

# Behaviour of Chilean and Peale's dolphins in southern Chile: interspecific variability of sympatric species

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*Assessing the behavioural patterns of animals is an increasingly important field in conservation biology, as it may assist in the prediction of how animals respond to rapid changes in the environment. Comparing the behavioural patterns of sympatric species can also give insights into the mechanisms that allow similar species to coexist. We undertook dolphin group follows in order to quantify the behavioural patterns of the sympatric Chilean and Peale's dolphins in southern Chile. Markov chains showed that these species differed significantly in time allocated to each of the five different behavioural states, but travelling was the most frequent behavioural state observed for both species. Six (out of 25) behavioural transitions were found to be different between species. In addition, group size and group dispersion were highly associated with specific behavioural states. Larger groups were more likely to socialize, while small groups were more likely to rest. For both species resting was mostly observed in tight groups, while foraging/feeding and travelling were related to intermediate group dispersion. Socializing differed between species, occurring in tight groups for Peale's dolphins and dispersed groups for Chilean dolphins. Overall, there were significant differences in behavioural patterns between the two species. These dissimilarities may represent evidence of different strategies (i.e. habitat use patterns and foraging) these two species employ which allow them to coexist. The information generated in this study will contribute to the development of better predictive models on how animals may respond to a changing environment and to the potential effects of human induced activities.*

**Keywords:** dolphin sympatry, behavioural patterns, northern Patagonian fjords, Markov chains

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## INTRODUCTION

The Chilean dolphin (*Cephalorhynchus eutropia*, Gray, 1846) and Peale's dolphin (*Lagenorhynchus australis*, Peale, 1848) are two species inhabiting the coastal waters of Chile and Argentina. Both species are sympatric on the Chilean coast from 33°S to 55°S (Goodall, 1994; Goodall *et al.*, 1997). Although that these two species are the most frequently observed of all cetaceans in southern Chile (Viddi *et al.*, 2010), our knowledge about their ecology and conservation status is limited. They are among the least known species in the dolphin family.

Due to their near-shore and restricted distribution, Chilean and Peale's dolphins are subject to direct and indirect anthropogenic threats, including incidental takes (by-catch) in local fisheries and the progressive destruction of potentially critical habitat (Hucke-Gaete *et al.*, 2006). The Chilean dolphin, the only endemic cetacean in Chile, is listed as 'Near Threatened' (Reeves *et al.*, 2008) and Peale's dolphins as 'Data Deficient' (Hammond *et al.*, 2008) by the International Union for the Conservation of Nature (IUCN).

In the last five years, there has been progress in the information generated on both Chilean and Peale's dolphins, though there are still important gaps in knowledge and therefore an urgent need for research on these species. Most research until

now has principally focused on distribution, habitat selection and patterns of movement (Viddi & Lescrauwaet, 2005; Heinrich, 2006; Ribeiro *et al.*, 2007; Viddi *et al.*, 2010, 2011), while other aspects have been overlooked, including behavioural patterns. This is mainly because some researchers mistakenly believe that data on behaviour have little applicability to understanding ecological processes or because these data have little contribution to make towards the conservation and management of species. However, the truth is that behaviour of animals characterizes the relationships among species and plays a significant role in ecological processes (Dingle *et al.*, 1997). Moreover, behaviour is an important component of the adaptive complex that allows animals to function (Bartholomew, 1970) and is shaped by the interactions between the environment and the genetic make-up of individuals (Wells *et al.*, 1999). Activity patterns of animals result from a complex balance and trade-offs of energy saving and expenditure, which is related to the needs of finding food, refuge, resting, reproduction and socializing (Nielsen, 1983). As this balance shifts, so do activity budgets. Consequently, behavioural patterns can indicate significant demographic or environmental alterations, resulting from natural phenomena or from human-induced activities (Parrish, 2005), as the development of behaviour is directly linked to the flexibility of animals to adapt to variable ecological conditions (Hall *et al.*, 1998).

Accordingly, behavioural studies can have direct application to conservation (Caro, 1998). For instance, changes in the behavioural patterns of several cetacean species have

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been related to boat traffic (Lusseau, 2003; Ribeiro *et al.*, 2005; Dans *et al.*, 2008, 2012; Lusseau *et al.*, 2009) and to climate variability (Lusseau *et al.*, 2004) and their potential negative effects on populations. Furthermore, understanding the behavioural patterns of sympatric species is crucial in order to gain insights into the mechanisms by which similar species coexist (Perri & Randall, 1999). Different activity budgets between species may indicate differences in energy requirements, foraging strategies and different ways of responding to the characteristics of the environment.

