



Importance of multi-sensor observations to advance species co-occurrence knowledge: a demonstration of two acoustic technologies

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ABSTRACT: Multi-sensor observations, integrated across time and space, may bridge knowledge gaps in ecosystem dynamics, one aspect of which is species co-occurrence. In the present work, we combined data streams from 2 acoustic technologies; passive acoustic monitoring (PAM) and acoustic telemetry (AT) jointly installed under the LifeWatch project. We made use of existing long-term data series from studies on single-species dynamics, to investigate the co-occurrence of multiple species: European seabass, Atlantic cod and cetaceans (harbour porpoise and dolphins), in the Belgian part of the North Sea. Common co-occurrence analyses were applied to a combined PAM and AT hourly presence–absence matrix at different spatial and temporal resolutions. The fish species were in the presence of harbour porpoise at least one-third (seabass) to nearly half (cod) of the time they were detected. At a seasonal resolution, we did not observe probabilities of occupancy to be higher or lower than what is expected by chance, while we could discern patterns of co-occurrence when using an hourly resolution. Analyses done at an hourly resolution showed that porpoises have a significantly higher probability of co-occurrence with cod or seabass during autumn and winter nights. Developing these large-scale networks of integrated acoustic instruments while considering species co-occurrences would further expand data applicability. Considering co-occurrence in ecological research is a step towards ecosystem-based management of our oceans.

KEY WORDS: Passive acoustic monitoring · *Phocoena phocoena* · Dolphins · Belgium · North Sea · Acoustic telemetry · *Dicentrarchus labrax* · *Gadus morhua*

1. INTRODUCTION

Ecological research has flourished from investigating single-species distributions to the interactions of various species across space and time in community and ecosystem research (Carmel et al. 2013). Different species having similar habitat requirements are drawn to the same environments. Over time, they may avoid or actively seek each other's presence for interactions such as competition, predation or collaboration (Blanchet et al. 2020). Anthropogenic impacts ranging from global climate change to local habitat

loss affect species differently, and the resulting cumulative effects on species interactions are poorly understood (Tulloch et al. 2018, Hodgson & Halpern 2019). Understanding how species co-occur within communities is therefore a vital step towards ecosystem-based management (EBM; Howell et al. 2021), wherein cumulative impacts are considered, and management is geared towards protecting the ecosystem as a whole (Rosenberg & McLeod 2005).

A key aspect of well-functioning marine ecosystems are predator–prey relationships and interactions (Hazen et al. 2019), involving, amongst others, various

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species of cetaceans and fish. Consuming significant amounts of prey biomass, marine predators can impact food webs through top-down forcing (Ballance 2018). In addition, as migratory predators make their way from one habitat to another, they are key transportation elements within nutrient cycles (McInturf et al. 2019). Marine species face a range of anthropogenic stressors, including fisheries, shipping, chemical, noise and waste pollution (Maxwell et al. 2013). As a result of interactions between marine species (competition, predation, collaboration), a threat to one species can impact co-occurring species. Fisheries bycatch in particular is one of the primary causes of the decline of some marine megafauna at risk, such as sea turtles, sharks and cetaceans (Lewison et al. 2004, Jog et al. 2022). For example, bycatch of common dolphins *Delphinus delphis* Linnaeus, 1758 in the pelagic trawl fishery in the Bay of Biscay has been attributed to the dietary overlap of common dolphins with the fisheries' target species, the European seabass *Dicentrarchus labrax* Linnaeus, 1758 (Spitz et al. 2013). Understanding patterns of co-occurrence of marine predators and prey is therefore key to establish better conservation and management plans that consider species ecology.

Some acoustic technologies gather long-term presence and behaviour data of aquatic animals. Passive acoustic monitoring (PAM) can be used to record sounds produced by aquatic animals, such as whistles and echolocation clicks of cetaceans (Schaffeld et al. 2016, Nuutila et al. 2017, Williamson et al. 2022). In acoustic telemetry (AT), an animal is fitted (externally or internally) with an electronic tag that transmits an acoustic signal which can be detected when in the detection range of an acoustic receiver (Hussey et al. 2015). Both acoustic technologies have greatly advanced marine ecological research, but have some (dis)advantages in observing these animals in the wild: in PAM, detecting the presence of a species relies on the animal effectively producing sounds, with its presence remaining undetected during silent periods, and PAM is unable to distinguish individuals. An acoustic receiver can only detect an animal tagged with an acoustic tag, but can provide information on individual movement behaviour (Brown-scombe et al. 2022).

In the present work, we combined PAM and AT technologies, making use of long-term data series from studies on single-species dynamics, to investigate the co-occurrence of multiple species. We therefore (1) described the jointly installed technologies and data management flow, (2) modified and applied species co-occurrence analyses that are commonly used to suit the combined long-term data series at

high temporal resolution from PAM and AT and (3) showed how the combined technologies can contribute to community and ecosystem ecology research.

