

Fine-scale movement patterns of the sympatric Chilean and Peale's dolphins in the northern Patagonian fjords, Chile

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ABSTRACT: Animal movement is a central topic in ecology, as movements are crucial to habitat selection, foraging and spatial population ecology. Movement is a primary mechanism coupling animals to their environment, as organisms respond to environmental heterogeneity at different spatio-temporal scales. The fjord system in southern Chile is highly heterogeneous and sustains poorly known dolphin species, including the sympatric Chilean *Cephalorhynchus eutropia* and Peale's *Lagenorhynchus australis* dolphins. Focal dolphin group follows were undertaken between January and April 2007, 2008 and 2009 to assess the fine-scale movement patterns of these 2 species in southern Chile. Correlated random walk models (CRW) overpredicted dolphin paths for both species, indicating that dolphins displayed a resident type of movement. Only a small number of dolphin groups fitted a Lévy flight model, thus suggesting that dolphins undertake a non-random searching strategy. First-passage time (FPT) models for both species showed that dolphins spent a large proportion of their time in small localised areas of only 100 m radius. Generalized additive mixed models (GAMMs) demonstrated that Peale's dolphin movements were highly associated with kelp beds while Chilean dolphin movements were associated with rivers. Movement patterns of both species are very similar in scale and form, but they differ in relation to the associated ecological features. Movement models may be useful for developing holistic and more realistic predictions of how dolphins may respond to shifting resources as a consequence of environmental change with clear implications for conservation.

KEY WORDS: *Cephalorhynchus eutropia* · *Lagenorhynchus australis* · Dolphin movement · Correlated random walk · Lévy flight · First-time passage · Generalized additive mixed models

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INTRODUCTION

Animals inhabiting a particular ecosystem are highly influenced by the degree of spatial heterogeneity, and this is reflected in animals' distribution patterns (Johnson et al. 1992b). However, the processes responsible for these patterns are linked to how organisms make use of their environment, either in search of food, mates or refuge against predators (Johnson 1980).

At the fine scale, distribution of animals results from the decisions that animals make to shape their

movement patterns; these decisions have important consequences on their fitness (Prasad & Borges 2006). Animals interact with their environment in complex ways at different spatial and temporal scales, and these interactions can produce varied movement patterns (Jonsen et al. 2003). How animals change their movement patterns in relation to the environment is a central topic in ecology (Turchin 1998), specifically regarding foraging, gene flow, dispersion, habitat selection, disease dispersal and spatial population ecology (Johnson et al. 1992b, Fryxell

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& Lundberg 1998, Fauchald & Tveraa 2003, Whitehead et al. 2008). Movement also plays an important function in the evolutionary history and evolutionary potential of a species (Bridle & Hayes 2007), as evolution has favoured life strategies that can take advantage of changing mosaics of suitable habitats (Cain 1985). Understanding animal movement also has important implications for conservation, as identifying critical areas for populations is of great importance for management (James et al. 2005).

A major reason for animals to move is to locate food and, in particular, to find food patches that provide optimal rewards (Charnov 1976). However, animals tend to move only as much as they must to maximise their access to resources (Stevick et al. 2002). In response to spatial heterogeneity and resource patchiness, animals may vary their movement patterns by intensifying search effort in rich resource areas. Furthermore, animals need to make decisions about how much time is spent in any particular patch; therefore, time allocated to an area is likely to indicate the patch profitability (Fauchald & Tveraa 2003). Accordingly, there is a trade-off between the departure from a food patch and the speed and likelihood of encountering a new one (Walsh 1996).

Many studies have demonstrated that animal movements and the time allocated to specific areas are correlated to environmental features and are shaped by differences in behaviour. The focus of these studies has been on understanding how dynamic variables, such as frontal systems, water currents, primary productivity, as well as fixed features, such as depth and topography, influence movement patterns. For instance, Suryan et al. (2006) found that foraging destinations, movement patterns and habitat use of short-tailed albatrosses *Phoebastria albatrus* were significantly associated with wind speed, bathymetry and chlorophyll concentration. Etnoyer et al. (2004) demonstrated that several species of sea turtles and blue whales *Balaenoptera musculus* spend considerable amounts of time off the Baja California peninsula in waters that exhibited high sea surface temperature gradients, indicative of frontal systems and therefore potential optimal foraging habitat.

The fjord region of southern Chile encompasses extremely heterogeneous marine ecosystems. It is also widely recognised as a highly productive area and a complex oceanographic system (Daneri et al. 2000). These complex conditions make the area a hotspot for marine species, including a high number of cetaceans (Hucke-Gaete et al. 2004, Viddi et al. 2010). Among these, Chilean dolphins *Cephalorhynchus eutropia* and Peale's dolphins *Lageno-*

rhynchus australis seem to be the most frequently observed (Hucke-Gaete et al. 2006, Viddi et al. 2010). However, these 2 species are among the least studied of the dolphin family. They are coastal species restricted to the waters of Chile and Argentina. The Chilean dolphin, the only cetacean endemic to Chile, is distributed from Valparaiso (33° S) to Cape Horn (55° S), while Peale's dolphins range along the Chilean coast from Valparaiso (33° S) southward to Tierra del Fuego and along the Argentinean coast northward up to San Matias Gulf (38° S). This species is also found around the Falkland (Malvinas) Islands (Goodall 1994). While recent studies have focused on the distribution and habitat selection of these species (Heinrich 2006, Ribeiro et al. 2007, Viddi et al. 2010), little is known about fine-scale patterns of movement and their implications for habitat use.

