Radboud Universiteit Nijmegen

Cetacean Behavioural Ecology and Environmental Drivers

Analysis of Observations at Fishguard Harbour Breakwater (2017–2025)

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Contents

1 Abstract **2**

2 Introduction **2**

2.1 Global Context . . . 2

2.2 Regional Overview: North-east Atlantic . . . 2

2.3 Site Characterisation: Fishguard Harbour . . . 3

2.4 Theoretical and Knowledge Gap . . . 3

2.5 Research Questions . . . 3

3 Methods **4**

3.1 Fieldwork and Data Collection . . . 4

3.1.1 Study Site . . . 4

3.1.2 Survey Protocol . . . 4

3.1.3 Environmental and Behavioural Recording Standards . . . 4

3.1.4 Historical Data Acquisition . . . 5

3.2 Data Cleaning and Verification . . . 6

3.2.1 Row-by-row Verification . . . 6

3.2.2 Species Identification . . . 6

3.2.3 Tidal Dynamics . . . 6

3.2.4 Behavioural Code Standardisation . . . 7

3.2.5 Boat Activity Metrics . . . 7

3.2.6 Time of Day Metrics . . . 7

3.3 Statistical Analysis . . . 7

3.4 Analytical workflow . . . 8

4 Results **8**

4.1 Tidal Influences on Cetacean Abundance . . . 8

4.2 Temporal Patterns and Species Segregation . . . 11

4.2.1 Diurnal Activity Patterns . . . 11

4.2.2 Species-Specific Patterns . . . 11

4.3 Anthropogenic Effects on behaviour . . . 12

4.3.1 Ferry Operations . . . 12

4.3.2 Boat Activity Responses . . . 12

4.4 Environmental Predictors and Advanced Modelling . . . 14

4.4.1 Zero-Inflated Modelling . . . 14

4.4.2 Generalised Additive Modelling . . . 15

4.4.3 Machine Learning Classification . . . 19

4.4.4 Model Comparison . . . 19

5 Discussion **20**
5.1 Ecological Interpretation of Tidal Patterns . . . 20
5.2 Temporal Niche Partitioning Mechanisms . . . 21
5.3 Anthropogenic Interactions . . . 21
5.3.1 The Ferry Paradox . . . 21
5.3.2 Surface Activity Amplification . . . 21
5.4 Methodological Insights . . . 22
5.4.1 Zero-Inflation Challenges . . . 22
5.4.2 Tidal-Temporal Interactions . . . 22
5.5 Conservation Implications . . . 22
5.5.1 Tourism Management Framework . . . 22
5.6 Limitations and Future Research . . . 23

6 Conclusions **23**

7 Acknowledgements **24**

8 References **24**

9 Appendices **25**
9.1 Appendix A: Statistical Model Specifications . . . 25
9.1.1 Tidal Phase Analysis . . . 25
9.1.2 Zero-Inflated Model Structure . . . 25
9.2 Appendix B: Data Dictionary and Variable Descriptions . . . 25
9.3 Appendix C: Survey Protocol Summary . . . 26
9.3.1 Site Setup: . . . 26
9.3.2 Observation Protocol . . . 26
9.3.3 Species identification key . . . 26
9.3.4 Data Recording Forms Example . . . 27
9.4 Appendix D: Data Quality Assurance Procedures . . . 27
9.5 Appendix E: Management Framework Support . . . 27
9.6 Appendix F : Research Data Management . . . 27

1 Abstract

Cetaceans play a critical role as apex predators in marine ecosystems, regulating food webs and enhancing nutrient cycling through mechanisms like the “whale pump”. Monitoring their behaviour provides important insights into ecosystem health and their responses to environmental stressors. Tidal cycles and diurnal patterns are known to influence cetacean foraging, but how these drivers interact with anthropogenic pressures in coastal habitats is not understood. In regions like Fishguard Harbour (Pembrokeshire, Wales), species such as harbour porpoises (*Phocoena phocoena*)

and bottlenose dolphins (*Tursiops truncatus*) face cumulative impacts from boat traffic and tidal variability. Current models lack any integration of these interacting drivers across multiple species. The combined effects of tidal phase, time of day, and boat activity on cetacean abundance and behaviour in coastal zones have not been determined.

This study shows that tidal phase significantly influences cetacean abundance, with peaks during early ebb tide and low tide, while species exhibit distinct temporal partitioning: harbour porpoises occur mostly at midday, whereas bottlenose dolphins display more flexibility. Contrary to expectations, scheduled ferry operations caused no detectable behavioural disruption, suggesting localised habituation. However, increasing boat counts amplified surface behaviours: leaping (OR = 2.19) and socializing (OR = 2.21) probabilities rose significantly per additional vessel. Tidal phase explained 2.8% of abundance variance ($\eta^2 = 0.028$), aligning with Fishguard's intermediate position in the Celtic Sea's tidal-energy gradient. Advanced modelling identified Seasonality, diel cycle and sea state as primary predictors of cetacean presence. The results suggest that tidal fronts concentrate prey during ebb phases, driving cetacean abundance, while diurnal niche partitioning reduces interspecific competition. Boat activity induces non-acoustic disturbance, manifesting as modified surface behaviour rather than avoidance.

These findings directly inform adaptive management frameworks for marine tourism, advocating for time-area closures during peak tidal foraging and vessel exclusion zones.

Keywords: tidal influences, anthropogenic impacts, species temporal partitioning, environmental predictors, coastal monitoring

2 Introduction

2.1 Global Context

Cetaceans play a critical role in marine ecosystems as apex predators, exerting both top-down and bottom-up effects on food web dynamics. They are able to maintain ecosystem stability by regulating prey populations. In addition, climate regulation is possible through the "whale pump mechanism". This occurs when migrations and defecation cycles facilitate nutrient transport and enhance primary production, thereby boosting carbon sequestration and supporting marine biodiversity (Roman and McCarthy 2010). Carcasses can also create deep-sea habitats, and marine mammals are known to transport nutrients vertically and horizontally which supports productivity. Cetaceans provide significant cultural and economic value, for example through whale-watching tourism with the potential to foster a sense of environmental stewardship (OSPAR Commission 2017).

Monitoring their behaviour and distribution provides insights into ecosystem health and responses to environmental stressors. For example, shifts in cetacean foraging behaviour or migration patterns have been linked to rising sea temperatures and prey availability changes during marine heat waves (Chambault et al. 2018). Similarly, avoidance of polluted areas or increased boat traffic can indicate habitat degradation (Pennino et al. 2016).

2.2 Regional Overview: North-east Atlantic

In the North-east Atlantic, cetacean populations exhibit varied trends across species and regions. Harbour porpoises, for example, have experienced a southward distribution shift in the Greater North Sea, with stable abundances in West Scotland, Ireland, and Iberia, but declines in the Celtic and Irish Seas. Coastal bottlenose dolphin (*Tursiops truncatus*) populations remain stable in most assessed areas, such as Cardigan Bay and Normandy/Brittany, though declines have been observed in the Sado Estuary, Portugal. Other species, including the short-beaked common dolphin (*Delphinus delphis*), white-beaked dolphin (*Lagenorhynchus albirostris*), and minke whale (*Balaenoptera acutorostrata*), show no clear declines and some even experienced an increase in abundance (OSPAR Commission 2023).

2.3 Site Characterisation: Fishguard Harbour

Fishguard Harbour is situated within a glacially carved valley in Ordovician volcanic bedrock. It offers sheltered, deep-water habitats shaped by ancient volcanism, glaciation, and faulting. The harbour's unique geomorphology and

hydrodynamics create favourable conditions for a variety of marine species, making it an important site for cetacean monitoring (Burt et al. 2012). The North Breakwater (Figure 1; Figure 2), constructed in the early 1900s, further shelters the area and provides an ideal vantage point for land-based systematic observations of cetacean behaviour and distribution (Fishguard and Goodwick Local History Society 2022). Land-based surveys are often advantageous as they provide zero disturbance to the cetaceans being surveyed, and they also provide long-term consistency.

Figure 1: Outer End of The Fishguard Outer Breakwater

Figure 2: Inner End of The Fishguard Outer Breakwater

2.4 Theoretical and Knowledge Gap

While existing research has established fundamental relationships between environmental variables and cetacean behaviour, significant knowledge gaps persist regarding species-specific responses to interacting drivers in coastal environments like Fishguard Harbour. Current literature demonstrates tidal influences on foraging behaviour in harbour porpoises (Nuuttila et al. 2018) and diurnal activity patterns in various cetacean species (Osiecka et al. 2020), but lacks comprehensive analyses of how tidal cycles, time-of-day effects, and anthropogenic pressures simultaneously influence behaviour across multiple species. This represents a critical theoretical gap.

Therefore, this study will specifically focus on small cetaceans regularly observed in Pembrokeshire waters, including harbour porpoises (*Phocoena phocoena*), bottlenose dolphins (*Tursiops truncatus*), Risso's dolphins (*Grampus griseus*), and short-beaked common dolphins (*Delphinus delphis*). These species are ecologically significant as they are highly responsive to environmental change and anthropogenic pressures (Sea Trust Wales 2023).

2.5 Research Questions

This study aims to address these knowledge gaps by investigating the effects of tidal variations, weather conditions, and anthropogenic factors on the number and behaviour of cetaceans observed at Fishguard Harbour breakwater. Specifically, it seeks to answer the following research questions:

- **Main Question:** What are the effects of tidal variations and weather conditions on the number and behaviour of small cetaceans observed at the Fishguard Harbour breakwater?
- **Sub-Question:** Is there any effect of time-of-day or boat activity on the number of cetaceans observed?

Previous research suggests tidal cycles strongly affect cetacean activity. For example, harbour porpoises in the North Sea forage more frequently during high or flood tides when tidal currents concentrate prey like herring (Nuuttila et al. 2018). Similarly, a calm sea may improve detection rates, due to the possibility that the number of cetaceans is the same in both rough and calm seas. However, the human eye can detect them better when the sea is calm (Teilmann 2003). Weather conditions may also influence behavioural diversity, as reduced wave action in calm seas allows clearer observation of behaviours like breaching or socializing as opposed to in rough seas (Mann and Würsig 2013). Calm seas not only aid observers but also improve dolphin foraging success and energy conservation. Hourly variations have been shown to significantly affect the presence of porpoises, indicating that there is a time-of-day effect (Nuuttila et al. 2018), with harbour porpoises mainly foraging at night (Osiecka et al. 2020). Boat traffic has been shown to cause

significant behavioural disruption in cetaceans, for example by increasing the occurrence of bow-riding in dolphins (National Marine Fisheries Service 2022).

