ARTICLE

Diving for food: a switch of foraging strategy of dusky dolphins in Argentina

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Abstract During winter, dusky dolphins (*Lagenorhynchus obscurus*) were observed in coordinated diving apparently in a feeding activity, contrasting with the surface feeding observed during summer. The aim of this work consisted in analyzing the diving activity as an alternative foraging strategy in Argentine dusky dolphins, based on sequential analysis. The study area was Golfo Nuevo, located in Northern Patagonia, Argentina. Random transects were surveyed by a research boat from 2001 to 2007. During behavioral sampling, group members were observed continuously and the predominant activity was recorded at 2-min intervals. Six predominant activities were identified. Each 2-min interval was classified according to the activity at the previous interval (preceding activity), the activity at the interval (following activity), and the season (cold or warm). Z scores were calculated and then used to construct sequence diagrams. An association between diving and milling behavior was observed. This could be another foraging tactics different to the surface foraging sequences and this could be related with the distribution or abundance of preys.

Introduction

The dusky dolphin (*Lagenorhynchus obscurus*) is a small dolphin inhabiting coastal temperate waters in the southern hemisphere. However, habitats and resources utilized by dusky dolphins vary widely along the distribution range. In Kaikoura, New Zealand (42°25′S, 173°42′E), dusky dolphins feed at night during the winter, mainly on fish (Myctophidae, *Macruronus novaezalandiae*, *Physiculus bacchus* and *Merluccius australis*) and squid (*Nototodarus* sp. and *Todaroides* sp.) associated with the deep scattering layer. In summer, they migrate northwards to Admiralty Bay (40°56′S, 173°53′E, a distance of approximately 200 km) and feed during the day on sardines (*Sardinops neopilchardus*; Benoit-Bird et al. 2004). From May to July, dolphins fed on mobile prey at depth, while from August to November they herd small schools of fish to the surface (Vaughn et al. 2007).

In Argentina, at a similar latitude, in Golfo San José and Golfo Nuevo (42°20′–42°50′S, 65°W), dusky dolphins primarily feed on schooling southern anchovy (*Engraulis anchoita*), which they hunt cooperatively during the day (Würsig and Würsig 1980; Degrati et al. 2008). Dolphin groups join up, and large prey schools may attract up to 300 dolphins and over 1,000 birds. In Golfo Nuevo, surface feeding bouts alternate with traveling bouts in long sequences (Vaughn et al. 2010). This would be a foraging strategy related to prey distribution, where dolphins find a prey patch, feed on it, and then move to the next patch (Degrati 2011).

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Although the main dusky dolphin prey is anchovy, other species such as juvenile hake (*Merluccius hubbsi*) and common, Patagonian, and South American long-fin squid, (*Illex argentinus*, *Loligo gahi*, and *Loligo sanpaulensis*), have also been recorded in their diet (Koen Alonso et al. 1998; Romero et al. 2011). In Golfo San José, Würsig and Würsig (1980) noted that surface feeding occurred less often in winter than in other seasons of the year. As a result, these authors suggest that dolphins were feeding on other prey and more individually during the winter in this area. In the North Patagonia ecosystem, the Argentine anchovy and the common and the South American long-fin squid are the most important pelagic resources (Brunetti et al. 1998; Barón and Ré 2002; Hansen et al. 2009). Hence, it seems that dusky dolphins forage opportunistically on available prey species (Romero et al. 2011).

Several studies on dusky dolphins' behavior have been carried on since 2001 in Golfo Nuevo. The main goal of these studies was to describe and quantify the activity budget of dolphins, mainly during summer (Degrati et al. 2008). More recent studies extended throughout the whole year. During winter, dusky dolphins were observed in coordinated diving apparently in a feeding activity, contrasting with the surface feeding observed during summer. Therefore, the aim of this work consisted in analyzing the diving activity as an alternative foraging strategy in Argentine dusky dolphins, based on sequential analysis, and its spatial and temporal variation.

Materials and methods

Study area

The study area was Golfo Nuevo (42°20′–42°50′S, 64°20′–65°00′W), located in Northern Patagonia, Argentina (Fig. 1). This gulf as well as Golfo San José is surrounded by Península Valdés, a protected area that was declared a World Heritage Site by UNESCO (United Nations Educational, Scientific, and Cultural Organization) in 1999. The surface of Golfo Nuevo is 2,500 km^2 and its maximum depth is 184 m (Mouzo et al. 1978). It is a semi-enclosed basin of approximately 70 km length and 60 km width. It is connected to the Atlantic Ocean through a shallow sill of an average depth of 44 m and a length of 16 km (Mouzo et al. 1978).

