Subsurface and nighttime behaviour of pantropical spotted dolphins in Hawai′i

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Abstract: Pantropical spotted dolphins (*Stenella attenuata*) are found in both pelagic waters and around oceanic islands. A variety of differences exist between populations in these types of areas, including average group sizes, extent of movements, and frequency of multi-species associations. Diving and nighttime behaviour of pantropical spotted dolphins were studied near the islands of Maui and Lana′i, Hawai′i, in 1999. Suction-cup-attached time–depth recorder/VHF-radio tags were deployed on six dolphins for a total of 29 h. Rates of movements of tagged dolphins were substantially lower than reported in pelagic waters. Average diving depths and durations were shallower and shorter than reported for other similar-sized odontocetes but were similar to those reported in a study of pantropical spotted dolphins in the pelagic waters of the eastern tropical Pacific. Dives (defined as >5 m deep) at night were deeper (mean = 57.0 m, SD = 23.5 m, *n* = 2 individuals, maximum depth 213 m) than during the day (mean = 12.8 m, SD = 2.1 m, *n* = 4 individuals, maximum depth 122 m), and swim velocity also increased after dark. These results, together with the series of deep dives recorded immediately after sunset, suggest that pantropical spotted dolphins around Hawai′i feed primarily at night on organisms associated with the deep-scattering layer as it rises up to the surface after dark.

Résumé : Les Dauphins tachetés pantropicaux (*Stenella attenuata*) fréquentent aussi bien les eaux des zones pélagiques que les eaux qui bordent les îles océaniques. Il existe un certain nombre de différences entre les populations de ces types de milieux, notamment dans le nombre moyen de dauphins par groupe, l'importance des déplacements et la fréquence des associations multispécifiques. Les plongées et les comportements nocturnes des Dauphins tachetés pantropicaux ont été étudiés au large des îles Maui et Lana′i, à Hawai′i, en 1999. Des chronobathymètres/marqueurs radio VHF ont été attachés à six dauphins au moyen de ventouses pendant 29 h au total. Les taux de déplacement des dauphins marqués sont considérablement plus faibles que ceux signalés dans les eaux pélagiques. La profondeur et la durée moyennes des plongées sont moins élevées que celles enregistrées chez des odontocètes de même taille, mais sont semblables à celles observées au cours d'une étude sur les Dauphins tachetés pantropicaux dans les zones pélagiques du Pacifique tropical oriental. Les plongées (de plus de 5 m) sont plus profondes (en moyenne = 57,0 m, écart type = 23,5 m, *n* = 2 individus, profondeur maximale de 213 m) la nuit que le jour (en moyenne = 12,8 m, écart type = 2,1 m, *n* = 4 individus, profondeur maximale de 122 m) et la vitesse de la nage augmente également à l'obscurité. Ces résultats, ajoutés à l'observation de plongées profondes immédiatement après le coucher du soleil, indiquent que les Dauphins tachetés pantropicaux se nourrissent surtout la nuit d'organismes associés à la couche diffusante profonde, pendant sa remontée vers la surface la nuit.

[Traduit par la Rédaction]

Introduction

As its name implies, the pantropical spotted dolphin (*Stenella attenuata*) is found throughout tropical oceans of the world. In the eastern tropical Pacific (ETP) groups are large and often numbering in the hundreds or thousands of individuals (Scott and Cattanach 1998). These groups form associations with yellowfin tuna (*Thunnus albacares*) and several other species of pelagic dolphins. Most of what is known about pantropical spotted dolphins comes from the ETP, as high levels of bycatch in the tuna purse-seine fishery have spurred research into pantropical spotted dolphin biology and ecology (e.g., Perrin 1975; Robertson and Chivers 1997; Scott and Cattanach 1998). Recently a study of the movements and diving behaviour of pantropical spotted dolphins has been undertaken, with several time–depth recorders (TDRs) deployed on animals in oceanic waters of the ETP (Scott et al. 1993). Results from tracking and food habits studies (Perrin et al. 1973; Robertson and Chivers 1997; Scott and Cattanach 1998) suggest that pantropical spotted dolphins in the ETP feed primarily at night on epipelagic species and on mesopelagic species that rise towards the water's surface after dark. Dolphins in these pelagic areas have also been documented to have large home ranges and move over large areas in relatively short periods of time, traveling

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from 50 to 100 km or more per day (Leatherwood and Ljungblad 1979; Perrin et al. 1979; Scott et al. 1993).

Pantropical spotted dolphins are also found in nearshore areas, both along continental coasts (e.g., Acevedo and Burkhart 1998) and around oceanic islands. Near the Hawaiian Islands, this species is often found in waters less than 200 m deep and group sizes are much smaller than observed in pelagic waters. Based on 23 sightings made during aerial surveys covering all of the main Hawaiian Islands, Mobley et al. (2000) found an average group size of 43 individuals. There is also some evidence that pantropical spotted dolphins around the Hawaiian Islands show much more limited movements and presumably have much smaller home ranges than those observed in the ETP. Scott and Wussow (1983) radio-tracked a pantropical spotted dolphin off the island of Hawai′i and found movements of only about 40 km over a 4-day period. In addition, pantropical spotted dolphins in relatively shallow areas (e.g., between the islands of Maui and Lana′i) have relatively low frequencies of scars associated with deepwater cookie-cutter sharks (*Isistius brasiliensis*) compared with pantropical spotted dolphins off the island of Hawai′i (R.W. Baird, personal observations). This suggests that animals in these shallow-water areas rarely move into deeper water, and thus may not regularly move across the deepwater (>1000 m) channels between some of the islands.

