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Diurnal and tidal influence on the spatial distribution and surface activity of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland

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Abstract

The interactions between oceanographic processes and topography have an important role in driving the formation of localised biodiversity hotspots. These hotspots create predictable prey resources utilised by many large coastal marine vertebrates, such as the bottlenose dolphin *Tursiops truncatus*. The abundance, behaviour and distribution of bottlenose dolphins is therefore largely driven by predator-prey interactions which are strongly influenced by physical ocean processes such as tides and the formation of hydrographic fronts. Understanding these interactions as well as the ecology of bottlenose dolphins is therefore vital for the effective conservation management of this species. Through the fine scale examination of the diurnal and tidal influences on bottlenose dolphin distribution, this paper aims to define the relationships driving the tidal temporal spatial distribution and habitat use of bottlenose dolphins in a tidally dominated system, as well as identify the drivers behind key foraging areas and the relationship between tidal influence and the direction of travel of dolphin schools. Shore-based observation data of dolphin surface activity were collected using a surveyor's theodolite from June to September 1996 and 1997 during standardised, systematic surveys of the lower Shannon Estuary, Ireland. Data relating to school position and surface activity were recorded to map species distribution relative to tidal temporal variables, as well as activity in order to infer regions of key habitat use for this species.

Observed surface activities were categorised and the relationships between them and tidal and temporal influences were tested statistically using Chi square analyses in RStudio. Kernel density plots were created to visually analyse diurnal and tidal phase influences on the spatial distribution of bottlenose dolphins in this region, and a 2-way ANOVA was used to test the significance of these interactions. Furthermore, focal follow data containing the sequential positions of observed dolphin schools and associated surface activities were collected in order to assess the extent of tidally mediated spatial distribution and direction of travel of schools within this region. A total of 529 dolphin schools were recorded during 55 shore-watches conducted within this study period. The spatial distribution of dolphin schools throughout the estuary were found to be both temporally and tidally mediated with concentrated foraging activity occurring almost exclusively during flooding tides, in the evening period and in mainly upper river regions with steep topography. Two critical foraging locations were identified within the study area: (1) Kilcredaun Point and (2) Beal Strand. The direction of travel of observed dolphin schools was not found to be significantly tidally mediated, though schools were observed to travel at greater frequencies against ebbing tidal flow, and with flooding tides. Tidally mediated spatial distribution was identified to be likely due to the interactions between tidal flow and the topography of the Shannon Estuary, resulting in the formation of hydrographic fronts and regions of intensified current velocities, utilised by the resident population of bottlenose dolphins for enhanced foraging efficiency. The identification of critical foraging locations for bottlenose dolphins in this region of the estuary highlights the importance for the protection of this region and further conservation of its resident populations.

Key words: behaviour, distribution, movements, conservation, oceanographic-topographic interactions, foraging, *Tursiops truncatus*.

Introduction

The bottlenose dolphin is a cosmopolitan species with distributions across tropical and temperate latitudes (Leatherwood 1983, pp. 296 – 299). Resident populations are found throughout UK and Irish waters, mainly in Southern Cornwall (Wood, 1998), the Moray Firth, Scotland (Hammon and Thompson, 1991), Cardigan Bay, Wales (Gregory and Rowden, 2001), and the Shannon Estuary, Ireland (Carmen, Berrow and O'Brien, 2021). They have coastal and oceanic ecotypes occupying a diverse range of habitats in warm shallow waters and deeper offshore areas respectively. Despite being able to use vast areas of the ocean, coastal ecotypes of bottlenose dolphins are typically found in estuarine environments, concentrating in localised regions and preferring depths of ~30 meters, where tidal currents and topography interact to create highly predictable ephemeral features which species exploit to enhance their foraging efficiency (Block et al., 2011; Cox, 2016; Hersh and Duffield, 1990). Estuaries provide a critical habitat for various fish species and therefore serve as a key habitat for bottlenose dolphins who are opportunistic feeders, foraging intensively when prey is in high abundance (Carmen, Berrow and O'Brien, 2021; Fruet, Möller and Secchi, 2021). As one of the most important Atlantic salmon (*Salmo salar*) rivers in Ireland, the Shannon Estuary is therefore utilised by its resident population of bottlenose dolphins for its high prey availability (Foley, et al., 2010). Throughout Ireland, bottlenose dolphin populations are found to occupy estuarine, coastal, and oceanic waters (Dinis, 2021; Ingram 2000; O'Brien et al., 2009). Furthermore, these populations have been found to be genetically distinct, presenting different breeding populations, and there is no evidence to date that the coastal population occupying the Shannon Estuary interacts with any other Irish population (Mirimin et al., 2011).

The higher accessibility to coastal populations of bottlenose dolphins has led to the movement patterns, habitat use and behavioural characteristics of this species being widely studied in a number of estuaries worldwide (Leatherwood 1983, pp. 296 – 299). In the Clarence Estuary, Australia and Cardigan Bay, Wales tidal influence on bottlenose dolphin spatial distribution has been thoroughly studied with tidal phase concluded to have a significant effect on the species spatial distribution, and dolphin schools observed to travel inshore during flooding tides (Fury and Harrison, 2011; Gregory and Rowden, 2001). Studies into the varying spatial distribution of bottlenose dolphins in relation to diurnal influences however, have revealed no significant patterns in distribution as a result of time of day (Gregory and Rowden, 2001; Ingram, 2000). In the Shannon Estuary, diurnal influence has been seen to have little effect on the spatial distribution of bottlenose dolphins, with dolphin schools seen to have uniform diurnal distribution across the mouth of the estuary (Ingram, 2000). Furthermore, studies into the habitat use of bottlenose dolphins have observed spatial distribution throughout the Shannon Estuary to be driven by surface activity with foraging occurring predominantly in upper river areas (Carmen, Berrow and O'Brien, 2021).

The influence of tidal phase on bottlenose dolphin surface activity, particularly foraging, has been widely studied with significant relationships between foraging and tidal state being observed in Cardigan Bay, and foraging being found to occur most frequently during flowing flood tides in the Shannon Estuary (Carmen, Berrow and O'Brien, 2021; Gregory and Rowden, 2001). There is more limited understanding regarding diurnal influences on the activity of bottlenose dolphins with many contradicting conclusions being drawn regarding this relationship. In Sanibel Island and Galveston Bay the observed surface activity of bottlenose dolphins is seen to vary in response to time of day, with foraging being most frequently observed in the afternoon in Sanibel Island, and socialising most frequently in the afternoon in Galveston Bay (Bräger, 1993; Shane, 1990). However, in Cardigan Bay no significant relationship has been concluded for diurnal influences on the observed surface activity of bottlenose dolphins (Gregory and Rowden, 2001).

The interaction between tidal current flow and the direction of dolphin school movement is another area with limited understanding and numerous studies into this interaction have drawn contradicting conclusions also. Studies off the coast of Florida and Argentina have concluded a significant relationship between tidal current flow and the direction of dolphin travel, with bottlenose dolphin schools observed to travel with tidal flow (Irvine and Wells, 1972; Würsig and Würsig, 1979). However in contrast, studies near Port Aransas, Texas have observed bottlenose dolphin schools to exhibit a tendency to travel against tidal flow, particularly during the ebb phase of the tidal cycle (Shane, 1990). Furthermore, studies in the Sado Estuary, Portugal and the Gulf of Guayaquil, Ecuador have concluded tidal flow to have no effect on the direction of bottlenose dolphin travel (Felix, 1995; Santos and Lacerda, 1987).

The Shannon Estuary situated on Ireland's west coast is the largest estuary in Ireland with a catchment equivalent to 18% of Ireland's total area (Raine, 1992). Tapering from ~15km across at the mouth to less than 100m in the inner estuary it is a highly tidal dominated environment with semidiurnal tidal forcing being the main driver of circulation (Fouz et al., 2022; Sheehan and Healy, 2006). The strong tidal currents of up to 2.30 ms^{-1} and 1.96 ms^{-1} at mid-ebb and mid-flood respectively, interact with the steep topography throughout the estuary to create hotspot areas which experience the highest current velocities (Fouz et al., 2022). Situated off Kilcredaun Point and Beal Strand, the interaction between bottom topography and tidal forcing creates an area with amplified tidal current velocities utilized by the Shannon Estuary's resident population of bottlenose dolphins (Fouz et al., 2022). Bottlenose dolphins have an abundance level of international importance and must therefore have measures implemented for their protection. Listed as an Annex II species in the European Union's Habitats Directive they require designations of Special Areas of Conservation (SAC) (Council Directive 92/43/EEC). As such, the Shannon Estuary is designated as one of two SACs for this species in Irish waters, alongside the west Connacht coast. The resident population of bottlenose dolphins in the Shannon Estuary are further protected under the Irish Wildlife Act 1976 and Wildlife (Amendment) Act 2000.