2. MATERIALS AND METHODS

2.1. Study area

The Belgian cetacean passive acoustic network (BCPAN) has been collecting long-term data on the presence of porpoises and dolphins in the Belgian part of the North Sea (BPNS) since 2016, as part of the Life-Watch observatory (<https://lifewatch.be/en/cetacean-passive-acoustic-network>). Echolocation signals of odontocete cetaceans (with the exception of sperm whales) can be recorded using C-PODs (Chelonia Ltd.). A C-POD is a PAM logger programmed to autonomously log echolocation clicks over long periods of time (up to 4 mo; Roberts & Read 2015). C-PODs listen continuously for high frequency clicks (20–160 kHz) and store the parameters of these clicks (e.g. frequency, bandwidth, sound pressure level, duration), and not the raw recording itself. Each BCPAN station consists of a multi-use platform moored on the seabed (Fig. 1): a tripod frame originally designed for acoustic telemetry studies (Goossens et al. 2020). The adapted frame fits a C-POD in the floatable collar in a fixed vertical position, together with a VR2AR acoustic receiver from InnovaSea Systems. Acoustic receivers detect acoustic signals at 69 kHz transmitted by electronic tags implanted in or attached to individual organisms. These tags allow the presence of individual animals to be detected when they are within the detection range of the acoustic receiver. The acoustic receivers are equipped with an acoustic release system, enabling the retrieval of all equipment (design and deployment protocol are detailed by Goossens et al. 2020). This multi-use platform collects PAM data for the BCPAN and AT data for the Permanent Belgian acoustic receiver network (Reubens et al. 2019).

In the BCPAN, 10 stations were installed across the BPNS, which extends 83 km (45 nautical miles) out to sea from the coast with a length of approximately 65 km (Fig. 2). The BPNS has a mean depth of 20 m, with a maximum depth of 45 m, and is characterized by a variety of sandbanks enriching the region's biodiversity (Belgian Federal Public Service Health, Food Chain Safety and Environment 2015). Anthropogenic activities in the BPNS are ubiquitous, including fishery activities, offshore wind energy production and shipping. Eight stations are located near shipwrecks, and 2 stations (Belwindreefballs and

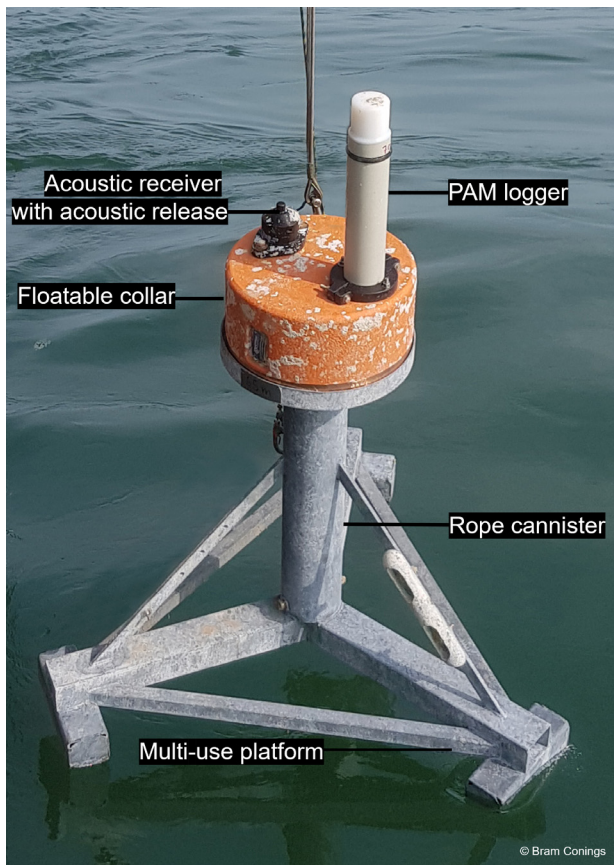


Fig. 1. Multi-use instrument mooring of the Belgian cetacean passive acoustic network (BCPAN), just before deployment: a passive acoustic monitoring (PAM) logger (C-POD) and an acoustic receiver with an acoustic release, fixed in a vertical position in the floatable collar held by the mooring. The rope cannister connects the floatable collar with the mooring and ensures full recovery

Cpowerreefballs) are installed next to biodiversity-increasing artificial reefs in 2 offshore wind farms (Fig. 2). Two stations (G-88 and Nauticaena; Fig. 2) were discontinued over time due to external problems, with G-88 being operational for less than a year (November 2018 to August 2019), and Nauticaena operational until January 2021.