These differences in group size and scale of movements of island-associated pantropical spotted dolphins versus those found in pelagic areas are matched by substantial differences between the mesopelagic prey community associated with islands and that of pelagic areas (Reid et al. 1991). Thus, it is unclear whether pantropical spotted dolphins around islands would exhibit the same feeding patterns as individuals in offshore areas. Little is known about the diet of pantropical spotted dolphins around the Hawaiian Islands; stomach contents of only two individuals have been recorded, and these primarily contained the remains of mesopelagic fish and squid (Shomura and Hida 1965; Clarke and Young 1998).

Here we report on a study of the diving behaviour of pantropical spotted dolphins off the islands of Maui and Lana′i, Hawai′i; the first diving behaviour study of this species in nearshore waters. We used TDRs and VHF-radio tags to study diving behaviour. These tags were remotely attached with suction cups, an approach that does not rely upon capturing animals (Baird 1998*a*; Hooker and Baird 2001).

Methods

Fieldwork was undertaken between 7 January and 9 December 1999 in the waters west of Maui, Hawai′i, using 5- and 6-m rigid-hull inflatable boats. The area between the islands of Maui, Lana′i, and Kaho′olawe was searched nonrandomly, with routes being determined to give as broad a coverage of the area as possible but being limited by strong trade winds and resultant high seas which commonly occur in the area. When dolphins were encountered, the species was identified and group size was estimated. If pantropical spotted dolphins began to bowride on the research vessel and tagging gear was onboard (approximately 70% of the days pantropical spotted dolphins were encountered), attempts to tag were made.

The tags used were the same as those used to examine diving behaviour of several other species of cetaceans (Baird 1998*a*; Hooker and Baird 1999; Baird et al. 2000). Each tag weighed about 400 g (approx. 0.5% of the body mass of a pantropical spotted dolphin) and contained a VHF-radio transmitter (MOD-125, Telonics, Mesa, Ariz., U.S.A.) with a 30-cm semi-rigid wire antenna and a TDR (Mk6, Wildlife Computers, Redmond, Wash., U.S.A.). The TDR recorded depth and velocity every second, and temperature and light levels every 5 s. All but one TDR measured depth in 1-m increments (accuracy ± 1 m), whereas the remaining instrument measured depth in 4-m increments (accuracy ± 4 m). The maximum depth range of these instruments was 250 or 1000 m, respectively. Velocity was measured by rotation of a paddlewheel. Velocity readings are presented as relative velocity, as readings vary with position of the tag on the body (Baird 1998*b*) and probably also with body size. The maximum temperature limit of the units was 22.7°C, which is less than the temperature of surface waters in Hawai′i, thus the only usable temperature records were those obtained below a depth of approximately 80 m. Light intensity was measured with a photodiode (BPX 63, Siemens Components Inc., Cupertino, Calif., U.S.A.), which had a spectral sensitivity of 350–1100 nm and peak sensitivity at 800 nm. Light values were recorded in uncalibrated units; calibration of the values followed McCafferty et al. (1999) with units converted to illuminance (lux) using the formula: $\ln(\text{lux}) = 0.13(\text{TDR output}) - 12$.

Tag bodies were constructed from syntactic foam (to cause tags to float after they fell off) and were attached with a 8-cm diameter suction cup (Canadian Tire). The inner surface of the suction cup was coated with silicone grease to increase adhesion. Tags were attached to the end of a 3-m pole and were deployed on bowriding dolphins by hitting the suction cup against the dorsal surface of a dolphin as it came to the surface to breathe.

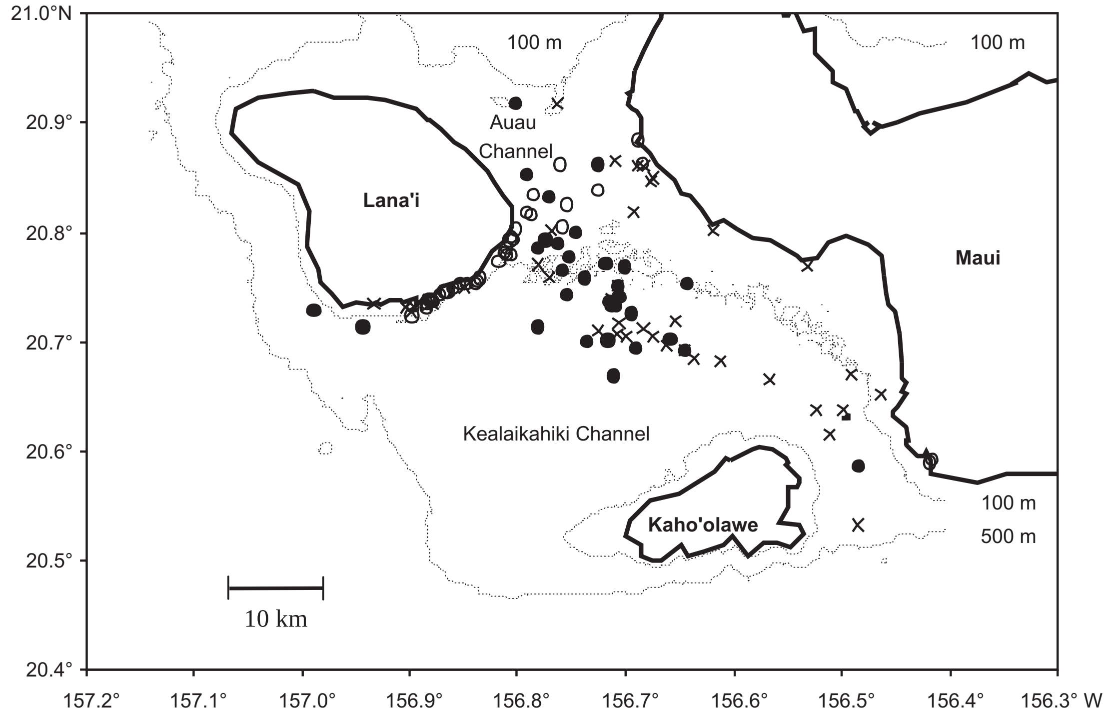
The magnitude of the immediate reactions of individuals to tagging was recorded. Once a tag was attached, the tagged animal or the group in which the tagged animal was present was tracked visually or using the VHF-tracking equipment. We recorded location on board our research vessel with a GPS at 5- to 10-min intervals when near the tagged dolphin or the group that it was in, and bottom depths were determined by interpolation off a nautical chart. Associations with seabirds, which might indicate feeding behaviour, were noted as were any observations of possible feeding (e.g., fish observed at the surface near dolphins or dolphins moving through schools of fish).

