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RESEARCH ARTICLE

Habitat use by dusky dolphin in patagonia: how predictable is their location?

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Abstract Off Patagonian coasts, Argentina, the dusky dolphin is one of the most common small cetaceans. This species is the aim of newly developed watching activities during summer in Golfo Nuevo. However, the real occurrence and movement pattern are unknown. The objectives of this work were to investigate the predictability of dusky dolphin distribution, group structure and behaviour in the western portion of Golfo Nuevo, with respect to environmental features (bottom depth, bottom slope, distance from shore and substrate). Random transects in the bay were searched by small boat during the summer and autumn of 2001–2004. When a group of dolphins was sighted, estimates of group size, composition (mothers with calves, adults and juveniles only, and mixed groups) and the predominant activity (*feeding*, *travelling*, *socialising*, *resting* and *milling*) were recorded and thereafter at 2 min intervals. A grid of 1.5 × 1.5 km was constructed and each cell was characterised by environmental features, Area Use Index (percent of total annual search effort) and Activity Index (predominant behaviour of groups observed in that cell). Mothers with calves and smaller groups and *resting* behaviour occurred in shallowest waters supporting the idea/hypothesis that movement to shallower water is related to increased safety for individuals. *Travelling* occurred in the deepest areas with other behaviours observed in intermediate depths. Dolphin distribution within the bay differed significantly between years, but this was not related to any of the factors analysed in this study. Although there was considerable variation between years, in general, dolphins were found in deeper waters further from shore (except for mother–calf groups) and over areas with steeper seafloor gradient. The high variability in the distribution of the animals does not allow for the generation of a simple, area-specific management plan.

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Introduction

The abundance of animals and the distribution of their populations vary in space and time, often predictably with the availability of the environmental components that are necessary for life (Litvaitis et al. 1994). Within the overall distribution range of a species there will be areas that are occupied to a greater or lesser extent and areas that may have specific behaviours associated with them (e.g. feeding, breeding or resting areas). An adequate identification of key habitats and core areas where biologically and socially important behaviours concentrate is an important task in understanding the species' ecology, and for the development of an effective conservation and management of any wild animal population (Karczmarski et al. 2000). It follows then that the fundamental unit in the conservation of biodiversity is not the species but the habitat.

The dusky dolphin has been incidentally caught in fishing nets off Patagonian coast showing unsustainable levels at least during the 1980s (Dans et al. 2003a, b). At the same time, this species is the target of newly developed cetacean watching activities in Golfo Nuevo, particularly during the summer months when it has arisen as an alternative focal animal to the southern right whale (*Eubalaena australis*) which is only present in the area in the winter months. At present dolphin watching in the area is unregulated and lacks a management scheme.

Coscarella et al. (2003) showed that dusky dolphins change their behaviour, including interrupting feeding, when approached by boats, with unknown long-term effects for the populations. In Shark Bay (Australia), Bejder et al. (2007) showed that dolphin-watching tourism has contributed to a long-term decline in dolphin abundance within the impact site. On the other hand, Lusseau and Higham (2004) showed that the disruption of bottlenose dolphins in two behavioural states (resting and socialising) has particularly significant consequences for the energetic budget (energetic budget is the pattern of energy allocation among different activities) of the species. For example, socialising is likely to be directly related to the reproductive output of a population, so that less time for socialising might result in lower pregnancy rates (Lusseau 2004). A spatially explicit management scheme that takes into account differential use of the environment by dolphins (particularly for behaviours or group types with greater sensitivity to disturbance) may be the most effective way to compromise between the conflicting interests of boat-based dolphin watching (BBDW) operators wanting unlimited access to dolphins and conservators wanting to minimise any potential impacts. If the distribution and behaviours of dusky dolphins is sufficiently predictable, it might be possible to define areas of limited or no interaction to allow the dolphins a refuge from watching boats.

The dusky dolphin inhabits waters of the continental shelf and slope of Argentina, Chile and Peru in South America, southwestern Africa and New Zealand (Leatherwood and Reeves 1983; Crespo et al. 1997) and shows a marked plasticity in its habitat use between these differing locations. In New Zealand, dusky dolphins forage at night in deeper waters on vertically migrating prey associated with the deep scattering layer, while in Argentina diurnal feeding on schooling prey was observed in shallower waters on the continental shelf (Würsig et al. 1997). Studies carried out in this last area, although limited to a small and closed bay, showed that larger groups and feeding groups tended to move faster and be in deeper water, suggesting a habitat shift related to foraging activities (Würsig and Würsig 1980). Line transect surveys off the Patagonian coast showed that dusky dolphins were not evenly distributed and the authors suggest that the high degree of concentration in some areas might be due to concentrations of important pelagic prey items such as the Argentine anchovy (*Engraulis anchoita*), and juvenile hake (*Merluccius hubbsi*) (Schiavini et al. 1999).

The distribution of cetaceans has been related to a variety of environmental variables, including bathymetric variables (Torres et al. 2003; Carreta et al. 2001; Hooker et al. 2002; Ballance 1990; Ferlt et al. 2003; Naud et al. 2003), sea surface salinity (Thompson et al. 1986), sea surface temperature (Bräger et al. 2003), substrate, distance from shore (Elwen and Best 2004a, b) thermoclines, eddies and fronts (Bjørge 2001; Baumgartner et al. 2001). These abiotic factors may be direct determinants of cetacean distribution through physiological limits, or may act by influencing prey distribution (Jaquet and Whitehead 1996; Fiedler et al. 1998; Redfern et al. 2006). For example, areas with steep gradients may provide greater feeding opportunities to cetaceans (Au et al. 1979; Hui 1979, 1985; Payne et al. 1986). For example, bottlenose dolphin exhibited preferential use of areas with greatest slope and depth in the Shannon estuary in Ireland (Ingram and Rogan 2002).

Some physical factors can influence cetaceans by providing some degree of protection. Elwen and Best (2004a) proposed that a sedimentary substrate might provide some protection for southern right whale calves (*Eubalaena australis*) in shallow water from both injury (avoidance of obstacles) and predation (acoustic damping) to some extent. Proximity to shore has also been suggested as an effective defence against killer-whale predation in bottlenose, dusky dolphins and right whale, especially in conjunction with continuous longshore movements (Würsig and Würsig 1979; Thomas and Taber 1984).

Given the present background, the objective of this work is to study the occurrence of dusky dolphins in Golfo Nuevo, to analyse the relationship with the following environmental variables: depth, slope, substrate and distance from shore, and to investigate if the areas where the groups of dolphins carry out different activities are related to these environmental features.

