ORIGINAL PAPER

Group size varies with climate and oceanographic conditions in bottlenose dolphins

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Abstract

An understanding of animal grouping patterns is essential to increase knowledge about their social systems. We used a 5-year continuous dataset to investigate grouping behavior in a free-ranging highly social mammal, the bottlenose dolphin. Our objective was achieved by examining the relationships between a set of oceanographic, climatic, topographic, anthropogenic and social variables and bottlenose dolphin group size. Modeling analysis revealed that bottlenose dolphin group dynamics was linked to both small-scale oceanographic variation and large-scale climatic variation. Larger groups of bottlenose dolphins were predicted with an elevated concentration of dissolved oxygen in the water column, a moderate concentration of chlorophyll-a 60 days before each encounter, and a neutral NAO index. The observed link between environmental variables and dolphin group size is likely associated to changes in dolphin prey availability. Bottlenose dolphin group dynamics are likely driven by multiple factors, and social variables may act synergistically with environmental parameters. Larger groups of bottlenose dolphins were indeed also predicted with a greater number of dependent calves, likely because of enhanced care towards the calves. This study illustrates the value of using multiple variables at different scales to explore the factors that shape animal societies. The current study therefore contributes to the growing body of literature on how environmental change, occurring at different spatio-temporal scales, is indirectly related to the social behavior of a marine top predator.

Introduction

Animals commonly form groups to reduce predation risk and to increase access to resources and to mating opportunities (Alexander 1974); yet forming groups is also associated with a number of costs (e.g., increase intraspecific competition for food resources; increase risk of being detected by predators) (Clark and Mangel 1986; Krause and Ruxton 2002). Consequently, some mammal species live in societies with flexible grouping patterns where group membership is

not spatio-temporally stable (i.e., fission–fusion dynamics) (e.g., African elephant, *Loxodonta africana*: Fishlock and Lee 2013; bottlenose dolphin, *Tursiops spp.*: Connor et al. 2000; chimpanzee, *Pan troglodytes*: Lehmann and Boesch 2004; giraffe, *Giraffa camelopardalis*: Muller et al. 2018; zebra, *Equus spp.*: Sundaresan et al. 2007). Within this flexible social system, individuals associate in groups that change in size and composition to limit the effect of intra-group competition (Smith et al. 2008). Thereby, while they limit the effect of competition through group splits during periods of high competition (Dunbar 1992), they enhance cooperative effects through group cohesion when the ecological costs of aggregating are low or when the benefits of grouping are high (Takahata et al. 1994; van Schaik 1999). Variation in group size is therefore a trade-off between predation pressure and prey availability, where the decision of each individual, to either leave or remain in the group will be strongly influenced by a combination of social and environmental factors (Sueur et al. 2011).

The fission–fusion social dynamic is taxonomically widespread in highly cognitive mammalian species living in

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environments with temporal and spatial variability. Among these species, the social dynamics of dolphins (Family *Delphinidae*) is often associated with a foraging pattern shaped by certain levels of environmental heterogeneity. Dolphins adapt their grouping pattern depending on the abundance and type of prey available in order to maximize their energy intake (e.g., killer whales, *Orcinus orca*: Baird and Dill 1996; bottlenose dolphins: Hanson and Defran 1993; dusky dolphins, *Lagenorhynchus obscurus*: Vaughn et al. 2010). When prey species form large schools, dolphins appear to use cooperative feeding behavior, an efficient way to herd prey into balls (Tardin et al. 2011; Vaughn et al. 2010). On the contrary, when prey is not a schooling species, or is distributed in a spatially heterogeneous area, dolphins form smaller groups to reduce intraspecific competition (Baird and Dill 1996; Díaz López 2006). As information on both distribution and abundance of dolphin prey is driven by environmental conditions and often hard to measure directly, environmental variables can be used as proxies of prey availability, thus taking into consideration the complexity of dolphin foraging environment. Not much is known, however, about the influence of both fine- and large-scale environmental factors on dolphin grouping patterns, as little research has been carried out on this topic to this day (but see: Lusseau et al. 2004 and Bouveroux et al. 2018), particularly in coastal waters under the pressure of intense anthropogenic activities.

An understanding of the relationship between environmental variables on coastal dolphin grouping pattern is becoming increasingly important since human activities (e.g., fisheries, marine traffic and aquaculture) induce significant changes in coastal ecosystems (Islam and Tanaka 2004; Edwards 2015). Human activities introduce spatial habitat complexity and fragmentation in coastal ecosystems leading to variation in dolphin group size by changes in dolphin prey availability. For example, common dolphins (*Delphinus delphis*) in Spain and Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand form larger aggregations in the presence of fishing vessels due to the concentration of fish schools in those areas (Díaz López et al. 2019; Rayment and Webster 2009). As fluctuations in dolphin group size can be indicative of the influence of human activities on coastal ecosystems, focused studies are needed to determine the key factors that drive changes in grouping patterns at particular locations. Studying such variation would therefore allow to understand and to predict the influence of human-induced environmental changes on dolphin behavior (e.g., Lusseau et al. 2004; Díaz López 2019).

Variation in dolphin group size can also be explained by social interactions between group members. For example, dolphin groups with calves are generally larger than those without calves (e.g., Gibson and Mann 2008; Kerr et al. 2005; Bearzi et al. 1997; Díaz López et al. 2013, 2018a). Larger group size reduces the probability that an individual can be attacked (dilution effect) and increases the probability of predator detection (detection effect) (Delm 1990). As parental care in dolphins is essentially provided by the mother (Mann 2019), groups with calves are generally composed of other females that assist the mother in caring for her calf (i.e., alloparental care) potentially allowing the mother to spend a greater proportion of time foraging to maintain the higher energy demand during lactation (Johnson and Norris 1986). Similarly, larger groups may increase protection of vulnerable calves from predators and potential infanticidal attacks (Díaz López et al. 2018b), thus providing a better learning environment for young dolphins (Gibson and Mann 2008). Finally, a larger group may also function to provide mating opportunities, learn courtship skills, or gain information on spatio-temporal variation in food resources (Baird and Dill 1996).

