acta ethologica
https://doi.org/10.1007/s10211-021-00363-0

ORIGINAL PAPER

Spatial segregation and interspecific killing of common dolphins (*Delphinus delphis*) by bottlenose dolphins (*Tursiops truncatus*)

Séverine Methion[1] · Bruno Díaz López[1]

Received: 3 November 2020 / Revised: 18 February 2021 / Accepted: 22 February 2021

Abstract
We described the spatial segregation of two species of cetaceans, the common dolphin and the bottlenose dolphin. We also document the first direct observation of interspecific killing of a common dolphin by bottlenose dolphins and of interspecific necrophilia in cetaceans. The study was conducted from 2014 to 2019 in the Ría de Arousa (Northwest Spain). This study highlights that both species use this area as a foraging ground, although they show different patterns of occurrence (bottlenose dolphins were always observed in the ria and common dolphins were mostly observed outside). During the study period, bottlenose dolphins and common dolphins were only observed on five occasions at the same time and in the same area, including three occasions which led to the displacement of the common dolphin(s), and one lethal interaction. In this event, several bottlenose dolphins, including adults and calves, and males and females, aggressively herded, chased, and assaulted a common dolphin. After approximatively 10 min, the common dolphin corpse appeared floating at the surface, and several adult male bottlenose dolphins repeatedly pushed the body underneath the water surface and an (attempted) copulation was witnessed. We suggest that the common dolphin could have been killed for competition for food resources or practice for infanticide, and sexual arousal might have been triggered by expression of dominance. Further information about the occurrence of such behaviors, and the outcomes through specific studies on fitness would be crucial to further understand the implication of such events.

Keywords Interspecific interaction · Aggressive behavior · Interspecific killing · Interference competition · Necrophilia · Cetaceans

Introduction

Accumulating evidence has revealed the existence of interspecific competition among mammals which commonly leads to species divergence in ecology, morphology, behavior, or physiology resulting in reduced competition outcomes (Hersteinsson and Macdonald 1992; Dayan and Simberloff 1998; Buchmann et al. 2013). Interspecific competition is commonly divided into (i) exploitative competition, whereby a species indirectly competes with other species for common resources (reducing the amount available for other species through resource use) and (ii) interference competition, whereby a species attempts to free resources by interfering directly with another species in the form of aggression, intimidation, harassment, competitive exclusion, or killing of the interspecific competitor (with or without consumption) (Palomares and Caro 1999; Lourenço et al. 2011).

Interspecific competitive killing unrelated to predation has been documented in various wild mammal species (e.g., white-tailed prairie dog *Cynomys leucurus*: Hoogland and Brown 2016; gray wolf *Canis lupus*: Mohammadi et al. 2017; red fox *Vulpes vulpes*: Mulder 1990; lion *Panthera leo*: Eloff 1984). The reasons for these killings include removing a source of mortality for the killer or its offspring and freeing up food resources that would otherwise be consumed by the victim (Palomares and Caro 1999). The interspecific killing of one species by another species can substantially influence the ecology and demography of both the killing and the victim species (e.g., Hoogland and Brown 2016) and can also shape the community structure of the ecosystem in which these species live (e.g., Bowers and Turner 1997).

Aggressive, non-predatory interactions between sympatric species of wild cetaceans have occasionally been documented

✉ Séverine Methion
severine@thebdri.com

[1] Bottlenose Dolphin Research Institute (BDRI), Avenida Beiramar 192, 36980 O Grove, Pontevedra, Spain

Published online: 12 March 2021

in the wild (e.g., long-finned pilot whale *Globicephala melas*: Weller et al. 1996; killer whale *Orcinus orca*: Jefferson et al. 1991; Pacific white-sided dolphin *Lagenorhynchus obliquidens*: Baird 1998). Possible explanations for antagonistic behavior include competition for resources, feeding interference, practice fighting and infanticide, and sexual frustration (Ross and Wilson 1996). There is, however, limited comprehensive knowledge of interspecific killing unrelated to predation in cetaceans, which impedes the understanding of its evolution, ecological importance, and conservation significance. Further documentation of such aggressive interactions among cetaceans would therefore contribute to additional examination of interaction patterns, determination of whether victim consumption occurs, a better understanding of direct and indirect effects on the populations involved, and identification of conservation and management implications.

The common bottlenose dolphin (*Tursiops truncatus*) (hereafter bottlenose dolphin) is found in temperate and tropical marine waters around the world and inhabits a wide range of habitats due to its behavioral plasticity (Connors et al. 2000). The length of adult individuals can range from 2.5 to 4.1 m, and the body weight varies from 150 to 650 kg (Jefferson et al. 2015). They are complex social animals often found in groups of varying size (Wells and Scott 2009). Infanticide has been recorded in wild bottlenose dolphin groups in Scotland (Patterson et al. 1998), on the East Coast of the USA (Dunn et al. 2002) and in North-western Spain (Díaz López et al. 2018). Violent, non-lethal interspecific attacks of bottlenose dolphins on other cetacean species have also been confirmed by direct observations in several locations around the world (e.g., commerson's dolphins *Cephalorhynchus commersonii* in Argentina: Coscarella and Crespo 2010; Guiana dolphins *Sotalia guianensis* in Brazil: Wedekin et al. 2004). Moreover, bottlenose dolphins have been involved in lethal attacks with various cetacean species, evidenced both by direct observation (harbor porpoise *Phocoena phocoena* on the West coast of the USA: Cotter et al. 2012) and from necropsies of stranded animals (e.g., harbor porpoise in the UK: Ross and Wilson 1996; Jepson and Baker 1998; long-finned pilot whale and Risso's dolphin *Grampus griseus* in the UK: Barnett et al. 2009; striped dolphin *Stenella coeruleoalba* and short-beaked common dolphin *Delphinus delphis* in the UK: Barnett et al. 2009; and in Canary Islands, Spain: Puig-Lozano et al. 2020). Because these interactions are rarely observed in the wild, especially for marine animals, reporting the time and location of direct observations of interspecific killing is valuable.

The two most common cetacean species along the North-western coast of Spain (Galicia) are bottlenose dolphins and short-beaked common dolphins (hereafter common dolphins) (Díaz López and Methion 2017; Díaz López et al. 2019). Bottlenose dolphins exhibit a high site fidelity for coastal waters and are considered resident (Methion and Díaz López 2018). They show a preference for shallow waters (< 30 m) and use the Galician rías as foraging and breeding grounds (Díaz López and Methion 2017; Methion and Díaz López 2019, 2020). Common dolphins are the most abundant cetacean in continental shelf waters of the northwest Iberian Peninsula (Pierce et al. 2010), exhibiting a preference for depths between 50 and 200 m (Giralt Paradell et al. 2019).

In this study, we describe the co-occurrence of these two species of cetaceans, the common dolphin and the bottlenose dolphin, in the Ría de Arousa (Northwest Spain). Additionally, we document the interspecific killing of a common dolphin by bottlenose dolphins and we discuss the potential causes of interspecific killing in these cetacean species.

Methods

The study was carried out in the Ría de Arousa and surrounding waters (Galicia, Northwest Spain) (Fig. 1). Several species of cetaceans have been recorded in these waters, and the most regularly observed are bottlenose dolphins and common dolphins (Methion and Díaz López 2018; Díaz López et al. 2019).