However, understanding the drivers behind this species use of, and behaviour within the Shannon Estuary SAC is vital to the implementation of effective management plans (Sutherland, 1998). Identification of the key habitat locations within the estuary and the variables driving their spatial distribution can benefit the integrative management of other coastal tidal-topographic systems. Understanding the habitat use of bottlenose dolphins in the Shannon Estuary in particular, is vital due to the industrial and touristic nature of this estuary. Housing numerous boat touring operations and being used by up to 1,000 ships annually (O'Brien et al., 2016), the estuary is likely to be subjected to developments in energy, maritime, tourism and port related industries, as well as increased shipping through harbour developments as highlighted in the Shannon Estuary's Strategic Integrated Framework Plan (Anon, 2012). Furthermore, identification of the Shannon Estuary as a suitable site for the future development of marine renewable energy installations poses numerous threats to the species and robust understanding of their ecology in this location is vital to their appropriate future protection (O'Rourke, Boyle, and Reynolds, 2010).

In order to make robust predictions on the spatial distribution of bottlenose dolphins and fully understand the influence of environmental variables on the ecology of this species, further site specific investigations are required at a population specific scale. For the Shannon Estuary, few investigations have been undertaken with the focus of tidally and temporally mediated habitat use of bottlenose dolphins. Therefore, this report aims to outline, firstly the influence of tidal phase on the observed surface activity and spatial distribution of bottlenose dolphins, as well as the direction and speed of travel of dolphin schools. And secondly, the temporal distribution of this population and the temporal influences on their activity.

Methods

Study site

Data were collected during land-based observations from Kilcredaun Point (Fig 1) at a height of 35 ft between 15th June and 20th September 1996 and 7th June and 2nd September 1997. This time period coincides with seasonal peaks in bottlenose dolphin abundance as identified by Rogan et al., 2000 and Kilcredaun Point offered a prime location for dolphin encounters with high concentrations of the species identified in this area (Rogan et al., 2000). The Kilcredaun site also helped to mitigate any observer interference, a common issue during boat-based surveys.

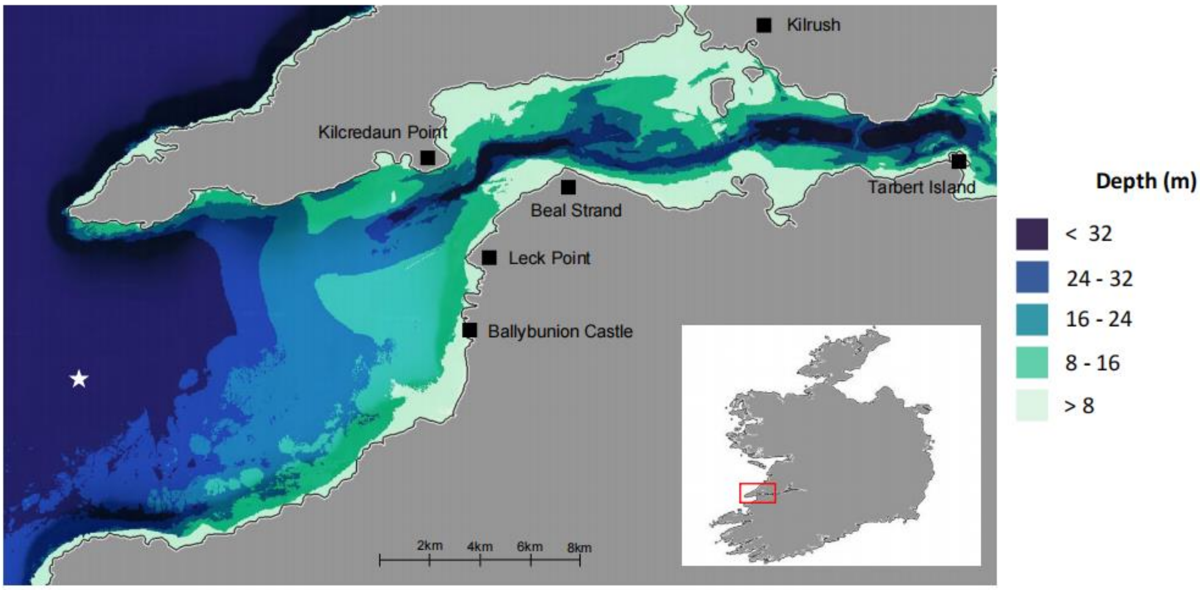

Figure 1: Bathymetry plot of the Shannon Estuary with inset of the Republic of Ireland, indicating the location of the Shannon Estuary (red box). Bathymetry data taken from the CV09_01 RV Celtic Voyager 2009 which contains Irish Public Sector Data (Geological Survey Ireland & Marine Institute) licensed under a Creative Commons Attribution 4.0 International (CC BY 4.0) licence. Map created using the Free and Open Source QGIS. Basemap: Googlemaps 2022. The white star represents the point used as the centre of the mouth of the estuary.

Field work methods

Data on the positions and observed surface activity of dolphin schools were collected from shore watches which typically lasted 4 hours, and 10-minute scans were conducted at half hourly intervals. This was in an attempt to minimise the probability of resampling dolphin schools in consecutive samples, and excluded any observer effects on the activity of dolphin schools through the use of non-contact, remote surveying methods. A ‘school’ was defined as a group of individuals engaging in similar activities within 100m of each other (as defined in Irvine et al., 1981). The scan samples contained data on all dolphin schools seen across the horizon from Kilcredaun Point and recorded details such as school size, direction of travel, activity, and position. Focal follow data were collected between scan samples and recorded the sequential positions of dolphin schools and as well as their surface activity at each position. In order to reduce the implication of sea-state on sighting probability, watches were confined to days of wind forces of three or less as defined by the Beaufort Scale.

Observations of surface activity were made using a TSN-1 Kowa telescope equipped with a 30x (wide) eyepiece and Minolta 10x50 binoculars and dolphin positions, with an accuracy of ± 50m, were derived using a surveyors theodolite equipped with a monocular 30x eyepiece. The theodolite, positioned at Kilcredaun Point, was situated ~35 ft above sea level and measured the vertical and horizontal bearing to an observed dolphin school. The vertical bearing was used to determine the distance offshore of the observed dolphin school with a bearing of 90_o indicating a dolphin school at eyeline, $>90^o$ indicating a dolphin school further offshore and $<90^o$ indicating a dolphin school situated closer to Kilcredaun Point. For the horizontal bearing, Ballybunion Castle (see Fig 1) was used as the 0^o reference point. The distance and bearing from Kilcredaun Point to an observed dolphin school was used to determine the co-ordinate position of the school using spherical trigonometry. The observed surface activities of sighted dolphin schools were classified as travelling, foraging, socialising or resting. These categories have been used throughout a number of similar studies on bottlenose dolphins and provide meaningful interpretations of surface activity without introducing ambiguity or subjectivity (Acevedo, 1991; Bräger, 1993; Shane, 1990). As numerous studies have defined resting as a dolphin school moving slowly at less than 2 mph (Arcangeli et al., 2009; Lusseau, 2006), for subsequent statistical analysis resting and slow-travel observations were combined. The activity classifications used throughout this report are therefore defined as follows (Ingram, 2000):

Travelling	School members surface regularly in a uniform direction with no aerial
behaviour	
Foraging	Observations of fish tossing rushes and lunges or surface milling with little or no overall progression of the school
Socialising	When contact was observed between individuals and/or members of a school displaying interactive aerial behaviours such as breaching, flipper waving or tail slapping
Resting	Inactive slow surfacing of dolphins with little or no forward progression of the school

Tidal data

Tidal data were extracted from an Oregon State University (OSU) TPXO7 tide model which best-fits, in a least-squares sense, the Laplace Tidal Equations and averaged ocean surface topography data obtained from 1992 to 2006, during the joint TOPEX/Poseidon venture (Egbert and Erofeeva, 2002; Fu et al., 1994). The detailed methods used to compute the model are described by Egbert and Erofeeva, 2002, and tidal data were obtained for a point in the mouth of the Shannon Estuary, at 52.5295° N, -9.7838° W. To validate this model, the modelled high water times were checked in correspondence to the 1996 Kilrush Creek Marina and Boatyard tide table, and the 1997 Shannon Estuary tide table. For the 1996 tide table data, an offset of -15 minutes, as computed by Ingram (2000), was added to account for the time delay in high water between Kilrush and Kilcredaun Point (see Fig 1 for locations). Similarly, as the 1997 tide table data were from Tarbert Island a +26 minute offset, again computed by Ingram (2000), was added to account for the time delay between this location and Kilcredaun Point (see Fig 1 for locations). Modelled tidal data corresponded accurately with data obtained from the relevant tide tables, so tidal data from the OSU TPXO7 tide model was used for the remainder of this report. The tide model supplied hourly sea surface elevation predictions, relative to the seabed, as shown in Fig 2. This information was used to calculate the predicted rate of sea surface height change (Δ) (Eq. 1).

