Behavior of free-ranging common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand

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ABSTRACT

Here we present the first data describing the behavior of common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. Activity budgets are used to assess the effects of diel, season, depth, sea surface temperature, group size, and composition on dolphin behavior. Additionally, the presence/absence of Bryde's whale (*Balaenoptera brydei*) and Australasian gannet (*Morus serrator*) is examined in relation to dolphin behavior. Behavioral data were collected from 686 independent dolphin groups during boat-based surveys conducted between February 2002 and January 2005. Foraging (46.7%) and social (7.2%) were the most and least frequently observed

behaviors, respectively. Travel (28.9%), mill (9.5%), and rest (7.7%) accounted for the remainder of the activity budget. Behavior varied seasonally, with the highest proportion of foraging and resting groups observed during the spring and autumn, respectively. Behavior also varied with water depth, with foraging animals observed in the deepest and resting groups recorded in the shallowest regions of the Hauraki Gulf. A correlation between group size and behavior was evident, although behavior did not vary with the composition of dolphin groups. Resting, milling, and socializing animals were more frequently observed in smaller group sizes. Foraging behavior was prevalent in both small and large group sizes, suggesting foraging plasticity exists within this population. Behavior differed between single- and multispecies groups, with foraging more frequent in multispecies groups. Resting, milling, or socializing was rarely observed in the presence of any associated species, indicating the primary mechanism for association is likely prey related.

Key words: common dolphin, *Delphinus*, seasonality, feeding area, Hauraki Gulf, New Zealand.

There is growing support within the international community for special consideration to be given for areas that are deemed significant ecosystems or habitats for a species or population. For example, habitats that are associated with fundamental biological processes (*e.g.*, feeding, resting, and breeding) may be nominated as special areas of conservation (SACs). However, the identification of such SACs for species conservation inherently relies on a sound understanding of the behavior of that species. Typically, cetacean behavior reflects habitat use, and thus may be influenced by parameters such as time of day (*e.g.*, Baird *et al*. 2002, Stafford *et al*. 2005), season (*e.g.*, Bräger 1993, Stockin *et al*. 2001), water depth (*e.g.*, Cañadas *et al*. 2002), bottom topography (*e.g.*, MacLeod and Zuur 2005), and tidal flow (*e.g.*, Acevedo 1991, Gregory and Rowden 2001). Such parameters act as correlates of food and shelter availability within the environment.

Very little is known about the behavior of free-ranging common dolphins (*Delphinus* spp.) worldwide. Foraging strategies (Gallo Reynoso 1991, Neumann and Orams 2003, Burgess 2006) and respiration patterns (Ferretti *et al*. 1998) have been examined in some populations, although there is a general lack of behavioral data available for the genus. In Greece, behavioral data have been systematically collected for short-beaked common dolphins (*Delphinus delphis*) for over a decade, although these data remain unpublished due to more urgent concerns regarding the critical conservation status of the population (*e.g.*, Bearzi *et al*. 2003, Bearzi 2007, Bearzi *et al*. 2008). Some insights into the behavior of Mediterranean common dolphins have recently been detailed by Cañadas and Hammond (2008), although those data represent habitat modeling rather than behavioral activity budgets *per se*. Other behavioral data for both short- and long-beaked (*D. capensis*) common dolphins observed off California have additionally been reported (Bearzi 2005, 2006), although currently, just one activity budget for the genus appears within the published literature (Neumann 2001). This activity budget describes the behavioral states of common dolphins in the Bay of Plenty, a region *ca.* 100 km east of the Hauraki Gulf, New Zealand. Thus, our understanding of common dolphin behavior is extremely poor. This should be of concern to managers because this information is necessary to identify critical habitats necessary for biological processes such as feeding and breeding.

New Zealand common dolphins (*Delphinus* sp.) lack taxonomic confirmation, yet exhibit extensive morphological variation (Stockin and Visser 2005). Despite being

the most abundant cetacean species in the Hauraki Gulf (Stockin *et al.* 2008*a*), little is known about their use of these waters. Thus, to better understand the use and importance of the Hauraki Gulf, we examined the activity budget of common dolphins using this region. Based on extrinsic and intrinsic factors that can affect behavior, we assessed the activity budget of common dolphins in relation to diel, season, depth, sea surface temperature (SST), group size, and group composition. Additionally, behavioral differences between single- and multispecies groups were investigated using presence/absence of the Bryde's whale (*Balaenoptera brydei*) and Australasian gannet (*Morus serrator*). The proportion of time that common dolphins spend devoted to key activity states (forage, mill, rest, social, and travel) was examined, and compared to Neumann (2001) and other available data in order to assess differences in habitat use. In particular, this study considered the importance of the Hauraki Gulf as a potential feeding ground for common dolphins.