Therefore, this study hypothesizes that cetacean sightings will be more frequent during high and flood tides, when tidal currents aggregate prey and enhance foraging efficiency. Sightings are also expected to increase during calm seas (Beaufort scale ≤ 2) due to improved visibility, though detection bias must be considered. Behavioural diversity is anticipated to rise under favourable conditions, as reduced wave action allows for clearer observation of complex behaviours. It is also likely to rise with an increase in boat activity. Lastly, cetacean sightings are predicted to peak during later hours of the day, reflecting their natural foraging rhythms.

This research will investigate how tidal variations, weather conditions, and the time of day influence the number and behaviour of cetaceans observed from the Fishguard Harbour breakwater. It will do this by analysing 689 standardized 15-minute observation intervals (2017–2025) using Generalised additive models (BAM) to quantify tidal-hour interactions, zero-inflated regression for abundance patterns, and behavioural GLMs to assess anthropogenic impacts. Understanding these dynamics can improve conservation efforts, inform marine management practices, and contribute to the ongoing monitoring programs conducted by Sea Trust Wales.

3 Methods

3.1 Fieldwork and Data Collection

3.1.1 Study Site

The study was conducted at Fishguard Harbour's Outer Breakwater in Pembrokeshire, Wales (51.996°N, 4.976°W), with surveys spanning multiple seasons from 2017 to 2025. Of the 249 surveys carried out, some were sourced from historical Sea Trust records, while those conducted specifically in April and May 2025 were performed exclusively for this research. Across the survey period, a total of 689 observation intervals (each lasting 15 minutes) were recorded, amounting to approximately 172 hours of observation. Notably, there were gaps in survey coverage during the years 2021 and 2023.

3.1.2 Survey Protocol

Between 7th April and 24th May, visual surveys were performed using marine binoculars. Observations were recorded at 15-minute intervals, capturing data on the number of individuals, group composition, animal behaviours, and prevailing environmental conditions, following the standardised cetacean monitoring protocol established by Sea Trust. Land-based surveys resulted in minimal to no disturbance of the cetaceans involved.

3.1.3 Environmental and Behavioural Recording Standards

The categorical environmental and behavioural variables recorded in this study were organised and defined in reference tables created by Sea Trust (Table 1 - Table 4). Consistent categories and codes were assigned to each variable to ensure that the data could be recorded in both a reliable and reproducible manner.

Table 1: Beaufort Sea State Scale

Beaufort	Description
0	Calm, glassy
1	Ripples
2	Small wavelets, no white caps
3	Large wavelets, few white caps
4	Small waves, frequent white caps
5	Moderate waves, many white caps
6	Large waves, many white caps
7	Sea heaps up, foam in streaks
8	Long, high waves, foam in streaks
9	Storm, high waves, rolling sea

Table 2: Cetacean Species Codes

Code	Species
HP	Harbour Porpoise
BND	Bottlenose Dolphin
CD	Common Dolphin
RD	Risso's Dolphin

Table 3: Cetacean Behaviour Codes

Behaviour	Description
Foraging/feeding	Active prey pursuit, fast swims, frequent direction changes
Travelling	Decisive movement from one point to another
Leaping	Full body breach
Tail slapping	Striking water surface with tail flukes
Socialising	Interactions between animals
Milling	Slow movements in same general area
Resting	Immobile or minimal movement near surface
Unknown	Unidentified behavior

Table 4: Precipitation Codes

Code	Meaning
0	None
L	Light/Showers
M	Moderate
H	Heavy

3.1.4 Historical Data Acquisition

To supplement recent surveys, historical data from 2017 to 2024 were obtained from Sea Trust archives, comprising 605 raw spreadsheet entries. These records included site location, position, date, observer names, tidal state, sea

state, wind speed and direction, visibility, cloud cover, precipitation, animal counts, behavioural notes, and additional observations. Survey coverage was interrupted in 2021 and 2023.

3.2 Data Cleaning and Verification

3.2.1 Row-by-row Verification

A total of 686 rows (representing 249 surveys) were manually cross-checked against archival data to identify and correct transcription errors. Historical sea temperature data was appended to the dataset to enhance environmental context.

3.2.2 Species Identification

The study focused on the following small cetacean species:

- Harbour porpoise (*Phocoena phocoena*)
- Bottlenose dolphin (*Tursiops truncatus*)
- Common dolphin (*Delphinus delphis*)
- Risso's dolphin (*Grampus griseus*)

3.2.3 Tidal Dynamics

All tidal logs were rechecked for accuracy. Tidal conditions for each survey were standardized by calculating a tidal index (ranging from 0 to 1, where 0 and 1 correspond to high tide). The index was calculated as:

$$\text{Tidal Index} = \frac{\text{Survey Time} - \text{First High Tide}}{\text{Second High Tide} - \text{First High Tide}}$$

This standardization process ensured comparability across all records (see Appendix A for full tidal index calculations). Standardizing tidal conditions using an index (0–1) enables direct comparison of surveys conducted at different times by translating clock times into proportional positions within the tidal cycle. This eliminates temporal confounding and quantifies cetacean behaviour relative to tidal phases (e.g., high/low tide) allowing for a statistically accurate analysis of tidal influences. Observations were then binned into tidal phases (Table 5).

Table 5: Tidal Phase Categories with Corresponding Tidal Index Ranges and Descriptions

Tidal Phase	Tidal Index Range	Description
Early Ebb	0.00 - 0.25	Early ebb
Mid Ebb	0.25 - 0.45	Mid ebb
Low	~0.50	Low tide
Early Flood	0.55 - 0.75	Early flood
Late Flood	0.75 - 1.00	Late flood

The tidal range was measured in meters and refers to the vertical difference between high and low tide. Differences in tidal range between surveys may occur due to varying lunar phases, seasonal changes, or minor differences in observation location along the breakwater.

3.2.4 Behavioural Code Standardisation

Free-text behavioural notes were mapped into standardized binary columns for key behaviours:

- Travelling
- Foraging/feeding
- Leaping
- Tail slap
- Social
- Milling
- Resting
- Unknown

Additional annotations were expanded to include mother-calf pairs (MC), juveniles (J), gannets (G), and grey seals (AGS). These were not analysed in this study, as they were not relevant to the research question.

3.2.5 Boat Activity Metrics

Two additional columns were introduced to the dataset, as a result of the expansion of the additional annotations, which contained information on:

- Boat Count: The number of boats present during each observation (including the ferry).
- Ferry Presence: Any ferry activity during the survey (recorded as a binary indicator).

3.2.6 Time of Day Metrics

Observation times were binned into three broad time-of-day categories to standardise temporal analyses of cetacean sightings and behaviour. These bins aligned with survey hours to detect diurnal patterns in the data (Table 6).

Table 6: Time of Day Categories with Hour Ranges and Descriptions

Time.of.Day	Hour.Range..24h.	Description
Morning	07:00 - 11:00	Morning
Midday	11:00 - 14:00	Midday
Afternoon	14:00 - 18:00	Afternoon

3.3 Statistical Analysis

All analyses were conducted in R version 4.5.1, with reproducibility ensured through seed setting (`set.seed(12345)`) and version control of analytical packages.

A sequence of statistical techniques were used that progressed from non-parametric group comparisons to machine learning classifiers. This (summarised in Table 7) allowed sequential examination of: 1) tidal phase effects on abundance distributions, 2) species-specific temporal associations, 3) localised anthropogenic impacts, and 4) complex behavioural responses.

Table 7: Overview of statistical methods applied in this study

Step	Method	Purpose
1	Kruskal-Wallis Tests	Non-parametric comparison of abundance across tidal phases
2	Fisher's Exact Tests	Species-time association analysis
3	Wilcoxon Signed-Rank Tests	Ferry effect on abundance (paired observations)
4	Generalized Linear Models (GLMs) + Post-hoc	Behavioural response modeling
5	Zero-Inflated Models	Address abundance zero-inflation
6	Generalised Additive Models (Big Additive Model)	Complex interaction modeling
7	Random Forest	Machine learning classification

3.4 Analytical workflow

The analytical workflow's hierarchical structure (Figure 3) allowed for a sequential examination of any distributional patterns before investigating complex ecological interactions through additive modelling and machine learning approaches.

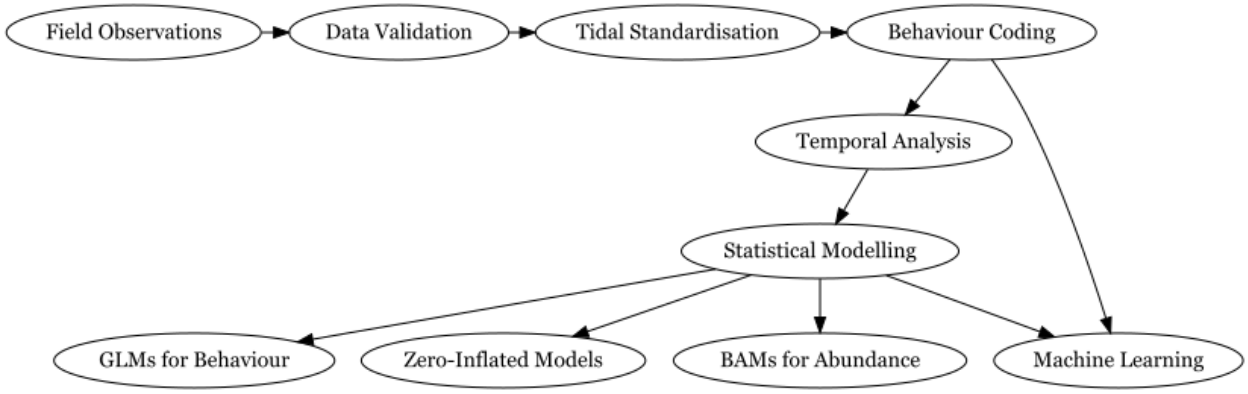

Figure 3: Flowchart of analytical workflow. From field observations to statistical modeling (including GLMs, BAMs, and machine learning).

4 Results

This study investigated how tidal cycles, diel patterns, and anthropogenic activities influence cetacean abundance and behaviour at Fishguard Harbour Outer Breakwater.

4.1 Tidal Influences on Cetacean Abundance

Cetacean abundance varied significantly across tidal phases at Fishguard Harbour (Kruskal–Wallis test: $\chi^2(5) = 19.4$, $p = 1.62\text{e-}03$, $n^2 = 0.028$, $n = 686$). Peak abundances occurred as the tide was dropping, with the highest counts observed during early ebb (tidal stage 0–0.25) and low tide (~0.5; Figure 4).

