

Behavior and seasonal variation in the relative abundance of Commerson's dolphin (*Cephalorhynchus commersonii*) in northern Patagonia, Argentina

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Abstract Commerson's dolphins (*Cephalorhynchus commersonii*) along the Patagonian coast of South America suffer incidental mortality in fisheries and are the target of a dolphin-watching industry. We describe the daily activity patterns and assess the variation in the relative abundance of the species near the northern boundary of its range. Information was gathered with a spotting scope from a cliff-top vantage point applying the method of scan sampling. Behaviors were categorized as individual feeding, cooperative feeding, directional swimming, socializing, and resting. These behaviors are similar to those observed in other species of small cetacean, but differences were found regarding the patterns of directional swimming and feeding techniques. Hunting tactics favored the association of terns with dolphin groups. No clear diel behavioral pattern was observed, but seasonal changes in the frequency of behaviors were recorded. Group and school sizes were larger during periods with colder sea surface temperature (SST). Seasonal abundance was correlated with SST, suggesting that at higher SST the species forsakes the area, probably in favor of coastal areas to the south with lower SST.

Keywords Commerson's dolphin · Behavioral ecology · Patagonia · Terns · Sea surface temperature

Introduction

Commerson's dolphin (*Cephalorhynchus commersonii*) is a coastal species ranging from 41°30'S to 55°S in the southwestern South Atlantic Ocean, including the Falkland (Malvinas) Islands (Goodall 1994). A separate subspecies occurs off the Kerguelen Islands (Indian Ocean) (Robineau et al. 2007). Although the species mainly inhabits shallow coastal waters, there have been several sightings as far as 200 nm from the shore (Pedraza 2008). They mostly congregate in groups of 2–10 individuals, although schools >100 individuals have been recorded near Tierra del Fuego and north of the Chubut and Santa Cruz provinces in Argentina (Goodall et al. 1988; Coscarella et al. 2003; Pedraza 2008). These exceptionally large schools are regarded as reproductive, feeding, or seasonal migratory aggregations (Goodall et al. 1988).

Throughout its range, Commerson's dolphins are incidentally killed in various fishing operations (Goodall et al. 1988; Crespo et al. 1997; Iñiguez et al. 2003). In addition, since the late 1990s, Commerson's dolphins have been increasingly used as a tourist attraction in at least three localities, and short-term effects on their behavior were reported (Coscarella et al. 2003).

Although this paper does not address the impact of such activities, in order to assess the short- and long-term impacts of dolphin watching, and to understand their population structure, habitat use, occurrence, and behavior is important before the dolphin-watching industry grows to the point where it affects the dolphin population irreversibly.

Despite concern for the need to evaluate the potential impacts of human activities on dolphins, published information on the behavior of Commerson's dolphin is scarce (Mermoz 1980; Robineau 1985; Goodall et al. 1988). Some behavioral information from captive animals has also been

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published (Gewalt 1979; Kastelein et al. 1993; Jhonson and Moewe 1999). On the other hand, no information is available on the behavior of this dolphin relative to the northern boundary of its distribution. The present study summarizes information on the behavior and daily activity patterns of Commerson's dolphin at Bahía Engaño, in northern Patagonia, examining at the same time the variables that can be responsible for seasonal changes in abundance.

Materials and methods

This study was done at Bahía Engaño, near the mouth of the Chubut river (43°20'S, 65°02'W). A vantage point was located 3 km south of the river mouth on a 21-m-high cliff (Fig. 1). Information was recorded from February 1999 to May 2002. A scan sampling method was applied (Lehner 1998), and the area was scanned from north to south every half an hour using a Spacemaster Bushnell spotting scope with a 20–45 × 60 zoom lens, covering approximately 30 km². Date, scan start time, Beaufort sea state, time of group sighting, activity, number of individuals in the group, interactions between bird flocks and dolphins, and scan finishing time were recorded. Activity is defined as the behavioral state recorded and was the same for all dolphins in the group. A group was defined as those dolphins associated closely and engaged in similar activities. The referred groups were ephemeral, and changed composition at an undetermined rate. The term group is hereafter only used for referring to this kind of aggregation. During a scan, all dolphins in the area (regardless of the number of groups) were considered to be a school (Coscarella et al. 2003).