MATERIALS AND METHODS

Study Site

The Hauraki Gulf (Fig. 1) is a shallow (60 m maximum depth), semi-enclosed body of temperate water (Manighetti and Carter 1999) on the east coast of North Island, New Zealand (36°10′–37°10′S, 174°40′–175°30′E). Influenced by the subtropical East Auckland Current (EAUC), this region is extremely productive (Booth and Sondergaard 1989), exhibiting high levels of nutrient availability and consequently, a high diversity of biological fauna (Chang *et al*. 2003). Unlike other regions around the New Zealand coast, common dolphins occur within the Hauraki Gulf year-round
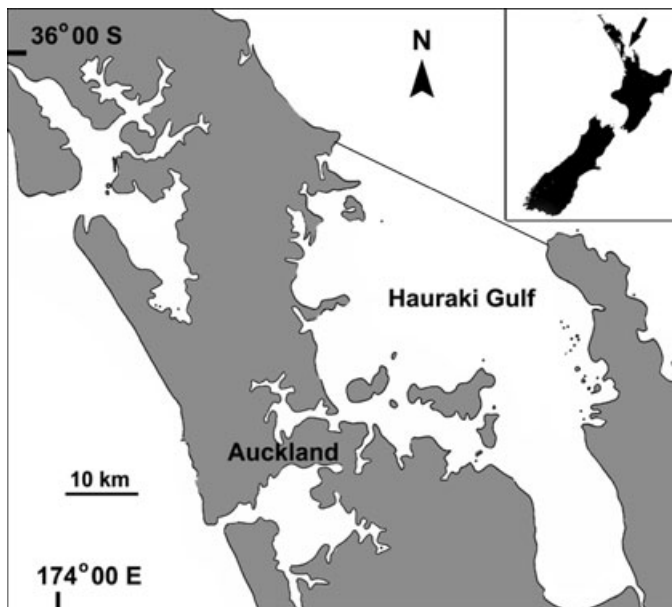

Figure 1. Map showing location of the Hauraki Gulf, North Island, New Zealand.

(Stockin *et al.* 2008*a*), and have proven susceptible to coastal accumulative impacts (*e.g.*, Stockin *et al.* 2007, 2008*b*).

Data Collection

Behavioral observations of dolphins were conducted between 28 February 2002 and 24 January 2005. Two platforms were used: (1) *Aihe*, a 5.5-m, center-console, rigid-hulled inflatable boat, fitted with a 90-hp four-stroke outboard engine at 0.5 m observer eye-height and (2) *Dolphin Explorer,* a 20-m catamaran powered by twin 350-hp diesel engines at 5 m observer eye-height. Owing to the lower height of *Aihe*, and consequent reduced detectability of cetaceans, only surveys conducted in good visibility ($\geq$1 km) and in Beaufort 2 or less were used in the analysis. Data collected from onboard *Dolphin Explorer* were included when visibility was good ($\geq$1 km) and in Beaufort 4 or less. Survey routes conducted from *Aihe* were considered nonselective in that they typically were governed by weather conditions (*e.g.*, swell and prevailing winds). However, equal survey coverage of all sectors of the Hauraki Gulf (northeast, northwest, southeast, and southwest) was achieved during each season owing to the alternation of search effort between quarters. Conversely, survey routes onboard *Dolphin Explorer* were less weather dependent, although they were occasionally influenced by the last known location of dolphins. Nonetheless, the greater number of surveys aboard this platform, in conjunction with the desire to optimize the opportunity of encountering additional species, resulted in representative coverage of the study area during the study period.

Observations by naked eye were conducted by experienced observers using a continuous scanning methodology (Mann 1999). Additionally, binoculars (Bushnell 8 × 42 magnification) were used onboard *Dolphin Explorer* to assist with the detection of animals. The increased elevation of this platform allowed distant observations of whales and seabirds to be used as sighting cues. Other sighting cues used to detect dolphins include splashing and silhouettes of porpoising animals, water disturbance due to surface activity of animals, and sighting of dorsal fins.

Once within 400 m of a focal group of dolphins, the boats would slow to an approach speed ($\sim$5 kn). At this point, behavioral data, group size and composition were recorded. Environmental parameters (*i.e.*, SST and water depth) were also noted at the start of each observation, in addition to the presence of any associated species. No attempt was made to quantify the number of birds and whales, but rather to confirm species presence/absence. SST ($^\circ$C) and depth (m) were recorded to one decimal place using a calibrated hand-held digital thermometer and onboard depth sounder. Once within 200 m of a dolphin focal group, the boat would slowly parallel animals, after approaching to the rear of the group. Once the boat was within approximately 100 m of the animals, the start time and location for the encounter were recorded using a hand-held Garmin GPS 12.

Focal group follows with instantaneous scan sampling of the predominant behavior (Altmann 1974, Mann 1999) was used to measure behavior. Animals were scanned from left-to-right for the entire group in order to include all individuals, and to negate attention being drawn to only specific individuals or behavior (Mann 1999). The predominant behavior was determined as the behavioral state in which more than 50% of the animals were involved at each instantaneous sample. Where groups exhibited an equal percentage of individuals engaged in different behaviors,

all represented behaviors were recorded. Focal groups were monitored for >30 min during each encounter. Only behaviors that could be recorded reliably and consistently (Mann 1999) were sampled. This methodology included the decision rule to remain with the larger group when one or more individuals departed the original focal group.

Despite the advantages of focal individual follows (Mann 1999), such sampling was neither feasible nor appropriate for this study owing to similar constraints highlighted by Neumann (2001), namely, the difficulties of identifying individuals in the field, and the increased probability of disturbance to the group as a result of tracking one individual. Furthermore, as a comparable study to Neumann (2001), it was necessary to replicate the methodologies and assess the activity budget using similar sampling procedures, where possible.

Dolphin behavior was recorded in two manners (1) every 3 min during independent focal follows (conducted from *Aihe* only, herein termed *focal follow* behavior) and (2) at the onset and 30 min after the approach of the viewing vessel (herein called *initial* and *lagged* behavior, respectively). No focal follows were attempted from *Dolphin Explorer*, because this platform frequently interchanged between subgroups during a single encounter. In contrast, *Aihe* remained with a single focal group and was maneuvered in a consistent manner to minimize the potential impacts associated with the boat. Photo-identification of individuals within a focal group was predominantly undertaken at the start and end of each focal follow using a Nikon D80 fitted with a Nikkor 70–300-mm lens. Occasionally, further opportunistic photo-identification was undertaken intermittently between scan samples if additional individuals were thought to have fused with the original focal group. All behavioral data were called by a single observer (KAS) in order to standardize observations between focal groups. Occasionally, more than one independent focal group was encountered during a survey. However, focal groups were only considered independent if they were separated spatially and temporally to a degree that would prevent individuals becoming resampled during a second focal follow (>5 km), and only when subsequent photo-identification analysis revealed no matches between the focal group members.