2.2. Data management and access

The data management of PAM and AT data was facilitated through the European Tracking Network (ETN) database (<https://lifewatch.be/etn>). The C-POD data were first processed with CPOD.exe software (Chelonia Ltd.) with an automatic click train detection classifier, 'KERNO'. The clicks from the raw data (.CP1 file) were identified as originating from

click trains of harbour porpoises *Phocoena phocoena* (Linnaeus, 1758) (narrowband high-frequency clicks) or dolphins (Delphinidae Gray, 1821) with a quality label (high, moderate or low). As the 'KERNO' classifier could not make a distinction between dolphin species, these were grouped together under the label 'Other cetaceans'. The click train classifications (.CP3 file) were manually validated by visual inspection with the CPOD.exe software. For this study, we only considered click trains with high and moderate quality labels. The data with a temporal resolution of 1 min were then exported per quality label. For every C-POD deployment, the data (TrainDuration.txt and DetEnv.txt files) and metadata were stored on the underwater acoustics component of the ETN database. The AT data and metadata were archived and accessed as described in detail by Reubens et al. (2019).

PAM and AT data from all deployments of all stations were accessed via the R packages 'lwdataexplorer' (Hernandez et al. 2021) and 'etn' (Desmet et al. 2022), respectively. PAM data were downloaded in units of detection-positive hours (DPH), defined as the observed odontocete presence (at least 1 echolocation click train) within a given hour. The acoustic detection data consisted of the dates and times of detection of individual tags at each receiver. AT data originated from electronic tags of different telemetry projects registered within ETN. We contacted the principal investigators of each of these projects to get permission to use the data. Our data set was therefore limited to detections that we had permission to use during the period of analysis. Detections that were time stamped on dates outside of the receiver and/or tag battery lifetimes were considered false detections and were excluded from the analyses.

2.3. Data analysis

All data processing and analyses were performed in R version 4.1.3 (R Core Team 2022), with scripts made available on the GitHub repository, 'species-co-occurrence' (<https://github.com/lifewatch/species-co-occurrence>). For each species, the data were organized in an hourly presence–absence matrix at every station (Table 1; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m727p049_supp.pdf). For the PAM data, the detection of at least 1 echolocation click train sufficed to consider a species present within the hour (DPH = 1). For the AT data, at least 1 tagged individual had to be detected at least once to label the species as present within the hour (DPH = 1). Absence of a species was defined for both techniques as the

