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Research paper

Natural and anthropogenic drivers of foraging behaviour in bottlenose dolphins: influence of shellfish aquaculture

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Abstract

1. In the coastal environment, marine mammals are exposed to one of the fastest-growing food production sector, i.e. the shellfish farming industry. Identification of critical habitats, such as foraging grounds in highly human-impacted areas, is essential to species conservation. Therefore, understanding the variables that influence a species' foraging behaviour is important for their conservation, especially for long-lived mammals such as cetaceans.
2. The aims of this study were: (i) to identify and quantify the environmental and anthropogenic drivers of wild bottlenose dolphin (*Tursiops truncatus*) foraging behaviour and (ii) to investigate whether the shellfish farming industry influences the behaviour of this species.
3. Behavioural observations were conducted along the north-western coast of Spain, an area affected by intensive human activities, particularly the shellfish aquaculture industry.
4. A multi-modelling approach highlighted the importance of shellfish farm areas as a foraging ground for bottlenose dolphins. Dolphins were predicted to be more likely found foraging inside shellfish farm areas than outside (57 vs. 43%).
5. Variability in bottlenose dolphin behaviour is likely a result of the interactions of environmental and anthropogenic drivers with prey availability and physiological needs of the dolphins. Although shellfish farm areas provide high prey density for dolphins, they can also pose threats in a number of ways (i.e. collisions with vessels, entanglement with ropes, habitat loss, noise and water pollution).
6. From a conservation perspective, aquaculture management should consider the presence of dolphins foraging and minimise the associated risks that this industry may pose to these coastal cetaceans.

Keywords

coastal, disturbance, estuary, habitat management, industry, mammals

1. Introduction

Human-induced behavioural disturbance of wild animals can implicate the reduction of foraging efficiency, therefore affecting energy intake with potential implications for individuals and possibly population-level fitness (Ashe, Noren, & Williams, 2010). Foraging behaviour is driven by multiple stressors including environmental variables (as indicators of prey availability) and in certain conditions, anthropogenic variables (Patterson, Basson, Bravington, & Gunn, 2009; Yirga et al., 2017). Examples in the literature link human activities to alteration in mammal foraging behaviour (e.g. black bears *Ursus americanus*: Beckmann & Berger, 2003; chimpanzees *Pan troglodytes verus*: Hockings, Anderson, & Matsuzawa, 2012; European hedgehogs *Erinaceus europaeus*: Dowding, Harris, Poulto, & Baker, 2010; key deer *Odocoileus virginianus clavium*: Harveson, Lopez, Collier, & Silvy, 2007; stonemarten *Martes foina*: Herr, Schley, Engel, & Roper, 2010; killer whales *Orcinus orca*: Williams, Lusseau, & Hammond, 2006). Likewise, some studies point out that anthropogenic food resources affect the foraging behaviour of several generalist mammal species (e.g. bottlenose dolphins *Tursiops truncatus*: Díaz López, 2006b, 2012, 2018; spotted hyenas *Crocuta crocuta*: Yirga et al., 2012). For instance, some species are able to persist at high human densities and to capitalize on human activities, taking advantage of the availability of food resources in a human-dominated

landscape (e.g. racoon *Procyon lotor*: Prange, Gehrt, & Wiggers, 2004; spotted hyenas *Crocuta crocuta* and African golden wolf *Canis anthus*: Yirga et al., 2017). Conversely, mammals being attracted by high food availability in anthropogenic areas face many threats such as direct persecution (Yirga et al., 2017), loss of natural food resources (Oriol-Cotterill, Macdonald, Valeix, Ekwanga, & Frank, 2015), habitat loss and modification (Rogala et al., 2011), accidental mortality (Díaz López, 2012), and pollution (Kannan, Corsolini, Focardi, Tanake, & Tatankawa, 1996). Therefore, identifying and quantifying the factors that influence a species' foraging behaviour is essential to implement appropriate future conservation measures.

In the marine environment, marine mammals are exposed to multiple human activities such as marine traffic (Constantine, Brunton, & Dennis, 2004), fisheries (Read, Drinker, & Northridge, 2006), and aquaculture (Díaz López, 2012). Marine aquaculture is one of the fastest-growing food production sectors in the world and continues to expand globally (FAO, 2014). Shellfish farming, which is the culture of filter-feeding bivalves, is the main sector of this industry comprising 60% of the marine aquaculture production (FAO, 2014). Several studies (reviewed in Callier et al., 2017) suggest that the three-dimensional scale of shellfish farming may reduce the coastal areas used by cetaceans for potentially important biological and social activities. Multiple species

of dolphins in various locations around the world appear to avoid areas occupied by shellfish farming, indicating a potentially large impact of this industry on small cetaceans (i.e. Dusky dolphin *Lagenorhynchus obscurus* in New Zealand: Markowitz, Harlin, Würsig, & McFadden, 2004; Pearson, 2009; Pearson, Vaughn-Hirshorn, Srinivasan, & Würsig, 2012; Chilean dolphins *Cephalorhynchus eutropia* in Chile: Ribeiro, Viddi, Cordeiro, & Freitas, 2007; and Indo-Pacific bottlenose dolphins *Tursiops aduncus* in Australia: Watson-Capp & Mann, 2005). In contrast, a recent study carried out along the north-western coast of Spain demonstrated that common bottlenose dolphins (*Tursiops truncatus*, hereafter bottlenose dolphin) are attracted by shellfish farm areas, suggesting that, depending on the culture method, these farms can provide an adequate foraging habitat for dolphins (Díaz López & Methion, 2017).