Once tags were recovered, data were downloaded to a computer in hexadecimal format. Data were processed in several ways using software provided by the TDR manufacturer (Wildlife Computers). The hexadecimal files were run through the program Minimum–Maximum–Mean (version 1.22) to produce raw ASCII files with all data values (e.g., for plotting and calculation of the percentage of time at depth). As well, hexadecimal files were processed with Zero–Offset–Correction (version 1.30) to correct for temperature-related drift in the surface values. The resulting files were processed with Dive Analysis (version 4.08) to calculate statistics for each dive (dive durations, maximum depths, rates of descent and ascent). The outputs of this program were ASCII files, which could then be imported into Excel (version 2000) and (or) Minitab (version 10.2) for statistical analyses and graphing. Rates of ascent and descent were calculated with the start and end points chosen using the Dive Analysis program, selecting periods of relatively constant descent or ascent covering at least 40% of the depth of each dive.

Results

A total of 640 h of boat-based search effort during 98 days resulted in 36 sightings of pantropical spotted dolphins. Group size ranged from 10 to approximately 150 individuals (median = 60, mean = 60, SD = 26). Most groups had infants present, indicating the presence of adult females. Although search effort was not random, pantropical spotted

Fig. 1. Sighting locations of pantropical spotted dolphins (*Stenella attenuata*) (●), spinner dolphins (*Stenella longirostris*) (○), and bottlenose dolphins (*Tursiops truncatus*) (×) from the study area during 1999. Only a single point is shown for each encounter, the location where each group was first seen. The 100- and 500-m depth contours are indicated.



dolphins were typically found at least 3–5 km offshore in the area between the islands of Maui, Lana′i, and Kaho′olawe and in waters ranging from 70 to 300 m deep (Fig. 1). Comparison with the sighting distribution of other recorded dolphin species (based on the same distribution of search effort) demonstrated their relatively distinct habitat use. Spinner dolphins (*Stenella longirostris*) were typically found closer to shore (particularly off the island of Lana′i) or in shallower water in the Auau Channel, and bottlenose dolphins (*Tursiops truncatus*) were distributed both close to shore along the coasts of Maui and Lana′i and further offshore (Fig. 1). Taking into account only group composition when first found (since the longer a group is followed the more likely it may come across another species), mixed-species groups were uncommon (9.1% of sightings of pantropical spotted dolphins), with associations occurring with bottlenose (two occasions) and spinner dolphins (one occasion).

Nineteen attempts were made to tag pantropical spotted dolphins, eight of which were successful. Attempts were not always successful primarily because of the angle at which the suction cup hit the dolphin (i.e., if the cup did not hit squarely it was unlikely to stick). The battery failed in the tag used in the first two deployments, thus dive data were obtained from only six individuals (hereafter referred to as "successfully tagged animals") on 5 days (Table 1). Based on the degree of spotting and relative body size estimated in the field, all six of the successfully tagged animals were thought to be adults or large subadults. Group sizes for groups in which animals were tagged were similar (mean = 70 individuals, SD = 18 individuals, n = 5 groups) to the overall average group size. For 1 of the 6 successfully tagged animals no reaction to tagging was observed; other reactions observed included a flinch and fast dive (2/6), a tail flick (2/6), and a slow barrel roll (1/6). Three of the six successfully tagged animals returned to ride the bow, and all tagged animals remained within the group and exhibited behaviours similar to other nearby dolphins. Tags remained attached for periods ranging from a few minutes to just over 12 h, resulting in a total of 29 h of dive data. Tagged dolphins were followed for periods ranging from 5 min to over 3 h (for a total of 12 h; Table 1), and we noted that they used the same areas as non-tagged dolphins (Fig. 2). Two of the tags remained attached after sunset, providing a total of 5.5 h of nighttime data. Taking into account the first and last known locations of tagged dolphins on each day, an average net speed of 1.8 km/h was calculated (Table 1). However, travel routes were clearly nonlinear (Fig. 2), so this average net speed does not represent true swimming speed. Bottom depths where tagged dolphins were followed ranged from 70 to 440 m (mean = 220 m, SD = 107 m, n = 137 depth readings at 5-min intervals) and in no case when dolphins were followed were dives near the bottom (Fig. 3). A regression of bottom depth against time of day during the periods when tagged dolphins were followed showed that tagged animals tended to move into deeper water later in the day ($r^2 = 0.54$, $p < 0.001$). Water temperature varied from approximately 22.5°C at a depth of 80 m to 19.5°C at a depth of 200 m.

