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Original Article

Tidally modulated burrow emergence rhythms of *Nephrops norvegicus*

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Abstract

The Norway lobster (*Nephrops norvegicus*) is one of the most important fishery resources in Europe and a key species for investigating biological rhythms in marine crustaceans, due its burrowing behaviour and wide depth distribution across continental shelves and slopes. Its availability to trawling is influenced by population-level burrow emergence events that vary in timing throughout the day. These emergence patters are known to depend on depth-related light intensity thresholds, but the effects of other environmental modulators remain less understood. Among them, the role of tidal cycles is poorly characterized, particularly in areas where strong hydrodynamic forcing may interact with day–night cues. Here, we assess the effects of tidal dynamics on *Nephrops* emergence in the Bay of Biscay (NE Atlantic, France), using a temporal analysis of population densities (i.e. by counting partially or fully emerged *Nephrops*) estimated from archived video-transects from 2016 to 2020 by Underwater Television surveys at depths between 28 and 133 m. Tidal data (i.e. sea level anomaly) were estimated to every transect, and 24-h variations in *Nephrops* density were analysed using Generalized Additive Models. Our results revealed a strong positive correlation between burrow emergence and the semidiurnal tidal cycle, with peaks typically aligned with flood currents and reduced densities with ebb phases, independently of the photoperiod. This finding contrasts with results from field studies in other regions using similar methodologies to analyse populations activity rhythms. It suggests that light intensity and tidal cycles influence burrow emergence patterns, with the strength of this modulation likely shaped by local habitat conditions. Behavioural responsiveness to tidal rhythms may therefore represent an adaptive trait in shelf-dwelling *Nephrops* populations inhabiting tidally dynamic environments.

Keywords: biological rhythms; stock assessment; demersal fisheries; sea level anomaly; day–night cycles; *Nephrops*

Introduction

The Norway lobster (*Nephrops norvegicus*), here after *Nephrops*, plays a key role in European fisheries, with annual catches typically around 60 000 tonnes (FAO 2023) and first-sale earnings of approximately €300 million (Issifu et al. 2022). Stock assessments are commonly based on Underwater Television (UWTV) surveys, which estimate burrow densities across known habitats to generate abundance indices. Over the past decade, these indices have fluctuated considerably, with a notable 40% decrease reported in 2024, coinciding with declining landing trends (ICES 2024). This has raised concern among fisheries managers regarding the sustainability of the stocks. Contributing factors may include trawling-induced alteration of benthic sediments from muddy to mixed types, elevated discard rates, and increasing water temperatures (ICES 2024). However, another key factor may be variation in the *Nephrops* burrow emergence behaviour, which depends on environmental and temporal conditions (Aguzzi et al. 2012), and is not yet fully understood.

Nephrops constructs and inhabits complex burrow systems and emerges periodically out onto the seabed; this behaviour is influenced by a biological clock and results in locomotor rates synchronized upon light and dark cycles (e.g. Atkinson and Naylor 1976, Chiesa et al. 2010, Sbragaglia et al. 2013, Aguzzi et al. 2023). On continental shelves (i.e. 50–150 m), populations typically exhibit two major emergence events at crepuscular hours, leading to dusk and dawn trawl catches peaks, whereas a single midday peak occurs at greater depths (Simpson 1965, Naylor and Atkinson 1976, Hammond and Naylor 1977, Redant and De Clerk 1984, Aguzzi et al. 2003). While diel emergence patterns have been well documented, the modulation of emergence by tidal phase, particularly at the visible population level, remains less clearly understood (e.g. Aguzzi et al. 2004, Sbragaglia et al. 2015).

Tides generate horizontal barotropic currents that can alter conditions throughout the water column, including near the seabed, where they may act as behavioural cues for benthic species like *Nephrops*. Laboratory experiments support this

idea, showing that under simulated tidal flow, *Nephrops* reduce emergence during periods of increasing current velocity, often orienting downstream, if flow occurred during the active locomotor phase (Sbragaglia et al. 2015). However, field evidence for this behaviour is limited. One study reported higher catches during high tidal elevation on the shelf (Bell et al. 2008), whereas UWTV surveys at similar depths around Ireland reported day–night but not tidally modulated emergence rhythms (Aguzzi et al. 2021). In the Mediterranean, acoustic telemetry has recently been used to investigate how individual locomotor rhythms contribute to the formation of population-level emergence peaks, in an effort to explain the diel catch patterns, historically reported on the upper slope (around 350 m depth). This research showed that individual emergence could be arrhythmic, depending on the phase dissociation between light and current cycles (Aguzzi et al. 2023).