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 (18–19 °C). In the cold season (May–October), the waters are mixed and the temperature
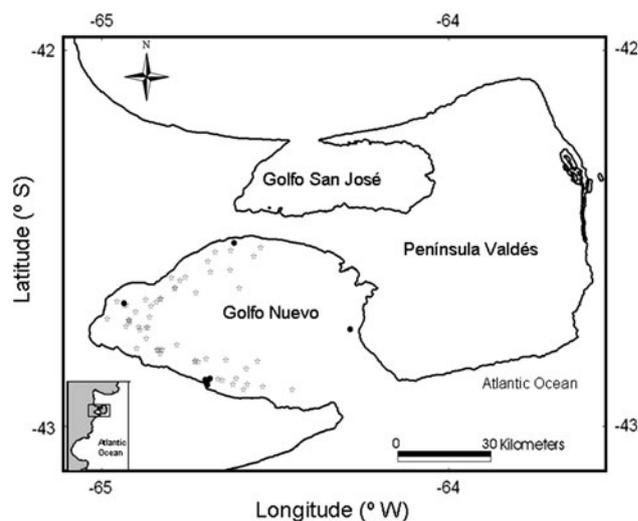

Fig. 1 The study area in Golfo Nuevo, Argentina. *Black points* represent groups of dusky dolphins (*Lagenorhynchus obscurus*) in diving behavior and *gray stars* represent groups in surface foraging sequences

is homogeneous vertically (12 °C both at surface and the bottom) and horizontally (11–13 °C, both at the coast and the middle area) (Rivas and Ripa 1989; Garaffo et al. 2010).

Behavioral data collection

The area was surveyed by means of a research boat from 2001 to 2007. One survey was completed each day between 0800 and 2000 hours. A total of 235 random surveys were conducted during this study. Most of the surveys were conducted by the first authors. The mean duration of trips was 5:23 ± SD 1 h (range, 1:30–9 h), the duration was determined by sea and weather conditions (Beaufort Sea state <4). A nonsystematic search method was used to locate dolphins, with a search speed of 10–12 knots. Once a group of dolphins was found, the transect was abandoned and the group was followed as long as possible. The location of dolphin groups was recorded by a GPS at 2-min intervals during the whole tracking. 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. No group was sampled more than once per day. When more than 1 group was found during the same trip, each was considered an independent sample. When new dolphins joined the focal group or the group split, the resulting collection of individuals was considered a new group. Thus, although we attempted to maximize the independence of our behavioral data, it is possible that some individuals were observed more than once in the same day. Bejder and Samuels (2003) indicated that the

Table 1 Behavioral states or activities of dusky dolphin (*Lagenorhynchus obscurus*) 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. This activity takes place at the surface or at low depth; therefore, we sometimes use the term feeding at the surface (FS)
Traveling	Persistent movement, with all group members swimming in the same direction
Socializing	Frequent interactions between 2 or more individuals, usually in the form of body contact accompanied by high-speed movements, frequent changes in direction, and aerial displays such as leaps, tail-over-head leaps, backslaps, headslaps, and tailslaps
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. No surface behaviors and no apparent physical contact between individuals, usually staying close to the surface
Diving	Entire dolphin group submerged under water in a coordinated movement, presumably encountering prey

group-follow protocol may result in over- or underestimation of the frequency of specific states or events. Bias could occur because observers are more likely to start or to continue following groups engaging in certain kinds of behavior (Whitehead 2004). At the same time, bias may result if, after group composition changes (e.g., a group fissions), there is a tendency to follow the more active subgroup (Mann 1999). To minimize these biases, we began group-follows after a collection of individuals was encountered, regardless of their current behavior; all group-follows continued until weather conditions became prohibitive or the animals were no longer visible. When a group split, the new group to be followed was selected randomly.

For behavioral data collection and analysis, a group was defined as any collection of individuals located in close proximity (<10 m) from one another (Smolker et al. 1992). The predominant activity of the focal group (Mann 1999), 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. During behavioral sampling, group members were observed continuously and the predominant activity was recorded at 2-min intervals using an instantaneous sampling protocol (Altmann 1974). Six predominant activities were identified (Table 1).