There are many studies of cetacean behaviour, but only a few have included an interspecific comparative approach (Parra, 2006). Regarding Chilean and Peale's dolphins, some studies have addressed behaviour (Lescrauwaet, 1997; Viddi & Lescrauwaet, 2005; Ribeiro *et al.*, 2007), but none have systematically and comparatively assessed the activity budgets and behavioural patterns of both species. Considering that dolphin-watching may become an important economic activity in southern Chile, here we compared the behavioural patterns of the Chilean and Peale's dolphins in southern Chile in order to build a practical baseline framework from which to assess potential effects of anthropogenic activities.

## MATERIALS AND METHODS

### Data collection

Boat-based surveys were conducted during January–April 2007, 2008 and 2009 in the waters off Guaitecas Archipelago in the Chilean Northern Patagonian fjords ( $43^{\circ}52'S$   $73^{\circ}45'W$ , Figure 1). Surveys were undertaken by two or three observers on-board a rigid-hulled inflatable boat 5 m long with an outboard four-stroke 25 hp engine. Observers

looked for dolphins with naked eye or  $7 \times 50$  binoculars, covering a strip of about 300 m ahead and  $90^{\circ}$  to each side, at a searching speed of 8 knots. Upon sighting a group of dolphins, search effort was interrupted in order to record dolphin behavioural states, group size and group dispersion. Data on weather conditions (sea state, cloud cover, wind direction and relative strength) were also recorded.

A group of dolphins was defined by spatial proximity. Animals within a radius of 50 m were considered to be part of the same group. Under this definition, dolphins are part of a group as long as they are within this radius. This 'distance measure' definition of a group was chosen over a 'coordinated activity' definition for its simplicity and because it does not rely on any explicit or implicit assumptions about the behaviour of a group's member (Mann, 1999).

Dolphin behavioural states were assessed by 'group-follow' protocol and 'scan sampling' method (Martin & Bateson, 1993; Mann, 1999). Instantaneous scan samples were taken at 2 min intervals of all individual dolphins on the surface. A behavioural state for the group was assigned as the predominant behaviour in which most of the individuals were engaged (more than 50% of the animals).

Behavioural states recorded included:

- Foraging/feeding (F): frequent dives characterized by steeply downward movements sometimes preceded by fluking up or peduncle arches. Dolphins may be seen swimming in circles, or swimming in parallel formation, with fast, directional and synchronized movements. Dolphins may be observed engaging in rapid chases of fish, or observed with fish in their mouth. Fish may be seen leaping out of the water.
- Milling (M): animals move slowly, with repeated unsynchronized dives in different directions in a determined

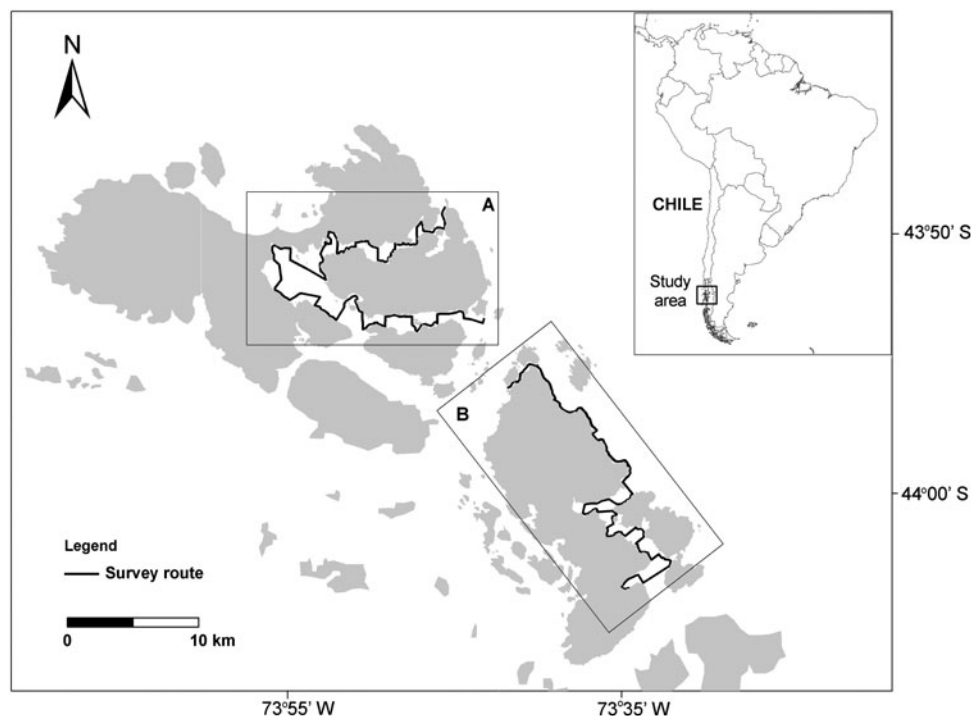


Fig. 1. Study area in Southern Chile, showing an inset of the location of Guaitecas Archipelago and the two sub-areas: (A) Puquiting; (B) Leucayec. Main boat routes also shown.

location. Movement has no apparent direction, short dives at different intervals.