Five categories of behavioral state were defined (Table 1), modeled on the definitions used by Neumann (2001). A behavioral state is defined as a broad category of activities, such as foraging behavior, that integrates a number of behavioral activities into a recognizable pattern (Bearzi 2005). A *group* was defined as any number of animals observed in *association*, moving in the same direction and usually engaged in the same activity (Shane 1990). Dolphins within five body lengths of any other dolphin were deemed to be in *association* (Fertl 1994). *Focal groups* were defined as any *group* for which instantaneous sampling of the predominant behavior was collected for >30 min during focal follows. Any other cetacean or avian species observed <100 m from the *focal group* was defined as an *associated species* (Bearzi 2006). *Neonates* were defined as small calves that exhibited diagnostic features indicative of newborns (*e.g.*, the presence of dorsoventral fetal folds); *calves* were defined as animals that were approximately one-half (or less) the length of an adult and were consistently observed in association with an adult animal (Fertl 1994); *juveniles* were defined as animals approximately two-thirds the size of an adult animal and frequently observed swimming in association with an adult animal, though not in the infant position, suggesting that they were weaned (Mann *et al.* 2000). *Adults* were defined as any animal >1.8 m.

Table 1. Definitions of behavioral states recorded for common dolphins in the Hauraki Gulf, New Zealand between 2002 and 2005.

Behavioral state	Definition
Forage	Dolphins involved in any effort to pursue, capture, and/or consume prey, as defined by observations of fish chasing (*herding*), coordinated deep diving and rapid circle swimming. Prey frequently observed at the surface during foraging activity of the dolphins.
Mill	Dolphins exhibited nondirectional movement, frequent changes in heading prevent animals from making headway in any specific direction.
Rest	Dolphins observed in a tight group (<1 body length between individuals), engaged in slow maneuvers with little evidence of forward propulsion. Surfacings appear slow and are generally more predictable than those observed in other behavioral states.
Social	Dolphins observed chasing, copulating, or engaged in any other physical contact with other dolphins (excluding mother–calf pairs). Aerial behaviors such as breaching frequently observed.
Travel	Dolphins engaged in persistent, directional movement, making noticeable headway along a specific compass heading.

Data Analysis

Diurnal and seasonal patterns in activity budget and relationships with environmental variables, that is, water depth and SST, were investigated. The effect of group size and composition on behavior was also examined. Finally, we assessed the effect of associated species independently, using presence/absence of Bryde's whales and Australasian gannets.

Diurnal patterns were investigated by assigning each observation to a 2-hr period within the sequence 0600–0759, 0800–0959, through to 1800–2000. Seasonal analyses were based on the austral seasons as follows: spring (September to November), summer (December to February), autumn (March to May), and winter (June to August). Group size was classified as: 1–10, 11–20, 21–30, 31–50, 51–100, 101–200, and 201 + animals. Group composition was analyzed by the youngest component within a group, classified either as *neonates*, *calves*, *juveniles*, or *adults*.

Water depth and temperature were both analyzed as continuous raw data. Statistical analysis was carried out using Minitab 14 (Minitab Inc., USA). The distributions of continuous response variables (SST and depth) were initially tested for normality and homogeneity using Anderson-Darling and Bartlett's and Levene's tests, respectively (Zar 1996). In most cases, data were nonnormal, so the nonparametric Kruskal–Wallis analysis of variance (ANOVA) test was used. Pearson χ^2 tests were applied to assess categorical data sets (*e.g.*, group size and composition). All tests were considered statistically significant at $P \leq 0.05$. To avoid pseudoreplication, each focal group rather than each individual data point, was treated as an independent sample.

To test for bias in the detection of conspicuous *vs.* inconspicuous behaviors, we compared *initial* behavioral states (*i.e.*, when the dolphins were first observed) with the *lagged* behavioral states (*i.e.*, after a 30-min habitation period). As expected, less-conspicuous behaviors were more frequently recorded during the habituation

period, although no significant difference was observed between the data sets. Thus, activity budgets were defined on the *initial* behavior because (1) this reduced the likelihood of an impact from the observing boat and (2) it allowed direct comparisons to be made with Neumann (2001). Potential differences in data collected from the two observation platforms were tested by segregation of the data sets by vessel. No significant difference was detected ($\chi^2_4 = 3.159$, $P = 0.532$) so subsequent analyses reported here used a pooled data set.

<div align="center">RESULTS</div>

Field Effort

Data were collected between February 2002 and January 2005 during 506 boat-based surveys. A total of 719 independent common dolphin encounters were observed, although behavioral data were collected for only 686 groups, 548 and 138 from *Dolphin Explorer* and *Aihe*, respectively. All observations occurred in the presence of only one boat, the observation platform.