Bottlenose dolphins show a high behavioural and ecological plasticity that allows them to live in coastal areas along with human activities (Díaz López, 2006b, 2018; Scott, Wells, & Irvine, 1990). Bottlenose dolphins inhabit a very wide range of habitats and are generalist animals that feed on locally abundant prey species (mainly demersal and pelagic fish, and cephalopods) (Santos, Fernandez, López, Martínez, & Pierce, 2007). Foraging behaviour in bottlenose dolphin is driven by a multitude of environmental and anthropogenic factors, and differs in different part of its range and among individuals of the same population (Díaz López, 2009; Sargeant, Wirsing, Heithaus, & Mann, 2007; Torres & Read, 2009). The bottlenose dolphin is an opportunistic species that is capable of developing, over its range, a multitude of adaptive strategies, including specialist feeding techniques, which involve a high degree of diet flexibility, social organization and behavioural adaptation (Connor, Wells, Mann, & Read, 2000; Díaz López, 2012, 2018; Díaz López & Shirai 2008). In different parts of the world, these strategies allow bottlenose dolphins to capitalize on human activities such as gillnet and trawl fisheries, and fin fish aquaculture (Chilvers & Corkeron, 2001; Díaz López, 2006b; 2012; Fertl & Leatherwood, 1997). In spite of this, little is known about the factors that affect bottlenose dolphin behaviour and, in particular, about the influence of shellfish farming on bottlenose dolphin foraging behaviour.

The north-western coast of Spain, being one of the world's most important areas for shellfish farming (Rodríguez, Villasante, & do Carme García-Negro, 2011) and supporting a resident population of bottlenose dolphins (Methion & Díaz López, 2018), exhibits the perfect conditions to carry out such a specific study. Building upon the study of the influence of shellfish farming on the habitat use of bottlenose dolphins in these waters (Díaz López & Methion, 2017), this present study attempted to investigate the influence of the shellfish aquaculture industry on the foraging behaviour of bottlenose dolphins. The aims of this study were to identify and quantify the environmental and anthropogenic drivers of wild bottlenose dolphin foraging behaviour and to investigate whether the presence of shellfish farms influences the behaviour of this species.

2. Material and methods

2.1. Study area

The north-western coast of the Iberian Peninsula (Galicia, Spain) lies at the northern edge of one of the major upwelling areas in the world, the eastern boundary system off NW Africa and SW Europe (Santos, Gómez-Gesteira, & Alvarez, 2011). The frequent upwelling of cold and dense North Atlantic Central Water results in nutrient enrichment of the water making this area one of the most productive oceanic regions in the world (Santos et al. 2011). This coast is characterized by high biodiversity, productive fisheries, and important aquaculture activities, particularly the production of mussels (*Mytilus galloprovincialis*) (Tenore et al., 1995). Shellfish farming has occurred in Galicia since the late 1940s (Miguez, Gil, & Lafuente, 2009) and has developed over the years, making this area the European leader in this sector (FAO, 2014). Galicia produces an average of 300 000 tons of mussels per year, making it the third most important producer in the world after China and Thailand (Fuentes, Gregorio, Giráldez, & Molares, 2000; Rodríguez et al., 2011) with 13% of the world's mussel production (50% of Europe and 98% of Spain) (FAO, 2014). In Galicia, the shellfish are grown on rectangular floating platforms, which is in contrast to other systems of production such as long-lines or poles (Perez Camacho, Gonzalez, & Fuentes, 1991). The rafts are generally made of wood and the bivalves are grown on ropes tied to the platforms. Each individual raft has a maximum of 500 ropes (no longer than 12 m) and covers an area of up to 500 m² used for shellfish cultivation (Fuentes et al., 2000).

The current study was conducted in the largest of the Galician rías, the Ría de Arousa (239 km²) (Prego, del Carmen Barciela, & Varela, 1999) (Figure 1). The ría is exposed to a semidiurnal, mesotidal regime, with the tidal range varying from 1.1 to 3.5 m during neap and spring tides respectively (Alvarez, Decastro, Gomez-Gesteira, & Prego, 2005). Around 2 370 mussel cultivation rafts are situated in the Ría de Arousa (Rodríguez et al., 2011) covering approximately 17% of the area (Díaz López & Methion, 2017). Abundance of bottlenose dolphins (*Tursiops truncatus*) ranges from 56 to 144 individuals in the Ría de Arousa (Methion & Díaz López, 2018). In this ría, bottlenose dolphins are frequently found in shellfish farm areas (Díaz López & Methion, 2017).