$$\Delta = \frac{H1 - H2}{3600} \qquad \text{Eq. 1}$$

Where, $H1$ is the first sea surface height (cm), and $H2$ is the second the sea surface height (cm)

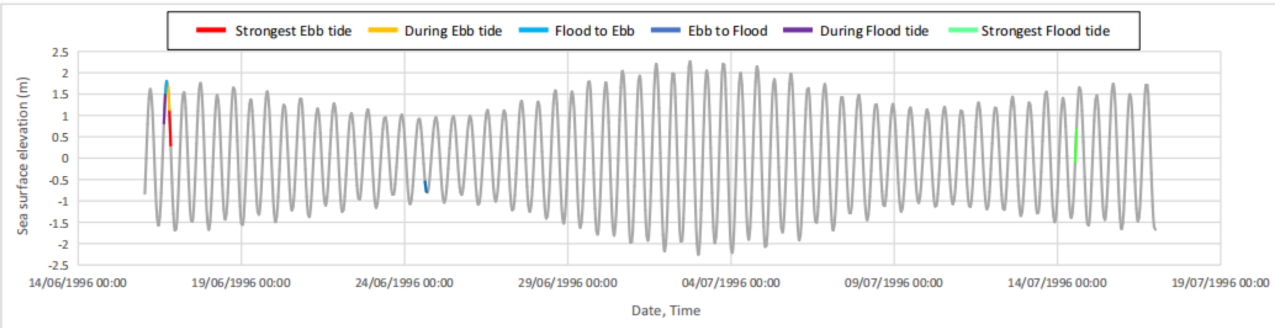

Figure 2: Modelled tidal curve for the Shannon Estuary from 16/06/1996 to the 16/07/1996. Predicted sea surface elevation data obtained from an Oregon State University (OSU) TPXO7 tide model. Colours represent the tidal bin categories used throughout this study.

The predicted rate of sea surface height change was used as a proxy for tidal phase. The tidal phase categories used throughout this report are defined as follows:

Strongest ebb tide	The maximum rate of sea surface height decrease, at rates of 0.02 cms^{-1} to 0.03 cms^{-1}
During ebb tide	Sea surface height decrease at a rate of 0.009 cms^{-1} to 0.019 cms^{-1}
Ebb to flood tide	The slowest rate of sea surface height decrease, leading into low water with zero rates of sea surface height change, and followed by the slowest rate of sea surface height increase. Rates of sea surface height change are within 0.006 cms^{-1} to 0.0089 cms^{-1}
During flood tide	Sea surface height increase at a rate of 0.009 cms^{-1} to 0.019 cms^{-1}
Strongest flood tide	The maximum rate of sea surface height increase, at rates of 0.02 cms^{-1} to 0.03 cms^{-1}
Flood to ebb tide	The slowest rate of sea surface height increase, leading into high water with zero rates of sea surface height change, and followed by the slowest rate of sea surface height decrease. Rates of sea surface height change are within 0.006 cms^{-1} to 0.0089 cms^{-1}

The predicted angle of tidal flow relative to north was computed between two points within the estuary at 52.538^{o}N, -9.736^{o}W and 52.587^{o}N, -9.648^{o}W. The angle of tidal flow was estimated as 45^o during flood tide and 225^o during ebb.

Time of day

Scan data were divided into 3 time of day categories, morning (08:00 to 12:00), afternoon (12:00 to 16:00) and evening (16:00 to 20:00).

Statistical analysis

Influences on spatial distribution:

Kernel density plots were created using QGIS software (V 3.20.3) and were used to visually analyse diurnal and tidal phase influences, as well as the influence of surface activity, on the spatial distribution and habitat use of this population. A 2-way ANOVA tested the influence of tidal phase and activity on dolphin spatial distribution at a significance level of 0.05. For this analysis, the spatial distribution of the bottlenose dolphins was quantified using their distance upstream from the centre of the estuary mouth (Fig 1), estimated using the QGIS measure line tool. The condition of homogeneity of variances was met.

Characteristics of observed dolphin schools:

Focal follow data were used to plot the tracks of dolphin schools observed throughout the study. The speed of travel of these schools (V) was computed for each leg between the recorded schools positions using Eq.2 (see Appendix B for illustration of these methods). During the analyses of speed of travel in response to tidal phase the conditions for normal distribution and homogeneity of variances were not met, so a Kruskal-Wallis statistical test was used to assess the significance of the tidal cycle on the speed of travel of observed dolphin schools.

$$V = \frac{d}{\Delta t} \qquad \text{Eq. 2}$$

Where, d is the distance (m) between the schools recorded position calculated using Pythagorean theorem in Eq.3, and Δt is the time difference between the recorded positions (s)

$$d = \sqrt{a^2 + b^2} \qquad \text{Eq. 3}$$

Where, a is the difference between the northing values of the two recorded positions, and b is the difference between the easting values of the two recorded positions

The angle of travel of observed dolphin schools (θ) relative to north was calculated using the trigonometric function in Eq. 4, for each recorded position along the schools track (see Appendix B). The mean angle of travel of observed dolphin schools were plotted in comparison to the tidal angle using the ggplot2 package of RStudio version 3.6.2 (R core team, 2019).

$$\theta = \tan^{-1}\frac{a}{b} \qquad \text{Eq.4}$$

Where, a is the difference between the northing values of the two recorded positions, and b is the difference between the easting values of the two recorded positions.

The frequency of travel with or against tidal flow during each section of an observed school's track was enumerated for both the ebb and flood phases of the tidal cycle. Dolphin schools were classified as travelling with flowing flood tides if their angle of travel was within +/- 10^o of the angle of tidal flow, and against tidal flow in the opposite case. The same classifications were used for the ebbing tide. A Chi square statistical test at a significance level of 0.05 was used to test the significance of the relationship between the angle of travel of observed dolphin schools and the angle of tidal flow.

Influences on activity:

The significance of the influence of time of day and tidal phase on the activity of dolphin schools was assessed using Chi square analysis at a significance level of 0.05. For the analysis of tidal phase on the observed surface activity, the tidal phase categories were combined into tidal phases of:

Ebb tide	Including surface activity records for strongest ebb and during ebb periods
Slack tide	Including surface activity records for the transition from ebb to flood tide, and flood to ebb tide periods
Flood tide	Including surface activity records for strongest flood and during flood periods

Results

Throughout the 55 shore-watches conducted between June and September 1996 and 1997 a total of 399 scan samples were obtained with 529 dolphin schools being recorded. The surface activity was recorded for 96.8% of the 529 dolphin schools. The greatest number of dolphin schools were observed during the ebbing tide, in the evening period, and performing travelling surface activities (Fig 3).

