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Occurrence and Behavior of Hawaiian Spinner Dolphins *(Stenella longirostris)* Along Oahu's Leeward and South Shores

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Abstract

The spinner dolphin (*Stenella longirostris*) is a delphinid that occurs in both pelagic and coastal tropical and subtropical habitats worldwide. A model of the behavior and ecology of this species was described for a resident population along the Kona coast of the island of Hawaii by Norris et al. (1994). To assess the applicability and variability of this model in divergent coastal habitats, the occurrence and behavior of spinner dolphins resident along the southern and western shores of the island of Oahu, Hawaii, was studied over a five-year period. The findings reveal that spinner dolphins off Oahu carry out their daily cycle in a manner similar to those off Kona, but that some noteworthy differences exist in the manner in which dolphins off Oahu use the nearshore habitat. Spinner dolphins exhibited strong preferences for specific locations along the west coast of Oahu, but not along the southern shore, where the average pod size was consistently larger. Resting and social behaviors were tied primarily to the time of day, rather than to any specific site along the coast. Spinner dolphins consistently exhibited a strong affinity for the 10-fathom isobath, indicating that shallow waters are likely the primary coastal feature promoting daytime residence. Foraging was initiated typically in the late afternoon along the edges of banks where vertically and horizontally migrating mesopelagic prey presumably first ascend to shallower depths. Spinner dolphins on Oahu use the coast opportunistically and, therefore, over time, could respond to recent increases in human encroachment by shifting the location and/or timing of their occurrence and behavioral activities.

Key Words: Spinner dolphin, Oahu, behavior, resting, foraging, activity index, *Stenella longirostris*

Introduction

The spinner dolphin (*Stenella longirostris*) is a cosmopolitan species with widespread distribution in tropical and subtropical oceans around the world (Perrin & Gilpatrick, 1994). The common name is derived from the aerial acrobatics that characterize the surface behavior of this species. Four subspecies—*S. l. longirostris*, *S. l. orientalis*, *S. l. centroamericana*, and *S. l. roseiventris*—and one race (the Hawaiian spinner dolphin) are recognized that vary from one another in geographical occurrence, size, shape, and coloration (Norris et al., 1994; Perrin, 1990; Perrin et al., 1999). Two of the subspecies—*S. l. centroamericana* and *orientalis*—are thought to represent ecotypes adapted to the pelagic environment of the Eastern Tropical Pacific (ETP); another—*S. l. roseiventris*—is a dwarf form restricted to shallow waters in Southeast Asia; and the fourth—*S. l. longirostris*—is found worldwide.

Spinner dolphins occur in both open ocean and coastal environments. Pelagic populations, such as in the ETP, often are found in waters with a shallow thermocline (Reilly, 1990). The thermocline concentrates pelagic organisms in and above it, upon which the dolphins feed. Coastal populations also are common and usually are found in island archipelagos, like Hawaii and French Polynesia, where they are tied to trophic and habitat resources associated with the coast (Norris & Dohl, 1980; Poole, 1995).

Despite their diversity in form and habitat use, all spinner dolphins (except the dwarf form) specialize in foraging on small (< 20 cm) mesopelagic fish, shrimp, and squid (Norris et al., 1994). Foraging takes place primarily at night when the mesopelagic community migrates towards the surface (Perrin et al., 1973). Spinner dolphins dive to meet the rising layer of prey organisms and forage cooperatively. Recent observations that were made using a modified sonar system revealed that spinners work as a group to systematically concentrate segments of the layer (Benoit-Bird & Au, 2003).

In Hawaiian waters, spinner dolphins are the most abundant of the delphinid species (Mobley et al., 2000). They occur along the leeward coasts of all the major islands and around several of the atolls northwest of the main island chain. Their presence in Hawaii and other Pacific archipelagos is attributed to the so-called "island mass" effect (Norris et al., 1994). Slow, nutrient-rich bottom currents are brought to the surface by the slopes of the islands (Gilmartin & Revelante, 1974). Localized nutrient-rich waters concentrate the mesopelagic community upon which the dolphins feed.

The behavior of spinner dolphins resident along the Kona coast of the island of Hawaii was detailed first by Norris and Dohl (1980) and later by Norris et al. (1994) and Östman (1994). These studies revealed that spinner dolphins engage in a very cyclical and largely predictable pattern of behavior. Dolphins on the Kona coast seek out shallow, wind-sheltered coves daily for protection from predation while resting. Groups of 20 to 100+ dolphins usually enter these coves in the morning and gradually descend into a state of lowered activity level for several hours. Periods of rest are characterized by very cohesive group formations and an almost total absence of acoustic activity. It is thought that these prolonged periods of quiescence are important for tissue regeneration in the sound producing structures so heavily used for echolocation at night (Norris et al., 1994). During rest, spinner dolphins rely on vision rather than echolocation for scanning their environment and, as a result, favor clear, calm waters and light bottom substrates that provide a less cryptic backdrop for predators like tiger sharks. In the late afternoon/early evening, following a period of renewed social activity, groups move offshore again towards their evening foraging grounds. The cycle is repeated almost daily, with the only seasonal changes being adjustments in the timing of events, which reflect shifts in day length.

The studies of the Kona population by Norris and his colleagues provide the current framework for our understanding of spinner dolphin behavior and natural history. Similar patterns of spinner dolphin foraging and resting cycles also have been observed at other island habitats such as Moorea in French Polynesia (Poole, 1995) and the Midway atoll (Karczmarski et al., 2001); however, little information presently exists about the variability of behavioral patterns typical of spinner dolphins at different locations.

Norris et al. (1994) suggested that the availability of prey and resting habitats are the primary limiting factors influencing the occurrence of spinner dolphins along the Kona coast. Presumably, these are the same constraints faced by populations on other islands. Yet, the Kona coast is rather unique in the Hawaiian Archipelago and among other tropical Pacific islands in its large size; availability of numerous protected coves; and vast stretches of calm (Beaufort sea state 0-2), clear leeward waters. Additionally, the mesopelagic community along Kona differs in density and distribution from communities found on other Hawaiian islands (Benoit-Bird et al., 2001). So, how do spinner dolphins near different islands with more exposed coastlines, few or no protected coves, and different prey fields exploit their environment and carry out their daily behavioral cycle?

To address this question, the patterns of habitat use and behavior of a population of spinner dolphins resident on the island of Oahu were investigated over a five-year period. The occurrence, movements, and behavioral patterns of spinner dolphins on the southern and western shores of Oahu were examined and compared with patterns previously described for the Kona coast.

Materials and Methods

Study Area

The western and southern shores of Oahu (the former is typically known as the Waianae coast) represent two different habitats occupied by spinner dolphins (Figure 1). The Waianae coast faces WSW and stretches 38 km from Barbers Point in the south (21º 17.5'N, 158º 06.5'W) to Kaena Point (21º 34.5'N, 158º 17'W) in the north. All but 2-4 km of the southern end of the coast are usually in the lee of prevailing northeasterly tradewinds. The Waianae mountain range parallels the coastline, impinging directly on it north of Kepuhi Point and south of Maili Point, creating a large valley between. Offshore tradewinds result in variable surface conditions along the coast. North to easterly winds are funneled and strengthened in the valley and are mostly blocked by the mountains elsewhere. Beaufort sea states on a typical tradewind day (10-20 mph) range from 1-3 along the different parts of the coast. The majority of human activities along Waianae are limited to small (< 20 m) commercial and private fishing, diving, and whale-watching craft.

