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On the behaviour of an under-studied population of bottlenose dolphins in the Southern Adriatic Sea

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Abstract

Perhaps the world's best-known cetacean, the bottlenose dolphin shows considerable variation in behaviour between and within populations in relation to differences in natural and anthropogenic conditions. Drivers of behavioural variation need to be identified to understand the dynamics of wild dolphin populations. Little research has been published on the bottlenose dolphin population found in the Southern Adriatic Sea. Using a set of spatial, temporal and social predictors, we aimed to investigate what variables are related to the behaviour of an under-studied population of bottlenose dolphins along the coastline of Montenegro. We present the results of a year-long study monitoring the behaviour of bottlenose dolphins along coastal Montenegro. We considered the effect of topography, seasonality and group size. A large proportion of travelling (55%) small groups (mean 4, range 1–9) in shallow waters (<50 m) was observed. We showed that seasonality alone explained behaviour best, with surface-feeding and socializing-resting increasing in autumn and winter. Group size was found to be a result of behavioural choice. We suggest seasonal changes in environmental conditions and anthropogenic pressure may explain the recorded behavioural pattern. This research points to the necessity of increased collaboration in the region to help understand complex patterns in behaviour and habitat use of local dolphin populations if effective conservation measures are to be developed.

Introduction

Since the late 20th century, concerns over the condition of the bottlenose dolphin (*Tursiops truncatus*) Mediterranean sub-population, listed as vulnerable on the IUCN Red List (IUCN, 2017), have increased. While *T. truncatus* is perhaps one of the most extensively studied dolphin species due to its cosmopolitan distribution, their population numbers in certain areas have decreased significantly since the 1940s (Folkens & Randall, 2002). Due to the species' predominantly coastal range, this decline is often attributed to anthropogenic factors (Wilson *et al*., 1997). Behavioural changes are associated with a combination of environmental cues and human pressures that can lead to changes in population-level dynamics (Nowacek *et al*., 2001; Bas *et al*., 2017). It is therefore important that we understand natural patterns of dolphin behaviour so any anthropogenic impacts can be mapped and quantified (Bearzi, 2002). Indeed, bottlenose dolphin behaviour is known to be complex and extremely fluid both within and between populations (Shane *et al*., 1986; Hanson & Defran, 1993; Connor *et al*., 2000; Gregory & Rowden, 2001). Factors related to geographic and temporal variability and group size have the potential to affect behaviour both directly and indirectly (Miller *et al*., 2010; Hwang *et al*., 2014).

Various studies have revealed relations between group size and behaviour in this highly social species. For example, diving and foraging groups are significantly smaller than socializing groups (Bearzi *et al*., 1997) whilst travelling groups tend to be significantly smaller than foraging groups (Rogers *et al*., 2004). It is still unclear whether it is group size that affects behavioural choices in bottlenose dolphins or whether the behaviours they engage in direct group size. Identifying the social processes influencing behaviour is central to understanding this species' habitat use and associated distribution patterns.

Furthermore, temporal variation in environmental conditions has been shown to affect *T. truncatus* behaviour (Shane *et al*., 1986; Connor *et al*., 2000). Although a conclusive daily behavioural cycle for bottlenose dolphins has yet to be determined (Bearzi *et al*., 1999), other factors that change diurnally, such as tide, currents, wind and prey presence are known to affect their behaviour (Hanson & Defran, 1993; Bearzi *et al*., 1997; Gregory & Rowden, 2001; Daura-Jorge *et al*., 2005; Miller *et al*., 2010). For instance, bottlenose dolphins in the South Atlantic engage in resting behaviour in the morning, when schooling fish are unavailable, with levels of activity increasing in the afternoon as prey availability increases (Würsig and Würsig, 1979). Linking diurnal changes to dolphin behaviour may point to further environmental variables that explain behavioural choices in bottlenose dolphins. Similarly, seasonal changes in water temperature, salinity and prey availability have been linked with changes in *T. truncatus* behaviour (Bräger, 1993; Hanson & Defran, 1993;

Miller *et al.*, 2010). Indeed, fluctuations in prey availability due to changes in sea temperatures with season are known to result in increased foraging or travelling behaviour as prey move in and out of the region (Bearzi *et al.*, 1999). Furthermore, identifying seasonal patterns in dolphin behaviour that correspond to changes in environmental and anthropogenic pressures can yield invaluable insight into local populations' life history and help establish more efficient conservation strategies (Miller *et al.*, 2010).