2.2. Data collection

Boat-based surveys were conducted between March 2014 and November 2017. The study area was monitored on-board a 12 m research vessel during daylight hours at a constant speed of 6 knots. At least three experienced observers were stationed on the flying bridge (4 m above sea level), scanning 360 degrees of the sea surface in search of bottlenose dolphins (with the naked eye or 10x50 binoculars). The minimum number of experienced observers and vessel speed remained consistent during the study period. Surveys were carried out when the sea conditions were no greater than 3 on the Douglas sea force scale (approximately equivalent to the Beaufort wind force scale) and visibility was not reduced by rain or fog (Díaz López & Methion, 2017). The surveyed area and daily routes were designed to cover all parts of the study area equally (Figure 1) (Methion & Díaz López, 2018).

Upon sighting a group of bottlenose dolphins the vessel slowly manoeuvred towards them in order to not alter their behaviour during the approach. A group of bottlenose dolphins was defined as one or more individuals observed within a 100-m radius, interacting with each other, and engaging in the same behavioural activity (Methion & Díaz López, 2018). Group size and composition were estimated before, during, and after the bottlenose dolphins had been approached. Individual dolphins were classified according to age at the time of the encounter (Scott, Wells, & Irvine, 1990). Age class definitions followed those of Díaz López & Methion (2017), whereby bottlenose dolphins were classified as either dependent calves or adults. Individuals were considered dependent calves when they were about two-thirds the length of an adult and were observed in close association with an adult. Individuals were considered adults when their length was more than 2.5 m.

The behavioural state of a group was determined every five minutes based on the activity performed by at least 50% of the individuals present in the group for at least 50% of the duration of the five-minute sample (Predominant group activity sampling) (Altmann, 1974; Karniski et al., 2015). The behavioural states were classified into four categories: foraging, resting, socializing, and travelling (Table 1). As the determination of cetacean behaviour from surface observation can be challenging, several parameters were considered to assess the behavioural state in order to reduce potential bias: behavioural events, dive duration, swimming speed and direction, inter-individual distance, and contact among individual dolphins (following Díaz López, 2006a). To eliminate inter-observer variability, the behavioural state was determined by the same observer during the full study period. All encounters continued until the group composition changed, the group was lost, or until weather conditions became unfavourable.

The variables listed below were initially considered to have potential significance on bottlenose dolphin foraging behaviour, and were available for each five-minute sample recorded during the study: time (UTC), group size, presence of dependent calves, number of dependent calves, depth (m), sea surface temperature (SST in ° Celsius), sea surface salinity (SSS in parts per thousand), wind speed (m/s), bottom slope gradient (the maximum rate of change in depth in a given area of grid cell and expressed as per cent slope), tide level (m), tidal cycle (flood; ebb), distance to the coast (m), and the presence of the group of bottlenose dolphins inside or outside the shellfish farm areas.

The date, time, position (UTM longitude and UTM latitude, WGS 84 UTM Zone 29N), depth, SST, SSS, wind speed, and the presence of the group of bottlenose dolphins inside or outside the shellfish farm areas were collected in situ along with the behavioural state of the group as an instantaneous point sample every five minutes.

Supplementary variables were extracted and linked to each behavioural state: bottom slope gradient, tide level, tidal cycle, and distance to the coast. Tide level and tidal cycle categories were obtained from the Galician weather service (<http://www.meteogalicia.gal>). Bottom slope gradient was computed from the bottom depth

obtained from a bathymetric chart data set (following Díaz López & Methion, 2018). All distances to coast were minimum distances in metres from the GPS position of each five-minute sample to the coastline, and calculated via spatial analyst tools using QGIS software.

Data collection in the present study complied with current laws of Spain, the country in which the study was performed.

2.3. Data selection

As reported in other areas (Díaz López, 2012), given the long-term nature of the study, the process of field data collection was not expected to cause significant behavioural changes to the animals studied. Following Díaz López (2009), at least 10 minutes of observation are needed to assess the behaviour of wild bottlenose dolphins. Consequently, all encounters with a duration of 10 minutes or less were discarded and only the third behavioural sample (corresponding to the interval between the minute 10 and 15 of observation) of each encounter was selected for further analysis. By down-sampling the data, the autocorrelation and pseudoreplication arising from consecutive samples was limited (Díaz López & Methion, 2018).