On a coarse scale, the proportion of time spent at depth for the four animals whose tags remained on for longer than 2 h was relatively consistent (Fig. 4). During the day, the dolphins spent the vast majority of the time in the top 10 m of the water column (mean = 88.5%, SD = 2.8%, n = 4), with the deepest dive to 122 m. At night, the dolphins spent

Fig. 2. Map showing tracks of tagged pantropical spotted dolphins. Arrows are shown giving the general direction of travel of tagged animals. The location where the 16-November tag was recovered (on 17 November) is shown. Location where the 16-March tag was recovered (on 17 March) is not shown, but this tag was recovered on the trackline from the previous day, 7 km north of the southernmost point shown for the dolphin on this day. The 100-m depth contour is indicated.

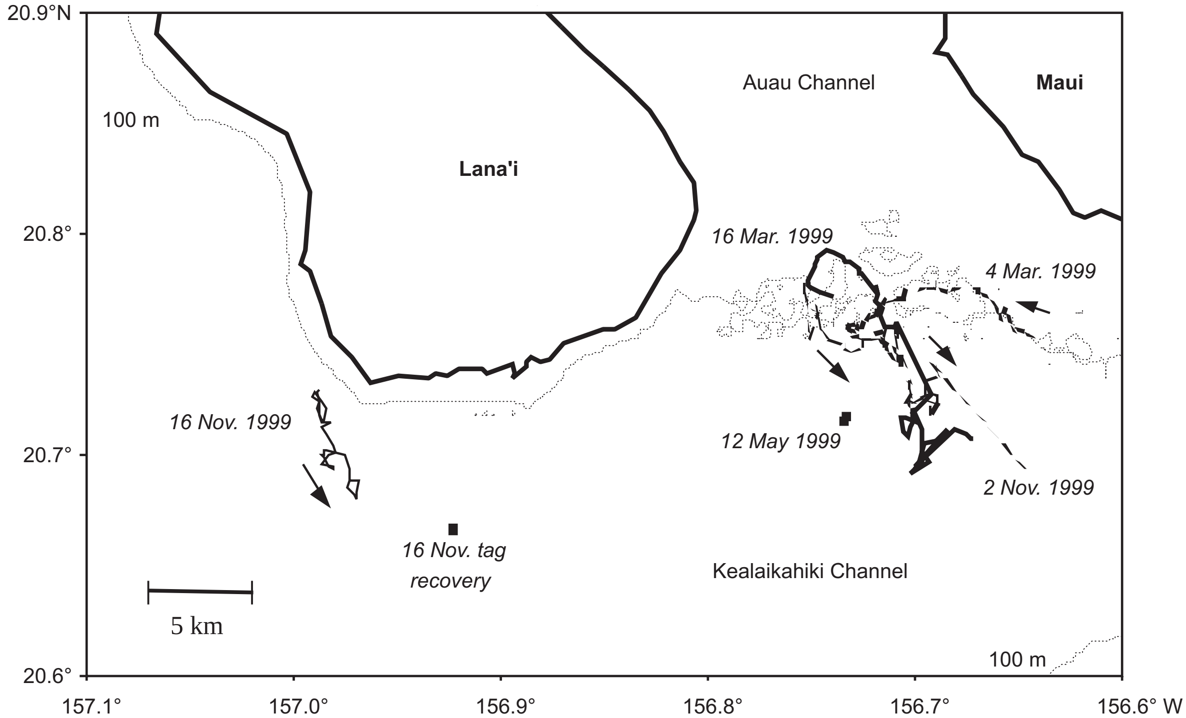


Table 1. Details of tag deployments for pantropical spotted dolphins (*Stenella attenuata*).