In addition to social and temporal factors, geographic features found in *T. truncatus*' range affect its behaviour (Ballance, 1992; Acevedo-Gutiérrez & Parker, 2000; Benoit-Bird & Au, 2003; Hastie *et al.*, 2004; Toth *et al.*, 2012; Hwang *et al.*, 2014; Temple *et al.*, 2016). Typically, distance from shore is directly linked to bathymetry and a slight change in oceanic depth can affect the entire ecology of a region (Bell, 1983). This heterogeneity of marine habitats plays a major role in the distributions and behaviour variations of bottlenose dolphins (Ballance, 1992; Hanson & Defran, 1993; Acevedo-Gutiérrez & Parker, 2000; Hastie *et al.*, 2004; Hwang *et al.*, 2014). In *T. truncatus*, diving and foraging behaviour are associated with deeper waters whilst travelling and resting are observed more often at shallower depths, which offer protection from predators and navigation guidance (Ballance, 1992; Acevedo Gutiérrez & Parker, 2000; Bearzi, 2005). Indeed, dolphins found closer to shore, on average, spend more time travelling, followed by feeding and socializing (Hanson & Defran, 1993; Bearzi, 2005).

Here, we focus on an under-studied population of bottlenose dolphins found in the South-eastern Adriatic Sea along the coastline of Montenegro. Despite the wide research on bottlenose dolphin behaviour globally, in Montenegro, peer-reviewed cetacean research is severely limited (Joksimović *et al.*, 2013; Gaspari *et al.*, 2015; Durović *et al.*, 2016). The current study was established in September 2016 as the first long-term cetacean monitoring project in Montenegro. To further our understanding of the local dolphin population, our study aimed to investigate the relationship between behaviour and a set of spatial, environmental and social factors. Specifically, we tested the hypothesis that (i) proximity to shore and depth influenced behavioural choices, (ii) the local population displayed seasonal and diurnal patterns in behaviour and (iii) behaviour varied significantly with group size. The information collected will be crucial in providing baseline data on the behavioural patterns of bottlenose dolphins in Montenegro that will help in the development of local marine conservation initiatives.

Materials and methods

Study area

The entire coastline of Montenegro was divided into three regions to allow for an evenly distributed sampling effort. Five land survey stations were then randomly selected based on these regions, two in the South (Ulcinj and Utjeha), two in the centre (Bar and Petrovac) and one in the North (Herceg-Novi). These stations allowed for a total coverage of 137.5 km^2 out of the 575.7 km^2 making up Montenegro's coastal waters (Figure 1).

Depth along the coastline of Montenegro ranged from 5 to 75 m. This depth range was maintained along most of the coastline with few deeper areas except in the Bay of Kotor area. These relatively shallow waters contrasted with some of the deepest waters of the Adriatic Sea, over 650 m, found further offshore (Figure 1).

Data collection

The coastal region of Montenegro was surveyed using land-based observation techniques to avoid potential behavioural changes as dolphins reacted to research vessels (Lemon *et al.*, 2006).

Each land station was visited, weather permitting, at least twice a month for an entire year from September 2016 to October 2017. Surveys, lasting from 3 to 4 h, were conducted from an elevated position on the shoreline via continuous scans using both 10×50 magnification binoculars and a Sokkia DT5A Electronic Theodolite. All observations recorded above 4000 m from shore were discarded as dolphin fins were not discernible from wave crests.