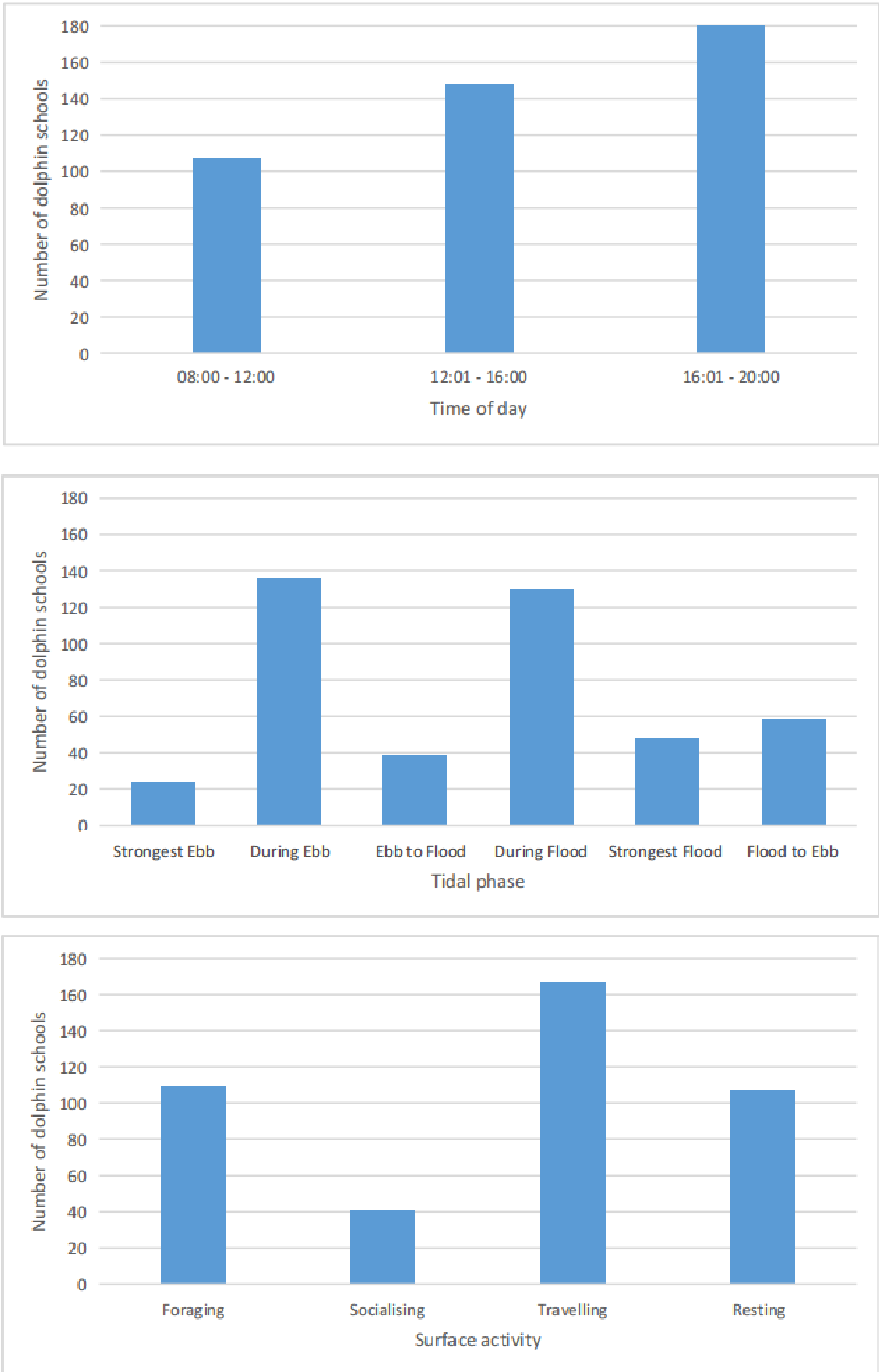

Figure 3: The distribution of observed dolphin schools in the Shannon Estuary during each time of day category, each tidal phase and performing each categorised surface activity.

Spatio-temporal changes in dolphin distribution through the estuary:
Visual analysis of all dolphin schools observed during the entirety of this study showed a spatial concentration close to Kilcredaun Point (Fig 4). Concentrations of observed dolphins were also found protruding into the estuary towards Beal Strand, as well as offshore focussing at Leck Point (see Fig 1 for locations).

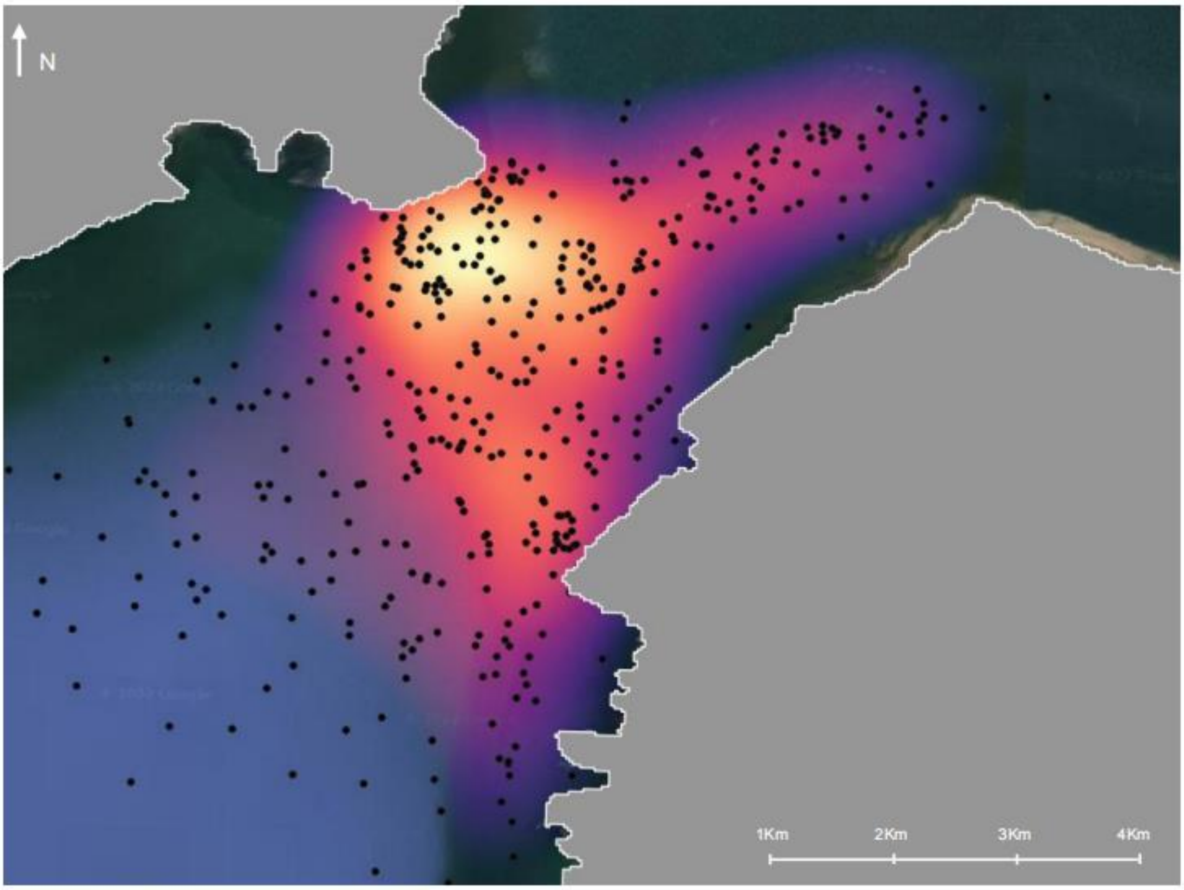

Figure 4: Kernel density plot of all observed bottlenose dolphins in the Shannon Estuary from June to September 1996 and June to September 1997. Colouring from purple to yellow indicates increasing species density and the black dots indicate individual dolphin positions. Map created using the Free and Open Source QGIS. Basemap: Googlemaps 2022.

Tidal influence on spatial distribution
During the flooding tidal phases schools showed a greater intrusion into the estuary concentrating in upper river areas close to Beal Strand. This spatial distribution was also shown during the transition from flood to ebb tide. During the ebbing tide dolphin Furthermore, during the transition from ebb to flood tide concentrations were seen to be close to Kilcredaun Point (Fig 5) (see Fig 1 for these locations).schools were observed more concentrated in outer river areas, close to Kilcredaun and Leck Point, with a reduced concentration of schools observed in upper regions.

