeding on schooling fishes; instead, we saw scattered small groups of three to six animals milling, resting, and occasionally engaging in apparent chases of prey. Only individual animals were detected acoustically. During these two days, there was a clear positive relationship between acoustic scattering, indicative of potential prey, and the relative abundance of dusky dolphins. Dolphins were rarely observed when volume scattering was below $2 * 10^{-6} \sigma/m^3$. Because the species and size of potential prey causing the acoustic scattering is unknown, the volume scattering cannot yet be related to numerical prey density or energy density. However, it may indicate that a lower limit of prey availability for effective foraging by dusky dolphins exists. With further work, it may be possible to model the energy cost of foraging using remotely sensed prey and dusky dolphin data, similar to what was done by Gorman *et al.* (1998) for wild dogs and Acevedo-Gutiérrez *et al.* (2002) for blue and fin whales.

Dusky dolphins in and near Kaikoura Canyon forage at night on mesopelagic myctophids and squid in a deep-scattering layer (Würsig *et al.* 1989, Cipriano

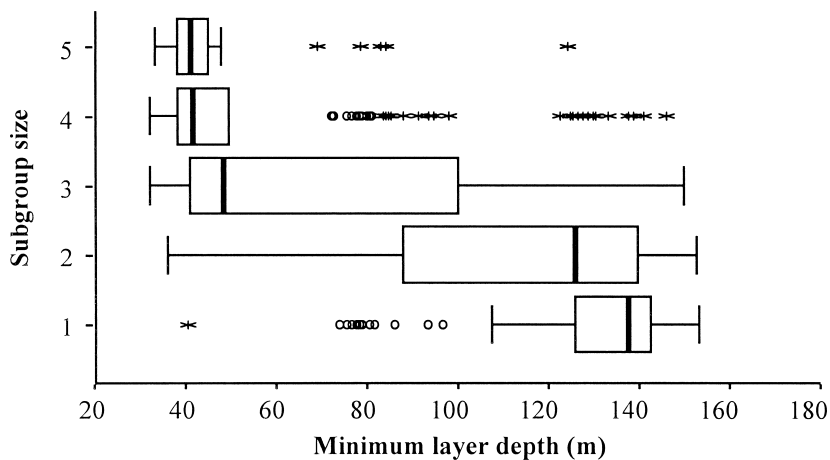


Figure 6. Boxplot of the minimum depth of the scattering layer as a function of the detected subgroup size. Alone, scattering layer minimum depth accounted for 44% of the variation observed in subgroup size. Dark bars show the median of the layer's depth at each subgroup size, the box shows the interquartile range, the error bars show the 95% confidence interval. The open circles represent outliers (values within three times the interquartile range) while stars show extreme cases (values more than three box lengths outside the interquartile range). The lower bound of the 95% confidence interval for groups of four dolphins was within the interquartile range.

1992, Würsig *et al.* 1997). Until this study, we did not know at what depths dolphins were utilizing the scattering layer. The equipment used was limited to the upper 150 m of the water column. However, this did not limit our study as dusky dolphins were not acoustically observed at depths >130 m. In the deep waters of and near Kaikoura Canyon, dusky dolphins began to overlap with the deep-scattering layer, apparently foraging, at about 2000 local time, after it came within 130 m of the surface. They continued to forage until 0500 when the layer again descended below 130 m. This provided a potential foraging window of 9 h. Collection of similar data for summertime would permit the influence of night duration to be investigated. Research on other vertically migrating animals suggests that the sound-scattering layer would be in shallow waters, accessible to dusky dolphins for much longer each night in the winter than the summer (Clarke 1970). The length of the summer foraging window will depend on the vertical migration behavior of the scattering layer and the depth range utilized by the dusky dolphins. It is unknown if the depth of about 130 m is the practical lower limit for dives of these smaller delphinids, or if they would dive deeper if prey were not available in more shallow depths. Because dolphins can expend less energy when diving less deeply (Williams *et al.* 1999), it is possible that foraging on more dispersed prey in shallower water is more advantageous energywise. Shallower dives were observed in Kaikoura. The full range of depths of detected dusky dolphins decreased as the layer migrated towards the surface, similar to the vertical distribution observed in spinner dolphins (Benoit-Bird and Au 2003). While dusky dolphins were capable of diving to 130 m, dolphins were not observed at these depths except when the majority of the scattering layer was deeper than 130 m. In all cases when there were two areas of high volume scattering within the scattering layer, they were found