- Travelling (T): directional and persistent movement at speed with regular patterns of surfacing. Dive angles shallow.
- Resting (R): very slow movements with no direction, or staying still at the surface from several seconds to minutes.
- Socializing (S): inter-individual interactions within a group, in frequent physical contact, rubbing, chasing each other, with frequent vigorous movements.

Group dispersion was defined by inter-individual spatial proximity, or spread between dolphins in groups, and was also recorded by instantaneous sample at 2 min intervals. Mode nearest neighbour distance in adult dolphin body lengths was classified as (a) tight: animals <1 body length apart; (b) intermediate: 1–3 body lengths apart; and (c) disperse: >3 body lengths apart.

Because group size in both Chilean and Peale's dolphins is relatively small (medians 2 and 4, respectively) and individual animals are hard to identify for both species, scan sampling on group follows was chosen as the best method to record behavioural data (Mann, 1999; Whitehead, 2004). Group-follow was chosen over a survey protocol, as dolphin group encounter rate is higher than the rate of change of behavioural state (Whitehead, 2004).

Focal group behavioural samples were designed to maximize time with dolphins, rather than collect a specific time with a single group and then continue the track in search of another new group. This rule was undertaken because sighting rate was, in general, low (Viddi, 2009). Dolphin follows were conducted as long as the group was in sight, so long as weather and light conditions permitted. To minimize disturbance of dolphins, and, therefore, reduce any bias due to the presence of the research boat, a four stroke engine was used and an average distance of 250 m was kept from the dolphins. Under many situations, the engine was in fact kept turned off. Finally, only groups which were followed more than 30 min and did not appear to react to the boat (e.g. bow-riding) were included in the analysis.

## Data analysis

Sequences of behavioural states for both species were assessed by transition probabilities and Markov chains. In this study the main interest was to understand the change in the likelihood that when a dolphin group was in a 'behavioural state A' they would be in 'behavioural state B' two minutes later (at the next sampling interval). In this case, it was assumed that the succeeding behavioural state was only dependent on the preceding state, thus the analysis on behaviour transition was based on first order Markov chains (Caswell, 2001; Lusseau, 2003).

Transition matrix analysis assumes that the transition probabilities remain constant across time, an assumption called stationarity (Martin & Bateson, 1993; Lehner, 1996). To assess stability over time, a three-way contingency table of  $5 \times 5 \times 4$  was designed (preceding behavioural state versus succeeding behavioural state versus season). Season included four time blocks: January–February 2007, March–April 2007, January–February 2008 and March–April 2008 (data from year 2009 were not included into transition matrices as sample size for this year was too small). If the transition

probability was stable over time, season had no effect on the outcome of the transition. The effect of season on transitions was analysed by log-linear models of the three-way contingency table. The fully saturated model was compared to the model with all two-way interactions using  $G^2$  statistics (Quinn & Keough, 2002).

By pooling data from all seasons, a two-way  $5 \times 5$  contingency table was developed for each species, which included the frequencies of preceding behavioural state versus succeeding behavioural state. From these, the transition probabilities were calculated as:

$$p_{ij} = \frac{a_{ij}}{\sum_{j=i}^5 a_{ij}} \quad \text{and} \quad \sum_{j=i}^5 p_{ij} = 1$$

where  $p_{ij}$  is defined as the transition probability in the Markov chain from behavioural state  $i$  to behavioural state  $j$ ,  $a_{ij}$  is the number of 2 min intervals in which state  $i$  was followed by state  $j$  ( $i$  and  $j$  ranges from 1 to 5 because there are five behavioural states).

To determine if the transition probabilities differed significantly from a random transition model, a  $\chi^2$  test was performed (Lehner, 1996). A significant difference would indicate that the behavioural patterns observed were in fact sequentially dependent (Martin & Bateson, 1993). The difference in the transition probability matrix between species was compared through a Pearson's  $\chi^2$  two-sample test for equality of proportions with continuity correction (Newcombe, 1998).