Table 8: Pairwise Wilcoxon test adjusted p-values

Group1	0-0.25	0.25-0.45	~0.5	0.55-0.75	0.75-1
0-0.25	0.0000000	1.000000	1.0000000	1.0000000	0.0083522
0.25-0.45	1.0000000	0.000000	1.0000000	1.0000000	0.0036880
~0.5	1.0000000	1.000000	0.0000000	0.5774430	0.0002619
0.55-0.75	1.0000000	1.000000	0.5774430	0.0000000	0.1947735
0.75-1	0.0083522	0.003688	0.0002619	0.1947735	0.0000000

Post-hoc Wilcoxon pairwise comparisons with Bonferroni correction (Table 8) revealed:

- Significantly lower abundance during late flood (0.75–1) as opposed to early ebb ($p = 0.008$), late ebb (0.25–0.45; $p = 0.004$), and low tide ($p < 0.001$)
- No significant differences between low tide/early flood, early ebb/low tide, or early/late ebb phases (all $p \approx 1$)

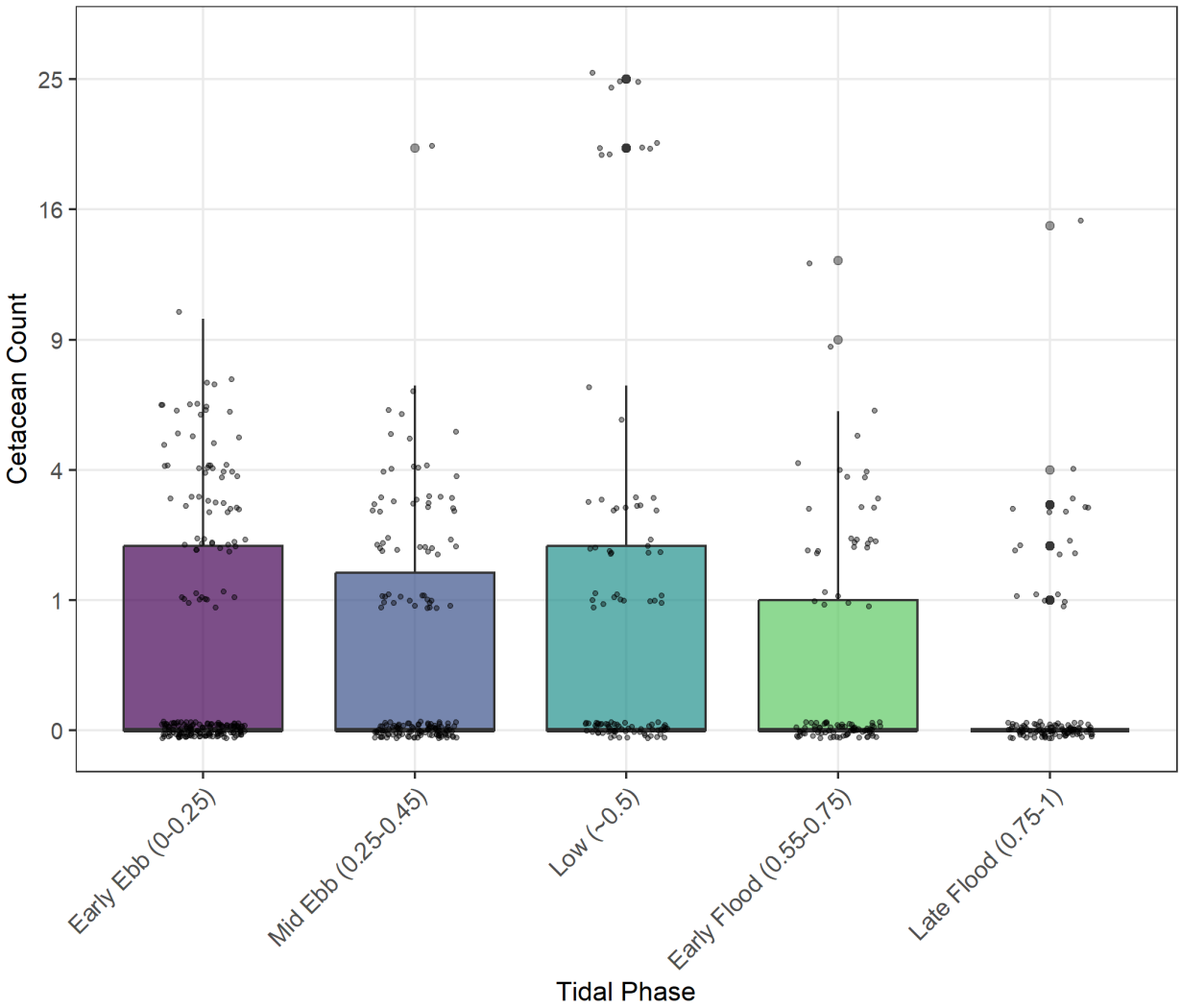

Figure 4: Boxplot of cetacean abundance across tidal phases at Fishguard Harbour (2017–2025). Each box represents the distribution of minimum cetacean counts for a given tidal phase. Points show individual observations, with a square root-transformed y-axis to improve visualization of low counts.

Figure 4 shows that despite median abundances of 0 across all tidal phases (reflecting zero-inflated data):

- Early ebb displayed frequent high-count outliers
- Low tide showed the highest variability
- Late flood had the highest proportion of zero counts

These results demonstrate that ebb phases, particularly early ebb and low tide, support the highest cetacean occurrence at the breakwater.

4.2 Temporal Patterns and Species Segregation

4.2.1 Diurnal Activity Patterns

Significant diurnal patterns characterized cetacean observations (Kruskal-Wallis test: $\chi^2(df) = 9.2786609$, $p = 0.0097$). Peak sighting rates occurred during the following hourly intervals: 11:00–12:00, 12:00–13:00, 13:00–14:00 with combined sightings representing 87.2% of total observations (and individual peak hour percentages ranging from 15.7% to 54.7%).

4.2.2 Species-Specific Patterns

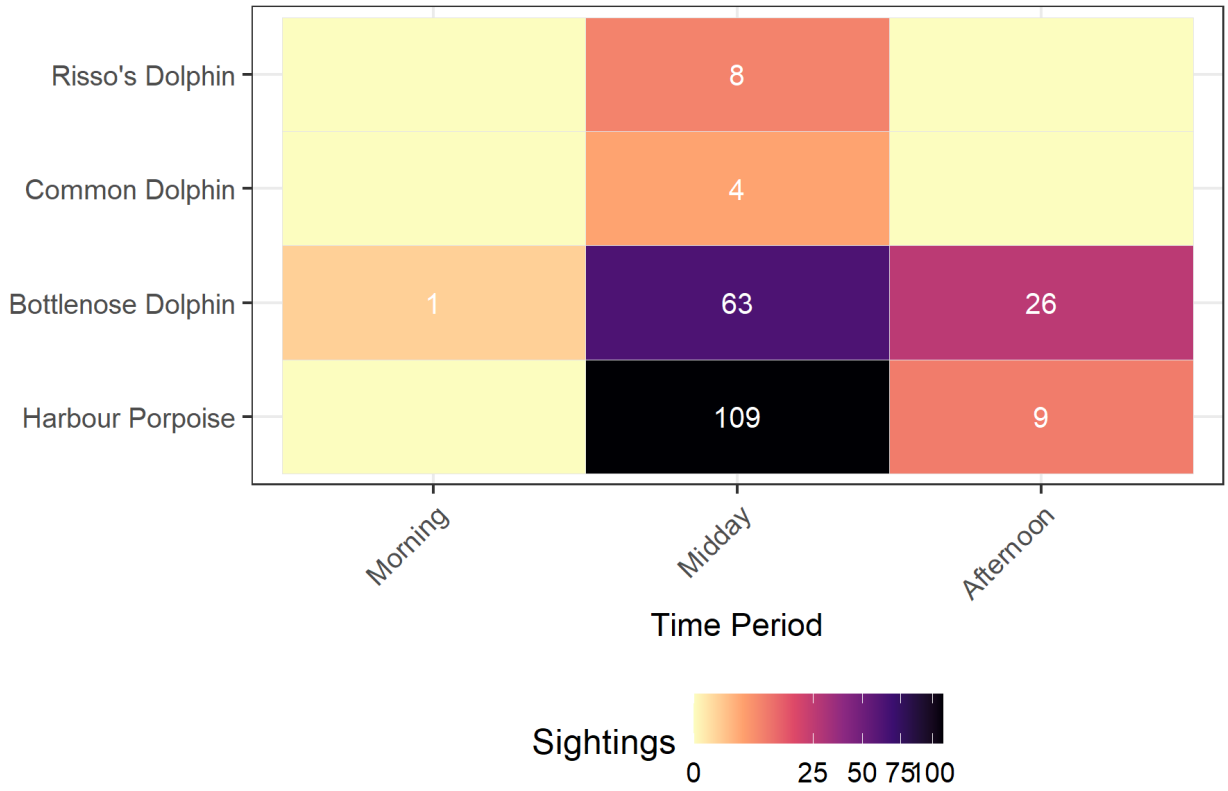

Figure 5: Heatmap showing the frequency of cetacean sightings by species across daily time periods (Morning, Midday, Afternoon) at Fishguard Harbour. Each cell represents the number of sightings for a given species and time period. The color scale uses a square root transformation for clarity.

Species-specific diurnal patterns were visualized in a heat map (Figure 5) and confirmed by statistical tests (Fisher's exact test: $p = 0.0006$):

- **Harbour Porpoise**: Observed predominantly at midday (92.4% of observations)
- **Bottlenose Dolphin**: Bimodal distribution (70.0% midday, 28.9% afternoon)
- **Rare species:** Common and Risso's Dolphins were exclusively observed during midday due to low sample sizes

These results indicate clear temporal partitioning, with midday representing the peak activity window for cetaceans at Fishguard Harbour.

4.3 Anthropogenic Effects on behaviour

4.3.1 Ferry Operations

Ferry presence showed no significant effect on abundance (Wilcoxon rank-sum test: $W = 11097.5$, $p = 0.529$, $d = 0.05$, 0.95, -0.29, 0.38).

