



Sequential foraging of dusky dolphins with an inspection of their prey distribution

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ABSTRACT

The aim of this work was to analyze the sequential foraging behavior of dusky dolphins (*Lagenorhynchus obscurus*). Foraging sequences were defined when more than two feeding bouts occur with a traveling bout between them. We hypothesized that traveling costs of searching for prey patches were related to the time spent feeding on a patch. In addition, the distribution and seasonal variation of anchovy schools were studied in the area to better understand dolphins' behavior. We observed dolphins from a research vessel from 2001 to 2007, and recorded their location and behavior. Anchovy data were collected during two hydro-acoustic surveys. Dusky dolphin behaviors varied seasonally; they spent a greater proportion of time traveling and feeding in the warm season (Kruskal-Wallis: $H = 172.07$, $P < 0.01$). During the cold season dolphin groups were more likely to exhibit diving behavior and less surface feeding. We found a positive correlation between searching and foraging time ($r = 0.88$, $P = 0.019$), suggesting that the costs associated with searching were compensated by an increase in the energy intake during the foraging bout. There was an association between dusky dolphin and anchovy distribution, in that they co-varied spatially and seasonally.

Key words: foraging strategy, foraging sequence, *Lagenorhynchus obscurus*, dusky dolphins, anchovies, Patagonia.

To cope with the high uncertainty associated with prey distribution and abundance, marine top predators have developed complex foraging strategies in heterogeneous environments (Russell *et al.* 1992, Viswanathan *et al.* 1996, Fauchald 1999, Pinaud and Weimerskirch 2005, Benhamou 2007). Foraging theory predicts that individuals, when searching, selecting, and eating food, choose those

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behaviors that allow them to get the greatest benefit with minimal effort and risk (Stephens and Krebs 1986, Krebs and Davies 1993). Within this theoretical framework, Charnov (1976) developed the marginal value theorem or the patch model. This model assumes that the forager encounters patches of food one after the other (sequential encounter) assuming that foraging consists of many repetitions of the following sequence: search-encounter-decide. Within this model the individual should decide how long to stay in a patch to maximize the long term average rate of energy intake. Considering some restrictive assumptions (all patches have the same gain function and search costs are zero), the marginal value theorem shows that the optimal residence time depends on travel to the patch time. When travel time is long, residence time is long and *vice versa* (Stephens and Krebs 1986).

The relationship between search patterns and the distribution of food has rarely been documented for large free-ranging animals (Ward and Saltz 1994, Mårell *et al.* 2002). In marine ecosystems, the distribution of fish prey is poorly known at small temporal and spatial scales, which makes the comparison between predator searching effort and prey density extremely difficult. Prey distribution and dynamics have strong effects on the foraging behavior of marine predators. The amount of work, and therefore energy expenditure that an animal invests in locating prey likely varies as a function of the energy content, availability, and location of the individual prey items (Stephens and Krebs 1986). Prey availability varies as a function of its density and its distribution in the environment.

Experiments that manipulate prey resources are difficult to carry out in the pelagic environment, therefore spatial and temporal variation in prey and predator distributions can be examined to provide insights into their interactions (Benoit-Bird and Au 2003, Benoit-Bird *et al.* 2004). Analysis of predator behaviors and prey distribution can improve our understanding of the foraging strategies of marine predators. Entire foraging sequences are relatively easy to obtain for terrestrial animals (*e.g.*, Clarke *et al.* 1995), allowing researchers to discriminate between feeding and searching behaviors. Among marine animals, foraging sequences have been more difficult to observe (but see Miller *et al.* 1995, Nowacek 2002).

Dusky dolphins (*Lagenorhynchus obscurus*) are small delphinids that inhabit select areas of coastal temperate waters in the Southern Hemisphere. They are semipelagic top predators that exhibit great behavioral flexibility in foraging. Off Argentina, dusky dolphins primarily feed on schooling southern anchovy (*Engraulis anchoita*), which they hunt cooperatively at the surface, during the day (Würsig and Würsig 1980, Degradi *et al.* 2008). However, other species, such as juvenile common hake (*Merluccius hubbsi*) and squids (Argentine short-fin squid, *Illex argentinus*, Patagonian long-fin squid, *Loligo gahi*, and South American long-fin squid, *Loligo sanpaulensis*), were also recorded in their diet (Koen Alonso *et al.* 1998, Romero *et al.* 2012). Dolphin groups at times join together during foraging, with feeding lasting for several hours.