The main objectives of this study were to assess the fine-scale movement patterns of Chilean and Peale's dolphins in northern Patagonian fjords, Chile, and to determine which environmental variables influence these patterns. To accomplish these objectives, a hierarchical framework approach of different models was used. (1) By using a correlated random walk model (CRW; Turchin 1998) we aimed to determine whether dolphins moved through the study area randomly, used the area in a persistent pattern (i.e. dolphins were residents) or used the area as a corridor. Deviations from this model can provide insights into the search strategy adopted by the dolphins within their home range. (2) By fitting Lévy flight models, we examined whether dolphin trajectories followed a deterministic or random movement search strategy (Viswanathan et al. 1999). Animal movement using Lévy flight models can provide important information about foraging strategies and the distribution of potential prey resources. (3) We used a first-passage time (FPT) model approach to determine the scale of searching behaviour and how much time dolphins allocated to specific areas, the so-called areas of restricted search (Fauchald & Tveraa 2003). (4) Generalized additive mixed models (GAMMs) were used to assess which environmental features were related to the observed movement patterns.

MATERIALS AND METHODS

Data collection

Dolphin group follows (Altmann 1974, Mann 1999) were conducted between January and April in 2007, 2008 and 2009 in the waters off Guaitecas Archipel-

ago in southern Chile (43° 52' S, 73° 45' W; Fig. 1). These follows were undertaken by 2 to 3 observers onboard a rigid hulled inflatable boat 5 m long. Observers searched for dolphins by naked eye and 7 × 50 binoculars, covering a strip of ~300 m on either side of the boat, at a searching speed of ca. 8 knots. Upon sighting a group of dolphins, search effort was interrupted in order to record dolphin geographical positions using a handheld GPS. Animals within a radius of 50 m were considered to be part of the same group. Dolphin group paths were generated by recording the location of the boat at 2 min intervals together with the distance to the dolphins (measured with a range finder) and angle with respect to magnetic north (using binoculars with a built-in compass). The corrected position of the dolphins was then derived by trigonometry and stored in ArcGIS 9.2, after correcting compass angles due to magnetic yearly variation. Lines connecting sequential move-points, and consequent estimation of movement parameters, such as distance between moves and turning angles, were derived using Hawth's Analysis Tools for ArcGIS (Beyer 2004).

Dolphin follows were conducted as long as the group was in sight, while weather and light conditions permitted. Each sample session, and therefore each dolphin group encounter, for a given day was

considered independent and became the unit for later analysis. Only groups that were followed for more than 30 min (Mann 1999) and did not react to the boat (e.g. bow-riding) were included in the analysis.

Correlated random walk model

For each group track, the observed net squared displacement was calculated, while distances and angles between successive locations were used to estimate the predicted net squared displacement using the CRW model of Kareiva & Shigesada (1983):

$$R_n^2 = nm_2 + 2(m_1)^2 \left(\frac{c}{c-1} \right) \left(n - \frac{1-c^n}{1-c} \right) \quad (1)$$

where R_n^2 is displacement (in m) from the first location, n is the number of moves from the first location, m_1 is the mean move distance (in m), m_2 is the mean squared move distance (in m^2), and c is the mean of the cosines of the move angles (in degrees).

A CRW model measures the rate of change in area over time by incorporating move lengths (the measured distance from one location to the next) and turning angles (the change in angle from one location to the next) into a quantitative description of