2.4. Data analysis

Explanatory variables were tested for multicollinearity by examining the variance inflation factor (VIF), and when $VIF > 5$, the variable was discarded (Dormann et al., 2013). Following this procedure, tide level, number of calves, and distance to the coast were excluded from the analyses. Coordinates were not included as covariates because they were correlated with sea-surface temperature, sea-surface salinity, presence of shellfish farms, and depth, which were included instead due to their biological interpretability (Díaz López & Methion, 2018; Forney, 2000). As a result, 10 predictor variables were selected: group size, presence of dependent calves, time, depth, SST, SSS, bottom slope gradient (hereafter slope gradient), tidal cycle, wind speed, and whether the dolphins were inside or outside the shellfish farm areas. A generalized additive modelling (GAM) framework was used to study variables correlated to the foraging behaviour of bottlenose dolphins. Presence-absence of foraging behaviour was modelled as a binomial GAM (presence of foraging behaviour, scored as 1; or absence of foraging behaviour, i.e. resting, socializing and travelling, scored as 0) with a logistic link function. The smooth functions were represented by cubic regression splines (Wood, 2006). The amount of smoothing was not fixed to a pre-set value but cross validation was used to estimate the optimal amount of smoothing (Wood, 2006). The mgcv package (Wood, 2006) in the software R (R Development Core Team 2011) was used to perform the GAMs. Model assumptions were checked by visual inspection of the residuals and regression fits were examined by using residual plots against fitted values. The Durbin-Watson test (from the package “lmtest”) (Zeileis & Hothorn, 2002) and auto-correlation functions (ACF) were used to check for serial correlation, both in the raw data and in the residuals from the models. The optimum final model (hereafter referred to as global model) was selected based on the lowest Unbiased Risk Estimator

(UBRE), and there were no clear patterns in the residuals (following Díaz López & Methion, 2018). A multi-model inference approach (referred as model averaging, i.e. several models used at once for making predictions) (Grueber, Nakagawa, Laws, & Jamieson, 2011) was used for model simplification and selection, because of the large number of potential combinations of predictor variables. Model averaging can lead to robust predictions accounting for uncertainty in model selection by making inferences from an assemblage of possible solutions (Burnham & Anderson, 2002). Model averaging was used to calculate the relative importance of predictor variables. The R package 'MuMIn' (Barton, 2011) was used to produce a candidate model set consisting of all simplified versions of the global model and compared them based on their Akaike Information Criterion (AICc), corrected for small sample sizes (Grueber, Nakagawa, Laws, & Jamieson, 2011). To ensure that the most parsimonious models were maintained within the best supported model set, the models with $\Delta AICc < 2$ were used to identify the relative importance of each model term in predicting the response variable and to estimate the effect sizes of the predictors (Burnham & Anderson, 2002). Models were ranked from best to worst using the difference in AICc and the relative importance of a predictor variable (RVI) was calculated as the sum of the Akaike weights over all of the models in which the predictor appeared (Burnham & Anderson, 2002). Partial predictions with 95% confidence intervals were plotted for each covariate included within the best supported model set.

3. Results

3.1. Survey effort, group size, and behavioural samples

From 2014 to 2017, 273 boat-based observations were carried out for a total of 1 015 h, covering 9 416 km (Figure 1). Overall, 712 groups of bottlenose dolphins (*Tursiops truncatus*) were encountered. The behaviour of the bottlenose dolphins was sampled for a total of 445 hours, and 2 566 km. The mean duration of encounters was 38.0 ± 1.3 minutes (median 25, minimum 1, maximum 253).

Group size ranged from 1 to 90 individuals (mean 11.87 ± 0.44 ; median 8). The groups were composed of 88% adults and 12% dependent calves. Dependent calves were present in 56% of the groups. The group size, presence of dependent calves, and number of dependent calves did not vary for groups present inside or outside the shellfish farm areas (Mann Whitney test, $p > 0.05$).

Overall, 5 296 five-minute behavioural samples were collected (of which 2 481 foraging, 148 resting, 675 socializing, and 1 995 travelling samples). A final dataset of 574 samples (11% of the total samples) was generated for further analysis.

3.2. Behavioural budget

Of the 574 selected behavioural samples, 282 were foraging samples (49.1 %), 220 were travelling samples (38.3 %), 51 were socializing samples (8.9 %), and 21 were resting samples (3.7 %). The frequencies of occurrence of the four behavioural states were not distributed uniformly inside and outside shellfish farm areas, with a

predominance of foraging activities inside shellfish farm areas (contingency table $\chi^2 = 10.1$, 3 df, $p < 0.05$) (Figure 2). On the contrary, resting and travelling behaviour occurred more frequently outside shellfish farm areas (Figure 3). Social behaviour was not related to any area in particular.

3.3. Factors influencing bottlenose dolphin foraging behaviour

A candidate model set was produced with all 1 024 simplified versions of the global model and the models were compared based on their AICc. Five models with $\Delta AICc < 2$ were used to produce model-averaged parameter estimates (Table 2). The shellfish farm areas, SST, and time were retained in each model within the candidate model set and had a relative variable importance (RVI) of 1 in the final average model (Table 3). The slope gradient was retained in five top models within the candidate model set and had a RVI of 0.89. The wind speed (as a measure of the sea state), group size, tidal cycle, and SSS, were only retained in one of the top models with a RVI lower than or equal to 0.20 (Table 3). Depth and presence of dependent calves were not present in the top model set, indicating that these covariates were not important predictors of bottlenose dolphin foraging behaviour. Bottlenose dolphin foraging activity was predicted to be driven by environmental variables (predominantly at low SST and during morning hours) and anthropogenic variables (higher inside shellfish farm areas ($57\% \pm 5\%$) than outside shellfish farm areas ($43\% \pm 4\%$)) (Figure 4, Table 3).