Understanding how both day–night and tidal cycles influence *Nephrops* burrow emergence is crucial to improve the accuracy of UWTV-based stock assessments in most European waters, which presently estimate stock densities from burrow counts rather than the counts of individual *Nephrops* (STECF 2023). In the future, incorporating the timing of day and phase of the tide into UWTV survey design may help account for better density estimations, where burrows and *Nephrops* counts are compared, under the assumption that one individual typically occupies a single burrow system (Aguzzi et al. 2023). Other factors such as seasonal temperature changes, reproductive state, and age structure also affect emergence patterns and may influence catchability (Farmer 1974, Tuck et al. 1994, Aguzzi et al. 2004, Aguzzi and Sardà 2008). In this study, we investigate *Nephrops* emergence dynamics on the continental shelf of the Bay of Biscay (NE Atlantic, France), a region characterized by a strong tidal regime (e.g. Karagiorgos et al. 2020). Using UWTV data collected at depths between 28–133 m over five consecutive years (2016 to 2020), we assess the potential influence of tidal cycles on short-term fluctuations in population density, beyond the classical light-driven emergence behaviour. The findings aim to support more accurate and ecologically informed survey strategies in tidally influenced environments.

Methods

Biological data collection and processing

UWTV surveys were conducted annually from 2016 to 2020 in the Bay of Biscay (NE Atlantic Ocean) at depths ranging from 28 to 133 m. All surveys followed the protocol established by the ICES Working Group on *Nephrops* Surveys for stock assessment purposes (ICES 2020). Surveys took place in spring (April–May) for 2016–2019 and in July 2020 to capture summer and minimize seasonal variation in emergence related to reproductive cycles and activity rhythms (Aguzzi et al. 2021). At each station, the UWTV sledge equipped with a high definition camera was deployed and towed for 10 min once stable. The vessel position was tracked using a Differential Global Positioning System (DGPS) and the sledge position was monitored using an on-board Ultra Short Baseline acoustic transponder. Positional data were recorded every 2 to 5 seconds and used to calculate the video-swept distance over the ground (~200 m), following ICES recommendations (Dobby et al. 2021). All visible *Nephrops* were counted from each video transect and classified as either fully emerged or partially emerged (i.e. door-keeping behaviour; Aguzzi et al. 2007). Densities (individuals per m^2) were calculated using the video-swept area (Aguzzi et al. 2021) and timestamped to the midpoint of each transect. In total, 782 transects were analysed. Hourly densities were aggregated and visualized using Hovmöller diagrams in R (R Core Team 2024), with time of day on the *y*-axis and sampling date on the *x*-axis. *Nephrops* emergence was measured as the number of visible individuals per m^2 in each UWTV frame. Density peaks were defined post hoc as temporal increases in *Nephrops* counts relative to preceding and following time steps, typically occurring during flood phases and recurring within 24-h cycles.

Tidal data and hydrodynamic variables

Tidal elevations and depth-averaged currents were estimated for each location with their time stamp corresponding to the observation dataset, using the global barotropic TPXO9-atlas-v5 tidal model (Egbert and Erofeeva 2002), which has a spatial resolution of 1/30° (~3–4 km). The model assimilates satellite altimetry and provide tidal constituents for coastal and shelf environments. Tidal predictions were computed in MATLAB® (The MathWorks Inc., Natick, MA, USA) using the Tide Model Driver (TMD) version 3.0 (Greene 2023), accessing the TPXO9 NetCDF dataset with tmd_predict function. For each UWTV observation, tidal elevation and current velocity components, zonal (u) and meridional (v), were extracted. The model provides a single current value that represents the average flow throughout the water column, calculated as the Euclidean norm $\sqrt{U^2 - V^2}$. Tidal volume transport was similarly derived from its U and V components. Transport (m^2 s^{-1}), which integrates horizontal velocity with the vertical structure of the water column, is commonly used to represent hydrodynamic process relevant to shelf ecosystems (Aguzzi and Sarda 2008). In our study, transport and current were highly correlated ($r^2 = 0.82$), therefore only one was retained to avoid redundancy. Given our focus on physical-biological interactions at the seabed, we selected current speed as the primary hydrodynamic predictor, as it more directly reflects near-bottom flow conditions experienced by *Nephrops*. Tidal predictions were validated against sea-level anomalies from Concarneau and Port-Bloc tide gauges, showing strong agreement ($r^2 = 0.96$; Supplementary Fig. S2). This confirms that survey transects encompassed both spring and neap tidal phases, with tidal elevations ranging from –2 to +2 m and current speeds from 0.01 to 0.5 m s^{-1} (Table 1).

Statistical analyses

Generalized Additive Models (GAMs; Hastie and Tibshirani 1990) were fitted using the mgcv package in R (Wood 2011). These flexible models were used to assess diel rhythms, i.e. hourly *Nephrops* densities, following the form:

$$E\,(NEP) = g - 1(\beta_0 + \beta_{year} + s\,(HD,\ bs = cc,\ k = 24) + te\,(lon, lat) + \varepsilon$$

where *E(NEP)* is the expected density, *g* is the log link function, β_0 is the intercept, β_{year} are the parametric coefficients for year (categorical factor), *s* is the smoothing function with the term *bs* = "*cc*" specifying the 24 h knot based ($k = 24$) cyclic cubic regression spline. *te* is the tensor smooth function for the interaction among transect locations (i.e. latitude and longitude) accounting for spatial dependence affecting the 24-h

Table 1. Annual descriptive statistics of biological and environmental variables measured at UWTV survey stations in the Bay of Biscay during the cruises from 2016 to 2020.