Boat-based observation surveys were conducted from April 2014 to November 2019 by the Bottlenose Dolphin Research Institute BDRI (www.thebdri.com) as part of a longitudinal study on the ecology of cetacean species (Díaz López et al. 2019). The study area was systematically monitored using either a 12-m or a 5.5-m research vessels during daylight hours. On each survey, at least three experienced observers scanned 360° of the sea surface in search of cetaceans (with the naked-eye and 10 × 50 binoculars). Surveys were performed when the visibility was not reduced by rain or fog, sea conditions were up to 4 on the Beaufort wind force scale, and wave height was < 1 m. Details on the data collection procedure can be found in Methion and Díaz López (2019).

A group of dolphins was defined as one or more individuals observed interacting with each other, and engaging in the same behavioral activity, within a 100-m radius for bottlenose dolphins (Methion and Díaz López 2019) and within a 500-m radius for common dolphins (Díaz López et al. 2019). Upon sighting a group of dolphins, the date, time, and position were recorded, and group size and composition were estimated. Photographs were taken for photo-identification purposes using digital single lens reflex (DSLR) cameras equipped with a 35- to 300-mm and a 150- to 500-mm telephoto zoom lens. Details on the photo-identification procedure can be found in Methion and Díaz López (2018). The predominant behavior of the group was assessed every five

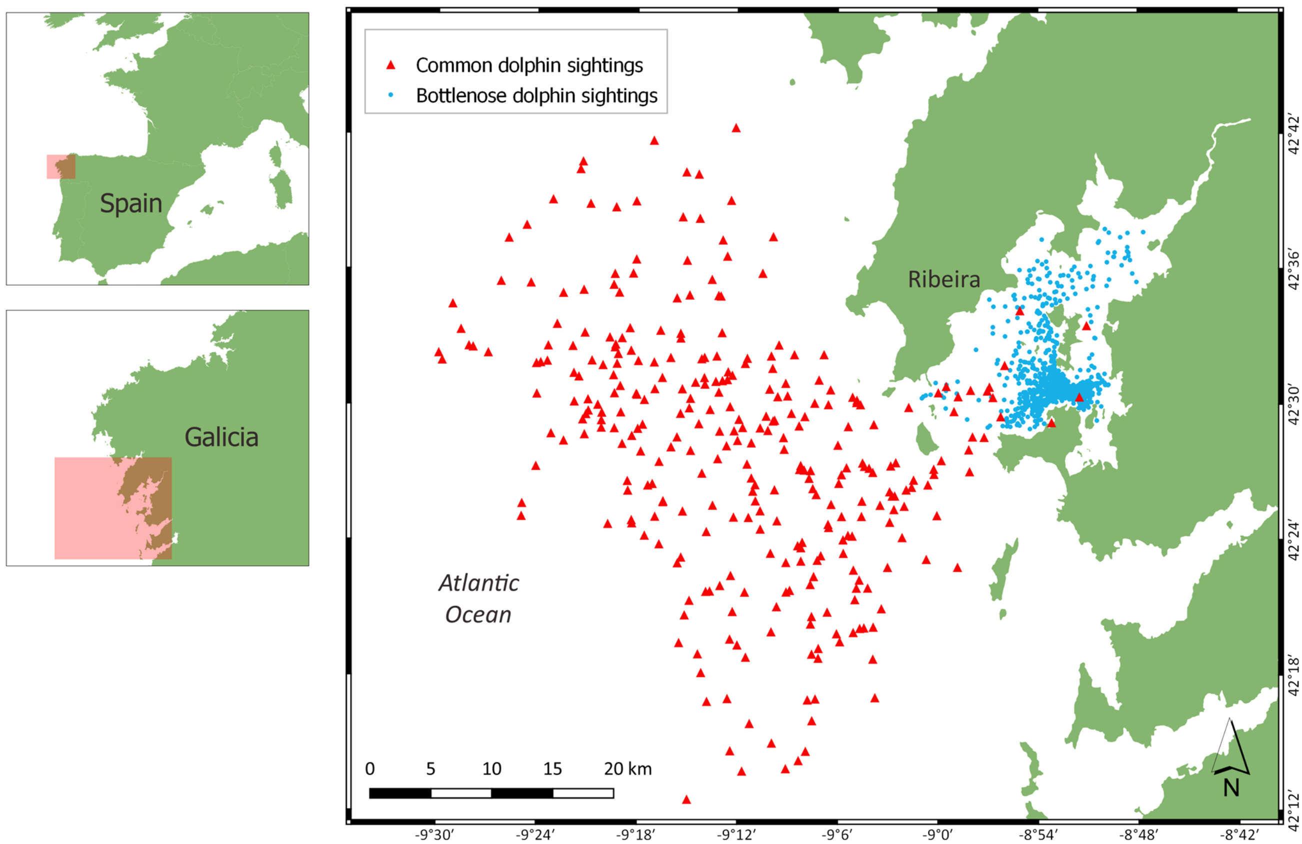

Fig. 1 Study area (Ría de Arousa and surrounding waters, Northwest Spain) with sightings of bottlenose dolphins (blue dots) and sightings of common dolphins (red triangles) throughout the entire six-year study period

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 5-min sample (predominant group activity sampling). The predominant behavior was classified into four categories: foraging, resting, socializing, and travelling (detailed in Methion and Díaz López 2019).

The age of bottlenose dolphin individuals was classified as either (i) dependent calves (including new-born dolphins born within the same calendar year, and immature dolphins born the previous calendar year or before), (ii) juveniles (independent dolphin, not sexually mature), or (iii) adults (independent dolphin, presumably sexually mature) based on behavioral cues, visual assessment of the size, and birth dates. The term calf was used to refer to dependent offspring that were still nursing, or not yet weaned (Mann et al. 2000). Birth dates were estimated from the last date a mother was sighted before the birth of the calf to the first date the mother was sighted with her calf, as well as physical features of the calf such as fetal folds, behavior and body size (Mann et al. 2000). Sex was determined by the observation of the genital region with photographs or by the repeated observation with a new-born calf swimming in infant position (Methion and Díaz López 2020).

The age of common dolphin individuals was classified as either dependent calves or adults (independent dolphin, sexually mature) based on behavioral cues and physical features (e.g., presence of fetal folds and body size).

The interspecific killing of a common dolphin by bottlenose dolphins was observed and filmed on September 12, 2019, by opportunistic observers aboard a recreational vessel from 16:58 to 17:25 UTC, in the Ría de Arousa. The behavior of the group of bottlenose dolphins responsible for the kill was monitored continuously by the BDRI research team before the kill event from 10:26 to 14:21 UTC. The videos of the interspecific interaction were analyzed frame by frame with a video-editing software. The time, identity (from the natural marks present on their dorsal fin; Methion and Díaz López 2018), and behavior of individual dolphins, including the occurrence of agonistic interactions, were recorded whenever possible.

Results

Occurrence, group size, group composition, and behavior of bottlenose dolphins and common dolphins in the Ría de Arousa

From April 2014 to November 2019, 423 daily boat surveys were conducted to monitor the Ría de Arousa and surrounding waters. Throughout this period, 955 groups of bottlenose dolphins (mean group size = 10.2 ± SE 0.3; minimum = 1; maximum = 64) and 317 groups of common dolphin were observed (Fig. 1). Only 6% of the common dolphins' group ($n = 20$) were seen inside the Ría de Arousa (Fig. 1). The mean group size of these 20 groups of common dolphins was 31.7 ± SE 8.6 (minimum = 1; maximum = 150). Common dolphin group size was significantly higher when compared with bottlenose dolphins (Mann Whitney $z = -3.2$, $P = 0.001$). Calves were present in 43% and 60% of the groups of bottlenose and common dolphins observed, respectively. Groups of bottlenose dolphins and common dolphins were composed of 12.2% and 13.7% dependent calves, respectively. Both bottlenose dolphin and common dolphin group sizes were positively correlated with the presence of dependent calves in the group (bottlenose dolphins: Spearman rho = 0.59, $P < 0.001$; common dolphins: Spearman rho = 0.76, $P < 0.001$). Likewise, the number of individuals in the group was significantly higher in the presence of dependent calves for both species (bottlenose dolphins, median with and without calves 11 v. 4 respectively; Mann–Whitney $z = -15.3$, $P < 0.001$; common dolphin, median with and without calves 24 v. 10 respectively; Mann–Whitney $z = -2.2$, $P = 0.026$).