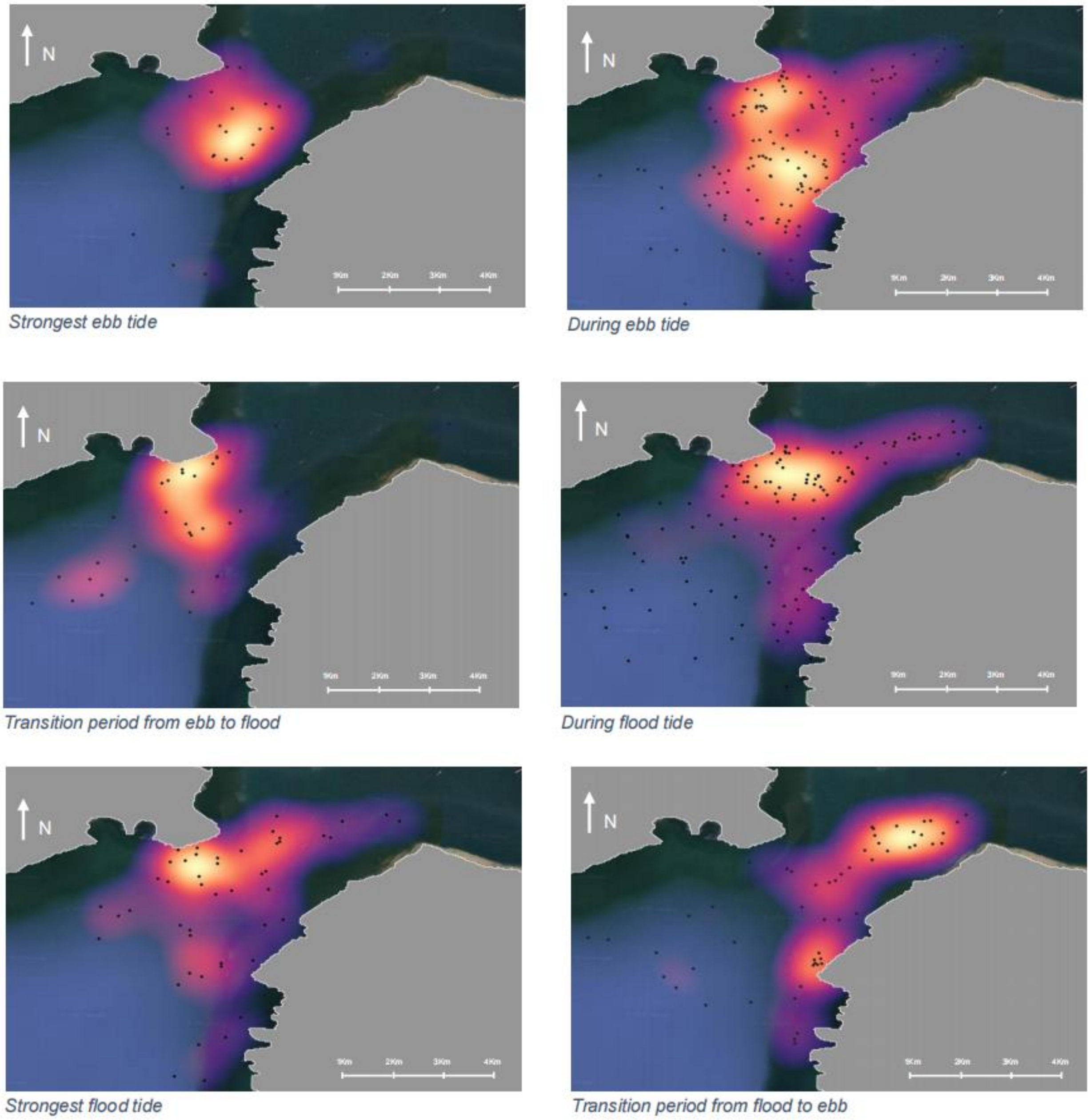

Figure 5: The spatial distribution of bottlenose dolphins in the Shannon Estuary, as represented by kernel density plots, during each tidal phase. Colouring from purple to yellow indicates increasing species density and the black dots indicate individual dolphin positions. Map created using the Free and Open Source QGIS. Basemap: Googlemaps 2022.

Influence of activity on spatial distribution:

Travelling and resting individuals were observed across the entirety of the study site with concentrations throughout the whole width of the estuary. Socialising individuals were concentrated off Kilcredaun Point and those foraging had clear aggregations at Kilcredaun Point and Beal Strand (Fig 6) (see Fig 1 for these locations).

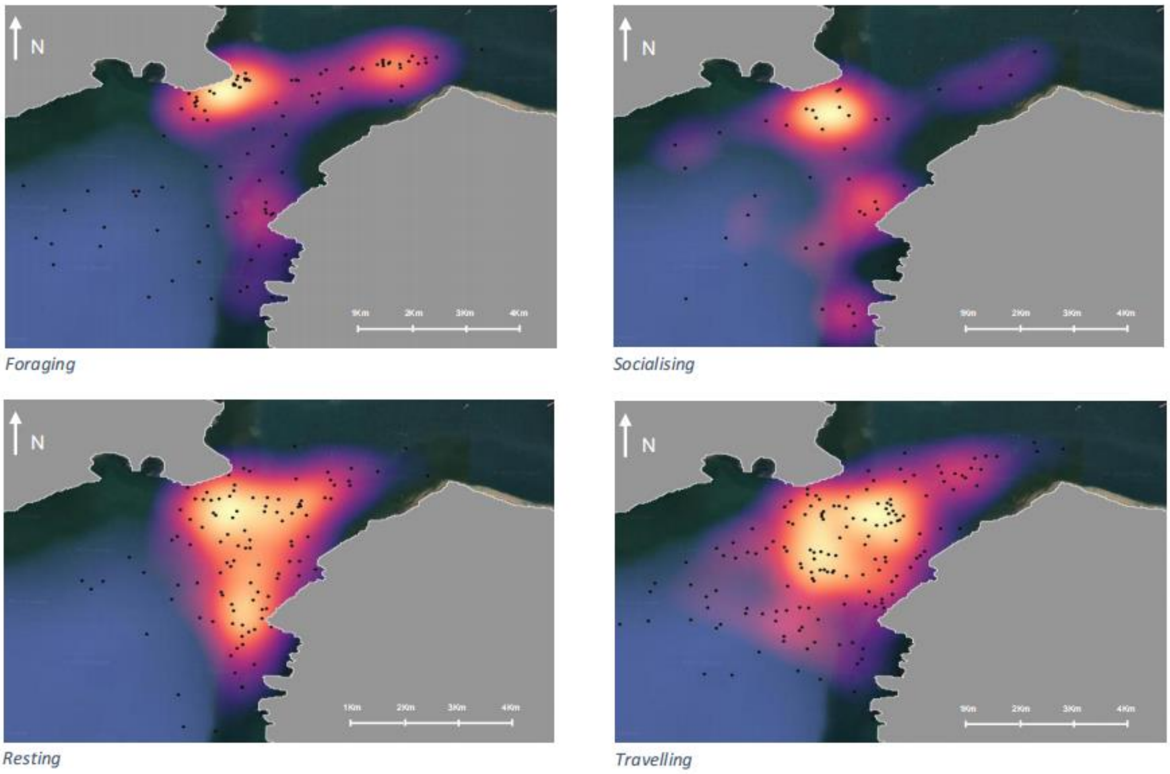

Figure 6: The spatial distribution of bottlenose dolphins in the Shannon Estuary, as represented by kernel density plots, during each performed surface activity. Colouring from purple to yellow indicates increasing species density and the black dots indicate individual dolphin positions. Map created using the Free and Open Source QGIS. Basemap: Googlemaps 2022.

Temporal influence on spatial distribution:

During the morning hours from 08:00 to 12:00 observed dolphin schools were seen to have a more offshore distribution with concentrations observed near Leck Point and downstream of Kilcredaun Point. In the afternoon, concentrations of observed schools were seen to be closely associated with Kilcredaun Point throughout a majority of the tidal cycle. Finally, the greatest upstream intrusion of observed dolphin schools was seen from 16:00 to 20:00 with concentrations moving towards Beal Strand (Fig 7) (see Fig 1 for locations).