Year	Sampling period	Number of stations	Parameter	Depth (m)	Door-keeping (Ind/m^2)	Outside (Ind/m^2)	Fraction of door-keeping individuals	Tidal elevation (m)	Current speed (m/s)	Water transport (m^2/s)
2016	From 04 May to 15 May	196	Mean	97.5	0.011	0.017	0.527	−0.006	0.178	17.571
			SD	19.9	0.024	0.042	0.378	1.309	0.080	10.062
			Min	46.0	0.000	0.000	0.000	−2.269	0.024	1.972
			Max	130.0	0.194	0.297	1.000	2.301	0.429	47.184
2017	From 06 May to 17 May	124	Mean	98.5	0.005	0.011	0.452	0.014	0.165	16.004
			SD	19.0	0.010	0.028	0.382	1.120	0.061	7.300
			Min	45.0	0.000	0.000	0.000	−1.812	0.037	2.164
			Max	133.0	0.051	0.210	1.000	1.828	0.341	35.369
2018	From 19 Apr to 01 May	183	Mean	101.0	0.003	0.009	0.315	−0.013	0.171	16.597
			SD	17.2	0.008	0.020	0.401	1.145	0.082	7.858
			Min	45.0	0.000	0.000	0.000	−2.135	0.033	2.277
			Max	130.0	0.071	0.119	1.000	1.999	0.505	44.577
2019	From 02 May to 14 May	145	Mean	97.6	0.003	0.004	0.566	0.032	0.152	14.273
			SD	18.5	0.006	0.009	0.419	1.168	0.078	7.878
			Min	45.0	0.000	0.000	0.000	−1.957	0.009	0.372
			Max	130.0	0.032	0.043	1.000	2.006	0.442	44.516
2020	From 22 Jul to 31 Jul	134	Mean	101.9	0.009	0.005	0.750	−0.031	0.155	15.434
			SD	17.6	0.013	0.015	0.176	1.177	0.079	8.537
			Min	28.0	0.000	0.000	0.000	−2.075	0.027	1.162
			Max	130.0	0.095	0.119	1.000	2.150	0.348	39.906
2016 - 2020		782	Mean	99.3	0.006	0.009	0.531	−0.001	0.165	16.117
			SD	18.5	0.015	0.027	0.401	1.206	0.078	8.556
			Min	28.0	0.000	0.000	0.000	−2.269	0.009	0.372
			Max	133.0	0.194	0.297	1.000	2.301	0.505	47.184

The fraction of door-keeping individuals refers to the proportion of all visible Nephrops observed at the burrow entrance but not fully emerged (i.e. door-keeping/[door-keeping + outside]). The final row (2016–2020) present statistics derived from the combined dataset across all surveys.

burrow emergence rhythms of *NEP*, and ε is the residual error term.

Model were fitted for (i) for fully emerged individuals only, (ii) door-keepers, and (iii) total densities (summing up fully emerged and door-keepers) per survey and for all the surveys.

For further alignment with *Nephrops* diel patterns, diel pattern of tidal elevation was assessed following the form:

$$E\,(TID) = \beta_0 + \beta_{year} + s\left(HD,\ bs = cc,\ k = 24\right),$$
$$corAR1(form \sim 1|Year), + \varepsilon$$

where E(TID) is the expected tidal elevation. The correlation term [corAR1(form = ~ 1 | Year)] assumes residuals autoregressive correlation structure of order 1 with respect to the sampling period (*Year*).

The effect of tidal elevation (*TideE*) on current velocity was assessed using GAMs of the form.

$$E(Y_i) = g - 1(\beta_0 + \beta_{year} + s(TideE) + te(lon, lat) + \varepsilon$$

where $E(Y_i)$ is the expected current velocity.

The same model structure was applied to evaluate the influence of tidal elevation on (i) total *Nephrops* density and (ii) the proportion of door-keeping individuals, with *Yi* representing the corresponding response variable in each case. For the case of proportion of door-keepers, *g* represented a logit link function to model the quasibinomial response (proportion data), following standard practice for bounded variables (Wood 2011).

The models were checked for residual patterns, and overfitting. The degree of smoothing was estimated using Generalized Cross-Validation scores. Visualization of smooth effects and spatial contours was performed using base R plotting functions and mgcv built-in plot routines.

Finally, correlations between the modelled 24-h burrow emergence patterns (by density data) and tidal elevation were carried out by non-parametric Spearman test, as the former data did not show normal distributions (being generally bimodal at crepuscular sunset and sunrise hours on the shelf; e.g. Hammond and Naylor 1977, Aguzzi et al. 2003).