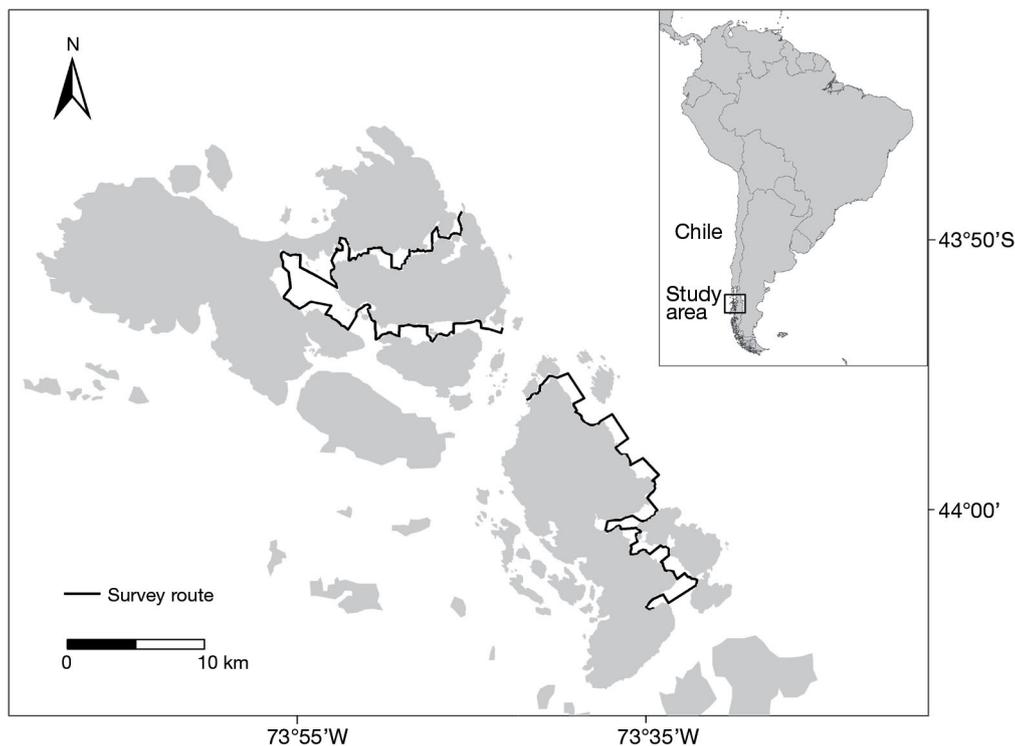


Fig. 1. The Guaitecas Archipelago of southern Chile. Survey routes used to locate Chilean and Peale's dolphins during summer (Jan–Apr) 2007–2009

movement, or in our case, the dolphin group's trajectory (Turchin 1998).

The model assumes that there is no predisposition to turn in a preferential direction and that move lengths are not serially correlated. These assumptions were tested by calculating the autocorrelation function (ACF) and the Ljung-Box Q-statistic for all lags up to 6 moves for move length. Angular correlation was determined by defining sequential turns as left or right and performing a runs test to check for non-randomness (Turchin 1998). If any track exhibited significant autocorrelation for either of these parameters, then tracks were divided until autocorrelation in both turning angle and step length was no longer present. When dividing groups, if one subgroup became too short (<30 min) then it was discarded from the analysis.

Using the empirical distribution of move lengths and turning angles from all dolphin groups, an expected R_n^2 was generated using a bootstrapped simulation of 1000 iterations with 95% CI determined by the percentile method (Turchin 1998). The observed and predicted net squared displacements were plotted over time to visualise how each dolphin group tracked fitted the CRW model. The tracks were then assigned a movement type based on whether more than 50% of the moves were within the 95% CI of the expected values for a CRW. Those groups that fit the model were termed 'correlated random walkers'. If a group's trajectories were smaller than that predicted by the CRW model, the group was then termed 'resident'. Conversely, if the observed trajectories were above the expected R_n^2 , then the dolphin group had greater displacement than predicted by the model and was therefore termed 'transient'.

Lévy flight

Lévy flights are a special class of random walks whose step lengths are not constant, but rather are chosen from a probability distribution with a power-law tail (Shlesinger et al. 1993). The distribution of move lengths, $N(x)$, of each dolphin group, as well as pooled for each species, was assessed for whether they fit a Lévy flight model of the form (Viswanathan et al. 1999):

$$N(x) \sim x^{-\mu} \quad (2)$$

where x is the move-step length (in m) between dolphin positions and μ is the power-law (Lévy) exponent ($1 < \mu \leq 3$). For each dolphin group and species,

move lengths between successive locations were divided into 10 equal-range bins, and the frequency of move lengths in each bin was calculated. The Lévy parameter μ was estimated from a regression model of log frequency vs. log move length. Model fit was assessed by examining trends in the residuals.

First-passage time model

First-passage time model (FPT) is a quantitative estimate of the time required for an animal to cross a circle of a given radius (Johnson et al. 1992a). FPT was calculated at every location along the track of every dolphin group followed for radii ranging from 50 to 500 m by 50 m increments. Excluding the first and last legs of the paths, as FPTs backwards and forwards from these end positions are unknown, the log transformed FPT variance was then plotted against radii for each group followed to determine a peak in FPT variance. The variance peak identifies which spatial scale is best to differentiate high (area of restricted search, ARS) vs. low (transitory) passage times (Fauchald & Tveraa 2003). The scale at which ARS was highest was then compared between species and used for assessment of which environmental variables were related to ARS. The scale was determined by estimating the average of the radius giving the highest relative variance for all trips pooled for each species.

Dolphin movement and habitat association

Generalized additive mixed models (GAMMs) were used to assess which environmental variables determined ARS in dolphins. GAMMs are an additive extension of GLMMs (generalized linear mixed models) in which part of the linear model predictor is specified in terms of smoothed functions of covariates (Lin & Zhang 1999). This class of models allows flexible functional dependence of an outcome variable on covariates by using nonparametric regression, while accounting for correlation between observations by incorporating random effects.

To assess the environmental variables determining ARS, the values of FPT in each location along a dolphin track were used as the response variable. Since the response variable had a log-normal distribution, GAMM was used with a log link function. Dolphin group was included as a random effect, whereas distance to kelp *Macrocystis pyrifera* beds, distance to rivers, tide height and tide rate of change were

included as fixed effects (explanatory variables) and were only retained if they significantly improved model fit. Akaike's information criteria (AIC) were used to identify the most parsimonious model. For competing models with a difference in AIC < 2, the model with the least number of parameters was selected (Lin & Zhang 1999). All possible combinations of main effects and interactions were considered.