Bottlenose dolphins were observed every month of the year from April 2014 to November 2019. While common dolphins were also observed every month of the year outside the Ría de Arousa, they were only seen occasionally from 2017 to 2019 inside the Ría de Arousa (six sightings from July to October 2017, one sighting in January 2018, three sightings in August 2018, and ten sightings from July to September 2019). Bottlenose dolphins were observed on 371 different days (88% of the daily surveys) for a total of 603 h, and common dolphins were observed on 18 different days (4% of the daily surveys) for a total of 18 h inside the Ría de Arousa. The occurrence of bottlenose dolphins was at a minimum in 2019 (contingency table Chi2 = 17.9, 5 df, $P = 0.003$), and there was a peak in occurrence in common dolphins in 2019 inside the Ría de Arousa (contingency table Chi2 = 22.4, 5 df, $P < 0.001$) (Fig. 2). Both species were predominantly involved in foraging behavior while observed in the Ría de Arousa (Table 1).

Co-occurrence of bottlenose dolphins and common dolphins in the Ría de Arousa

During the study period, there were four occasions (excluding the lethal interaction described below) when both species

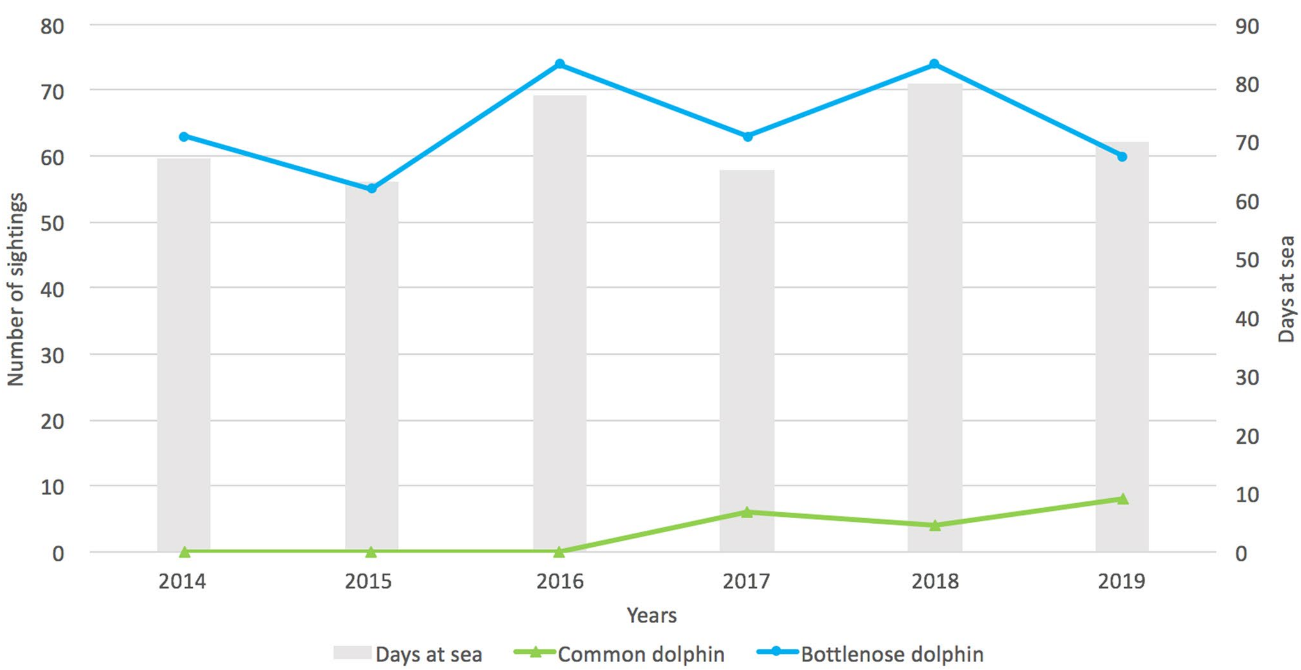

Fig. 2 Number of days spent at sea and number of sightings of bottlenose dolphins and common dolphins over the study period in the Ría de Arousa

Table 1 Behavioral budget of bottlenose dolphins and common dolphins in the Ría de Arousa

Behavioral budget	Foraging	Travelling	Resting	Socializing
Bottlenose dolphin	48%	37%	4%	11%
Common dolphin	81%	17%	2%	0%

were observed at the same time and less than one nautical mile away from each other (Fig. 3). The behavior of the dolphins is presented chronologically, as observed in the field.

Case 1. On July 21, 2017, from 10:00 to 10:40 UTC, a group of 100 common dolphins (including 30 dependent calves) was observed foraging close to the eastern shoreline of Sálvora Island (Fig. 3). At 10:40 UTC, a group of five bottlenose dolphins (including two females with their dependent calves) arrived in the area (1500 m away). The bottlenose dolphins were engaged in foraging behavior on the north-eastern side of the island. Upon the arrival of the bottlenose dolphins, the common dolphins changed their behavior, all performing sequences of fast surfaces and full leaps, leaving the Ría de Arousa along the coastline of Sálvora island from the South (towards the open ocean). No direct interaction between the two species was observed.

Case 2. On August 26, 2017, at 8:10 UTC, a group of bottlenose dolphins was spotted along the southern shoreline of the Ría de Arousa (Fig. 3). The group was composed of 16 adult individuals, including 15 males and one female (without a dependent calf). The bottlenose dolphins were performing sequences of regular dives along the shore and heading Southwest. At 8:45 UTC, at least seven of the bottlenose dolphins in the group entered a semi-enclosed bay, locally named Porto Meloxo, performing sequences of regular dives followed by tail-stock and flukes-up dives. The other bottlenose dolphins were engaged in foraging behavior at the entrance of the bay. At 8:50 UTC, one solitary adult common dolphin was