Results

The environmental and biological conditions characterizing each annual UWTV survey are summarized in Table 1. These data provided the background for interpreting subsequent analyses of diel and tidal emergence patterns.

Diel trends were first visualized using a Hovmöller diagram (Fig. 1), which provided an overview of density variation (as a proxy for burrow emergence patterns) across dates and hours. Although the diagram revealed broad temporal structure, variability among individual transects and gaps in sampling obscured consistent daily patterns. This variability highlighted the need for statistical modelling to more robustly characterize diel and tidal rhythms. GAMs fitted to the 24-h cycle (Fig. 2; Table S1) revealed clear diel emergence patterns. The bimodal rhythm, characterized by two daily peaks, was primarily driven by fully emerged individuals (Fig. 2a), whereas door-keeping individuals showed no significant diel structure (Fig. 2b). To ensure full behavioural representation and increase statistical power, we therefore combined both categories in subsequent analyses. This approach aligned with UWTV survey practices, which consider both fully emerged and door-keeping individuals in abundance estimates.

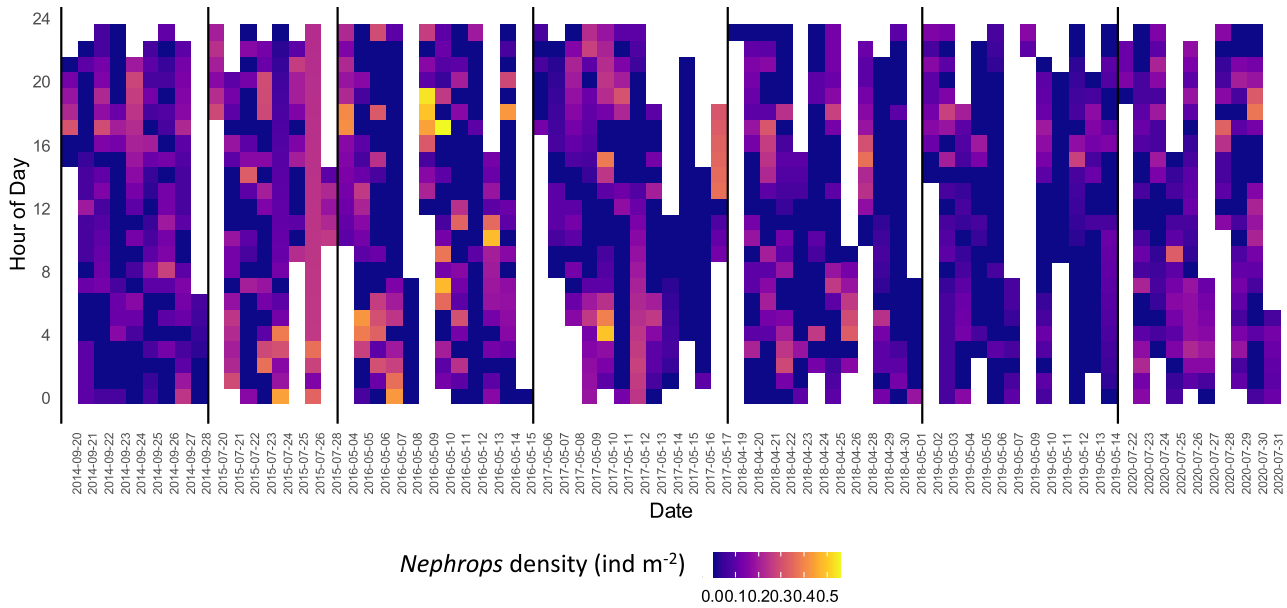

Figure 1. Hovmöller diagram of *Nephrops* burrow emergence (considering both door-keeping and fully outside the burrows) by date (*x*-axis) and hour of day (*y*-axis) from UWTV surveys (2016–2020). Colour scale indicates *Nephrops* density. Missing values shown (in white) represent time bins within the 10-min video transects for which density could not be reliably estimated due to image quality or observational constraints, as per ICES UWTV survey protocols. Start and end times of the recordings vary between surveys (conducted in different months) and sometimes between transects.