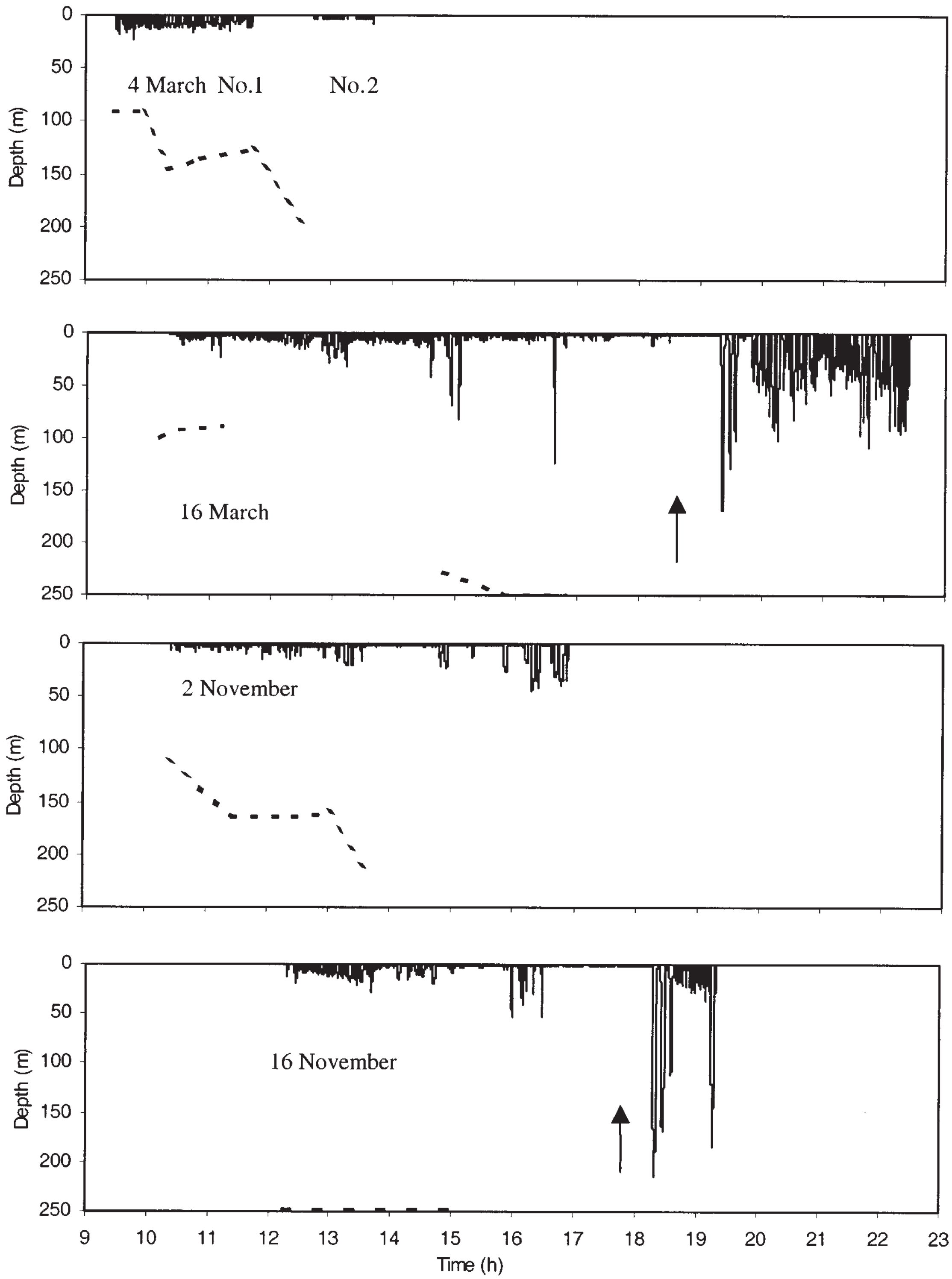
Date	Time	Tag duration (h, min)	Periods when tagged dolphin/group followed[a]	Average travel speed (km/h)
4 March No. 1	09:28–11:42	2, 14	09:28–10:58, 11:34–11:42 (1, 28)	2.3[b]
No. 2	12:34–13:44	1, 10	12:34–13:13 (0, 39)	2.3[b]
16 March	10:13–22:33[c]	12, 10	10:13–11:18, 14:35–17:14 (3, 44)	0.7
12 May	11:12–11:17	0, 5	11:12–11:17 (0,5)	—
2 November	10:26–16:52	6, 26	10:26–13:35 (3, 9)	2.2
16 November	12:18–19:19[d]	7, 1	12:18–15:10 (2, 52)	2.1
Total[e]		29, 6	11, 57	
Mean				1.8

[a] Numbers in parentheses are hours and minutes.
[b] This travel speed estimate was for both dolphins that were tagged on 4 March, as they were in the same group. Only one value was used in calculating the mean.
[c] Sunset on this date was at 18:37, thus 3 h and 56 min of data were obtained after sunset.
[d] Sunset on this date was at 17:46, thus 1 h and 33 min of data were obtained after sunset.
[e] Total values are given in hours and minutes.

less time in the top 10 m (mean = 59.4%, SD = 9.2%, n = 2) and more time at greater depths with dives as deep as 213 m. Within the top 10 m of the water column, exactly where individual dolphins spent their time varied considerably (Table 2). Approximately half an hour after sunset the frequency of deep dives increased (Fig. 3). The initial deep dives after sunset are to depths where the light levels were equal to those recorded near the surface later during the night (Fig. 5). Velocity readings for the two individuals whose tags remained on into the night showed that velocity at night was generally higher and more variable than velocity readings during the day (Fig. 6).

For the purposes of presenting dive statistics, we used two definitions: (*i*) any dive lasting longer than 6 s and (*ii*) dives to greater than 5 m in depth (Table 3). Dives during the day were generally shorter and shallower than dives at night (Table 3). Regressions of dive depth versus duration during the night resulted in high r^2 values (mean = 0.81, SD = 0.11, n = 2), whereas during the day r^2 values were lower (mean = 0.34, SD = 0.23, n = 4). Rates of descent and ascent were

Fig. 3. Depth data with time of day for five dolphins for which tag attachment was greater than 1 h. Bottom depth, when known, is shown by the broken lines (broken lines are shown on the *x* axis when the bottom depth was greater than 250 m). Arrows indicate the time of sunset for the 2 days when the tags remained on after dark.