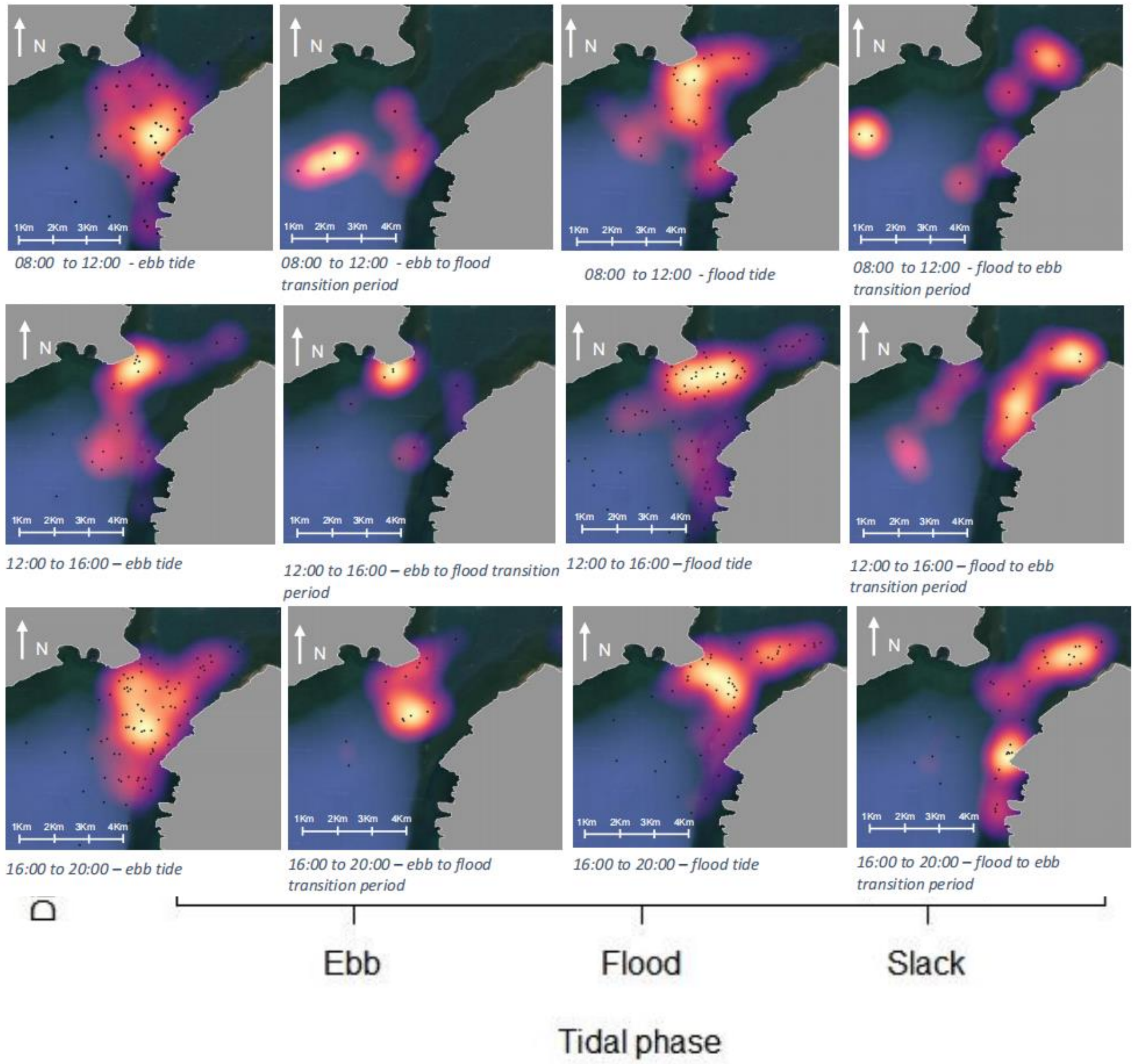

Figure 7: The temporal spatial distribution of bottlenose dolphins in the Shannon Estuary, as represented by kernel density plots. Each time of day category is further divided into each tidal phase to account for tidal influence on the spatial distribution of observed dolphin schools. Colouring from purple to yellow indicates increasing species density and the black dots indicate individual dolphin positions. Map created using the Free and Open Source QGIS. Basemap: Googlemaps 2022.

*Tidal phase*activity influence on spatial distribution*

Both tidal phase and surface activity were observed to have a significant effect on the intrusion of dolphin schools upstream relative to the centre of the mouth of the Shannon Estuary (Fig 1) (Table 1). Travelling and foraging activities during the flood tide were found to have the greatest upstream intrusion with average distances of 19.4km and 18.8km respectively. Furthermore, foraging individuals during flood tide were found to have an average greater upstream intrusion of 500m compared to those foraging during the ebbing tide (Fig 8). The interacting effect of tidal phase and activity was also found to have a significant influence on the upstream intrusion of dolphin schools (Table 1).

Figure 8: The distance upstream of observed bottlenose dolphins in the Shannon Estuary, measured from the centre of the mouth of the estuary (see Fig 1) during each performed activity (top) and each tidal phase (bottom).

Table 1: Output of a 2-way ANOVA statistical test to analyse the influence of tidal phase and bottlenose dolphin surface activity on the upstream distance of observed dolphin schools.

Dependent variable: Distance upstream					
Source of variation	Sum of squares	df	Mean squares	f	P-value
Tidal phase	4.28	2	2.14	4.64	0.11
Activity	9.66	3	3.22	6.97	<0.01
Tidal phase: Activity	9.99	6	1.67	3.60	<0.01

Tidal influence on dolphin schools

Spatial distribution of dolphin schools

Plotting of the tracks of observed dolphin schools revealed clear varying spatial use of the Shannon Estuary depending on tidal phase. During the flooding tide schools were observed in the central channel of the estuary travelling upstream (Fig 9a). Likewise, during the transition from flood to ebb tide schools were observed using the deep central channel to travel offshore in a south-westerly direction (Fig 9b). During the ebbing tide schools were observed associated with the steep topography near Kilcredaun Point, and were seen travelling inland in close proximity to the coast (Fig 9c). See appendix A for the tracks of all observed dolphin schools.

Figure 9: Tracks of dolphin schools during the flood phase of the tidal cycle (a), during the transition from flood to ebb tide (b), and during the ebb tide (c). Map created using the Free and Open Source QGIS. Basemap: Googlemaps 2022.

a) Track 19 3a. A total of 6 positions recorded over 30 minutes.

b) Track 68 4a. A total of 15 positions recorded over 15 minutes.

c) Track 80 8a. A total of 51 positions recorded over 32 minutes.

Speed of travel of observed dolphin schools

The speed of travel of dolphin schools was significantly different throughout the tidal cycle ($H(2) = 19.9$, $p < 0.05$). The lowest speed of travel occurred during the flood tide with an average school travel speed of 0.92 ms^{-1}. During slack water schools were observed to travel the fastest at average speeds of 2.33 ms^{-1} (Fig 10).

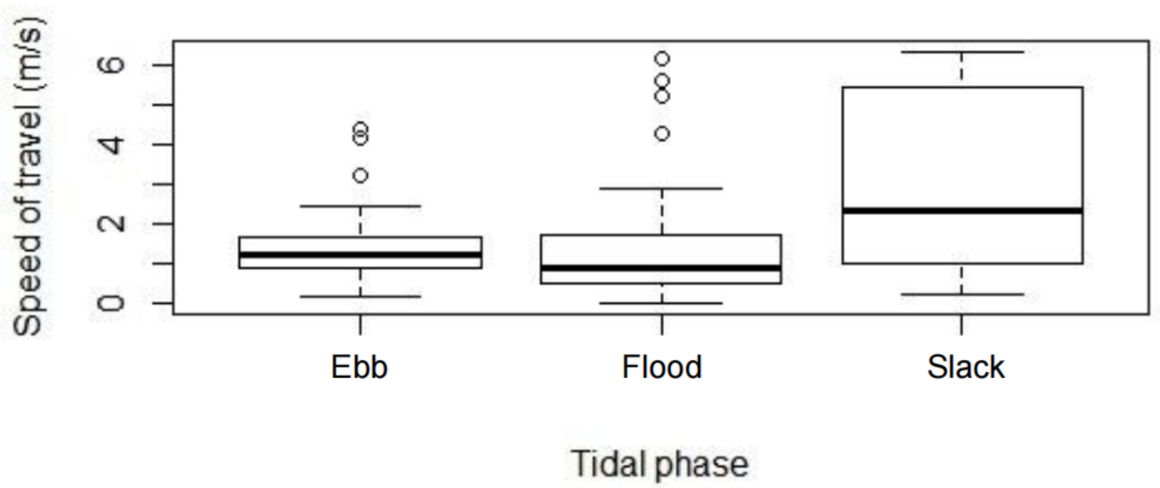

Figure 10: The speed of travel of observed dolphin schools during each tidal phase.

Tidal influence on the direction of travel of observed dolphin schools

The relationship between the direction of travel of observed dolphin schools and tidal flow was not found to be significant ($X^2 = 1.13$, df = 1, $p = 0.288$) and schools during the flooding tide were rarely seen to be travelling against tidal flow, but more commonly with or across flowing water (Fig 11 and Fig 12). Alternatively, during the ebb tide the angle of tidal flow was seen to have little influence on the direction of travel of dolphin schools, with similar frequencies of schools being observed to travel with and against the tidal flow (Fig 12). Observed dolphin schools were also shown to exhibit a tendency to travel across flowing ebb tides, most commonly in a north-westerly direction (Fig 11).

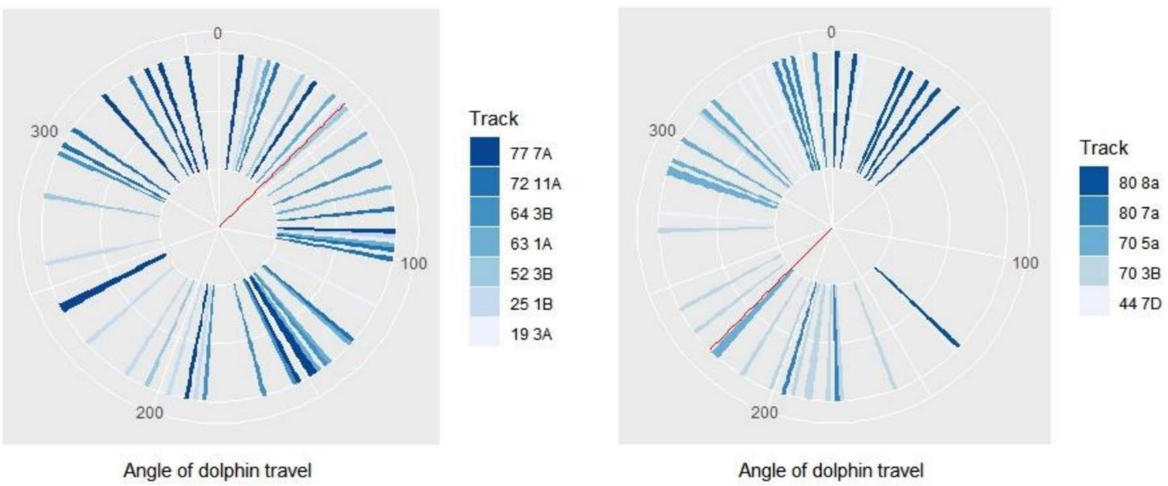

Figure 11: The angle of travel of observed dolphin schools between recorded consecutive positions during the flood (left) and ebb (right) phases of the tidal cycle. The angle of tidal flow is represented by the red line.