As part of a long-term research program in Golfo Nuevo, northern Patagonia, behavioral sequences of dusky dolphins foraging during daylight hours were described (Vaughn *et al.* 2010). Within these sequences, dolphins alternate feeding bouts with traveling bouts in long sequences. This behavior may be a foraging tactic related to prey distribution, whereby dolphins find a prey patch, feed on it, and then move to the next patch.

The aim of this work was to analyze the sequential foraging behavior of dusky dolphins. We hypothesized that traveling costs of searching for prey patches were related to the time spent feeding on a patch. This hypothesized relationship was tested at two spatial scales: (1) At a small spatial scale: if traveling bouts within the foraging sequence are searching bouts, one might expect that, in a given sequence, the more time dolphins spend traveling, the more time they will spend feeding subsequently. (2) At a larger spatial scale: dolphins move to areas with high concentrations of prey and then start feeding. Based on these assumptions, we hypothesized that the more time dolphins spent in a traveling bout before the foraging sequence started, the longer the sequence duration would be. In addition, the distribution and seasonal variation of anchovy schools were studied in the area to better understand dolphin foraging sequences.

METHODS

Study Area

Golfo Nuevo (42°20'–42°50'S, 64°20'–65°00'W; Fig. 2) is located in northern Patagonia, Argentina. It is surrounded by Península Valdés, a protected area that was declared a World Heritage Site by the UNESCO (United Nations Educational, Scientific, and Cultural Organization) in 1999. The gulf is a semi-closed basin approximately 70 km long and 60 km wide with a total area of 2,500 km². The average depth is 80 m with a maximum depth of 184 m (Mouzo *et al.* 1978). The mouth of the gulf is 16 km long and connects to the Atlantic Ocean by shallow waters with an average depth of 44 m (Mouzo *et al.* 1978).

We define two seasons (cold and warm) in relation to the sea water temperature. During the warm season (November–April), Golfo Nuevo is strongly stratified both vertically (18°C at surface and 11°C at bottom) and horizontally, with lower temperatures occurring along the southern and northern coasts (16°C) and higher temperatures occurring in the central area of the gulf (18°C–19°C). In the cold season (May–October) the water is mixed and the temperature is homogeneous both vertically (12°C both at the surface and the bottom) and horizontally (11°C–13°C both in the line coast and in the central area of the gulf) (Rivas and Ripa 1989, Garaffo *et al.* 2010).

Dolphin Data

Random transects were surveyed onboard a research vessel from 2001 to 2007. Three research vessels were used: a 6 m fiberglass boat with a 50 hp outboard engine from 2001 to 2003, a 7 m fiberglass boat with a 105 hp outboard engine, and an inflatable boat of 6 m with a 90 hp outboard engine from 2004 to 2007. One survey was completed each day between 0800 and 2000. The mean duration of surveys was 5:23 ± 1 SD h:min (range = 1:30–9:00); the duration was determined by sea state and weather conditions (Beaufort sea state ≤ 3). For behavioral data collection, a group of dolphins was defined as any collection of individuals located in close proximity (<10 m) to one another (Smolker *et al.* 1992).

To minimize our potential impact on the dolphins' behavior, each group was approached slowly, from the side and rear, with the vessel moving in the same direction as the animals. Dolphins were followed at a constant distance of about

100 m, with minimal changes in vessel heading and speed. When a group of dolphins was sighted their size, predominant activity, and location were recorded. Groups were classified into the following arbitrary size categories: <10, 10–20, 21–50, 51–70, 71–100, and >100 individuals. The predominant activity or “behavioral state” was defined as the activity in which >50% of group members were engaged; for our study population, typically >90% of the animals in a group were engaged in the same activity, indicating that this form of sampling provided a robust measure of the behavior of group members. Six predominant activities, diving, feeding, milling, resting, socializing, and traveling were used to categorize behavioral state (Table 1). During behavioral sampling, group members were observed continuously as long as possible, and the predominant activity was recorded at 2 min intervals using an instantaneous sampling protocol (Altmann 1974). The location of the group was also recorded every 2 min by a Global Positional System and stored as a track file.