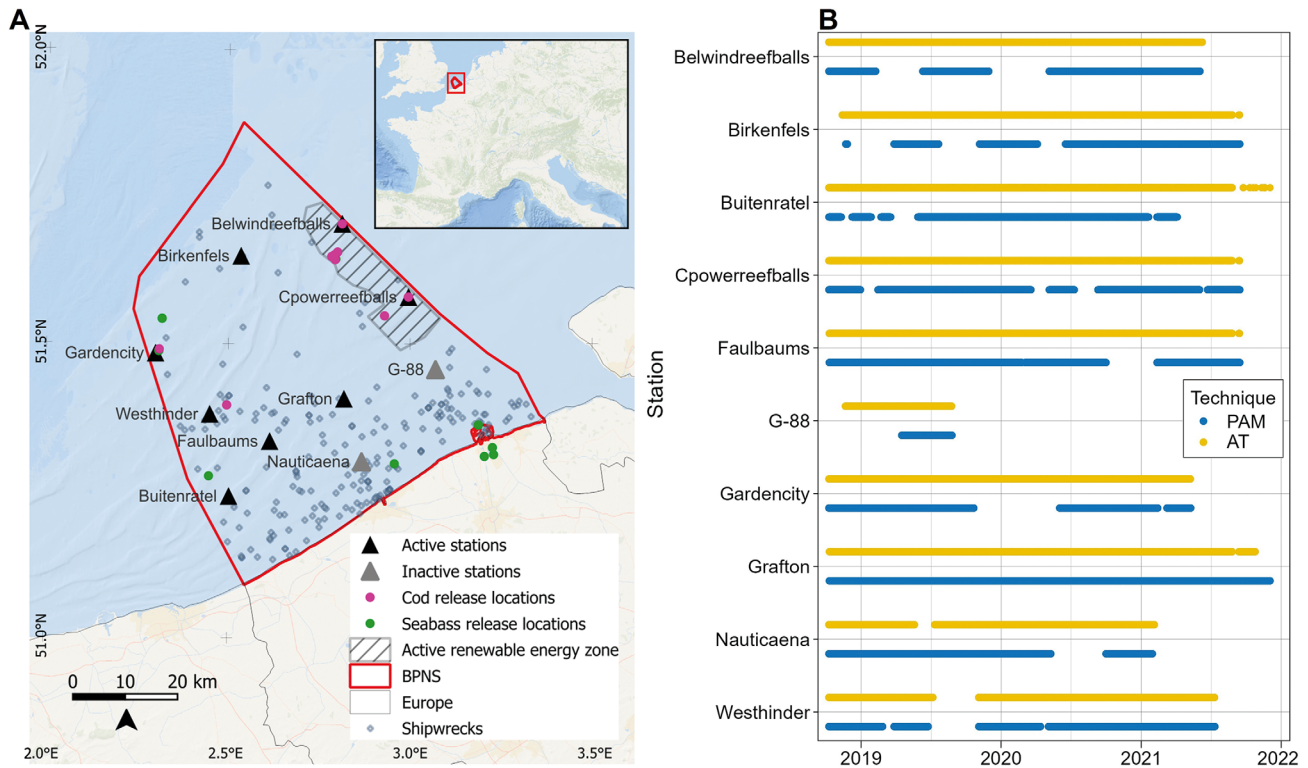


Fig. 2. (A) The 10 stations of the Belgian cetacean passive acoustic network (BCPAN). Red polygon corresponds to the area of the Belgian part of the North Sea (BPNS). Striped, grey polygon shows the presently active renewable energy zone (offshore wind farm) in the BPNS. Distribution of shipwrecks in the BPNS (<https://wrakkendatabank.afdelingkust.be>) is also overlaid on the map. Stations Nauticaena and G-88 were discontinued in 2019 and 2021, respectively, due to external problems. (B) Temporal availability of passive acoustic monitoring (PAM, blue) and acoustic telemetry (AT, yellow) data for each BCPAN station

Table 1. Definition of values of detection-positive hour (DPH) in the presence–absence matrix for species of fish (acoustic telemetry, AT) and odontocete cetaceans (passive acoustic monitoring, PAM). NA: not applicable

Value of DPH	PAM	AT
1	Detection of at least one echolocation click train	Detection of at least one transmission of one acoustic tag
0	No detection of an echolocation click train	No detection of an acoustic tag
NA	Inactive C-POD	Inactive acoustic receiver or no acoustic tag with active batteries

lack of detecting the species in an hour (DPH = 0). If a C-POD or acoustic receiver was inactive, or if there were no animals of that species with active acoustic tags (i.e. with active batteries), then the value for that hour was regarded as not applicable (DPH = NA). The hours of detections, regardless of the exact minute, were classified as day or night using the local sunrise and sunset timings in UTC from the 'Stream-Metabolism' package (Sefick 2016) based on the NOAA sunrise and sunset calculator. Dates of equinoxes and solstices were used to mark the beginning and end of each season (Table S1).

Using these hourly presence–absence matrices, we investigated spatiotemporal patterns in occupancy and co-occurrence. Occupancy, indicating similar patterns in habitat use, was expressed by the presence of different species in the vicinity of the same station, while co-occurrence was indicated by the presence of different species at the same time (hour) in the vicinity of the same station. We defined co-occurrence as the detection of 2 or more species at a station within a given hour on the same day. An overlap in occupancy indicated 2 or more species detections at a station in the same season.

Five different analyses commonly used in species co-occurrence studies were performed to investigate occupancy and co-occurrence at different temporal scales, and are detailed in the following sections (Table A1 in the Appendix). The combined hourly presence–absence matrices were therefore transformed to suit the hourly analyses (C-score and co-occurrence modelling) and reduced to a lower temporal resolution to suit the other analyses (pairwise species monthly occupancy and seasonal diel overlap; Fig. S1).

2.3.1. Pairwise species monthly occupancy

A probabilistic pairwise species monthly occupancy analysis was performed using the R package ‘co-occur’ (Griffith et al. 2016). This package computed the probability that species *A* was present at a station, given the presence of species *B* (at least 1 DPH) for a particular month. A simplified data frame was used, solely considering the monthly presence–absence of the species for each station (Fig. S1). The probability P_j of 2 species both occurring at j number of stations in the same month is:

$$P_{ji} = \frac{\binom{N_{Ai}}{j_i} \times \binom{N - N_{Ai}}{N_{Bi} - j_i}}{\binom{N}{N_{Bi}}} \quad (1)$$

where N_{Ai} and N_{Bi} are the number of sites where species *A* and species *B* occur in a given month i , respectively, and N is the total number of sites of the network. The value P_{ji} can be interpreted as the proportion of N_{Bi} sites where species *A* is occurring, given that both species occupy j sites during month i (Griffith et al. 2016).

If a species pair was not observed to share any site for a given month, this would result in less than 1 expected site of occupancy (Veech 2013). For each month, results were therefore limited to species pairs whose expected shared occupancy is ≥ 1 site.

2.3.2. Co-occurrence percentage

For each species, we calculated the co-occurrence percentage as the amount of time (number of DPH) one species co-occurred with each of the other species out of its total DPH. In the case of detecting only one species for a given hour at a particular station, we made the distinction between the cases where (1) co-occurrence was undetermined since the detection of another species was not possible because of inactivity

of the C-POD, receiver or tags (DPH = NA), and (2) no other species were detected within the detection range of that station (DPH = 0). In the latter case, a true absence of other species could not be distinguished from the presence of untagged fish of that species.