Activity Budget

Overall, forage (46.7%, $n = 321$) and travel (28.9%, $n = 198$) were the most frequently recorded behavioral states. Social (7.2%, $n = 49$) and rest (7.7%, $n = 53$) were the least observed behavioral states (Fig. 2). Foraging dolphins were more frequently observed from *Dolphin Explorer* than *Aihe*, although differences for this and other behaviors were not found to be significant between platforms ($\chi^2_4 = 3.159$, $P = 0.532$).
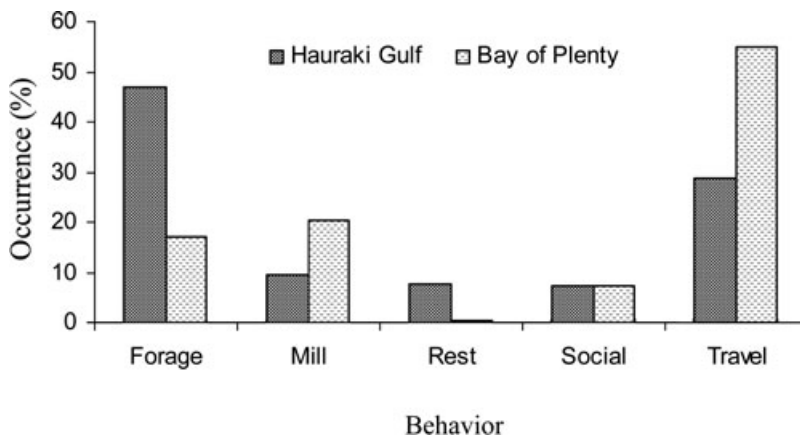

Figure 2. A comparison of activity budget for common dolphin groups reported by Neumann (2001) for the Bay of Plenty and for the Hauraki Gulf (this study). Behavior assessed as the *initial* state observed at the onset of each independent encounter, as detailed in Neumann (2001).
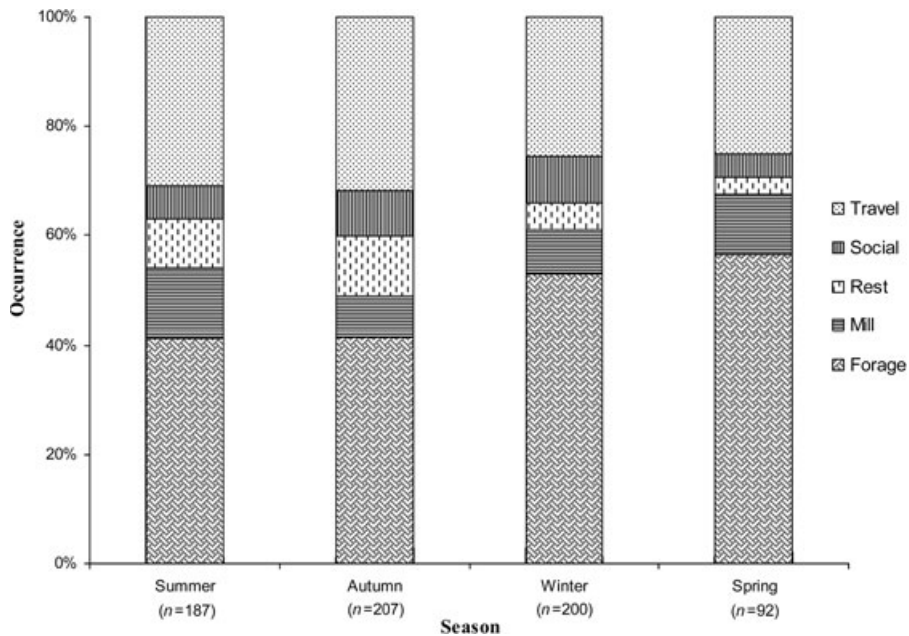
Figure 3. Seasonal behavior of common dolphin groups ($n = 686$) in the Hauraki Gulf, New Zealand observed between 2002 and 2005. Behavior assessed as the *initial* state at the onset of each independent encounter, as detailed in Neumann (2001).

Temporal Variance

Diurnal differences in behavior were not detected ($\chi^2_8 = 7.422$, $P = 0.494$), although seasonal variance was evident ($\chi^2_{12} = 22.249$, $P = 0.035$). Foraging and resting groups were most prevalent in winter and autumn, respectively (Fig. 3). Foraging (16.2%, $n = 52$) was observed more frequently than expected during the winter and spring, whereas resting (5.7%, $n = 3$) groups were observed significantly less than expected.

Environmental Variance

Behavior varied significantly with water depth (Kruskal–Wallis $h_4 = 24.76$, $P = <0.001$) with foraging groups observed in the deepest ($n = 315$, median $= 42.5$ m, SE $= 0.39$) and resting groups observed in the shallowest ($n = 53$, median $= 37.0$ m, SE $= 1.4$) waters. Traveling and socializing groups were observed in median water depths of 39.8 m ($n = 195$, SE $= 0.61$, range 13.0–53.9) and 41.6 m, ($n = 48$, SE $= 0.77$, range 26.0–51.4), respectively. Milling groups were observed at a median water depth of 41.0 m ($n = 63$, SE $= 0.99$, range 17.0–51.1) (Table 2).

Behavior varied significantly with SST (Kruskal–Wallis $h_4 = 12.77$, $P = 0.012$), with foraging groups observed in the coolest (median $= 17.9°C$, SE $= 0.18$) and resting groups observed in the warmest (median $= 20.3°C$, SE $= 0.35$) waters, respectively. Milling common dolphins were observed at a median water temperature of 19.1°C ($n = 56$, SE $= 0.414$). Traveling and socializing groups were observed

Table 2. Depth of water (m) by season for each behavioral state recorded for common dolphin groups ($n = 686$) observed in the Hauraki Gulf, New Zealand between 2002 and 2005.