River mouths in the study area were digitised from satellite image composites using ArcGIS 9.2. Kelp beds were digitised, also using ArcGIS, from data taken *in situ* during low tide. Kelp beds were represented spatially by polygons generated from GPS locations at the edges of kelp beds. Only polygons >300 m² were included in the analysis to avoid overestimating the presence of kelp beds due to dispersed plants or small patches. These 2 map layers were then overlapped with dolphin movement locations to calculate the distance from each of these point locations to river mouths and kelp beds.

Tide height was extracted from the software WXTide32 version 4.7 (available at <http://wxtide32.com>), which gives complete tide tables with 1 minute accuracy. To account for water current during tidal cycle, a proxy of tide rate of change was calculated, which consisted of the proportion of change of tide height at 30 min intervals. Values close to 0 represented slack tide at high and low tide, whereas high positive and high negative values represented peak water current at flood tide and at ebb tide, respectively.

All statistical and modelling analyses were made using the statistical package R version 2.9.1. (R Development Core Team 2009). Direct comparisons of time following dolphins, FPT radius and time within ARS between species were assessed using *t*-tests or the nonparametric equivalent, Wilcoxon rank tests. FPT was calculated using the R package *adehabitat* (Calenge 2006), while GAMMs were fitted in R using the package *mgcv* (Wood 2006).

RESULTS

Survey effort and data summary

Over the 3 fieldwork summer seasons a total of 54 surveys were conducted, which encompassed 290 h of effort searching for dolphins. Group follows were attempted for 173 dolphin groups which were encountered. However, only 90 groups were included in the analysis (those followed for >30 min), representing 95.9 h following dolphins. The mean (\pm SE) duration of a group follow was 82.8 ± 9.9 min (range = 30 to 240 min) for Chilean and 67.7 ± 4.6 min (range = 30 to 196 min) for Peale's dolphins. Time following dolphins was not significantly different between species (*t*-test; $t = -1.34$, $df = 34.5$, $p = 0.189$). However, the number of dolphin groups sighted, time with dolphins and dolphin group size all varied between species (Table 1).

Correlated random walk model

Twelve tracks showed significant autocorrelation in either move length or turning angle. These tracks were subdivided into 3 paths, and at this scale, autocorrelation was no longer present. After subdivision, 35 paths were analysed for Chilean dolphins and 72 for Peale's dolphins.

Overall, CRW modelling for both species indicated that most groups showed a resident type of movement. For Chilean dolphins, 45.7% of the paths were classified as 'residents' and 63.9% for Peale's dolphins, indicating that individuals of both species remained closer to their initial location than would be expected if they were moving randomly. Chilean dolphin paths were consistent with assumptions of CRW models for 34.3% of the paths and therefore termed 'correlated random walkers', compared to only 11.1% for Peale's dolphins. Paths classified as 'transients' encompassed 20% and 25% of paths for Chilean and Peale's dolphins, respectively (Fig. 2)

Table 1. *Cephalorhynchus eutropia* and *Lagenorhynchus australis*. Survey data collected during focal follows of Chilean and Peale's dolphin groups in 3 consecutive summers off southern Chile

Year	No. of surveys	Search effort (h)	No. of groups followed (total detected)		Time spent with dolphins (h)		Group size (ind. group ⁻¹)	
			Chilean	Peale's	Chilean	Peale's	Chilean	Peale's
2007	23	118.6	9 (19)	22 (38)	12.3	25.6	5.1	6.2
2008	26	142.3	16 (24)	36 (73)	16.7	34.9	5.2	6.7
2009	5	29.8	2 (3)	5 (16)	2.5	3.9	3.2	4.3
Total	54	290.7	27 (46)	63 (127)	31.5	64.4	5.1	6.3