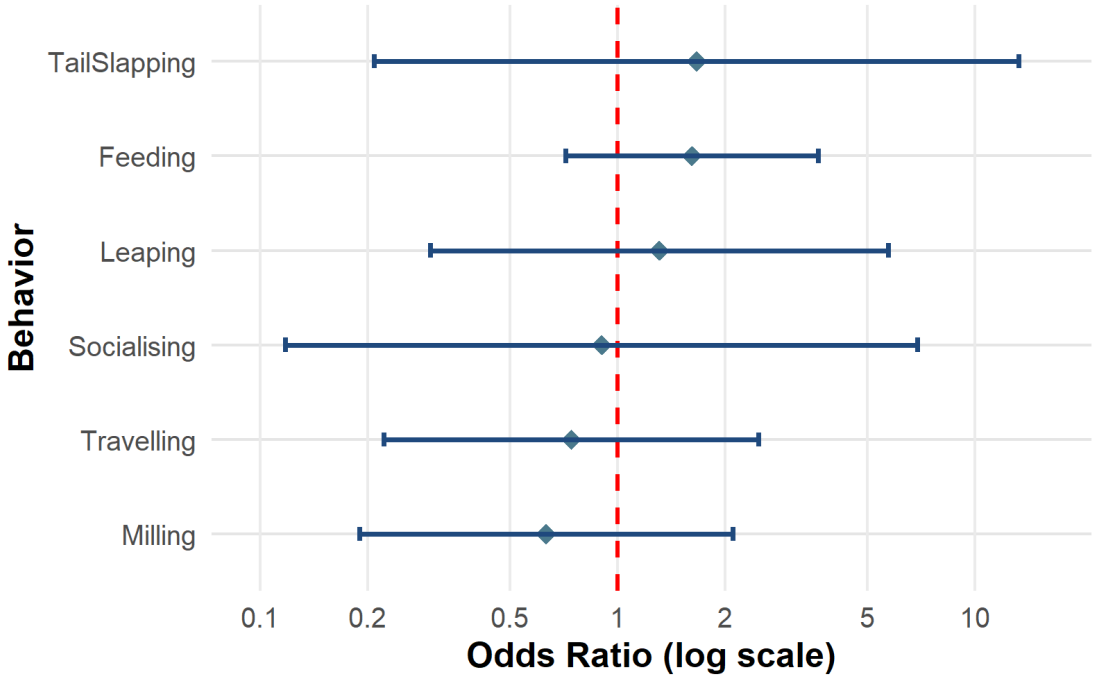

Figure 6: Generalized linear models evaluating the effect of ferry presence on the probability of observing each cetacean behaviour (binary response).

Figure 6 indicates that ferry presence alone does not significantly influence behaviour probabilities as all Odds Ratio 95% CIs overlapped 1.

4.3.2 Boat Activity Responses

While presence of an individual boat (the ferry) showed no significant effect on overall cetacean abundance or behaviour, generalised linear models revealed boat count was associated with an increased likelihood of behaviour occurrence (Table 9).

Table 9: Generalised linear models with binomial error distribution. Coefficients represent log-odds of behavioural occurrence per unit increase in boat count.

behaviour	Coefficient	P-value	Odds Ratio	95% CI
Leaping	0.783	<0.001	2.19	1.45-3.30
Socializing	0.794	<0.001	2.21	1.47-3.32
Tail Slapping	0.565	0.065	1.76	0.96-3.22
Travelling	0.307	0.091	1.36	0.95-1.94

Significant effects (Table 9) were observed for:

- Leaping (OR = 2.19 [1.45–3.30], $p < 0.001$)
- Socializing (OR = 2.21 [1.47–3.32], $p < 0.001$)

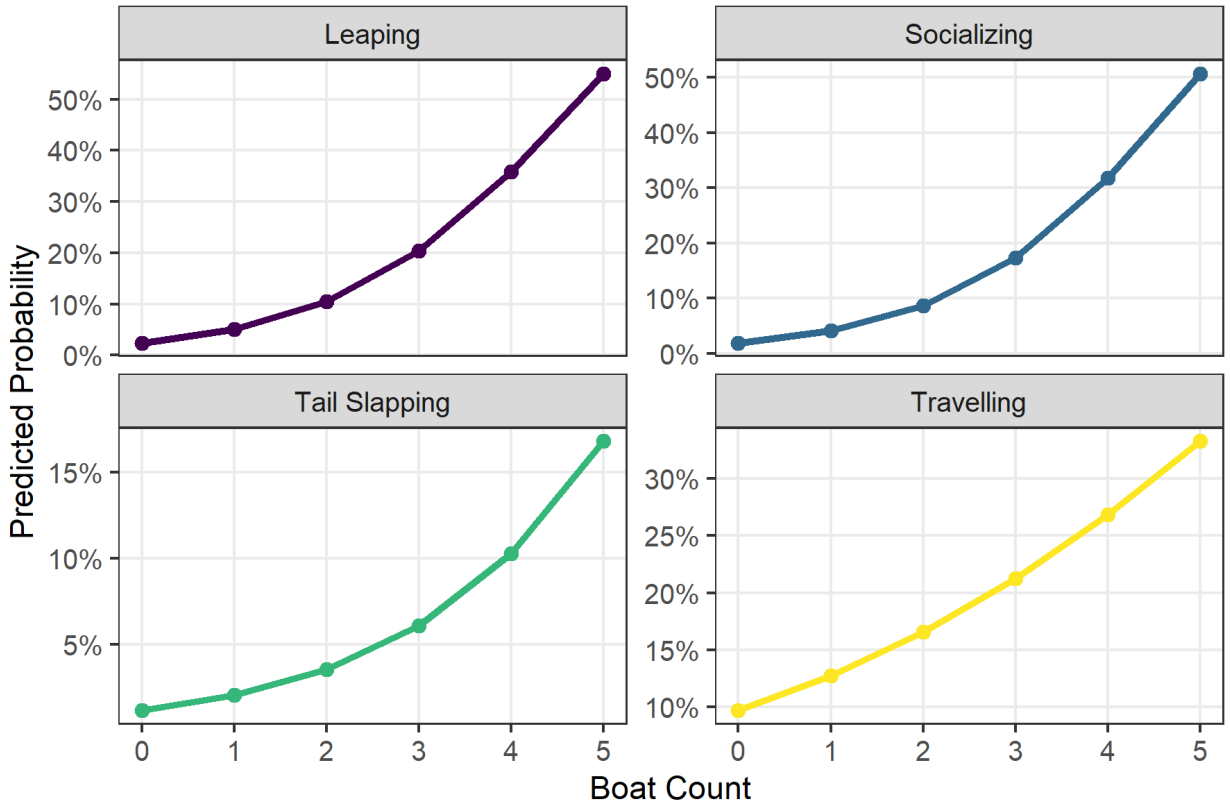

Figure 7: Model-predicted probabilities of cetacean behaviours in response to increasing boat counts, holding hour constant at median value. Lines and points represent predictions for Leaping, Socializing, Tail Slapping, and Travelling behaviours.

Travelling and tail slapping showed non-significant positive trends (Figure 7).

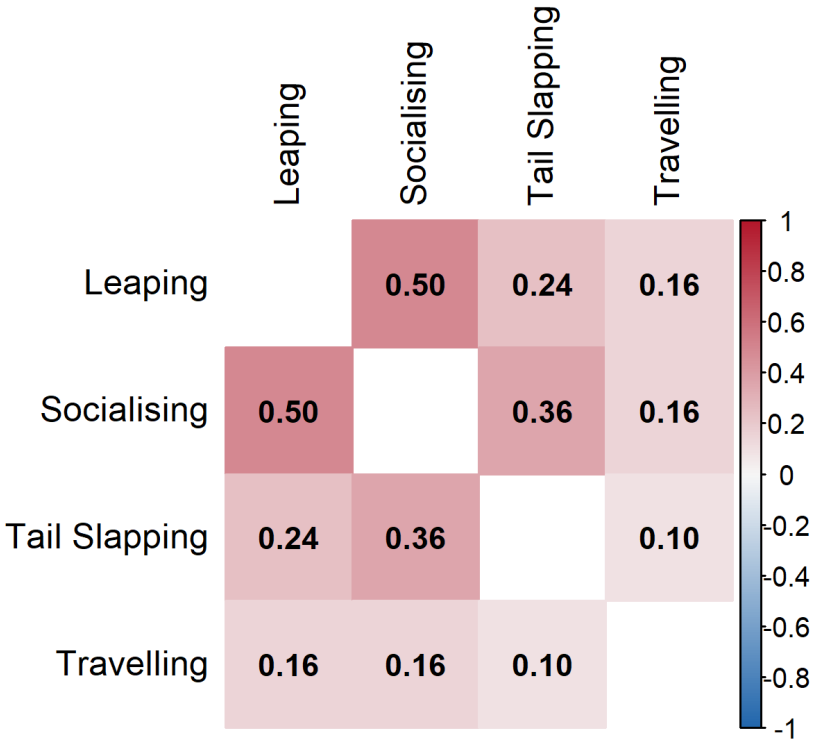

Figure 8: Correlation plot illustrating Spearman correlations between selected behaviours (Leaping, Socialising, Tail Slapping, Travelling).

Behavioural correlations were strongest between leaping and socializing (Spearman's correlations: $\rho = 0.50$; Figure 8). While scheduled ferries resulted in no significant response, higher boat density amplified surface behaviours.

4.4 Environmental Predictors and Advanced Modelling

4.4.1 Zero-Inflated Modelling

Zero-inflated negative binomial models (Table 10) addressed the high frequency of zero observations (68.1%) of records. Specifications of the model can be found in Appendix A.

Table 10: Zero-Inflated Negative Binomial Regression Coefficients

component	Term	Estimate	Std. Error	z value	p-value
Count	Intercept	-3.111	0.970	-3.207	0.001
Count	Tidal Range	0.114	0.103	1.111	0.267
Count	TidalStage	-0.665	0.358	-1.859	0.063
Count	Sea State	-0.310	0.105	-2.949	0.003
Count	Hour of Day	0.197	0.068	2.891	0.004
Count	Julian Day	0.008	0.001	6.030	0.000
Count	Log(theta)	-1.010	0.128	-7.896	0.000
Zero-inflation	Intercept	42.672	10.840	3.937	0.000
Zero-inflation	TidalStage	-0.292	0.773	-0.378	0.705
Zero-inflation	Hour of Day	-3.723	0.942	-3.952	0.000

The main predictors of counts (Table 10) were:

- Positive: Later hours ($\beta = 0.197$, $p = 0.004$) and Julian day (seasonal progression: $\beta = 0.008$, $p < 0.001$)
- Negative: Sea state ($\beta = -0.310$, $p = 0.003$) and Tidal stage (marginal effect: $\beta = -0.665$, $p = 0.063$)

The large intercept (42.672, SE = 10.840, z = 3.937, $p < 0.001$) reflected the large proportion of structural zeros. This potentially indicates absence or non-detection.

4.4.2 Generalised Additive Modelling

A Big Additive Model (BAM) is a generalised additive model designed to fit large datasets. The BAM explained 41.9% of deviance (Adjusted $R^2 = 0.35$) with key non-linear effects:

- Tidal range and hour jointly shaped response. Red denoted conditions associated with above-average sighting rates, while blue denoted below-average rates. Sightings were more likely at tidal ranges between 2 and 4 and around 12.5 to 17.5 hours (Figure 9)
- Tidal stage effects varied by time of day, with the most pronounced negative influence observed during the morning (Figure 10 - Figure 12)
- A generally negative association was observed between sea state and sighting rates. As sea state increased, expected sightings declined (Figure 13)
- There was a cyclical seasonal pattern, with sighting rates exhibiting distinct peaks and troughs throughout the year (Figure 14)

When the confidence band crossed or included zero, the effect was not statistically significant.