Season	$\bar{x}$	Median	I.Q.R.	SD	SE	Range	n
Forage							
Spring	40.7	41.8	7.9	6.5	0.9	21.3–52.5	50
Summer	40.3	43.2	11.2	8.2	0.9	13.5–51.8	76
Autumn	41.8	43.3	4.8	6.5	0.7	14.3–52.0	86
Winter	40.2	41.8	8.2	6.4	0.6	19.0–54.8	103
Mill							
Spring	42.3	43.2	5.0	3.6	1.2	34.5–46.0	9
Summer	35.0	34.2	12.0	9.6	2.0	17.0–51.1	23
Autumn	38.9	40.4	10.3	8.0	2.1	20.9–51.1	15
Winter	41.7	41.6	4.2	3.5	0.9	34.8–48.1	16
Rest							
Spring	44.1	42.0	8.3	4.5	2.6	41.0–49.3	3
Summer	30.8	32.5	20.5	12.8	3.1	7.0–46.4	17
Autumn	36.6	36.3	12.2	7.8	1.6	20.4–49.6	23
Winter	39.3	42.0	10.0	7.0	2.2	26.0–46.8	10
Social							
Spring	41.3	41.8	7.1	3.7	1.9	36.7–45.0	4
Summer	41.5	42.5	4.1	6.4	1.9	26.7–51.4	11
Autumn	39.7	41.8	7.4	5.5	1.3	28.0–46.4	17
Winter	40.5	40.5	6.3	4.9	1.2	31.1–48.6	16
Travel							
Spring	38.3	41.8	6.1	8.7	1.8	17.0–48.0	23
Summer	35.8	37.6	12.6	9.3	1.2	13.0–50.0	58
Autumn	39.3	41.6	7.2	7.6	0.9	15.6–50.4	66
Winter	38.6	39.0	10.2	8.3	1.2	14.4–53.9	48

at median temperatures of 19.3°C ($n = 169$, SE = 0.223) and 19.3°C ($n = 44$, SE = 0.429), respectively (Table 3).

Effect of Group Dynamics on Behavior

Behavior varied significantly with group size ($\chi^2_{24} = 46.224$, $P = 0.004$), with foraging ($n = 15$) and traveling ($n = 3$) groups accounting for 90% of all large (200+ animals) groups observed. Foraging ($n = 28$) and traveling ($n = 33$) also comprised the largest proportion of small (1–10 animals) groups recorded, accounting for 30.4% and 35.9%, respectively. Resting was more frequent in smaller group sizes and was most observed in groups comprising 11–20 animals (32%, $n = 16$). Resting was recorded least in group sizes that exceeded 100 animals ($n = 4$), with just 8.2% of all resting behavior observed in groups of 100+ animals. Milling was also more frequent in smaller group sizes, and was more frequent in groups comprising 11–20 animals (26.2%, $n = 16$). Additionally, milling was also less frequently observed in group sizes over 100+ animals ($n = 2$), with just 3.3% of all resting behavior observed in groups of more than 100 animals. Socializing was frequently recorded in smaller group sizes, and was most observed in groups comprising 21–30 animals (27.1%, $n = 13$). Socializing was least recorded in the group sizes over 100+ animals

Table 3. Sea surface temperature (SST, °C) by season for each behavioral state recorded for common dolphin groups ($n = 686$) observed in the Hauraki Gulf, New Zealand between 2002 and 2005.

Season	$\bar{x}$	Median	I.Q.R.	SD	SE	Range	n
Forage							
Spring	16.6	16.7	1.4	1.2	0.2	14.0–19.6	37
Summer	21.2	21.3	1.8	1.5	0.2	17.7–24.4	63
Autumn	19.6	19.5	2.9	1.7	0.2	16.7–23.4	80
Winter	15.0	14.9	2.3	1.4	0.1	12.0–18.8	96
Mill							
Spring	16.6	17.0	2.4	2.6	1.0	13.1–21.2	7
Summer	21.1	21.3	2.6	1.8	0.4	18.0–24.9	21
Autumn	20.0	20.2	2.0	1.4	0.4	17.3–22.8	14
Winter	14.9	14.9	1.7	1.1	0.3	13.0–17.4	14
Rest							
Spring	16.4	16.4	1.3	0.7	0.4	15.7–17.0	3
Summer	21.0	21.2	2.5	1.5	0.4	18.8–23.7	16
Autumn	20.3	20.5	0.6	1.0	0.2	18.0–22.2	20
Winter	15.6	16.1	1.8	1.1	0.4	14.2–17.2	9
Social							
Spring	16.9	16.9	N/A	0.8	0.6	16.3–17.4	2
Summer	21.5	21.8	1.5	0.8	0.3	20.1–22.5	10
Autumn	20.3	20.5	2.3	1.3	0.3	17.9–22.3	17
Winter	15.5	14.7	2.6	1.4	0.4	13.7–17.7	15
Travel							
Spring	16.7	16.8	1.4	1.3	0.3	14.1–18.7	15
Summer	20.7	20.5	2.3	1.5	0.2	17.8–24.1	47
Autumn	20.1	20.2	1.4	1.2	0.1	17.4–22.4	60
Winter	14.8	14.5	1.6	1.6	0.2	10.5–18.5	47

($n = 2$), with just 4.2% of all social behavior observed in groups comprising more than 100 animals.

Behavior did not vary with group composition ($\chi^2_{24} = 10.168$, $P = 0.601$). All group compositions based on youngest component engaged in foraging more often than any other behavioral activity. Traveling was the second most prevalent behavior in each of the group compositions. Overall, resting behavior was least observed in groups that comprised adults only (23.5%, $n = 12$). Conversely, groups comprising calves as their youngest component were recorded to rest most ($n = 23$), accounting for 45.1% of all resting groups observed. Both milling (36.0%, $n = 19$) and social (34.7%, $n = 17$) behaviors were observed most in groups that contained calves.