The south shore is flanked by Barbers Point in the west and Koko Head Crater (21º 15.5'N, 157º 42.5'W) in the east. Most of the 48-km coastline faces due south, except for a 7-km stretch between Honolulu Harbor and Diamond Head Crater where it faces SW. The tradewinds refract around the Ko'olau mountain range that parallels the east side of the island, resulting in sideshore easterly winds along most of the south shore. Surface conditions are considerably rougher than along Waianae on most days, with a Beaufort sea state typically

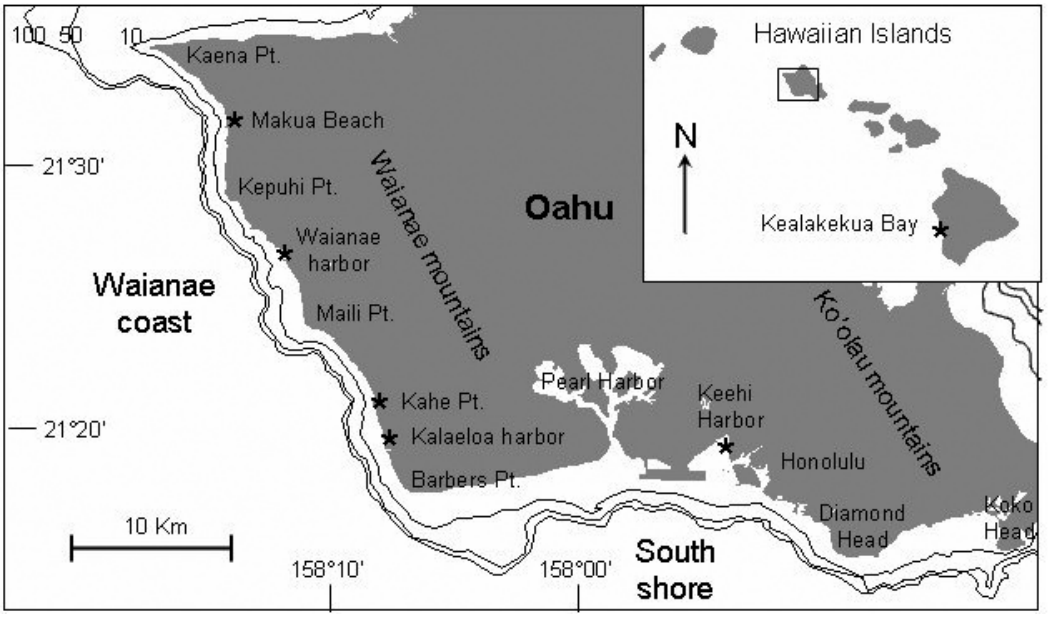

Figure 1. Map of study area showing 10-, 50-, and 100-fathom isobaths

ranging between 2 and 4. The south shore is also much more heavily navigated than the Waianae coast with commercial, industrial, and military shipping, as well as private crafts, operating in large numbers each day out of Honolulu Harbor, Pearl Harbor, and four small boat harbors.

Data Collection

Data for this study were obtained within the operating framework of a larger effort to study the acoustic signaling of spinner dolphins between June 1996 and November 2001 (Lammers, 2003). Observations of the occurrence, movements, and behavior of dolphins were made systematically by visually following the movements of groups and also opportunistically when transiting through the study area on other research matters. All observations were made from either a 5.2-m Boston Whaler with a 40-hp outboard engine or from a 9.7-m Grand Banks with a 120-hp inboard diesel engine.

The primary approach for data collection was to locate groups of dolphins occupying the study area and visually track their movements and record their behaviors for extended periods of several hours. When tracking or behavioral sampling of a group was not feasible, only the time, number of animals, and GPS location of the sighting was recorded. The search for dolphin groups typically was launched between 0700 and 1200 h from Waianae Harbor, Kalaeloa Harbor, or Keehi Harbor (Figure 1). Initial search routes along Waianae alternated between exploring the northern coast up to Kaena Point one day and the southern end towards Barbers Point the next. On the south shore, the waters east of Keehi Harbor up to Diamond Head and west of the harbor to Barbers Point were explored. Surface conditions were too rough on most days to effectively search the waters east of Diamond Head.

Once encountered, a group of dolphins was tracked and observed as long as the animals could be kept in sight or until surface conditions became too rough to continue. Spinner dolphin groups typically were tracked from a distance of 150-500 m. At 30-min intervals, groups were approached to within 50-100 m and several variables were recorded, including the time, the number of animals present, the GPS position, the water depth, and a series of behavioral measures used to establish their relative level of activity. An activity index (AI) was developed as a composite metric of the behavioral state of spinner dolphin groups. It is based on three measures: (1) the degree of coordination among individuals in a group, (2) the duration of dives, and (3) the amount of surface activity observed. These measures were defined in the following manner:

Coordination Index (CI) – Group coordination was classified into three types (Figure 2): Type I – A group composed mostly of animals occurring as singles, pairs, or triplets swimming with little cohesion (CI = 1); Type II – A core group of animals moving in a synchronized fashion with a

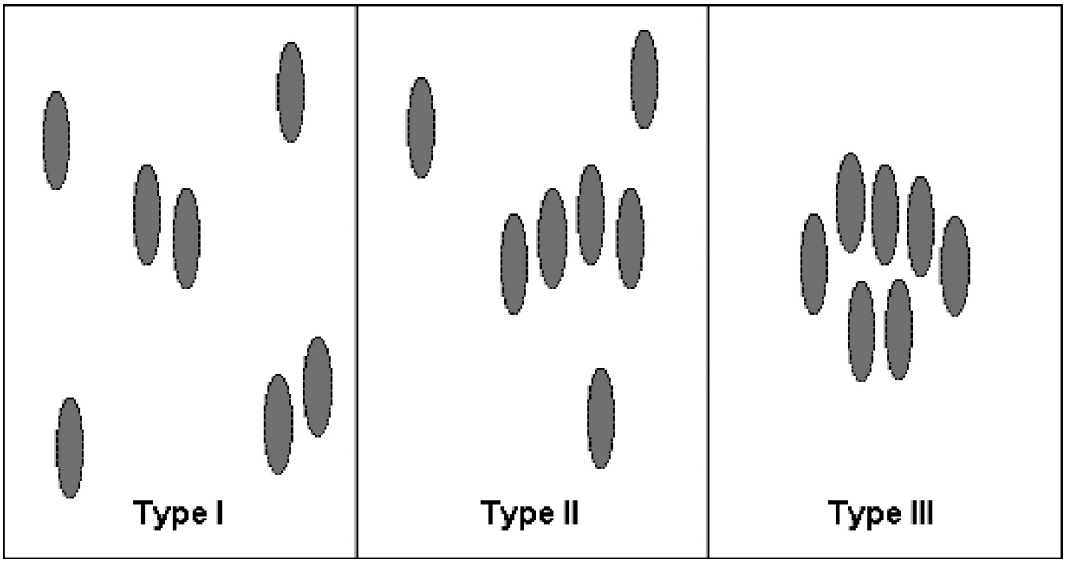

Figure 2. Classification criteria of spinner dolphin group coordination based on the relative spacing among individuals; the gray ovals represent dolphins.

number of individuals continuing to swim independently on the periphery (CI = 2); and Type III – All animals in the group integrated into a tight cohesive unit (CI = 3).