Despite the information outlined above, few studies have focused on the variation in dolphin group size using both social and environmental variables. This approach would be particularly recommended for monitoring dolphin species with a coastal distribution such as the common bottlenose dolphin (*Tursiops truncatus*, hereafter referred to as bottlenose dolphin). Exhibiting social systems characterized by fission–fusion dynamics, bottlenose dolphins provide a useful framework for analyzing variation in group size in relation with the characteristics of their foraging environment. Determining the importance of environmental and social variables on dolphin grouping pattern would involve manipulating these factors independently, which is not conceivable in wild dolphin populations. Observational studies in the wild, where free-ranging animals are exposed to varying environmental and anthropogenic pressure, however, may help unravel the factors related to dolphin group size.

Resident, coastal bottlenose dolphins inhabit the coastal waters of the Ría de Arousa (Northwest Spain, Atlantic Ocean) (Díaz López and Methion 2017). Their seasonal abundance ranges from 56 to 144 individuals, and is thought to mainly vary due to food availability, as dolphins do not have natural predators in this region (Methion and Díaz López 2018). This area is an important feeding ground for bottlenose dolphins (Methion and Díaz López 2019) and the distribution and abundance of their prey is likely indirectly influenced by intense upwelling events (Arístegui et al. 2004), land runoff (Varela et al. 2005), fisheries activities (Surís-Regueiro and Santiago 2014), and the presence of one of the world's most important shellfish farming industry (Rodríguez et al. 2011). These dolphins live in a fluid social system, being found in groups of varying size that form and split on a daily basis (Methion and Díaz López 2019, 2020). Given bottlenose dolphins fission–fusion social system and the high spatio-temporal changes (i.e., in anthropogenic and environmental conditions) occurring in the Ría de Arousa, this study site therefore provides advantageous conditions to

study group size variation in dolphins inhabiting a heterogeneous coastal environment.

In light of the above considerations, we used a five-year continuous dataset to investigate grouping behavior in free-ranging resident bottlenose dolphins. Our objective was achieved by examining the relationships between a set of oceanographic (tides, water temperature, water salinity, dissolved oxygen concentration, chlorophyll-a concentration), climatic (NAO index, wind speed), topographic (location, depth), temporal (date, time), anthropogenic (number and type of vessels, aquaculture farms, fisheries), and social (number of dependent calves) variables and bottlenose dolphin group size. Through this framework, we aimed to advance our understanding of the relative influence of multiple variables on coastal bottlenose dolphin grouping patterns.

Methods

Study area

The study was performed along the north-western coast of the Iberian Peninsula, Spain, specifically in the Ría de Arousa (240 km^2), the largest of the Galician rias (ancient drowned tectonic valley taken over by the sea; Evans and Prego 2003) (Fig. 1). This ria is an estuarine coastal embayment with a large tidal range (between 1.1 and 3.5 m during neap and spring tides, respectively) (Álvarez et al. 2005). The average depth is 19 m and the maximum depth is 70 m. Water circulation is mainly driven by the tide, wind regime

over the continental shelf, wind regime over the ria, and freshwater discharge (Otto 1975; Álvarez et al. 2005). Residence time of water in the Ría de Arousa is 5–10 days (Álvarez-Salgado et al. 1996).

The marine environment in the ria is heterogeneous. The ria is divided into deeper zones under an external oceanic influence (exposed to oceanic processes) and shallower and secluded areas under an internal estuarine influence with an important tidal range (exposed to fluvial processes) (Evans and Prego 2003). The internal estuarine area is more exposed to changes in salinity and temperature due to the input of freshwater (Álvarez et al. 2005). The main freshwater input is located in the innermost part of the Ría de Arousa and comes from two rivers: the Ulla River (river flow = 79.3 m^3/s) and the Umia River (river flow = 16.3 m^3/s) (Álvarez et al. 2005). These rivers show a high seasonal variability in river flow, with the highest value in winter and the lowest in summer, following the rainfall pattern (Álvarez et al. 2005). The frequent upwelling of cold and dense Eastern North Atlantic Central Water (ENACW) results in nutrient enrichment of the water, making this one of the most productive oceanic regions in the world (Arístegui et al. 2004; Santos et al. 2011). Oceanographic patterns in the region are modulated by the seasonal cycle of wind direction, where the prevalence of north-eastern winds between April and September (Álvarez-Salgado et al. 2008; Pardo et al. 2011) is the main cause of coastal upwelling events that significantly increase primary production (Álvarez et al. 2011). The ria behaves as a partially mixed estuary where the partial stratification is maintained by the river discharge in winter and by solar heating and coastal upwelling in summer (Álvarez et al. 2005). Under upwelling conditions,

Fig. 1 Map of the study area (Ría de Arousa, north-west Spain) where bottlenose dolphin behavior surveys were conducted. Red circles represent the 6 oceanographic stations from which oceanographic parameters were collected
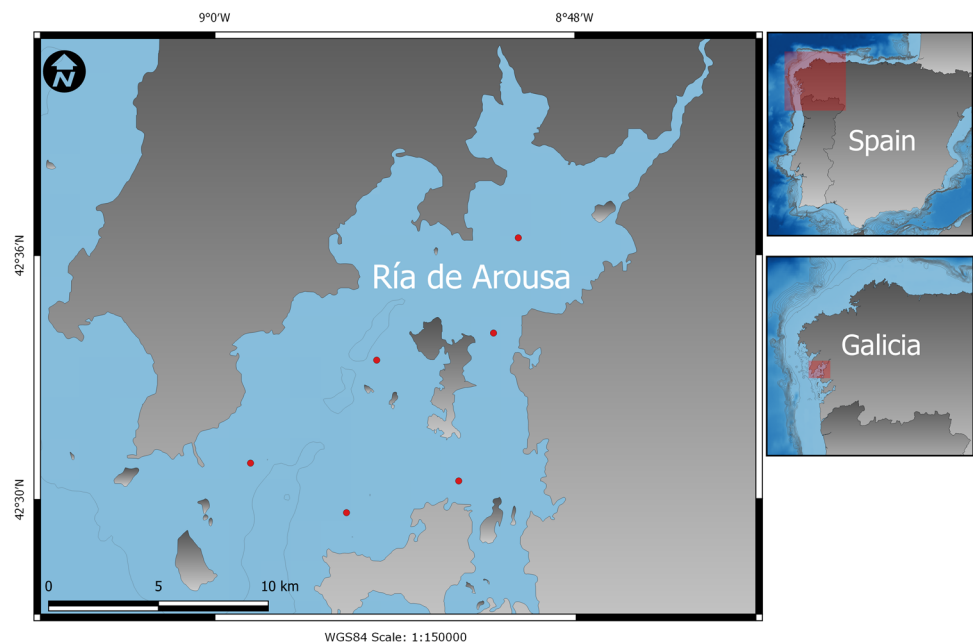
nutrient-rich subsurface ENACW enters the ria by positive estuarine circulation (Prego and Fraga 1992). The rest of the year, there is a dominance of downwelling conditions (Figueiras et al. 2002), during which warmer, nutrient-depleted surface waters move inshore and downward reducing the strength of the exchange flow (Álvarez et al. 2005).