Methods

Study area

The study area is located in Golfo Nuevo (42°20′–42°50′ S; 64°20′–65°00′ W) (Fig. 1). This gulf as well as Golfo San

José is surrounded by Península Valdés, which constitutes a protected area that has been declared World Heritage by UNESCO since 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). The area surveyed in this study corresponded to the western portion and it was of 905 km^2. This area was selected because it represents the area where dolphin-watching commercial trips are performed. Boats operate from Puerto Madryn, and they usually look for dolphins as far as Baliza 25 de Mayo on the north and Punta Conscriptos on the south (Fig. 1).

Survey procedures

Random transects were done by a research boat (January to May 2001, January to April 2002, January to April 2003 and January to June 2004). Once a group of dolphins was found, transect was abandoned and the group was followed as long as possible. During January 2001 and 2002, a commercial dolphin-watching boat was also used, because the research boat was unavailable. During commercial trips, searching effort was mostly allocated at random although trips and follows were shorter.

A group was defined as any group of animals closely engaged in the same activity and moving in the same direction. When a group of dolphins was sighted, location (recorded by a GPS), group size and composition, and the predominant group-activity were assigned. According to their composition, groups were classified as: adults and juveniles, mother with calves (when more than 80% of the individuals were mothers with their calves) and mixed (combination of mother and calves, juveniles and adults). Group size was assigned to one of the following categories: <10, 11–20, 21–50, 51–70, 71–100 and more than 100 animals. Predominant group-activity was defined as the activity in which most of animals were engaged (Mann 1999). This activity was classified into one of the five categories: *feeding, travelling, socialising, resting and milling* (Degrati et al. 2007). During *feeding*, dolphins swam in circles and zigzags and enclose the school of fishes. The presence of birds feeding with or following the dolphins was a good indicator of feeding behaviour. *Travelling* consisted of persistent and directional movement, where all group members swim synchronously. *Socialising* was characterised by interactions between individuals, usually in the form of body contact, with high-speed movements and with frequent direction changes and leaps. *Resting* consisted of a low level of activity, where the dolphins apparently float stationary and motionless on the surface, with some occasional slow forward movement. *Milling* consisted of low speed movements with frequent changes in direction.

Coscarella et al. (2003) found that dolphins changed their behaviour when boats approached them, with feeding being the most sensitive behaviour. The distance and behaviour of the approaching boat affected the strength of the reaction, dolphins changing from feeding to travelling

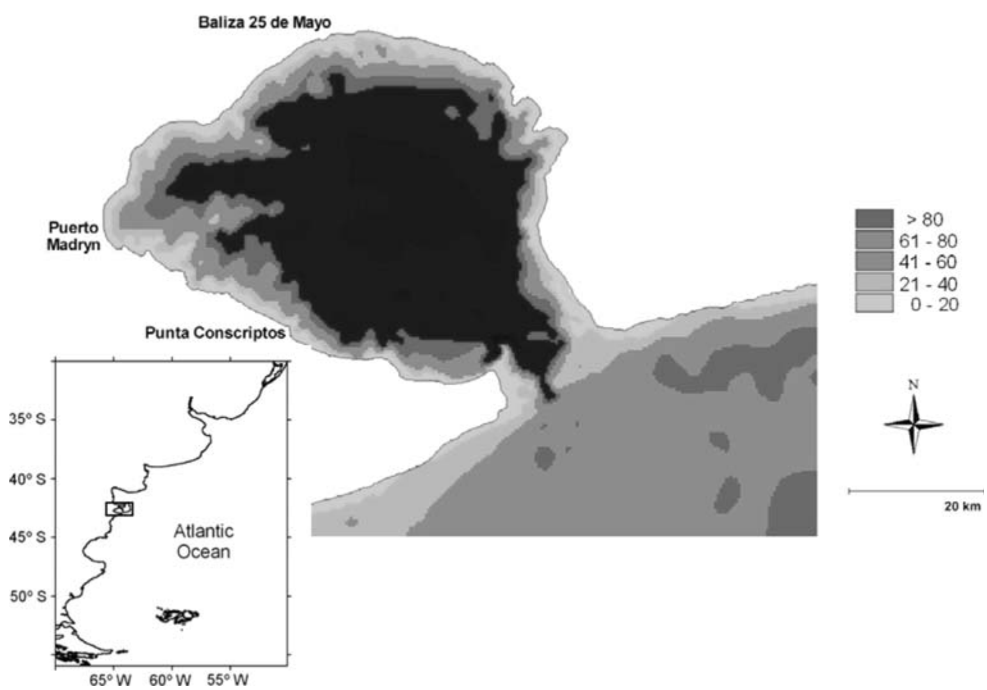

Fig. 1 Map of Golfo Nuevo showing its bathymetry (*m*). The study area included the western portion, located on the left of an imaginary line between Baliza 25 de Mayo and Punta Conscriptos. Surveys were done from Puerto Madryn

most frequently when commercial boats were at a distance of 50 m or less from the dolphins. In the present study, we attempted to reduce the potential impact of the research boat on dolphin behaviour by approaching dolphins from the side in the same direction and speed of dolphins movements, and attempting to keep boat behaviour and distance constant throughout (100 m). This type of sampling has been used in other studies (Lusseau and Higham 2004).

Each group was considered as a focal group and followed as long as possible (Altmann 1974). When new dolphins were added to the focal group or the group split, this was considered as a new group and it was recorded as a new tracking. During the tracking, group size, composition, the predominant activity and location were recorded at 2 min intervals once the group was sighted.

Given the potential use of the nearshore environment for protection by dolphins, the direction in which the different types of groups moved after the boat started to follow the group was analysed. Direction was considered as categorical variable and defined as: *onshore*, *offshore*, *parallel to shore*. There was no relation between movement direction and type of group ($G = 0.69$, $df = 4$, $P = 0.95$, $n = 193$).

Data analysis

Nautical charts (H-218, 1:110,000, Naval Hydrographic Service) containing depth data and a substrate distribution map (Mouzo et al. 1978) were used to gather information about environmental features (depth, substrate, slope and distance from shore). A grid of $1.5 \times 1.5\ \text{km}^2$ was constructed for the study area. A Geographic Information System (GIS) was used to integrate the environmental data with the grid. Once the grid, nautical charts and substrate map were overlapped, each cell of the grid was characterised by depth, slope, substrate and distance from shore.