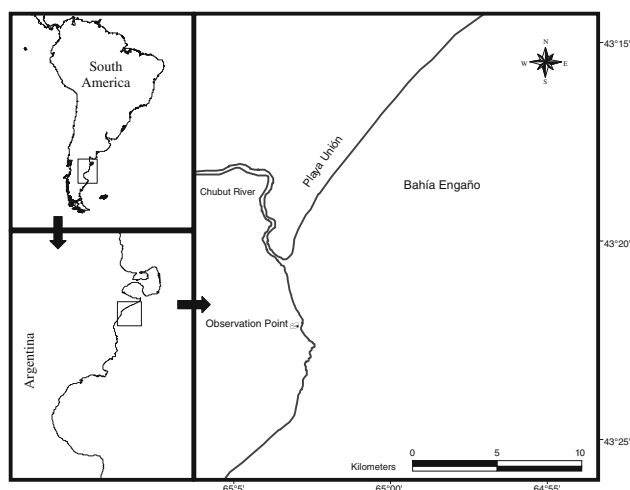


Fig. 1 Study area and location of the observation point

Sample sessions were carried out from dawn to dusk but interrupted when Beaufort sea state was above 3. This was done in order to avoid the influence of the weather condition on the precision of the counts, because the breaking waves on the surface made it difficult to detect dolphins. A negative correlation was found between the mean number of animals and the Beaufort sea state for an observed range from 0 to 6 (Spearman $r = -0.9$; $P < 0.05$).

Behaviors were assigned to the following mutually exclusive and exhaustive categories:

- *Individual feeding* Individual dolphins or small groups (2–4 dolphins) move erratically with sudden changes of direction and speed. During these movements, lone dolphins can swim fast in closed circles while chasing prey. They also may burst and change their swimming direction by 180° in a sudden manner.
- *Cooperative feeding* Individuals surface at regular intervals in a coordinated manner, exhibiting a circular swimming pattern. Other dolphins cross inside the circle with no clear direction. The size of the groups can reach up to 30 individuals. Dolphins were also seen displaying coordinated swimming, creating a front line of 5–10 individuals, moving in the same direction. Dolphins in the edge of the formation suddenly overtake the others and turn 180°. At this moment (at very close range observation), it was possible to see dolphins feeding on small fishes that were trapped by this maneuver.
- *Resting* Resting dolphins remain stationary at one location, with their heads facing one direction. They often rest alone although resting groups of up five individuals are not uncommon. Dolphins remain at the surface floating motionless for up to 1 min while drifting, generally followed by two to five short dives. Occasionally, these short dives are followed by a longer submersion.
- *Socializing* This behavioral state includes events like jumps, slaps, mating, chase, and rubbing. No forward movements are detected. When an individual in a group was seen performing an aerial display (not porpoising), the entire group was recorded as socializing.
- *Directional swimming* During directional swimming, individuals maintain a constant swimming direction up to a couple of minutes. The directional swimming could be classified as slow, characterized by a slow movement where only the upper part of the head and the dorsal fin are visible, or fast, where movements are faster and a greater portion of the dolphin body may be observed out of the water with intermediate speeds between the two. Finally, within this type of behavior, we included porpoising, when almost all the body comes out of the water but the flippers remain in contact with the water surface.

Usually, dolphins in a group were engaged in the same behavior. When dolphins in the group displayed different behaviors, the behavior displayed by the majority of the individuals was assigned to the group. When the activity of a group could not be assigned to any of these categories, it was recorded as undefined.

To assess the monthly relative abundance, a sighting per unit effort (SPUE) index was calculated as:

$$\text{SPUE} = \frac{\text{No. of sighted animals in the month}_i}{\text{No. of scans in the month}_i} \quad (1)$$

Sea surface temperature (SST) was recorded by an electronic thermometer onboard a boat once a week when the weather conditions allowed it. The median of the transformed SPUE (transformation $\ln\text{SPUE}$) was regressed against the monthly average SST using the Nair-Bartlett method for a Type II regression model (Sokal and Rohlf 1995). To explore cyclic changes in SPUE and SST, a polynomial regression against month was applied (Sokal and Rohlf 1995). Correlations between tide height and tide gradient were assessed by means of the Kendall's concordance test (Conover 1999).