Owing to the high primary production along this coast, this is an important area for fisheries and shellfish aquaculture. In this ria, there are twelve commercial fishing harbours, which are used by more than 3000 commercial fishing boats (Instituto Galego de Estadística 2018 https://www.ige.eu/). These boats operate both in inshore and offshore waters, using traps, trawls, gill-nets and longlines and target fish, mollusks and crustaceans (Instituto Galego de Estadística 2018 https://www.ige.eu/). Around 2370 shellfish cultivation rafts (about 500 m² each) are located in the Ría de Arousa (Rodríguez et al. 2011), covering approximately 17% of the area (Díaz López and Methion 2017). One study estimated that nearly 85% of the biomass of the Ría de Arousa is removed yearly by anthropogenic activities (Outeiro et al. 2018). These highly productive and heterogeneous waters are an important year-round feeding ground for coastal bottlenose dolphins (Methion and Díaz López 2019).

Field data collection

Boat-based surveys were conducted year-round over 49 months from March 2014 to November 2018. The Ría de Arousa was monitored onboard a research vessel during daylight hours at a constant speed of 6 knots. The minimum number of experienced observers and vessel speed remained consistent during the study period. While the surveyed area and daily routes were designed to cover the study area equally, the spatial distribution of the effort varied according to weather conditions and time constraints throughout the study period (Methion and Díaz López 2018). Surveys were carried out when the wind speed was lower than 5.5 m/s (3 on the Beaufort wind force scale) and visibility was not reduced by rain or fog. A group of bottlenose dolphins was defined as one or more individuals observed within a 100 m radius and, if more than one individual, interacting with each other and engaging in the same behavioral activity (Methion and Díaz López 2019).

Upon a bottlenose dolphin group encounter, searching effort ceased and the vessel slowly maneuvered towards the animals in order to minimize disturbance during the approach. Group size and group composition was estimated and digital photographs were taken using digital single-lens reflex (DSLR) cameras equipped with telephoto zoom lens during each bottlenose dolphin encounter. Group size estimated in the field was verified with photographs taken during each encounter and was adjusted by increasing the number of individuals present if more individuals were identified

from the photographs (Methion and Díaz López 2020). The age of individuals was assessed based on behavioral cues and visual assessment of the size (following Methion and Díaz López 2018, 2020) and classified as: (i) adults; (ii) immature dolphins (dependent calves, < 2/3 length of an adult, in association with an adult); or (iii) new-born dolphins (dependent calves, < 1.5 m, swimming in the infant position, in association with an adult, born within the same calendar year).

For each bottlenose dolphin encounter, a suite of data was recorded: the date, initial time, location (with a Global Positioning System (GPS)), depth, and wind speed (m/s) (as an associated measure of sea state). The date, time, location, and depth were obtained by a GPS-Plotter Map Sounder associated with an 83–200 kHz echo-sounder transducer. The wind speed was measured when the vessel was stationary (one minute at the beginning of each encounter) using a cup anemometer. Five anthropogenic variables were also recorded within a 1 nautical mile visual range of the position of each bottlenose dolphin group: (i) number of fishing boats; (ii) number of recreational boats; (iii) number of mussel farm boats; (iv) presence of fishing buoys (indicating the occurrence of bottom set gill-nets); and (v) the presence of the group of bottlenose dolphins inside or outside the shellfish farm areas (Methion and Díaz López 2019).

Extraction of environmental predictors

The vertical profile of four oceanographic parameters were obtained from records of oceanographic data provided by the INTECMAR observation network of 6 sampling stations distributed within the Ría de Arousa (Instituto Tecnolóxico para o Control do Medio Mariño, http://www.intecmar.gal) (Fig. 1): seawater temperature (in degrees Celsius, °C; hereafter 'WT'), seawater salinity (in practical salinity unit, PSU; hereafter 'SAL'), dissolved oxygen (in μmol/kg; hereafter 'DO'), and seawater fluorescence intensity as an indirect measure of chlorophyll-a concentration (in mg/m³; hereafter 'Chla'). These parameters were recorded using a CTD (Conductivity, Temperature, and Depth profiler) and a fluorometer. As changes in levels of primary production require time to be transferred through the various trophic levels from phytoplankton to dolphin prey, the effect of this covariate was evaluated over different temporal scales. Chlorophyll-a data was therefore extracted at the date of each encounter ('Chla'), 15 days before each encounter (hereafter 'Chla15'), 30 days before each encounter (hereafter 'Chla30'), and 60 days before each encounter (hereafter 'Chla60'). Data obtained included weekly measurements of the first 15 m of the water column, of these oceanographic parameters, at each station. For each variable, data were averaged over three depth ranges (0–5 m, 5–10 m, and 10–15 m). Moreover, standard deviation values were calculated throughout

the water column for WT (hereafter 'SD-WT'), SAL (hereafter 'SD-SAL'), and DO (hereafter 'SD-DO'), as a factor of stratification in the first 15 m of the water column. The frequency of sampling (weekly) and the number of stations (6) distributed along the Ría de Arousa provide a thorough understanding of the spatial and temporal variability of the oceanographic conditions in the area.

Oceanographic data were transformed to raster format by interpolating the values of each station using the inverse distance weighted (IDW) interpolation in a Geographical Information System (QGIS 2.18 2016 www.qgis.org). The creation of rasters allowed us to link each variable to the location of the bottlenose dolphin encounters taking into account the spatio-temporal environmental variability. IDW is a spatial interpolation method that has been widely used to predict environmental variables and assumes that values of nearby points are more similar than values of more distant points (Li and Heap 2008). Hence, it estimates values at unknown locations by giving a heavier weight to closer sampled points (Li and Heap 2008; Lu and Wong 2008). The 'point sampling' tool in QGIS was then used to extract the raster values (of each oceanographic variable), at each bottlenose dolphin encounter position, in order to link the group size with the environmental variables (SAL, WT, DO, Chla, Chla15, Chla30, Chla60, SD-SAL, SD-WT, and SD-DO).