Activity Pattern Analysis

For activity patterns analyses each dolphin group-follow was considered an independent observation. Dusky dolphins are characterized by a fluid, fission–fusion society and their associations are not static over time (Markowitz *et al.* 2004). As a result, groups sighted on different days were considered distinct. When new dolphins joined the focal group or the group split, the resulting collection of individuals was considered a new group. Only one group per day was considered in the statistics analysis. Because behavior at consecutive 2 min intervals was not independent, the proportion of time spent in each of the six defined activities was

Table 1. Behavioral states or activities of dusky dolphin groups in Golfo Nuevo.

| Activity | Description |
|-------------|---|
| Feeding | Dolphins move fast, diving and emerging in all directions. At times it is possible to see dolphins harassing fish, fish jumping out of water, and marine birds like terns, gulls, albatrosses, giant petrels, shearwaters, cormorants, jaegers, and others, feeding at the same time. Dolphins move fast but the group does not change location. Two types of feeding: <i>feeding in sequences (F)</i> , when a feeding bout occurred in a foraging sequence and <i>isolated feeding</i> when a feeding bout occurred before or after a nontraveling activity. |
| Traveling | Persistent movement, with all group members swimming in the same direction. Two types of traveling bouts: traveling bouts following any activity except feeding (<i>T'</i>), and traveling bouts between two feeding bouts (<i>T</i>). |
| Socializing | Frequent interactions between two or more individuals, usually in the form of body contact accompanied by high-speed movements, frequent changes in direction. Aerial displays such as leaps, tail-over-head leaps, backslap, headslaps, and tailslaps are common. |
| Resting | Low level of activity, with individuals remaining stationary, at times floating motionless on the surface, with occasional slow forward movement. |
| Milling | Low-speed movement with frequent changes in direction, resulting in little overall directional movement by the group. |
| Diving | Entire dolphin group submerged under water in a coordinated movement, presumably encountering prey. |

calculated from each group-follow. The nonparametric Kruskal-Wallis test was used to assess differences in activities among cold and warm seasons. Nonparametric tests were selected because assumptions regarding normality and homogeneity of variance between samples were not met and because the existence of outliers made the median more representative than the mean for these samples (Lehner 1998).

Foraging Sequences Analysis

A foraging sequence was defined by at least two feeding bouts (F) occurring with a traveling bout (T) between them, and was completed when an activity different than traveling occurred after a feeding bout. A bout was defined as a period of time in which a single behavioral state occurred (Martin and Bateson 1993). A feeding bout was distinguished as the set of consecutive 2 min intervals in which feeding was recorded as the behavioral state. In a similar way, a traveling bout was defined as the set of consecutive 2 min intervals in which traveling was recorded. The duration and distance dolphins moved during a bout and during the whole sequence were determined.

The relationship between time traveling and time feeding was analyzed at two spatial scales. A smaller scale was defined taking into account the distance dolphins moved during a feeding bout within a sequence (mean = 571 m, SD = 353 m, $n = 37$) and a larger spatial scale was defined considering the distance dolphins moved during the whole foraging sequence (mean = 3,724 m, SD = 2,965 m, $n = 37$). A Spearman correlation was used to test the relationship between the time in consecutive feeding and traveling bouts within a sequence, and to test the correlation between the time dolphins spent in a traveling bout before foraging (T') and the whole foraging sequence ($T + F$).

Prey Distribution Data

Two hydro-acoustic surveys were carried out during 2007. A total distance of 99 and 120 nmi were surveyed during the cold season (24–29 May) and the warm season (27 November–2 December), respectively. Weather conditions deteriorated during the first survey precluding the completion of some transects.

The acoustic sampling consisted of systematic zigzag transects (Fig. 1). A research vessel of 7 m with a 105 hp outboard engine was used for data collection. If during the acoustic route a group of dolphins was sighted, the track was abandoned and the group was followed to record behavioral data. At the end of observations the transect was continued at the same point where it was abandoned. Acoustic data sets were obtained using a portable echo sounder SIMRAD EY-500 operating a 38 kHz split beam transducer. The transmitted pulse duration was 1 ms and a wide bandwidth was used. The echo sounder was calibrated with standard targets following Foote *et al.* (1987). Data were collected continuously during between 0900 and 1900 local time and then stored on digital media for future processing and analysis. Interpretation of the echogram was performed by personnel experienced in using visual echo trace. Fish school data analysis was performed using EchoView (v.4.10.67).² Anchovy school density

²The latest version (5.2) is available from Myriax Software Pty. Ltd., Hobart, Tasmania, Australia.

