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ABSTRACT

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Temporal variations in the numbers of foraging seabirds usually coincide with concurrent variations in physical processes influencing prey availability. Responses to periodic tidal currents are commonly reported, with certain tidal states being favoured. By contrast, responses to intermittent meteorological events have rarely been reported, even though winddriven exchanges of water masses or intrusion of estuarine plumes could have similar consequences. As large-scale offshore constructions (e.g. aquaculture, coastal defences, ports and marine renewable energy installations) and climate variations alter periodic tidal currents and intermittent meteorological events, respectively, quantifying responses to these physical processes identifies potential impacts on seabird communities. This study quantifies responses of foraging seabirds to physical processes in the Ria de Vigo, north-western Spain. The numbers of foraging European Shags *Phalacrocorax aristotellis* and Yellow-legged Gulls *Larus michahellis* showed no response to variations in current direction and speed. By contrast, both increased in number during an estuarine plume intrusion (the Western Iberian Buoyant Plume: WIBP) following an extreme river discharge event and southerly winds. These increases may be explained by the temporary combination of marine and brackishwater fauna, increasing prey biomass. The frequency of extreme river discharge events is likely to decrease in north-western Spain. If WIBP intrusions consistently enhance prey availability, observations of large numbers of foraging seabirds using the ria could become rarer.

Key Words: estuarine plume, foraging ecology, European Shag, *Larus michahellis, Phalacrocorax aristotellis,* vessel-based surveys, Yellow-legged Gull

INTRODUCTION

For foraging seabirds, coastal environments represent important habitats due to physical processes that enhance prey availability (Cox *et al.* 2018). However, numerous physical processes in coastal environments are susceptible to anthropogenic-driven changes. Largescale offshore constructions (e.g. aquaculture, coastal defences, ports and marine renewable energy installations; Carter 2013) alter tidal currents (Cazenave *et al.* 2016, De Dominicis *et al*. 2017, Fraser *et al*. 2017, Shields *et al.* 2011) whereas climate change and oscillations (e.g. North Atlantic Oscillation, El Nino Southern Oscillation) alter meteorological events (Stenseth *et al.* 2003, Harley *et al.* 2006). Identifying the responses of foraging seabirds to tidal currents and meteorological events in coastal environments would highlight potential impacts of anthropogenic-driven changes.

In coastal environments, periodic changes in the direction/speed of tidal currents and depth across ebb-flood cycles are a conspicuous physical process (Simpson *et al.* 2012). These changes influence prey availability. For seabirds targeting pelagic prey, a certain current direction or speed could advect prey from productive neighbouring areas, increasing encounters with prey (Zamon 2001). In other cases, certain combinations of current direction/speed and topography create turbulent eddies and shear-lines, entraining and aggregating prey (Johnston *et al.* 2007). For seabirds targeting benthic prey, the energetic cost of dives is reduced at slow current speeds and shallow depths, increasing the accessibility of prey (Heath *et al.* 2010). Studies showing the number of foraging seabirds increasing during certain tidal states are numerous and widespread (Hunt *et al.* 1999, Benjamins *et al.* 2015; Waggitt *et al.* 2016a, 2016b).

In some coastal environments however, meteorological events (e.g. extreme river discharge or intense wind) also represent important physical processes. Estuarine plumes following extreme river discharge events alter salinity and temperature (Gillanders *et al.* 2002), whereas exchanges of water masses during intense wind events have similar effects (Kämpf *et al.* 2016). As with tidal currents, these meteorological events could also influence prey availability. For instance, onshore advection of productive water masses encourage prey to form denser schools (Benoit-Bird *et al.* 2019). Estuarine plumes encourage brackish-water species into the open-ocean, increasing prey biomass (Kingsford *et al.* 1994). The frequency of these meteorological events is usually seasonal, with the highest numbers of foraging seabirds seen when favourable meteorological events are most likely (Cox *et al.* 2018). However, the timing of individual meteorological events within seasons are intermittent and unpredictable. Studies showing changes in the number of foraging seabirds during an intermittent meteorological event are scarce (Cox *et al.* 2018).