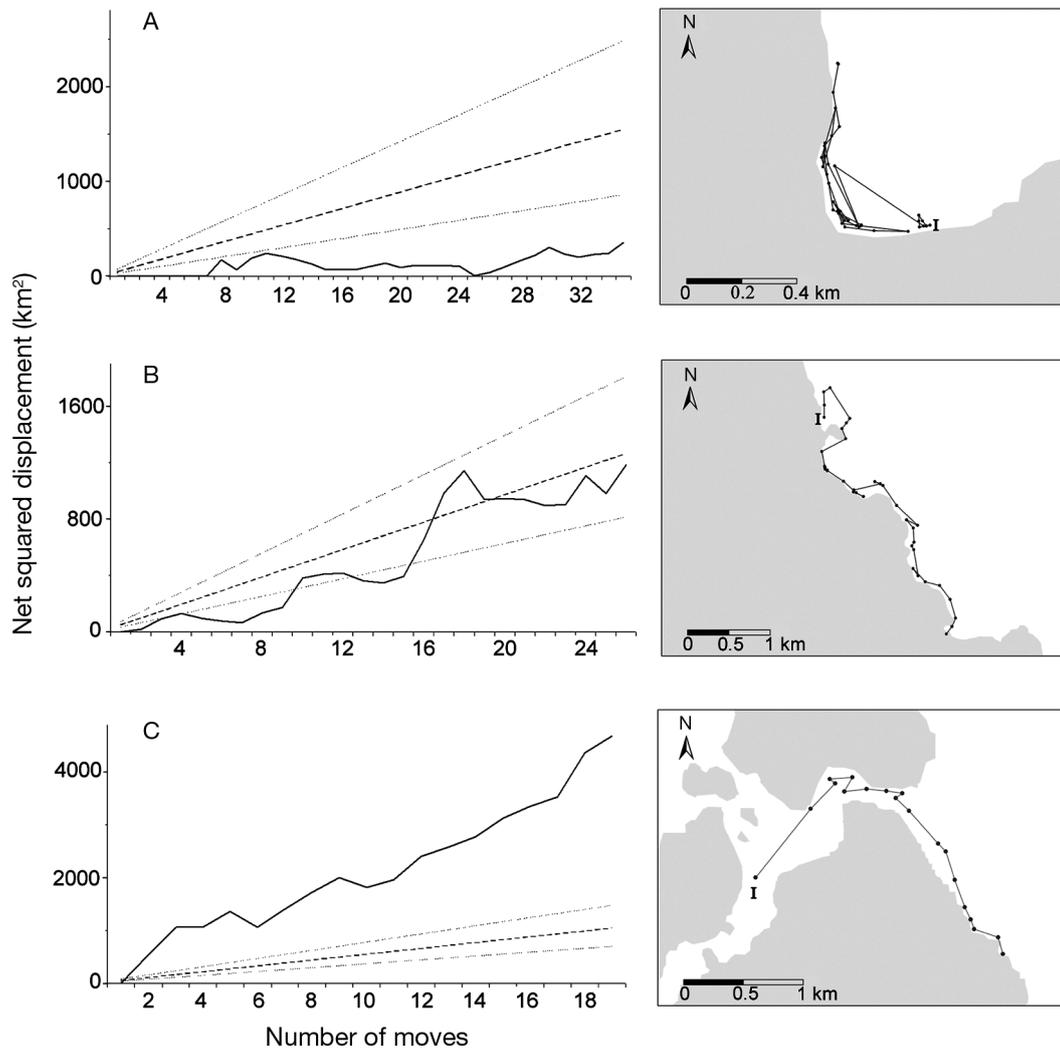


Fig. 2. *Cephalorhynchus eutropia* and *Lagenorhynchus australis*. Examples of observed (—) versus expected (---) net squared displacement and lower 25% and upper 95% (···) CIs and corresponding trajectories plotted within the survey area for 3 dolphin groups demonstrating different movement types: (A) Chilean dolphin group ID9 classified as 'resident'; (B) Peale's dolphin group ID24 classified as 'correlated random walker'; and (C) Peale's dolphin group ID6 classified as 'transient'. I: beginning of trajectory

Lévy flight

The frequency distribution of move lengths of all trajectories pooled for each species resembled the distribution function of a Lévy flight model (Chilean: $\mu = 1.94$, $r^2 = 0.734$, $p < 0.001$; Peale's: $\mu = 2.12$, $r^2 = 0.76$, $p < 0.001$). However, when assessing each track separately, only 5 Chilean dolphin groups (18.5%) and 10 Peale's dolphin groups (15.9%) had frequency distributions of move lengths that fit the negative power of a Lévy flight.

Three of the Chilean groups that fit the Lévy flight model also fit a CRW model, while 2 were classified as 'residents'. From those Peale's groups that fit a

Lévy flight, only 1 group also fit the CRW model and 9 were deemed 'residents'. None of the dolphin groups classified as 'transients' fit the Lévy flight distribution model. Transient groups had a frequency distribution characterised by more long move-lengths than short ones, resulting in a distribution with no descending right tail.

First-passage time model

Eleven Chilean dolphin groups (40.7%) and 38 Peale's dolphin groups (60.3%) showed clear peaks of variance in FPT. On average, ARS among all

groups occurred within a 105 m radius for Chilean dolphins and 123 m radius for Peale's dolphins, a difference that was not significant (t -test, $t = -0.833$, $df = 19.8$, $p = 0.415$). ARS for Chilean dolphins varied between 50 and 200 m radii, whereas for Peale's dolphins, the range was between 50 and 300 m radii. In contrast, the remaining number of groups for both species had relatively low FPT variance and no clear peaks, indicating that these dolphins did not concentrate their search effort in any particular area or scale along their paths during the observation period.

Chilean dolphins remained within their ARS for a median duration of 4.69 min, ranging from 0.53 to 65.2 min, while Peale's dolphins remained within their ARS for a median duration of 4.15 min, ranging from 0.81 to 57.9 min. The interspecific difference in the time that dolphins remained within their ARS was not significant (Wilcoxon rank-sum test, $W = 685902.5$, $p = 0.115$).

Dolphin movement and habitat association

The median search radius for both species was 100 m, and hence the values for FPT under this radius were used in GAMMs to determine association with habitat. The time that Chilean dolphins remained within their ARS was significantly associated with distance to rivers, distance to kelp beds and tide regime (Table 2). Dolphins that spent long times in their ARS (high values of FPT) were in general far from kelp beds (>4500 m), had movement distances <500 m and were also >3000 m from river mouths; time spent in ARS was also inversely related to tide height and generally positively related to tide rate of change (higher FPT values at flood tide; Fig. 3).