Effect of Associated Species on Behavior

Dolphins were observed in association with four cetacean and eight avian species including the Bryde's whale, killer whale (*Orcinus orca*), bottlenose dolphin (*Tursiops truncatus*), striped dolphin (*Stenella coeruleoalba*), Australasian gannet, flesh-footed shearwater (*Puffinus carneipes*), Buller's shearwater (*P. bulleri*), sooty shearwater (*P. griseus*), gray-faced petrel (*Pterodroma macroptera*), black-backed gull (*Larus dominicanus*), white-fronted terns (*Sterna striata*), and blue penguin (*Eudyptula minor*) (Stockin *et al*. 2008*a*). However, only the presence/absence of Bryde's whale and

Australasian gannets is considered here due to the limited sample size of other associations. Furthermore, percentages given relate to the proportion of dolphin groups for which dolphin behavior was recorded (*i.e., n* = 686, as opposed to *n* = 719, as quoted in Stockin *et al*. 2008*a*).

Dolphin-only groups (*i.e.*, common dolphins only) were observed during 74.3% of encounters (*n* = 510). Dolphin–whale groups (*i.e.*, common dolphins with Bryde's whales) accounted for 25.7% (*n* = 176) of groups. Behavior varied significantly between these single- and multispecies groups (χ^2_4 = 44.884, *P* < 0.001) with 68.2% of all foraging behavior observed for common dolphins (*n* = 120), occurring in the presence of Bryde's whales. Travel observed in dolphin-only groups was almost double that recorded in the presence of whales (17.6 and 32.8%, respectively). Most resting common dolphin groups (84.9%, *n* = 45) were typically observed in the absence of whales. Milling (*n* = 58) and social (*n* = 39) behavior was more predominant in single- rather than multispecies groups, accounting for 89.2% and 79.6% of all observed milling and social behavior.

Australasian gannets were observed in association with common dolphins during 56% of observed dolphin groups (*n* = 384). Behavior varied significantly during gannet associations (χ^2_4 = 178.354, *P* < 0.001), with 81.3% of foraging groups (*n* = 261) occurring in the presence of gannets. The number of traveling groups observed in the presence of gannets (*n* = 64) was over half that recorded in the absence of gannets (*n* = 134), accounting for 32.3% and 67.7%, respectively. The majority of resting common dolphin groups (77.4%, *n* = 41) were typically observed in the absence of gannets, with only 22.6% (*n* = 12) of all resting groups occurring in the presence of gannets. Milling (*n* = 45) and social (*n* = 22) groups were also more predominant in the absence of gannets, accounting for 89.2% and 79.6% of all observed milling and social behavior, respectively.

DISCUSSION

Understanding spatial and temporal fluctuations in behavior is necessary for an appreciation of how a population uses its environment, and moreover, how to effectively manage a population. We found that the behavior of common dolphins in the Hauraki Gulf was mostly influenced by season, water depth, group size, and the presence of associated species. Group composition and diurnal cycles had no apparent influence on behavior of common dolphins in this region.

Food availability is considered the single most important factor in determining an animal's activity budget (*e.g.*, Powers and McKee 1994, Adeyemo 1997, Baldellou and Adan 1997). Behavioral data presented here reveal 46.8% of the activity budget of Hauraki Gulf common dolphins is attributable to foraging. This is significantly greater than the 17% foraging activity reported by Neumann (2001) for common dolphins studied in the adjacent waters of the Bay of Plenty, *ca.* 100 km north east of the Hauraki Gulf. Such a discrepancy may partially be due to the more inclusive definition used in this study. For example, *feeding* used by Neumann (2001) is similar to that of *forage* described herein, in that both were defined by the pursuit and capture of prey. However, a specific behavioral event *herding,* frequently observed during foraging bouts in the Hauraki Gulf, may potentially have been absent from Neumann's study. Unfortunately, exclusion of *herding* from the present data set for comparative purposes was not possible because behavioral events were not always recorded. Nonetheless, the comparatively higher proportion of time devoted to

traveling in the Bay of Plenty compared to the Hauraki Gulf likely reflects differences between the two environments, for example, open seas off the Bay of Plenty *vs.* relatively enclosed waters of the Hauraki Gulf.

In the Bay of Islands, a region *ca.* 240 km north of the Hauraki Gulf, 40% of common dolphin groups ($n = 17$) were observed to be *feeding* when initially encountered (Constantine and Baker 1997). This is comparable with our studies in the Hauraki Gulf, although small sample size obtained from the Bay of Islands region prevents further comparison. In the Mediterranean, the Alboran Sea was described as an important feeding ground after surface feeding by short-beaked common dolphins was observed in just 11.2% of groups (Universidad Autónoma de Madrid and Alnitak 2002). Furthermore, Bearzi (2003) reported common dolphins (*Delphinus* spp.) off Santa Monica Bay, California spending approximately 30% of their time foraging and diving, a proportion considered high and a likely consequence of available primary productivity (Bearzi 2005). Thus, it would appear reasonable to suggest that the productive waters of the Hauraki Gulf likely offer similar feeding opportunities to New Zealand common dolphins.