2.3.3. C-score

Using the ‘EcoSimR’ package (Gotelli et al. 2015), a C-score (Stone & Roberts 1990) was calculated to quantify the association between species pairs based on the number of shared stations. The C-score for species *A* and *B* is:

$$C_{AB} = (R_A - SS)(R_B - SS) \quad (2)$$

where R_A and R_B are the number of stations where species *A* and *B* occurred, respectively, and SS is the number of stations where the species pair co-occurred. The C-score would therefore range from 0 (maximally aggregated) to a maximum of $R_A R_B$ (maximally segregated with no shared sites). C-scores were calculated for every hour of the data set, excluding stations where the species occurred for less than 10 h throughout the period of the data set. A non-parametric Kruskal-Wallis test (Kruskal & Wallis 1952) was used to test for significant differences in C-scores between seasons (Table S1) and between day and night. As a post hoc test, we performed pairwise comparisons using a Wilcoxon rank-sum test (Wilcoxon 1945).

2.3.4. Diel overlap pattern

Similarity between species’ diel occupancy, expressed by species’ presence, during different seasons was estimated with the R package ‘overlap’ using the ‘overlapEst’ function (Meredith & Ridout 2021). The function fits kernel density estimates to the data set to calculate a coefficient (Δ) — the overlap in 24 h diel patterns per season. The coefficient ranges from 0 (no overlap) to 1 (complete overlap). The data sets for each species had to be reduced to DPH values of 1, removing NAs and 0s, since only the presence of species for each diel hour had to be considered (Table 1; Fig. S1).

We used a type 4 overlap estimator (Δ_4), which compares densities at the actual times of observation of species, and it is only recommended if both samples are larger than 50 (Meredith & Ridout 2021). Only stations where the species occurred for at least 10 h were included in this analysis.

2.3.5. Co-occurrence modelling: logistic regression

Finally, spatiotemporal patterns in co-occurrence of different pairs of species were analysed with generalised linear mixed effects models (GLMM) using the 'lme4' package (Bates et al. 2015). Separate models were used to investigate co-occurrence from the point of view of one species: when species *A* is present, what is the probability of it co-occurring with species *B*? The data subset for each model was therefore limited to the hours where species *A* was present (DPH = 1). Hours when the detection of species *B* was technically not possible (i.e. DPH = NA) were removed. Locations where the species were detected for less than 10 h were excluded from the analysis. The co-occurrence of species *A* and *B* was modelled with a GLMM with a Bernoulli distribution, a type of binomial distribution wherein the value of co-occurrence is only either 0 or 1 for every DPH. The GLMM estimated the probability of co-occurrence as a function of the fixed effects season, day–night and their interaction, with the interaction of station and season as random effect:

$$\text{Co-occurrence} \sim \text{Diel} \times \text{Season} + (1 | \text{Station/Season}) \quad (3)$$

Models were evaluated by backwards model selection, using Akaike's information criterion (AIC) (Akaike 1974) and a chi-squared test. If the GLMM resulted in a singular fit (Barr et al. 2013, Matuschek

et al. 2017), the random effect was simplified by removing the interaction effect. The random effect was then assessed by computing the intra-class correlation coefficient (ICC) of its variance (Snijders & Bosker 2012). Low or zero ICC indicated independence of groups, implying that the random effects should be dropped from the analysis (Solorio-Rivera et al. 2007). In this case, a generalised linear model (GLM) with a Bernoulli distribution was used instead. The model's assumptions of the distribution from an exponential family and independence of cases were satisfied.

3. RESULTS

The BCPAN recorded the presence of harbour porpoises, dolphins and 9 acoustically tagged fish species (Fig. 3). The detections originated from fish tagged during different projects (Table S2). Considering the limited number of DPH for some species, we applied the analyses on harbour porpoise (PAM), dolphins (PAM), European seabass (AT) and Atlantic cod *Gadus morhua* Linnaeus, 1758 (AT). Therefore, the data set was limited to the period when data for all 4 species were available, i.e. from 9 October 2018 to 3 December 2021.

Within this study period, harbour porpoises were registered for 84 431 DPH (almost half of the time the C-PODs from the 10 stations were active). Porpoise