This study compares responses of foraging seabirds to periodic tidal currents and an intermittent meteorological event in the Ria de Vigo, north-western Spain (42° 15' 04" N, 8° 53' 30" W) (Fig.1). During the study, an estuarine plume (the Western Iberian Buoyant Plume, WIBP; Sousa *et al.* 2014) originating from the Minho Estuary (Fig.1) entered the ria, following an extreme river discharge event and southerly winds. In the same area, tidal currents flow through a narrow (2.8 km) and shallow (~25 m) channel (Fig.1), causing periodic variation in their direction/speed. This study uses the co-occurrence of these tidal currents and the WIBP intrusion to ask whether: (1) temporal changes in the number of foraging seabirds are correlated to these physical processes, (2) the strength of correlations are greater for physical processes associated with tidal currents or the WIBP intrusion?

METHODS

Study Area

This study was conducted on seven days between 4 and 15 June 2018. This period coincided with the breeding seasons of the dominant seabird species in the ria: European Shag *Phalacrocorax aristotellis* and Yellow-legged Gull *Larus michahellis*. The study area covered approximately 48 km^2 in the northern ria (Fig.1). The latter encompasses sand-banks known to be exploited by shags and gulls feeding predominantly on sandeel *Ammodytidae* (Velando *et al.* 1999) and Henslow's swimming crab *Polybius henslowii* (Munilla 1997), respectively. The recording of temporal variations in the numbers of foraging seabirds and physical processes occurred exclusively within the study area.

Seabird Abundance

A single observer recorded temporal variation in the number of foraging seabirds during 40 zig-zag transects of approximately 10.3 km in length (Fig. 1). Transects were performed from a rigid inflatable boat moving at an average speed of 14 kt (11.2 – 17 kt), and lasted an average of 23 min (19 – 30 min). The numbers of transects were spread relatively evenly between ebb (n = 19) and flood (n = 21) tides. Throughout the transects, the observer followed European Seabirds At Sea (ESAS) methodology (Tasker *et al.* 1984). However, the observer was only 1 m above sea-surface. To ensure that the observer recorded representative numbers of animals, transects were only performed when the sea state was less than Beaufort

Scale 3. Nevertheless, estimations of sea state were recorded at the start of each transect to account for possible changes in the detectability of animals during rough weather (Camphuysen *et al.* 2004). These estimations represented a mean across the study area, and included non-integer values if there were spatial variations in weather conditions. Animals seen diving, dip-feeding and searching were considered as foraging seabirds (Camphuysen *et al.* 2012). As transects were performed away from breeding colonies, animals sitting on the sea-surface were likely resting between foraging bouts rather than alongside nests (Waggitt *et al.* 2016a, 2016b), and were also considered as foraging seabirds. Yellow-legged Gulls seen scavenging around fishing vessels were not considered as foraging seabirds (Valeiras 2003).

Physical Processes

Periodic tidal currents were quantified using outputs from an existing Finite Volume Community Ocean Model (FVCOM) (Chen *et al.* 2003) developed for the ria. Outputs were available at 15 min and approximately 100 m resolution. Mean depth averaged speed would summarise general conditions over the study area, whereas maximum or surface speeds may detect the presence or absence of strong hydrodynamic features at certain locations (Benjamins *et al*. 2015). Analyses was concerned with variations in the number of foraging seabirds across the study area, rather than associations between foraging seabirds and strong hydrodynamic features (e.g. Waggitt *et al.* 2016a). Therefore, for each transect, periodic tidal currents were represented by the mean depth averaged speed ($m\ s^{-1}$) across the study area at the start of observations (Supplementary Material, S1). To discriminate between current directions, currents from the north were converted into negative values. Therefore, negative values show ebb currents, and positive values represent flood currents.

The WIBP intrusion was quantified using outputs from an existing Nucleus for European Modelling of the Ocean (NEMO) model (Madec 2008) developed for the Iberian region (Sotillo *et al.* 2015) (http://marine.copernicus.eu). Outputs were available at daily and 7 km resolution. For each transect, the influence of the WIBP was represented by the mean salinity (ppt) across the study area on the day of observations (Sousa *et al.* 2014). The arrival and departure of the WIBP intrusion in the study area would be identified by decreasing and increasing salinities, respectively. Data processing was performed in the ‘raster’ package (Hijmans 2013) in R (version 3.5.1, R Development Core Team 2018).