Table 2. *Cephalorhynchus eutropia* and *Lagenorhynchus australis*. Generalized additive mixed models (GAMMs) for first-passage time of Chilean and Peale's dolphins in relation to environmental variables. na: not available; edf: estimated degrees of freedom

	Chilean dolphins			Peale's dolphins		
	Estimate	t	p	Estimate	t	p
Intercept	2.56	35.3	<0.001	2.45	75.84	<0.001
Smoother terms	edf	F	p	edf	F	p
Distance to kelp beds	7.80	3.59	<0.001	4.82	9.74	<0.001
Distance to rivers	4.24	4.49	0.001	6.72	4.51	<0.001
Tide height	1.00	23.58	<0.001	8.04	9.17	<0.001
Tide rate of change	7.58	7.27	<0.001	na	na	na

For Peale's dolphins, time spent in ARS was significantly associated with distance to rivers, distance to kelp beds and tide height (Table 2). In general, Peale's dolphins spent a longer time closer to kelp beds, farther from river mouths and at intermediate tide heights (Fig. 4).

DISCUSSION

This study is the first to comparatively assess the fine-scale movement patterns of Chilean and Peale's dolphins. In general, both species have a tendency to remain in the same locations, spend a great part of their time in small, localised areas and use movements that are influenced by specific conditions of the environment. Peale's dolphin movements are highly influenced by the presence of kelp beds while Chilean dolphin movements are shaped by proximity to river mouths.

The CRW model explained the movement behaviour of less than half of the dolphin groups. However, CRW model prediction provided a useful first step in describing and differentiating among types of movement for both species: (1) those dolphin groups that moved in a random fashion, the CRWs; (2) those whose moves were characterised by short return trips from a single place, the residents; and (3) those that undertook long distance movements, the transients. Nevertheless, most of the trajectories for both Chilean and Peale's dolphins were overpredicted by the model and therefore fell under the category of 'residents'. The lack of fit of Chilean and Peale's dolphin to CRW models suggests that these species do not undertake movement patterns typical of dispersal, but rather have a tendency to reside in the same locations. Theory predicts that movements characterised by CRW should increase the likelihood of successful dispersal (Zollner & Lima 1999). The results for CRW models in this study gave first insights indicating a preference for particular habitat characteristics, probably to aid dolphins in finding food.

Overall for both species, <20% of the dolphin groups fit a Lévy flight model, which indicates that other search tactics are involved and that prey items consumed by dolphins may not be randomly distributed at the scale at which this study was developed. Prey distribution and resources may be more predictable and may not respond as a function of

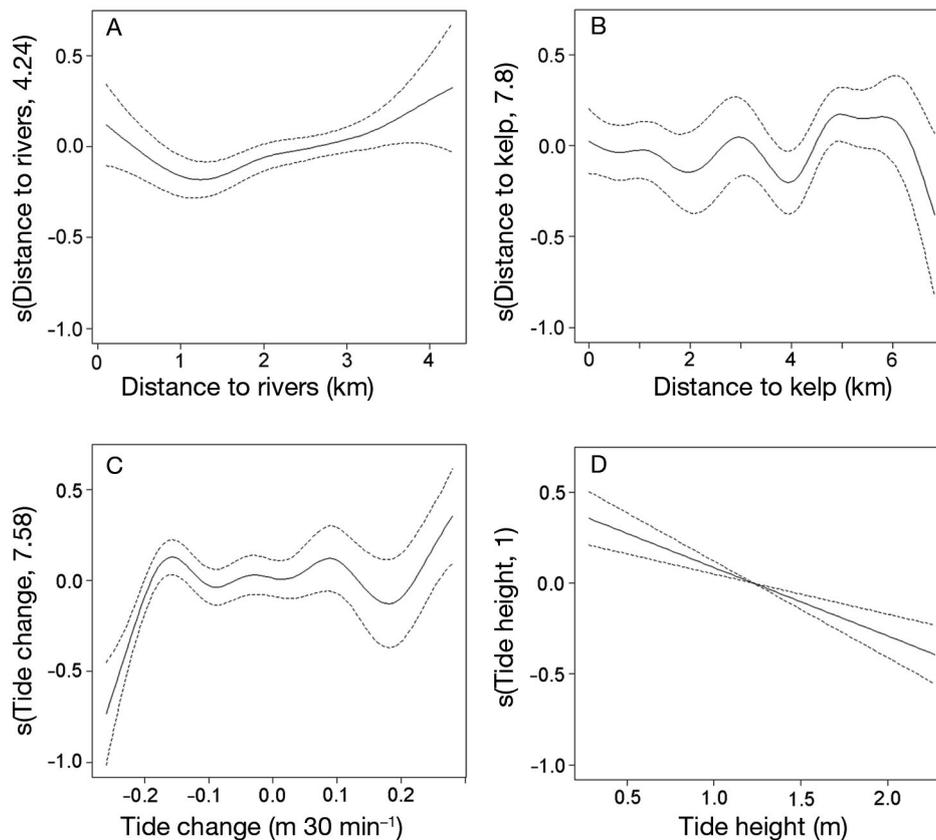


Fig. 3. *Cephalorhynchus eutropia*. Generalized additive mixed model (GAMM) function (—) and 95% CIs (---) of first-passage time (FPT) in relation to explanatory environmental variables for Chilean dolphins: (A) distance to rivers; (B) distance to kelp beds; (C) tide rate of change; and (D) tide height. Estimated degrees of freedom are in the parentheses on the y-axes