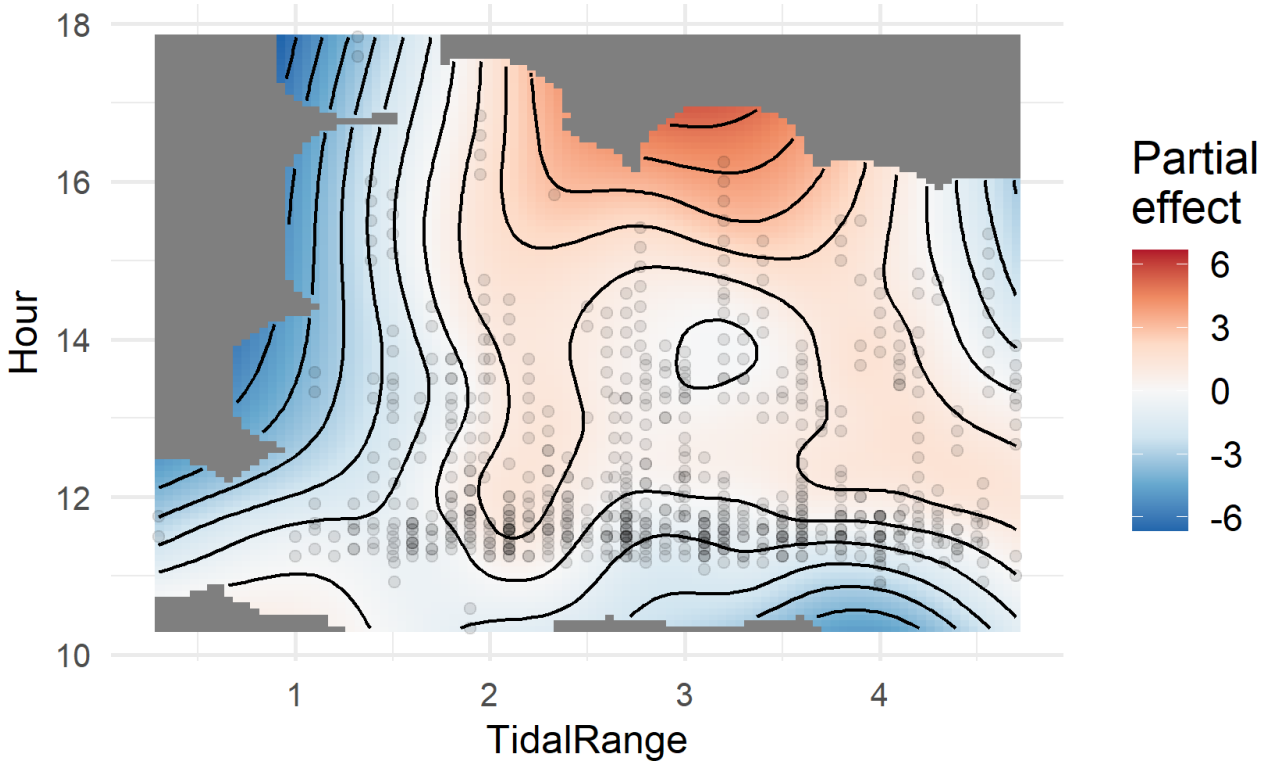

Figure 9: Visualization of a big additive model fit to minimum count data, showing the combined effects of tidal range and hour of day.

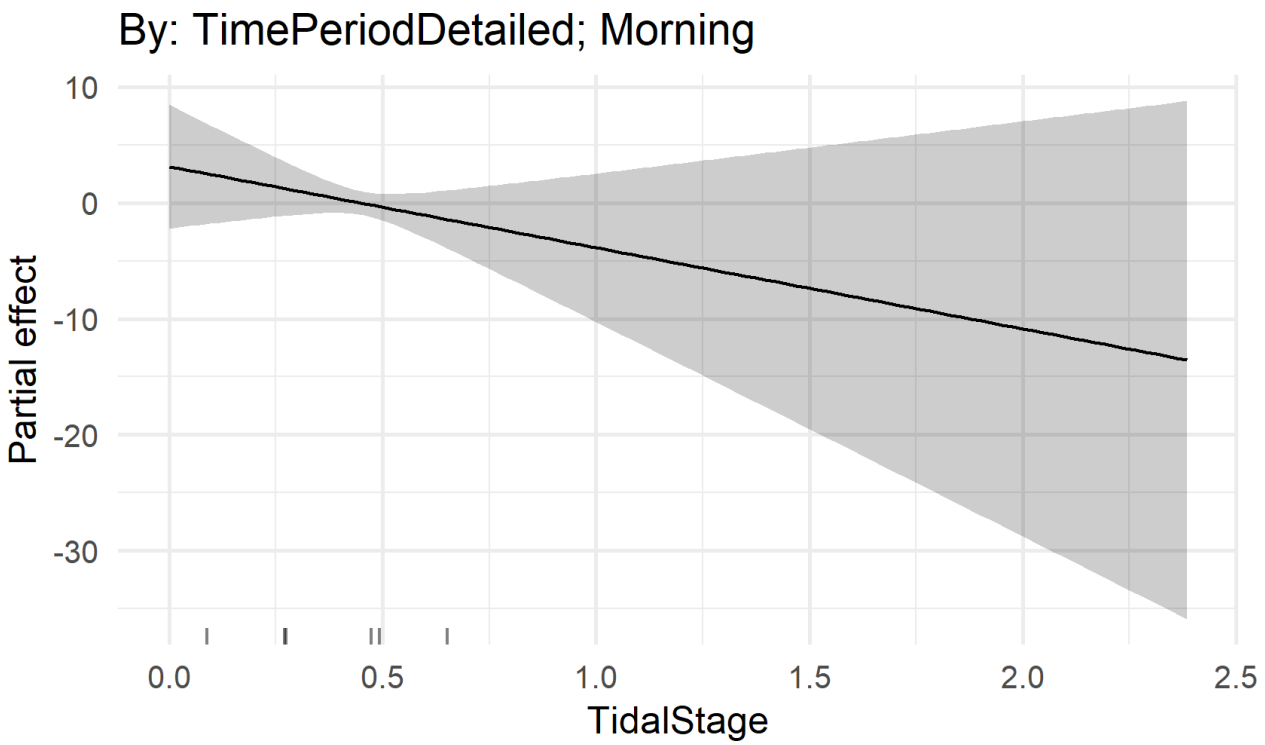

Figure 10: Visualization of a big additive model evaluating how the effects of tidal stage on minimum count data vary by morning periods.

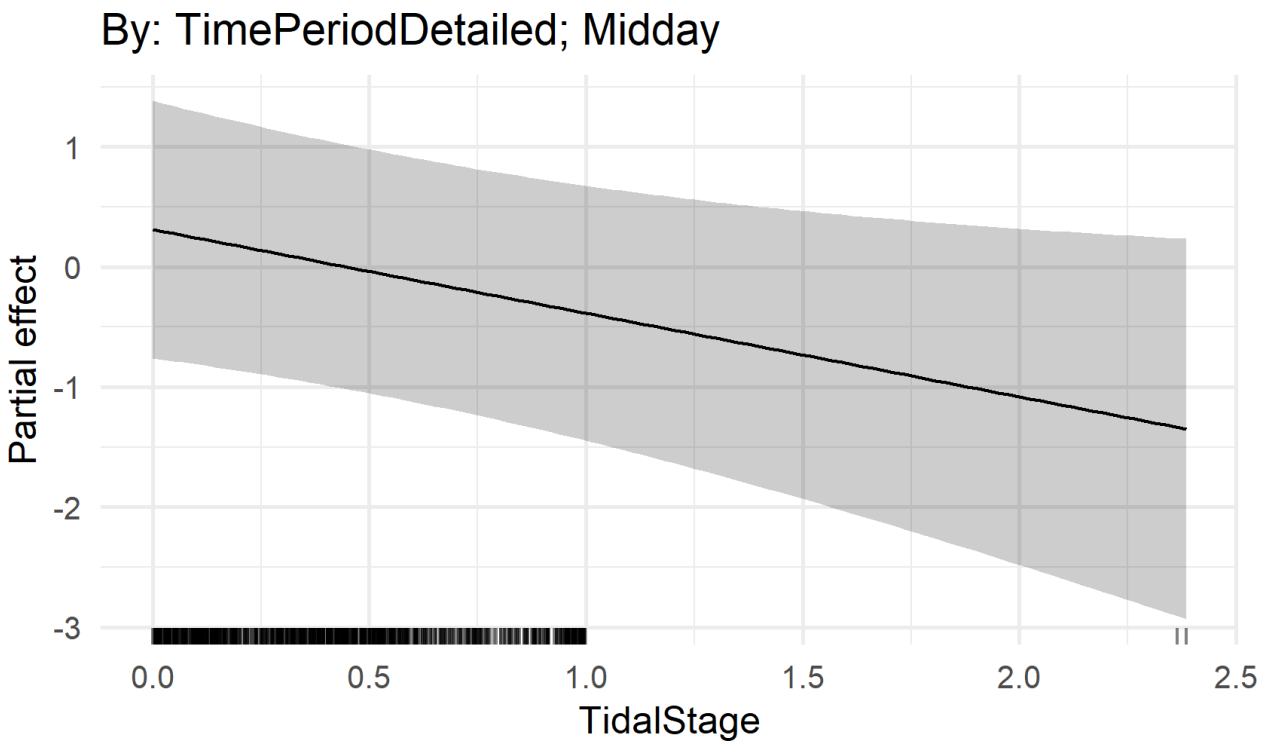

Figure 11: Visualization of a big additive model evaluating how the effects of tidal stage on minimum count data vary by midday periods.