A Kruskal–Wallis test was used to compare SPUE values among years and a Mann–Whitney test was used to compare group and school size between warm and cold periods. Warm periods, extending from December through April, were designated as “summer”, while the remaining months were grouped into the “winter” category. A Kruskal–Wallis test was also used to compare group and school size among different daily time periods. These periods were defined as morning (0700–1059 hours), noon (1100–1459 hours) and afternoon (1500–1859 hours). Differences in behavior frequencies between seasons and among blocks were assessed by means of a Chi-square test.

Results and discussion

Dolphins were recorded in the study area during 79 of the 114 sampling days. A total of 1051 scans were performed during the scan sampling. A total of 5048 groups of Commerson's dolphins were sighted in 479 scans. Of these groups, 716 were interacting with a dolphin-watching vessel and thus excluded from the analysis, because their behavior is altered by the presence of the boat (Coscarella et al. 2003).

School size

When dolphins were present in the sampling area, on average 18.40 ± 25.71 (mean \pm SE) dolphins were sighted during a scan. The maximum number of dolphins in the area (recorded in a single scan) was 218 individuals

forming 88 groups. The mean school size was smaller in summer (12.89 ± 16.49) than in winter (19.44 ± 26.99) (Mann–Whitney U test, $P = 0.028$). No significant differences were found in the size of the school over the three time blocks during summer (Kruskal–Wallis, $P = 0.486$) or winter (Kruskal–Wallis, $P = 0.095$). The mean size of the schools in the study area was large for this species when compared to previous reports. The majority of the sightings near Tierra del Fuego and the Kerguelen Islands comprised less than 15 individuals (Goodall et al. 1988; Robineau 1985). During this study, more than 20% of the schools comprised over 20 dolphins. This is likely to be an underestimated value as the actual number of individuals in the area could be higher than the reported depending on swimming synchronization, dive length, and the distance to the vantage point.

Group size

Mean group size was slightly smaller in summer (1.68) than in winter (1.81; Mann–Whitney U test, $P = 0.041$). For summer, no differences were found in the size of the group regarding the time block (Kruskal–Wallis, $P = 0.186$). For winter, it differed between time blocks (Kruskal–Wallis, $P = 0.0489$), with the larger groups recorded during the afternoon. Group size varied with behavior (Kruskal–Wallis, $P < 0.001$). Dolphins occurred in larger groups when performing activities related to feeding (Table 1). The size of the group while socializing, resting, and displaying directional swimming did not differ from each other (Table 1). Our results indicated that average size of the groups is 1.72 dolphins; this value is close to the reported in previous works from South America and the Kerguelen Island, where the reported group size is 2 individuals (ranging from 1 to 4 individuals) (Robineau 1985; Venegas and Atalah 1987; Goodall et al. 1988; Venegas 1996; Lescrauwaet et al. 2000; Pedraza 2008).

Behavior patterns

Individual feeding was recorded for 938 (21.47%) groups, of which 51.34% were associated with terns. The individual feeding behavior recorded in this study is similar to those described for Chilean (*C. eutropia*) and Hector's dolphins (*C. hectori*) (Crovetto and Medina 1991; Bräger 1998). Several individuals in close proximity can simultaneously perform individual feeding.

Cooperative feeding can be considered as a rarely observed behavior, as it was only performed by 48 (1.1%) groups. Terns were associated with 84.62% of these groups. Cooperative feeding has been described for Hector's and Chilean dolphins, representing up to 9% of

Table 1 Q nonparametric multiple comparisons test for the hypothesis that the group sizes of Commerson's dolphin (*Cephalorhynchus commersonii*) are the same for all the behaviors ($Q_{0.05,6} = 2.936$)

	Directional swimming	Resting	Individual feeding	Undefined	Socialization	Cooperative feeding	Mean group size \pm SE
Directional swimming		1.393	10.338*	4.082*	0.083	13.005*	1.59 \pm 0.96
Resting	41.260		8.692*	4.692*	0.608	12.605*	1.71 \pm 1.25
Individual feeding	45.368	47.346		9.199*	5.41*	10.002*	2.11 \pm 1.51
Undefined	86.119	87.177	89.194		3.185*	13.711*	1.30 \pm 0.64
Socialization	82.223	83.330	85.439	112.508		11.831*	1.82 \pm 2.46
Cooperative feeding	161.676	162.242	163.335	178.987	177.146		6.27 \pm 3.25