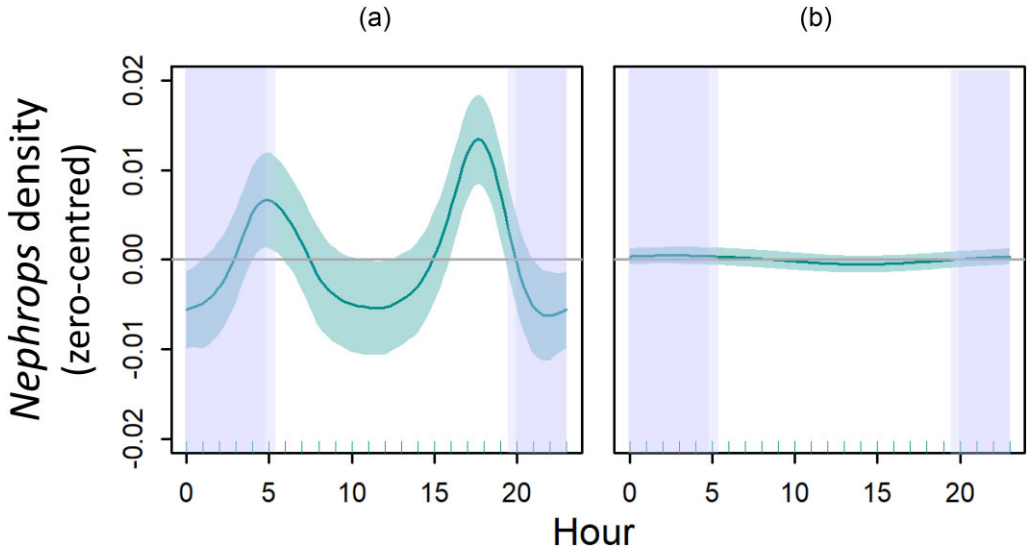

Figure 2. GAM smooths showing diel patterns of *Nephrops* density as a function of hour of the day; (a) fully emerged individuals only, (b) door-keeping individuals only. Shaded areas indicate 95% confidence intervals. Night-time hours are indicated, with lighter shading representing the range of night-time periods across surveys conducted in different months.

Diel emergence peaks aligned closely with tidal phases, generally mirroring the semi-diurnal tidal cycle (Fig. 3 a–e; Table S2). However, the bimodal pattern in *Nephrops* density was not always evident; in some years, either the dusk peak (e.g. 2017) or the dawn peak (e.g. 2019 and 2020) was reduced. Both peaks were clearly present only in 2016 and 2018. GAMs fitted to tidal elevation over the full study period and confirmed the usual presence of two dominant episodes of burrow emergence, corresponding to semi-diurnal tidal peaks: one around dawn (04:00–07:00) and another ~2 h before dusk (17:00–19:00) (Fig. 3 f).

Nephrops densities on the seabed, as estimated by the general GAM fitted to data from all annual surveys, showed a strong correlation value with tidal elevation ($r = 0.73$, $P < 0.01$). The weakest correlation was observed in 2019 (($r = 0.14$, $P = 0.17$), when no density peak was detected around sunrise. Nevertheless, when restricting the analysis to the period between midday and midnight, the correlation became significant and increased to $r = 0.55$. In 2017 and 2020, which both exhibited a single density peak. The correlation between *Nephrops* density and tide height strengthened markedly when focussing only on the corresponding peak period (12:00 to 24:00 in 2017 and 00:00 to 12:00 in 2020). In