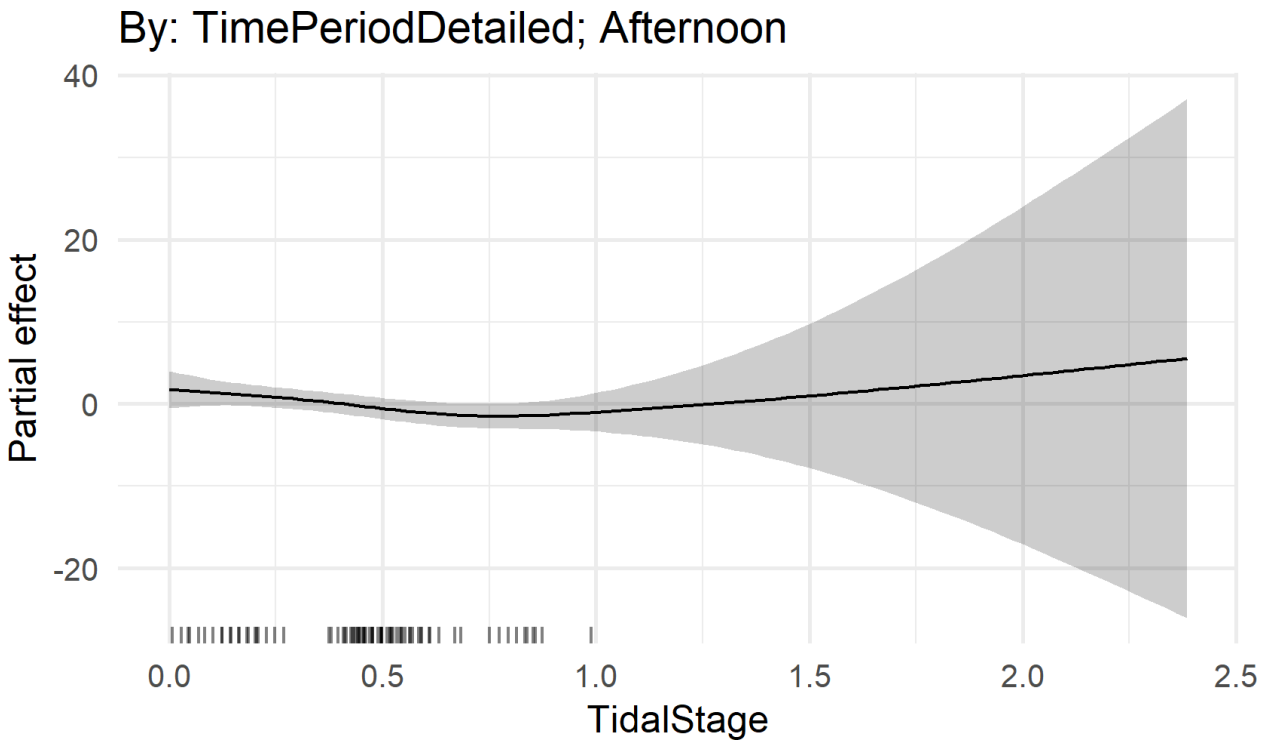

Figure 12: Visualization of a big additive model evaluating how the effects of tidal stage on minimum count data vary by afternoon periods.

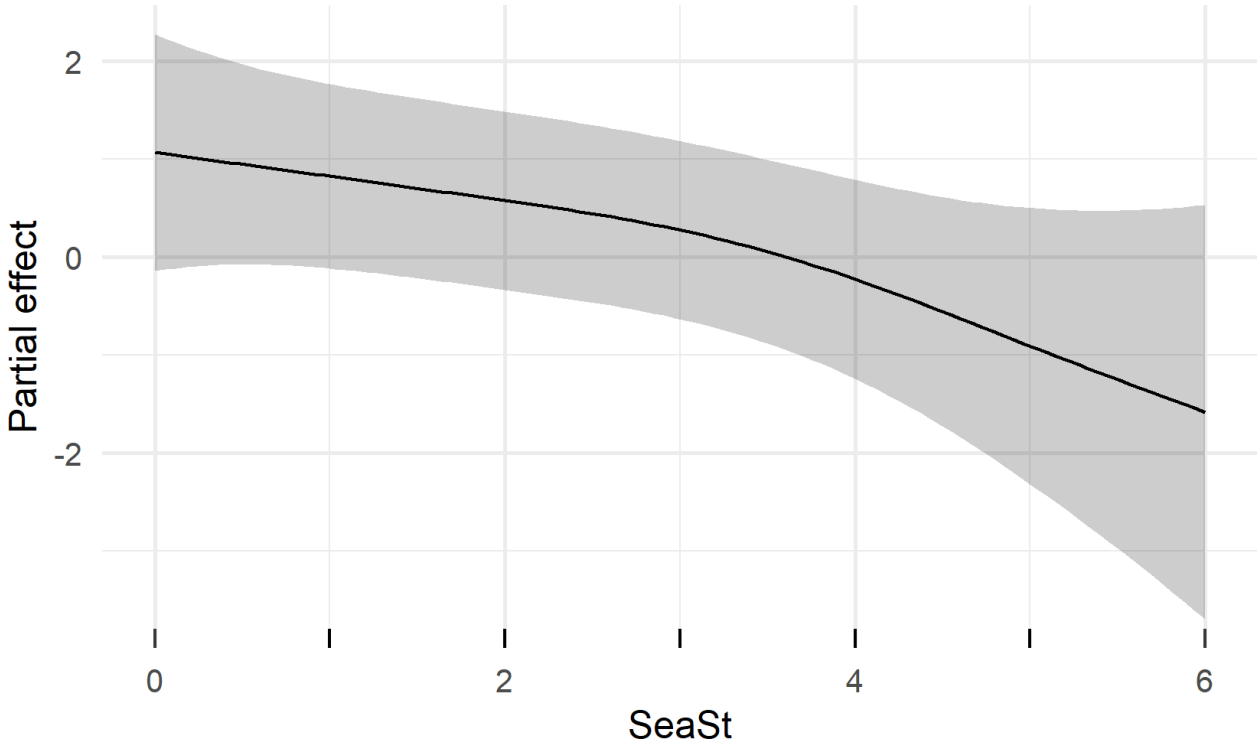

Figure 13: Visualization of a big additive model fit to minimum count data, showing the effects of sea state.

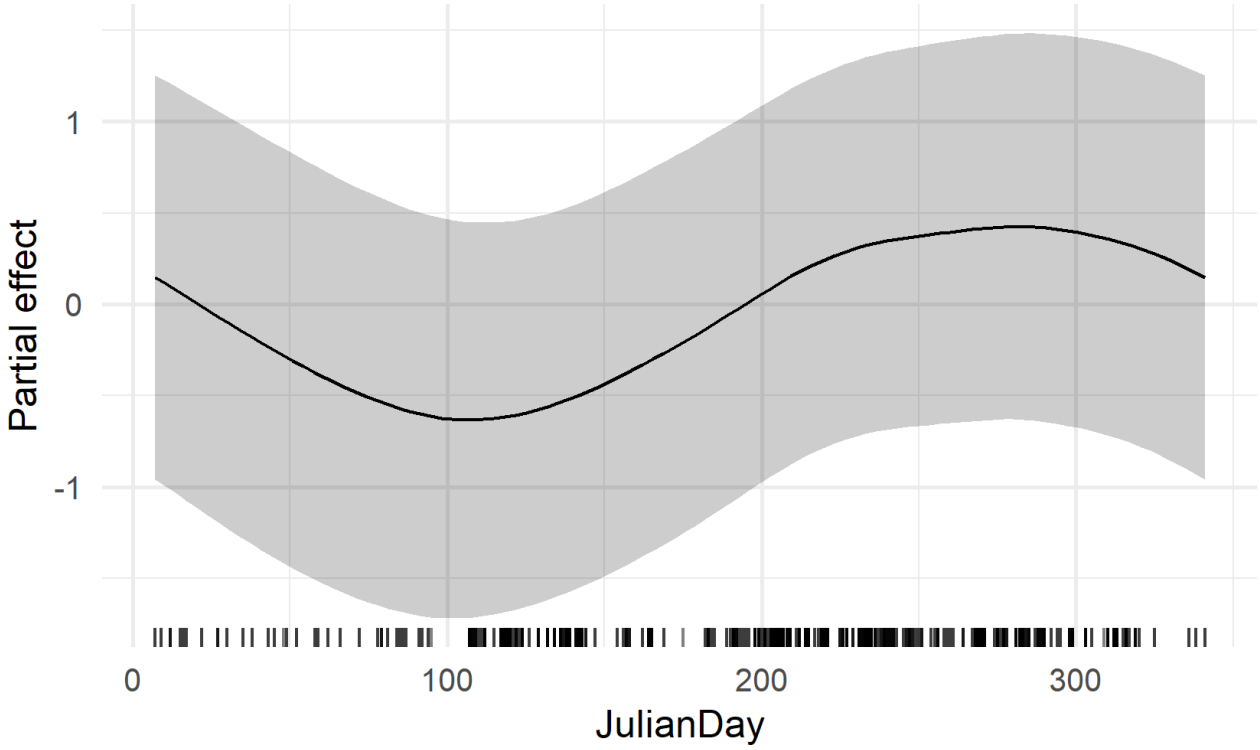

Figure 14: Visualization of a big additive model fit to minimum count data, showing the effect of Julian Day.

These plots collectively reveal that cetacean detection probabilities are maximized at intermediate tidal ranges, during

specific times of day, and under calmer sea states; seasonal peaks are also apparent.

4.4.3 Machine Learning Classification

Random Forest models achieved an out-of-bag (OOB) accuracy of 85.7% accuracy in predicting cetacean presence.

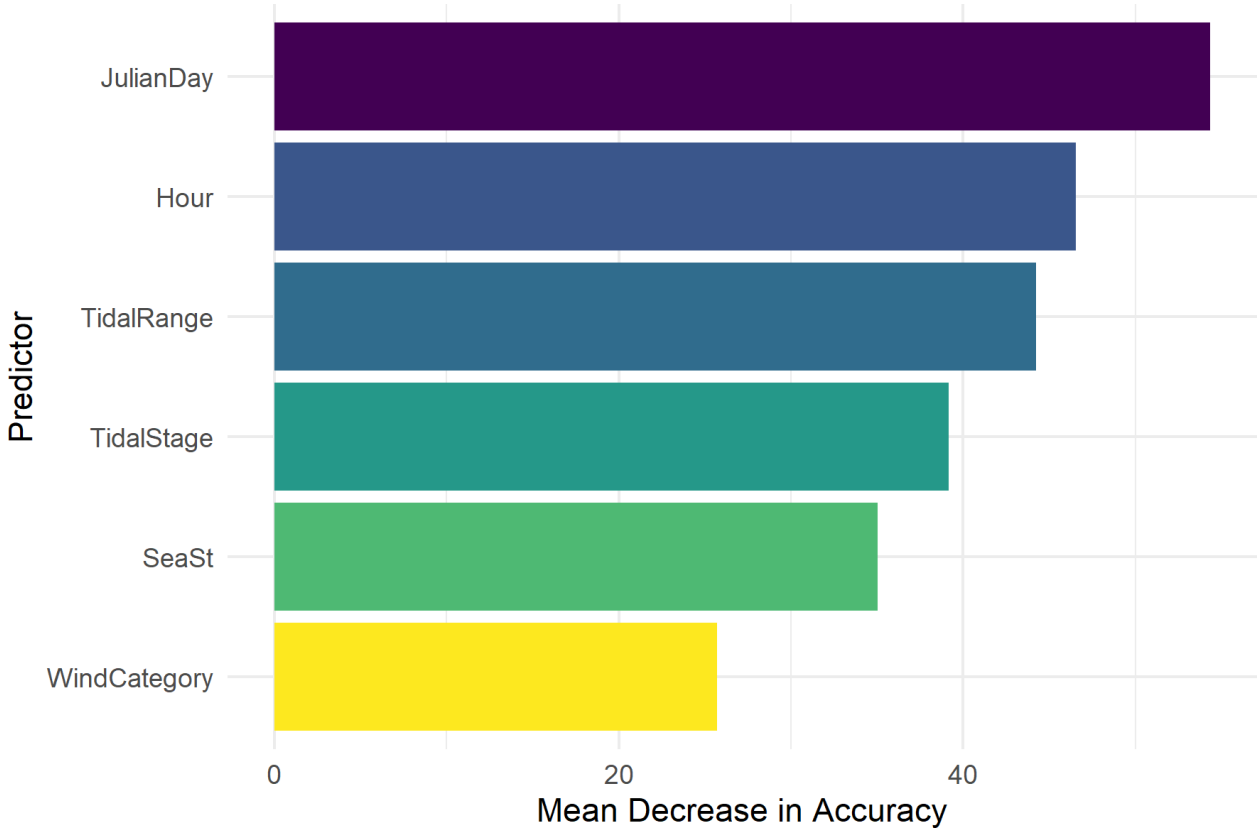

Figure 15: Variable importance plot from a random forest classification model predicting cetacean presence (Present vs. Absent) based on environmental and temporal factors.