Tidal cycle (presence/absence of flood tide) at the initial time of each dolphin encounter was obtained from the harbor of Ribeira (42°33′N, 008°59′W), from the Galician weather service (http://www.meteogalicia.gal). The North Atlantic Oscillation (hereafter 'NAO') index was obtained from the NOAA—National Weather Service (http://cpc.ncep.noaa.go). The monthly mean NAO index is based on the surface sea-level pressure difference between the Subtropical (Azores) High and the Subpolar Low. In South-western Galicia (North Western coast of the Iberian Peninsula), a positive NAO index induces an anticyclone weather type, and therefore a reduced rainfall (Lorenzo et al. 2008).

Data analysis and modeling framework

All variables were explored to detect measurements errors with two R packages (R Development Core Team 2011). The package 'lubridate' was used to work with dates and the package 'dplir' was used for data manipulation (to filter and summarize the data). Twenty-six predictors were initially considered to have potential ecological significance and were available for each group of dolphins encountered (Table 1).

Generalized additive models (GAMs) were used to explore the predictor variables that might have affected bottlenose dolphin group size (response variable). GAMs are widely-used for interpreting ecological interactions and are particularly well-suited for the type of non-linear responses

that are expected in species-environment relationships (Hastie and Tibshirani 1990). Data exploration protocols described by Zuur et al. (2010) were used to identify outliers, data variability, and relationships between predictor variables and the bottlenose dolphin group size. Modeling was initiated using a full General Linear Model (GLM), which included all predictor variables that could potentially drive bottlenose dolphin group size. Possible collinearity between predictor variables was investigated by calculating pairwise Spearman correlation coefficients (r) and variance inflation factors (VIFs). When variables showed high correlation (above $r = 0.7$ and VIF > 3), they were not used together in the same model (Dormann et al. 2013). To find a set of explanatory variables that did not contain collinearity, variables were removed one at a time and then the VIF values were recalculated. Following this procedure, SD-SAL (highly correlated to SAL, $r = -0.81$, $P < 0.01$) was excluded before starting the GAM fitting. Likewise, 'month of year' was not included as covariate, because it was related with environmental variables exhibiting monthly changes (i.e., WT, $r = 0.61$, $P < 0.01$; SAL, $r = 0.56$, $P < 0.01$) which were included instead due to their biological interpretability (Burnham and Anderson 2002).

Bottlenose dolphin group size was modeled using a GAM with a negative binomial distribution and logarithmic link function to account for overdispersion. The negative binomial distribution is appropriate for overdispersed count data, such as group size, in which the variance is larger than the mean (Ver Hoef and Boveng 2007). The smooth functions were constructed as cubic splines and their optimal shape was estimated by minimizing the general cross validation (GCV) criterion. GCV automatically chose the number of knots for the model so that simplicity was balanced against explanatory power (Wood 2006). Latitude and longitude were excluded from the initial model in order to explain the observed variation in the data using more informative environmental predictors. By excluding coordinates, we therefore reduced the concurvity amongst spatial and temporally dynamic environmental variables. Interaction terms were not considered (i.e., interactions between environmental variables) as the primary aim was to identify potential 'bottlenose dolphin group size'—drivers, instead of maximizing explained deviance (Beekmans et al. 2010).

The optimal GAM was selected using a combination of backward and forward model selection procedures based on the Akaike Information Criteria (AIC). Thus, the optimal model was the model with the lowest AIC. Model assumptions were checked by visual inspection of the residuals and regression fits were examined using plots of residuals against fitted values. The Durbin-Watson test (from the R package 'lmtest', Zeileis and Hothorn 2002) and auto-correlation functions (ACF) were used to check for serial correlation, both in our raw data and in the residuals from the models.

Table 1 List of predictor variables initially considered to have potential ecological significance

Type	Predictor variable	Description
Temporal	Month of year	Calendar month of each dolphin encounter
	Year	Calendar year of each dolphin encounter
	Time	Initial time of each dolphin encounter
Topographic	Depth	Water depth at the initial time of each dolphin encounter; meters
	Longitude	UTM-X at the initial time of each encounter; UTM (Universal Transverse Mercator) projection, zone 29 N; meters
	Latitude	UTM-Y at the initial time of each dolphin encounter; UTM projection, zone 29 N; meters
Social	Number of immature dolphins	Number of immature dolphins in each dolphin group
	Number of new-born dolphins	Number of new-born dolphins in each dolphin group
Anthropogenic	Number of fishing boats	Number of fishing boats within 1 nautical mile (nm) visual range at the initial time of each dolphin encounter
	Number of recreational boats	Number of recreational boats within 1 nm visual range at the initial time of each dolphin encounter
	Number of mussel farm boat	Number of mussel farm boats within 1 nm visual range at the initial time of each dolphin encounter
	Position within shellfish farms	Presence of dolphins within shellfish farms at the initial time of each dolphin encounter; Yes/No
	Presence of gillnets	Presence of bottom-set gillnets within 1 nm visual range at the initial time of each dolphin encounter; Yes/No
Climatic	Wind speed	Wind speed at the initial time of each dolphin encounter; meters/second
	Daily NAO index	Daily North Atlantic Oscillation Index at the date of each dolphin encounter
Oceanographic	Tidal cycle	Tidal cycle category at the initial time of each dolphin encounter: Flood, Ebb
	WT	Seawater temperature at the date of each dolphin encounter; degrees celsius (°C)
	SAL	Seawater salinity at the date of each dolphin encounter; PSU (Practical Salinity Units)
	DO	Seawater concentration of dissolved oxygen at the date of each dolphin encounter; µmol/kg
	Chla	Seawater concentration in chlorophyll-a at the date of each dolphin encounter; mg/m^3
	Chla15	Seawater concentration in chlorophyll-a 15 days before each dolphin encounter day; mg/m^3
	Chla30	Seawater concentration in chlorophyll-a 30 days before the dolphin encounter day; mg/m^3
	Chla60	Seawater concentration in chlorophyll-a 60 days before the dolphin encounter day; mg/m^3
	SD-WT	Standard deviation of seawater temperature (thermal stratification) at the date of each dolphin encounter; degrees Celsius (°C)
	SD-SAL	Standard deviation of seawater salinity at the date of each dolphin encounter; PSU
	SD-DO	Standard deviation of the concentration in dissolved oxygen; µmol/kg

GAMs results and diagnostic information about the fitting procedure were implemented using the mgcv (Wood 2006) and MASS (Venables and Ripley 2002) packages in R v. 1.8.1 (R Development Core Team 2011). Partial predictions with 95% confidence intervals were plotted for each statistically significant covariate included within the final GAM. The data are presented as means ± standard error (SE).