Statistical Analysis

Generalised Additive Models (GAMs) identified and quantified correlations between the number of foraging seabirds and physical processes (Wood 2006). A negative binomial distribution was used to account for overdispersion in the number of seabirds. The response variable was the number of foraging seabirds seen per transect. The explanatory variables were the corresponding measurements of depth averaged current speed, salinity and sea state. Salinity and sea state were modelled as continuous and linear variables. Whilst sea state is sometimes modelled as a categorical variable, a general decrease in detectability with increasing sea state was expected, making a linear variable more appropriate. Depth averaged current speed was modelled as a continuous and non-linear variable, with the number of knots fixed at 3. This setup allowed relationships with maximum speed, maximum speed in a particular direction (south or north), and slack water to be detected. Salinity was modelled as a continuous and linear variable. Sea state was included to account for possible decreases in the detectability of foraging seabirds in rough weather (Camphuysen *et al*. 2004). GAM were constructed using the ‘mgcv’ package (Wood 2006) in R.

Backwards model-selection based on *p*-values was performed (Zuur *et al.* 2009). Residuals from resultant models showed no evidence of temporal autocorrelation (Supplementary Material S2). Predicted variances in the number of foraging seabirds across gradients in physical processes were calculated from model parameters. In these calculations, the physical process of interest was varied between its minimum and maximum value, whilst other physical processes were held at their mean values. The magnitude and strength of relationships between numbers of foraging seabirds and physical processes were quantified using proportional differences (*Pd*). *Pd* represented the absolute difference between the maximum and minimum predicted values divided by the minimum predicted value, allowing direct comparisons between physical processes (Waggitt *et al.* 2017, 2018). Model selection and prediction were performed using the ‘mgcv’ package in R.

RESULTS

The WIBP intrusion originated from the Minho estuary following an extreme river discharge event on June 6. Southerly winds (see https://www.meteogalicia.gal) then advected the WIBP towards the study site between 7 and 9 June (Fig. 2). Decreasing salinities indicated the arrival of the WIBP on June 10, with increasing salinities indicating its dispersal on June 12 (Fig. 3). Periodic tidal currents were considerably faster when flowing from the north than from the south, with rapid changes in direction seen at slack water (Fig. 3).

The mean daily count of foraging European Shags peaked at 64.8 on 11 June, coinciding with the WIBP intrusion (Fig.3). The highest count in one transect on 11 June was 100 animals. On the remaining six days, the daily mean count was considerably lower. However, counts were generally higher before 11 June (lowest = 15.3, highest = 22.6) than after (lowest = 4.7, highest = 16.5) (Fig.3). The decrease after 11 June coincided with higher occurrence of rough weather; 71% of transects experienced sea states greater than Beaufort Scale 1.5. Accordingly, European Shags showed negative relationships with salinity and sea state (Fig.4). No relationships were found with depth averaged current speed. When accounting for the effect of sea state, *Pd* values indicated that (on average) 3.6 times more European Shags were encountered during WIBP intrusions than typical scenarios (Fig.4).

The daily mean count of foraging Yellow-legged Gulls also peaked on 11 June (56.3), again coinciding with the WIBP intrusion (Fig.3). The highest count in one transect on 11 June was 94 animals. Daily mean counts after 11 June were comparable to those during the plume event (lowest = 34.3, highest = 44.6); those before were considerably lower (lowest = 9.0, highest = 16.5) (Fig.3). The former coincided with higher numbers of transects being performed in rough weather (see above) (Fig.3). Accordingly, Yellow-legged Gulls showed negative relationships with salinity, and positive relationships with sea state (Fig.4). No relationships were found with depth averaged current speed. When accounting for the effect of sea state, *Pd* values indicated that (on average) 4.2 times more Yellow-legged Gulls were encountered during WIBP intrusions than typical scenarios (Fig.4).