strict stochastic processes. A Lévy flight strategy implies that animals can visit more new and randomly distributed foraging sites than using a simple random walk under typical Brownian motion (Sims et al. 2008). For foragers, employing a Lévy flight search tactic would be more advantageous when resources are randomly and sparsely distributed, because the probability of revisiting previously visited sites is smaller than for a normal distribution (Viswanathan et al. 1996, Viswanathan et al. 1999, Ramos-Fernández et al. 2004, Sims et al. 2008). This specialised random walk model has super-diffusive properties comprising 'walk clusters' of short move step lengths with longer reorientation jumps between them (Sims et al. 2008). This pattern quickly takes the forager to more distant sites, reducing the likelihood that it will walk on its own steps again (Ramos-Fernández et al. 2004). Furthermore, this clustered pattern of step lengths is repeated across all scales, with the resultant scale-invariant clusters creating trajectories with fractal patterns (Bartumeus et al. 2005). A Lévy flight would then represent an

optimal solution for searching complex landscapes (Viswanathan et al. 1996).

Lévy flight type of movement has been proposed to be widespread among a diverse range of marine organisms and has evolved in response to patchy resource distribution (Sims et al. 2008). However, this is clearly dependent on differences between individuals, populations, species, spatial and temporal scales and ecosystems that will shape the variations in movement strategies. The interpretation from the Lévy flight model in this study suggests that Chilean and Peale's dolphins movement patterns reflect fine-scale patterns on more predictable and on less scale-invariant resources and are therefore more deterministic rather than probabilistic (i.e. 'blind'). Thus, these coastal species may have a complex mental map about resource locations; hence, the underlying resource landscape determines the distribution of move steps.

Thus, although spatial and environmental features influence movement (With et al. 1997), non-random search tactics such as those observed for Chilean and

Peale's dolphins may also be influenced by intrinsic factors such as memory and social behaviour. These factors have been previously suggested to affect the movements of grey seals *Halichoerus grypus* (Austin et al. 2004), spider monkeys *Ateles geoffroyi* (Ramos-

Fernández et al. 2004) and baboons *Papio hamadryas* (Sigg & Stolba 1981) and are also likely the case for dolphins given their high levels of sociability (Connor et al. 1998). Social behaviour is particularly important when considering the social influences on foraging vertebrates in relation to where, when, what and how they forage (Galef & Giraldeau 2001).

Optimal foraging theory assumes that animals should attempt to minimise time spent between patches and maximise time within them (Pyke 1978). Predators need time to find prey patches, and the time spent searching is thought to be a function of patch characteristics (Stephens & Krebs 1986). However, long distance travel should only be taken if there is a high chance of reward from the distant patch (Austin et al. 2004). An optimal foraging strategy would imply moves with low speed and high turning rates in areas of high prey density and high speed, straight moves between these dense areas, which is the so-called ARS strategy (Fauchald & Tveraa 2003). Chilean and Peale's dolphins showed search activities confined to small ARS (radii < 130 m) with high FPT in these small localised areas. The sites of concentrated search effort appeared to be foraging locations and may explain the dolphin's preference for these areas.

Just as observed by Bailey & Thompson (2006), the results of the present study suggest that the small search radii could be a consequence of large, highly nutritional food being taken in this area, or alternatively, it may reflect the size of prey patches. Furthermore, the scale at which dolphins concentrate their movements may therefore be potential evidence that prey patches are clustered at these small scales, as proposed before for Antarctic petrels *Thalassoica antarctica* (Fauchald & Tveraa 2003), bottlenose dolphins *Tursiops truncatus* (Bailey & Thompson 2006) and short-tailed albatrosses (Suryan et al. 2006).

Many studies on marine organisms have shown that movement is strongly influenced by environmental features (Johnston et al. 2005, Phillips et al. 2006, Suryan et al. 2006). In the present study, FPT for Peale's dolphins was higher near kelp beds, far from rivers and at slack tide during high tide. Kelp beds are known to host a myriad of organisms, including species of fish and squid (Moreno & Jara 1984), many of which may be fed upon by Peale's dolphins. Unfortunately, no data were available on which potential prey species are found in these kelp beds. These results provide further evidence on the importance of specific habitats for Peale's dolphins, an association previously documented in Argentinean waters (de Haro & Iñiguez 1997) and in Chile