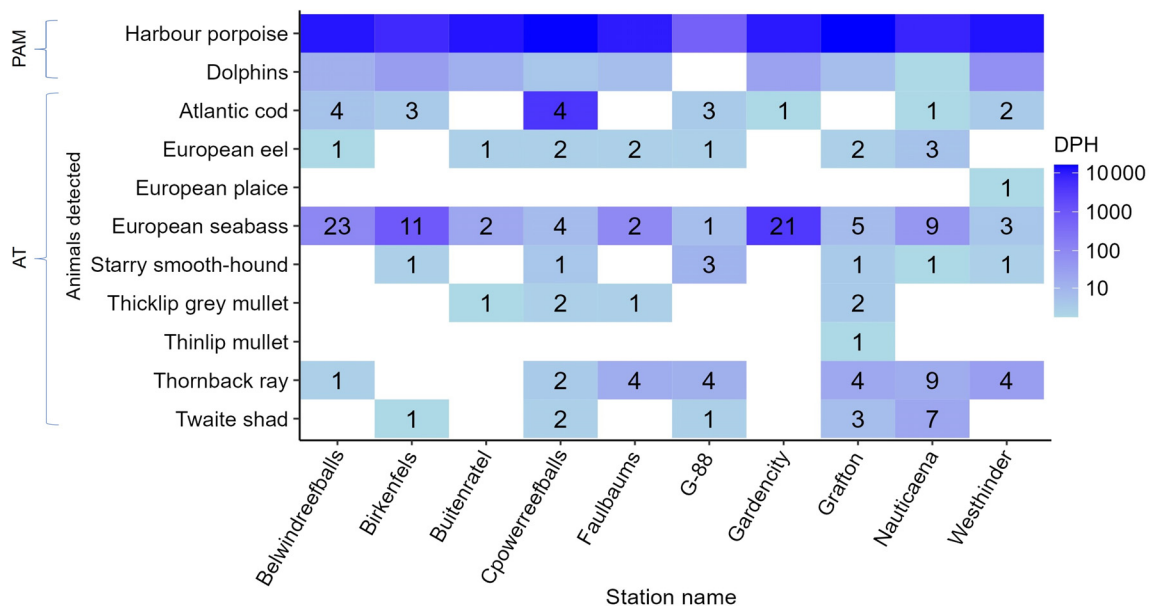


Fig. 3. Detections of various species at each station of the Belgian cetacean passive acoustic network (BCPAN). For fish (identified by acoustic telemetry, AT), the numbers indicate the number of individuals detected at each station. For cetaceans (identified by passive acoustic monitoring, PAM), only detection-positive hours (DPH) are shown

click trains were observed year-round at all stations. Dolphins only accounted for 160 DPH, mainly at the stations Westhinder and Birkenfels (Figs. 2 & 3). Both species were observed slightly more frequently during the night (64.4% of dolphin DPH, 56.7% of porpoise DPH).

The acoustic receivers from the 10 stations of BCPAN registered a total of 4704 DPH (out of 215 374 possible detection hours) for seabass and 4538 DPH (out of 69 607 possible detection hours) for cod. The majority of detected cod (13 individuals, 39–42.5 cm in total length) were caught and tagged near the offshore wind farms (Fig. 2), while seabass (47 individuals, 33–66 cm in total length) were tagged along the coast and near shipwrecks (Fig. 2). The majority of DPH for seabass was found at the offshore stations Gardencity (76%) and Birkenfels (19%), mainly in the period from November to January (Fig. 4). During spring, seabass were detected at all stations, albeit in very low numbers of DPH, whereas seabass detections during summer were limited to offshore wind farm stations. Almost all (99.6%) of the cod DPH were observed at the station Cpowerreefballs (Figs. 2 & 4). Here, cod were detected in autumn, winter and spring, but not in summer. Like the cetaceans, the fish were observed more frequently during the night (64.0% of seabass DPH and 55.0% of cod DPH).

3.1. Pairwise species monthly occupancy

Due to very low probabilities of occupancy, not all pairs of species were expected to share at least one site every month (Fig. 5). However, where suitable data were available, monthly co-occurrence was observed for most of the pairs of species. The harbour porpoise paired with the other 3 species have the highest probabilities of occupancy compared to the rest of the species pair combinations. Seabass and harbour porpoises consistently had the highest probability of occupying the same stations (at least 3) throughout the year except during the months of January, February, July and August. In May, seabass and porpoises were predicted to occupy all stations (probability = 1). During the months of January, February, July and August, dolphins and porpoises had the highest probabilities of occupancy. The probability for cod and porpoises to occupy the same stations was highest around autumn (probability = 0.45 in September). Based on the probabilistic analysis of monthly occupancy of the stations, none of the species pairs was significantly associated, either positively or negatively (all $p > 0.05$).

3.2. Co-occurrence percentage

Dolphins, European seabass and Atlantic cod were frequently observed to co-occur with harbour porpoises (Table 2). Out of the total hours these species were observed, porpoises were present during 48.1% of the DPH of dolphins, 44.0% of the DPH of Atlantic cod, and 32.9% of the DPH of European seabass. Conversely, for the highly prevalent harbour porpoise, the other species were only detected during 4.4% of its DPH. Atlantic cod and dolphins were detected at the same station for 1 h and were never found to co-occur with European seabass.

In the subsequent analyses (see Sections 3.3–3.5), we investigated the co-occurrence of harbour porpoises with each of the other species.

3.3. C-scores

European seabass and harbour porpoises were maximally aggregated (C-score = 0), co-occurring in the greatest number of stations during winter and autumn nights with similar C-score distributions (Wilcoxon rank-sum test, $p < 0.001$; Fig. 6A). During the summer, European seabass and harbour porpoises had higher C-scores (C-score = 1–2) indicating segregation; species were rarely detected at the same stations and thus had lower probabilities of co-occurrences within BCPAN.