DISCUSSION

This study quantified the influence of periodic tidal currents and an intermittent meteorological event on the number of foraging seabirds in the Ria de Vigo in north-western Spain. Foraging European Shags and Yellow-legged Gulls showed no responses to periodic tidal currents. By contrast, numbers of both species increased during a WIBP intrusion on 11 June. The numbers of foraging seabirds were also correlated to measurements of sea state.

The discussion focusses on responses of foraging seabirds to periodic tidal currents, intermittent meteorological events, and comparisons between these physical processes. The potential impacts from anthropogenic-driven changes within the ria are also discussed.

Periodic Tidal Currents

Increases in the numbers of foraging seabirds during certain tidal states are commonplace in areas of both strong (> 1 m s^{-1}) (Benjamins *et al.* 2015) and weak currents (< 0.5 m s^{-1}) (Embling *et al.* 2012, Scott *et al.* 2013). The absence of responses to periodic tidal currents in the ria suggests that the amount of prey advected from surrounding areas is consistent across tidal states and/or turbulent eddies and shear-lines emerging during certain tidal states do not increase prey availability. Alternatively, limited numbers of surveys across different tidal states and/or strong responses of foraging seabirds to the WIBP intrusion could prevent responses to periodic tidal currents being detected. Extending studies over longer periods could investigate these possibilities further by increasing the number of surveys performed across different tidal states and outside WIBP intrusions. In any case, this study shows that strong tidal patterns in numbers of foraging seabirds cannot be assumed in coastal environments, even though they represent a conspicuous physical process.

Intermittent Metrological Events

Increased numbers of foraging seabirds in areas and seasons of persistent estuarine plumes are commonly reported (Cox *et al.* 2018). However, evidence of responses to an individual estuarine plume intrusion are scarce (Cox *et al.* 2018). As with previous examples, increases in the numbers of foraging seabirds during the WIBP intrusion are presumably explained by higher prey biomass. Local Yellow-legged Gulls forage primarily on Henslow's swimming crab (Munilla 1997). This detritivorous crab benefits from terrestrial-matter entering the water column (Vinagre *et al.* 2012), and observers noted Yellow-legged Gulls catching swarming crabs at the water surface. Whilst local European Shags forage consistently on sandeel, they sometimes exploit sand smelt *Atherina presbyter* in large numbers (Velando *et al.* 1999). This brackish-water fish (Wheeler 1969) is locally abundant, and it is speculated that European Shags exploited schools moving into the ria. However, whilst WIBP intrusions are commonplace in the ria (Des *et al.* 2019), studies over longer periods are needed to determine if responses occur during all WIBP intrusions.

Sea state is usually included in analyses to account for decreased detectability of animals during rough weather (Camphuysen *et al.* 2004). As expected, observers detected fewer European Shag in higher measurements of sea state. However, they detected more Yellowlegged Gull under the same circumstances. This could still indicate variation in detectability. The authors observed that Yellow-legged Gulls became restless during rough seas, and the tendency to take-off and land frequently could increase their detectability. However, it could also indicate differences in behaviour. European Shags detect and capture prey on the seabed using pursuit-dives. Therefore, European Shags may remain onshore during rough weather due to increased dive costs (Daunt *et al.* 2006, Lewis *et al.* 2015). By contrast, Yellow-legged Gulls detect and capture prey at the sea surface using dip-feeding or pecking. Animals could benefit from rough weather due to decreased flight costs (Haney *et al.* 1994) and resuspension of sub-surface material (Simpson *et al.* 2012). Therefore, relationships with sea state could be explained by both detectability and behaviour.

Comparisons

Periodic tidal currents are known to influence prey availability, initiating responses by foraging seabirds (Hunt *et al.* 1999, Benjamins *et al.* 2015) . However, this study shows that an intermittent meteorological event can cause stronger responses in some circumstances. These two processes almost certainly function synergistically, with numbers of foraging seabirds responding to the resultant conditions. Nevertheless, the relative influence of periodic tidal currents and intermittent meteorological events may relate to their control on conditions at a location. For instance, foraging Black-legged Kittiwakes *Rissa tridactyla* showed a greater response to periodic tidal currents in locations where current speeds were stronger (Trevail *et al.* 2019). Whilst the speed of periodic tidal currents cannot be considered weak in the ria, intermittent meteorological events have a much greater control on conditions in this area (Arıstegui *et al.* 2006). This study suggests that the dynamics of foraging seabirds are intrinsically linked to that of the dominant process at a location.