4. Discussion

Integrating behavioural studies into conservation strategies is an important step for the protection of wildlife and contributes to reducing the consequences of human disturbances (Buchholz, 2007; Sutherland, 1998). Identification and protection of critical habitats, such as foraging grounds, are particularly difficult tasks and essential to the conservation of species in the marine environment. Therefore, defining the variables that influence the foraging behaviour of a marine top predator, such as the bottlenose dolphin, can help with the protection, management and conservation of this potentially vulnerable species.

This study provides additional understanding on the environmental and anthropogenic factors that drive bottlenose dolphin foraging behaviour in a highly human-impacted area. The results highlight the importance of shellfish farm areas as potential foraging grounds for this species. The model averaged parameter estimates revealed that foraging behaviour is correlated to both environmental (sea surface temperature and time of the day) and anthropogenic (shellfish farm areas) variables. Variability in bottlenose dolphin behaviour is likely a result of the interactions of these drivers with prey availability and physiological needs of the dolphins. The observed influence of environmental parameters (such as the sea surface temperature and time of the day) on foraging behaviour may in fact be related to temporal changes in abundance of pelagic and demersal fish species. Indeed, pelagic and demersal fish species, which are the most important prey species of bottlenose

dolphins in the region (Santos et al., 2007), show clear temporal changes (seasonal and circadian) in abundance and distribution inside of the Ría de Arousa (Chesney & Iglesias, 1979; Tenore et al., 1995). As a result, during seasons characterized by low sea surface water temperature, dolphins might tend to increase the time spent foraging due to higher energy requirements (Bräger, 1993; Díaz López, 2012; Shane, 1990).

The observed preference that bottlenose dolphins show for foraging inside shellfish farm areas contrasts with other studies claiming that dolphins avoid shellfish farm areas (i.e. Hector's dolphins in New Zealand (Würsig & Gailey, 2002), Indo-Pacific bottlenose dolphins in Australia (Watson-Capp & Mann, 2005), Chilean dolphins in Chile (Ribeiro, Viddi, Cordeiro, & Freitas, 2007)). The difference in these results might be due to varying shellfish culture methods used (i.e. floating rafts vs. long-lines). In Galicia, the use of square floating rafts with a concentration of ropes in the same area in the water, has introduced spatial habitat complexity (Chesney & Iglesias, 1979; Iglesias, 1981). Indeed, shellfish aquaculture has fragmented bottlenose dolphin habitat in the Ría de Arousa causing certain areas to become more attractive to dolphins (Díaz López & Methion, 2017). Shellfish farms lead to a variation in food resource distribution and abundance in the form of modified habitat that is favourable for bottlenose dolphin foraging activity (high diversity and abundance of fish species and physical space for the dolphins to move in between the rafts). The rafts provide a physical structure acting as a fish aggregating device (FAD), thus increasing the abundance of fish species within shellfish farm areas relative to adjacent areas (Chesney & Iglesias, 1979; Romero, González-Gurriarán, & Penas, 1982; Tenore & González, 1976). Consequently, the pelagic and demersal fish species concentrated in the aquaculture areas, feeding directly on the shellfish-line associated community or using the structures as resting sites (Freire & González-Gurriarán, 1995; Iglesias, 1981), provide bottlenose dolphins with an important source of food. Similar results have been found in studies on the interaction between bottlenose dolphins and finfish aquaculture (Bonizzoni et al., 2014; Díaz López, 2006a, 2012). In Mediterranean waters, bottlenose dolphins feed more efficiently in areas with high concentration of prey around finfish cages, allowing them to shorten their dive time and consequently giving them more flexibility with speed and swimming mode as a result of higher oxygen availability (Díaz López, 2009). In this way, dolphins reduce the proportion of time spent searching for food and increase the quantity of food consumed (Díaz López, 2012).

Previous studies have shown that interaction between dolphins and marine aquaculture can cause damages to both the aquaculture industry (i.e. damage to gear, depredation of farmed fish) and to dolphins (i.e. fatal entanglement, habitat loss and degradation, introduction of diseases) (Díaz López, 2012; Würsig & Gailey, 2002). While dolphins around finfish farm areas can feed on both wild and farmed fish, often causing damages to the equipment and the stock (Díaz López, 2006a), dolphins in shellfish farm areas only feed on wild prey, thus not affecting the aquaculture product.

Therefore, attempts to dissuade bottlenose dolphins, through the use of predator nets or acoustic harassment devices, are not necessary in shellfish aquaculture. Nevertheless, shellfish aquaculture can pose threats to bottlenose dolphins in number of ways: (1) increased mortality as a result of fatal collisions with vessels working in the area (Ribeiro, Viddi, Cordeiro, & Freitas, 2007), or entanglement with ropes, (2) habitat loss (Watson-Capps & Mann, 2004), (3) increased levels of noise pollution due to the high number of vessels in the area, and (4) water pollution due to the use of antifouling paint biocides containing toxic compounds (i.e. lead, arsenic, mercury, copper, cuprous oxide, organotin compounds, or tributyltin), associated with the maintenance of the floating rafts and working vessels (Terlizzi, Frascchetti, Gianguzza, Faimali, & Boero, 2001). These biocides diffuse at the paint-water interface and wash away with time. Some authors claimed that the accumulation of biocides may cause bottlenose dolphin mortality by suppressing their immune system (Kannan, Corsolini, Focardi, Tanabe, & Tatsukawa, 1996).