Data analysis

Behavioral data recorded by group-follows were treated as behavioral sequences, considering them as sequences or chains of behavioral states. Two-event sequences were constructed considering that consecutive states cannot repeat. In this study, six behavioral states were considered corresponding to activities defined previously. Thus, there were 30 (6 × 5) possible two-event sequences. Chains from different groups were pooled and only separated by season. Two seasons were considered, cold and warm, based on previous knowledge. For each group-follow, 2-min intervals were classified according to the activity at the previous interval (preceding activity P), the activity at the interval (following activity F), and the season (cold or warm). The frequency for each two-event sequence was computed by counting the number of intervals the activity F was preceded by the activity P. These frequencies were arranged in separate tables, one for each season, where rows represent the preceding activity and columns represent the following activity (Table 2).

The z score statistic was used to determine if particular behavior transitions occur significantly more or less frequently than expected by chance (Bakeman and Gotman 1997). In this study, z scores were used as an index of strength of the sequential dependence of two behaviors. They were calculated by dividing the difference between observed and expected frequency by their standard deviation, following the formula (Bakeman and Gotman 1997):

$$Z_{PF} = \frac{x_{PF} - m_{PF}}{\sqrt{m_{PF}(1 - p_{P+})(1 - p_{+F})}}$$

where x_{PF} is the sum of the observed frequencies in the given row, m_{PF} is an estimate of the expected frequency, p_{P+} is the sum of the observed frequencies in the given row divided by the total number of tallies in the table, and p_{+F} is the sum of the observed frequencies in the target columns divided by the total number of tallies in the table. Values of z score >1.96 (or <−1.96) are considered statistically significant at the 0.05 probability level (Bakeman and Gotman 1997). The z score was then used to construct sequence diagrams (Slooten 1994).

To relate dolphins feeding tactics to depth and distance from shore, nautical charts (H-218, 1:110,000, Naval Hydrographic Service) containing depth data (Mouzo et al.

Table 2 Observed frequencies for two-event sequences for which consecutive code cannot repeat

Preceding activity	Following activity						
	Feeding	Diving	Resting	Milling	Socializing	Travelling	Total
Warm season							
Feeding	–	0	3	25	17	152	197
Diving	0	–	0	1	0	0	1
Resting	0	0	–	20	4	26	50
Milling	27	1	26	–	19	90	163
Socializing	15	0	2	12	–	72	101
Travelling	123	0	22	113	59	–	317
Total	165	1	53	171	99	340	829
Cold season							
Feeding	–	0	0	2	0	11	13
Diving	0	–	1	12	0	2	15
Resting	0	1	–	15	1	8	25
Milling	2	15	15	–	6	26	64
Socializing	1	0	0	6	–	6	13
Travelling	8	1	9	26	4	–	48
Total	11	17	25	61	11	53	178

1978) were used. A grid of 1.5×1.5 km was constructed for the study area. A Geographic Information System (GIS) was used to integrate the environmental data with a grid. Each cell of the grid was characterized by bottom depth and distance from shore. Mean depth was calculated by averaging values of depth. Distance from shore was calculated as the distance from the central point of each cell to the closest part of the coast. For each dolphins group, the position (in latitude and longitude) of the first 2-min interval, where a particular activity (feeding or diving) was recorded, was considered. Then these locations were overlapped with the grid. A Kruskal–Wallis H test was used to assess differences in depth and distance from shore between foraging tactics and the seasons. In all cases, a significance level of $\alpha = 0.05$ was used (Siegel and Castellan 1995; Conover 1999).

Results

During the whole study period, 227 groups were observed and followed, 183 and 44 in the warm and cold seasons, respectively. Almost half of these groups were involved in foraging activities during the behavioral sampling, 98 in the warm season and 15 in the cold season. Diving was recorded in 9 groups, 2 and 7 for each season, respectively. Groups were followed during totals of 3,678 and 823 2-min intervals during the warm and cold seasons, respectively. During the warm season, diving represents 0.1 % of the total number of intervals, while it represents 9.5 % during the cold season. On the other hand, surface feeding decreased from 20 to 6 % of sampled intervals. In both seasons, most of the groups observed diving were small (<10 dolphins) and the animals were in close proximity (<1 body length).

A total of 829 and 178 two-event sequences were sampled in the warm and cold seasons, respectively (Table 2). The sequence diagrams (Fig. 2a) revealed an association between feeding and traveling in both seasons, although during the warm season this association was stronger, as revealed by higher z score values. During the cold season, another association was observed (Fig. 2b), in which diving was related with milling.