Results

Survey effort and bottlenose dolphin group size

Overall, 340 daily boat surveys over a period of 49 months of research and covering 7495 nautical miles were undertaken between March 2014 and November 2018 for a total of 1340 h. During the study, 846 bottlenose dolphin groups were encountered (Fig. 2). A total number of 9009 bottlenose dolphins were observed on 313 different days at sea (92% of total number of daily surveys) throughout all the 49 months. Bottlenose dolphins were encountered all throughout the Ría de Arousa and in all months of the year. Table 2 and Table 3 display the average environmental conditions across the 5 years of research and across months, respectively.

Group size ranged from 1 to 64 dolphins (mean = 10.7 ± SE 0.3, median = 7). Sixty-nine percent of the groups were composed of a least 5 individuals, 42% of at least 10 individuals, and 25% of at least 15 individuals. The groups were composed of 88% adults and 12% dependent calves (of which 1.7% new-born dolphins). The first new-born dolphins of the year, of any given female, were always

Fig. 2 Bottlenose dolphin encounters in the Ría de Arousa during the study. The size of the circles represents the observed size of the groups
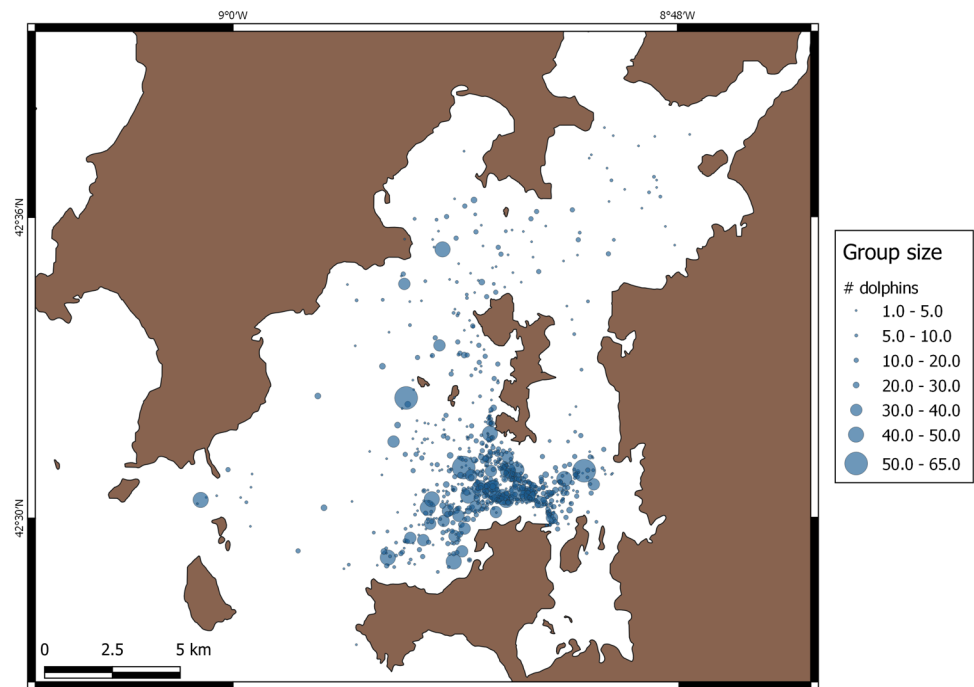
observed from June to September every year, with a peak in July and August. Dependent calves were present in 55% of the observed groups. New-born dolphins specifically were present in 11% of the observed groups.

Drivers of bottlenose dolphin group size

Based on AIC scores, the most parsimonious GAM included number of immature and new-born dolphins, dissolved oxygen in the water column, standard deviation of temperature in the water column (as a measure of thermal stratification), chlorophyll-a concentration 60 days before each encounter, and daily NAO index as explanatory variables of bottlenose dolphin group size (Table 4). This model explained 42.2% of the variation in the group size data ($n = 846$, R-sq = 0.448, AICc = 5271).

The number of bottlenose dolphins in a group was predicted to be significantly influenced by the number of dependent calves in the group (both immature and new-born dolphins), concentration of dissolved oxygen in the water column, chlorophyll-a concentration 60 days before each encounter, and daily NAO index (Fig. 3). Group size showed a linear relationship with the chlorophyll-a concentration 60 days before each encounter and with the number of newborn dolphins within the group. Number of immature dolphins within the group, dissolved oxygen concentration, and the daily NAO index showed a non-linear relationship with bottlenose dolphin group size.

Larger groups of bottlenose dolphins were predicted by larger numbers of dependent calves (both new-born and immature dolphins) (Fig. 3), in conditions of elevated concentrations of dissolved oxygen, negative to neutral NAO index, and medium abundance of primary producer (chlorophyll-a concentration) 60 days before each encounter. Thermal stratification did not contribute significantly to the observed variation in group size ($P > 0.05$).

Discussion

A comprehensive continuous 5-year dataset was used to investigate group size variation in a highly social mammal, the bottlenose dolphin, in a highly impacted coastal area. This study reveals that both social and oceanographic conditions—both on a small-scale (water oxygenation and chlorophyll-a concentration) and large-scale (NAO index) are related to the spatio-temporal aggregation patterns of bottlenose dolphins. It is well established that environmental changes can condition the phenology and demography of animals, but few studies have recorded such an influence on marine top predators. The current study therefore contributes to the growing body of literature on how environmental change, occurring at different spatio-temporal scales, is indirectly related to the social behavior of a marine top predator by influencing the abundance of its prey.