From a conservation perspective, aquaculture management should consider the presence of bottlenose dolphins foraging in shellfish farm areas and minimise the associated risks that this industry may pose to these coastal cetaceans. Management action for the shellfish industry threats listed in this study should be implemented following the European Union legal obligations under the Habitats Directive to protect bottlenose dolphins, a species listed under the annexes II and IV (species in need of strict protection and which require the designation of Special Areas of Conservation). Speed regulations for vessels operating inside the shellfish farm areas and control of antifouling paints containing biocides used for the floating rafts could minimise the potential impacts of this industry on bottlenose dolphins. In addition, the implementation of shellfish farms in areas of particular ecological importance for bottlenose dolphins should be regulated.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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Table 1. Description of the behavioural states observed in bottlenose dolphins in the Ría de Arousa (north-west Spain).

Behavioural state	Description
Foraging	Solitary or aggregation of bottlenose dolphins swimming in different directions in the same area. Dolphins usually stay in the same area, involve carousel and cross swimming. If large group, the group can be split into two or more subgroups spread over a large area (100m); or the individuals can be completely spread between each other. Surface-feeding: includes fast surfacing (chase prey close to the surface), feeding rush towards the surface or towards obstacles (e.g. rocks, shellfish platforms), catching prey, fish kicking or tossing, ventral swimming. Deep diving: sequence of regular dives followed by steep dives (tail-stock or flukes-up dives), and then long dives (> 60 seconds) (Díaz López, Shirai, Bilbao Prieto, & Méndez Fernández, 2008).
Resting	Solitary or aggregation of bottlenose dolphins surfacing at a slow and constant speed (< 2kt). Group is tight (< 1 body length, 3 meters). Surfacing usually involves synchronous dive behaviour between two or more individuals and floating at the surface. Most of the ventilations are regular and the dives are short (< 60 seconds), with absence of steep dives. When this behavioural state finishes, there is a drastic change of behaviour (important changes of speed, direction, dive interval and behavioural events).
Socializing	Aggregation of bottlenose dolphins interacting at the surface and underwater with one other or, several other, dolphins. Can include synchronous dives, body contact, biting, rolling, charging, chasing, somersault, mating, genital inspections, tail slaps, leaps, bows, and breaches. Individuals change position in the group and swimming direction varies. The group can be split into small subgroups spread over a large area. The dive interval is short (<60 seconds).
Travelling	Solitary or aggregation of bottlenose dolphins regularly surfacing (constant dive intervals) (<60 seconds) at a constant speed (>2 kt) and one goal direction. If there are several individuals in the group, the group is generally cohesive and the inter-individual distance is usually less than 3 bodies (approximately 9 meters).

Table 2. Summary of the 6 best-supported models of bottlenose dolphin foraging behaviour.

Models	df	logLik	AICc	Δ_i	w_i
SF + SST + T + S	9.53	-379.36	778.14	0.00	0.30
SF + SST + T + S + W	10.65	-378.60	778.93	0.79	0.20
SF + SST + T + S + G	10.57	-379.04	779.66	1.51	0.14
SF + SST + T + S + TC	10.47	-379.18	779.73	1.59	0.13
SF + SST + T	5.83	-384.14	780.07	1.92	0.11
SF + SST + T + S + SSS	10.44	-379.40	780.11	1.97	0.11

Only six most candidate models ($\Delta_i \leq 2$) of the 1024 are presented. df degrees of freedom, Δ_i difference in AIC between the particular model and the first-ranked model, w_i Akaike weight showing the relative support of a given model compared to the others, SF shellfish farms, S slope gradient, SST sea-surface temperature, T time, W wind speed, G group size, TC tidal cycle, and SSS sea surface salinity.

Table 3. Model-averaged relative variable importance (RVI) estimated by a generalized additive model to determine the effects of shellfish farms (SF), sea surface temperature (SST), time (T), slope gradient (S), wind speed (W), group size (G), tidal cycle (TC), and sea surface salinity (SSS) on bottlenose dolphin foraging behaviour (n=574).

	RVI
SF (Yes)	1
SST	1
T	1
S	0.89
W	0.2
G	0.14
TC (Flood)	0.13
SSS	0.11

Figure 1. Map of the study area (Ría de Arousa, north-west Spain) with survey tracks, bottlenose dolphin encounters (indicated by filled circles), and polygons representing the shellfish farm areas.