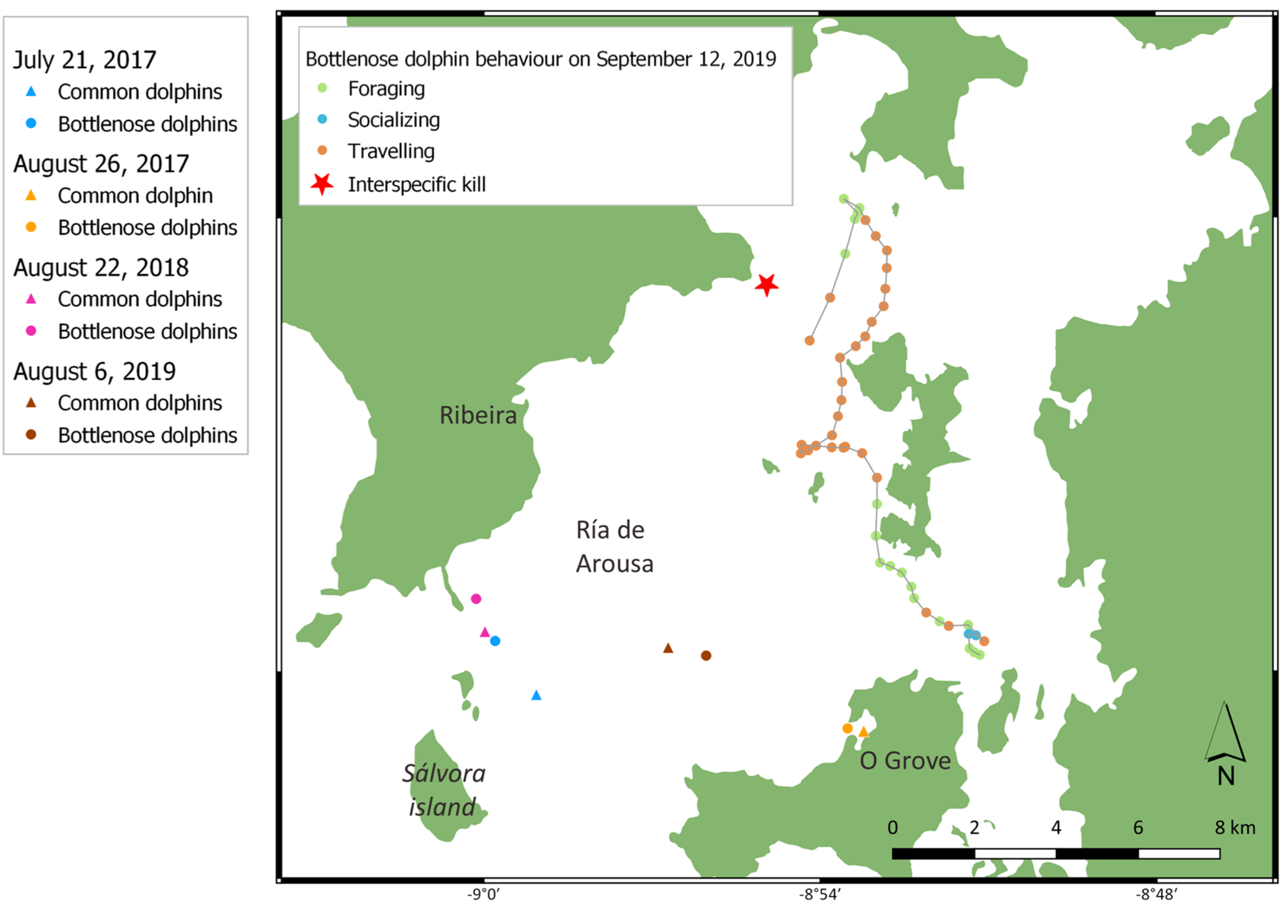

Fig. 3 Position and date of co-occurrence events (< 1 nm between bottlenose dolphins and common dolphins) with no direct interactions throughout the study period and associated behaviors (colored dots on grey line) of the bottlenose dolphin group (every five minutes) before the interspecific kill (star)

spotted in the bay, very close to the shoreline (< 10 m) (Fig. 3). The bottlenose dolphins were observed as close as 100 m away from the common dolphin but no direct interaction between the two species was observed. At 9:05 UTC, the bottlenose dolphins that were in Porto Meloxo left the bay heading Northeast. The group of bottlenose dolphins was observed foraging and socializing at the entrance of the bay up to 11:00 UTC. The behavior of the common dolphin was followed continuously from 8:50 to 13:45 UTC. During that time, the common dolphin was observed swimming in shallow waters (< 5-m depth) very close to the shore (< 10 m) frequently changing directions but staying in the same area. On six occasions, the respiratory pattern of the common dolphin was recorded to the nearest second using a digital stopwatch, for a total 46 min. The solitary common dolphin performed shallow dives only (mean dive duration = 11.7 ± SE 0.3 s; minimum = 1 s; maximum = 33 s; $n = 238$) and was observed floating several times. The common dolphin left the bay heading West at 13:45 UTC. There were no bottlenose dolphins in the area at this time.

Case 3. On August 22, 2018, at 6:32 UTC, a group of 40 common dolphins (including 10 dependent calves) were engaged in foraging behavior at the northern entrance of the Ría de Arousa (Fig. 3). The common dolphins were spread over a 300-m radius. Several species of seabirds were flying over the common dolphins, feeding in the same area. These included yellow-legged gulls *Larus michahellis*, great black-backed gulls *Larus marinus*, sandwich terns *Sterna sandvicensis*, Balearic shearwaters *Puffinus mauretanicus*, and cormorants *Phalacrocorax spp*. At 6:45 UTC, the group of common dolphins became more compact (inter-individual distance less than 10 m) and dolphins started to perform sequences of fast surfaces heading Southwest (towards the southern entrance of the Ría de Arousa). At 6:50 UTC, a group of bottlenose dolphins was spotted in the same area (750 m away). The bottlenose dolphins were engaged in foraging behavior, and the group was composed of 24 individuals, including six adult males and 12 adult females, six of which had a dependent calf (five immature dolphins and one new-born dolphin). The common dolphins left the Ría de Arousa swimming around the island of Sálvora from the South upon the arrival of the bottlenose dolphins. No direct interaction between the two species was observed.

Case 4. On August 6, 2019, at 8:54 UTC, a group of bottlenose dolphins composed of four individuals, including two adult males, one adult female and her dependent calf, was observed in the middle of the Ría de Arousa (Fig. 3). These bottlenose dolphins were travelling at a constant speed and direction (East). At 9:16 UTC, a group of 22 common dolphins (including three dependent calves) was spotted 950 m West of the group of bottlenose dolphins (Fig. 3). The common dolphins were engaged in foraging behavior and the individuals were spread over a 200-m radius. The bottlenose dolphins kept travelling in the same direction and the common dolphins stayed foraging in the same area until 10:00 UTC. No direct interaction between the two species was observed.

Interspecific killing of a common dolphin by bottlenose dolphins

On September 12, 2019, from 16:58 to 17:25 UTC, opportunistic observers aboard a recreational motor boat filmed the interaction between bottlenose dolphins and common dolphins along the northern shoreline of the Ría de Arousa (N 42°35′07; W 008°54′56) (Fig. 3). The behavior of the dolphins during the interspecific interaction is presented chronologically, as seen from the surface videos recorded on the opportunistic vessel (see video in Online Resources):

16:58–17:00 UTC. At least five common dolphins were engaged in foraging behavior, performing sequences of full leaps in different directions along the northern shoreline of the Ría de Arousa. Several yellow-legged gulls were flying in circles over the common dolphins.

17:01 UTC. A group of at least eleven bottlenose dolphins arrived in the area, performing sequences of fast surfaces, from the Southeast of the Ría de Arousa, towards the group of common dolphins (Northwest). Yellow-legged gulls were still flying over the common dolphins.

17:02 UTC. Five bottlenose dolphins were seen chasing the group of common dolphins. The bottlenose dolphins then isolated one common dolphin from the rest of the group and chased it, performing sequences of full leaps and fast surfaces with abrupt direction changes. Other bottlenose dolphins (including at least three females and their dependent calves) were present in the area and were performing fast surfaces towards the bottlenose dolphins chasing the common dolphin. In the meantime, the other common dolphins were leaving the area, performing sequences of fast surfaces in a Southwest direction.