Diurnal peaks in foraging activity have been frequently observed in other species (*e.g.*, Bräger 1993, Scott and Cattanach 1998). However, no such patterns were observed for common dolphins in either the Bay of Plenty (Neumann 2001) or during this study. Neumann (2001) did report a high frequency of early morning feeding activity but hypothesized that a second peak in foraging activity was possibly undetected due to its nocturnal occurrence. An increased frequency in foraging activity was also detected in the Hauraki Gulf, although this was not found to be significant. In many worldwide populations, common dolphins have been shown to feed on species of the deep-scattering layer (*e.g.*, Young and Cockcroft 1994, Scott and Cattanach 1998). Recent investigations into the diet of New Zealand common dolphins concur (Meynier *et al*. 2008), indicating dietary differences because of diurnal movements within the New Zealand population. This is further supported by recent studies that show common dolphins in New Zealand waters exhibit a high degree of foraging plasticity (Neumann and Orams 2003, Burgess 2006).

Unlike in the Bay of Plenty, seasonal variation in foraging activity was evident in the Hauraki Gulf, with most foraging observed during spring. A potential reason for this is seasonal fluctuations in primary productivity (Booth and Sondergaard 1989, Chang *et al*. 2003), and the consequent availability of prey. Fuller (1953) reported the composition of plankton in the inner Gulf to be stable year-round, but suggests oceanic waters in the outer Gulf become dominated by chaetognaths and copepod species during the winter. This primary productivity change, and its consequential effect along the marine food chain, may potentially explain the increased feeding activity observed in the Hauraki Gulf during winter and spring. Fish species that were observed to be taken by common dolphins in the Bay of Plenty, for example, kahawai, *Arripis trutta*; jack mackerel, *Trachurus novaezelandiae*; yellow-eyed mullet *Aldrichetta forsteri*; flying fish, *Cypselurus lineatus*; parore *Girella tricuspidata*; and garfish, *Hyporamphus ihi* (Neumann and Orams 2003), appear to be locally abundant in the Hauraki Gulf (Kendrick and Francis 2002).

The activity budget of common dolphins in the Bay of Plenty revealed *Travel* as the most prevalent behavioral state, accounting for 54.8% of the activity budget (Neumann 2001). However, in the Hauraki Gulf common dolphins spent considerably less time traveling, accounting for just 29.8% of the activity budget. Neumann (2001) argued that a large amount of time spent traveling was reasonable if dolphins were to gain access to suitable foraging habitats and conspecifics. In the Bay of Plenty,

it was suggested that food resources are rarely uniform, and that traveling allows dolphins to move between different foraging locations (Neumann 2001). However, the Hauraki Gulf exhibits high levels of primary productivity (Booth and Sondergaard 1989, Chang *et al*. 2003) and consequently, is an area of high marine biodiversity. Food resources are less patchy in this enclosed region compared with Bay of Plenty waters (Neumann 2001), thus, dolphins are likely to spend more time foraging with reduced traveling. This hypothesis is supported by the availability of key prey species occurring within the Hauraki Gulf (Kendrick and Francis 2002).

Neumann (2001) reported just 0.4% of the activity budget for common dolphins in the Bay of Plenty was attributable to rest, although he argued this was likely an underrepresentation given the inconspicuous surface activity of resting common dolphins. In the Hauraki Gulf, resting accounted for 7.7% of the activity budget. Neumann suggested that the approach of the research vessel may trigger a switch from resting to other behaviors, thus producing a bias. However, in previous tourism impact studies, rest was reportedly the most stable behavioral state for common dolphins in the Bay of Islands (Constantine and Baker 1997) and the Hauraki Gulf (Stockin *et al*. 2008*b*). Notably, the research vessel (*Aihe*) used by Neumann (2001) in the Bay of Plenty was the same as that used during this study in the Hauraki Gulf. However, the adoption of a stringent approach protocol and upgrading of the outboard engine to a four-stroke may potentially have had some influence on the observed differences. Conversely, apparent discrepancies in resting between these two regions may represent real differences in activity budget.

Despite its inshore sheltered nature, the Hauraki Gulf is arguably less well suited for resting dolphins, especially given the heavy commercial and recreational traffic within the region (Baker and Madon 2007). Impacts associated specifically with tourism in this area (Stockin *et al*. 2008*b*) have already been shown to be higher than those reported elsewhere for this species (Constantine and Baker 1997, Neumann and Orams 2006). Furthermore, vessel collisions involving common dolphins (Massey University, unpublished data) and Bryde's whales (Stockin *et al*. 2008*c*, Wiseman 2008) have been recorded in this region. Nonetheless, resting behavior was observed mostly in groups comprising calves as their youngest component. This supports earlier suggestions that the Hauraki Gulf is an important area for calves (Stockin *et al*. 2008*a*), further confirming its potential as a nursery area for this population (Schaffar-Delaney 2004, Stockin *et al*. 2008*a*).

Milling accounted for just 9.5% of the activity budget for Hauraki common dolphins, considerably less than the 20.5% reported by Neumann (2001). Possible reasons for this include the extended amount of feeding activity evident within the Hauraki Gulf. Neumann (2001) suggested that milling could mark an early stage of foraging, when dolphins have reached a potential patch and are investigating the area for available prey. If correct, less milling would be expected in the Hauraki Gulf because prey in this region is considered less patchy, and thus dolphins would engage more in foraging as opposed to moving between patches of prey. Neumann (2001) also argued that milling may act as a brief rest-stop between bouts of traveling. Given that less traveling was observed within this region compared to the Bay of Plenty, this suggestion also seems plausible. However, no seasonal difference was observed in the frequency of milling or traveling groups in the Hauraki Gulf, whereas a seasonal difference in the number of foraging groups was detected.