Environmental variables (Beaufort sea state, cloud cover and glare) were collected hourly and surveys were abandoned when sea state increased to 3 or more. Data were collected during daylight hours with surveys always starting and ending at sunrise or sunset. Time of day was classified as 'morning' when surveys started at sunrise and 'afternoon' when surveys ended at sunset. Seasons were defined by 3-month intervals: spring (March, April, May), summer (June, July, August), autumn (September, October, November) and winter (December, January, February).

Dolphin coordinate recordings gathered with the Theodolite were converted to geographic coordinates using Pythagoras software (Pythagoras 1.2; Würsig *et al.*, 1991; Lerczak & Hobbs, 1998), and information about depth and distance from shore were inferred using ArcGis (ESRI, 2011, version 10.3.1).

Focal group scan sampling was used to assess group behaviour, assuming that the surface behaviour was representative of that underwater (Lusseau, 2003; Bas *et al.*, 2017). Behavioural states were recorded according to a study-specific ethogram (Table 1) along with group size at 5 min intervals upon dolphin sighting. Groups were defined as the number of individuals within 50 m of each other. The predominant behaviour at each 5 min interval (over 50% of animals from a defined group engaged) was recorded as the group behaviour. Whenever the group was not sighted at the end of the 5 min interval, the next sighting started the interval sampling anew. If the group was not observed for 20 min, the next sighting was categorized as a new group.

During focal follows, one observer was tasked with continuous scanning of the area while two observers recorded behaviours and followed the group and one observer tracked the dolphins with the theodolite. If the focal group split or another group was sighted, continuous scanning stopped, and one observer followed each group whilst the remaining observer guided the theodolite user between groups. Continuous scans were restarted when one of the groups was not spotted for more than 15 min. Sightings were often short (less than 15 min), thus 5 min intervals were deemed long enough to avoid a bias from temporal autocorrelation of the data as few groups had more than two behaviour recordings.

Statistical analysis

We tested for the independence of all explanatory environmental variables (depth, time of day, distance from shore and season) and behaviour by using a series of Chi-square tests. In order to perform such tests, the data for distance from shore and depth were transformed into integer categories of 500 m increments for distance from shore and 10 m increments for depth, as environmental conditions were not expected to vary within these ranges (Bell, 1983; Ballesteros, 1989; Micheli *et al.*, 2005). Any explanatory variable failing to show a significant relationship ($P > 0.05$) with behaviour was discarded in further analyses. Additionally, we tested for correlation between depth and distance from shore.

Behaviour in this study was an unranked categorical variable with four levels (Table 1). Behaviour could thus be modelled against the chosen explanatory environmental variables using a