17:03–17–09 UTC. The group of five bottlenose dolphins was observed herding the isolated common dolphin towards the rocky shoreline (North). The bottlenose dolphins were chasing the common dolphin in a small area, very close to the rocky shoreline, for several minutes. The isolated common dolphin was performing sequences of full leaps at a very high speed and in different directions, followed closely (< 10 m) by five bottlenose dolphins, including four adult males (identified as Z5, Z8, C4, and A9) (Z5 and Z8 were first observed as fully grown individuals in 2017, C4 and A9 were first observed as fully grown individuals in 2009 and 2003, respectively (López et al. 2019) and one dependent male calf (identified as B7C2, born in Summer 2018). The bottlenose dolphins were performing sequences of fast surfaces following the isolated common dolphin. The individual Z5 was in front of the group, followed by Z8, C4, A9, and B7C2. The mother of B7C2 (B7), and two other females (I4 and X4) with their new-born calves (born in Summer 2019) were also present in the area (< 30 m), although not actively chasing the common dolphin.

17:10–17:12 UTC. The isolated common dolphin was encircled by at least eleven bottlenose dolphins (including three dependent calves, identified as B7C2, I4C1, and X4C2) (< 10 m). The bottlenose dolphins were circling around the common dolphin, performing sequences of fast surfaces and tail-stock dives, with abrupt changes in direction. The bottlenose dolphins were harassing the common dolphin in an apparently coordinated manner while the common dolphin was performing sequences of fast surfaces in different directions.

17:13 UTC. The bottlenose dolphin identified as Z5 was forcing the common dolphin between itself (Z5) and the bottlenose dolphin identified as Z8. Z5 was ramming and pushing the common dolphin underwater while it was trying to surface to breathe. The common dolphin was then able to perform regular dives in different directions, but was followed very closely by Z5 and Z8. The individual Z5 then tossed the body of the common dolphin out of the water. After being tossed up, the common dolphin tried to surface but Z5 rammed the common dolphin with its rostrum from underwater and lifted the common dolphin out of the water. The common dolphin became gradually less vigorous. Z5 then breached over the common dolphin and performed sequences of tail-stock dives over the common dolphin, pushing and holding it underwater.

17:14–17:15 UTC. The common dolphin appeared lying motionless on its right side, floating at the surface. At least ten bottlenose dolphins (including three females and their dependent calves) were performing sequences of tail-stock dives close to the floating and inert body of the common dolphin. The individual Z5, in particular, was performing tail-stock dives over the motionless common dolphin. Z5 subsequently slapped the motionless body with its flukes, repeatedly, while in a belly up position. Afterwards, Z5 lifted the inanimate body of the common dolphin out of the water by laying with its ventral surface against the common dolphin's belly. Z5 was then observed rolling around the dead common dolphin body and positioning itself belly up, underneath the motionless common dolphin that was floating on its right side. Z5 had an erection, with its penis protruding above the surface and near the common dolphin's genitals, and an attempt of intromission was observed (the quality of the video did not allow us to confirm the intromission). All the other bottlenose dolphins continued to perform tail-stock dives in different direction, around the inert common dolphin (< 10 m away).

The opportunistic observers confirmed that the bottlenose dolphins left the area, leaving the common dolphin lying motionless at 17:25 UTC. While it was not possible for the opportunistic observers to recover the body of the common dolphin, its death was confirmed by the fact that it was observed floating and motionless at the surface for more than ten consecutive minutes.

Overall, ten individual bottlenose dolphins were identified during the interspecific interaction. The behavior of the bottlenose dolphins present during this interspecific interaction was previously monitored by the BDRI research team on the same day from 10:26 to 14:21 UTC (235 min) in the Ría de Arousa (Fig. 3). During that time, the water depth, sea surface temperature, and sea surface salinity varied from 6.7 to 52.8 m, 14.2 to 14.9 °C, and 33 to 35 Practical Salinity Unit, respectively. The group was composed of 17 individuals: seven adult males, five adult females (four of which had a dependent calf), one independent juvenile male (born in July 2017), and four dependent calves (two of them born in Summer 2018 and two of them born in Summer 2019). These bottlenose dolphins are resident individuals that have been followed by the BDRI research team since 2014. From 10:26 to 14:21 UTC, these bottlenose dolphins were engaged in foraging (85 min, 36%), travelling (120 min, 60%), and socializing behavior (10 min, 4%) (Fig. 3).

Discussion

In this study, we described the co-occurrence of two cetacean species in the Ría de Arousa (Northwest Spain) and we documented, to our knowledge, the first direct observation of interspecific killing of a common dolphin by bottlenose dolphins.

Bottlenose dolphins were studied for six consecutive years (1700 h in the field, including 603 h following dolphin behavior), and such an event was never observed by our research team. The fact that such a short (less than 15 min) and unanticipated interspecific kill was witnessed by opportunistic observers highlights the fleeting nature of this event and the importance of documenting it. As direct observations are rare in the wild, this type of study provides valuable information to better understand the occurrence of this phenomenon in highly mobile marine top predators.

This 6-year monitoring study highlights that both bottlenose dolphins and common dolphins use the Ría de Arousa as a foraging ground, although they show different patterns of occurrence. Bottlenose dolphins were observed on most of the daily boat-surveys (88%), while common dolphins were only sporadically sighted in the Ría de Arousa (4% of the daily boat-surveys). In Galician waters, bottlenose dolphins and common dolphins are part of the same trophic level (Giralt Paradell et al. 2020) and have a similar diet, with the same top seven most commonly consumed fish species (i.e., blue whiting *Micromesistius poutassou*; European pilchard *Sardina pilchardus*; European hake *Merluccius merluccius*; Atlantic mackerel *Scomber scombrus*; *Trisopterus* spp.; *Atherina* spp.; *Trachurus* spp.) (Santos et al. 2007; 2013; Méndez-Fernández et al. 2012). Yet, while bottlenose dolphins are mostly observed along the shore and show high-site fidelity to the Ría de Arousa (Díaz López and Methion 2018; Methion and Díaz López 2018), common dolphins are mostly observed in pelagic waters above the continental shelf (Fig. 1) (Giralt Paradell et al. 2019). Common dolphins indeed show a lower level of stable isotope ratios of carbon (δ13C) in the study area, which is thought to result from exploitation of more oceanic resources when compared with bottlenose dolphins (Méndez-Fernández et al. 2012). When observed in the Ría de Arousa, both species were engaged in foraging activity most of the time (81% for common dolphins; 48% for bottlenose dolphins). The Ría de Arousa is therefore an important foraging ground for these cetacean species and may contain high-quality and quantity resources that attract these two species. Both common dolphins and bottlenose dolphins might therefore be attracted to the same areas when searching for food, which may increase the probability of encounters.

Bottlenose dolphins and common dolphins are sympatric over a large part of their geographic range (Mediterranean Sea: Bearzi et al. 2005; Gulf of California: Silber et al. 1994; New Zealand: Dwyer et al. 2016; North-East Atlantic: Hammond et al. 2013). However, as observed in other areas (e.g., Azzellino et al. 2008), temporal and spatial segregation is also expected to occur in this area. During the study period, bottlenose dolphins and common dolphins were only observed on five occasions at the same time and in the same area. On three of these occasions, interspecific aggression without physical contact by bottlenose dolphins have been observed, which led to the displacement of the common dolphin(s) upon arrival of bottlenose dolphins. On one occasion, the common dolphins did not show avoidance to the bottlenose dolphins, as the bottlenose dolphins were travelling in the opposite direction. On the last occasion, a lethal interaction occurred.