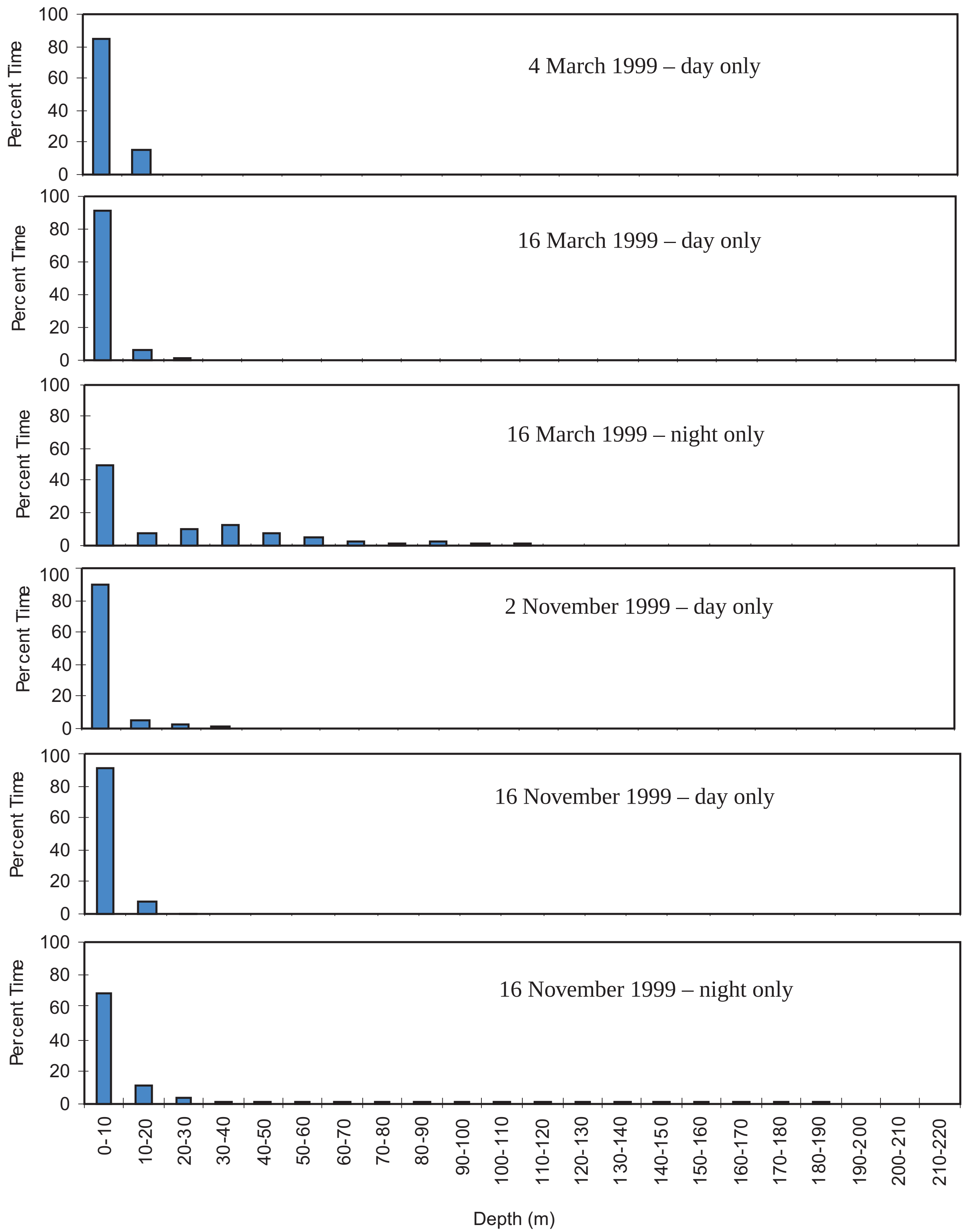


higher at night than during the day (e.g., 16 March night: descent mean = 1.64 m/s, SD = 0.51 m/s; ascent mean = 1.46 m/s, SD = 0.38 m/s; n = 46; 16 March day: descent mean = 1.00 m/s, SD = 0.72 m/s; ascent mean = 0.92 m/s, SD = 0.58 m/s; n = 13). Occasional surface feeding behaviour may have occurred during the daytime, as dolphins in the group were observed moving through schools of small fish and seabirds were seen feeding at the surface in association with the dolphins.

Discussion

The minimal and short duration responses observed following remote deployment of suction-cup-attached tags sug-

Fig. 4. Proportion of time spent at depth.



gest that the study animals are not affected to any great extent by the tagging procedure. The consistency of their behaviour compared with non-tagged animals in the same group further supports this fact. As such, we believe this technique did not impact the short-term behaviour of the dolphins and our results are likely representative of the diving behaviour of other dolphins in the groups.

On average, dive depths and durations documented for pantropical spotted dolphins in Hawai′i were generally shallower and shorter than has been reported for similar-sized

Table 2. Percentage of time spent in the upper 10 m of the water column during daylight hours for the four pantropical spotted dolphins tagged with 1-m resolution TDRs[a].

Depth (m)	4 March No. 1	16 March	2 November	16 November	Mean	SD	CV
0–2	29.4	25.7	80.5	75.9	52.9	29.3	0.55
2–4	7.2	41.1	3.8	3.2	13.8	18.3	1.32
4–6	7.1	10.3	1.7	3.0	5.5	3.9	0.71
6–8	16.4	7.8	1.4	3.2	7.2	6.7	0.93
8–10	23.7	6.0	1.7	4.8	9.1	9.9	1.10
Total	83.8	90.9	89.1	90.1	88.5	2.8	0.03

[a]The second tag used on 4 March contained a 1000-m rated TDR with a 4-m depth resolution, and thus the data obtained from this tag were not suitable for this analysis (nor for results presented in Table 3).

Fig. 5. Change in light levels (lower line) and dive depth (upper line) in relation to time of day for pantropical spotted dolphins tagged on 16 March 1999 (*a*) and on 16 November 1999 (*b*). Arrows indicate the time of sunset.