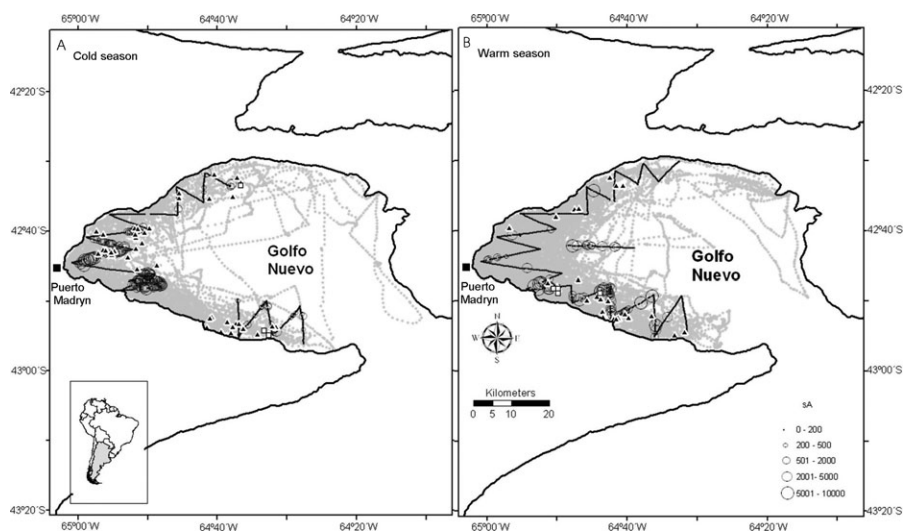


Figure 1. Dolphin and anchovy locations recorded during (A) cold season and (B) warm season, in the study area. Black triangles are dolphin sightings between 2001 and 2006 and white squares are dolphins sightings of 2007; size of gray circles is proportional to the square root of the sound scattering values (sA) assigned to anchovy schools; black lines show the transect followed during anchovy surveys and gray dotted lines represent the random transects traveled during dolphin surveys.

was calculated using the echo-integration method (MacLennan and Simmonds 1992). The sound scattering values (sA) assigned to anchovy were obtained from the analysis of the echograms in which regions were defined for each of the registered schools. A minimum threshold was established at -70 dB. In order to show the horizontal distribution of the echo-integration values of anchovy an ESDU (Elementary Sampling Distance Unit) was set at 0.1 nmi.

The shape, density, and location in the water column of each school were obtained. The school boundaries were determined using the algorithm provided in the school program module of EchoView. Some school descriptors were extracted, and grouped into energetic (sA), morphological (length, height, perimeter, area, volume), and bathymetric (depth) categories. All morphological measurements were corrected for beam width effects (Diner 2001). In addition, distances between the anchovy schools were calculated using Geographic Information System tools (GIS).

Prey and Predator Analysis

For spatial analysis the location of dolphin groups and anchovy schools was overlapped with a grid characterized by depth data. The location of a dolphin group was considered as the position at which a group was first sighted. The whole data set of dolphin groups sighted was used (2001–2007). Anchovy data were obtained from acoustic surveys performed in 2007 as explained above.

A preliminary assessment of whether depth and distance from shore are independent was done using data obtained from Nautical charts (H-218, 1:110,000,

Naval Hydrographic Service) (Mouzo *et al.* 1978). A grid of 1.5×1.5 km was constructed for the study area. A GIS was used to integrate the nautical chart with the grid. Each cell of the grid was characterized by depth and distance from shore. Mean depth was calculated by averaging values of depth. Distance from shore was calculated as distance from the central point of each cell to the closest line coast. Dolphins and anchovy locations were overlapped on the grid. A Kruskal-Wallis test was used to test for statistical differences in bottom depth between dolphins and anchovy locations as well as temporal variation. In all cases, a significance level of $\alpha = 0.05$ was used (Siegel and Castellan 1995, Conover 1999).

RESULTS

Dolphin Groups' Activity Pattern

A total of 235 random surveys were conducted during this study (Table 2). During the whole period 263 groups were reordered. Group size varied between the seasons. During the warm season more than 40% of groups were larger than 20 animals while during the cold season they were only observed 20% of this and most of them were less than 10 individuals ($\chi^2_5 = 11.45$, $P < 0.05$).