In what way(s) would killing common dolphins benefit bottlenose dolphins?

Increasing bottlenose dolphin fitness

Interspecific killing possibly reduces interspecific competition for food near the bottlenose dolphin foraging grounds. The area where the interspecific killing occurred is in fact used more than 80% of the time as a foraging area by bottlenose dolphins (see Fig. 2 in Methion and Díaz López 2019). Our results also show that common dolphins were mostly involved in foraging behavior when present in the Ría de Arousa (81% of the time). The removal of common dolphins from bottlenose dolphin foraging grounds over a long period of time might lead to the spatial exclusion of common dolphins, reduce competition for resources and possibly increase fitness of bottlenose dolphins. In white-tailed prairie dogs (*Cynomys leucurus*), interspecific killing unrelated to predation is indeed a strategy to decrease interspecific competition for food resources and is a strong predictor of lifetime fitness (Hoogland and Brown 2016).

When killers are larger than their interspecific competitors, the cost (e.g., risk of injury) of killings is considered smaller for killers, but the cost (e.g., death) can be much higher for victims (Hoogland and Brown 2016). The massive and muscular morphology of bottlenose dolphins compared with that of common dolphins (Jefferson et al. 2015) might make the costs of interspecific aggression negligible for bottlenose dolphins, rendering the attacks on the common dolphins profitable.

The group of bottlenose dolphins responsible for the kill was composed of several adult mature males and lactating females with dependent calves. The energy requirement of lactating females is greater than non-lactating females (Reddy et al. 1994; Kastelein et al. 2002). Likewise, male bottlenose dolphins might also need a higher energy intake in periods of breeding activity, as males incur energetic costs associated with sperm production, courtship, mate guarding and male-male competition (as observed in other mammals: Key and Ross 1999). In addition, bottlenose dolphins usually give birth from late June to late September in Galicia (Methion 2019) and, assuming a gestation period of 12 months (Wells and Scott 2009), the breeding period in Galicia most likely occurs from June to September. Peak sperm density, indicative of breeding activity, has in fact been detected in male bottlenose dolphins in the month of September (Northern hemisphere) (Schroeder and Keller 1989).

This interspecific killing event occurred in September, a period in which the water temperature starts to decrease in the study area (INTECMAR observation network; http://www.intecmar.gal). Bottlenose dolphins need a higher daily energy intake as water temperature lowers (Cheal and Gales 1992) and bottlenose dolphins indeed spend more time engaged in foraging behavior with lower water temperature in Galicia (Methion and Díaz López 2019).

This interspecific killing occurring in September, during the bottlenose dolphin breeding period, with decreasing water temperature, and with the confirmed presence of several adult mature males and lactating females with newborns may therefore be consistent with the hypothesis of interspecific killing to increase fitness.

Training for infanticide

As hypothesized by and Patterson et al. (1998) and Cotter et al. (2012), interspecific killing by bottlenose dolphins could also be considered a form of object-oriented play aimed at training for infanticide. Several infanticide events have indeed been reported in this area during the same time of year (i.e., September) (Díaz López et al. 2018). As mentioned earlier, this interspecific kill coincided with the breeding season, a period in which male bottlenose dolphin use sexual coercion and exert more aggression than usual (Smuts and Smuts 1993). The killing of a common dolphin by bottlenose dolphins could therefore serve to develop or practice skills used in infanticidal attacks. Interspecific killing of other cetaceans by bottlenose dolphins is thought to be because bottlenose dolphin calves and the individuals of the species killed (i.e., harbor porpoises, common dolphins; juvenile pilot whales) are of approximately similar lengths (Patterson et al. 1998; Barnett et al. 2009). In this study, there is no available measurement (length) of the common dolphin killed, but it could have been targeted to practice for infanticide, as common dolphins are of similar length (average length in Galician waters = 180 cm; López 2003) than bottlenose dolphin calves (around 150 cm; Díaz López et al. 2018) and as this interspecific killing occurred in September.

Sexual frustration

Interspecific attacks, as seen in other marine mammals, may result from re-directed aggression or sexual frustration, where access to females or other resources is limited (Higgins and Tedman 1990; Rose et al. 1991; Le Boeuf and Campagna 1994). Here, the interaction was indeed mostly led by two fully grown male bottlenose dolphins and the witnessed (attempted) copulation from one fully grown male bottlenose dolphin with the common dolphin corpse may support this hypothesis. Sexual arousal may be triggered by physiological responses related to stress or may be an expression of dominance, with no reproductive purpose (Bearzi et al. 2017, 2018). In captivity, bottlenose dolphins indeed establish or assert dominance through sexual displays (Ostman 1991). Sexual behavior toward corpses (necrophilia) of non-conspecifics has been observed in several taxa, including mammals (e.g., sea otters *Enhydra lutris*: Harris et al. 2010; Hooker's sea lion *Phocarctos hookeri*: Wilson 1979) and amphibians (e.g., *Dendropsophus columbianus:* Bedoya et al. 2014). This is yet, to our knowledge, the first report of interspecific necrophilia in cetaceans.

Improving fighting skills

Interspecific killing by bottlenose dolphins may also serve as practice for fights, as male bottlenose dolphins may constantly need to improve their fighting skills to gain access to females. Male sexual-competition is high in bottlenose dolphin societies, and male reproductive success depends on their fighting abilities (Connor et al. 2000). Common dolphins may therefore be safe targets for improvement of the male bottlenose dolphin combat skills that are essential for reproductive success. Some studies in birds also suggest that such killings may serve as displays of fighting ability in males (Nuechterlein and Storer 1982).

Victim consumption

In other mammalian species, individuals that kill competitors of different species sometimes consume their victims (e.g., lion: Eloff 1984; gray wolf: Boyd et al. 1994; brown bear *Ursus arctos*: Ballard 1980), and distinguishing between predation and interspecific killing not related to predation is therefore difficult. The bottlenose dolphins in this study were not observed feeding on the common dolphin. The lack of victim consumption has also been described in other cases of interspecific killing of other cetacean species by bottlenose dolphins (e.g., Barnett et al. 2009; Cotter et al. 2012). Sustenance from consuming common dolphins is thus unlikely to be a benefit of this interspecific killing, or a reason for its occurrence.

Why do common dolphins continue to use the same areas as bottlenose dolphins?

Living with bottlenose dolphins involves a compromise for common dolphins: a higher risk of mortality from interspecific killing, contrasted by the ability to access high-quality and quantity of food resources. If bottlenose dolphins live in areas with high-nutrition resources, then using the same area gives common dolphins access to the same food resources. Consequently, common dolphins might overall benefit from using the same areas as bottlenose dolphins.

As a result, common dolphin may adjust their behavior to reduce encounters with bottlenose dolphins and the potential risk of being killed. Simple patterns of interspecific aggression (Ferretti 2010) were indeed observed on several occasions during the study, which led to the displacement of the common dolphin(s). As common dolphin group size was higher than that of bottlenose dolphins, grouping might also allow common dolphins to obtain antipredator advantages or compete more successfully for food. The behavior of common dolphins is therefore likely influenced by the regular presence of bottlenose dolphins and the distribution of common dolphins in coastal waters might therefore be limited by the presence of bottlenose dolphins. This was further supported by the observed peak of common dolphin presence (2019) that corresponded with the lowest occurrence of bottlenose dolphins within the ría.