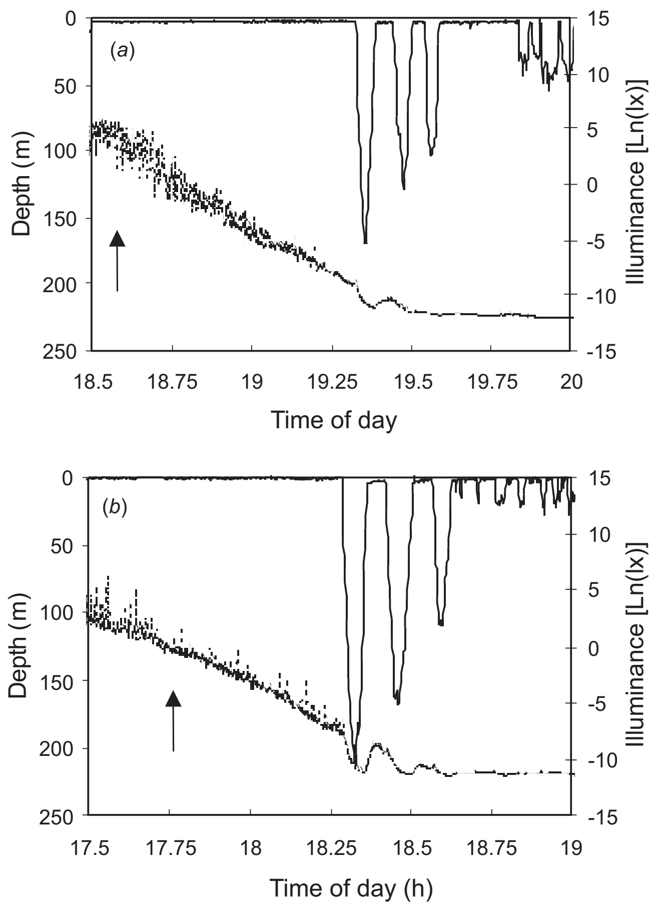
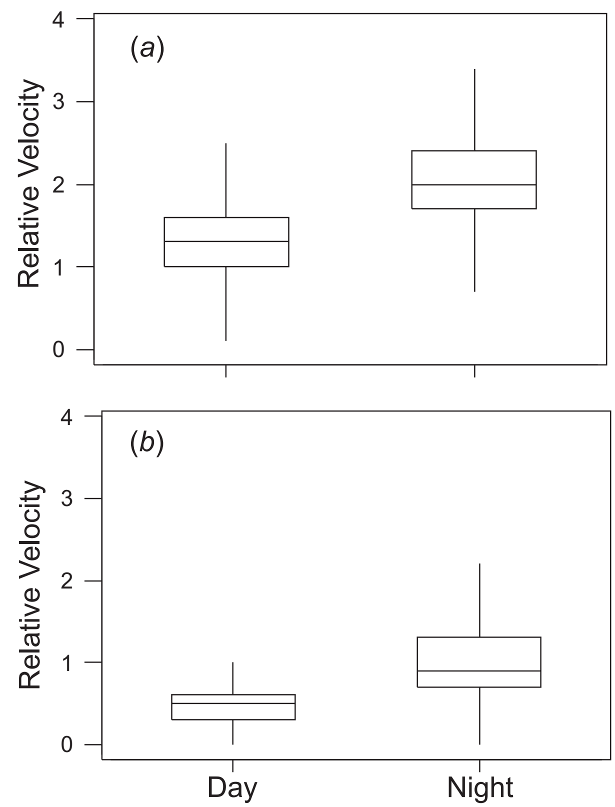


Fig. 6. Box plot of velocity readings for two pantropical spotted dolphins recorded on 16 March 1999 (*a*) and on 16 November 1999 (*b*).



cetaceans (e.g., harbour porpoise, *Phocoena phocoena* (Westgate et al. 1995); Dall's porpoise, *Phocoenoides dalli* (Baird and Hanson 1998)). However, a comparison of maximum dive depth and duration indicates that pantropical spotted dolphins closely match diving capacity predicted based on body size (Schreer and Kovacs 1997). The discrepancy comparing average values between these species may result from several factors, including taxonomic differences (little detailed dive data are available for similar-sized delphinids), differences in dive patterns based on time of day (see below), or differences in myoglobin concentrations in skeletal muscles. Breath-holding capability for odontocetes varies both with body size and with myoglobin concentration in skeletal muscles (Noren and Williams 2000). The myoglobin level of skeletal muscles of pantropical spotted dolphins are about 60% of those of harbour porpoises (Castellini and Somero 1981; Noren and Williams 2000), and thus pantropical spotted dolphins might be expected to generally exhibit shorter dives. At no time were dives thought to be near to the bottom, so diving depths were not limited by bottom depth.

During the day, pantropical spotted dolphins off southern Lana'i and western Maui were typically found in relatively small, single-species groups, which is in contrast to the large and frequently multi-species aggregations that are found in more pelagic waters (Scott and Cattanach 1998). Although some activity suggestive of foraging was observed, during the day these dolphins appear to spend the vast majority of their time in the top 10 m of the water column (Figs. 3, 4), which is similar to the behaviour of the pantropical spotted dolphins in the ETP (M.D. Scott, personal communication).

Table 3. Dive depth and duration values for pantropical spotted dolphins during the day and night.