Approximately 7% of the activity budget for Hauraki Gulf common dolphins was attributed to social behavior. This is consistent with that previously reported by Neumann (2001), and similar to that reported by Cañadas and Hammond (2008)

Figure 4. Common dolphins observed in the Hauraki Gulf, New Zealand during assumed copulation. Photograph by Karen Stockin.

for the southwestern Mediterranean. Neumann (2001) recorded similar behavioral events to those observed during the present study, *e.g.*, belly-to-belly contact (both with and without copulation), rubbing of the pectoral flippers and biting of the tail flukes. Assumed copulation (Fig. 4) was observed during most bouts of social activity in the Hauraki Gulf, occasionally involving the repetitive intromission of the same female by different males during a single observation. The significance of this remains unclear, although life history studies of common dolphins from the northeast Atlantic suggest promiscuous mating systems and sperm competition are evident within the *Delphinus* genus (Murphy *et al*. 2005). In the Hauraki Gulf, socializing was evident during autumn and winter, and most frequently recorded in smaller group sizes, and in groups comprising calves as the youngest component of the group. This suggests that social behavior exhibited by common dolphins in this region is important beyond the scope of just reproduction, *i.e.*, possibly for bonding and/or cultural learning (Rendell and Whitehead 2001).

Approximately 70% and 80% of foraging common dolphin groups observed in the Hauraki Gulf occurred in the presence of Bryde's whales and Australasian gannets, respectively. A bias in both the amount of foraging behavior and multispecies groups recorded from *Dolphin Explorer* was anticipated because both whales and gannets were commonly used as sighting cues to find dolphin groups from this platform. Surprisingly however, the proportion of foraging activity recorded from *Aihe* remained similar, thus negating the possibility of our results being an artifact of indicative search methodologies. Furthermore, this suggests that the high degree of foraging behavior observed for common dolphins in the Hauraki Gulf represents a true reflection of actual habitat use.

Multispecies aggregations, such as those observed in this study, have frequently been reported in mammals, and are known to serve various functions including among others, increased predator protection and foraging opportunities (see Stensland *et al*. 2003 for a review). Delphinids frequently form multispecies groups with other

cetaceans (*e.g.*, Frantzis and Herzing 2002, Herzing *et al.* 2003), but are also observed in multispecies groups containing large tunas *Thunnus* sp. (*e.g.*, Buckland *et al.* 1992, Das *et al.* 2003, Rogan and Mackey 2007) and various avian species (*e.g.*, Evans 1982, Martin 1986, Clua and Grosvalet 2001, Svane 2005). Further research conducted on other associated marine taxa, particularly fish species, would be helpful to our understanding of these multispecies feeding aggregations.

Study Limitations

The systematic following of groups or individuals in a population can contribute greatly to our understanding of the behavior of a species. However, inevitably with vessel-based follows of dolphins, the potential impact of the boat itself has to be taken into consideration when studying behavior. In this study, it was not possible to undertake land-based theodolite surveys because dolphin distribution was wide and occurrence close to shore was not predictable (Stockin *et al.* 2008*a*). Since boat-based surveys were necessary, we adopted protocols proven to minimize the potential impact of the observing vessel (Stockin *et al.* 2008*b*), and used a four-stroke outboard engine for reduced noise and exhaust emissions.

The frequency of multispecies groups was greater from *Dolphin Explorer*, and undoubtedly overestimated owing to the use of binoculars to detect seabirds and whales. However, less bias was anticipated from *Aihe* due to important differences in survey methodology. Areas searched from this platform were neither dependent upon previous dolphin encounters nor the presence of indicator species. Moreover, the conscious decision not to use binoculars to detect indicator species from *Aihe*, balanced the probability of observing both single- and multispecies groups.

We acknowledge that conspicuous surface activity and the presence of indicator species can arguably bias the activity budget. *Dolphin Explorer* frequently used feeding Australasian gannets as indicator species to locate dolphins, thus providing bias toward feeding groups of common dolphins. However, comparison of the *initial* and *lagged* behavioral states revealed no significant difference in the prevalence of foraging or other more conspicuous surface behaviors. Thus, it would appear that the importance of the Hauraki Gulf as a feeding ground for common dolphins is not merely an artifact of the way the dolphins were detected, but an accurate representation of how these waters are used by common dolphins.

Management Implications

Within New Zealand, the Hauraki Gulf is already acknowledged as a significant coastal, marine, and island ecosystem and given special status through the Hauraki Gulf Marine Park Act (2000). However, there is a strong argument for explicit and specific management strategies to be developed and applied for species that rely on this region for important biological processes, for example, feeding. Here, we present evidence that common dolphins utilize the Hauraki Gulf extensively for foraging. Foraging activity recorded in this region appears considerably higher than that reported by Neumann (2001) for the Bay of Plenty, or that reported for other common dolphin populations overseas. This is likely the result of a combination of factors, including prey availability, and possibly the need to meet the energetic demands related to calving and lactation (Bernard and Hohn 1989), especially because Hauraki Gulf waters are used as a calving/nursery area (Stockin *et al.* 2008*a*). Understanding

the importance of Hauraki Gulf waters for feeding is of notable importance, particularly given the apparent susceptibility of foraging common dolphins to tour boat interactions (Stockin *et al*. 2008*b*).

This study provides evidence to suggest that the Hauraki Gulf is a unique habitat that offers significant opportunities for common dolphins, allowing them to spend less time traveling and searching for food and, consequently more time foraging, resting, breeding, and raising calves. The Hauraki Gulf is clearly an important ecosystem for common dolphins, thus wise management of its marine resources is critical given the increasing demands being placed on it by nearby urban population growth and increasing recreational use.

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