Mean depth was calculated by averaging values of depth. Slope was calculated as $(D_{\max} - D_{\min})/\text{DI}$ where $D_{\max}$ the maximum depth in the cell, $D_{\min}$ is the minimum depth in the cell, and DI the distance in meters between the points of maximum and minimum depth of the cell and expressed in units of meters per km (Cañadas et al. 2002). Then, three categories of slope were defined: *plane*, slope ≤ 20 m/km; *medium*, slope between 21–40 m/km and; *steep*, slope ≥40 m/km. Four categories of substrate were defined as: *sandy*, more than 50% of cell presents sandy substrate; *sandy with gravel*, more than 50% of cell present sandy with gravel substrate; *sandy–silty*, more than 50% of cell presents sandy–silty substrate, and *muddy*, more than 50% of cell presents muddy substrate. The variable substrate was utilised in the analysis since in certain occasions the dolphins were seen carrying out long divings. This would be able to constitute a different feeding strategy in which the dolphins would be fed benthically. Distance from shore was calculated as distance from the central point of each cell to the closest part of the coast and categories were defined: ≤ 4 km, 4–8 km and ≥8 km.

Each cell was characterised by dolphin use intensity and dolphin tracks were overlapped with the grid, calculating the time dolphins spent in a specific cell. A coefficient of area use was calculated as:

$$\text{AU} = (D_i/T) \times 100$$

where D_i is the cumulative time following dolphins in the cell i and T is the total time following dolphins during the sampling period of each year. AU indicates the intensity of use of each specific cell, representing the proportion of time that dolphins spend in a particular cell. Therefore, AU is relative to the total time following dolphins during each year and it allows making comparisons between years. In theory, a cell will show the maximum value of AU (100) when all the time following dolphins in one sampling period was concentrated in this cell. Cells were classified according to the intensity of use into three categories: low use ($0\% < \text{AU} < 0.75\%$), medium use ($0.75\% < \text{AU} < 1.5\%$) and intense use ($\text{AU} > 1.5\%$).

Dolphins' activity in each cell was quantified using an activity index AI_{ij} (Karczmarski et al. 2000). This index was used to represent the time the animals were engaged in a particular activity within a particular cell. It was calculated as:

$$\text{AI}_{ij} = \frac{1}{n}\sum_{k=1}^{n} D_{ijk}/S_{ik}$$

where D_{ijk} is the time that a group of dolphins k was engaged in the activity j within the cell i, and S_{ik} is the total time spent by the group k in the cell i. Then, each cell was characterised by a AI_{ij} that is the average over n groups.

The interannual variation in the location of dolphins was evaluated using only cells searched in each of the 4 years using a Cochran Q test. Then McNemar test for pairwise comparisons was employed considering each cell as a block (Zar 1996). Those years that did not show significant differences were pooled for further analysis.

Depth of cells where dolphins were observed was compared to their expected distribution (total distribution of depth) from searched cells using a Chi-square analysis. Then, the same analysis was carried out for slope, substrate and distance from shore (Conover 1999; Siegel and Castellan 1995).

In order to reduce the number of entries in the contingency tables and to avoid a large proportion of zeros, possible explanatory variables were pre-selected by multivariate descriptive techniques. All the visited cells were considered and Principal Components Analysis (PCA) was carried out on all continuous variables (*depth*, *slope*, *distance from shore*). *Depth* and *substrate* type are related in the bay, with the deepest areas being muddy and shallowest areas sandy (Mouzo et al. 1978).

Relationships between *use* (low, medium and intense) and environmental factors: (a) *depth* (<40 m, 40–80 m and >80 m), (b) *slope* (plane, medium and steep), and (c) *distance from shore* (three categories: <4 km, 4–8 km and >8 km); were analysed by log-linear analysis with *year* (2001, 2002, 2003 and 2004) included to investigate possible interannual differences in the relations. The following abbreviations are used in the descriptions of the models: *U* for *use*, *D* for *depth*, Sl for *slope* and Di for *distance from shore*. The effects of the factor on use were analysed using the technique described by Caswell (2001). Different models were tested incorporating the interaction of interest to the null model. In comparing these hierarchical models, ΔG^2 statistic was used, which measures the impact of the terms excluded on the goodness of fit (Caswell 2001). ΔG^2 is distributed as χ^2 with degrees of freedom equal to the increment in degrees of freedom in the two models to be compared.

The relationship between environmental variables and group size and composition was also explored using PCA as above but, only using the initial sighting position of each group. Composition and group size were considered as second matrix to the environmental variables. In addition, the time of day when each group was sighted was also included as a second matrix, with three time periods defined as morning (09:00–11:59 h), noon (12:00–14:59 h) and afternoon (15:00–17:59 h).

Dolphins' activity in relation to environmental variables was also analysed. In this case, the depth, slope and distance from shore were considered as continuous variables and Kruskal–Wallis test was employed to evaluate differences among activity categories (Conover 1999; Siegel and Castellan 1995). Substrate was considered as categorical variable and then *G* test was used. Only cells with $AI_{ij} \geq 0.5$ were used so that they could represent the activity. When more than one activity was observed within the same cell, activity with the highest AI was assigned.

Results

Detecting areas used by dolphins and inter-annual variation

During the 4 years, 203 trips were performed, 138 trips with at least one group of dolphins. From a total of 562.5 h looking for dolphins, it took 127.5 h to sight and track 199 groups of dusky dolphins. A total of 402 cells were surveyed (904.5 km^2) (Fig. 2) and dolphins were recorded in 256 cells (576.5 km^2).

Dolphins used different parts of the bay in different years, predominantly the west in 2001 and 2002, the south in 2004 and both the western and northern areas in 2003 (Fig. 3). The Cochran *Q* tests showed differences among years ($Q = 55.2$, $df = 3$, $P < 0.0001$, $n = 150$). The location of dolphins was only similar between 2002 and 2003 (McNemar test, $P = 0.08$). The proportion of cells used with a different intensity varied among years and the location of areas used by dolphins also changed along the years. In 2001 a larger proportion of cells (64% of total cells) was used with a low intensity while in 2004 the *use* was more spatially concentrated (46% of total cells were used with high intensity) (Table 1). Also, in this last year, the total surface used with high intensity was larger, although dolphins used only 25% of the total surface surveyed (153 km^2 from 603 km^2; Table 1), suggesting again a more concentrated use by dolphins in this year (Fig. 3).

Relationship between use and environmental variables

When the depth where dolphins were observed was compared to their expected distribution in the searched area (total distribution of depth in the region), differences were observed in 2001 and 2002–2003 ($G = 11.08$, $df = 5$, $P = 0.049$ in 2001; $G = 36.28$, $df = 5$, $P < 0.00001$ in 2002–2003). In 2001, dolphins showed a preference for areas between 40 and 100 m, and avoided areas with depths less than 20 m. In 2002–2003 dolphins showed a preference for areas between 20 and 80 m, and avoided depths over 100 m. Finally a trend towards deeper areas (over 60 m) was observed in 2004 although differences were not significant ($G = 10.21$, $df = 5$, $P = 0.069$) (Fig. 4a–c).