As shown in Figure 15, there was variable importance ranking:

1. **Julian Day** (seasonality; MDA = 54.3)
2. **Hour** (diel pattern; MDA = 46.5)

4.4.4 Model Comparison

Table 11: Model Performance Comparison

Model	Deviance Explained (%)	AIC	Accuracy (%)	Key_Predictors
Zero-Inflated	NA	1744.10	NA	Hour, JulianDay, SeaSt
BAM	41.9	1681.78	NA	TidalRange × Hour, SeaSt
Random Forest	NA	NA	85.7	JulianDay, Hour, SeaSt

Based on the evaluation metrics presented in Table 11:

- The Zero-Inflated model explains 41.9% of deviance and has an AIC of 1681.78, indicating better fit.
- The BAM model has the highest AIC and no deviance explained, suggesting it does not fit the data as well. Interpreting generalised additive models like BAM can be challenging due to issues with identifiability and constraints on smooth terms.
- The Random Forest model achieves the highest accuracy (85.7%) but lacks deviance and AIC measures, reflecting a more predictive (less inferential) approach.

Advanced modelling consistently identified tidal range, diel cycles, and seasons as the primary drivers of cetacean occurrence.

5 Discussion

This study investigated how tidal dynamics, diel cycles, and anthropogenic activities influence cetacean abundance and behaviour at Fishguard Harbour. The key findings confirm a statistically significant relationship between tidal phase and cetacean occurrence, with peak abundances occurring during early ebb (tidal stage 0–0.25) and low tide (~0.5), while late flood (0.75–1) showed significantly lower abundance. Furthermore, strong temporal partitioning was observed among species, with harbour porpoises predominantly active at midday and bottlenose dolphins exhibiting bimodal patterns. Ferry presence had no significant effect on abundance or behaviour, though increasing boat counts amplified surface behaviours like leaping (OR = 2.19) and socializing (OR = 2.21). Advanced modelling (zero-inflated, BAM, Random Forest) consistently identified Julian day (seasonality), hour (diel cycle), and sea state as primary predictors of cetacean presence.

5.1 Ecological Interpretation of Tidal Patterns

Tidal cycles structure cetacean abundance as shown by the statistically significant influence of tidal phase on cetacean abundance ($p = 0.0016$). This is consistent with the "tidal conveyor hypothesis" proposed by Scott et al. (Scott et al. 2019) which proposes that ebb tides generate frontal systems which aggregate prey biomass. Peak cetacean abundances were observed during early ebb tide (tidal phase 0.0–0.25) and at low tide (~0.5) (Figure 4), suggesting that foraging efficiency was enhanced by the following mechanisms:

1. **Hydrodynamics**: Strong tidal currents concentrate plankton along convergence fronts, which creates feeding hotspots for forage fish and subsequently for cetaceans (Genin 2004).
2. **Energy conservation**: Cetaceans may exploit tidal currents to reduce movement costs during foraging, as seen in porpoise populations in the Bay of Fundy (Johnston et al. 2005).

At Fishguard Harbour, tidal phase explained approximately 2.8% of the variance in cetacean abundance ($\eta^2 = 0.028$). This effect size aligns with the region's intermediate position within the Celtic Sea's tidal energy gradient (Robins et al. 2018):

- **High-energy west** (Pentland Firth): 7 m/s currents, $\eta^2 = 0.12$ (Benjamins et al. 2016)
- **Intermediate central** (Fishguard): 2-4 m/s currents, $\eta^2 = 0.028$ (UK Hydrographic Office 2023)
- **Low-energy east**: <2 m/s currents, $\eta^2 < 0.01$ (Jones et al. 2021)

This west-to-east decrease in tidal energy alters benthic habitat structure and prey availability (Hoskins et al. 2019), which in turn drives spatial variation in tidal phase effects on cetacean abundance across sites (Pierpoint 2008, Scott et al. 2019). The intermediate η^2 value observed at Fishguard reflects this gradient.

It is important to note that tidal phase explained only 2.8% of variance in abundance ($\eta^2 = 0.028$), suggesting it is one of multiple drivers. These findings highlight the importance of the tides in shaping cetacean spatial distribution.

5.2 Temporal Niche Partitioning Mechanisms

The strong species-specific temporal segregation (Fisher's exact p = 0.0006) supports mechanisms of temporal niche partitioning which potentially reduce interspecific competition.

Harbour porpoises exhibited strict diurnal foraging patterns (92.4% midday detections), consistent with their high metabolic demands of approximately 10% body weight daily. This requires continuous feeding (Wisniewska et al. 2016). Their midday peak coincides with vertical migration of myctophid fishes, their primary prey in this region (Santos and Pierce 2013). By synchronizing their feeding with the predictable availability of these vertically migrating prey, harbour porpoises effectively optimize energy intake while avoiding temporal overlap with other species.

In contrast, bottlenose dolphins displayed greater temporal flexibility in their foraging activities, likely capitalizing on a broader range of demersal prey that are less tightly coupled to diel cycles.

On the other hand, bottlenose dolphins showed greater temporal flexibility, and probably capitalised on demersal prey less constrained by diel cycles. This flexibility in foraging behaviour may reduce direct competition with harbour porpoises by exploiting different prey types or feeding at alternate times.

However, these interspecific interactions are further complicated by well-documented aggressive behaviour from bottlenose dolphins towards Harbour Porpoises. This includes ramming, tossing, and forcibly pushing porpoises underwater. This is generally thought to be motivated by competition for space or food resources as well as social dominance (Cotter et al. 2011). This harassment may influence harbour porpoises' temporal distribution, reinforcing their strict midday foraging to potentially limit overlapping habitat use.

Rare species such as Risso's and common dolphins were observed too infrequently in this study to draw definitive conclusions regarding their temporal patterns, apart from indicating that they are very rarely found at Fishguard Harbour.

Temporal segregation may reflect competition avoidance, but as this study did not measure spatial overlap or aggressive interactions, these patterns could equally result from species-specific prey synchrony.

5.3 Anthropogenic Interactions

5.3.1 The Ferry Paradox

The non-significant ferry effect on abundance (p = 0.529) and behaviour (Figure 6) despite substantial noise emissions presents an interesting case of anthropogenic habituation. This likely reflects:

1. **Predictability**: Fixed schedules allow cetaceans to develop spatio-temporal avoidance strategies (Pirotta et al. 2015)
2. **Acoustic masking**: Consistent engine frequencies may facilitate neural adaptation in auditory processing (Schlack et al. 2007)
3. **Behavioural compensation**: Energy budget models suggest ferry noise represents only 3-5% of daily energy expenditure in porpoises, below avoidance thresholds (New et al. 2023).

In contrast to the non-significant effects of the ferry (a single boat), multiple boats elicited significant increases in the probability of leaping (OR=2.19) and socializing (OR=2.21) happening.

5.3.2 Surface Activity Amplification

The increased probability of leaping (OR = 2.19) and socializing (OR = 2.21) behaviours with boat presence may reflect adaptive responses, an idea which is validated by marine mammal regulatory frameworks:

1. **Attention Diversion**: Vessels disrupt foraging focus, triggering investigatory leaps consistent with Level B harassment thresholds (behavioural disruption) under NMFS guidelines (National Marine Fisheries Service 2011).

2. **Play Facilitation**: Dolphins exploit bow waves for energy-efficient travel, incorporating leaping behaviours that represent behavioural modification under MMPA definitions (National Marine Fisheries Service 2022).

3. **Communication Compensation**: Increased surface activity may compensate for engine-noise masking, aligning with acoustic interference responses in seismic survey Incidental Harassment Authorisations (National Marine Fisheries Service 2022).

These findings show a need for more nuanced management approaches in order to counteract the ecological impacts of boat traffic.

5.4 Methodological Insights

5.4.1 Zero-Inflation Challenges

The high prevalence of zero observations (68.1% of records) presented significant analytical challenges. This necessitated the use of zero-inflated statistical models which reflected real world conditions. Zeros may have fallen into the following categories:

1. **True ecological zeros**: The study took place in an area outside of the preferred habitat
2. **Perceptual zeros**: Animals were present but were not detected due to sea state limitations (The BAM model indicated a negative relationship between sea state and sightings)

Complementary application of Random Forest classification improved detection accuracy (out-of-bag accuracy = 85.7%) by incorporating complex detection covariates in order to similarly address the zero-inflation challenge. This machine learning technique trades ecological interpretability for predictive power. It reveals the importance of variables such as Julian Day (Figure 15), but not how they influence behaviour through measurable effect sizes.

5.4.2 Tidal-Temporal Interactions

The Big Additive Model (BAM) further revealed significant interactions between tidal range and hour of day (Figs. 9–10), with tidal effects predominating during daylight hours. The BAM accounted for 41.9% of deviance in cetacean abundance data, though residual patterns suggest there could be an influence of unmeasured variables such as prey density and distribution.

5.5 Conservation Implications

5.5.1 Tourism Management Framework

The behavioural responses to boats suggest need for revised management protocols, and therefore the following hypothetical tourism management framework was developed (Figure 16).