Behavioral data were recorded for 184 groups during the warm season and 45 during the cold season. Dusky dolphins showed seasonal variation in their behaviors (Kruskal-Wallis: $H = 172.07$, $P < 0.01$, $n_{\text{warm}} = 69$, $n_{\text{cold}} = 26$). They spent a greater proportion of time traveling and feeding in the warm season, and a greater proportion of time milling and resting in the cold season (Fig. 2). Additionally, feeding at the surface decreased during the cold season ($\chi^2_2 = 21.32$, $P < 0.001$) while feeding behaviors were almost entirely at the surface in the warm season (Fig. 3).

Dolphin Foraging Sequence

Forty-one percent of dolphin groups that were feeding showed traveling-feeding sequences. The average duration of foraging sequences was 42 min (range = 8–134 min). Sequences contained 2–6 feeding bouts. Within a foraging sequence, there was no relationship between the duration of consecutive traveling (T) and feeding (F) bouts (Spearman rank correlation: $r = 0.068$, $P = 0.58$, $n = 70$). However, a positive correlation was found between time spent traveling

Table 2. Summary of the effort during the dolphin groups survey in Golfo Nuevo.

| Year | Survey hours | Hours with dolphins | No. of groups |
|------|--------------|---------------------|---------------|
| 2001 | 132 | 56 | 59 |
| 2002 | 148 | 20 | 55 |
| 2003 | 133 | 25 | 39 |
| 2004 | 143 | 29 | 39 |
| 2005 | 221 | 32 | 74 |
| 2006 | 89 | 13 | 27 |
| 2007 | 135 | 13 | 19 |

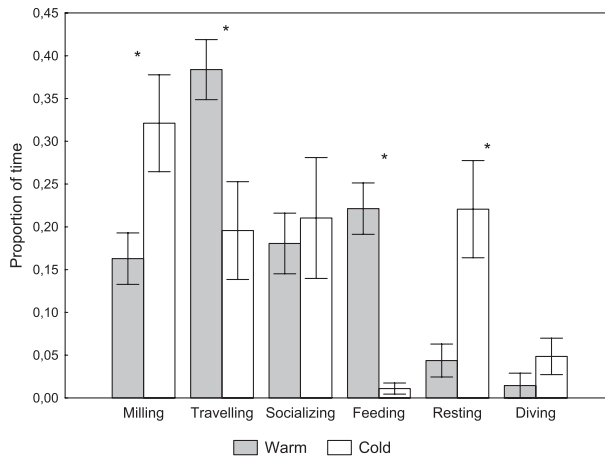


Figure 2. Proportion of time dusky dolphins exhibited different behaviors during the seasons. Bars represent mean values; lines represent standard errors for these means. Significant differences are indicated by asterisks.

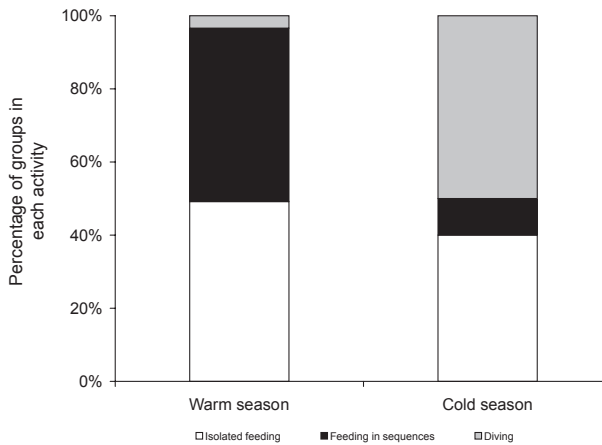


Figure 3. Proportion of dolphin groups recorded in different foraging behaviors during warm and cold seasons.

before a foraging sequence (T'') and time spent in the complete foraging sequence (Spearman rank correlation: $r = 0.88$, $P = 0.019$, $n = 6$, Fig. 4).

Anchovy's Schools and Their Relation with Dolphins' Spatial Distribution

Although anchovy data came from one year we assumed that the variation among years was negligible. It is expected that anchovy distribution changes with sea surface temperature (SST) and concentration of chlorophyll *a* (chlorophyll) (Bakun and Parrish 1991, Hansen *et al.* 2001). In order to check for any possible variation in these environmental variables along the study period, SST and chlorophyll data were inspected. Mean SST for each month was extracted