Markov chains have ergodic properties because the transitions between all states are possible (Caswell, 2001). A group of dolphins could be involved in a transition from any state to another, as there are no biological restrictions preventing dolphins from changing between one state and the others (Lusseau *et al.*, 2009). Hence, the probability of observing a specific activity at a specific time for each species was calculated from the left eigenvector,  $\mathbf{v}$ , of the matrix. This vector represented the stationary distribution of a Markov chain, and its components  $v_i$  summed up to 1. Here,  $\mathbf{v}$  represents the behavioural budget of dolphins and each,  $v_i$ , represents the proportion of time spent in activity,  $i$ . The left eigenvector was obtained with PopTools 3.1 (available from <http://www.cse.csiro.au/cdg/poptools>). The difference between the behavioural budgets between Chilean and Peale's dolphins was assessed by Pearson's  $\chi^2$  two-sample test for equality of proportions with continuity correction.

The association between behavioural states and group size was assessed by Kruskal–Wallis rank sum test. The association between behavioural states and group dispersion, as well as frequency of events was evaluated by correspondence analysis (Lehner, 1996).

All statistical analyses were made in R v.2.9.1 (R Development Core Team, 2009).

## RESULTS

### Survey effort, data summary and temporal patterns

Over the three fieldwork summer seasons of 2007, 2008 and 2009, a total of 54 surveys were conducted, which

**Table 1.** Total number of surveys, hours of effort, number of dolphin groups followed and analysed (number in parenthesis are the total number of groups encountered), time with dolphins and group size for each species for each field season.

	2007	2008	2009	Total
Number of surveys	23	26	5	54
Effort (h)	118.6	142.3	29.8	290.7
Groups of Chilean dolphins	9 (19)	16 (24)	2 (3)	27 (46)
Groups of Peale's dolphins	22 (38)	36 (73)	5 (16)	63 (127)
Total number of groups	31 (57)	52 (97)	7 (19)	90 (173)
Time with Chilean dolphins (h)	12.3	16.7	2.5	31.5
Time with Peale's dolphins (h)	25.6	34.9	3.9	64.4
Total time with dolphins (h)	37.9	51.6	6.4	95.9
Chilean dolphin average group size	5.1	5.2	3.2	5.1
Peale's dolphin average group size	6.2	6.7	4.3	6.3

encompassed 290 h on effort searching for dolphins. 173 dolphin groups were encountered for which groups follows were attempted. However, only 90 groups were analysed, which were followed for more than 30 min, representing 95.9 h of total net time following dolphins. Mean duration of group follows was 82.8 min (standard deviation (SD) = 51.31) for Chilean dolphins, ranging from 30 to 240 min, whereas for Peale's dolphin mean duration time was 67.7 min (SD = 36.39) ranging from 30 to 196 min. The difference in time following dolphins was not significant between species (*t*-test,  $t = -1.34$ , d.f. = 34.5,  $P = 0.189$ ). Number of dolphin groups sighted, time on effort, time with dolphins and dolphin group size all varied between species and are summarized in Table 1.

### Markov chains: behavioural sequence and budget

The transition probability matrices for both Chilean and Peale's dolphins were stable over time ( $G^2 = 59.95$ , d.f. = 48,  $P = 0.116$  and  $G^2 = 58.87$ , d.f. = 48,  $P = 0.135$ , respectively). The transition probabilities for both species were significantly different from a random transition model (Chilean dolphins,  $\chi^2 = 1934.8$ , d.f. = 16,  $P < 0.001$ ; Peale's dolphin,  $\chi^2 =$

3504.4, d.f. = 16,  $P < 0.001$ ), indicating that the behavioural patterns showed by these species are sequentially dependent (Figure 2).

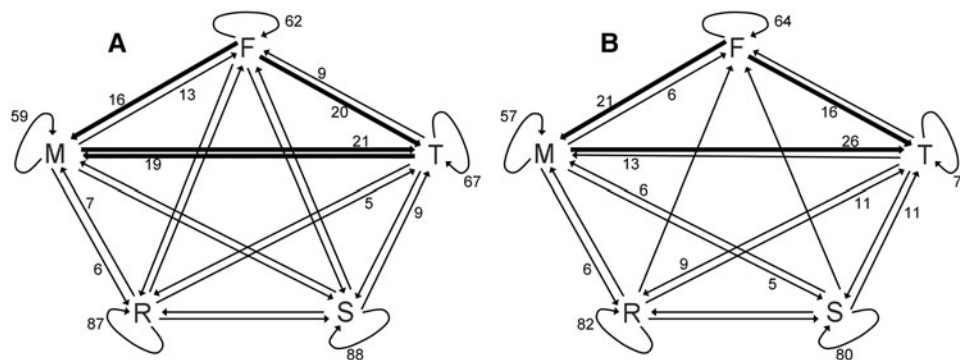
From the 25 behavioural transitions, only six were significantly different between species. The transition probabilities  $M \rightarrow F$ ,  $T \rightarrow F$  and  $T \rightarrow M$  were higher for Chilean dolphins, whereas the transitions  $M \rightarrow S$ ,  $R \rightarrow T$  and  $T \rightarrow R$  were higher for Peale's dolphins (Figure 3).