The SE for the test values are in the lower diagonal of the matrix, while the statistic values (q) are in the upper diagonal

* Statistically significant

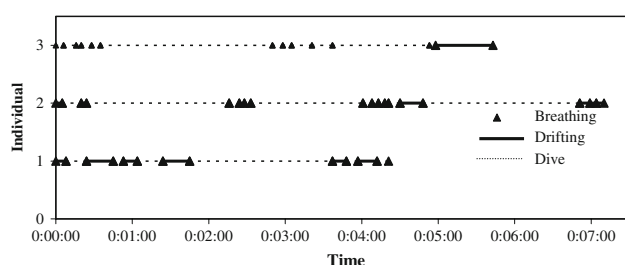


Fig. 2 Breathing sequences of three individual Commerson's dolphins (*Cephalorhynchus commersonii*) during resting. The pattern shows the sequence of short dives followed by long dives intermingled with drifting episodes

the observed behavior for the latter species (Crovetto and Medina 1991; Bräger 1998; Ribeiro et al. 2007). Dusky dolphins (*Lagenorhynchus obscurus*) feeding on Argentine anchovy (*Engraulis anchoita*) in Patagonia only feed cooperatively (Würsig and Würsig 1980; Degrat et al. 2008). Anchovy is also a prey species for Commerson's dolphin (Crespo et al. 1997), and thus it is possible that Commerson's dolphins may feed on this species in the study area.

Resting was recorded for 1,292 (29.58%) groups of Commerson's dolphins. Rest in the species includes drifting episodes. While at the surface, we observed resting individuals take several breaths, and then dive for up to 2 min and emerge to breathe near the same location (Fig. 2). In captivity, Commerson's dolphins present a "bobbing" or "hanging" behavior, floating motionless at the surface for a few moments, usually accompanied by hyperventilation (Shochi et al. 1982; Kastelein et al. 1993; Cornell et al. 1998; Shpak et al. 2009). While submerged, dolphins show no sign of activity, and this behavior was always accompanied by a series of inspirations (2–6) with short intervals (Shpak et al. 2009).

Socializing occurs at low frequency (it was recorded for only 203 or 4.65% of the groups) possibly because part of the social interactions may take place underwater.

Although highly conspicuous at the surface, they are barely visible underwater, so it is extremely difficult to follow the entire behavioral sequence. This can negatively bias the frequency of this behavior.

Directional swimming This species is characterized by erratic swimming patterns, although this behavior was displayed by 1,604 (36.72%) groups. The directional swimming displayed by Commerson's dolphin is a behavioral state which does not exactly match previously described behavior of other species. When engaged in this behavior, Commerson's dolphins swim in a straight line, maintaining the same direction while moving forward at different speeds. Directional swimming does not last long, and is usually intermingled with other behaviors such as feeding. This kind of behavioral sequence has also been suggested for dusky dolphins in northern Patagonia (Garaffo et al. 2007).

Frequencies of the behaviors

The frequencies of the behaviors change between periods. More dolphin groups are found in directional swimming during winter while resting is more common during summer (Fig. 3; Chi-square test, $n = 4,268$, $df = 6$, $P < 0.001$). Individual feeding did not change its relative frequency between periods. Frequencies of behaviors also change with the time blocks during winter (Chi-square test, $n = 3,763$, $df = 10$, $P < 0.001$). The main activity in the three time blocks is directional swimming, followed by resting and individual feeding. The highest individual feeding frequency was recorded during the morning, progressively decreasing during the day, and reaching the lowest frequency during the afternoon. Resting peaked at noon and directional swimming during the afternoon. The socializing frequency reached its highest point after the decrease in feeding activities, suggesting that social activities take place after the dolphins had fed (Fig. 3). This pattern has also been suggested for other species (i.e., dusky and bottlenose dolphins *Tursiops truncatus*) (Würsig