Diving Index (DI) – Dive patterns were timed and classified over a 5-min period by observing individuals with naturally occurring marks and scars from the beginning of one surfacing event (often composed of consecutive breaths) to the beginning of the next. Dive intervals were classified as short – lasting less than 1 min (DI = 1), medium – lasting between 1 and 2 min (DI = 2), or long – lasting longer than 2 min (DI = 3).

Surface Index (SI) – The surface and aerial acrobatic behaviors displayed by a group were recorded over a 5-min sampling period using the classification nomenclature of Norris et al. (1994). Observed behaviors were dictated into a tape recorder and later classified according to their relative level of intensity and/or their presumed behavioral function. Surface behaviors were divided into moderate effort – acrobatics where more than ¼, but less than the entire animal's body broke the water's surface (e.g., head slaps, back slaps), high effort – when the entire animal's body left the water (e.g., tail-over-head and arcuate leaps), and social – behaviors linked to direct interaction with other individuals (e.g., chases, tail slaps).

The SI was calculated for the subgroup based on the number of animals present using the following equation:

$$SI = 0.5(M) + H + 0.5(S)$$

where, M, H, and S represent the number of moderate effort, high effort, and social behaviors, respectively, per animal divided by the upper 95% confidence interval value of each class calculated from the entire dataset. High effort surface behaviors were weighed more than moderate effort and social behaviors to reflect the perceived disparity in the energy required to perform them. These weights were arbitrarily selected. The resulting SI values ranged between 0 and 2. All observations, although made by multiple individuals over the course of the study, were continuously calibrated for consistency by the author, who was always present in the field.

Norris et al. (1994) characterized alert and socially interactive spinner dolphin groups as having loose swimming formations, short dive times, and as displaying frequent aerial acrobatic behaviors. Conversely, they described resting groups as forming tight clusters, diving for long periods, and suppressing most surface activity. The Activity Index (AI) used in this study was developed to follow the shifts in behavioral state quantitatively of a group of spinner dolphins through the day as a function of these behavioral cues. For each 5-min sampling period, the AI was calculated using the following equation:

$$AI = CI + DI - SI$$

This formula was selected so that all AI values ranged between 0 and 6, with low behavioral indices (0-2) representing alert, socially active groups, and higher indices (4-6) representing progressively more subdued groups. At a maximum AI value of 6, all animals in a group were tightly clustered, dove for periods longer than 2 min, and were coordinated to the point of synchrony.

Data Analysis

The GPS positions of spinner dolphin groups were plotted on digital NOAA navigation charts using *Nobletec Visual Navigator 4.1* software. The distance to shore and to the 10-, 50-, and 100-fathom bathymetric contours were measured for each waypoint. Additionally, the bearing of travel was calculated for successive positions. This provided a measure of the change in direction of travel over time. Tracks with three or more waypoints provided multiple "legs" for which changes in travel angle and rate could be calculated.

To examine the occurrence of dolphins and their patterns of activity over time and at different locations, data were grouped by the time of day and by the location along the coast where the animals occurred. Time of day was classified as early morning (0700-0959 h), late morning (1000-1159 h), midday (1200-1359 h), early afternoon (1400-1559 h), late afternoon (1600-1759 h), and evening (1800-1959 h). Locations along the Waianae coast were divided by latitude into three areas: north Waianae (21º 34.5'–21º 29'), central Waianae (21º 28'–21º 24'), and south Waianae (21º 23'–21º 17.5'). On the south shore, the coast also was divided by longitude into three areas classified as Barbers Point (158º 06.5'–158º 01'), Pearl Harbor (158º 00'–157º 54'), and Honolulu Harbor (157º 53'–157º 49'). To examine patterns of behavior in more detail, the three areas in some cases were grouped further into smaller segments of coastline spanning only 2 latitudinal/longitudinal min (3.45 km).

The data revealed that pods of spinner dolphins rarely remained cohesive for more than one to two hours at a time. Groups changed in a fission-fusion pattern of occurrence, whereby large groups fragmented into smaller subgroups, which periodically rejoined other groups to form a new pod (Figure 3). As a result, the number and composition of individuals in a group of dolphins being tracked frequently changed. Often, recognizable animals disappeared from groups being monitored only to rejoin them several hours later or occur with some of the same animals in a new group on a different day. To account for this variation, data points on the location and behavior of groups were averaged over two-hour periods. Each two-hour period was considered to represent a distinct makeup of animals and treated as a separate data point. So, for example, a four-hour track composed of eight 30-min sampling periods would be averaged to represent two data points. For statistical analysis, data points obtained within the same

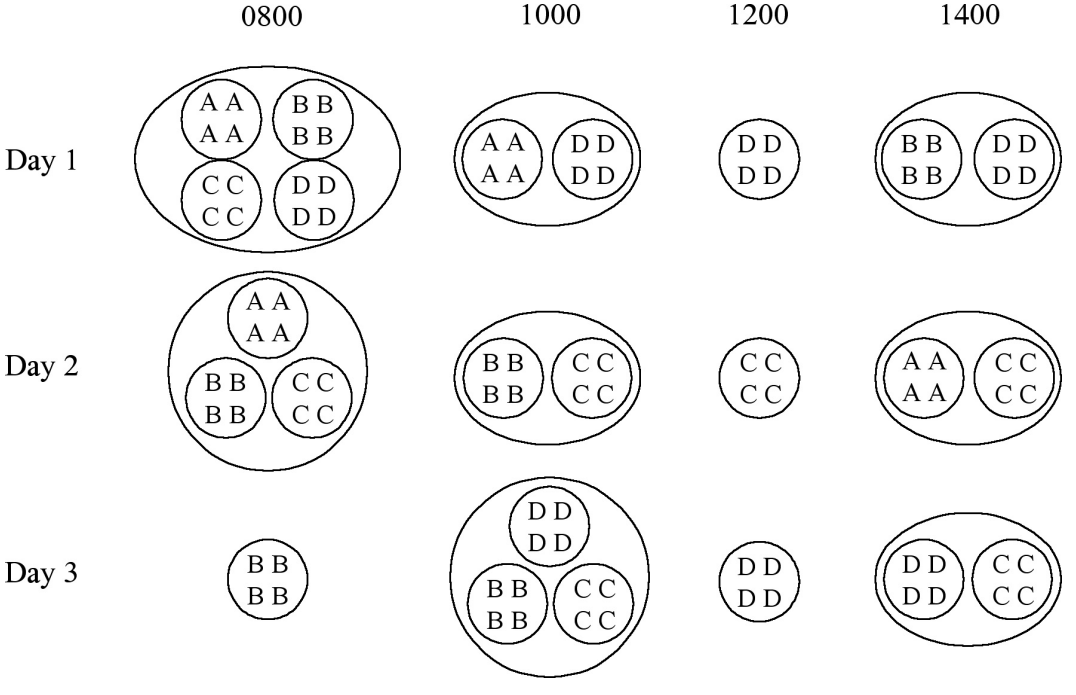

Figure 3. A hypothetical representation of the fission-fusion pattern of occurrence of spinner dolphin pods along the coast over a period of three days; circles with letters represent subgroups which may or may not remain cohesive over time. The illustration shows how over several hours the composition of pods being observed can vary as much as that of pods observed on different days.