Habitat selection with respect to sea floor gradient was not clear from our data, and a significant difference from

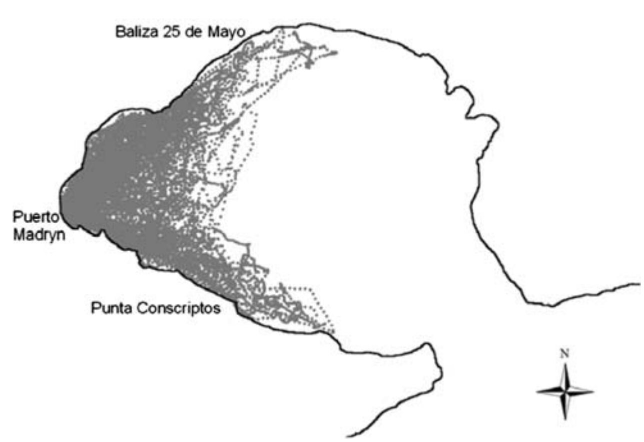

Fig. 2 Map showing the boat transect carried out from 2001 to 2004

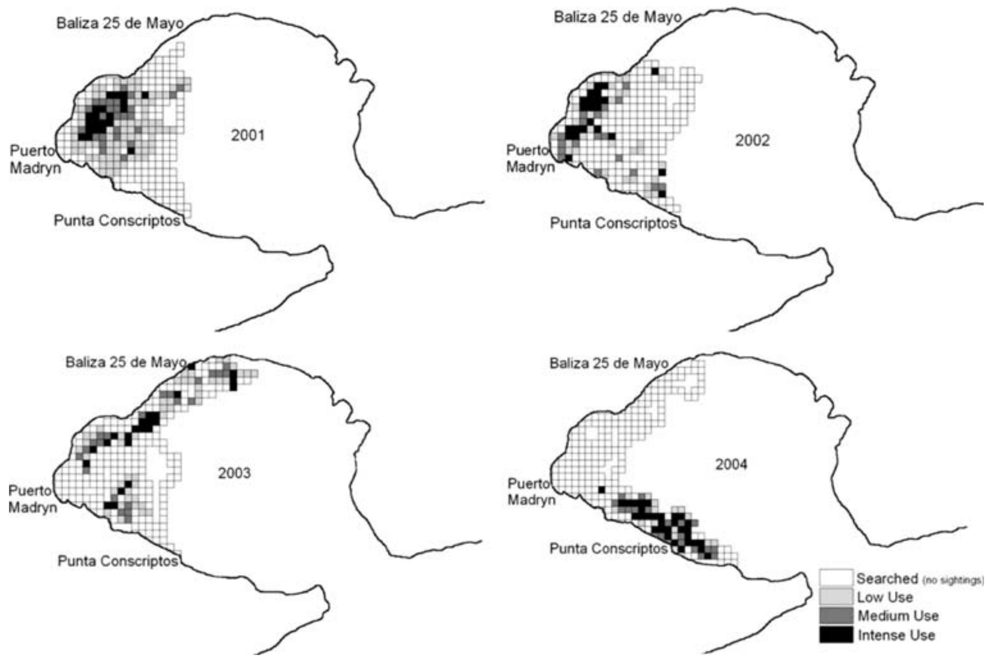

Fig. 3 Study area subdivided in cells of 1.5 × 1.5 km. Each cell was characterised by a coefficient of area use (See text). Hours searched in each year: 2001, 304 hs; 2002, 188 hs; 2003: 189 hs and 2004, 143 hs

Table 1 Distribution of the Coefficient of Area Use among different cells by dusky dolphins per year of survey in the western portion of Golfo Nuevo during summer and autumn

	2001	2002	2003	2004
AU intense	45 (15)	52 (32)	52 (25)	70 (46)
AU médium	61 (21)	41 (25)	52 (25)	47 (31)
AU low	189 (64)	70 (43)	101 (49)	36 (24)
Surface used by dolphins	295	162	205	153
Surface surveyed	608	572	617	603

Surface of cells used with different intensity are expressed in km^2 and the value between parentheses represents the percentage of total surface used by dolphins each year. Surface used by dolphins and surface surveyed per year are expressed in km^2

expected values was only observed in 2002–03 ($G = 7.94$, $df = 2$, $P = 0.019$) when dolphins were observed more often than expected over areas with steeper slopes. The distance from shore where dolphins were observed and their expected distribution in the searched area differed significantly in 2001 and 2002–2003. In 2001 dolphins were seen more frequently than expected in areas farther from shore (>4 km) ($G = 13.05$, $df = 2$, $P = 0.0015$), but in 2002–2003, they were seen more frequently in areas closer to shore ($G = 32.45$, $df = 2$, $P < 0.0001$). It is important to emphasise that during 2004, the dolphins always were observed within 8 km of shore.

In all years, dolphins were seen more frequently than expected over areas with sandy–silty substrate ($G = 9.45$, $df = 3$, $P = 0.024$ in 2001; $G = 17.56$, $df = 3$, $P < 0.0005$ in 2002–2003; $G = 9.97$, $df = 3$, $P = 0.019$ in 2004).

The first principal component accounts for about 60% of the variation in the data. This component represents an average between *depth* and *distance from shore*. Therefore log-linear analysis was carried out considering *use* as response variable and *year*, *depth* and *distance from shore* as explanatory variables.

Within the range used by dolphins, all depth categories were used with the same intensity (the DU interaction was not significant) but the distance from shore had a significant effect on intensity of use (the UDi interaction was significant), although this differed between years (the UdiY interaction was significant). It is important to emphasise that *depth* and *distance from shore* are related (DDi interaction was significant) (Log-linear analysis, Table 2) (Fig. 5a–c). A similar log-linear analysis was performed with slope replacing *depth*. Similar results were obtained. On the one hand *distance from shore* and *slope* are found related (DiS interaction was significant) and on the other hand *distance from shore* had a significant effect on use (the UDi interaction was significant) (Log-linear analysis, Table 3).