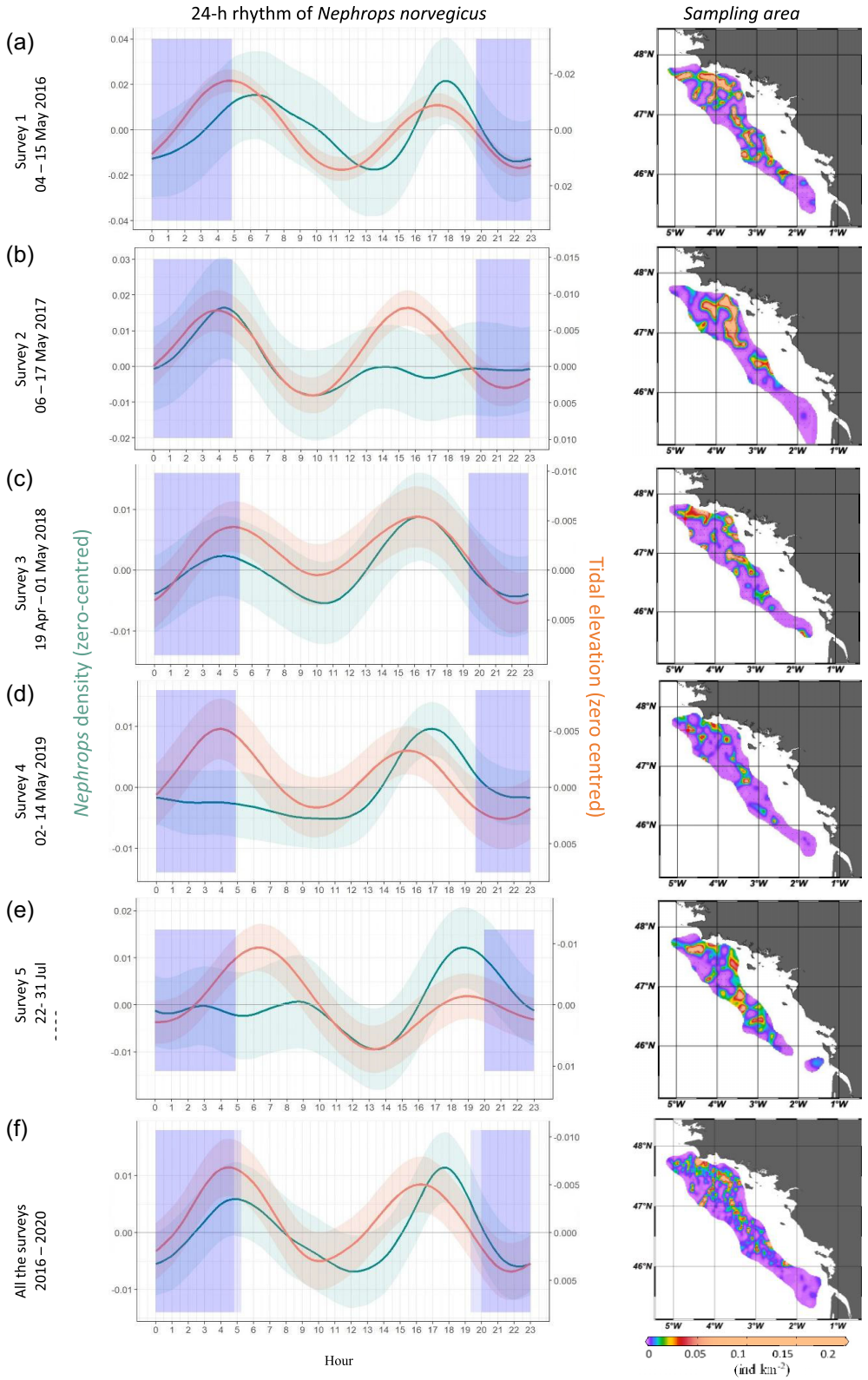

Figure 3. GAM fits (left panels) showing diel pattern of *Nephrops* density in relation to tidal elevation and the day–night cycles in the Bay of Biscay. Panels (a)–(e) correspond to each annual surveys; panel (f) shows the combined model across all surveys. The fitted curves represent *Nephrops* density and tidal elevation, with shaded areas indicating 95% confidence intervals. Night-time hours are indicated, and in panel (f) the range of night-time periods across surveys conducted in different months is shown with lighter shading. Maps on the right show sampling locations and *Nephrops* densities for each survey (a–e) and for the combined dataset (f). Maps were produced using Ocean Data View (Schlitzer, 2024).

both cases, the correlation rose from $r = 0.58$ and $r = 0.48$, respectively, to 0.99.

Tidal elevation had a clear influence on current speed, with maximum velocities occurring near mid-tide (around mean sea level) and decreasing towards both low and high water (slack) (Fig. 4a; Table S3). It also exhibited a non-linear effect on total *Nephrops* density (Fig. 4b; Table S3) and the proportion of individuals displaying door-keeping behaviour (Fig. 4c; Table S3). At low tide (below −1 m), total density declined markedly, likely indicating that more individuals remained within their burrows. This is supported by a simultaneous rise in the proportion of door-keeping individuals, suggesting that emergence was largely limited to partial exposure. As tidal elevation increased towards mean sea level and high tide, both responses flattened, indicating a reduced influence of tidal height beyond mid-tide.

The observed tidal modulation of *Nephrops* emergence was further supported by correlation analyses between surface density and tidal state (Table 2). Spearman rank correlation tests revealed strong positive associations between modelled 24-h *Nephrops* surface densities (as a proxy for burrow emergence) and tidal elevation. Across all surveys, emergence peaks were consistently aligned with periods of high tidal elevation, typically during the flooding phase of the tide, while lower surface densities coincided with low tidal elevation values, corresponding to ebb tides. Particularly high correlation coefficients were observed in 2016 ($r = 0.72$), 2018 ($r = 0.89$), and for the combined dataset across all years ($r = 0.73$), all with $P < 0.001$. In years where only a single emergence peak was evident (2017, 2019, and 2020), additional 12-h correlations yielded even stronger associations, with *r*-values approaching 0.99.

Discussion

The present work shows a relationship between *Nephrops* burrow emergence and tidal cycles on the NE Atlantic shelf, extending beyond the traditionally established effects of photoperiod. In doing so, it seeks to explore additional ecological factors that may modulate behavioural responses to environmental cues, such as strong tidal current flows. In the region of the Bay of Biscay where the UWTV surveys were conducted, the observed tidal regime includes several weaker constituents beyond the dominant semidiurnal M2 one (see Supplementary Tables S4 and S5), resulting in a stable tidal signal with no visible damping over weekly time scales (see Fig. 3). The M2 constituent represents the principal lunar semidiurnal tide, with a period of ∼12.42 h, and is typically the strongest tidal component in many shelf seas. This stability ensures that the timing of maximum flood and ebb currents, which typically occur around mid-tide (near mean sea level) and weaken towards high and low water (slack periods), remains consistent throughout each survey period.