Similar to the European seabass and harbour porpoise, C-scores of 0s for the dolphins and porpoises were more frequent than the rest of the C-scores (1–2) during autumn and winter, indicating maximal aggregation in these seasons (Fig. 6B). During spring, for every hour that both a dolphin and a harbour porpoise were detected, the 2 species were maximally aggregated (C-score = 0), sharing the same sites. However, differences between seasons and diel variation were statistically insignificant for this species pair (Kruskal-Wallis test, $p = 0.057$ [season], $p = 0.139$ [diel]). The C-scores of Atlantic cod and harbour porpoise were not assessed due to insufficient data.

3.4. Diel overlap pattern

Diel patterns of detected presence were analysed for the 3 pairs of species (namely, harbour porpoise with cod, seabass and dolphins, Table 3). Higher diel overlap coefficients of cod and seabass with porpoises during autumn ($\Delta_4 = 0.95$) and winter ($\Delta_4 = 0.94$) showed similar diel occupancy during these seasons. This

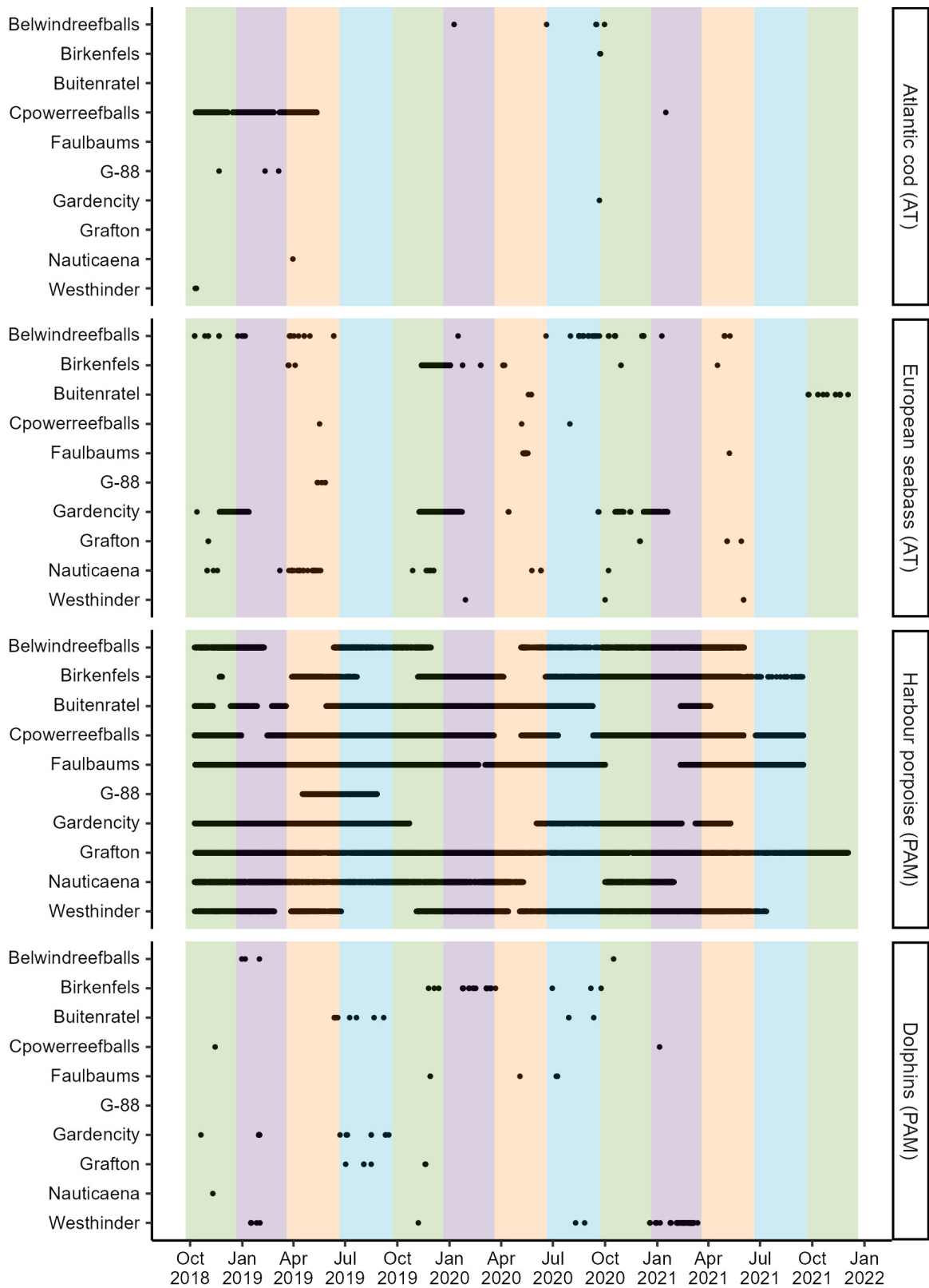


Fig. 4. Detections per species from each station during the study period (9 October 2018 to 3 December 2021) indicated by black dots. Seasons are marked by the colour of the shading (autumn: green; winter: purple; spring: orange; summer: blue). AT: acoustic telemetry; PAM: passive acoustic monitoring