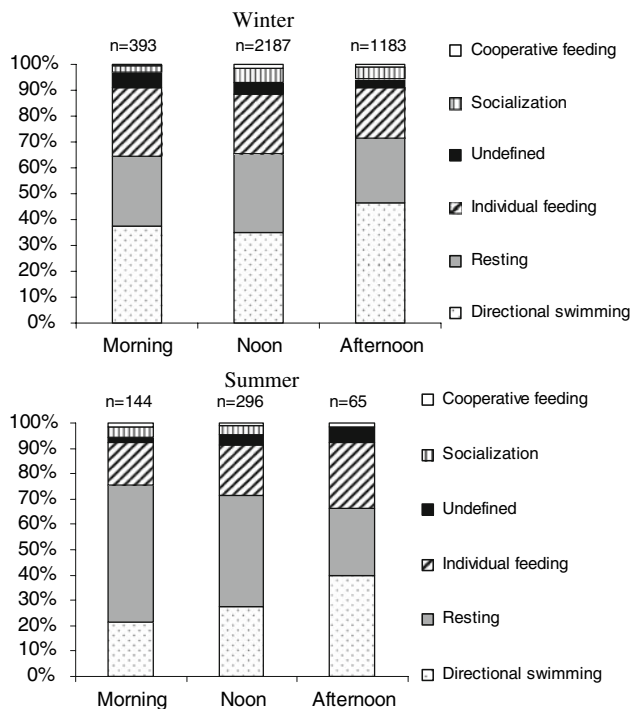


Fig. 3 Relative frequency of activities performed by dolphin groups in the area for winter and summer

and Würsig 1980; Bräger 1993). The changes in frequencies of behaviors with time blocks follow a different pattern during summer (Chi-square test, $n = 505$, $df = 10$, $P = 0.025$). More groups rest during the morning and early afternoon, with directional swimming and feeding behaviors increasing during the afternoon and evening (Fig. 3). In captive animals, resting was reported as occurring after feeding and at the time of the day when the temperature was highest (Shochi et al. 1982; Kastelein et al. 1993). This may well explain why more groups are found resting during summer than in winter. Likewise, during the winter, the peak of resting activities occurred at noon, after feeding, which constituted the second most recorded activity during the morning.

It is remarkable that directional swimming increases during the afternoon in both periods. This may indicate that dolphins move progressively away from the area during the night. This kind of movement between daytime and nighttime areas was recorded for other species, including the spinner (*Stenella longirostris*) and the dusky and Hector's dolphins; all of these cases were related to the bathymetry or geographic features of the area (Norris and Dohl 1980; Würsig and Würsig 1980; Stone et al. 1995). This is not likely that this is the case for the Commerson's dolphins in the Bahía Engaño area, where deep water is far away from the coast. It is more likely that these movements could be related to feeding activities as in the case of the Heaviside's dolphin (*C. heavisidii*) (Elwen et al. 2006).

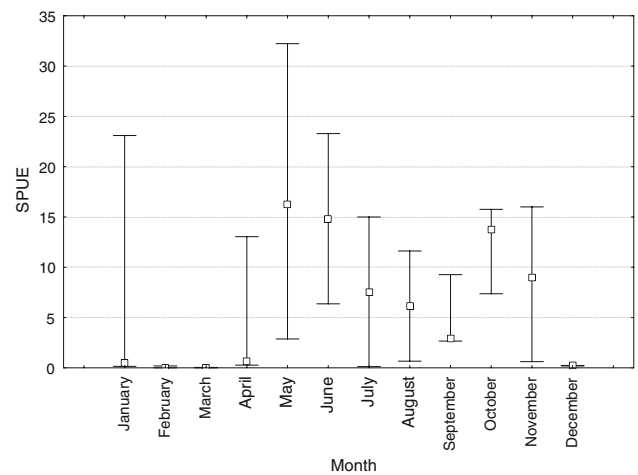


Fig. 4 Monthly median SPUE. The error bars are the minimum and maximum values of the PSUE

Variation in the relative abundance related to environmental parameters

The median value of SPUE was 2.66 (0.1924; 13.75). The SPUE values showed no differences between years (Kruskal–Wallis, $P = 0.352$), but were different between months (Kruskal–Wallis, $P < 0.020$) and between periods (Mann–Whitney U test, $P < 0.001$). Figure 4 shows that the lower SPUE values are recorded from December to April.