Findings of this study highlight the importance of year-round monitoring to identify possible environmental changes

Table 2 Yearly variation in bottlenose dolphin group size and in predictor variables across the study

Variables	2014	2015	2016	2017	2018	Total
Response variable						
Group size	12.89±1.01	11.61±0.81	13.61±0.82	8.07±0.49	7.07±0.48	10.65±0.34
Predictor variables						
Topographic						
Depth (m)	15.27±0.86	18.99±0.95	16.28±0.67	16.85±0.71	14.63±0.79	16.45±0.35
Social						
Number of immature dolphins	1.76±0.13	1.27±0.14	0.98±0.09	0.85±0.11	0.78±0.13	1.09±0.05
Number of new-born dolphins	0.21±0.05	0.22±0.07	0.30±0.06	0.05±0.02	0.12±0.03	0.18±0.02
Anthropogenic						
Number of fishing boats	3.48±0.35	2.79±0.24	5.11±0.34	4.18±0.31	4.57±0.43	4.11±0.15
Number of recreational boats	7.91±0.57	3.75±0.26	4.97±0.26	4.57±0.26	5.33±0.63	5.20±0.18
Number of mussel farm boat	18.19±1.57	20.45±1.44	19.65±1.35	21.77±1.35	19.38±1.24	20.02±0.63
Climatic						
Wind speed (m/s)	2.48±0.18	2.24±0.18	2.71±0.18	2.49±0.16	1.91±0.16	2.40±0.07
Daily NAO index	− 0.24±0.10	− 0.12±0.12	− 0.14±0.07	0.01±0.08	1.23±0.06	0.12±0.04
Oceanographic						
WT (°C)	16.32±0.05	14.51±0.14	13.90±0.12	14.57±0.07	14.26±0.12	14.63±0.06
SAL (PSU)	34.89±0.03	35.13±0.04	34.68±0.10	35.21±0.04	34.93±0.07	34.97±0.03
DO (µmol/kg)	247.68±1.76	241.95±2.35	231.84±2.96	228.18±1.57	194.94±1.52	228.89±1.15
Chla (mg/m³)	2.55±0.14	4.01±0.19	4.01±0.24	4.04±0.20	3.45±0.22	3.68±0.10
Chla15 (mg/m³)	2.24±0.12	3.61±0.19	3.70±0.16	3.52±0.19	3.26±0.17	3.32±0.08
Chla30 (mg/m³)	2.42±0.12	3.53±0.21	3.87±0.24	3.11±0.16	3.60±0.22	3.34±0.09
Chla60 (mg/m³)	2.19±0.11	2.83±0.15	3.60±0.19	2.76±0.21	2.92±0.14	2.91±0.08
SD-WT (°C)	0.65±0.04	0.51±0.04	1.56±0.17	0.54±0.03	0.67±0.05	0.82±0.05
SD-SAL (PSU)	0.33±0.3	0.30±0.03	0.75±0.09	0.19±0.02	0.43±0.05	0.41±0.03
SD-DO (µmol/kg)	9.74±0.49	23.60±1.38	14.52±1.06	10.33±0.45	9.78±0.78	13.49±0.44

WT water temperature, *SAL* water salinity, *Chla* fluorescence, *DO* dissolved oxygen, *NAO* North Atlantic Oscillation

affecting bottlenose dolphin group dynamics over differing spatial and temporal scales. Modeling analysis reveals that bottlenose dolphin group dynamics were linked to both small-scale oceanographic variation and large-scale climatic variation. The observed link between these variables and dolphin group size is likely associated to changes in the availability of dolphin food resources (Lusseau et al. 2004). Bottlenose dolphins are known to feed on a variety of schooling fish species such as blue whiting (*Micromesistius poutassou*), European pilchard (*Sardina pilchardus*), common grey mullet (*Mugil cephalus*), Atlantic horse mackerel (*Trachurus trachurus*), and European seabass (*Dicentrarchus labrax*) (Díaz López 2009; Santos et al. 2007), whose availability in the study area varies both in space and time (Banon et al. 2010). When environmental conditions in specific zones lead to a low availability of schooling prey, bottlenose dolphins could, therefore, form smaller groups while foraging to reduce inter-individual competition (Methion and Díaz López 2020). Smaller groups may also be advantageous when prey items occur singly, and cooperative or coordinated foraging is inefficient (e.g., Heithaus and Dill 2002; Mann and Sargeant 2003). In contrast, dolphins could increase prey-finding and capture abilities by forming large groups when the environmental conditions (well-oxygenated waters where medium-concentration of chlorophyll-a occurred 60 days prior) facilitated a higher availability of schooling fish.

Concentration of dissolved oxygen and chlorophyll-a indeed play a fundamental role in fish dynamics in coastal ecosystems, impacting the ecology of fish species (Ware and Thomson 2005; Stevens et al. 2006). Dissolved oxygen is an important factor affecting the distribution and abundance of both demersal and pelagic fish communities (Howell and Simpson 1994), with fish diversity and abundance increasing in well-oxygenated waters (Mas-Riera et al. 1990; Howell and Simpson 1994). Similarly, chlorophyll-a concentration (i.e., primary producer abundance) is also directly linked to the abundance and distribution of marine fish, being the foundation of the marine food web (Ware and Thomson 2005). The combination of well-oxygenated waters (found close to the sea surface) and medium abundance of primary producer 60 days prior in surface layers could induce the presence of large schools of zooplanktivorous fish close to the sea surface which might also lead to the occurrence of large bottlenose dolphin groups. Direct behavioral observations during this study (S.M. and B.D.L., personal observations) confirm the presence of large fish schools often concentrated in the first meters of the water column (characteristic of the distribution of schooling fish) during feeding events of large groups of bottlenose dolphin.

The significant relationship between the NAO index and bottlenose dolphin group size provides further support to the relationship between large-scale climate indices and variation in grouping patterns in marine top predators. The NAO is a dominant mode of climate variability over the North Atlantic which can exert a strong influence on numerous marine organisms through changes in ocean temperature and salinity as well on vertical mixing and circulation patterns (Drinkwater et al. 2003; Hurrell and Deser 2010). Here, bottlenose dolphin group size was largest with negative to neutral NAO values and this relationship is likely associated with changes in bottlenose dolphin resources' availability. The NAO index has indeed been linked to variation in assemblage composition, abundance, and growth of marine fish (Guisande et al. 2001; Attrill and Power 2002; Baez et al. 2011). In Galicia (NW Spain), the NAO has mainly been linked to precipitation, river flow, and water resources (Lorenzo and Toboada 2005). Particularly, positive trends in NAO values correspond to cold and dry winters, therefore contributing to a significant decrease in freshwater discharge in the rias in winter (Trigo et al. 2004). On the contrary, a negative trend in the NAO values corresponds to warm and wet winters, contributing to a significant increase in freshwater discharge (Trigo et al. 2004). In Galician waters, lower NAO values have been associated to higher abundance of a bottlenose dolphin prey, the European pilchard (Guisande et al. 2001). Significant increase in freshwater discharge (negative trend in the NAO values) in the study area would, therefore, lead to an increase in bottlenose dolphin prey availability, which may in turn drive bottlenose dolphins to form larger aggregations to increase prey finding and capture abilities. In Scotland and in Canada, cetacean group size also varied from year to year in relation to large-scale climate variation, and local indices of prey abundance were linked to both climate indices and dolphin group size (Lusseau et al. 2004). These similar effects of climate variation on the aggregation patterns of coastal cetaceans provide further evidence that the effects of climate variation can filter up to higher trophic levels by altering the social structure of top predators.