Differential use by group composition and size

The results of the PCA performed with the three variables (*distance from shore*, *depth* and *slope*) showed the first principal component accounts for about 60% of the variation in the data. This component represents an average between *depth* and *distance from shore*. On the other hand, the second component represents *slope*. First two principal components, Z_1 *y* Z_2, account for 90.4% of the variation in

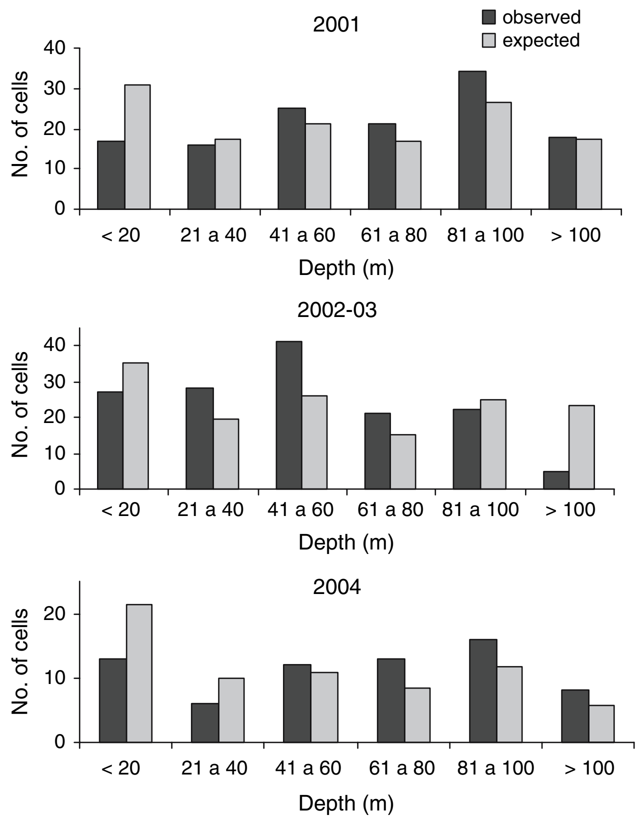

Fig. 4 Number of cells used by dolphins in each depth category (*m*) and expected distribution in the searched area, based on area search in each year for the study years 2001, 2002–2003 (pooled as distribution shown to be similar) and 2004

the data (Fig. 6a–c). The Fig. 6a, b show how groups of mothers with calves and the smallest groups occurred in shallowest areas and closer to shore. On the other hand, Fig. 6c shows that groups of dolphins occurred in further areas from shore in the mornings. The mean depth and mean distance from shore for the different types of groups and for groups with different size are shown in Figs. 7a, b and 8a, b.

Environmental variables and activities

Among activities, dolphins spent most of their time *resting* in the shallowest areas while *travelling* in the deepest areas. Cells used mainly for *socialising*, *milling* and *feeding* showed intermediate depth (KW = 10.78, $df = 4$, $P = 0.029$, $n = 105$ in 2001; KW = 20.05, $df = 4$, $P = 0.0005$, $n = 124$ in 2002–2003; KW = 11.96, $df = 4$, $P = 0.0176$, $n = 64$, in 2004) (Fig. 9). Dolphins rested in areas closer to shore (<4 km) (KW = 14.02, $df = 4$, $P = 0.0072$, $n = 108$ in 2001; KW = 12.33, $df = 4$, $P = 0.015$, $n = 124$ in 2002–2003; KW = 12.25, $df = 4$, $P = 0.016$, $n = 64$, in 2004) (Fig. 10). Although areas used for *feeding* showed a higher percentage of steep gradients, there was no significant

Table 2 Log-linear analysis of data classified by use (U), year (Y), distance from shore (Di) and depth (D)

Model	*df*	G^2	*P*
UY D Di	92	275.5	
UY Ddi	88	130.66	
Ddi	4	144.84	<0.001
UY Ddi	88	130.66	
UY DDi UD	84	124.09	
UD	4	6.57	0.160
UY Ddi	88	130.66	
UY DDi UDi	84	118.76	
Udi	4	11.9	0.018
UY DDi UDi	84	118.76	
UY DDi UDiY	66	63.99	
UdiY	18	54.77	<0.001

Notation: the model *UY, DDi* contains the terms *D, Di, Y, U*. The *UY* and *DDi* interactions imply the presence of the *D, Di, Y and U*

difference in depth gradient among areas in which dolphins carried out different activities. It must be denoted that areas used mainly for *feeding* represent a more coastal strip, while less coastal and deeper areas were mainly used for *travelling*.

Discussion

This paper contributes to the available knowledge on dusky dolphins' ecology, in particular, by exploring how dolphins are using the physical habitat and the possible determinants of their distribution within Golfo Nuevo, Argentina. The results obtained here highlight two important relationships between occurrence and environment. First there is clear evidence that dolphins are not evenly distributed throughout the environment of the gulf; and second, the location of animals varied within the gulf between years and different parts of the gulf were used by animals in different years. Although our observations were limited to summer and autumn, they allow us to hypothesise about processes occurring within the larger surrounding habitat as well as about group dynamics within this environment.

Dolphins used a relatively wide range of depth, although with some preference for areas between 40 and 100-m-deep. The relationship between slope and use only showed a trend towards steep slope and the link with the substrate could be better explained by a correlation between depth and substrate than an actual effect of substrate on dolphins' movements. Although, in other species sedimentary substrate may provide some protection from both injury (avoidance of obstacles) and predation (acoustic damping) when compared with more rocky substrates (Elwen and

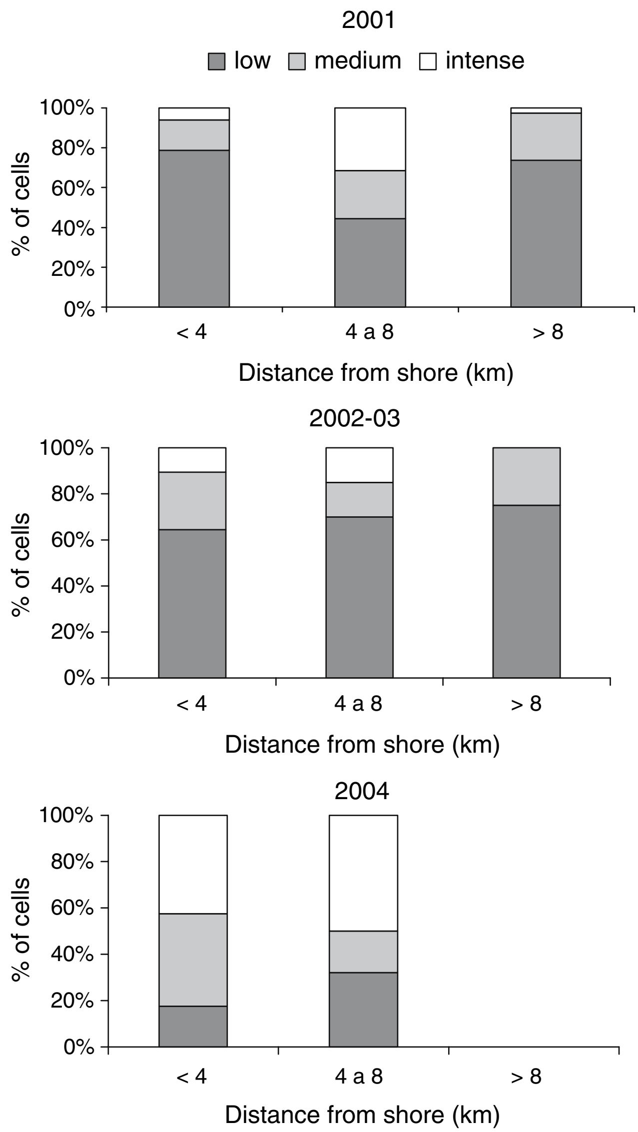

Fig. 5 Percentage of cells used by dolphins with different use intensity in each distance from shore category (km) during each years: 2001, 2002–03 and 2004