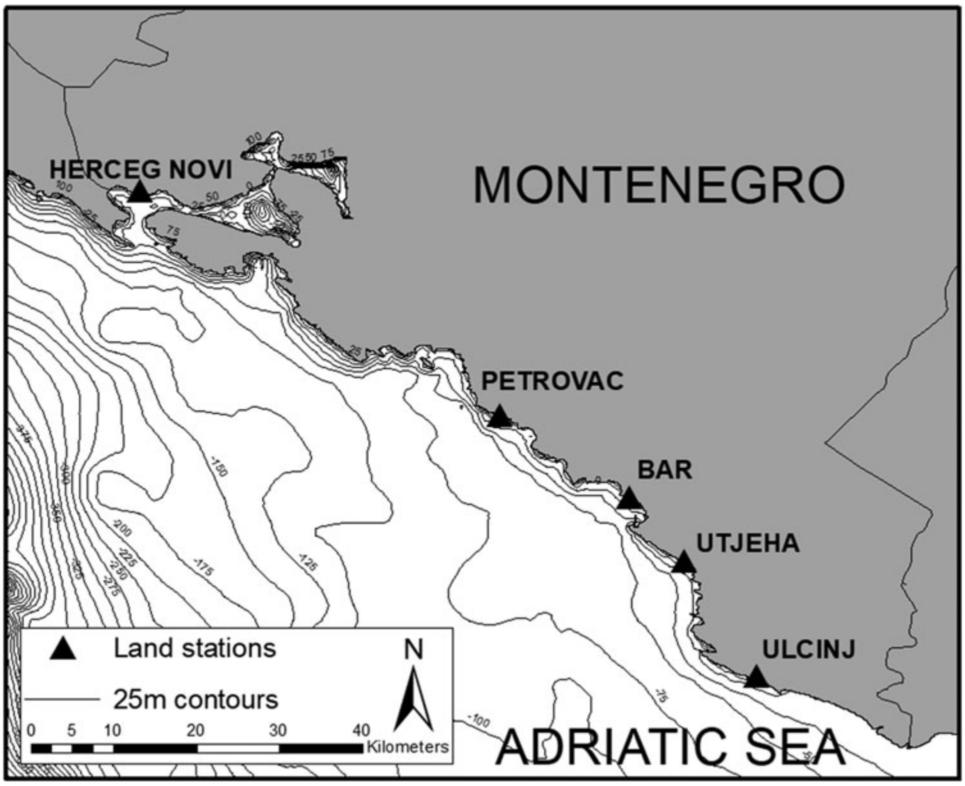

Fig. 1. Map of Montenegro's coastline and all survey stations used in this study: Ulcinj (19°12′38″E 41°55′29″N, 92 m above sea level), Utjeha (19°08′46″E 42°03′01″N, 78 m), Bar (19°04′19″E 42°07′11″N, 23 m), Petrovac (18°55′17″E 42°12′31″N, 148 m) and Herceg-Novi (18°32′25″E 42°27′11″N, 84 m). Bathymetry contours show 25 m increases in depth (data from: IOC, IHO & BODC, 1994).

Table 1. Ethogram of *T. truncatus* behaviour based on previous studies: Lusseau (2003) and Bas *et al.* (2017)

Behaviour	Description
DV	Dolphin is underwater for a long period of time (>20s) before resurfacing. Directional movement of the group may vary. Group dives synchronously.
TR	Dolphins engage in persistent, unidirectional movement with short, regular (usually 3–5 s) dive intervals. Group spacing may vary.
SU-FE	Dolphins engage in circular dives with rapid directional changes. Large amount of dolphin activity at the surface (likely to be associated with bird and fish presence on the surface).
SOC-RE	Category including both socializing (SOC) and resting (RE) behaviours due to small sample size. SOC: Dolphins are interacting with one another. Physical contact can be observed. Large diversity of behavioural events. Dive intervals may vary. RE: Dolphins are drifting near the surface of the water, moving slowly in a constant direction. There is little activity or splashing.

multinomial distribution. Multinomial regression allowed for the estimation of the relative risk ratios for a unit change in predictor variables of both continuous and categorical types (Blizzard & Hosmer, 2007). In turn, we estimated the probability of each behaviour outcome with respect to a baseline behaviour for any independent variable. Assuming our ethogram described all behavioural states observed in our population, the independence of irrelevant alternatives was not violated and made multinomial logistic regression an ideal tool to analyse the effect of the aforementioned variables on behavioural probabilities (Steckenreuter *et al.*, 2012). Furthermore, as most groups (50%) only accounted for 1–2 observations we considered the assumption of independence of data not to be broken. We thus ran a series of multinomial regressions from a fully saturated model, where all interaction and additive terms between explanatory variables were considered, to the simplest model, where only one explanatory variable was considered. We chose the best-fit model out of all combinations based on both AIC and BIC values.

Following the results of our multinomial regression, we further analysed the relationship between group size and behaviour considering that behaviour may have been affecting group size more than the inverse. Thus, we ran an analysis of variance (ANOVA) model to test for a specific effect of behaviour on group size. We then ran a *post-hoc* Tukey honest significant difference test to identify which behaviours, if any, were significantly affecting group size.