If environmental drivers of prey availability are related to bottlenose dolphin group size, these variables would be linked to the decision individuals have to make to stay or leave the group therefore guiding the structure of dolphin social community and inducing changes in their dispersal rate, survival, or reproduction (Lusseau et al. 2003). The observed aggregations of this study (mean = $10.7 \pm$ SE 0.3) are larger than the average group size in other coastal bottlenose dolphin populations (e.g., California, US = 8.8, Bearzi 2005; Shannon Estuary, Ireland = 8.5, Berrow et al. 2012; Kvarneric bay, Croatia = 6.8, Bearzi et al. 1997; Sarasota, US = 4.8, Irvine et al. 1981; Golfo Aranci, Italy = 4.4, Díaz López 2019; but see Moray Firth, Scotland = 14.2; Robinson et al. 2017; Golfo San José, Argentina = 14.9, Würsig 1978; Doubtful Sound, New-Zealand = 17.2, Lusseau et al. 2003),

Table 3 Monthly variation in bottlenose dolphin group size and in predictor variables across the study

|	January	February	March	April	May	June	July	August	September	October	November
Group size	9.16±1.67	13.47±2.03	9.91±1.04	11.32±1.43	10.30±1.04	9.83±0.77	10.19±0.79	10.85±0.85	11.17±0.98	11.22±1.20	6.73±1.24
Number of immature dolphins	1.13±0.20	2.26±0.45	1.30±0.17	1.12±0.17	0.86±0.13	0.74±0.11	1.02±0.12	0.99±0.13	1.10±0.12	1.16±0.23	0.82±0.23
Number of new-born dolphins	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.02±0.02	0.03±0.02	0.11±0.04	0.34±0.07	0.521±0.11	0.32±0.10	0.55±0.24,5
Depth (m)	15.60±1.83	13.68±0.79	20.33±1.27	14.00±0.91	15.21±1.02	15.79±0.97	16.46±1.23	16.92±0.93	17.123±0.95	17.70±1.34	10.08±2.10
WT (°C)	12.97±0.10	12.81±0.11	12.70±0.06	13.73±0.07	14.33±0.11	15.22±0.11	15.45±0.26	14.84±0.15	15.99±0.17	15.65±0.16	14.81±0.56
SD-WT (°C)	0.27±0.05	0.27±0.05	0.15±0.01	0.36±0.02	0.61±0.04	0.94±0.05	1.989±0.27	1.72±0.17	0.62±0.04	0.190±0.03	0.19±0.04
SAL (PSU)	33.59±0.29	33.61±0.27	34.61±0.07	34.23±0.11	35.00±0.05	35.09±0.07	35.40±0.03	35.50±0.05	35.41±0.04	35.23±0.04	34.37±0.16
SD-SAL (PSU)	1.08±0.31	1.51±0.29	0.81±0.07	0.80±0.07	0.32±0.03	0.27±0.04	0.15±0.01	0.11±0.02	0.15±0.02	0.09±0.02	0.783±0.16
DO (μmol/kg)	204.28±7.61	204.83±7.45	255.56±2.31	244.66±2.65	242.05±1.81	229.59±2.78	247.47±3.59	227.93±2.48	214.25±2.41	199.02±2.70	191.40±10.04
SD-DO (μmol/kg)	4.67±0.55	5.65±0.54	21.55±1.14	9.37±0.71	9.01±0.65	12.05±1.05	15.14±0.85	13.14±0.65	22.73±2.21	8.32±0.96	14.12±1.37
Chla (mg/m^3)	0.80±0.03	1.28±0.27	4.95±0.18	2.86±0.18	3.82±0.30	3.81±0.16	3.652±0.31	4.71±0.26	4.62±0.36	2.40±0.17	1.121±0.46
Chla15 (mg/m^3)	0.64±0.03	1.03±0.10	2.74±0.23	2.80±0.13	2.64±0.13	3.59±0.20	3.82±0.24	4.12±0.27	4.52±0.19	3.75±0.21	2.01±0.38
Chla30 (mg/m^3)	0.47±0.02	0.70±0.04	1.43±0.22	2.72±0.18	3.05±0.14	3.87±0.26	3.79±0.25	3.71±0.18	4.90±0.20	5.10±0.51	2.16±0.56
Chla60 (mg/m^3)	1.29±0.10	0.67±0.04	0.82±0.04	1.71±0.16	3.32±0.20	3.09±0.13	3.11±0.16	3.39±0.19	3.71±0.20	5.28±0.46	3.84±0.59
Wind (m/s)	2.48±0.32	1.62±0.28	3.01±0.23	2.28±0.30	3.09±0.21	1.97±0.19	2.07±0.22	2.47±0.18	2.30±0.22	2.57±0.27	0.98±0.31
NAO	0.70±0.09	1.32±0.04	0.90±0.07	0.86±0.07	-0.56±0.15	0.17±0.07	-0.44±0.20	-0.92±0.10	0.48±0.09	0.17±0.08	0.18±0.12
Number of fishing boats	4.29±1.19	7.60±0.90	5.48±0.61	3.24±0.34	3.46±0.39	1.56±0.15	4.41±0.43	3.43±0.31	3.98±0.40	5.95±0.63	8.45±1.37
Number of mussel farm boat	11.03±2.79	19.95±2.36	16.30±1.80	21.89±2.37	13.99±1.53	17.75±1.29	29.04±1.61	21.189±1.66	20.81±1.88	23.71±2.52	15.27±6.76
Number of recreational boats	3.52±0.78	3.21±0.27	2.69±0.21	3.63±0.27	4.36±0.36	4.843±0.30	6.39±0.44	9.9925±0.83	5.00±0.32	3.87±0.33	2.55±0.45