Anthropogenic Impacts

The frequency of extreme river discharge events is likely to decrease in north-western Spain

(Cardosa Pereira *et al.* 2019). Studies over longer periods are needed to investigate responses to periodic tidal currents better, and whether responses to WIBP intrusions are commonplace. However, if WIBP intrusions consistently enhance prey availability, then observations of large numbers of foraging seabirds using the ria could become rarer. Moreover, if animals breeding/roosting in the ria depend on occasional WIBP intrusions for their subsistence, they could suffer from decreased prey encounters and increased searching efforts. This study shows that investigating responses to periodic tidal currents and intermittent meteorological events identifies potential impacts from anthropogenic-driven changes in coastal environments.

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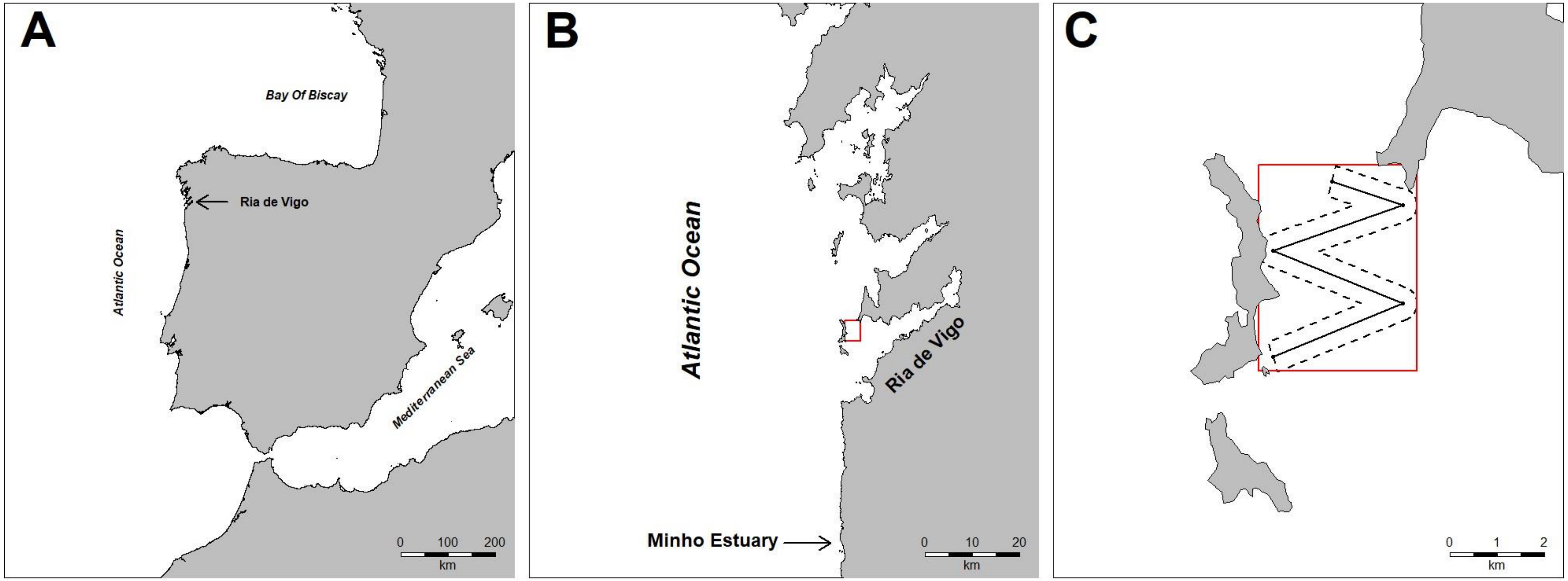

Fig 1: (A) The location of the Ria de Vigo in north-western Spain, (B) the area surrounding the ria, and (C) the zig-zag transects (solid black line) and observation area (dashed line) used to count numbers of foraging seabirds. The study area is shown by a red box.