day and/or track were pooled with those obtained on different days. This approach assumed that the variation in the composition of groups within each day was approximately equivalent to the variation between days and that any lack of independence between points resulting from shared individuals among groups would average out over the course of the study. When a group separated and both subgroups could be located, the one with the most animals was typically followed.

The manner in which groups moved along the coast was classified according to whether they milled in a restricted location or traveled down the coast. Milling behavior was defined on the south shore as movement limited to less than one longitudinal min over a two-hour period and an average change in travel angle greater than 90º over that same period. On the Waianae coast, which faces WSW, milling was defined by a north/south displacement of less than 0.83 latitudinal min over two hours (the equivalent distance in meters as on the south shore) and by an average change in travel angle greater than 90º. Conversely, traveling was characterized by a net movement of more than one and 0.83 latitudinal min along each respective coast and an average change in travel angle of less than 90º.

Results

A combined total of 131 surveys of the three areas along Waianae and 89 surveys of the three south shore locations were conducted, totaling 905 hours of searching and tracking effort. The frequency with which spinner dolphins were encountered somewhere along the coast during a survey was 75.1% on Waianae and 56.1% on the south shore. Along Waianae, spinner dolphins were tracked 63 times and sighted on 42 other occasions. On the south shore, dolphins were tracked 12 times and sighted 27 other times. Tracks lasted on average 3 h 21 min (SD = 2 h 32 min) on Waianae and 3 h 32 min (SD = 2 h 15 min) on the south shore.

Occurrence

Table 1 presents the relative occurrence of spinner dolphins on the coast in terms of the frequency with which they were encountered in each area adjusted for survey effort. Along Waianae, groups of spinner dolphins were found in the early morning period with roughly equal frequency along the northern and southern parts of the coast, and less so on the central part. Within these two areas, dolphins were found disproportionately at two specific 1.5 km^2 shallow water (< 10 fathoms) sites (Figure 4a). In north Waianae, 95.2% of all initial sightings were made along the stretch of coast in front and just north of Makua Beach. In south Waianae, 52.4% of sightings occurred in front of Kahe Beach Park. Only 15.1% of pods encountered were found in central Waianae. Of these, 87.5% occurred in front of Pokai Bay, adjacent to the Waianae Harbor entrance. In total, 37 out of 49 of all sightings (75.5%) made in the early morning occurred at these three sites over a combined area of 4.2 km^2. This represents only 13.2% of all the nearshore habitat less than 10 fathoms deep on the Waianae coast.

Table 1. The frequency of spinner dolphin encounters on different parts of the Waianae coast and south shore for surveys conducted in the early morning and late morning

Location	Frequency of encounter (# of surveys) 0700-0959h	1000-1159h
Waianae		
N. Waianae	71.9% (32)	80.0% (10)
C. Waianae	26.6% (33)	64.5% (13)
S. Waianae	78.6% (28)	73.3% (15)
South Shore		
Barbers Point	18.2% (11)	28.6% (14)
Pearl Harbor	36.0% (25)	40.0% (20)
Honolulu	61.5% (13)	16.7% (6)

The pattern of occurrence after 1000 h was different than in the early morning hours (Figure 4b). Spinner dolphins were found in approximately equal proportions along all three coastal areas. Dolphins remained common in north and south Waianae, but also were frequent in central Waianae. Only 27 out of 50 (54.0%) pods encountered or tracked during the late morning occurred at Makua, Pokai Bay, or Kahe. This proportion decreased further as the day progressed. During the midday, early afternoon, late afternoon, and evening periods, 18 of 39 (45.9%), 13 of 39 (33.3%), 7 of 28 (25.0%), and 0 of 5 (0%) pods, respectively, occurred at the three sites.

On the south shore, the pattern of occurrence of spinner dolphins was different than along the Waianae coast. In the early morning, dolphins were most commonly found along the shoreline adjacent to Honolulu (Table 1). While there, however, they did not exhibit a preference for any specific location as they did along Waianae (Figure 5a). During the late morning period, dolphins became more common in the Pearl Harbor area, but again did not show any consistent preference for a specific site (Figure 5b). At midday, seven out of 11 pods (63.6%) sighted or tracked occurred near Pearl Harbor, compared with four pods (36.4%) off Honolulu and none off Barbers Point. Only four pods were tracked into the early afternoon period of which three occurred off Honolulu and

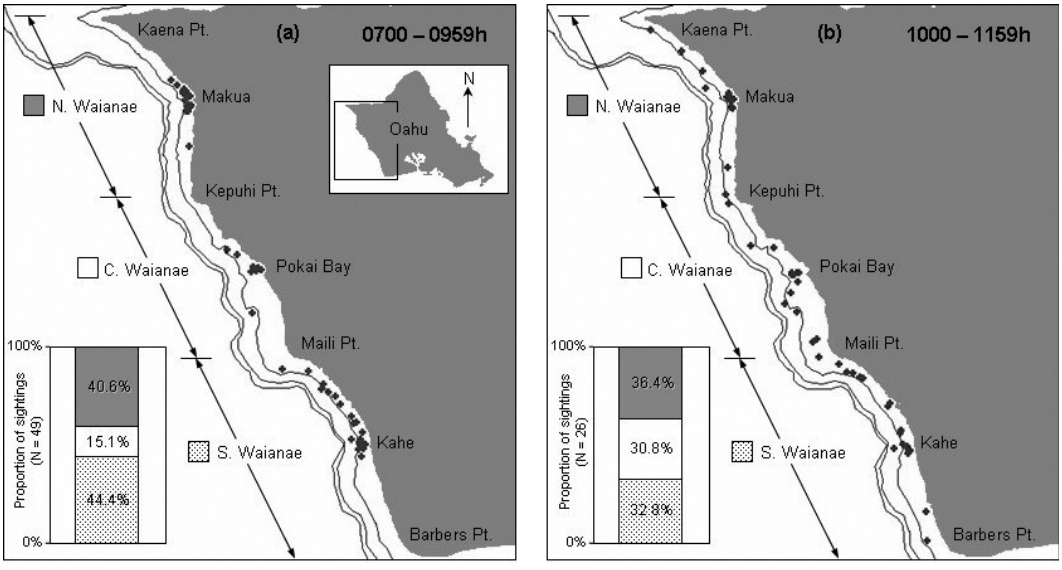

Figure 4. Occurrence of spinner dolphins on the Waianae coast in the (a) early and (b) late morning periods; percentages indicate the proportion of sightings (from initial encounters and tracks) recorded during the course of the study on the different parts of the coast.

one traveled east of Diamond Head. Two of these remained off Honolulu into the late afternoon period while the rest were lost from sight.