Both depth and distance from shore where dolphins were observed changed depending on the foraging tactics (Kruskal–Wallis test, $H = 14.39$, $P < 0.01$ for depth, and $H = 18.91$, $P < 0.001$ for distance from shore). Diving occurred in shallower waters and closer to shore areas than surface feeding. This pattern is shown in both seasons (Fig. 3).

Discussion

This work reports seasonal variation in the behavioral pattern of dolphins related to feeding tactics. Behavioral sequences showed an association between diving and milling behavior, in addition to the traveling–feeding sequence previously reported. During milling, dolphins swim erratically possibly searching for prey, and once they

Fig. 2 Sequence diagrams for 2-min intervals between the preceding and following behaviors, showing all links with z score ≥2. *Numbers* are z score, and *arrow thickness* represents these values. **a** Warm season, n = 829, **b** cold season, n = 178. D diving, M milling, R resting, T traveling, S socializing, F feeding
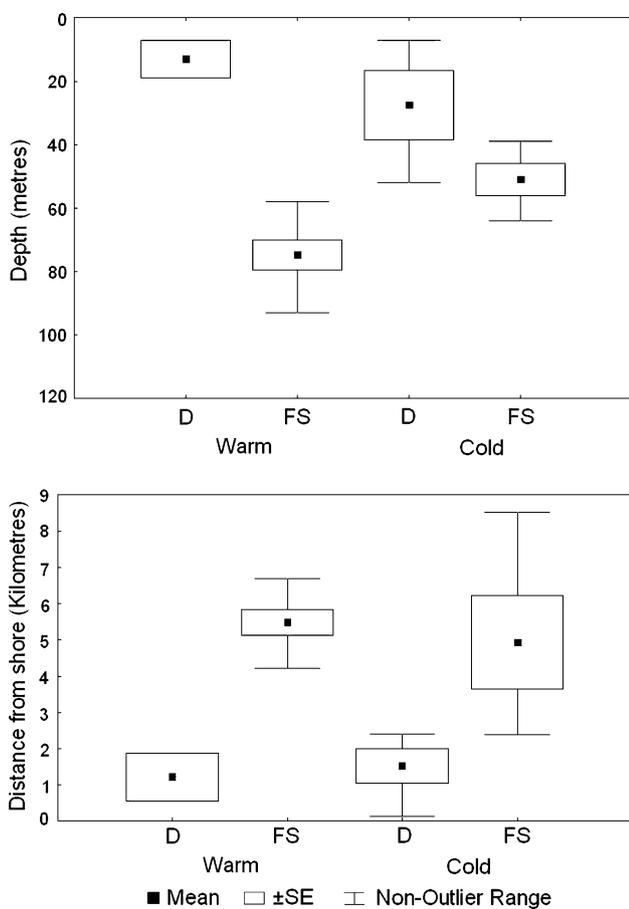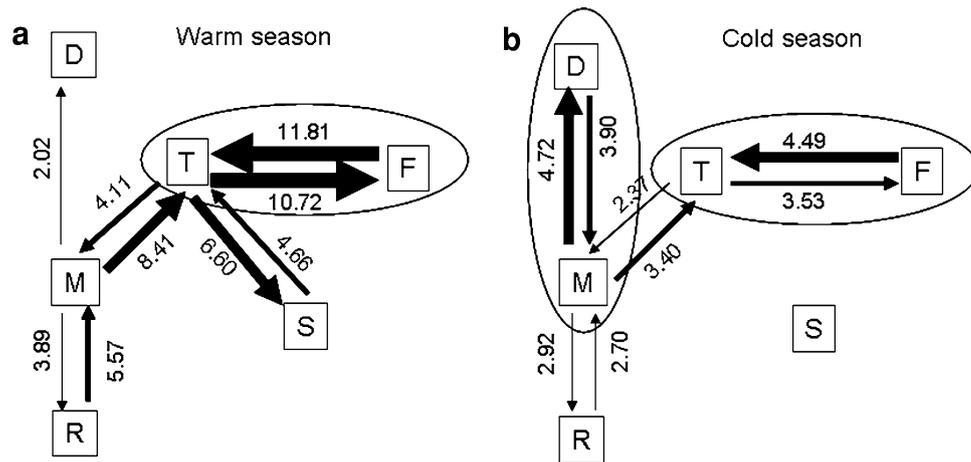

Fig. 3 Bottom depth (m) and distance from shore (km) where dolphins were observed in different foraging tactics for two seasons (warm and cold). *D* diving, *FS* feeding at the surface

with traveling bouts in long sequences. In the present study, prey were not surveyed at the same time that dolphins dived. However, some groups of shearwaters (*Puffinus gravis*) were observed submerging with the dolphins and then emerging with squid in their beaks. This could indicate that the inference of dolphins feeding activity would be accurate by this confirmation of available prey.