Best 2004a, b). On the other hand, the dolphins showed a preference for areas closer to shore and this behaviour could be related to increased safety from predators, particularly for mother–calf pairs (Würsig and Würsig 1979). Several authors postulated a similar function for nearshore movements (Norris and Dohl 1980; Saayman and Tayler 1979). Sharks have been observed on several occasions when dolphins were feeding during the present study as well as in Golfo San José (Würsig and Würsig 1980). In addition, several pieces of the body of dolphins, like flukes and tails, were found in stomach contents of broad-nose sharks (*Notorhynchus cepedianus*) along the Patagonian coast (42°–46°S) (Crespi et al. 2003). It is also known that killer whales (*Orcinus orca*) may prey on dusky dolphins (Würsig and Würsig 1980; Constantine et al. 1998).

Table 3 Log-linear analysis of data classified by use (U), year (Y), distance from shore (Di) and slope (S)

Model	*df*	G^2	*P*
UY S Di	92	138.54	
UY SDi	88	113.12	
SDi	4	25.42	<0.001
UY SDi	88	113.12	
UY SDi UDi	84	101.22	
UDi	4	11.9	0.018
UY SDi	88	113.12	
UY SDi US	84	106.87	
US	4	6.25	0.181
UY SDi UDi	84	118.76	
UY SDi UDiY	64	58.5	
UDiY	20	42.72	0.002

Notation: the model *UY, SDi* contains the terms S, *Di, Y, U*. The *UY* and *SDi* interactions imply the presence of the S, *Di, Y and, U*

The observed patterns in distribution may also be a result of association to the distribution of preys, since depth and changes in depth have been shown to concentrate prey (Sutcliffe and Brodie 1977). For species of cetacean prey, such as pelagic fish or cephalopods, physiography could play an indirect role through mechanisms such as topographically induced up welling of nutrients (Guerra 1992; Rubin 1997). The preferential use of areas with steep slope has been shown in studies of other cetacean populations (Ingram and Rogan 2002; Baumgarther 1997; Wilson et al. 1997; Ballance 1992). The abundance and distribution of Argentine anchovies, the main prey item of dusky dolphins (Koen Alonso et al 1998), are unknown inside the Golfo Nuevo and the available information comes from open waters (continental shelf). Hansen et al. (2001) concluded that main concentrations of anchovies were present in front of Península Valdés (42°–43° S) mainly on the inner and intermediate shelf 70-m-deep. This is similar to the range of depth mostly used by dolphins in Golfo Nuevo in this study. However, further studies about abundance and distribution of anchovies, as well as the whole pelagic assemblage, inside Golfo Nuevo, are required for a better understanding of dolphins' movements.

The second important finding is the fact that dolphins used different parts of the gulf from one year to the next but the location remained mostly unchanged within the year. This may explain, in part, the high variation in the depth of the areas used by dolphins in different years. Also, the observed pattern suggests that the distribution of different groups of dolphins could be highly contagious and then the presence of a group could be not independent from the presence of another group, and that there would be a residence time at a specific patch.

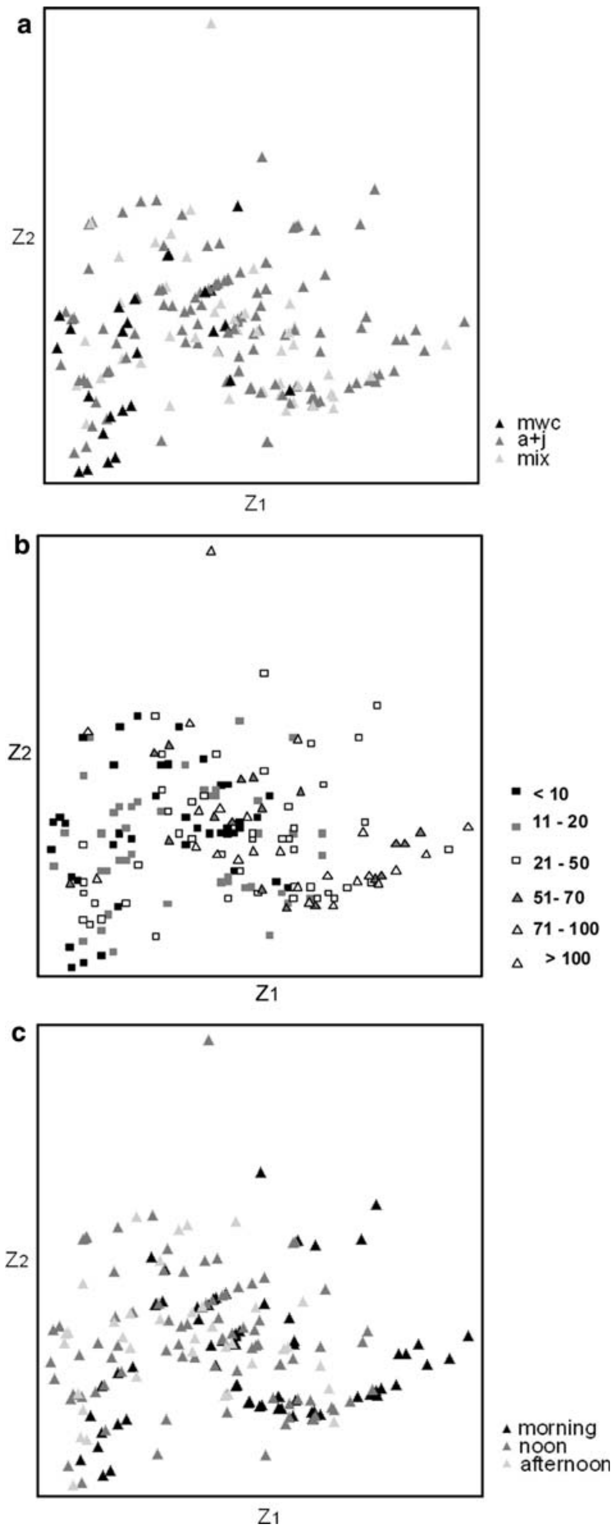

Fig. 6 Results of PCA. Plot of 199 groups of dolphins sighted during all study period, against values for the first two principal components, Z1 (depth and distance on *x*-axis) and Z2 (slope on *y*-axis). **a** Types of group, **b** size group and **c** time-blocks