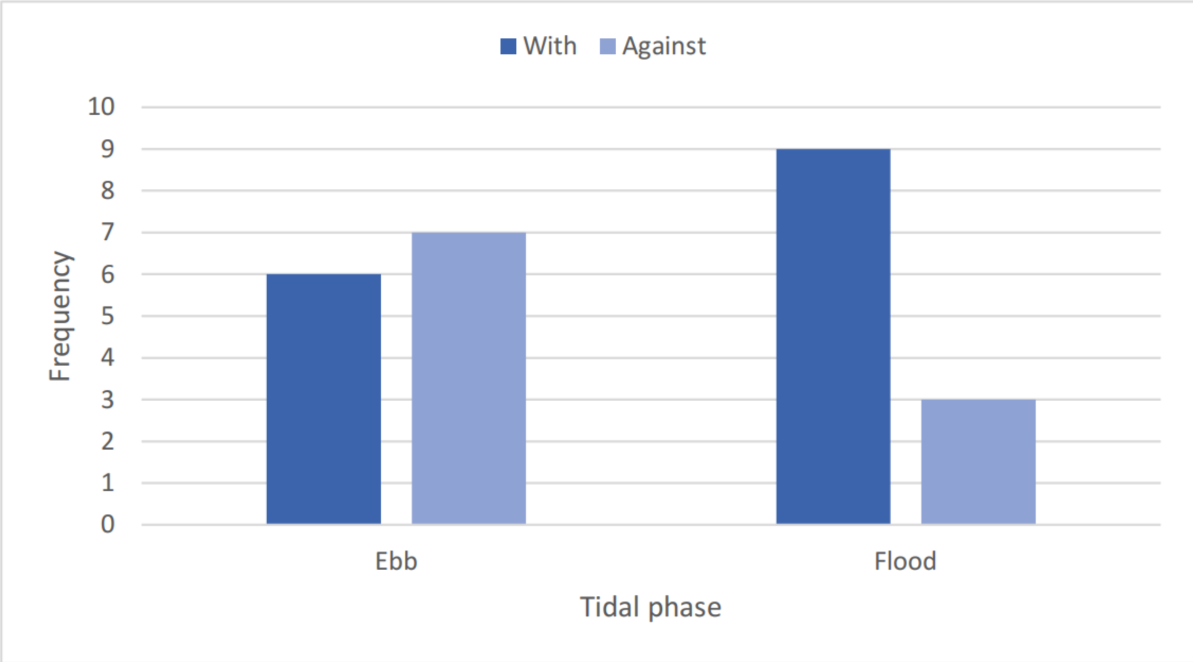

Figure 12: The frequency of observed dolphin schools in the Shannon Estuary travelling with or against flowing tidal water during the ebb and flood phases of the tidal cycle.

Diurnal and tidal influence on surface activity:

Diurnal influence on surface activity:

Resting was recorded at greater frequencies in the morning period, and during the afternoon greater foraging activities were observed. Travelling was found to be the dominant activity throughout the day and occurred greatest in the evening (Fig 13). However statistically, time of day was not found to have a significant influence on the surface activity performed by bottlenose dolphins ($X^2 = 8.28$, df = 6, p = 0.218).

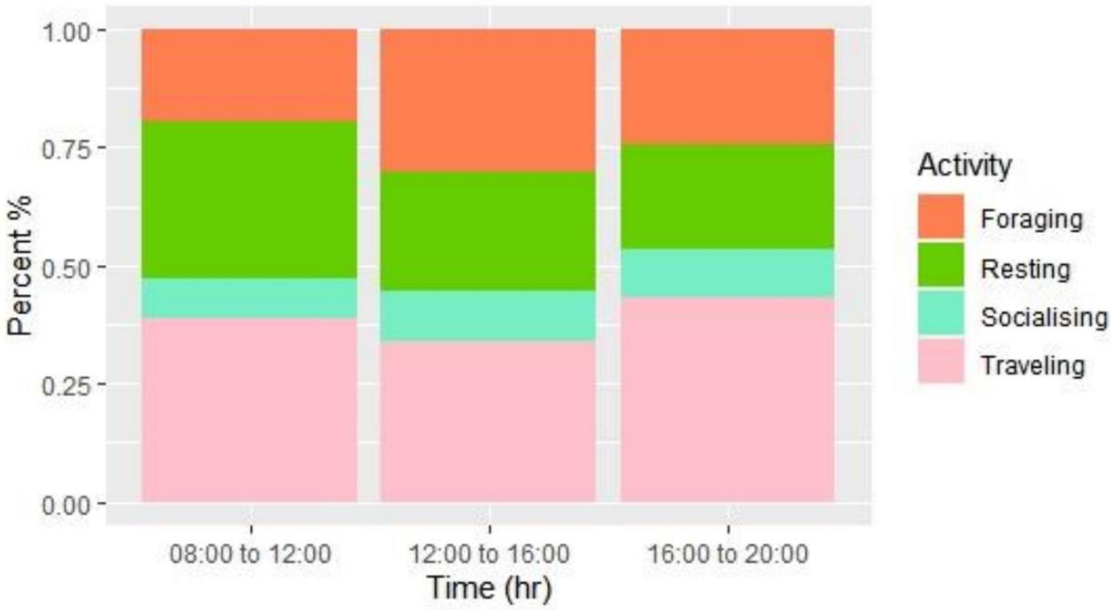

Figure 13: Distribution of the observed surface activity of dolphin schools during each time of day.

Tidal influence on surface activity
The surface activity of observed dolphin schools was found to be significantly affected by tidal phase (X^2 15.086, df=6, p <0.05). Foraging was observed most frequently during the flood tide, accounting for 34% of the activities recorded in this tidal phase, and least frequently during the ebb tide, at 17% of the recorded activities. During slack water and ebb tide travel was the dominant activity accounting for around 40% of the observed surface activities in both cases (Fig 14).

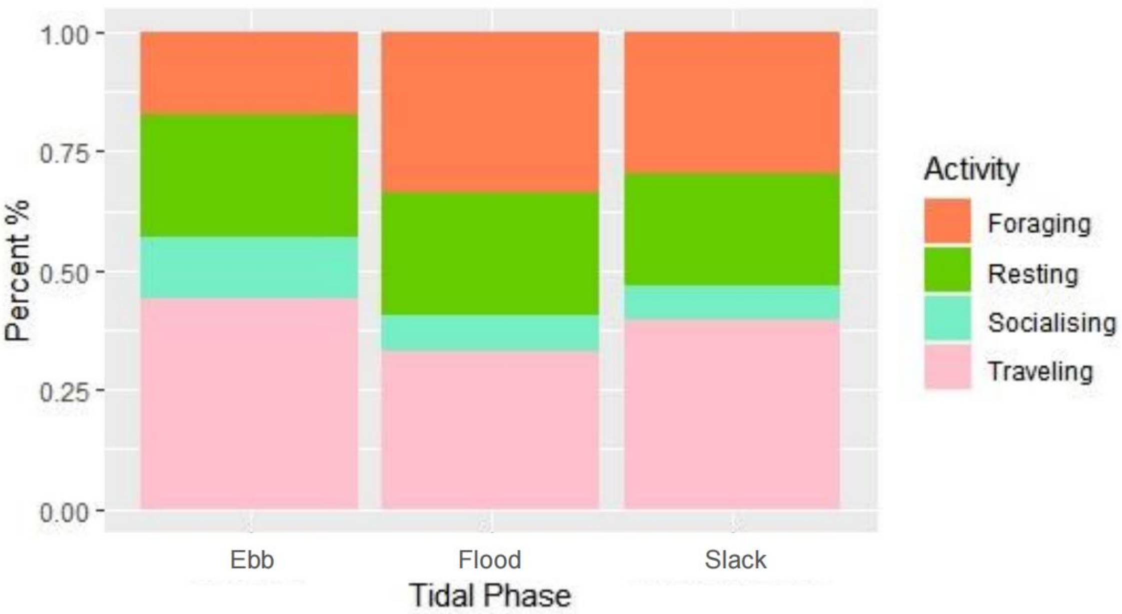

Figure 14: Distribution of the observed surface activity of dolphin schools during each phase of the tidal cycle.