All analyses in this paper were conducted using the statistical software R (R Core Team, 2018) and multinomial regression was performed using the nnet package (Venables & Ripley, 2002).

Results

Sampling

A total of 180 surveys (537 h) were carried out and dolphins were sighted on 60 different surveys during the study period, totalling 51 followed groups, and 134 behavioural observations. The number of observations per group ranged between 1–10 with the median equal to 2. Of the total number of surveys, 31% were carried out in Ulcinj, 21% in Utjeha, 17% in Bar, 15% in Petrovac and 16% in Herceg-Novi. Dolphins were sighted most in Ulcinj (46% of observations), followed by Utjeha (24%), Bar (10%), Petrovac (9%) and Herceg-Novi (11%) (Figure 2).

Group sizes varied from 1 to 9 with a mean and median of 4 individuals per group. The most commonly observed behaviour

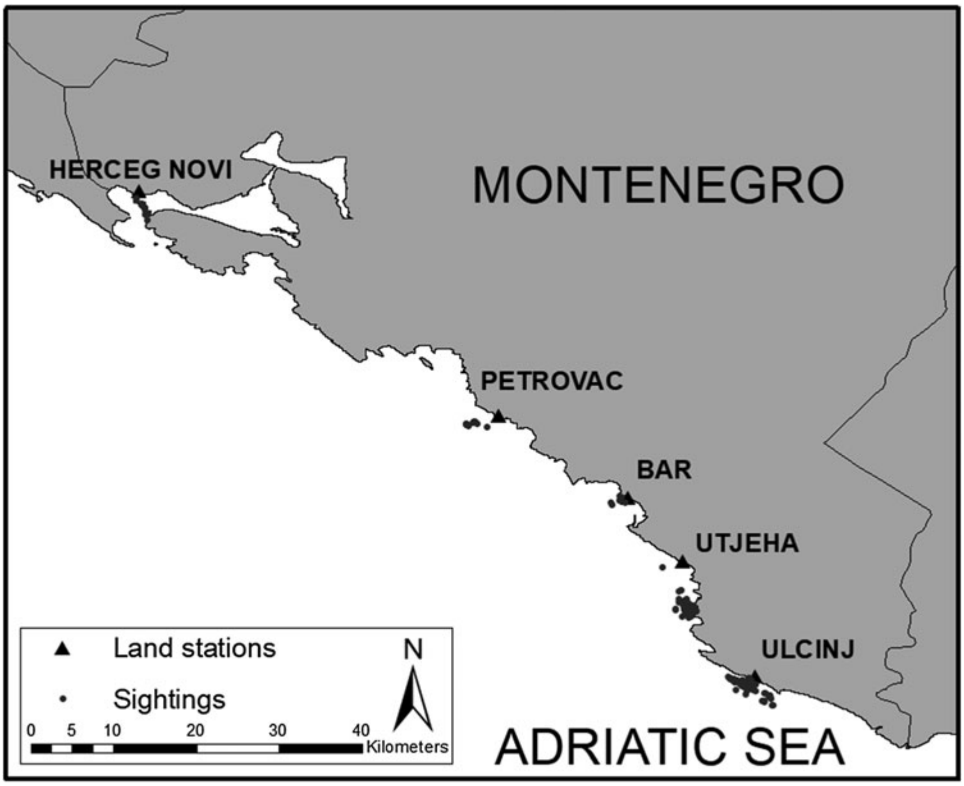

Fig. 2. Map of Montenegro's coastline and all individual dolphin sightings used in this study.

was found to be travelling (55% of the time) followed by diving (22%), socializing-resting (15%) and surface feeding (8%).

Of the total observations recorded, 44% occurred in the morning and 56% in the afternoon. More dolphin groups were observed in the autumn months (30%) followed by winter (28%), summer (25%) and spring (17%).