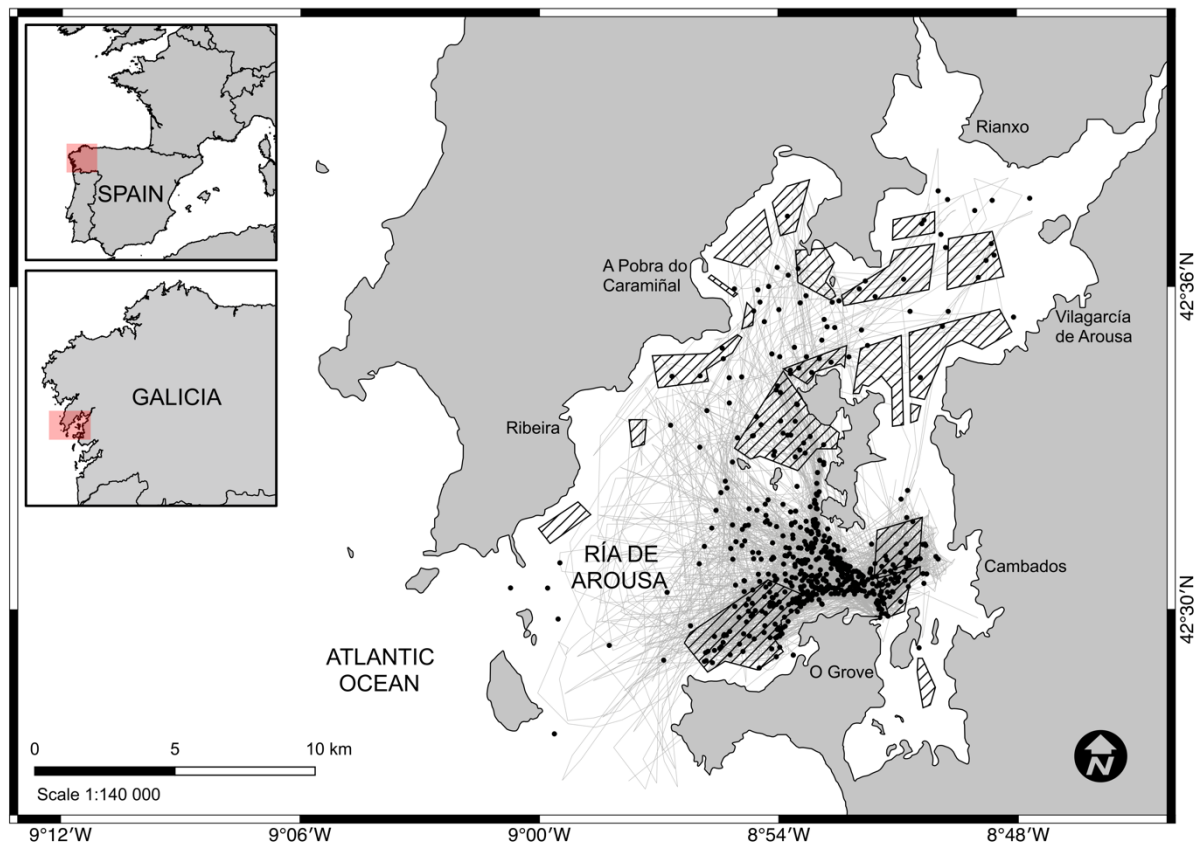


Figure 2. Map of the study area with grid representing bottlenose dolphin foraging budget and polygons representing the shellfish farm areas.