Spinner dolphins on both coasts exhibited a strong affinity for waters inside and near the 10-fathom isobath between the early morning and late afternoon periods (Figure 6a). During this time, 92.6% of all pods sighted or tracked along Waianae and 80.5% of pods on the south shore occurred in waters less than 17 fathoms deep. Dolphins on the Waianae Coast, however, occupied shallower waters than on the south shore. Before 1600 h, groups along Waianae occurred on average 210 m (SD = 358 m) inshore of the 10-fathom isobath in waters with a median depth of 11 m. On the south shore, they were found 56 m (SD = 417 m) offshore of the 10-fathom isobath in waters with a median depth of 19 m (Wilcoxon rank sum test, $p < 0.001$). In the late afternoon, dolphin pods on both coasts began to transition to deeper waters. By the evening, pods on Waianae typically occurred directly over the 100-fathom isobath (Figure 6b). All tracks on the south shore ended by the late afternoon due to rough surface conditions, so no data were obtained for the evening period.

Group Size

The size of dolphin pods varied considerably on both coasts. The largest pod encountered was estimated between 110-120 individuals, while the smallest group was composed of only two animals. No lone spinner dolphins were observed during the course of this study.

Figure 7 shows the average group size along both coasts as a function of the time of day. There was a significant trend on both the Waianae Coast (one-way ANOVA; $p = 0.006$) and the South Shore (one-way ANOVA; $p = 0.03$) for groups to change size over the course of the day. Groups tended to be larger in the morning than in the afternoon. This difference was greatest between the early morning and early afternoon periods on Waianae and the late morning and early afternoon periods on the South Shore. In addition, pods on the South Shore were consistently larger than along Waianae. These differences were significant (Tukey's pairwise comparisons; $p < 0.05$) during both morning periods and in the early afternoon, but not during midday. There were insufficient data points from the late afternoon on the south shore for statistical comparison with Waianae.

Movement

Pods of milling spinner dolphins were more common than traveling groups along Waianae in the early morning hours (Figure 8). After 1000 h, they were approximately equally likely to engage in either pattern of movement. On the south shore, dolphins milled and traveled in roughly equal proportions throughout most of the day, except during the midday period when all seven pods that were tracked traveled along the coast.

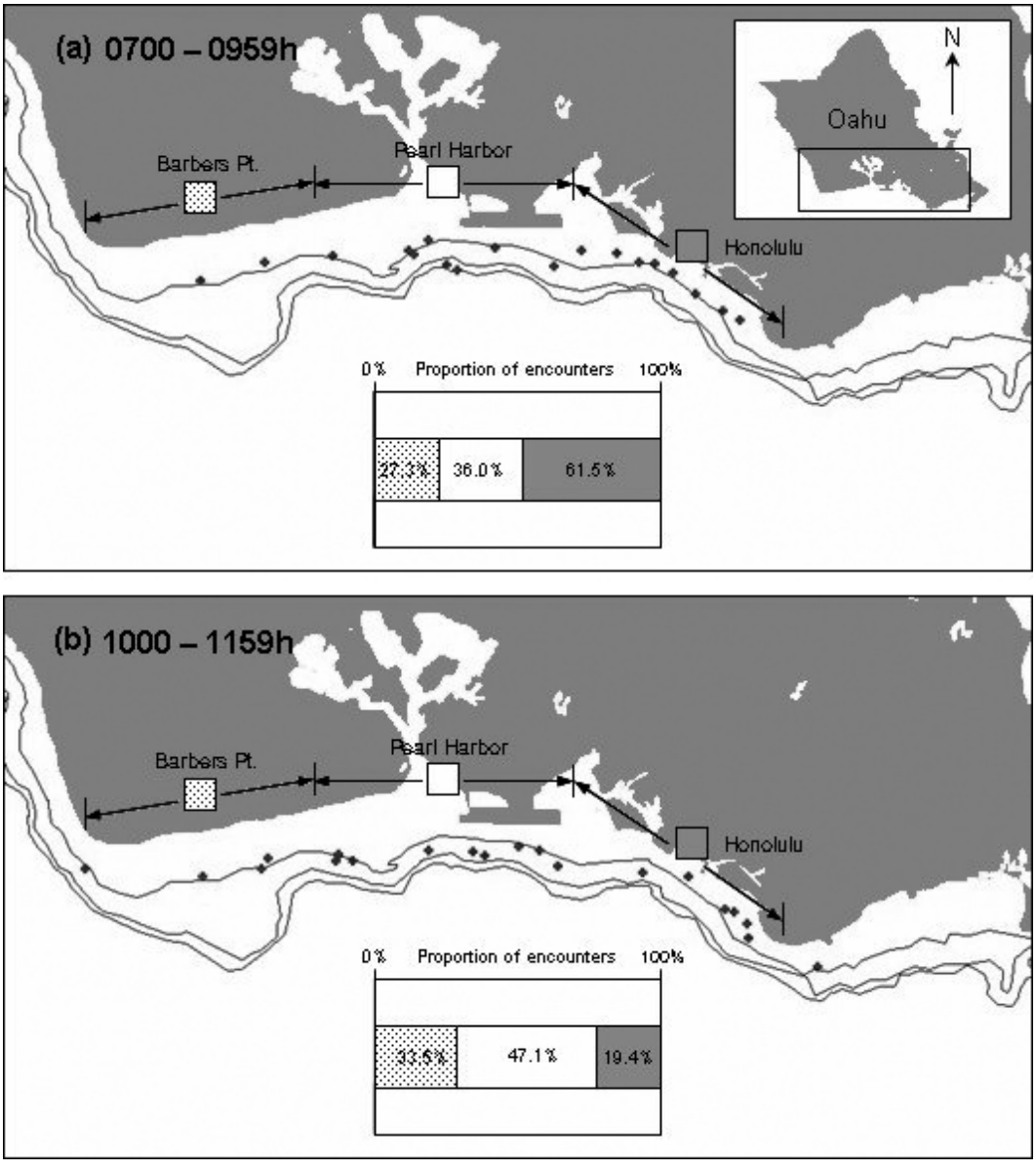

Figure 5. Occurrence of spinner dolphins on the South Shore in the (a) early and (b) late morning periods; percentages indicate the proportion of sightings (from initial encounters and tracks) recorded during the course of the study on the different parts of the coast.

Movement patterns along Waianae differed between specific locations. Figure 9 shows the proportion of milling vs. traveling pods as they occurred in latitudinal 2-min bins along the coast. Dolphins engaged in the greatest proportion of milling behavior in the three bins that coincided with the Makua, Pokai Bay, and Kahe sites. Milling also occurred to a lesser extent in bins adjacent to these sites. It is notable that almost all pods occurring at two of the sites in central Waianae and one in south Waianae only traveled while in these areas.