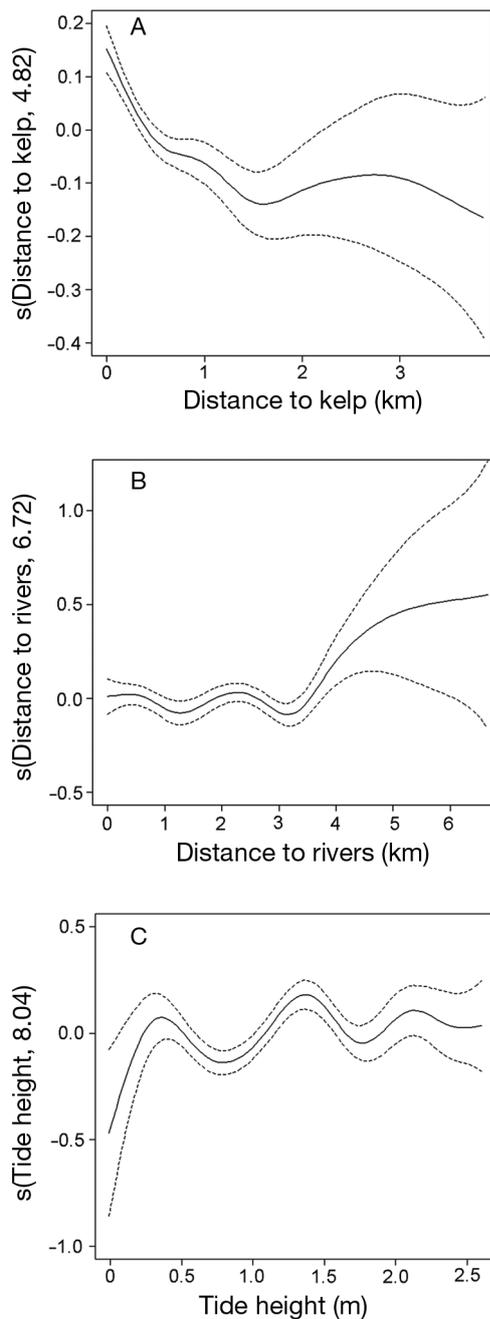


Fig. 4. *Lagenorhynchus australis*. Generalized additive mixed model (GAMM) function (—) and 95% CIs (---) of first-passage time (FPT) in relation to explanatory environmental variables for Peale's dolphins: (A) distance to kelp beds; (B) distance to rivers; and (C) tide height. Estimated degrees of freedom are in the parentheses on the y-axes

(Lescrauwaet 1997, Viddi & Lescrauwaet 2005, Viddi 2009). All these studies have suggested that the preference by Peale's dolphins for these habitats is highly related to finding food resources. Peale's dolphins are the only cetacean known to be highly associated with kelp beds (Viddi 2009). Certainly, other marine vegetated ecosystems are known to be important areas for food for other coastal dolphins, such as seagrass beds for bottlenose dolphins in Florida (Allen et al. 2001).

FPT for Chilean dolphins was higher close to rivers, far from kelp beds and associated with tide regime. Rivers and tide regime combined are suggested to be important to this species as they may represent hotspots of prey resources (Heinrich 2006, Ribeiro et al. 2007). In fact, rivers and estuaries have been identified as key features shaping habitat selection of several inshore cetacean species (Ingram & Rogan 2002, Goetz et al. 2007). The interaction between freshwater run-off and tidal phases are also known to generate tidal fronts (Iriarte et al. 2007), which act as convergence zones and may concentrate plankton and weak swimming nekton (Mann & Lazier 1991). These aggregations, in turn, result in localised patches of food for marine predators that feed on lower trophic levels (Wolanski & Hamner 1988), such as dolphins and porpoises (Mendes et al. 2002, Johnston et al. 2005).

Overall, the results of this study illustrate that movement patterns of the sympatric Chilean and Peale's dolphins are very similar in scale and type. Main differences arise from the distinct ecological factors that shape dolphin movements, in particular, the associations with kelp beds for Peale's dolphins and rivers for Chilean dolphins. However, these results alone do not suggest strict habitat partitioning. Both species have been observed in mixed groups during travelling and feeding behaviours, yet this study does propose a specific preference for different habitats.

Animal movement models may be useful for developing more holistic and realistic approaches to predicting how animals may respond to shifting resources as a consequence of environmental change. The present findings provide important information for focused management efforts, and they highlight the importance of northern Patagonian fjords for coastal dolphin conservation. The coastal habits of these dolphins and their prevalence to concentrate in well-defined, small areas make them vulnerable to human activities such as fishing, vessel traffic, aquaculture, pollution and tourism, among others. Conservation of these dolphin species and their habitats

could be achieved by incorporating habitat preference and movement pattern data into coastal management plans and regulations. In practice, areas covered by kelp beds and/or influenced by rivers must be taken into account when designing a conservation plan aimed at maintaining a healthy and functional ecosystem under a legal framework such as a Multiple Use Marine Protected Area (MUMPA). As 'flagship' species due to their emblematic significance, dolphins and other species such as the blue whale (Hucke-Gaete et al. 2004) can be used for their popularity to bring large marine areas into some degree of protection. Every effort made to conserve higher order predators and their ecosystems will also protect less emblematic species through an 'umbrella' species effect. This study provides an initial baseline on the importance of some specific areas of the Chilean coast to these 2 species based on their movement patterns and residency among patches. These areas could be among those in dire need of protection and have been included in a proposal to the Chilean Government (Hucke-Gaete et al. 2010).

The data presented here come from 3 restricted summer seasons only, so inferring similar findings about the ecological conditions and movement patterns of dolphins during other seasons through the year is not possible. Productivity of the area may fluctuate seasonally; thus, the data must be considered with caution for non-summer months. Future research over multiple years and covering all seasons should focus on long range dolphin movements, model replication into new areas, the environmental characteristics shaping movements and the implications for conservation.

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