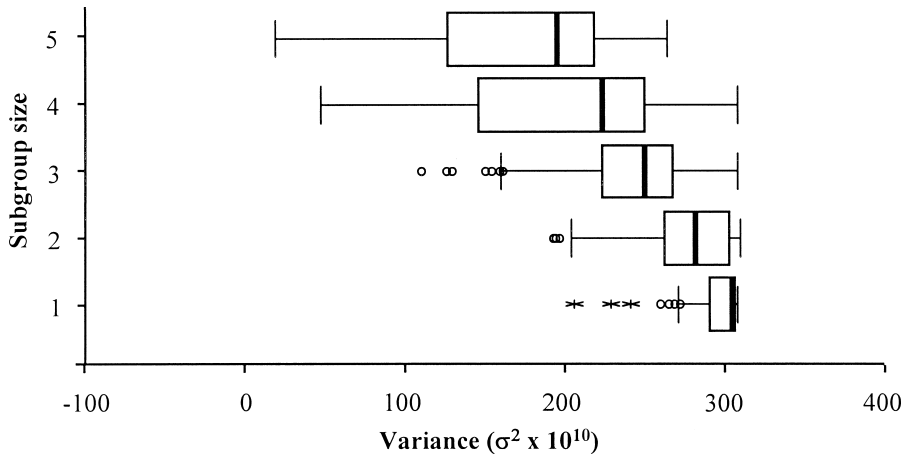


Figure 7. Boxplot of variance in the volume scattering of the prey layer off Kaikoura as a function of subgroup size of foraging dusky dolphins. Alone, prey variance accounted for 43% of the variation observed in subgroup size. Dark bars show the median of the variance for each subgroup size, the box shows one interquartile range in variance, the error bars show the 95% confidence interval for prey variance. The open circles represent outliers while stars show extreme cases.

only in the shallower one; for example, within the high density region between 50 and 65 m instead of the high density region at 100–120 m depth. In fact, the mean depth of dusky dolphins was within this shallow, high-scattering region nearly every time in which one was observed. Killer whales were observed to consistently work only the shallower layer when two were present (Similä 1997), whereas spinner dolphins used the shallower high-scattering region more often than the deeper one, but could be found in both (Benoit-Bird and Au 2003).

In addition to changing the depths at which dolphins were found, the diel migration of the prey was also correlated with a change in the subgroup sizes observed. Subgroup size varied from solitary animals to groups of five animals swimming in the same direction in close proximity to each other. These subgroups were not related to nearby subgroups. In contrast, foraging spinner dolphins in Hawaii were found almost exclusively in pairs that were part of much larger coordinated groups (Benoit-Bird and Au 2003). In Kaikoura Canyon, before foraging began, animals were almost exclusively found swimming individually. During foraging in Kaikoura Canyon, the subgroup sizes of dolphins increased with decreasing depth of the prey layer. Subgroups of dolphins were the largest during the middle of the night. This indicates that dolphins may be coordinating movements during feeding differently as prey depth changes. Since group foraging reduces variance in prey capture per individual, animals tend to forage solitary where prey availability is less than or equal to their needs, and in groups where prey availability is greater (Uetz and Hodge 1990). The volume scattering of prey increased as the layer's depth decreased with the addition of a high scattering region near the top of the layer. In addition, we hypothesize from available dive time and behavioral data that time limitations may be affecting the degree of coordination by dusky dolphins. Dusky dolphins tend to dive for about 1.5 min when "working" a school of fish in the shallow waters of Patagonia (Würsig 1982), with the

Table 2. Multiple regression summary for effects of prey characteristics on dusky dolphin subgroup size. Each regression is the best fit from the individual regressions.

Model	r^2	Change statistics				
		r^2 change	F change	df1	df2	P
Variance _(cubic)	0.51	0.51	499.60	1	655	<0.0001
Variance _(cubic) , Time _(quadratic)	0.61	0.10	132.81	1	654	<0.0001
Variance _(cubic) , Time _(quadratic) , Minimum depth	0.63	0.02	36.36	1	653	<0.0001
Variance _(cubic) , Time _(quadratic) , Minimum depth, night	0.63	0.00	0.65	1	652	0.42

occasional dive as long as 3 min in Kaikoura Canyon (Cipriano 1992). Sustained directional travel speeds at the surface are about 3.4 m/sec or 12.2 km/h (Cipriano 1992). If similar to dive speeds, then a round trip to 130 m (the lowest detected dives in this study) takes about 76 sec, or 1.3 min, with a maximum of only another 1.0–1.8 min available for feeding at depth. At 30 or 40 m depth, the amount of time available for feeding is increased, as only about 20 sec are needed for round-trip travel. It is possible that the difference in travel times at shallower depths allows for working cooperatively. Similä (1997) found that killer whales feed on herring to at least 98 m depth, and do so almost always alone below about 20 m; while at depths of 1–19 m, they are more often in groups of two to three (and, on two occasions, were in groups of 12).