Not enough tracking data points were obtained from the south shore to be divided into latitudinal 2-min bins; however, a broader comparison between the two coastal areas for which several observations were made revealed that pods milled and traveled in approximately equal proportions off Honolulu and Pearl Harbor (Fisher's exact test;

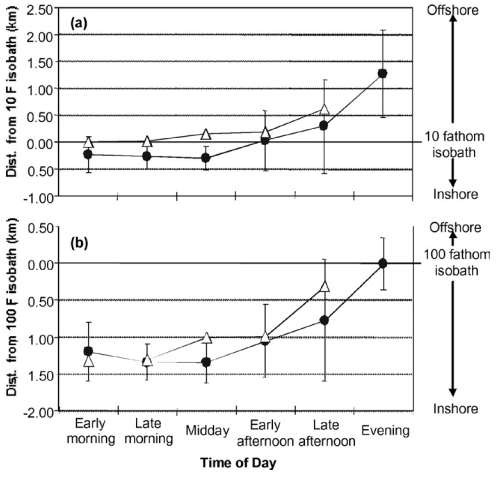

Figure 6. Average distance of spinner dolphin pods from (a) the 10-fathom and (b) 100-fathom isobath as function of the time of day; closed circles are for pods along Waianae and open triangles are for pods on the south shore. For clarity, standard deviation bars are shown only for the Waianae values.

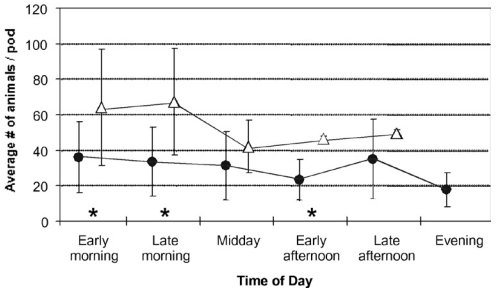

Figure 7. The average size and standard deviation of spinner dolphin pods along Waianae (•) and the South Shore (Δ) as a function of the time of day. Stars (*) indicate significantly different ($p < 0.05$) values between the two coasts.

$p = 0.147$). Only a single data point of a milling group was collected for the Barbers Point area.

Activity Level

The level of activity of spinner dolphins along Waianae, as measured by the AI (Figure 10), was significantly influenced by time of day (one-way ANOVA; $p < 0.001$). Activity levels were statistically equivalent during both morning periods, but differed from the midday and early afternoon when AI values increased significantly (Tukey's pairwise comparisons; $p < 0.0065$). In addition, while the latter two periods did not differ from one another, both did differ significantly from the late

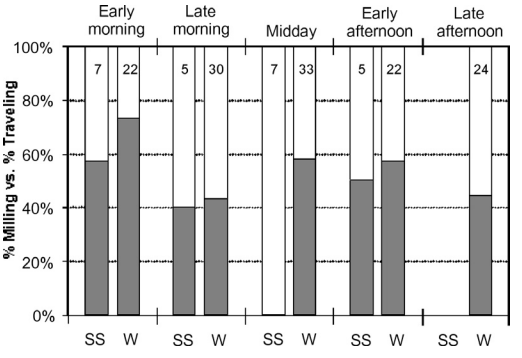

Figure 8. Proportion of spinner dolphin pods milling (■), and traveling (□) on the South Shore (SS) and Waianae (W) as a function of the time of day; the number of pods observed is indicated at the top of each column.

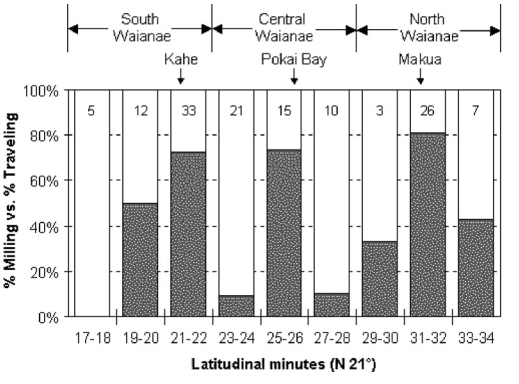

Figure 9. Proportion of milling (■) and traveling (□) spinner dolphin pods on different parts of the Waianae coast; the number of pods observed at each location is indicated at the top of each column.

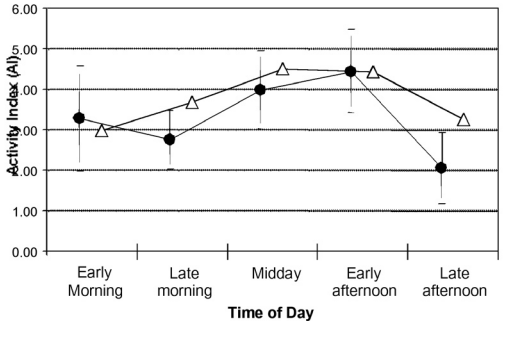

Figure 10. Average activity indices (AI) measured on Waianae (•) and the South Shore (Δ) at different times of the day

afternoon period when AI values were the lowest of the day (Tukey's pairwise comparisons; $p < 0.0065$). Similar inference tests for data obtained on the South Shore were not warranted, as only three to four data points were available for each time period. The trend of the means, however, followed the same pattern observed on the Waianae Coast (Figure 10).

A comparison of the activity levels of dolphin pods on the different segments of the Waianae Coast revealed no significant differences between latitudinal 2-min bins (one-way ANOVA; $p = 0.253$). Milling and traveling pods also did not differ significantly in their average activity levels (two-sample t-test; $p = 0.31$).

Foraging

Spinner dolphins were tracked until they began foraging on 15 occasions along the Waianae Coast. A group of dolphins was assumed to be foraging (Norris et al., 1994) when animals began to dive for several minutes at a time in the late afternoon/evening periods while over deep water (≥ 100 m). Figure 11 shows where dolphin pods went to begin foraging relative to where they were between 1400 and 1500 h. All but one pod traveled to one of three sites: the edge of the shallow water bank off Kaena Point, the bank off Maili Point, or the edge of the bank off Barbers Point. Animals occurring in north Waianae in the afternoon traveled either to Kaena Point or Maili Point, while those in south and central Waianae went to either Maili Point or Barbers Point. Foraging typically began between 1700 and 1900 h, although on at least one occasion a group of approximately 65 animals was tracked to the offshore edge of the Barbers Point bank where they began foraging shortly after 1600 h.