Discussion

Tidal influence on spatial distribution and surface activity

This study provides a useful insight into the fine-scale physical processes that drive activity and habitat use of bottlenose dolphins in a tidally dominated system. It outlines the spatial distribution of dolphin schools across the Shannon Estuary which was determined to be significantly dependent on tide. Identification of Beal Strand as a key foraging area during flooding phases of the tidal cycle coincides with the findings of Carmen, Berrow and O'Brien (2021) who identified dolphin schools to show a greater inland intrusion during the flooding tide and considerably higher proportions of foraging activities to occur in upper areas of the Shannon Estuary. This outlines the importance of the inner estuary as a key foraging site for bottlenose dolphins.

The dynamic characteristics of estuarine systems means numerous processes could underlie the spatial distribution of prey and therefore the locations of key foraging habitats for bottlenose dolphins in this estuary. The narrow topographic channel throughout the Shannon Estuary can act as a bottleneck to the movement of fish species forcing prey into densely packed aggregations and providing the resident dolphins with a predictable foraging resource during flowing flood tides (Bailey and Thompson, 2010). Similarly, the resident dolphins likely utilise regions of steep sided channel during the ebbing tide due to the associated increased foraging opportunities as prey species advect out of the estuary (Cox 2016). The foraging efficiency of the Shannon Estuary's bottlenose dolphins is also thought to be further enhanced by the formation of a hydrographic front (Cox, 2016). This front has associated upwelling and downwelling features found to further herd prey species into dense aggregations exploited by the resident population of bottlenose dolphins (Cox, 2016; Cotté and Simard, 2005). The critical areas of observed high concentrations of foraging schools around Kilcredaun Point and Beal Strand during ebb and flood tides respectively, as identified in this study and others, therefore likely occur due to the interaction between tidal flow and the steep topography in these locations (Cox, 2016; Ingram, 2000).

Diurnal influence on spatial distribution and surface activity
The spatio-temporal variations in bottlenose dolphin distribution throughout the Shannon Estuary point to concentrated uses of areas in close proximity to Leck Point, Kilcredaun Point and Beal Strand during morning, afternoon, and evening periods respectively. This is opposed to the findings of previous studies in the Shannon Estuary and Cardigan Bay, with diurnal influence being observed to have no effect on bottlenose dolphin spatial distribution (Gregory and Rowden, 2001; Ingram, 2000). The dolphins use of particular regions of the estuary in relation to time of day could be related to their surface activity (Daura-Jorge et al., 2005). With foraging activities occurring most frequently in the afternoon and evening periods, and these activities being observed to correlate with a more upstream distribution of dolphins, the observed upstream intrusion towards Beal Strand during the evening could be observed as a result of schools undertaking foraging activities during this period. However, despite a greater frequency of foraging activities being recorded in the afternoon and evening periods during this study, the overall relationship between time of day and the surface activity performed by bottlenose dolphins was not found to be significant. This is notable, as it compares well with results found during studies in Cardigan Bay (Gregory and Rowden, 2001). In contrast, these results are opposed to findings found previously in the Shannon Estuary where the relationship between time of day and surface activity was concluded to be significant, with foraging occurring most frequently in the morning period (Carmen, Berrow and O'Brien, 2021).

Tidal influence on the direction of travel of dolphin schools
Analysis of the tracks of dolphin schools revealed schools to utilise the tidal currents of the Shannon Estuary, travelling to the identified key foraging areas during flood and ebb tides, where tidal flow and topography interact to create favourable foraging conditions (Cox, 2016). Furthermore, during the flooding tide schools were more frequently observed to travel with the tidal current than against, and in comparison, during the ebbing tide a higher frequency of schools were observed moving against tidal currents. These results are similar to those reported by Irvine et al. (1981). As estuarine systems are energetically expensive for bottlenose dolphins to inhabit, minimising their energy expenditure by avoiding countercurrent travelling can be a behavioural strategy to conserve energy (Cox, 2016). However, despite the above findings, overall the direction of tidal flow through the Shannon Estuary did not have a significant effect on the direction of travel of observed dolphin schools. This result has similarly been concluded in the Gulf of Guayaquil, Ecuador, the Sado Estuary, Portugal and the Indian and Banana Rivers, Florida (Felix, 1995; Leatherwood, 1979; Santos and Lacerda, 1987).

Furthermore, a clear conclusion regarding the relationships between foraging activity, and the direction of travel of observed dolphin schools relative to tidal flow cannot be drawn from the findings of this study. The recorded higher frequency of foraging activity and greater concentration of dolphin schools in upper regions of the

Shannon Estuary during flooding tides corresponds closely with the findings of Carmen, Berrow and O'Brien (2021). However, the absence of evidence of dolphin schools to swim into flowing flood water does not support the observed increase in foraging activities during flood tide as encounters with prey species will not be maximised in this scenario (Sims et al., 2006). In contrast, the clear concentrations of dolphin schools situated off Kilcredaun Point during ebbing tides, as well as the increased frequency of dolphin schools to be observed swimming against flowing ebb water would provide the species with optimum foraging conditions and maximised prey encounters (Sims et al., 2006). The steep topography off Kilcredaun Point can aid in the formation of dense prey aggregations exploited by dolphin schools swimming into the ebbing tide and feeding on the rich foraging resource as prey species advect out of the estuary (Cox, 2016; Cotté and Simard, 2005). However despite this, foraging was recorded least frequently during this phase of the tidal cycle.

The contrasting drivers behind bottlenose dolphin foraging activity may likely be due to a simplification of the calculation of tidal angle used within this report and the issues that occur with defining surface activity. Visualisation of the central channel of the Shannon Estuary shows a right angled bend in topography in this region, and the curvature in the profile of the channel likely causes tidal flow to undergo this angular change also (Jay, 1991). Therefore, the crude method of defining tidal angle with a straight line through the study area was likely a vast oversimplification. To better understand the tidal characteristics throughout this estuary, as well as its relationship with resident species, a full tidal model with more precise tidal direction vectors would be required. However, this was beyond the scope of this study. In terms of surface activity categorisation, the methods implemented throughout this study did not allow for the observation of subsurface activities. In cases where defining surface behaviours were absent schools were recorded as travelling but may have been engaging in other activities such as foraging or socialising. Therefore, implementing methods to survey the subsurface behaviour of dolphin schools may alter activity classifications in future studies.

The use of passive acoustic techniques and multibeam sonar could be used to correlate sea surface activities and acoustic data, as well as provide real-time images of individuals, used to further increase the understanding of bottlenose dolphin behaviour (Janik, 2000; Ridoux et al., 2006). Furthermore, inaccuracies surrounding the determination of school position, as derived from the theodolite methods, likely occurred. A computer system was not used for data input within this study increasing the risk of transcription errors. Furthermore, due to the curvature of the earth angular errors were likely to be introduced alongside changes in tidal hight across the region (Piwetz et al., 2018).

Implications to conservation and management

Identification of the mouth of the Shannon Estuary as an important area for bottlenose dolphins in this report and others (Acevedo, 1991; Ballance, 1992; Shane, Wells, and Würsig, 1986) underlines the need for the careful habitat protection of this species. Identification of Kilcredaun Point and Beal Strand as key foraging areas is likely to increase the potential for disturbance to these species by dolphin watching boat touring operations which target areas of highest dolphin site use for more sightings. This should be considered within the management of the Shannon Estuary SAC, as well as the effects of future marine renewable energy instillations (MREIs) now the estuary has been identified as a potential site for MREIs (O'Rourke, Boyle, and Reynolds, 2010). MREIs have been identified to impact the current regimes of estuarine systems which could impact the identified critical habitat areas of these dolphins having implications to their ecology (Shields et al, 2011). Therefore, understanding the drivers of the spatial and temporal distribution of bottlenose dolphins in this area is required for the appropriate continued and future conservation of this species.

Conclusion

This study shows that the spatial distribution and behaviour of bottlenose dolphins in the Shannon Estuary is significantly dependent on the tidal cycle. The inner estuary was identified as a key foraging site with tidal and topographic interactions driving the formation of dense prey aggregations. These are known to be exploited by the resident bottlenose dolphin population for a predictable prey resource. The Shannon Estuary's bottlenose dolphins were observed to concentrate in specific regions within the estuary at certain times of the day. However, this may have been related to their surface activity and it is difficult to determine with the utmost certainty the diurnal influences driving bottlenose dolphin spatial distribution due to alternative variables that may have an influence. In dynamic environments such as estuarine systems, numerous processes are likely to influence the behaviour and habitat use of bottlenose dolphins and therefore consideration must be given to all processes that influence these species within these dynamic systems. Future studies should use a full tidal model with more precise tidal direction vectors to better understand the tidal characteristics throughout this estuary as well as consider the use of passive acoustic techniques and multibeam sonar to further increase the understanding of bottlenose dolphin behaviour and account for subsurface activities. This study outlines the clear importance for the protection of the mouth of the Shannon Estuary as it is a key foraging site for this population of bottlenose dolphins. Though in a world of ever-increasing threats to our marine environment further monitoring of the species in this area is required for their effective future conservation.

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