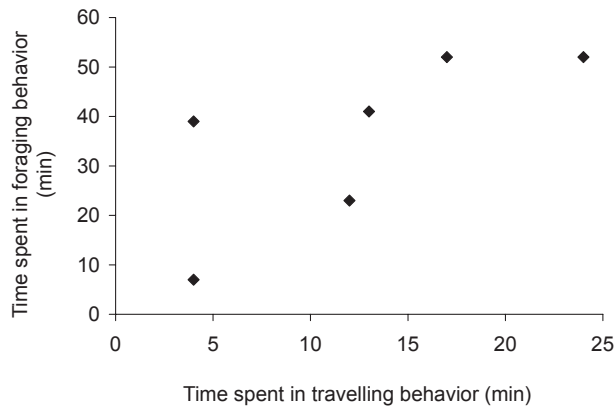


Figure 4. Relationship between the time that dusky dolphin groups spent traveling before a sequence, and time spent foraging (considering the whole sequence, $n = 6$).

from satellite images without clouds (NOAA Advanced Very High Resolution Radiometer, <http://www.conae.gov.ar>) at a spatial resolution 1.1 km^2 and from the Giovanni online data system, developed and maintained by the NASA GES DISC. In addition, mean concentration of chlorophyll a (mg/m^3) data for each month were extracted from the Giovanni online data system from 2001 to 2007. SeaWiFS images were used by this source. The monthly variation pattern of sst was kept over the years (ANCOVA, $P_{\text{months}} < 0.001$ and $P_{\text{years}} > 0.84$) as were chlorophyll values. Neither showed changes among the study period (ANCOVA, $P_{\text{months}} > 0.40$ and $P_{\text{years}} > 0.37$). Therefore we did not expect large changes in anchovy distribution among the years.

Anchovies were detected in both hydroacoustic surveys, 160 schools during the warm season, and 441 during the cold season, which were clumped in different areas of the gulf. The areas where dolphins and anchovies were sighted are shown in Figure 1. Although the area covered by the surveys was larger, dolphin groups were mostly found in the area covered during hydroacoustic surveys.

The analysis of the schools showed that during the cold season anchovy schools were larger and located deeper in the water column (Table 3). In addition, anchovy schools were acoustically denser (sA) and were found closer to each other in the warm than in the cold season (Table 3).

Spatial analysis showed that dolphins and anchovy locations varied between seasons. Both predator and prey were located in deeper waters during the cold season (Kruskal-Wallis: $H = 145.3$, $P < 0.001$, Fig. 5). We obtained the same results if we only used a data set of dolphins sighting in the same year that acoustic surveys were carried out (Kruskal-Wallis: $H = 114.5$, $P < 0.001$). Depth and distance from shore are correlated variables ($r = 0.82$, $P < 0.001$), therefore we only analyzed data relative to depth. During this season, dolphins were located in areas 68.3 m deep, 4.6 km from shore, while anchovies were located in areas 85 m deep and 5 km from shore. During the warm season dolphins were located in waters of 36.1 m deep and 2.5 km from shore while anchovies were located in waters 55 m deep and 3.7 km of distance from shore (Fig. 6).

Table 3. Mean values of each anchovy schools descriptors obtain in Golfo Nuevo during the surveys.

| School descriptor | Mean value | | Unit | P^a |
|-------------------|-------------|-------------|----------------------------------|--------|
| | Cold season | Warm season | | |
| Length | 41.68 | 29.41 | m | 0.0151 |
| Height | 10.99 | 10.13 | m | 0.1507 |
| Perimeter | 206.78 | 149.30 | m | 0.0246 |
| Area | 308.89 | 241.88 | m ² | 0.1730 |
| Volume | 2,570.39 | 2,298.18 | m ³ | 0.3677 |
| School depth | 52.15 | 23.78 | m | 0.0001 |
| sA | 618 | 1,340 | m ² /nmi ² | 0.0001 |
| Distance | 742 | 286 | m | 0.0001 |

^a P -values are the probabilities obtained from the comparison of two independent samples (Mann-Whitney U test, cold *vs.* warm season).

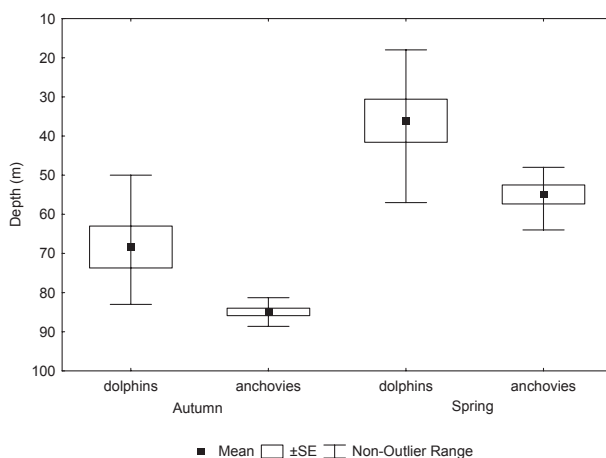


Figure 5. Bottom depth where dolphin groups and anchovy schools were found during both seasons.