The fitted regression model was

$$SPUE = e^{(7.042 - 0.494 \cdot SST)}, \quad (2)$$

where r^2 is 0.617 and 95% CI of a coefficient on SST is -0.751 to -0.257 . This shows that dolphins are less abundant during summer than during winter.

The SPUE was regressed against the month using cubic polynomial model, with a $r^2 = 0.65$ (analysis of variance, $F = 4.994$, $P = 0.032$; Fig. 5). Commerson's dolphins remained in Bahía Engaño throughout the year, although the sightings were significantly reduced during warmer months. SST in the study area ranged from 6.5 to 19.9°C, with December–April as the months when the average temperature increases above 15°C, and the abundance tended to be low. Goodall et al. (1988) suggested that 16°C is the maximum temperature where this dolphin species will occur.

The decrease of the relative abundance during the summer can be interpreted as a change in seasonal abundance in the northern boundary of the species range. Seasonal shifts towards deeper waters during colder months in South America have been proposed (Venegas and Atalah 1987; Goodall et al. 1988; Venegas 1996). For the Kerguelen population, Robineau (1985) proposed that dolphins

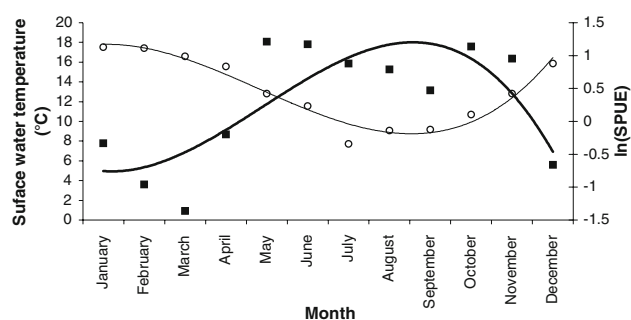


Fig. 5 Fitting of the $\ln(\text{SPUE})$ and the surface water temperature to the month. The lesser values of the $\ln(\text{SPUE})$ are obtained for the month where the surface water temperature is over 15°C , while the largest are attained during months with a mean water temperature below 15°C . Open circles mean monthly temperature, thin line fitted curve for the temperature, filled squares $\ln(\text{SPUE})$, thick line fitted curve for the $\ln(\text{SPUE})$

change their location from the Morbiham Gulf for other coastal areas of the island but do not migrate to open waters. We propose that dolphins in Bahía Engaño move southward during warmer months, since dolphins photo-identified in the study area were sighted in Bahía Camarones during summer, over 250 km to the south (Coscarella 2005).

Generally, changes in the distribution and local abundance of cetacean species are considered to be strongly related to prey availability (Gowans et al. 2001; Weir et al. 2007). Particularly for Commerson's dolphin, it has been suggested that seasonal movements occur primarily as a response to variation in prey abundance (Goodall et al. 1988). In central Patagonia, post-larval hake (*Merluccius hubbsi*) appear as the most important prey found in entangled dolphins (Crespo et al. 1997), but during this study, Commerson's dolphins were seen chasing and feeding on small silverside-like fishes, such as *Sorgentinia incisa* and *Odonthestes* spp. (Atherinidae) and Argentine anchovy, even though no species determination was possible. According to Mermoz (1980), silversides and anchovies are important food items for this dolphin. Moreover, silversides and the anchovy-like fuegian sprat (*Sprattus fueguensis*) are important food items for Commerson's dolphin in Santa Cruz and Tierra del Fuego provinces (Bastida et al. 1988; Iñiguez et al. 2000).

Changes in prey availability might also be related to water temperature. The Patagonian stock of Argentine anchovy is considered to be present between 41°S and 45°S in coastal waters ranging from 12.5 to 16°C of SST and concentrated around Isla Escondida ($43^{\circ}30'\text{S}$) during spring (Hansen et al. 2001). Nonetheless, anchovies are widespread and abundant throughout the year in the area, and Commerson's dolphins are rarely found farther north than 42°S (warmer waters). On the other hand, little is

known about the seasonal distribution of the silversides (*S. incisa* and *Odonthestes* spp.), which, as suggested by fishing records and a few oceanographic surveys, seem to remain in coastal waters throughout the year (Cosseau and Perrotta 1998). All the information concerning movements of the potential prey species is based on a regional scale, and how fine-scale environmental conditions affect the distribution of these fishes within small estuarine areas like Bahía Engaño is unknown.