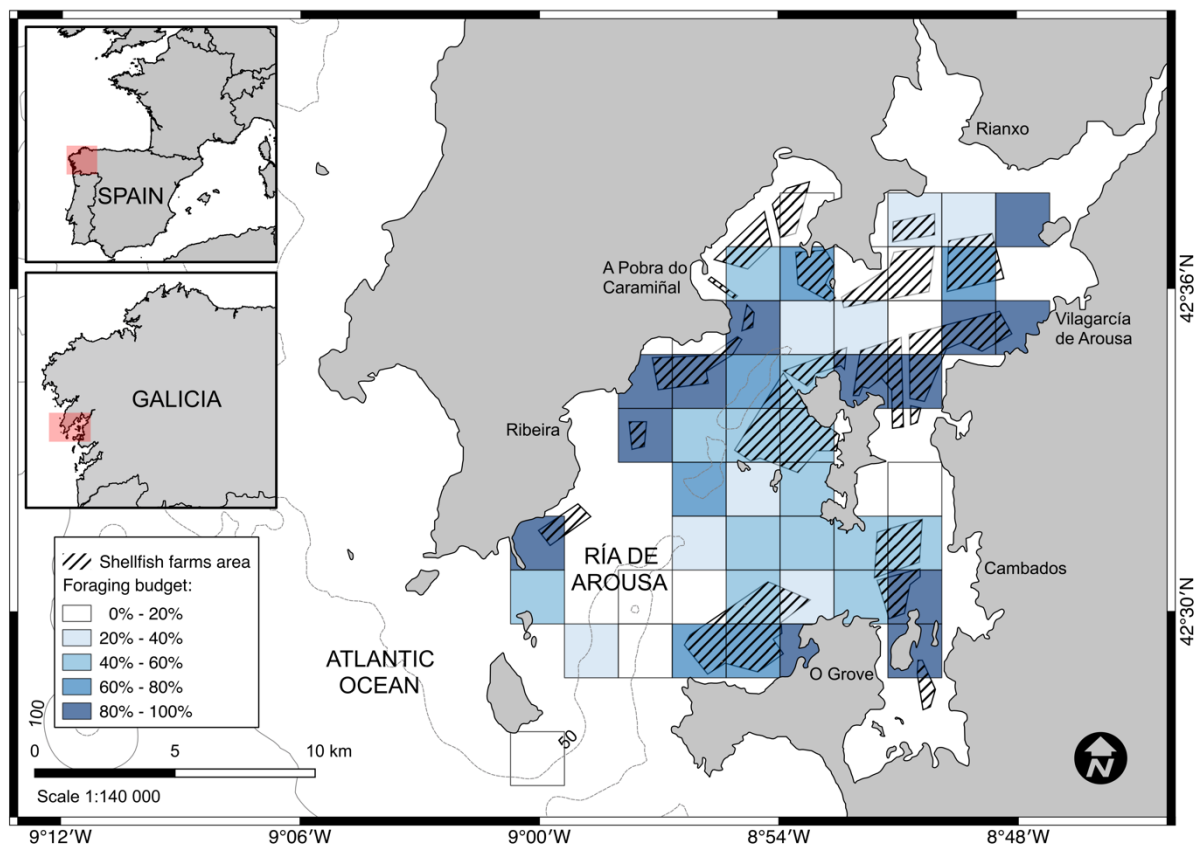


Figure 3. Bottlenose dolphin behavioural budget inside and outside shellfish farm areas.

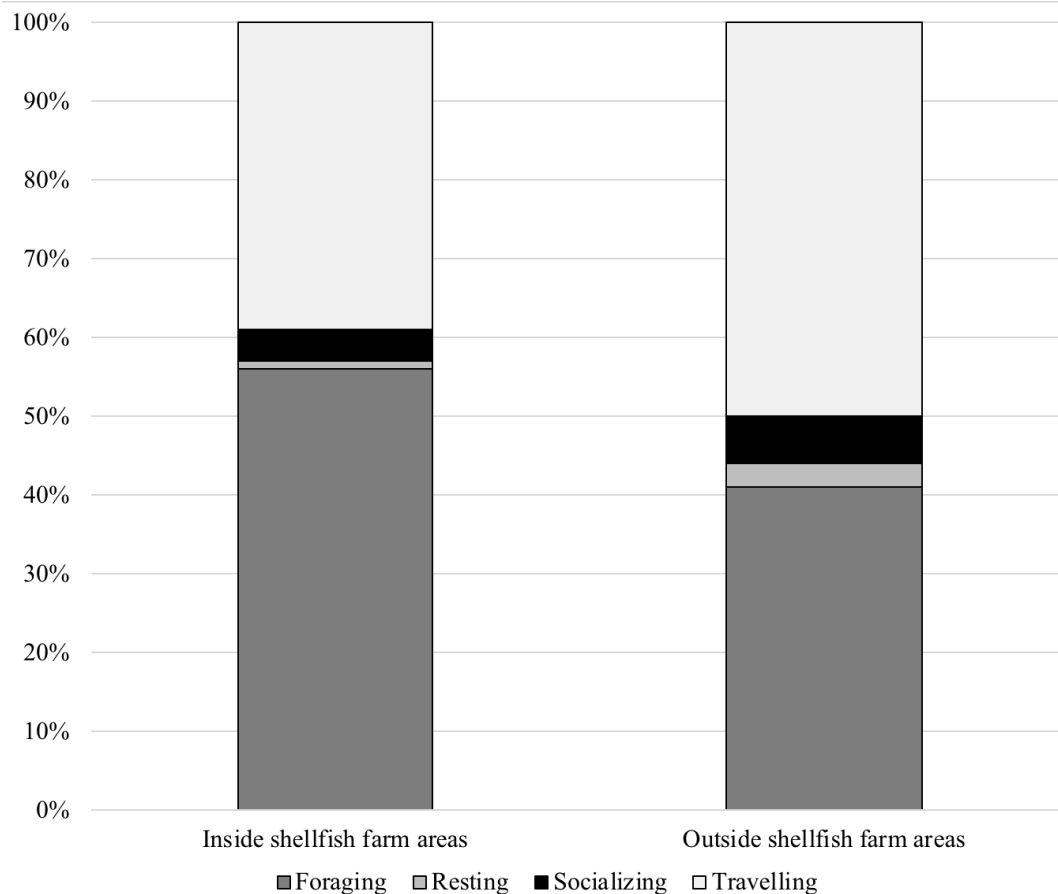


Figure 4. Averaged predictions of bottlenose dolphin foraging behaviour for each covariate present in the confidence set of models and their 95% confidence limits when all other variables are fixed on their mean value.