The Markov chain model predicts that Chilean dolphins invest most of their time in travelling and less in socializing (30.8% and 7%, respectively). Peale's dolphins also invest more time in travelling, but less in feeding/foraging (35.6% and 8.8%, respectively, Table 2). For all behavioural states, Chilean and Peale's dolphins differed significantly in the time allocated to each behavioural state (behavioural budget). The Markov chain model predicts that Chilean dolphins invest more time in feeding/foraging and milling than Peale's dolphins, whereas the latter invest more time in resting, socializing and travelling when compared with Chilean dolphins (Table 2)

### Behavioural states versus group size, group dispersion

For Peale's dolphins, bigger groups engaged mostly in socializing and feeding/foraging while small groups were more associated with resting (Kruskal–Wallis test,  $K-W = 216.4$ , d.f. = 4,  $P < 0.001$ ). Chilean dolphins bigger groups were also significantly more associated with socializing, and as Peale's dolphins, small groups were related with resting (Kruskal–Wallis test,  $K-W = 205.9$ , d.f. = 4,  $P < 0.001$ ; Figure 4).

Correspondence analysis showed that group dispersion and behavioural state for Peale's dolphins was significantly associated ( $\chi^2 = 190.41$ , d.f. = 8,  $P < 0.001$ ). Two eigenvectors were extracted which explained 100% of the total inertia (88.5% and 11.5%, respectively). Socializing and resting were associated with tight groups, feeding/foraging and travelling with intermediate dispersion and milling was more associated with dispersed groups (Figure 5). For Chilean dolphins, the association between group dispersion and behavioural state was also significant ( $\chi^2 = 118.01$ , d.f. = 8,  $P < 0.001$ ). Two eigenvectors were extracted which explained 100% of the total inertia (72.5% and 27.5%, respectively). Resting was associated with tight groups, feeding/



**Fig. 2.** Markov chains representing probabilities of transition in behavioural states: (A) Chilean dolphins; (B) Peale's dolphins. Values represent round percentages. Values less than 5% have been omitted. Thicker arrows represent values over 15% and the absence of arrows represents lack of transition between any two particular behavioural states.



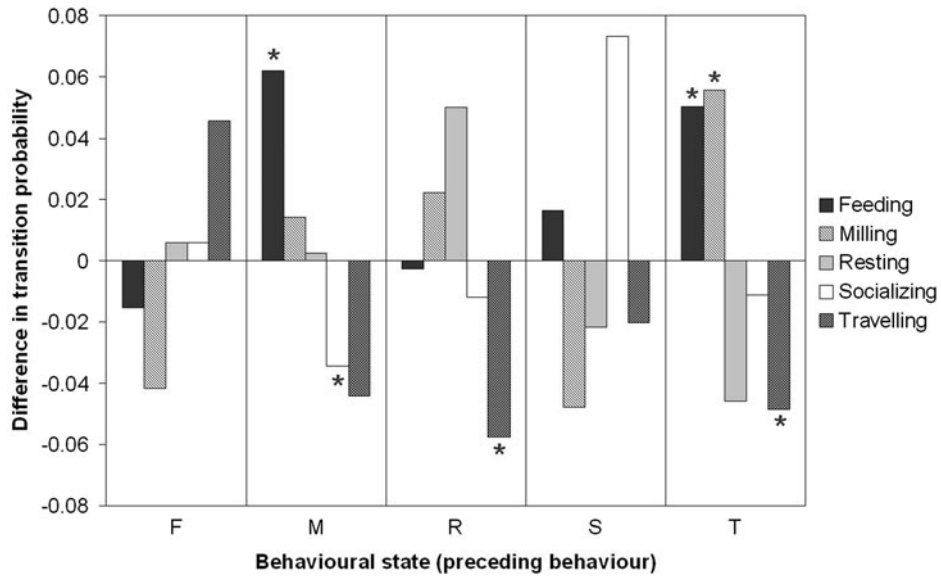


Fig. 3. Differences in transitions probabilities in behavioural states between Chilean and Peale's dolphins ( $p_{ij}(\text{Chilean dolphins}) - p_{ij}(\text{Peale's dolphins})$ ). Negative values indicate that the transition probability for behavioural states for Chilean dolphins is lower than for Peale's dolphins. The six transitions with a significant difference ( $P < 0.05$ ) are denoted by (\*).