The sequence analysis shows that, during the warm season, dolphins mostly forage using a feeding–traveling sequence. However, in the cold season, a greater proportion of diving activity appeared and surface feeding decreased. Hydro-acoustic surveys of prey in the study area showed that, in the cold season, anchovy schools are widely dispersed and deeper in the water column (Degrati 2011). Then, dolphins would need more time traveling longer distances between prey patches, and would spend more energy to carry the school to the surface. It is expected that, during the cold season, dolphins explore an alternative strategy allowing them to get the required energy at lower costs than using anchovies. Squid would be the target, as the second more important prey in their diet (Koen Alonso et al. 1998), while diving could be the strategy to catch them.

Most dolphin groups that were recorded diving were observed on the west coast of the gulf (Fig. 1), at depths less than 50 m. In this area, Crespi-Abril et al. (2010) reported the presence of paralarvae and juveniles of squid (*Illex argentinus*, *Loligo sanpaulensis*) in near-shore waters. The paralarvae were found during the summer and autumn (warm season) at depths lesser than 30 m, while juveniles appear in September (cold season), which is also the season when diving behavior was observed in greater proportions. Both this and the observation of squid in the shearwaters' beaks, associated with diving dolphin groups, support the idea that, during diving, dolphins were feeding on squid.

find them, they dive to catch them. This could represent an alternative foraging tactic different to the foraging sequences that have been described previously (Vaughn et al. 2010; Degrati 2011), where feeding bouts alternate

Delphinids may change feeding tactics intra-annually owing to changes in prey abundance, distribution, or schooling behaviors (Bowen and Siniff 1999; Baird 2000; Ballance et al. 2006). Diving as a foraging strategy has been reported for other cetacean species like bottlenose dolphins (*Tursiops truncatus*) (Shane 1990; Acevedo-Gutierrez and Parker 2000) and tucuxi (*Sotalia fluviatilis*) (Edwards and Schnell 2001). Dusky dolphins in New Zealand also show this feeding tactic (Benoit-Bird et al. 2004). In Golfo San José, Argentina, Würsig and Würsig (1980) suggested that dolphins were feeding below and not at the surface during winter, possibly on different prey, more individually, and in small groups near the shore. The results of this work are in concordance with this suggestion by Würsig and Würsig (1980), and proposes a foraging sequence of diving and milling as an alternative feeding tactic during the cold season. Nevertheless, a long-term study of dolphin activity patterns, simultaneously gathering prey and oceanographic data throughout the year, is necessary to better understand dolphin foraging tactics in Patagonia.

References

Acevedo-Gutierrez A, Parker N (2000) Surface behavior of bottlenose dolphins is related to spatial arrangement of prey. Mar Mamm Sci 16:287–298

Altmann J (1974) Observational study of behaviour: sampling methods. Behaviour 49:227–267

Bakeman R, Gotman JM (1997) Observing interaction. An introduction to sequential analysis, 2nd edn. Cambridge University Press, Cambridge

Baird RW (2000) The killer whale: foraging specializations and group hunting. In: Mann JC, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, pp 127–153

Ballance LT, Pitman RL, Fiedler PC (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. Prog Oceanogr 69:360–390

Barón PJ, Ré ME (2002) Reproductive cycle and population structure of *Loligo sanpaulensis* in the northeastern coast of Patagonia. Bull Mar Sci 71:175–186

Bejder L, Samuels A (2003) Evaluating impacts of nature based tourism on cetaceans. In: Gales N, Hindell M, Kirkwood R (eds) Marine mammals: fisheries, tourism and management. CSIRO, Collingwood, pp 229–256

Benoit-Bird KJ, Würsig B, McFadden CJ (2004) Dusky dolphin (*Lagenorhynchus obscurus*) foraging in two different habitats: active acoustic detection of dolphins and their prey. Mar Mamm Sci 20:215–231