DISCUSSION

Seasonal variation in activity budgets was observed for dusky dolphins. Dolphins spent a greater proportion of time traveling and feeding at the water surface during the warm season, while they spent a greater proportion of time diving during the cold season. The only data available on prey distribution obtained in the present work were from 2007 and hence our results cannot be generalized to the whole study period. Results obtained showed that anchovies and dolphins moved to deeper waters in the cold season, at the same time anchovies are located deeper in the water column. This result suggests that dolphins are following their prey, moving accordingly their location. During the cold season anchovy were concentrated in a small portion of the gulf (in front of Puerto Madryn coast), while during the warm season they were

distributed over a larger area (along the southwest coast of the gulf, Fig. 1). These results were concordant with the habitat use pattern described for dusky dolphins (Garaffo *et al.* 2007, 2010). During the warm season dusky dolphins used larger areas, staying less time in a particular location, but for the rest of the year, they were more concentrated in a smaller area.

Although the main feeding strategy of dusky dolphins in Patagonia is surface feeding, we would expect that during the cold season dolphins would use alternative feeding tactics that allow them to get more energy at lower costs. An association between diving and milling behavior was observed during this season (Degrati *et al.* 2012) suggesting that feeding at depth could be this alternative strategy; however, the energy budgets that these activities represent in the survival and reproduction of each individual is unknown. Marine mammals that feed within the water column must interrupt foraging activity to go to surface to breathe, decreasing the time available for food intake. Feeding at the surface would be advantageous to dolphins, but in situations where prey are not accessible at the surface, an alternative tactics must be used. In Admiralty Bay (New Zealand), dusky dolphins exhibit temporal changes in their feeding tactics, possibly in response to a change in prey species or behavior. From August to November dolphins herd small schools of fish to the surface, while from May through July, they feed on mobile prey at depth (Vaughn *et al.* 2007). Some of these same dolphins also forage at night on the deep scattering layer (Benoit-Bird *et al.* 2004, Markowitz *et al.* 2004).

According to foraging theory, it is expected that patch residence time depends on travel time (Stephens and Krebs 1986). When we considered an entire sequence as a foraging episode ($F + T$ bouts), we found a positive correlation between searching (T) and foraging time. On a larger spatial scale dusky dolphins move to areas of large concentration of prey. Within such broad scale areas, dolphins start foraging, and then alternate feeding and traveling bouts. In this case, the time spent by dolphins in traveling would be part of the handling time of prey or the displacement between schools within the foraging area. Therefore, there is no single characteristic scale that describes foraging tactics, but rather several scales that may reveal different processes (Fauchald *et al.* 2000).

In Golfo Nuevo dusky dolphin group size changed with the season. Larger groups were found in the warm season. This variation could be a function of the foraging tactic in response to the prey distribution. Dusky dolphins are group foragers and the amount of energy gained will depend on the number of individuals into the group. Having to sharing food resources with other group members causes within-group feeding competition, which reduces the foraging success of individuals within the group (Janson 1988, Janson and van Schaik 1988). Within group feeding competition increases with increasing group size (Janson and Goldsmith 1995, Steenbeek and van Schaik 2001). However, individuals in a group have some benefits in terms of the efficient discovery of food patches (Clark and Mangel 1986) and protection from predators. In addition, Würsig and Würsig (1980) reported that dusky dolphin appear to have more success when working together driving schooling fish to the surface, since they can contain "prey balls" more effectively. These authors also reported that dusky dolphin groups pay close attention to each other, with one group finding prey and another group joining in (Würsig and Würsig 1980). During our study, we observed the same pattern, but as explained in the methodology,

when new dolphins joined the focal group or the group split, the resulting collection of individuals was considered a new group in the statistical analyses. In our work, foraging sequence data were not analyzed in relation to group size because of the small sample size. However our results help to better understand foraging behaviors of pelagic dolphins and serve as a starting point for the more complex studies about the functional relationship between predator performance and prey distribution and abundance. This is critical to understanding the dynamics of trophic interactions and pathways of energy flow in pelagic marine ecosystems.

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