UWTV data, in conjunction with modelled tidal elevation and current velocities, indicate that *Nephrops* densities at the seabed surface increase during the flood phase and decline during ebbing, suggesting a positive association between emergence and rising tidal flow. This pattern suggest that emergence behaviour is modulated by the tidal cycle, whereby stronger currents during flooding may act as cues promoting emergence, in contrast to ebb tides, which coincide with reduced densities. This duality contrasts with previous studies reporting only a negative correlation between current speed and catchability (Hillis 1996). Laboratory studies simulating photoperiod and current flow (Sbragaglia et al. 2015) showed that strong currents can inhibit emergence, but *Nephrops* already emerged during the darkness remained outside the burrow. In our case, emergence increased during flooding and decreases during ebbing, forming a bimodal pattern centred around sunrise and anticipating sunset. These observations suggest that current speed alone does not fully explain emergence patterns.

The analysis of modelled surface densities and tidal elevation (see Table 2) reinforces this interpretation. Significant positive correlations between Nephrops emergence and tidal elevation were observed across most years, especially over full 24-h cycles (e.g. $r = 0.72$ in 2016; $r = 0.89$ in 2018). Notably, when correlations were restricted to 12-h periods aligned with observed emergence peaks (i.e. flood tides), coefficients increased markedly ($r = 0.99$ in 2017, 2019, and 2020). In contrast, full-day correlations weakened in some years (e.g. $r = 0.14$ in 2019), likely due to the asymmetrical emergence response between rising and falling tides. These results indicate a consistent synchrony between emergence and the flooding phase, possibly modulated by hydrodynamic and ecological conditions that differ between flood and ebb tides.

The bimodal emergence pattern was not constant across years. In some surveys, one of the two peaks was absent, for instance, at sunset for 2017 or before sunrise in 2019 and 2020. This inconsistency suggests that while emergence may be driven by an optimum light intensity range (Chapman 1985), the synchrony and amplitude of flow and ebb tides, may modulate expression of this rhythm, ensuring that at least one emergence peak occur every 24 h. Other factors, including geophysical cycles and unconsidered ecological variables, may also contribute.

Internal tides have been shown to synchronize the movement of deep-sea megabenthic species, with the strength of synchrony varying by locomotion mode, stronger in swimmers (e.g. fishes), moderate in walkers such as *Nephrops*, and weakest in crawlers (e.g. gastropods) (Aguzzi et al. 2010). These stratified internal flows, interacting with seabed topography, also influence the pulsing intensity of the Benthic Boundary Layer (BBL). We suggest that BBL currents may synchronize *Nephrops* burrow emergence behaviour along the Atlantic margin, with local bathymetric variation modulating the strength of this influence. This may explain why emergence modulation was not detected in Galway Bay UWTV data (Aguzzi et al. 2023), but was evident in the Farn Deeps by trawling (Bell et al. 2008) and the Bay of Biscay (present study).

Secondly, the pattern of maximum current velocity occurring near mid-tide or around mean sea level and decreasing at very low and very high tides, reflects the dynamics of tidal currents, which are strongest during rising and falling tides. At tidal extremes, velocity slows down to "slack water" as the current change direction. This progression in tidal height and flow is commonly approximated by the rule of twelfths, a heuristic used in navigation to describe how the rate of tidal height change accelerates toward mid-tide and slows near high and low water. Because barotropic tidal currents are largely proportional to this rate of change, the heuristic is consistent with our observation that current velocities peaked at mid-tide and weakened at tidal extremes (Fig. 4a). When compared with *Nephrops* densities (see Fig. 4b, c), this pattern suggests

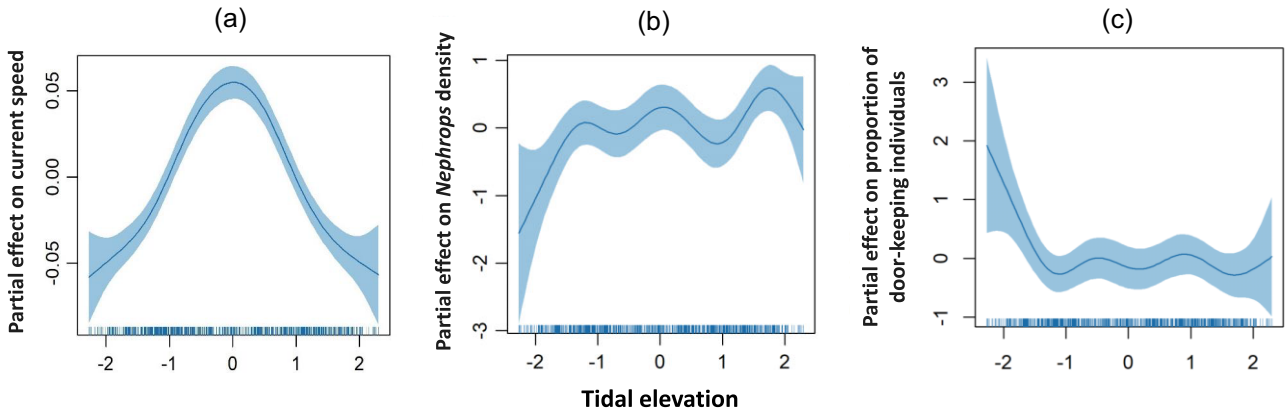

Figure 4. Non-linear effect of tidal elevation as estimated by a GAMs, on (a) current velocity, (b) the total *Nephrops* density, and (c) on the proportion of door-keeping individuals relative to the total *Nephrops* count per unit of area. Shaded areas represent 95% confidence intervals. Tick marks along the *x*-axis indicate the distribution of observed tidal elevation values.