WT water temperature, *SAL* water salinity, *Chla* fluorescence, *DO* dissolved oxygen. *NAO* North Atlantic Oscillation

Table 4 Summary of contributions of predictors to the best fitting GAM

	edf	Ref.*df*	Chi. sq	*p* value
Number of immature dolphins	4.150	9	428.7	$< 2e{-}16^{*}$
Number of new-born dolphins	1.12	2	14.4	$8.1e{-}05^{*}$
Mean DO	4.8	9	41.2	$2e{-}16^{*}$
WT standard deviation	0.87	9	2.7	0.054^{*}
NAO	3.7	9	23.0	$2.3e{-}05^{*}$
Chla60	1.3	9	3.9	0.048
R-sq (adj)	0.448			
Deviance explained	42.2%			
N	846			
AIC	5271			

edf effective degrees of freedom for the spline smoother, *Ref.df* reference degrees of freedom, *R-Sq (adj)* adjusted r-squared for the model, *UBRE* unbiased risk estimate, *AIC* Akaike information criterion

*Denotes a *p*-value of < 0.05
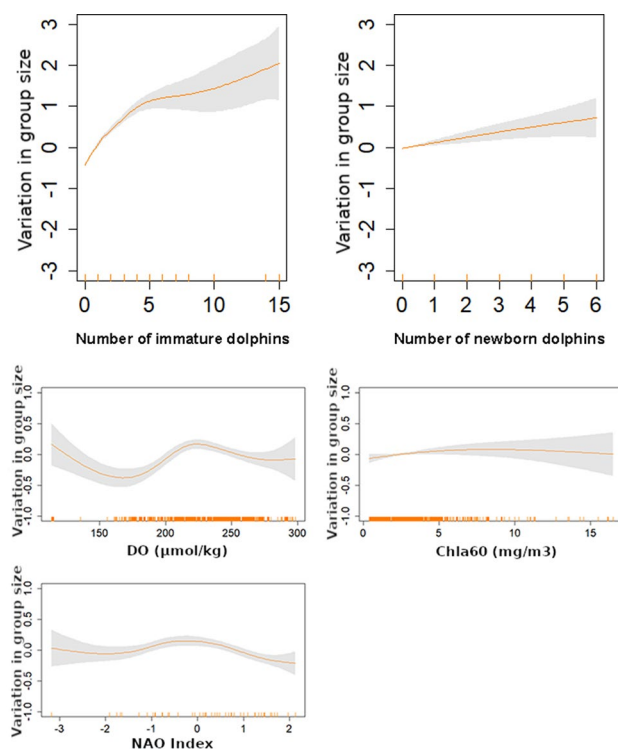
Fig. 3 Average predictions of bottlenose dolphin group size for each significant covariate in the final GAM (with 95% confidence limits)

which might be due to differences in food availability and predation risk. In the coastal waters of North-West Spain, bottlenose dolphins are not known to have natural predators (Methion and Díaz López 2018) and the area is highly

productive because of upwelling enrichment and land run-off, contributing to a significant abundance of bottlenose dolphin prey species (i.e., European pilchard, blue-whiting, and Atlantic horse mackerel) (Giralt Paradell et al. 2021; Santos et al. 2007; Tenore et al. 1995). This large food availability likely minimizes competition between individuals to access resources, and facilitates prey capture through cooperation, therefore helping bottlenose dolphins to maximize their energy intake. Previous studies in the study area in fact indicated that these bottlenose dolphins use different foraging techniques, including cooperative feeding, which involve a high degree of social organization and behavioral adaptation (Methion and Díaz López 2019, 2020).

In this study, we did not find a direct relationship between monitored anthropogenic activities (marine traffic, fisheries, and aquaculture) and the size of bottlenose dolphin aggregations. This could be explained by the fact that these human activities, despite causing changes in the surrounding environment, do not directly condition the availability (both in type and quantity) of dolphin prey as much as oceanographic variables (i.e., oxygenation and chlorophyll-a concentration of the water).

Bottlenose dolphin group dynamics are likely driven by multiple factors, and other variables such as behavior, parental care, and protection from predators and conspecifics (Gowans et al. 2008) may act synergistically with environmental parameters. The observed link between dependent calves (new-born and immature dolphins) and bottlenose dolphin group dynamics is in concordance with previous studies reporting larger groups in the presence of dependent calves (Gibson and Mann 2008; Kerr et al. 2005; Bearzi et al. 1997; Díaz López 2012). As several cases of infanticide have been reported in this area (Díaz López et al. 2018b), the formation of large groups likely increase calf protection from conspecifics by reducing the probability that a calf be attacked by other conspecifics (through both the dilution effect and the detection effect). On the other hand, forming large groups may also allow mothers to spend a greater proportion of time foraging to maintain the increased energy required for lactation by being assisted by other females in caring for their calves. In addition, by being part of larger groups, nursing females may benefit from an increased ability to search for and catch fish that aggregate in large schools thanks to cooperation with other group members, therefore ensuring sufficient energy intake for nursing. Further studies about parental care, alloparental care, and cooperation could help develop a better understanding on grouping patterns in bottlenose dolphins.

This study identifies a link between environmental changes and social behavior in a top marine predator and illustrates the importance of using multiple variables at different scales to explore the factors that shape animal societies. The findings provide valuable information on how

bottlenose dolphin grouping patterns are linked to both fine-scale and large-scale environmental changes and suggest that dolphin group size could act as a useful indicator of environmental change in coastal ecosystems. As with previous studies using regression techniques, this study has, however, the limitation of not being able to demonstrate causal links between environmental variation and dolphin grouping behavior. The observed fluctuation in dolphin group size could also be driven by unmeasured oceanographic events occurring at different temporal and spatial scales than the ones monitored in this study (e.g., outside the Ría de Arousa and in periods of time previous to the research). Further studies with larger temporal and spatial scales would therefore allow a better understanding of dolphin grouping patterns associated with broader environmental changes.

Data availability Data will be provided under request.

Code availability Not applicable.

Declarations

Conflict of interest None declared.

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

Consent to participate Not applicable.

Consent for publication All authors consent to publish.

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