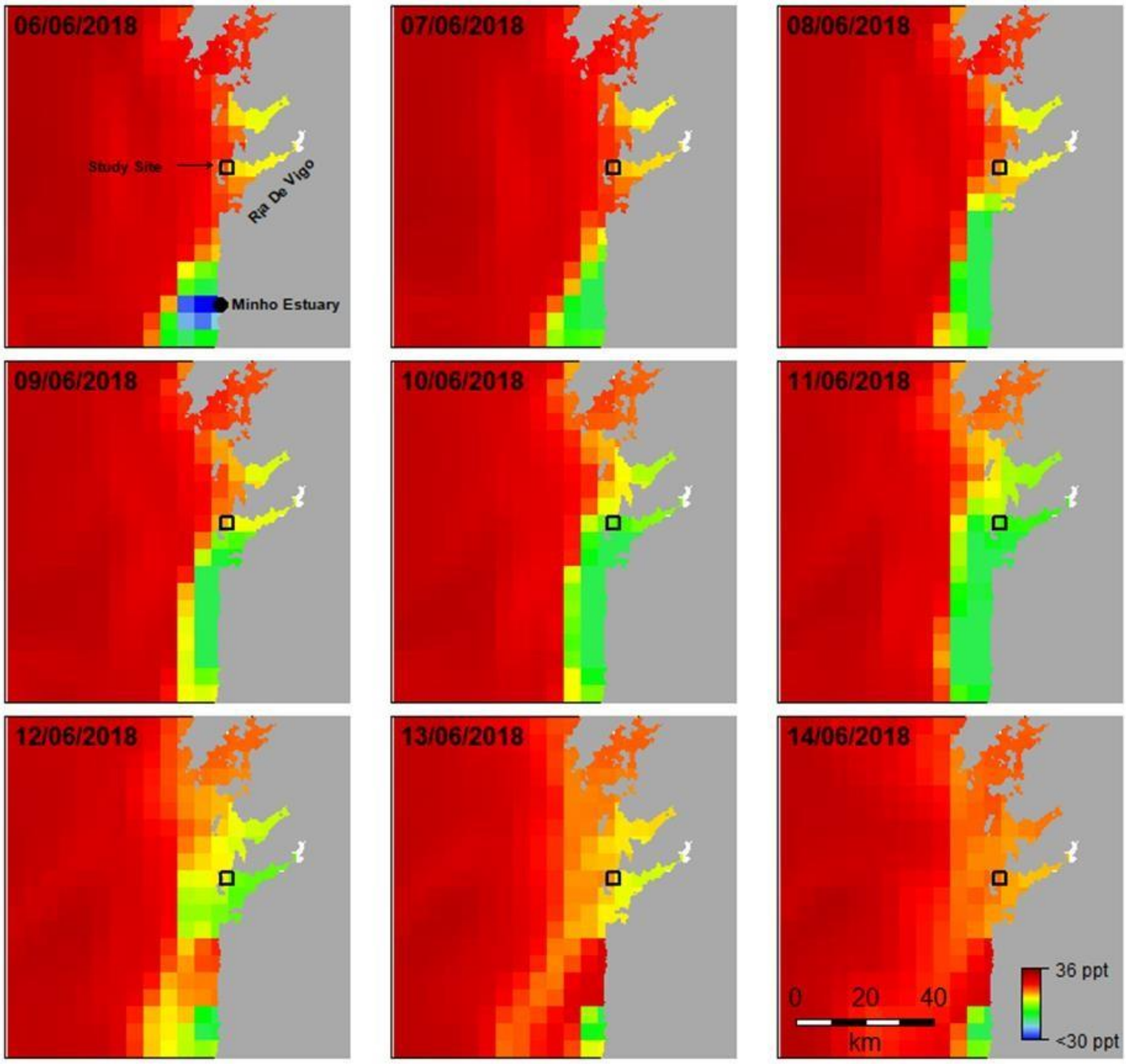

Fig 2: Variations in salinity between 6 and 14 June 2018 in the Ria de Vigo and the area surrounding the ria in north-western Spain. Values were sourced from an existing Nucleus for European Modelling of the Ocean (NEMO) model (Madec 2008) developed for the Iberian region (Sotillo *et al*. 2015). The study area is shown by a black box.