Dolphins were recorded at depths of 10–100 m over distances of 100–4000 m away from the shoreline, beyond which theodolite readings were discarded. Median recorded depth was 8 m and 75% of observed dolphins were found between 3 and 25 m deep. Median recorded distance from shore was 900 m and 75% of the observations were made between 600 and 1500 m.

Statistical analysis

Individual Chi-square test results showed that two of the four categorical or integer variables, season ($\chi^2 = 36.10$, $P < 0.001$) and distance from shore ($\chi^2 = 34.47$, $P < 0.05$), considered here were significantly not independent from behaviour. As behaviour was not found to significantly depend upon time of day or depth ($P > 0.05$), both variables were dropped from all subsequent analysis. Depth and distance from shore were found to be highly correlated ($r = -0.88$, $t = -21.64$, $P < 0.001$), supporting the use of distance from shore alone in further analysis.

Stepwise multinomial regression carried out with the remaining two explanatory environmental variables (season and distance from shore) and group size led us to reject all variables but one. Indeed, the best-fit model (AIC = 287.89 and BIC = 322.67) was that considering season as the sole explanatory variable (Figure 3). The model revealed a significant increase in surface-feeding ($z = 2.13$, SE = 0.42, $P < 0.05$) and a near significant increase in socializing ($z = 1.91$, SE = 0.31, $P = 0.056$) over the course of the year. This considerable increase in both surface-feeding and socializing behaviours came mainly at the expense of travelling (Figure 4), although this relationship was not found to be significant ($P > 0.05$).

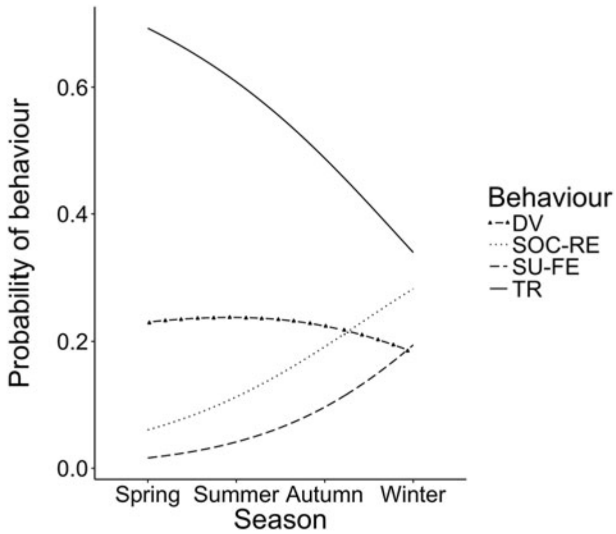

Fig. 3. Season model from stepwise multinomial regression of bottlenose dolphin behaviour.

The second best model, including both season and group size as additive terms, was found to fit the data as well as the season model on AIC alone but not when BIC was considered alongside it (AIC = 287.60 and BIC = 331.07). Thus, we considered the effect behaviour may be having on group size. The ANOVA test result suggested that the variance in group size within each behaviour category was significantly different from the overall variance in group size ($F = 4.33$, df = 3, $P < 0.01$). The *post-hoc* Tukey test revealed that travelling groups were significantly smaller than those engaged in surface-feeding behaviour (difference = 2, $P < 0.01$). No other pairwise differences were found to be significant.

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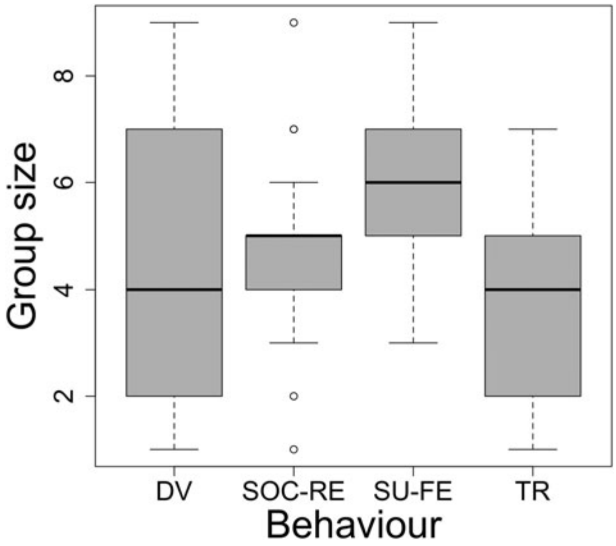