	Dives >6 s in duration			Dives >5 m in depth		
Date	Depth (mean ± SD, m)	Duration (mean ± SD, min)	*n*	Depth (mean ± SD, m)	Duration (mean ± SD, min)	*n*
Day						
4 March No. 1	8 ± 4 (24)	1.2 ± 1.0 (3.3)	89	11 ± 3	1.7 ± 0.8	55
16 March	6 ± 8 (122)	0.5 ± 0.5 (3.9)	417	11 ± 14	1.1 ± 0.7	126
2 November	7 ± 8 (44)	0.6 ± 0.9 (4.6)	156	15 ± 10	1.5 ± 1.3	44
16 November	10 ± 10 (54)	1.0 ± 0.9 (3.6)	89	14 ± 11	1.4 ± 0.8	54
Mean	7.8 ± 1.7	0.83 ± 0.33		12.8 ± 2.1	1.43 ± 0.25	
Night						
16 March	46 ± 50 (169)	1.7 ± 1.5 (3.8)	18	74 ± 46	2.6 ± 1.1	11
16 November	36 ± 53 (213)	1.2 ± 1.3 (5.0)	32	40 ± 56	1.3 ± 1.4	28
Mean	41.0 ± 7.1	1.45 ± 0.35		57.0 ± 23.5	1.95 ± 0.92	

Note: Values in parentheses are the maximum depths and maximum duration measured during dives.

However, movements of these dolphins appeared to be limited compared with the pantropical spotted dolphins in the ETP, based both on the distance traveled while tagged (Table 1, Fig. 2; see also Scott and Wussow 1983) and locations where the two tags that remained attached during the night were recovered the next day (Fig. 2). Both suggest that no long-range movements (e.g., greater than a few kilometres) were made during the nighttime period when the tags were on, even though there was a general movement into deeper water as the day progressed. Comparisons with the other two common species of dolphins found in the study area (Fig. 1) indicate differences in habitat use, with pantropical spotted dolphins showing a preference for deeper portions of the study area. Why would pantropical spotted dolphins show a general movement into deeper water as the day progresses, or conversely, why would they spend day-time periods in relatively shallow water (100–300 m)? The sympatric spinner dolphin in coastal Hawaiian waters typically spends daytime hours in very shallow areas, sometimes in less than 10 m of water, apparently to minimize predation by sharks (Fig. 1; Norris et al. 1994). Information on the depth distribution of sharks that might feed on dolphins in Hawaiian waters is sparse, however, there is some evidence that tiger sharks (*Galeocerdo cuvier*) spend a substantial proportion of their time in deeper (>400 m) waters around Hawai'i (Holland et al. 1999). Thus it is possible that the time spent in shallower water earlier in the day functions in part as shark avoidance.

The two pantropical spotted dolphins for which dive data was collected both during the day and night showed a distinct difference in dive patterns between day and night (Table 3, Fig. 4). For both individuals, the deepest dives occurred approximately half an hour after sunset (Figs. 3, 5), coincident with a reduction in light levels, and average dive depths and durations at night were greater than those during the day (Table 3). The relationship between dive depth and duration also appeared to differ between the day and night. At night, dive depths were strongly predicted by dive duration (i.e., almost all long dives were also deep dives), whereas during the day this relationship was relatively weak. Rates of descent and ascent, and velocity readings (Fig. 6), were also higher at night than during the day. Combined, these suggest that activity levels at night were higher than during the day, supporting our suggestion that feeding behaviour occurs more at night for these dolphins than it does during the day. These observations support recent information on the nighttime predominance of feeding for pantropical spotted dolphins elsewhere (Scott et al. 1993; Richard and Barbeau 1994; Robertson and Chivers 1997).

We suggest that the first few deep dives after sunset were "exploratory" dives, as the dolphins dove to the rising deep-scattering layer (Reid et al. 1991). In Hawaiian waters, this deep-scattering layer makes both vertical movements associated with a reduction in light levels after sunset and horizontal movements onto the shelf itself (Reid et al. 1991). Dives that did occur after these exploratory dives, approximately an hour after sunset, were deeper than those during the day, although shallower than the exploratory dives (Fig. 3). Exactly what species these dolphins are feeding on is unclear; as noted above, stomach contents from only two pantropical spotted dolphins in Hawai'i appear to have been collected, and these contained various mesopelagic fish and squid remains (Shomura and Hida 1965; Clarke and Young 1998). The most common fish documented in one stomach were myctophids, along with several squid species (*Enoploteuthis* sp., *Abraliopsis* sp. *Abralia astrosticta* and *Ommastrephes hawaiiensis*), all of which appear to be associated with the deep-scattering layer (Shomura and Hida 1965; Clarke and Young 1998).

As with the sympatric spinner dolphins (Norris et al. 1994), a variety of differences between pelagic and island-associated populations of pantropical spotted dolphins seem apparent. In both species, island-associated populations appear to be found more often in smaller, single-species groups, and obviously spend more time in shallower water. In the case of pantropical spotted dolphins, our results suggest that feeding and general activity patterns may be similar between pelagic and island-associated populations. Certainly average dive durations and depths during both the day and night (Table 3) were very similar to those found during these periods for pantropical spotted dolphins in the ETP (M.D. Scott, personal communication). Thus it appears that "how" and "when" prey resources are used is relatively conservative between pantropical spotted dolphins in these disparate habitats. However, the spatial predictability associated with islands and the possible shallow-water "refuge" from predation may cause these differences, not only in group size, but also in "where" and "how far" the animals move. Further studies in such areas, focusing on long-term movements or site fidelity of individuals, will help demonstrate how habitat contributes to the structure and dynamics of dolphin communities.

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