Table 2. Differences in time budget of behavioural states for Chilean and Peale's dolphins.

Behavioural state	Time budget (%)		$\chi^2$	P
	Chilean dolphins	Peale's dolphins		
Feeding/foraging	16.4	8.80	44.87	<0.001
Milling	24.1	18.00	11.04	<0.001
Resting	21.7	25.80	15.9	0.015
Socializing	7	11.70	10.07	<0.001
Travelling	30.8	35.60	6.93	<0.001

foraging, travelling and milling were associated with intermediate dispersion and socializing was related strongly with dispersed groups (Figure 5).

DISCUSSION

In this study, Chilean and Peale's dolphin behavioural states did not show any association with season or time of the day. Many studies have demonstrated that other dolphin species exhibit daily and seasonal patterns in their behaviour, which is suggested to be in response to variations in prey abundance and distribution, predator avoidance, reproduction and breeding (Bearzi *et al.*, 1999; Mann *et al.*, 2000; Markowitz, 2004). For instance, studies of bottlenose dolphin (*Tursiops truncatus*), have shown that there is a trend towards increased feeding in the morning and again later around dusk, increased socializing in the afternoon and increased travelling in the afternoon and evening (Hansen & Defran, 1993; Bearzi *et al.*, 1999). Bearzi *et al.* (1999) found extreme variability in bottlenose dolphin behaviour in the Adriatic Sea, particularly

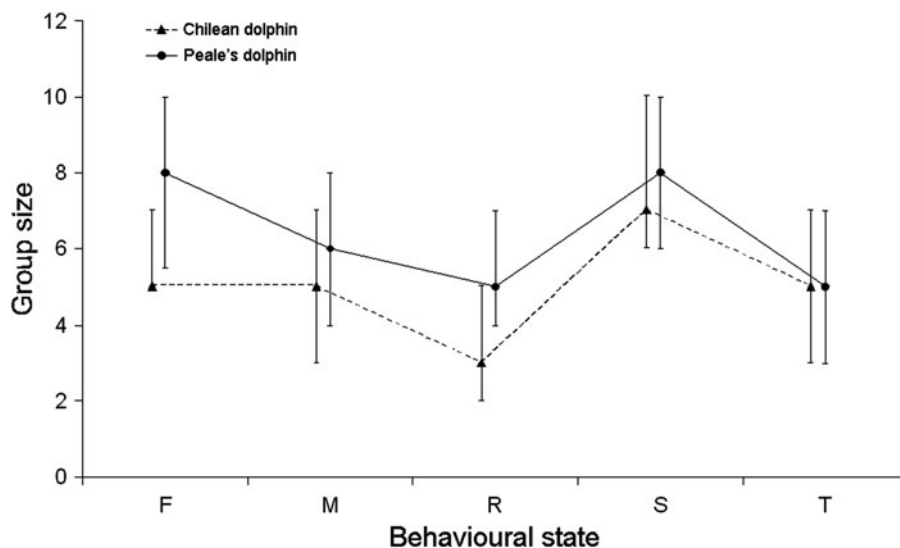


Fig. 4. Behavioural state of Chilean and Peale's dolphins relative to group size. Dots and triangles indicate average, bars represent standard deviation.

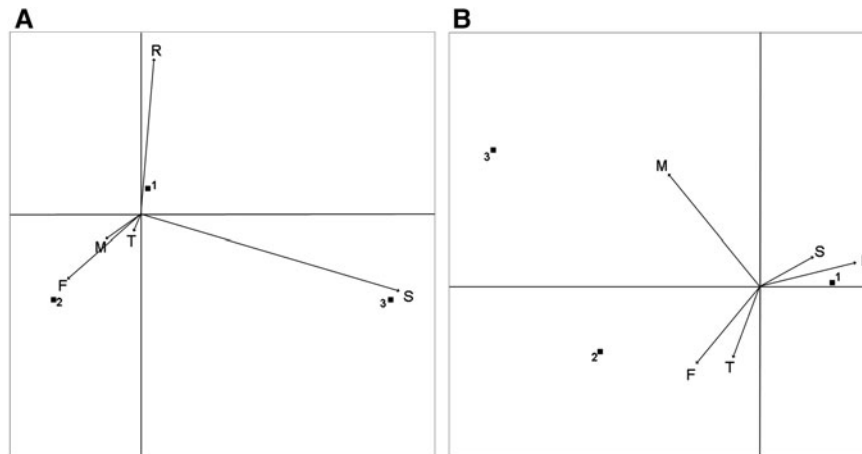


Fig. 5. Correspondence analysis joint plot. Behavioural states in relation to group dispersion for: (A) Chilean dolphins; (B) Peale's dolphins. Group dispersion category: (1) tight; (2) intermediate dispersion; (3) dispersed. F, foraging/feeding; M, milling; T, travelling; R, resting; S, socializing.