Bowen WD, Siniff DB (1999) Distribution, population biology, and feeding ecology of marine mammals. In: Reynolds JE III, Rommel SA (eds) Biology of marine mammals. Smithsonian Institution, Washington, pp 423–484

Brunetti NE, Ivanovic M, Rossi G, Elena B, Pineda S (1998) Fishery biology and life history of *Illex argentinus*. In: Okutani T (ed) Paper to international symposium on large pelagic squid. Contributed Japan Marine Fishery Resources Research Center, Tokyo, pp 217–232

Crespi-Abril AC, Dellatorre F, Barón P (2010) On the presence of *Illex argentinu*s (Castellanos, 1960) (Cephalopoda: Ommastrephidae), paralarvae and juveniles in near-shore waters of Nuevo Gulf, Argentina. Lat Am J Aquat Res 38:297–301

Conover WJ (1999) Practical nonparametric statistics, 3rd edn. Wiley, New York

Degrati M, Dans SL, Pedraza SN, Crespo EA, Garaffo GV (2008) Diurnal behaviour of dusky dolphins, *Lagenorhynchus obscurus*, in Golfo Nuevo. J Mamm 89:1241–1247

Degrati M (2011) Patrón de actividad y estrategias de alimentación del delfín oscuro (*Lagenorhynchus obscurus*) en el norte de Patagonia. PhD thesis, Universidad Nacional del Comahue, Bariloche, Argentina

Edwards HH, Schnell GD (2001) Body length, swimming speed, dive duration, and coloration of the dolphin Tucuxi (*Sotalia fluviatilis*) in Nicaragua. Caribb J Sci 37:271–298

Garaffo GV, Dans SL, Crespo EA, Degrati M, Giudici P, Gagliardini A (2010) Dusky dolphins: modeling habitat selection. J Mamm 91:54–65

Hansen JE, Buratti CC, Garciarena AD (2009) Estado de la población de anchoíta (*Engraulis anchoita*) al sur de 41°S y estimación de capturas biológicamente aceptables en el año 2009. INIDEP Technical report 11/09, pp 1–16

Koen Alonso M, Crespo EA, García NA, Pedraza SN, Coscarella MA (1998) Diet of dusky dolphins, *Lagenorhynchus obscurus*, in waters off Patagonia, Argentina. Fish Bull 96:336–374

Mann J (1999) Behavioural sampling methods for cetaceans: a review and critique. Mar Mamm Sci 15:102–122

Markowitz T, Harlin A, Würsig B, McFadden C (2004) Dusky dolphin foraging habitat: overlap with aquaculture in New Zealand. Aquat Conserv Mar Freshw Ecosyst 14:133–149

Mouzo FH, Garza ML, Izquierdo JF, Zibecchi RO (1978) Rasgos de la geología submarina del Golfo Nuevo. Acta Oceanogr Argent 2:15–32

Rivas A, Ripa P (1989) Variación estacional de la estructura termo-halina de Golfo Nuevo, Argentina. Geofís Int 28:3–23

Romero MA, Dans SL, García NA, Svendsen GM, González R, Crespo EA (2011) Feeding habits of two sympatric dolphin species off North Patagonia, Argentina. Mar Mamm Sci. doi: 10.1111/j.1748-7692.2011.00477.x

Shane SH (1990) Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studding dolphin behavior. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphins. Academic, San Diego, pp 541–558

Siegel S, Castellan NJ (1995) Estadística no paramétrica aplicada a la ciencia de la conducta, 4th edn. Editorial Trillas, Distrito Federal, México

Slooten E (1994) Behavior of Hector's dolphin: classifying behaviour by sequence analysis. J Mamm 75:956–964

Smolker RA, Richards AF, Connor RC, Pepper JW (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38–69

Vaughn RL, Shelton DS, Timm LL, Watson LA, Würsig B (2007) Dusky dolphin (*Lagenorhynchus obscurus*) feeding tactics and multi-species associations. N Z J Mar Freshw Res 41:391–400

Vaughn RL, Degrati M, McFadden CJ (2010) Dusky dolphins foraging in daylight. In: Würsig B, Würsig M (eds) The dusky dolphins. Masters acrobat off different shores. Academic Press, New York, pp 115–132

Whitehead HJ (2004) The group strikes back; follow protocols for behavioral research on cetaceans. Mar Mamm Sci 20:664–670

Würsig B, Würsig M (1980) Behaviour and ecology of dusky dolphins, *Lagenorhynchus obscurus*, in the South Atlantic. Fish Bull 77:871–890