Conclusion

The distribution of bottlenose dolphins and common dolphins appears to be parapatric in South Galicia, with bottlenose dolphins residing in coastal habitats and common dolphins using these areas only occasionally. The observed aggressive behavior of bottlenose dolphins towards common dolphins is a manifestation of interspecific dominance and may be a mechanism that contributes to the spatial segregation of these two cetacean species.

Bottlenose dolphin killing other cetacean species is likely to be driven by multiple factors acting synergistically, including competition for food resources, practice for infanticide, sexual frustration, or to improve fighting skills. In this case, the common dolphin could have been killed for competition for food resources or practice for infanticide and, sexual arousal might have been triggered by expression of dominance. This observation may have further implications for both victim and killer, such as significant consequences for fitness. Further information about the occurrence of such behaviors, and the outcomes through specific studies on fitness would therefore be crucial to further understand the implication of such events.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10211-021-00363-0.

Acknowledgements We thank Oriol Giralt Paradell, Sara de Almeida Simoes, Olga Mosca, Victoria Hope, Niki Karagouni, and BDRI volunteers for their contribution to support field and laboratory work. Thanks also to Francisco Redondo and his crew for providing the videos and to Olga Mosca for reviewing the English grammar of the manuscript. We also thank the editor Dr. Ana M. Faria and two anonymous reviewers for their constructive comments that helped improve the manuscript. Data collection complies with the current laws of Spain, the country in which it was performed. This research was conducted under various research permits, issued by the sub-directorate general for the protection of the sea in the Spanish ministry for ecological transition and demographic challenge.

Author contribution Séverine Methion and Bruno Díaz López designed the study and collected the data in the field. Séverine Methion analyzed the data and wrote the manuscript with significant input from Bruno Díaz López. Séverine Methion and Bruno Díaz López read and approved the final manuscript.

Funding This research is part of a long-term study supported by funding from the Bottlenose Dolphin Research Institute (www.thebdri.com).

Availability of data and material Data will be provided under request.

Declarations

Ethics approval This is an observational study, and no ethical approval was required.

Consent for publication All authors consent to publish.

Conflict of interest The authors declare that they have no conflict of interest.

References

Azzellino A, Gaspari S, Airoldi S, Nani B (2008) Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. Deep Sea Res Part I 55(3):296–323

Baird RW (1998) An interaction between Pacific white-sided dolphins and a neonatal harbor porpoise. Mammalia 62(1):129–133

Ballard WB (1980) Brown bear kills gray wolf. Canadian Field-Naturalist 94:91

Barnett J, Davison N, Deaville R, Monies R, Loveridge J, Tregenza N, Jepson PD (2009) Postmortem evidence of interactions of bottlenose dolphins (*Tursiops truncatus*) with other dolphin species in south-west England. Vet Rec 165(15):441–444

Bearzi G, Politi E, Agazzi S, Bruno S, Costa M, Bonizzoni S (2005) Occurrence and present status of coastal dolphins (*Delphinus delphis* and *Tursiops truncatus*) in the eastern Ionian Sea. Aquatic Conserv Mar Freshwat Ecosyst 15(3):243–257

Bearzi G, Eddy L, Piwetz S, Reggente MA, Cozzi B (2017) Cetacean behavior toward the dead and dying. Encyclopedia of animal cognition and behavior 1–30

Bearzi G, Kerem D, Furey NB, Pitman RL, Rendell L, Reeves RR (2018) Whale and dolphin behavioural responses to dead conspecifics. Zoology 128:1–15

Bedoya SC, Mantilla-Castaño JC, Pareja-Márquez IM (2014) Necrophiliac and interspecific amplexus in *Dendropsophus columbianus* (*Anura: Hylidae*) in the Central Cordillera of Colombia. Herpetology Notes 7(1):16

Bowers RG, Turner J (1997) Community structure and the interplay between interspecific infection and competition. J Theor Biol 187(1):95–109

Boyd D, Ream RR, Pletscher DH, Fairchild MW (1994) Prey taken by colonizing wolves and hunters in the Glacier National Park area. J Wildl Manag 58:289–295

Buchmann CM, Schurr FM, Nathan R, Jeltsch F (2013) Habitat loss and fragmentation affecting mammal and bird communities—the role of interspecific competition and individual space use. Eco Inform 14:90–98

Cheal AJ, Gales NJ (1992) Growth, sexual maturity and food-Intake of Australian Indian-Ocean bottlenosed dolphins, *Tursiops truncatus*, in captivity. Aust J Zool 40(2):215–223

Connor RC, Wells RS, Mann J, Read AJ (2000) The bottlenose dolphin: social relationships in a fission–fusion society. In: Mann J, Connor R, Tyack PL, Whitehead H (eds) Cetacean Societies: Field Studies of Dolphins and Whales. University of Chicago Press, Chicago, IL USA, pp 91–126

Coscarella MA, Pedraza SN, Crespo EA (2010) Behavior and seasonal variation in the relative abundance of Commerson's dolphin (*Cephalorhynchus commersonii*) in northern Patagonia. Argentina Journal of Ethology 28(3):463–470

Cotter MP, Maldini D, Jefferson TA (2012) "Porpicide" in California: Killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). Mar Mamm Sci 28(1):E1–E15

Dayan T, Simberloff D (1998) Size patterns among competitors: ecological character displacement and character release in