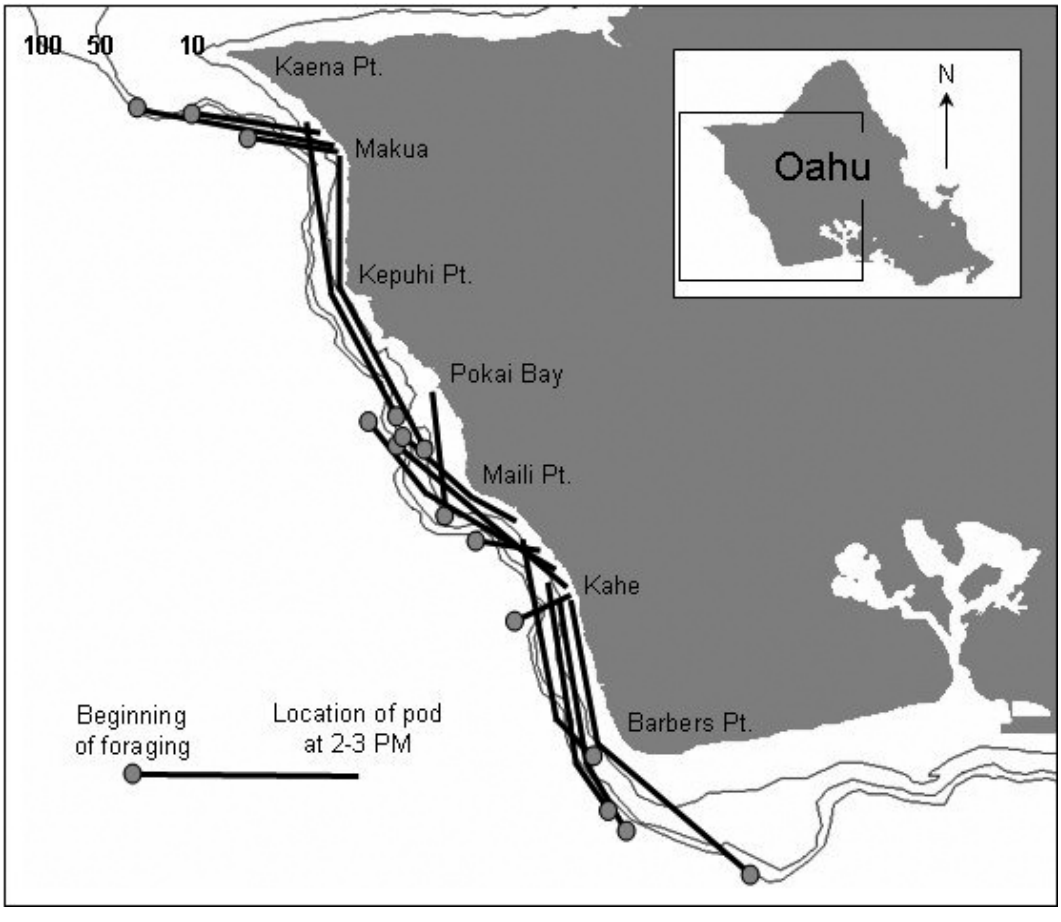

Figure 11. Locations along Waianae where spinner dolphins are believed to have begun foraging relative to where they were during the peak of the resting period (1400-1500 h)

Discussion

Spinner dolphins off Oahu carry out their daily cycle in the same general manner as they do off the Kona coast of Hawaii in the sense that groups come into shallow waters during daytime hours to rest and socialize, then move further offshore in the late afternoon or early evening to forage. Beyond this basic similarity, however, some noteworthy differences exist in the manner in which dolphins on Oahu use the nearshore habitat.

Patterns of Occurrence

Along the Waianae Coast, spinner dolphins seek out specific locations each morning as they do along Kona. Makua Beach, Kahe Point, and to a lesser extent Pokai Bay are essentially analogs of Kealakekua Bay on Hawaii where spinner dolphins occur almost daily (Norris et al., 1994). Two common features shared between these sites are that they are usually more sheltered from prevailing tradewinds than adjacent areas and that the bottom substrate is dominated by large stretches of white sand bottom rather than the prevailing reef and rock bottom found along most other parts of the coast.

These locations appear to serve as gathering sites where multiple pods meet after foraging at night. The function of forming large aggregations at specific locations is likely related to social processes that occur prior to groups descending into rest. High levels of acoustic and social activity typically characterize the early morning hours at these locations (unpublished data obtained in parallel with this study). Chases between individuals, affiliative behaviors (caressing, sexual, and pseudosexual interactions), and the production of whistles and so-called "burst pulse" acoustic signals are all very frequent during this time. These activities appear to be important in establishing or reaffirming social relationships between individuals in newly emerging subgroups. Norris et al. (1994) suggested that because spinner dolphin pods are so fluid in composition, a period of reacquaintance between members is probably necessary to establishing an effective resting group.

On the south shore of Oahu, no specific aggregating sites were identified. Spinner dolphins did not appear to prefer any particular place along the coast, but, instead, remained in consistently larger groups regardless of location. Pods on both coasts typically started off large in the morning and gradually fragmented into smaller subgroups until a minimum size was reached at the peak of the resting cycle in the early afternoon. The fact that pods on the south shore were consistently larger suggests that a tradeoff may exist between the number of animals required to form an effective resting group and the physiography of a particular area. Norris & Schilt (1988) proposed that polarized dolphin schools (and probably most other types of schools, herds, and flocks) rely on what they termed a sensory integration system (SIS) to protect themselves from predation. An SIS in action is characterized by the receipt of environmental information by individual members of a group monitoring different segments of three-dimensional space, followed by the rapid passage of a response reaction in all directions throughout the group (Norris & Dohl, 1980). Resting spinner dolphins on the South Shore may require larger numbers to achieve an effective SIS than on Waianae. On most days, the South Shore habitat is considerably more exposed to tradewinds and, as a result, waters tend to be more turbid than along Waianae. In addition, no sites were observed with large stretches of white sand bottom. Therefore, decreased visibility and a more cryptic bottom substrates may require animals on the south shore to maintain higher numbers to achieve adequate vigilance. Although highly reduced during rest, the overall echolocation activity of larger groups is likely to be greater than that of smaller ones. This could allow larger groups to remain aware of nearby threats even in reduced visibility. Alternatively (or additionally), by being in a larger group, individuals may simply gain greater protection through a higher dilution effect (Foster & Treherne, 1981).

Movement Patterns

The patterns of movement of spinner dolphins along the Kona Coast have not been described in detail to date; however, Östman-lind (pers. comm.) reported that, during the day, spinner dolphins resident there usually seek out and remain at specific resting sites along the coast until they move offshore again to their foraging grounds late in the afternoon. This is different than what was observed on Oahu. Spinner dolphins on both the Waianae Coast and the South Shore moved around quite a bit during the day. In fact, other than in the early morning period, they were equally as likely to mill at or near an aggregating site as they were to travel along the coast. On the South Shore, where no specific aggregating sites were identified, groups spent more time traveling than milling, especially during the midday period. Interestingly, spinner dolphins were almost never observed milling to the north and south of Pokai Bay and at the southern end of Waianae near Barbers Point. These areas were consistently more exposed to wind and dominated by shallow (< 10 m) reef bottom topography (pers. obs.). It seems spinner dolphins qualitatively distinguished between these and other locations along Waianae, choosing only to transit through certain areas.

When dolphins traveled along the coast, they did not do so haphazardly. Rather, they exhibited a strong affinity for staying near the 10-fathom isobath. As the coastline twisted and turned, rarely did a traveling group of animals choose to take the shortest path between two points separated by deeper water, preferring instead to follow the outline of the coast. This pattern became so obvious during the first two years of observation that the band of water centered on the 10-fathom contour was nicknamed the "spinner expressway." Groups of dolphins traveling in opposite directions often met on this expressway, sometimes interacting briefly and shuffling individuals, and other times (especially during rest) reacting in indifference or even avoidance.