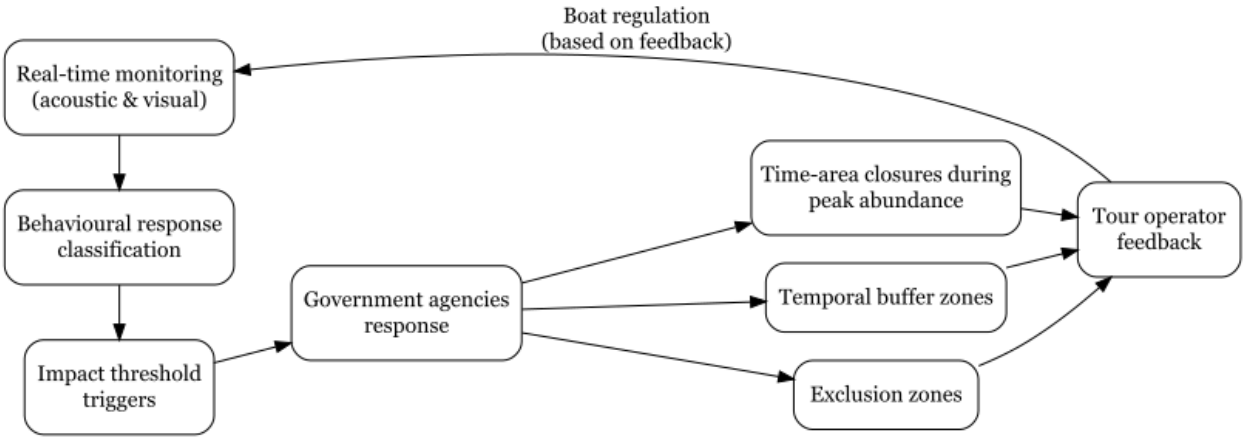

Figure 16: Proposed adaptive management framework for marine tourism.

Figure 16 proposes an adaptive management framework to mitigate vessel impacts on cetaceans. This is an evidence-based system that will integrate real-time monitoring (acoustic and visual) with behavioural response classification to establish impact thresholds. When thresholds are exceeded then government agencies enact targeted interventions: (1) time-area closures during peak abundance, (2) temporal buffer zones around tidal fronts, and (3) exclusion zones. Tour operator feedback should continuously refine vessel regulations, to create a feedback loop that ensures responsive management. The recommendations underpinning Figure 16 are expanded on in Appendix E. The proposed solutions require consultation with stakeholders and real-world testing.

5.6 Limitations and Future Research

Table 12: Summary of study limitations and mitigation strategies.

Table 12: Summary of Observational Limitations and Mitigations

Issue	Description	Impact	Mitigation
Zero-inflation	68% of observations recorded zero sightings, limiting count modelling	High	Used zero-inflated negative binomial models
Temporal coverage	Limited observations during night hours and winter months	Medium	Focused analysis on well-sampled periods
Boat activity data	Low variability in boat counts	Medium	Interpreted boat effects with caution
Overrepresentation of harbour porpoises and dolphins	More frequent observations of certain species may bias results	Medium	Results interpreted in context; caution advised when generalizing to all cetaceans
Detection bias (Beaufort state)	Beaufort >3 reduces detection probability	Medium	Detection conditions noted in analyses and interpretations
Tidal model limitation	Did not account for neap-spring amplitude modulation	Medium	Tidal effects interpreted within observed tidal range only
Absence of prey sampling	Lack of direct prey data limits ability to infer cetacean distribution drivers	Medium	Causal interpretations made with caution; recommend prey data inclusion in future studies
Boat type homogeneity	All vessels treated equally despite likely differences in impact	Medium	Interpreted boat activity effects with awareness of unmeasured vessel differences

Based on the limitations found in Table 12, future research should prioritize year-round sampling to capture seasonal variations, incorporate acoustic monitoring for comprehensive behavioural assessment, and expand spatial coverage to examine landscape-scale patterns. It should also include prey sampling and differentiate between boat types.

6 Conclusions

This study resolved how tidal dynamics, diel cycles, and anthropogenic activities shape cetacean distribution and behaviour at Fishguard Harbour. The hypothesis that sightings peak during high or flood tides was refuted. Peak abundance occurred during early ebb and low tide (tidal stages 0–0.25 and ~0.5), directly supporting the tidal conveyor hypothesis ($\eta^2 = 0.028$, $p = 0.0016$), with tidal phase being a statistically significant but minor predictor of abundance. Conversely, the hypothesis predicting crepuscular activity maxima was not supported; harbour porpoises exhibited strict midday presence (92.4% of occurrences), while bottlenose dolphins displayed flexible bimodal patterns, confirming strong temporal niche partitioning ($p = 0.0006$).

The anticipated link between boat activity and behavioural diversity was partially upheld: while ferry operations elicited no significant response (indicating habituation), general boat counts significantly amplified surface behaviours like leaping (OR = 2.19) and socializing (OR = 2.21), revealing non-acoustic disturbance pathways. The hypothesis regarding sea state was corroborated, as calmer conditions improved detection and revealed a true negative association between sea state and sightings ($\beta = -0.310$, $p = 0.003$).

Advanced modelling (zero-inflated GLMs, BAMs, Random Forest) overcame the issue of zero-inflation (68.1% zeros), identifying Julian day (seasonality), hour (diel cycle), and tidal-hour interactions as key predictors of occurrence (41.9% deviance explained).

These results demonstrate that cetacean ecology at Fishguard Outer Breakwater is governed by predictable environmental rhythms, species-specific behaviour, and responses to human activity. This understanding provides a framework for targeted conservation strategies in coastal habitats.

7 Acknowledgements

I would like to thank my daily supervisor, Nadia, and my first examiner, Dr. Marieke, for their support and guidance; Dr. Marlee Tucker for acting as my second examiner; staff, volunteers, and fellow interns at Sea Trust Wales for their assistance throughout this project; and my family for their encouragement.

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9 Appendices

9.1 Appendix A: Statistical Model Specifications

9.1.1 Tidal Phase Analysis

$$H_0 : \text{Median abundance equal across tidal phases}$$

$$H_1 : \text{At least one median differs significantly}$$

Test statistic: Kruskal-Wallis H = 15.400

9.1.2 Zero-Inflated Model Structure

$$\ln(\mu_i) = \beta_0 + \beta_1 \text{TidalRange}_i + \beta_2 \text{Hour}_i + ...$$
$$\text{logit}(p_i) = \gamma_0 + \gamma_1 \text{TidalStage}_i + \gamma_2 \text{Hour}_i$$

Where μ_i represents expected count and p_i represents zero-inflation probability.

9.2 Appendix B: Data Dictionary and Variable Descriptions

The data sources used to obtain the variables present in Table 13 were as follows:

- Historical
- Field recording
- Calculations

Table 13: Complete data dictionary for cetacean observation dataset

Variable_Name	Description	Data_Type	Units_Categories
DateTime	Observation date and time	datetime	YYYY-MM-DD HH:MM:SS
Species	Cetacean species observed	factor	HP = Harbour Porpoise
Species	Cetacean species observed	factor	CD = Common Dolphin
Species	Cetacean species observed	factor	RD = Risso's Dolphin
Species	Cetacean species observed	factor	BND = Bottlenose Dolphin
MinCount	Minimum number of individuals	integer	Count
TidalStage	Proportion of tidal cycle completed	numeric	0 (high tide) to 1 (next high tide)
TidalRange	Vertical difference between tides	numeric	Meters
SeaSt	Beaufort sea state	integer	0-9 (0=calm, 9=storm)
Hour	Time of observation	numeric	Decimal hours (0-24)
JulianDay	Day of year	integer	1-366
BoatCount	Number of vessels present	integer	Count
FerryPresent	Ferry activity during observation	binary	0=absent, 1=present
Travelling	Travelling behaviour observed	binary	0=absent, 1=present
Feeding	Feeding behaviour observed	binary	0=absent, 1=present
Leaping	Leaping behaviour observed	binary	0=absent, 1=present
TailSlapping	Tail slapping behaviour observed	binary	0=absent, 1=present
Socialising	Social behaviour observed	binary	0=absent, 1=present
Season	Seasonal category	factor	Spring, Summer, Autumn, Winter

9.3 Appendix C: Survey Protocol Summary

9.3.1 Site Setup:

- Position: Outer Breakwater, Fishguard Harbour (51.996°N, 4.976°W)
- Equipment: Marine binoculars containing compass bearings
- Timing: Daylight hours (07:00-18:00), optimal conditions (Beaufort ≤3)

9.3.2 Observation Protocol

- Scan duration: Continuous
- Scan method: Systematic 180° arc scan (seaward-facing)
- Data recording: Environmental conditions (every 15 minutes)
- Cetacean sightings: Minimum count that appeared (during 15 minute interval)

9.3.3 Species identification key

Harbour Porpoise - Small, triangular dorsal fin - Rounded head with no distinct beak, dark grey back and pale underside

Bottlenose Dolphin - Tall, curved dorsal fin - Rounded forehead (melon) with a short, stubby beak

Common Dolphin - Slender, curved dorsal fin - Hourglass colour pattern (yellowish patch in front, grey behind), long slender beak

Risso's Dolphin - Tall, curved dorsal fin, rounded blunt head with no distinct beak - Grey body covered in white or light grey scars and scratches

9.3.4 Data Recording Forms Example

Table 14: Example: Data Recording Form

Variable	Value
Site	Breakwater
Position	End
Date	2017-09-13
Observers	HD,TB
High_Tide	13:00
Low_Tide	19:45
HT_Height	4
LT_Height	1.8
Time	13:00
SeaSt	4
Wind_Direction	W
Visibility	3
Cloud_Cover	4
Precipitation	0
Min_Animals_Seen	3
Behaviour	T
Location	0
No_Porpoises_Photographed	0
Notes	Mother & Calf plus another adult

9.4 Appendix D: Data Quality Assurance Procedures

- Missing values were removed (including their spreadsheet rows)
- Invalid species entries were removed
- Temporal coverage was complete except for 2021 and 2023

9.5 Appendix E: Management Framework Support

Table 15: Evidence-based management recommendations

Recommendation	Scientific_Basis	Implementation_Level
Time-area closures (12:00-14:00)	92.4% HP sightings occur midday	High priority
Vessel exclusion zones	Surface behaviours increase >2 boats	Medium priority
Year-round monitoring	Julian Day β=0.008 ($p<0.001$)	Ongoing

9.6 Appendix F : Research Data Management

All research data, including primary observational records, tidal indices, and behavioural coding frameworks provided by Sea Trust Wales, was managed in strict compliance with Radboud University's Research Data Management Policy and the Data Sharing Agreement (DSA) with Sea Trust Wales. During active research phases, data was stored exclusively on Radboud University's OneDrive platform with role-based access restricted to the primary researcher (Mae McGinley Smith) and examiners (Dr. Marieke Van Katwijk, Dr. Marlee Tucker). No personal cloud storage, external drives, or unencrypted devices were used. Data processing occurred exclusively in R version 4.5.1, with all analytical scripts version-controlled and stored alongside the data in secured OneDrive folders.

Data usage adhered to the DSA, limiting analysis to environmental impacts on cetacean behaviour at Fishguard Harbour Outer Breakwater without reprocessing beyond agreed behavioural variables or linkage to identifiable entities. Post-project, processed datasets (aggregated counts, tidal-phase analyses, anonymised outputs) will be archived in the Radboud Data Repository (RDR), implementing FAIR principles.

All publications will attribute Sea Trust Wales as the data source, and original files will be deleted post-project per the DSA, retaining only anonymised derivatives in the RDR.