Subgroup size of foraging dusky dolphins in Kaikoura also varied as a function of prey heterogeneity. As the variance of the prey's volume scattering (a measure of patchiness) increased, the subgroup size also increased. It is not clear whether the increase in variance is causing a change in the dolphins' foraging behavior or if the variance is being caused by the behavior of the dolphins. There is no correlation between the horizontal distribution of the scattering layer and the abundance of dusky dolphins, suggesting that dusky dolphins are not actively aggregating their prey as has been observed for dusky dolphins near the surface off Argentina (Würsig and Würsig 1980) and in spinner dolphins well below the surface off Hawaii (Benoit-Bird and Au 2003). However, consumption of prey by dolphins could increase the prey's heterogeneity and would be expected to be higher with more dolphins. Alternatively, dusky dolphins may be increasing their foraging group size in response to the prey's variance as has been shown in other animals, including mole rats and pelagic fish (Ryer and Olla 1992, Spinks and Plaganyi 1999, Le Comber *et al.* 2002). Cooperation may decrease starvation risk in heterogeneous habitats (Spinks and Plaganyi 1999) or increase foraging efficiency through social facilitation in the ephemeral patches that are so common in pelagic systems (Ryer and Olla 1992). An additional benefit of group foraging may be an increase in prey-finding ability (Le Comber *et al.* 2002). When food is evenly distributed, there is little benefit to searching for food in a group as all areas have the same density of prey. However, as the prey becomes more patchily distributed, finding these high-density patches may become more important, and more difficult, increasing the advantages of group foraging. A final benefit of foraging as part of a group may be a decreased risk of predation through increased group vigilance (Swenson 1993). We do not know how this would be altered along with the

distribution of prey. However, the size of subgroups is likely not the appropriate measure of this as subgroups were observed in parts of larger, uncoordinated groups.

Radio-tracking studies in and near Kaikoura Canyon (Cipriano 1992, Würsig *et al.* 1997) showed that dusky dolphins traveled into deeper waters farther offshore at night than during the day. This travel was not a simple "offshore-inshore" pattern during the night, however, and it is possible that the dolphins were following the best-developed and shallowest areas in the deep-scattering layer. During this study, we did not gather enough data to fully describe the horizontal distribution of the deep-scattering layer in Kaikoura Canyon. However, the layer was remarkably homogeneous over the deep-water areas of the canyon. Over the shelf areas surrounding the canyon, the volume scattering of the layer decreased rapidly, suggesting that there is no directed horizontal movement of this layer towards shore like the movement that has been observed in the scattering layer consumed by spinner dolphins in Hawaii (Benoit-Bird *et al.* 2001).

Our data, combined with results from previous behavioral and tagging studies, suggest that the differences between the habitats used by dusky dolphins result in differences in how, when, and in what social groupings dusky dolphins forage. In the shallow nearshore waters of Admiralty Bay where dusky dolphins forage on schooling fish, our limited observations showed a correlation between dusky dolphins and potential prey, even when very little prey was available. Dolphins detected in these preliminary observations as overlapping with potential prey were foraging individually and were observed at the surface exhibiting behavior indicative of foraging. Dusky dolphins in the deep waters of the Kaikoura Canyon did not exhibit a correlation in horizontal space with their potential prey, likely because of its relative homogeneity within the canyon. Surface behavior was not a good indicator of the onset of foraging in Kaikoura Canyon, as overlap between dusky dolphins and potential prey did not occur until 2000, although surface indications of foraging began at 1800. In Kaikoura Canyon dusky dolphins can forage on the scattering layer only when it is within their depth range and, thus, are time-limited by the vertical migration behavior of this prey resource. The vertical range used by dusky dolphins closely matched the vertical distribution of the scattering layer, suggesting they followed its diel vertical migration. The mean depth of dusky dolphins closely followed the depth of a higher volume scattering region found near the top of the layer. Dusky dolphins in Kaikoura Canyon were found foraging alone, but also in groups of up to five animals. We did not see evidence of active aggregation of prey by the dolphins as has been observed by much larger coordinated groups of spinner dolphins (Benoit-Bird and Au 2003) and by dusky dolphins in other locations (Würsig and Würsig 1980). The degree of group coordination in Kaikoura depended on the characteristics of prey, suggesting a change in the risk-benefit tradeoff throughout the night. Changes in the benefits and risks throughout the year in these temperate waters may present an opportunity to examine the causes underlying the behavior of pelagic predators foraging on scattering layers, perhaps the most abundant source of food for these large predators worldwide (Cushing 1973).

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