Fig. 4. Variation in group sizes among behaviour categories. Boxplots show median, quartile, minimum, maximum and outliers.

Discussion

Our results suggest that spatial variables and time of day do not have an effect on the behavioural patterns of coastal Montenegro's bottlenose dolphins while season explains most of the observed variation in behaviour. Indeed, depth and distance from shore failed to explain the observed variation in behaviour. Depth and distance from shore are highly correlated variables that we expect to have analogous effects on dolphin behaviour via their effect on habitat complexity (Sargeant *et al.*, 2007). Montenegro is home to some of the deepest waters in the Adriatic Sea whilst its territorial waters are shallow (Blake & Topalović, 1996). In this study, no recordings were made at depths beyond 50 m or further than 4 km away from the coast. Thus, the variability in depth and distance of this study is very low and a gradient of 50 m within 4000 m may not be enough to promote a heterogeneous habitat that warrants specific behavioural changes (Ballance *et al.*, 1992; Sargeant *et al.*, 2007). Furthermore, these predominantly shallow waters and the high incidence of travelling behaviour supports previous findings that suggest travelling occurs primarily at shallow depths that offer protection from predation and enable the use of the coastline as a navigation tool (Ballance, 1992; Bearzi, 2005). Despite the lack of support for spatial effects on behaviour in our study, we expect that increased survey area coverage will reveal behavioural patterns that can be linked to depth and distance from shore (Di Sciara *et al.*, 1993; Hanson & Defran, 1993). Nevertheless, the high occurrence (75%) of dolphin groups in very shallow waters corresponds to the coastal distribution of this species' coastal ecotype described globally (Ballance, 1992; Di Sciara *et al.*, 1993).

Additionally, we do not detect any effect of diurnal changes on the behaviour of bottlenose dolphins. With the exception of diel light conditions, daily changes in abiotic factors are small in large marine basins such as the Adriatic Sea (Cushman-Rosin *et al.*, 2013) and are likely insufficient to cause habitat level changes that require behaviour modification in a homoeothermic species such as *T. truncatus*. Further, anthropogenic activity in the coastal waters of Montenegro does not vary greatly during the day with boat traffic remaining constant from morning to afternoon, as tankers arrive all day long and small fishing vessels leave at dusk and dawn (personal observations). However, splitting the dataset into two, morning and afternoon, may be too coarse a categorization to allow for the detection of a crepuscular pattern identified in previous studies.

Bottlenose dolphins in our study area display a seasonal pattern in behaviour, with sighting rates and behaviours such as surface-feeding and socializing-resting increasing over the colder autumn and winter months. Conservation efforts are directed by the identification of areas ecologically important for foraging and reproduction in bottlenose dolphin populations (Shane *et al.*, 1986; Connor *et al.*, 2000), which, here, are intrinsically linked to these times of year. Possible explanations for these changes in behaviour include increased productivity in winter and higher prey abundance or availability, favourable environmental conditions and decreased human presence (Hanson & Defran, 1993; Lusseau & Higham, 2004; Lusseau *et al.*, 2004). Indeed, Montenegrin waters are considerably warmer in summer months that are characterized by weaker maritime currents, which provide less nutrients and upwelling in the region (CAU, ELARD, ITI, 2014; UNEP, 2015). Moreover, Montenegro's economy relies heavily on tourism, with the peak season taking place in warmer months where boat traffic increases dramatically and high-speed loud boats such as jet skis are encountered on a regular basis (personal observations). Increases in boat traffic have been linked to a decrease in foraging and socializing behaviours in bottlenose dolphins in the Mediterranean (Papale *et al.*, 2012; Bas *et al.*, 2017) and elsewhere (Nowacek *et al.*, 2001; Bejder *et al.*, 2006). In fact, socializing and resting are the most sensitive behaviours to human disturbance (Lusseau & Higham, 2004). The relationship between behaviour and season combined with the increase in sighting rates in autumn and winter suggests that a temporal change in both anthropogenic pressure, comparable to that in other Mediterranean basins (Pennino *et al.*, 2016), and environmental conditions is prone to be responsible for the observed patterns in behaviour.