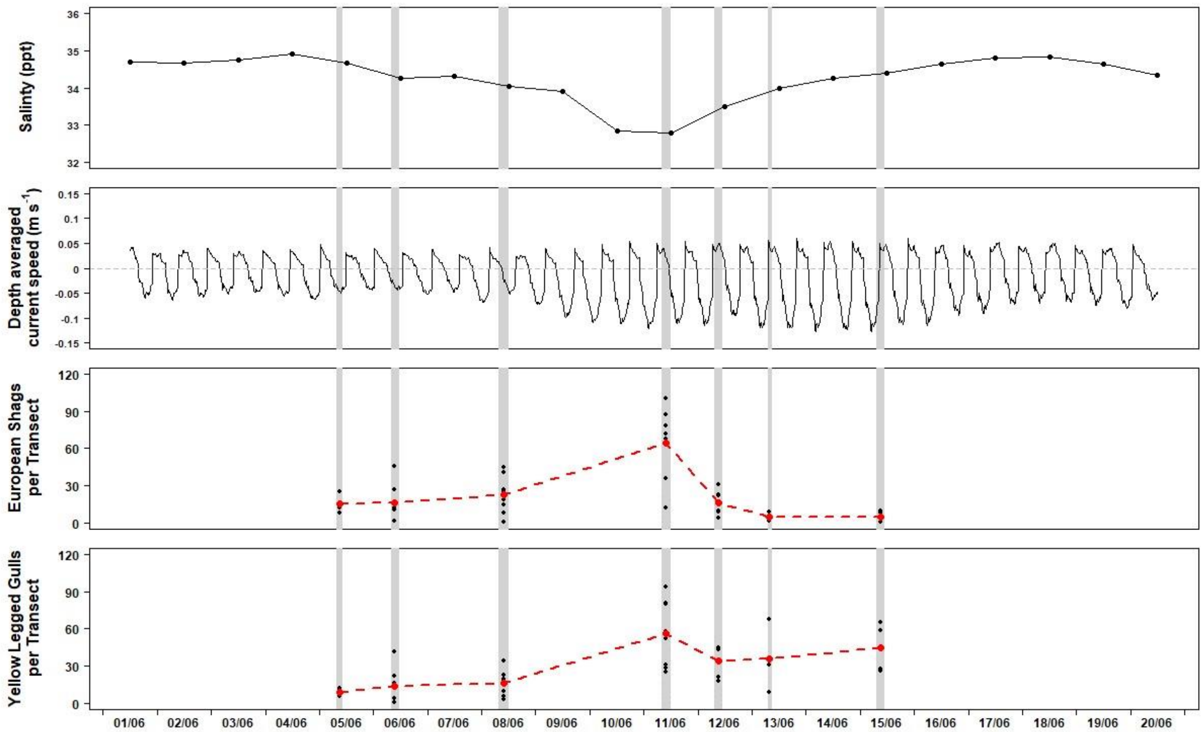

Fig 3: Temporal variations in salinity (ppt), depth-averaged tidal current speed (m s^{-1}) and numbers of foraging seabirds during June 2018 in the Ria de Vigo, north-western Spain. Values of salinity were sourced from an existing Nucleus for European Modelling of the Ocean (NEMO) model (Madec 2008) developed for the Iberian region (Sotillo *et al.* 2015). Values of depth-averaged tidal current speeds were sourced from an existing FVCOM (Chen *et al.* 2003) developed for the ria. Negative values of depth-averaged tidal current speed represent flows from the north, whereas positive values represent flows from the south. Grey bars indicate times of zig-zag transects recording the numbers of foraging seabirds. Black points represent individual counts of foraging seabirds from zig-zag transects. Red points and lines illustrate daily mean counts of foraging seabirds among zig-zag transects.