mammals, with special reference to island populations. Mammal Rev 28(3):99–124
Díaz López B, Methion S (2018) Does interspecific competition drive patterns of habitat use and relative density in harbour porpoises? Mar Biol 165:92
Díaz López B, López A, Methion S, Covelo P (2018) Infanticide attacks and associated epimeletic behaviour in free-ranging common bottlenose dolphins (*Tursiops truncatus*). J Mar Biol Assoc UK 98(5):1159–1167
Díaz López B, Methion S (2017) The impact of shellfish farming on common bottlenose dolphins' use of habitat. Marine Biology 164 (4)
Díaz López B, Methion S, Giralt Paradell O (2019) Living on the edge: overlap between a marine predator's habitat use and fisheries in the Northeast Atlantic waters (NW Spain). Prog Oceanogr 175:115–123
Dunn DG, Barco SG, Pabst DA, McLellan WA (2002) Evidence for infanticide in bottlenose dolphins of the western North Atlantic. J Wildl Dis 38(3):505–510
Dwyer SL, Clement DM, Pawley MDM, Stockin KA (2016) Distribution and relative density of cetaceans in the Hauraki Gulf, New Zealand. NZ J Mar Freshwat Res 50(3):457–480
Eloff FC (1984) Food ecology of the Kalahari lion *Panthera leo vernayi*. Koedoe 27:249–258
Ferretti F (2010) Interspecific aggression between fallow and roe deer. Ethol Ecol Evol 23(2):179–186
Giralt Paradell O, Díaz López B, Methion S (2019) Modelling common dolphin (*Delphinus delphis*) coastal distribution and habitat use: insights for conservation. Ocean Coast Manag 179:104836
Giralt Paradell O, Díaz López B, Methion S, Rogan E (2020) Foodweb interactions in a coastal ecosystem influenced by upwelling and terrestrial runoff off North-West Spain. Ocean Coast Manag 157:104933
Hammond PS, Macleod K, Berggren P, Borchers DL, Burt L, Cañadas A, Gordon J (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biol Cons 164:107–122
Harris HS, Oates SC, Staedler MM, Tinker MT, Jessup DA, Harvey JT, Miller MA (2010) Lesions and behavior associated with forced copulation of juvenile Pacific harbor seals (*Phoca vitulina richardsi*) by Southern sea otters (*Enhydra lutris nereis*). Aquat Mamm 36(4)
Hersteinsson P, Macdonald DW (1992) Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos 505–515
Higgins LV, Tedman RA (1990) Effect of attacks by male Australian sea lions, *Neophoca cinerea*, on mortality of pups. J Mammal 71(4):617–619
Hoogland JL, Brown CR (2016) Prairie dogs increase fitness by killing interspecific competitors. Proceedings of the Royal Society B: Biological Sciences 283(1827):20160144
Jefferson TA, Stacey PJ, Baird RW (1991) A review of killer whale interactions with other marine mammals: predation to co-existence. Mammal Rev 21(4):151–180
Jefferson TA, Webber MA, Pitman RL (2015) Marine Mammals of the world: a comprehensive guide to their identification, 2nd edn. Academic Press, London, UK, p 616
Jepson PD, Baker JR (1998) Bottlenosed dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). Vet Rec 143:614–615
Kastelein RA, Vaughan N, Walton S, Wiepkema PR (2002) Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. Mar Environ Res 53(2):199–218
Key C, Ross C (1999) Sex differences in energy expenditure in non–human primates. Proceedings of the Royal Society of London. Series B: Biological Sciences 266(1437):2479–2485
Le Boeuf BL, Campagna C (1994) Protection and abuse of young in pinnipeds. In: Parmigiani S, vom Saal F (eds) Infanticide and parental care. Harwood Academic Publishers, London, pp 257–276
López A (2003) Estatus dos pequenos cetáceos da plataforma de Galicia. PhD thesis. Universidade de Santiago, Spain. pp. 337
López A, Martínez Cedeira J, Mariscal P (2019) Catálogo TurGaSur de fotoidentificación dos arroaces (*Tursiops truncatus*) de Galicia Sur e manual de boas practices de navegación. CEMMA, Fundación Biodiversidad-Ministerio para la Transición Ecológica
Lourenço R, Penteriani V, del Mar DM, Marchi-Bartolozzi M, Rabaça JE (2011) Kill before being killed: an experimental approach supports the predator-removal hypothesis as a determinant of intraguild predation in top predators. Behav Ecol Sociobiol 65(9):1709–1714
Mann J, Connor RC, Barre LM, Heithaus MR (2000) Female reproductive success in bottlenose dolphins (*Tursiops sp.*): life history, habitat, provisioning, and group-size effects. Behav Ecol 11(2):210–219
Méndez-Fernández P, Bustamante P, Bode A, Chouvelon T, Ferreira M, Lopez A, Caurant F (2012) Foraging ecology of five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen isotope ratios. J Exp Mar Biol Ecol 413:150–158
Methion S (2019) Ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in a coastal area subject to shellfish farming. Université de Bordeaux, Thèse de doctorat
Methion S, Díaz López B (2018) Abundance and demographic parameters of bottlenose dolphins in a highly affected coastal ecosystem. Mar Freshw Res 69:1–10
Methion S, Díaz López B (2019) Natural and anthropogenic drivers of foraging behaviour in bottlenose dolphins: influence of shellfish aquaculture. Aquatic Conservation: Marine and Freshwater Ecosystems 29(6):927–937
Methion S, Díaz López B (2020) Individual foraging variation drives social organization in bottlenose dolphins. Behav Ecol 31(1):97–106
Mohammadi A, Kaboli M, López-Bao JV (2017) Interspecific killing between wolves and golden jackals in Iran. Eur J Wildl Res 63(4):61
Mulder JL (1990) The stoat *Mustela erminea* in the Dutch dune region, its local extinction, and a possible cause: the arrival of the fox *Vulpes vulpes*. Lutra 33:1–21
Nuechterlein GL, Storer RW (1982) The pair-formation displays of the western grebe. The Condor 84(4):351–369
Ostman J (1991) Changes in aggressive and sexual behavior between two male bottlenose dolphin (*Tursiops truncatus*) in a captive colony. In: Pryor K, Norris KS (eds) Dolphin societies: discoveries and puzzles. University of California Press, Berkeley and Los Angeles, CA, pp 305–317
Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153(5):492–508
Patterson IAP, Reid RJ, Wilson B, Grellier K, Ross HM, Thompson PM (1998) Evidence for infanticide in bottlenose dolphins: an explanation for violent interactions with harbour porpoises?. Proceedings of the Royal Society of London. Series B: Biological Sciences 265(1402):1167–1170
Pierce GJ, Caldas M, Cedeira J, Santos MB, Llavona Á, Covelo P, Martinez G, Torres J, Sacau M, López A (2010) Trends in cetacean sightings along the Galician coast, north-west Spain, 2003–2007, and inferences about cetacean habitat preferences. J Mar Biol Assoc UK 90(8):1547

Puig-Lozano R, Fernández A, Saavedra P, Tejedor M, Sierra E, De la Fuente J, Xuriach A, J Díaz-Delgado MA Rivero M Andrada Y Bernaldo de Quirós M Arbelo 2020 Retrospective study of traumatic intra-interspecific interactions in stranded cetaceans. Canary Islands Front Vet Sci 7:107

Reddy M, Kamolnick T, Curry C, Skaar D, Ridgway S (1994) Energy requirements for the bottlenose dolphin (*Tursiops truncatus*) in relation to sex, age and reproductive status. Marine Mammals: Public Display and Research 1(1):26–31

Rose NA, Deutsch CJ, Le Boeuf BJ (1991) Sexual behaviour of male northern elephant seals. III The mounting of weaned pups. Behaviour 119:171–192

Ross HM, Wilson B (1996) Violent interactions between bottlenose dolphins and harbour porpoises. Proceedings of the Royal Society of London. Series B: Biological Sciences 263(1368):283–286

Santos MB, Fernandez R, López A, Martínez JA, Pierce GJ (2007) Variability in the diet of bottlenose dolphin, *Tursiops truncatus*, in Galician waters, north-western Spain, 1990–2005. J Mar Biol Assoc UK 87(1):231–41

Santos MB, German I, Correia D, Read FL, Cedeira JM, Caldas M, López A, Velasco F, Pierce GJ (2013) Long-term variation in common dolphin diet in relation to prey abundance. Mar Ecol Prog Ser 481:249–268

Schroeder JP, Keller KV (1989) Seasonality of serum testosterone levels and sperm density in *Tursiops truncatus*. J Exp Zool 249(3):316–321

Silber GK, Newcomer MW, Silber PC, Pérez-Cortés MH, Ellis GM (1994) Cetaceans of the northern Gulf of California: distribution, occurrence, and relative abundance. Mar Mamm Sci 10(3):283–298

Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. Adv Study Behav 22:1–63

Wedekin LL, Daura-Jorge FG, Simões-Lopes PC (2004) An aggressive interaction between bottlenose dolphins (*Tursiops truncatus*) and estuarine dolphins (*Sotalia guianensis*) in southern Brazil. Aquat Mamm 30(3):391–397

Weller DW, Würsig B, Whitehead H, Norris JC, Lynn SK, Davis RW, Brown P (1996) Observations of an interaction between sperm whales and short-finned pilot whales in the Gulf of Mexico. Mar Mamm Sci 12(4):588–594

Wells RS, Scott MD (2009) Common bottlenose dolphin: *Tursiops truncatus*. In: Encyclopedia of marine mammals 249–255. Academic Press

Wilson GJ (1979) Hooker's sea lions in southern New Zealand. NZ J Mar Freshwat Res 13(3):373–375