Tide is yet another environmental variable likely to affect the distributional pattern of Commerson's dolphins. Bahía Engaño is an open bay, with a 12-h tidal cycle and annual average amplitude of about 2.81 m. Our field observations revealed that the tidal cycle had no effect on the presence of the dolphins in the area as no concordance was found between the number of dolphins in a particular scan versus the height of the tide for that scan (two-tailed $\tau = 0.030$, $Wp = -0.13$), the gradient of the tide height (one-tailed $\tau = 0.108406$, $Wp = -0.11$), nor the module of this gradient (one-tailed $\tau = -0.022$, $Wp = -0.11$). In Tierra del Fuego, in the Strait of Magellan, no relationship was found whatsoever with tide (Leatherwood et al. 1988), but in Santa Cruz province, Commerson's dolphins occurring inside closed bays and sea lochs move up the loch during flood tides and exit during ebb tides (Tomsin et al. 2002). This is probably related to the physical and geographical characteristics of this area, such as depth and presence of prey during ebb tide.

Terns associations with dolphins

Three tern species were identified interacting with dolphins: the South American tern (*Sterna hirundinacea*), the Cayenne tern (*Thalasseus sandvicensis eurygnatha*), and the Royal tern (*T. maximus*). During the association episodes, the terns hovered from 2 to 10 m above the dolphin following changes in the dolphin's direction, usually plunge-diving in front of dolphins. In the present study, terns were associated with 15.89% of the dolphin groups independently of the behavior exhibited. From the total number of groups with which the terns interacted, those engaged in feeding activities accounted for 72.53%, reaching a proportion of 84.62% when only the groups of dolphins engaged in cooperative feeding are considered. The median number of terns hovering over the dolphins was different depending on the behavioral state (Kruskal–Wallis, $n = 667$, $P < 0.01$). The larger flocks were associated with feeding activities. These associations could be interpreted as a commensal feeding behavior of terns. A correlation was found between the number of birds comprising the flock and the number of dolphins in the group for cooperative feeding (Spearman $r = 0.671$, $P < 0.001$). This correlation indicates that the larger the feeding group,

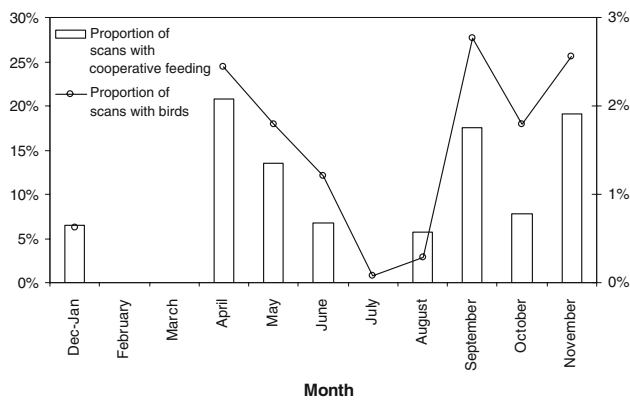


Fig. 6 Proportion of scans where cooperative feeding was recorded (right axis) and proportion of scans with birds hovering over dolphins (left axis)

the larger the associated flock. A similar association was also reported for white-fronted tern (*Sterna striata*) with Hector's dolphin off New Zealand, but only 2.9% of the Hector's dolphin groups were associated with terns, with a tendency for terns to occur more frequently over larger groups of dolphins (Bräger 1998).

The proportion of terns associated with dolphin groups throughout the year was variable. The highest proportion of associations occurred in April, then declined until July, and rose again between September and November. From December until March, the proportion was again low, less than 6% (Fig. 6). The higher frequency of associations recorded during September–November (spring) may also be reflecting an increase in concentrations of Argentine anchovies around the Bahía Engaño area (Hansen et al. 2001). The Cayenne and the Royal terns are known to feed upon Argentine anchovies and silversides in the area (Mermoz 1980; Quintana and Yorio 1997), the same putative prey species for Commerson's dolphins in Bahía Engaño. However, information regarding stock abundance and migration patterns of Argentine anchovy (or for that matter of silverside species) is scarce, making it difficult to evaluate the potential relationship between the increase in tern-dolphin associations and prey abundance.

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