with travelling and feeding, and they associated this with prey availability.

The lack of temporal patterns in behaviour for both Chilean and Peale's dolphins may be a response to relatively constant prey availability, also suggested for bottlenose dolphins (Hansen & DeFran, 1993) and dusky dolphins, *Lagenorhynchus obscurus* (Degradi *et al.*, 2008), in Argentina. This may be the case for Peale's dolphins, as they rely strongly on kelp beds (Viddi & Lescrauwaet, 2005; Viddi *et al.*, 2011), which may sustain a more constant prey availability. In addition, a lack of temporality may be also explained by patterns of prey availability other than circadian, such as tidal cycle, which is not constant during the day and changes from one day to the next. Certainly, it has been determined that Chilean dolphins are highly associated with tide regime (Ribeiro *et al.*, 2007; Viddi, 2009).

However, the results presented in this study come from a restricted period of time (only from January to April), so true seasonal patterns through the year are unknown. Reproductive and breeding seasonality is known for Chilean and Peale's dolphins (De Haro & Iñiguez, 1997; Lescrauwaet, 1997). Accordingly, seasonal variation in activity budgets might occur if energy requirements differ through the year, for example if reproduction is temporally concentrated, as has been observed for dusky dolphins in New Zealand (Markowitz, 2004) and bottlenose dolphins in the Adriatic Sea (Bearzi *et al.*, 1999).

All behavioural budgets differed significantly between Peale's and Chilean dolphins, and within species, behaviours were not performed evenly. Peale's dolphins spent most time travelling (>35%), followed by resting, milling, socializing and foraging/feeding. Chilean dolphins, on the other hand, also spent most of their time travelling (>30%), but followed by milling, resting, foraging/feeding and socializing. The proportion of time that Chilean dolphins spent travelling has also been observed in other studies, but the total proportion that this species is engaged in foraging/feeding is below the time it has been documented previously (Ribeiro *et al.*, 2007). However, the results of this study support the notion that Chilean dolphins spend only a small fraction of time in social activities (Heinrich, 2006; Ribeiro *et al.*, 2007).

Peale's dolphins spending more time on travelling is consistent with the observations by Heinrich (2006), but

inconsistent with those by Viddi & Lescrauwaet (2005). These authors found that Peale's dolphins spent most of their time in feeding and foraging behaviours, followed by travelling. Difference in behavioural patterns within the same species has also been observed in the eastern fjords. Peale's dolphins seem to spend more time milling and Chilean dolphins more time feeding and socializing (F. Viddi, unpublished data). It seems reasonable to suggest that activity budgets may vary with habitat and foraging strategies, as different ecological processes would influence energy requirements, as well as the abundance, distribution and quality of prey. Differences in behavioural patterns within species in different habitats have been observed in dusky (Degradi *et al.*, 2008), bottlenose (Bearzi *et al.*, 1999) and humpback dolphins, *Sousa chinensis* (Karczmarski & Cockcroft, 1999). Spending less time foraging/feeding, and also more time resting and socializing, as is the case for Peale's dolphins, is a potential indication that they may be preying on high quality items. The opposite would be the case for Chilean dolphins, as they spend more time in foraging activities and less time in socializing and resting. The relationship between prey quality and behavioural budgets has been the focus of research in several other species (Estes *et al.*, 1982; Doran, 1997; Cruz-Rivera & Hay, 2000).

The difference in behavioural patterns between sympatric species may indicate differences in foraging tactics, selection for different habitat and prey of dissimilar quality, distribution and abundance of prey, as well as specific energy requirements (Ewald & Bransfield, 1987; Perri & Randall, 1999). Indeed, Shane (1990) pointed out that dolphin behaviour can be influenced by a number of ecological variables, and behavioural responses can differ considerably depending on the habitat.