Behavioural choices are responsible for group dynamics in Montenegro's bottlenose dolphin population. Behaviour and group size are fundamentally linked in bottlenose dolphins (Shane *et al.*, 1986). Typically, group sizes are smaller in shallow waters where habitats provide relatively predictable food patches in space and time (Campbell *et al.*, 2002; Gowans *et al.*, 2007). Our results show that choices in behaviour are likely driving group size. Despite the lack of significance in pairwise differences, socializing and foraging show larger group sizes expected from behaviours requiring advanced coordination and the presence of conspecifics (Connor *et al.*, 2000; Sargeant & Mann, 2009). Populations in Croatia and Greece display larger group sizes associated with foraging behaviour than in neighbouring coastal Montenegro (Politi *et al.*, 1992; Bearzi *et al.*, 1992, 1999; Genov *et al.*, 2008). The smaller average group size found in Montenegrin waters can be linked to the predominance of travelling behaviours recorded in this study (Bearzi *et al.*, 1992; Rogers *et al.*, 2004). These findings support the idea that *T. truncatus* are using these waters as travelling grounds for small groups between feeding sites where they form larger assemblages.

Critical habitat delineation, using key biological behaviours, forms the baseline of marine protected area implementation (Hoyt, 2005; Pennino *et al.*, 2017). We suggest that combining our approach with new studies of *T. truncatus* found offshore and photo-identification of the local population will help to understand both its variation in behaviour and movement patterns. Mark-recapture analysis of bottlenose dolphins in the area can further reveal whether the same individuals are regularly seen travelling along the coast over time and if these are sighted in larger foraging groups in other territorial waters. Such an approach would benefit tremendously from a yet lacking international collaboration of all scientists working in the Adriatic. Additionally, long-term monitoring of the local population will be necessary to identify if the seasonal patterns found here, and their implications, are consistent over years. This effort, combined

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with specific analysis of behavioural responses to human presence (Lusseau, 2003) will reveal whether there is a chronic anthropogenic pressure on the present dolphins (Nowacek *et al.*, 2001; Bas *et al.*, 2017), forcing them to reduce ecologically important behaviours and avoid the area over summer months. This is especially important in the face of recorded changes in dolphin behaviours and abundance due to seasonal variations in marine vessel traffic and type across the Mediterranean (La Manna *et al.*, 2013; Pennino *et al.*, 2016; Campana *et al.*, 2017).

Our work provides the very first data on South-eastern Adriatic Sea bottlenose dolphin behaviour. We do not find any support for the effect of spatial variables on the observed variation in behaviour, possibly due to the limited geographic range of our sample and the homogeneous habitat found within it. However, we find patterns of seasonality in dolphin behaviour and sightings that suggest coastal Montenegrin waters are more favourable over autumn and winter. Disentangling which effects, natural and/or anthropogenic, are having the greatest impact on *T. truncatus* behaviour is crucial to designing effective management in these waters. Indeed, elucidating what role Montenegro's territorial waters play in these dolphins' life history and what effect human disturbance is having on the local population is of paramount importance for the proper identification of threats to the local population. Further effort should focus on collaborative work covering the entire Adriatic basin to better our understanding of local *T. truncatus* status throughout its range.

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