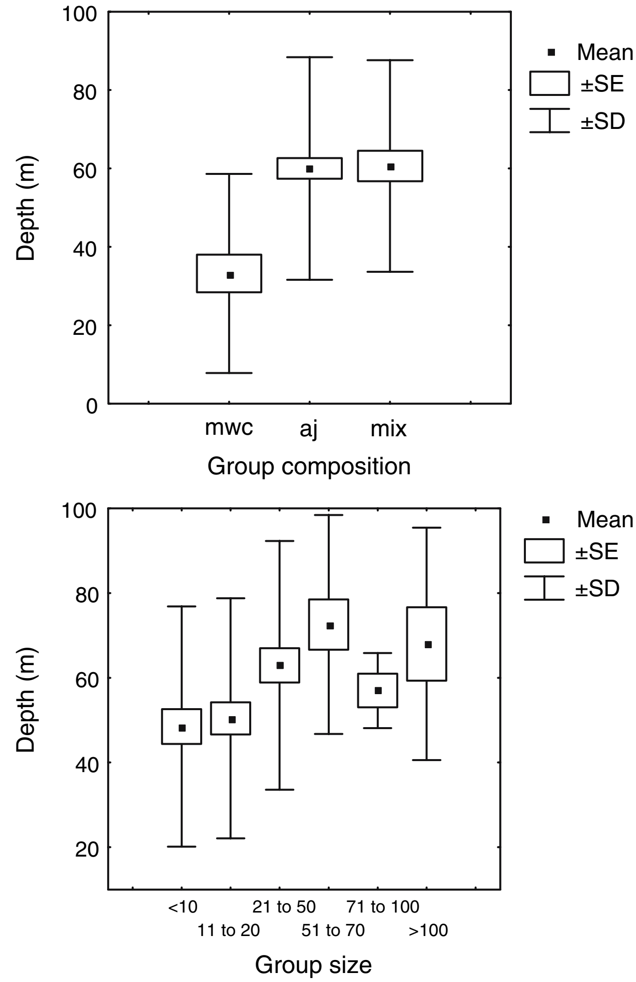

Fig. 7 Mean depth for: **a** the different types of groups and **b** groups with different size

Within the range of environmental variables used by dolphins, there was a differential use according to group size and composition. Smaller groups and those consisting of mothers with calves occurred in the shallowest areas closest to shore while mixed and larger groups occurred in deeper areas further from shore. The groups of mothers with calves may remain closer to the coast as a protection mechanism from predation. Degrati et al. (2007) suggest that the segregation of mothers with calves from larger groups of adults and juveniles may be explained by differences in activity requirements. On the other hand it is possible that male harassment of mothers might be reduced if the mothers and calves separate from the males and move inshore. Consequently, it is possible that once mothers and calves segregate from the other groups, they locate in shallower waters as a protection strategy.

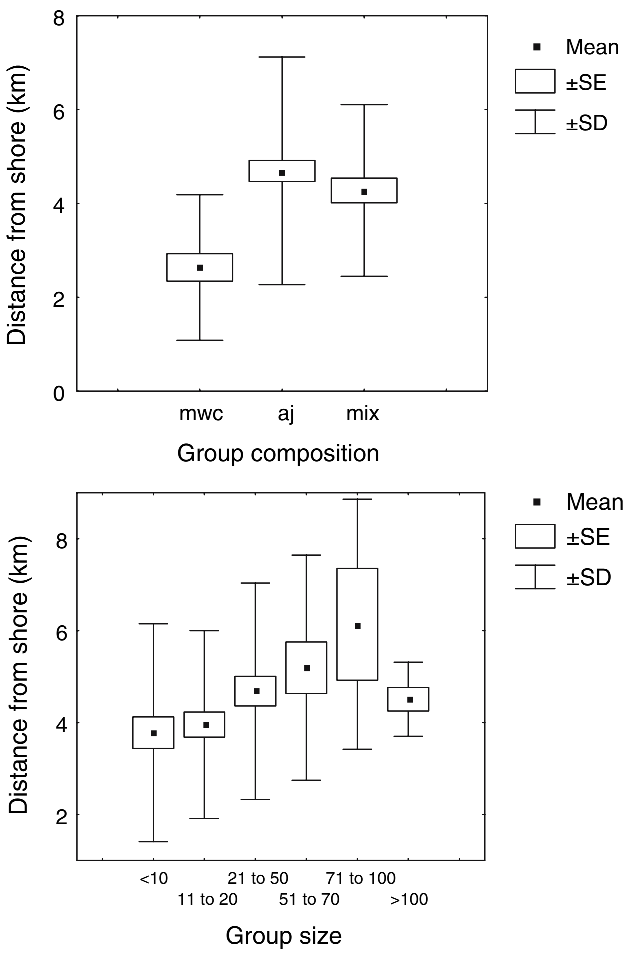

Fig. 8 Mean distance from shore for: **a** the different types of groups and **b** groups with different size

The location of dusky dolphins is also related to their activities as resting behaviour was observed to take place closer to shore than all other behaviours while *travelling* and *feeding* were recorded in the deepest areas. Würsig and Würsig (1980) showed some evidence that killer whales (*O. orca*) may prey on dusky dolphins and when killer whales came close to dolphin groups, the dolphins moved into extremely shallow waters. It is likely that nearshore movement for *resting* is a defence strategy against predation. Other works suggested that shark predation could be a major factor for the selection of *resting* habitats (Wells and Norris 1994; Heithaus and Dill 2002) and calving habitats (Wells et al. 1980; Mann et al. 2000) in various dolphin species.

Sequences of *travelling* and *feeding* were observed where travelling intervals of less than 20 min were alternated with feeding intervals (Degrati et al. 2007). Also *socialising* occurred after *feeding*. These sequences suggest that the other activities could be subordinates to *feeding*. For example, the periods of *travelling* between periods of *feeding* may represent displacements of the group of dolphins among patches of preys. Then, the time dolphins spend in a specific location will depend on the density of the prey-patches and the distance between them. The final outcome will be the overlapping of areas used for travelling and feeding.