Resting Behavior

Following an early morning phase of social activity, spinner dolphins on both coasts almost invariably entered into a period of rest. Unlike on the Kona Coast, however, spinner dolphins on Oahu did not restrict their resting behavior to specific sites. Rather, time of day appeared to be a greater influence on their activity level than location. Although resting behavior could occur at all hours of the day, it was observed with the greatest consistency during the midday and early afternoon periods. Whether a group was milling or traveling, between approximately 1200 and 1600 h, it typically entered into a behavioral pattern where all members of the pod were tightly polarized, coordinated, and doing long dives. Traveling groups tended to cycle between this pattern and somewhat looser swimming formations, whereas milling groups often persisted this way for several hours at a time.

The ability to rest while minimizing predation risks is undoubtedly the primary reason spinner dolphins occupy the nearshore habitat during daylight hours. Not surprisingly, they appear able to adopt more than one strategy to achieve rest. Besides the well-established approach of seeking sheltered areas with light bottom substrate, spinner dolphins are clearly also able to rest while on the move. By traveling over shallow water, they diminish the ability of a predator to attack from below, which is probably why they exhibit such a preference for the 10-fathom isobath. Pods also may choose to maintain large numbers and alternate vigilance responsibilities between subgroups. Often, the larger pods observed were made up of distinct subgroups in different phases of the active/resting behavioral cycle. Which strategy spinner dolphins ultimately employ to rest is probably dictated by the habitat available to them and the number of animals present in the group.

Movement Towards Foraging Sites

During the late afternoon, spinner dolphin groups that had spent the day separated while resting often rejoined or met up with new groups. This period was marked by an increase in overall behavioral activity. As on the Kona Coast, prior to moving towards their foraging grounds, pods typically engaged in what Norris & Dohl (1980) termed "zigzag" swimming. During this time, groups would suddenly become highly active aerially and make a concerted push towards offshore waters, only to double back and settle again into a resting pattern. This often was repeated several times until the group finally continued in its offshore progression. Acoustic activity at this time also rapidly increased and reached a crescendo of whistle choruses when the group finally made its offshore move (Lammers, unpublished data). Norris et al. (1994) compared this behavior to the acoustic "pep rallies" of Cape African hunting dogs (*Lycaon pictus*) that perform similar false starts and choruses in preparation for a hunt (Estes & Goddard, 1967). In both cases, the function of this behavior is thought to be to alert all members of the group's intentions and readiness to move off.

When dolphins on the Waianae Coast finally left their shallow water daytime refuge. they spread out widely (over a square km or more) and almost invariably traveled to one of three areas: Barbers Point, Maili Point, or Kaena Point. Specifically, they headed toward the 100-fathom isobath that marks the edge of the banks at these locations. While there, they often were joined by groups of bottlenose dolphins (*Tursiops truncatus*) and/or spotted dolphins (*Stenella attenuata*), and it was at these locations that they usually began making extended dives in coordinated groups of several animals.

The fact that spinner dolphins traveled to nearby banks to look for mesopelagic prey, rather than simply moving to the closest deep water, is indicative of an adaptive approach to finding their food. Recent studies of the mesopelagic boundary community along the Waianae Coast have shown that this layer of organisms migrates not only vertically but also horizontally towards shore at night (Benoit-Bird et al., 2001). The distance of the layer from shore is a function of the time of night relative to midnight. Mesopelagic organisms begin their shoreward movement in the evening and by midnight are densest within 1 km of the shore. Their migration is then reversed so that by dawn they are again offshore in deep waters. Spinner dolphins begin foraging at a protruding bank most likely because the prey layer enters shallow waters here before anywhere else along the coast. This has two important consequences:

to maximize the dolphins' overnight exposure time to the layer and to reduce the depth of the dives they need to perform (and, therefore, the energy they need to expend) to reach their prey. Both of these advantages are significant in light of recent findings by Benoit-Bird (2004) that the caloric content of typical mesopelagic organisms requires that spinner dolphins consume at least one organism per minute over an 11-hour foraging period to maintain a positive energy balance. Not surprisingly, spinner dolphins appear to be quite efficient at obtaining their prey.

Human Interactions

In recent years, spinner dolphins on Oahu and on other islands have increasingly become the focus of human attention. Their acrobatic surface displays and predictable occurrence have made them a profitable attraction for local dolphin and whale-watching tour companies. In addition, approaching and swimming with dolphins at places like Makua Beach and Kealakekua Bay have become popular with residents and tourists alike despite being illegal. This has raised concerns with some about the long-term effects of chronic human encroachment on these populations.

How spinner dolphins react to vessels and swimmers appears primarily determined by their behavioral state and the manner in which they are approached. Socially active groups often are quite tolerant of a human presence provided they are not actively pursued (pers. obs.). As they become more polarized and coordinated, groups tend to shy away from direct interactions with people. By the time they are at rest, they usually avoid being engaged and will sometimes leave an area if forced to interact (Norris et al., 1994).

Presently, no data exist to predict how the rising level of daily human encroachment will affect the lives of these animals in the long term. It is reasonable to suspect, however, that the ability to rest effectively will play a key role in determining future patterns of their occurrence and behavior along the coast. Spinner dolphins in Hawaii are probably also capable of resting while offshore since in other parts of the world populations exist that live nowhere near land. Aerial survey data indicate that pods do indeed sometimes occur offshore and in the channels between the islands in Hawaii during the day (Mobley et al., 2000). Should human encroachment become too great and their preferred coastal sites be reduced in the ability to support resting behavior, local populations could gradually become less frequent near shore, choosing instead to remain at sea. Tour industry operators and regulatory agencies should consider this and similar consequences in their efforts to manage this resource. Formulating policies and approach guidelines based on the known behavioral patterns of local populations will help ensure that spinner dolphins remain a common feature of Hawaii's nearshore environment.

Conclusions

Spinner dolphins occurring on Oahu's leeward and south shores are closely tied to the island's coastal environment. They rely on the physiographical and trophic resources provided by the nearshore habitat for nearly all phases of their life history. There is evidence that the animals on these coasts have long-term site fidelity. Marten & Psarakos (1999) photographically identified two uniquely scarred individuals on the Waianae Coast that had previously been identified twenty years earlier. This implies that the home ranges of at least some individuals are probably quite stable over time.

Resting behavior on Oahu appears to occur somewhat more opportunistically than has been described for Kona. Sheltered sites like Makua Beach and Kahe Point are clearly of high importance to spinner dolphins since they occur there almost daily; however, they also consistently occupy adjacent areas along the coast and can rest while traveling. Therefore, it would be more accurate to conclude that shallow waters are the primary daytime attraction for spinner dolphins rather than any one specific site. The local features found at places like Makua Beach and Kahe Point probably represent the optimal end of a continuum of conditions spinner dolphins are able to exploit.

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