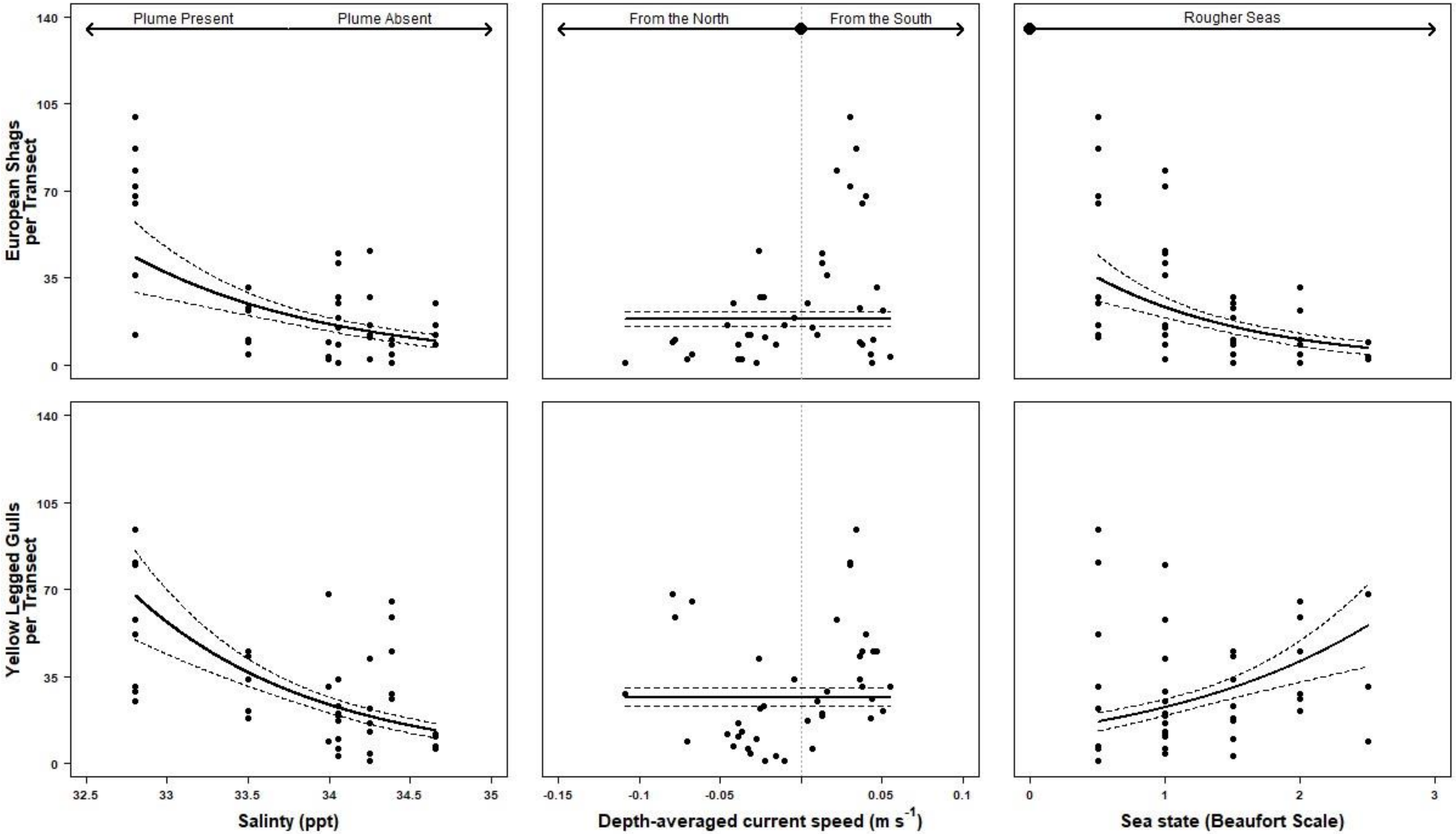

Fig 4: Predicted variations (± standard error) in counts of foraging seabirds across different physical conditions from 4 to 15 June in the Ria de Vigo, north-western Spain. Predictions were made using generalized additive models (GAM) with a negative binomial distribution.