As expected, the probability of a particular behaviour being followed by the same behaviour was high for all behavioural states for both Peale's and Chilean dolphins. From the 25 behavioural sequences, Chilean and Peale's dolphins differed only in six. In general, Chilean dolphins showed a greater probability of transition from milling and travelling to foraging/feeding than Peale's dolphin. This pattern, which may be an important functional component of Chilean dolphins, may be associated with the spatial distribution of prey. The association between travelling and feeding, in which animals move rapidly over areas that are poor in resources and stay

longer in feeding grounds, has been widely reported in cetaceans and other species (Bergman *et al.*, 2000; Mårell *et al.*, 2002; Stevick *et al.*, 2002; Austin *et al.*, 2006; Viddi *et al.*, 2011; Degradi *et al.*, 2012). Peale's dolphins, on the other hand, showed higher probabilities of transition from milling to socializing, resting to travelling and travelling to resting. This pattern is consistent with the behavioural budgets observed for this species, supporting the fact that this species spends only a small fraction in foraging/feeding activities. Indeed, the dissimilar behavioural patterns shown by both Chilean and Peale's dolphins is consistent with the difference found on their habitat preference patterns. Chilean dolphins prefer more turbid waters, areas close to rives and influenced by tide regimes, while Peale's dolphins prefer shallow and clearer waters and are very associated with kelp beds (Viddi, 2009). Interspecific variation on habitat selection and behavioural patterns are a good indicator of difference that dolphins may pose regarding prey quality and abundance consumed, preying tactics and predator avoidance.

Chilean and Peale's dolphin group size differed significantly in relation to behavioural states. For Peale's dolphins, travelling and resting were mostly carried out by small groups, while socializing and foraging/feeding was performed by bigger groups. For Chilean dolphins, groups also tended to be small when resting and bigger when socializing. These results are consistent with the observations by Heinrich (2006) at Chiloe Island and by Viddi & Lescrauwaet (2005) in the Magellan Strait, southern Chile. Patterns of association between group size and behavioural states are well documented for dolphin species. It is suggested that grouping in dolphins decreases predation risk, enhances foraging efficiency (Würsig, 1986) and increases the probabilities of finding reproductive mates while socializing (Connor, 2002). However, as proposed by Connor (2002), the size of prey schools may restrict the size of cooperative groups. An ideal group size must optimize energy intake (Baird & Dill, 1996; Wells *et al.*, 1999); thus, for example, cooperative feeding in large groups of dolphins has been linked to large schools of prey (Connor, 2002). When prey is dispersed, patchy or in low abundance, dolphins have a propensity to forage in small groups or individually (Würsig, 1986). Grouping also results from protection against predation risk, which has been documented for several cetacean species (Heithaus & Dill, 2002). Group size and behaviour are closely related regarding the cost and benefits of associations between individuals, which are linked to functional ecological processes of the life history of the species: predation risk, foraging, information exchange, access to mates, access to helpers to raise infants, disease transmission and thermoregulation (Lee, 1994). More specifically, for marine mammals, group size and behaviour have been shaped by three major ecological characteristics which include where animals give birth, where they forage and what they eat (Connor, 2002).

Group cohesiveness was highly associated with specific behavioural patterns for both Peale's and Chilean dolphins. For both species, tight groups were mostly observed during resting, and intermediate dispersion during travelling and foraging/feeding. The major difference between these species was for socializing, in which Peale's dolphins mostly formed tight groups whilst in this behavioural state, while Chilean dolphins formed dispersed groups. To our knowledge, there is no other precedent documenting loose group cohesion in dolphins while socializing. However, due to the low proportion of

time that Chilean dolphins were engaged in a social context, these observations are not conclusive for the species.

Tight cohesiveness in dolphin species is generally related to social behaviours (Wells *et al.*, 1999; Markowitz, 2004), as seen with Peale's dolphins. Tight formation is also a common tactic as a 'defensive posture' against predators (Wells *et al.*, 1999; Connor, 2002; Markowitz, 2004). Moreover, grouping pattern and cohesion differ relative to habitat, demography and geographical isolation, with a tendency towards smaller populations (communities) having larger parties (groups). In other words, the smaller the population, the higher the cohesion between society members (Karczmarski *et al.*, 2005).

Habitat and ecological processes in general may play an important role in shaping the behavioural patterns of species. However, differences in behavioural patterns in sympatric species, as observed for Chilean and Peale's dolphins, may reflect differences in foraging strategies, habitat and/or energy requirements, or even social differences. Understanding interspecific differences in behavioural patterns may reveal essential ecological relationships that allow these species to co-exist. In addition, the information generated in this study will assist in contributing to the development of better and holistic predictive models on how animals are responding or will respond to a rapidly changing environment and the potential effects of human activities.

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