Areas with steep slopes were expected to concentrate the feeding activity of dolphins, since areas of high sea floor relief often result in greater nutrient mixing due to topographically induced up welling (Svedrup et al. 1942; Guerra 1992; Rubin 1997). In the present study, only a slight trend toward steeper slopes where dolphins feed was observed and there was no observable relationship between gradient and other behaviour. This lack of a clear pattern may be explained by the apparent dependence among activities.

The physical variables that affect the presence of dusky dolphin preys, would indirectly affect the presence of these dolphins. However the distribution of different groups of dolphins and its temporal variation suggest that other factors may explain the habitat-use pattern observed. One interesting result observed in this work is the fact that, on

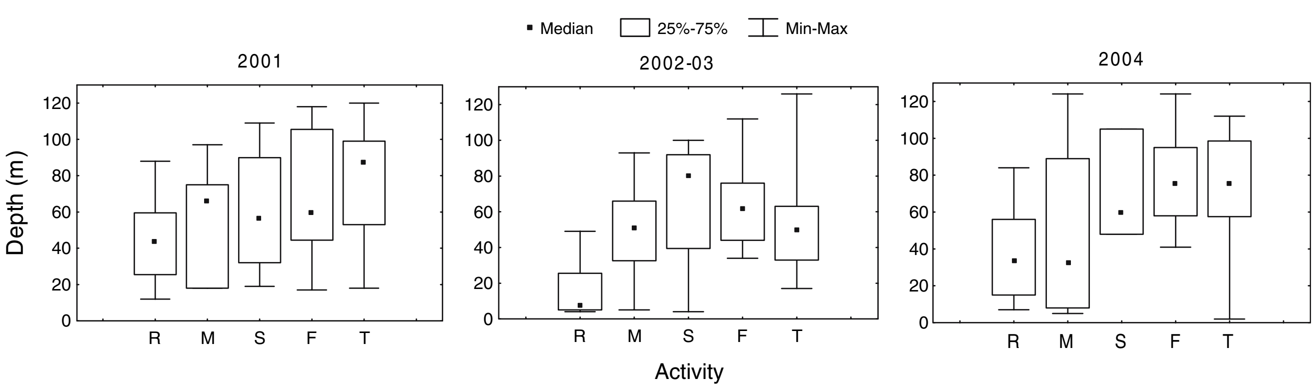

Fig. 9 Mean depth of the areas where *AI* for each activity was higher than 0.5 in Golfo Nuevo (*R* resting, *M* milling, *S* socialising, *F* feeding, *T* travelling) for **a** 2001, **b** 2002–2003, **c** 2004

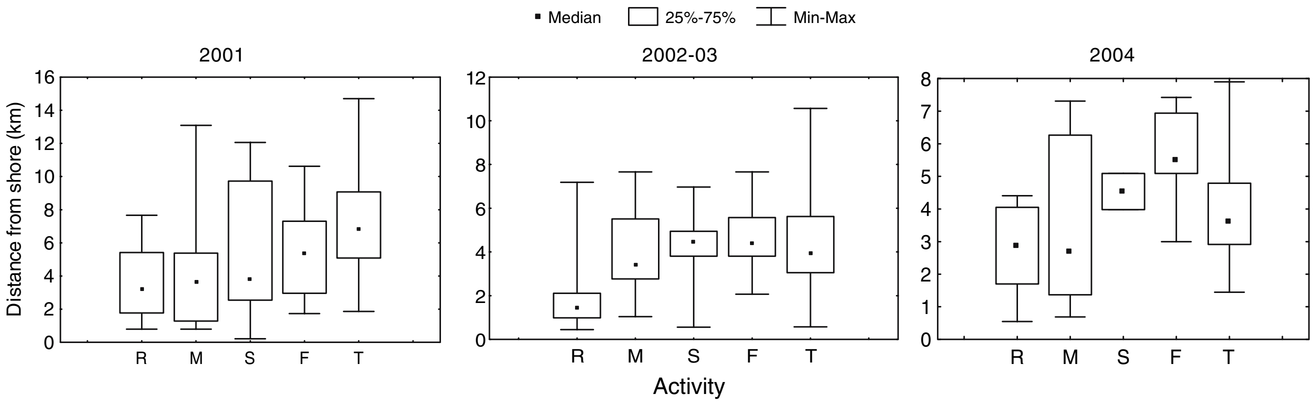

Fig. 10 Mean distance from shore where *AI* for each activity was higher than 0.5 in Golfo Nuevo (*R* resting, *M* milling, *S* socialising, *F* feeding, *T* travelling) for **a** 2001, **b** 2002–2003, **c** 2004

the one hand, several groups of dolphins remain in a relatively constant location during a long period of time (i.e. several months), and that, on the other hand, these groups switch location in a coordinated way. Although dusky dolphins are in fission–fussion society, fotoidentification studies that are being carried out indicate that at least some animals may remain in the gulf year after year. Unless only a few prey patches are available inside Golfo Nuevo, such an aggregation pattern may be the consequence of social relationships.

The distribution pattern mentioned above also has consequences for the logistic and analytical tools when studying the habitat use. In other studies, the number of encounters with dolphins in each cell is quantified (Ingram and Rogan 2002). The present work shows a novel methodology to quantify the use of different areas. It was decided to quantify the time that dolphins spend in every cell instead of other more traditional measurements, like sighting for effort unit. This decision was taken based on the fact that dolphin groups are scarce, which led to a very low encounter rate per sampling trip.

Finally, it is necessary to place the results of this study within a management and conservation context. Groups of dusky dolphins in Golfo Nuevo are exploited as a tourism resource. Interactions between whale/dolphin-watching vessels and wild dolphins have been shown to produce both short (Coscarella et al. 2003; Lusseau 2003; Constantine et al. 2004) and long-term disturbances (Bejder et al. 2006), such as potential changes in occurrence and local abundance. The definition of appropriate restricted times or areas where only authorised boats or interactions would be permitted, is a potentially powerful way to reduce these impacts on cetacean populations (Bejder et al. 2006; Lusseau and Higham 2004). The spatial dynamics of the dolphins found in the present study showed a high annual variability in their location. This result suggests that it will not be possible to identify more sensible areas, and, consequently, restricted areas. Therefore alternative management tools should be taken into account, such as keeping whale-dolphin watchers away from shore or depths greater than 40 m to avoid resting animals and mother–calf pairs.

At present, Península Valdés constitutes a protected area with managed resources. However, only the northern portion of Golfo Nuevo is included in this area. Obviously, this plan does not take into account the movements of dusky dolphins. Such aspects as well as short and long-term responses of dolphins to boats must be considered when deciding the management scheme of dolphin-watching activities.

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