Table 2. Spearman rank correlations between modelled 24-h Nephrops surface densities and tidal elevation.

Survey	Hours of peak emergence	Range of hours for correlation	Correlation results		
			S	*r*	*P*
2016	6–7 & 18	0 -24	46755	0.72	<0.001
2017	4–5	0 -24	69676	0.58	<0.001
		0 -12	264	0.99	<0.001
2018	4 & 16–17	0 -24	18334	0.89	<0.001
2019	17	0 -24	143665	0.14	0.171
		12–24	8384	0.55	<0.001
2020	18–19	0 -24	87067	0.48	<0.001
		12–24	126	0.99	<0.001
All the surveys	5 & 18	0 -24	44319	0.73	<0.001

Surface density was used as a proxy for burrow emergence. Additional 12-h correlations were included for surveys with a single daily peak (2017, 2019, 2020). *S*-values is the Spearman test, *r* is the correlation coefficient, and *P* the probability of observing the result under the null hypothesis ($P < 0.05$ indicates statistical significance).

a tidal modulation of emergence behaviour, with Nephrops more likely to remain partially emerged during low tide and more likely to be fully emerged as the tide rises. This may reflect a still unknown combination of ecological factors acting differently during rising and falling tides.

Seasonal temperature changes can influence the burrow emergence rhythms of *Nephrops norvegicus*. In northern waters such as the Irish Sea and NE Atlantic, emergence increases in late spring and summer as bottom temperatures rise and ovigerous females complete incubation (Farmer 1974, Aguzzi and Sardà 2008). Catch rates and burrow counts are typically higher in summer and lower in winter, indicating temperature-modulated seasonal rhythms (Tuck et al. 1994, Aguzzi et al. 2004). Even in the more thermally stable Mediterranean, emergence is still elevated during warmer months (Aguzzi et al. 2004). Although not assessed in this study, temperature likely interacts with other environmental drivers to influence emergence timing and catchability. Behavioural factors such as predator avoidance, fishing disturbance, and density-dependent competition may also modulate emergence rhythms. Individuals exposed to repeated trawling or high conspecific density may reduce emergence duration or shift activity to safer periods (Aguzzi et al. 2004). Similarly, high population density may promote competition for shelter or food, leading to altered emergence dynamics (Aguzzi et al. 2021). These behavioural modulations may interact with ecological factors, including predator–prey interactions and chemical signalling.

Nephrops is a generalist predator and scavenger feeding on crustaceans, echinoderms, polychaetes, molluscs, and fish (Baden et al. 1990, Cristo and Cartes 1998, Zacchetti et al. 2022), whose chemical cues may be conveyed by currents. Adult stages are preyed upon by cod, (*Gadus morhua*) in the Atlantic (Björnsson and Dombaxe 2004) and by elasmobranchs and demersal fishes in the Mediterranean (Vigo et al. 2022). Many benthopelagic species display vertical migrations into the BBL (Aguzzi et al. 2015), eliciting intermittent responses in benthic predators and prey (Angel 1990). However, to our knowledge, no study has demonstrated a suppression of *Nephrops* emergence in the presence of food or predator stimuli, even under laboratory conditions.

Conclusions

Our results show a strong correlation between tidal cycles and *Nephrops* burrow emergence in the Bay of Biscay, with population densities at the seabed surface generally peaking twice daily. This bimodal pattern highlights the interplay between tidal dynamics and sunlight in modulating the species biological rhythms. The phase of the tidal cycle and current speed play a key role in shaping emergence behaviour. However, consistency with this pattern varied between years, suggesting the

influence of additional, yet unidentified, ecological factors on the species biological clock. These findings support the integration of tidal phase and current dynamics into UWTV survey design, particularly in hydrodynamically active areas, to improve the accuracy of abundance estimates and minimize behavioural bias in stock assessments. Incorporating tidal status at the time of the observation, along with contextual ecological data such as predator and prey abundances, would strengthen the ecological interpretation of emergence patterns. Such an approach, aligned with Ecosystem-Based Management principles, would provide a more comprehensive understanding of *Nephrops* behaviour in response to both abiotic and biotic drivers.

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Supplementary material

The supplementary material is available at *ICESJMS* online.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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