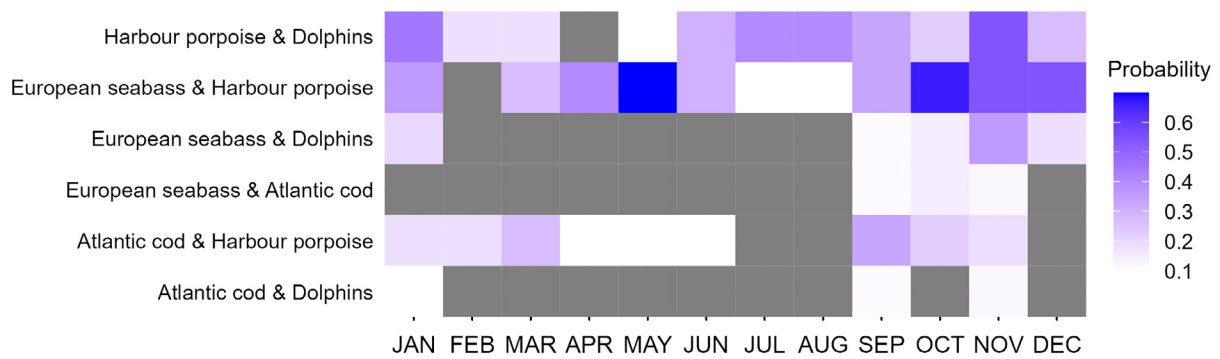


Fig. 5. Pairwise monthly occupancy of all species pairs. Grey zones indicate species pairs which did not share any site because not enough data were available for the analysis

Table 2. Co-occurrence of species as a percentage of each species' total detection-positive hours (DPH) recorded in the data set used for this study. Total DPH of each species is summed for all 10 stations and categorized into percentages as (1) 'Alone,' where DPH of all the other species was 0, (2) co-occurring with the other species, where DPH of the other species was 1, and (3) 'Undetermined,' where DPH of one of the other species was NA (thus, detecting one of the species was not possible)

Species	Total DPH (DPH = 1)	Alone (%)	With cod (%)	With seabass (%)	With dolphins (%)	With harbour porpoise (%)	Undetermined (%)
Atlantic cod	4538	16.7	—	0.0	44.0	0.0	39.3
European seabass	4704	7.8	0.0	—	32.9	0.0	59.3
Harbour porpoise	82431	26.3	2.4	1.9	—	0.1	69.3
Dolphins	160	18.1	1.3	0.0	48.1	—	32.5

implies that the species pair occurred at similar hours of the day throughout the season, although not necessarily during the same days. During the high diel overlap seasons of autumn and winter, cod and seabass seemed to be continuously detected regardless of the hour of the day, while the presence of porpoises dropped during the day (Fig. 7). Cod had very few DPH during the summer (DPH = 4) and was thus excluded from this analysis. Dolphins and harbour porpoises had lower diel overlap coefficients compared to the other 2 species pairs, as the diurnal presence of dolphins varied for each season. Dolphins and porpoises had the highest diel overlap during winter ($\Delta_4 = 0.86$, Table 3).

Since presence/detection densities varied per station, it is expected that these diel overlap patterns per species pair were not representative of the species pair's diel overlap pattern for each station in the BCPAN. Diel overlap coefficients were observed to vary considerably per station across the BCPAN, especially for seabass and porpoises.

3.5. Model probabilities of co-occurrence

For the 3 pairs of species (harbour porpoise with cod, seabass and dolphins), GL(M)Ms were fitted (detailed

in Table 4). The GLMMs fitted for the porpoise and seabass, and porpoise and dolphin models resulted in a singular fit—an indication that the models were overfitted. Singular fits were resolved by simplifying the random effect factor. For the models chosen for these 2 species pairs, the random effect factor (station and season interaction) was dropped, reducing the initial GLMMs to GLMs with diel and season as fixed effect factors. For the harbour porpoise and Atlantic cod model, only a GLM was fitted; the station factor was not considered as a random effect, since there was only data for 1 station (Cpowerreefballs) where DPH of Atlantic cod was at least 10.

AIC and chi-squared test model selection resulted in season and diel factor as significant factors for the 3 pairs of species (Fig. 8). When a European seabass was present, it had the highest probability of co-occurring with a harbour porpoise during autumn and winter nights, and the lowest during summer days. Co-occurrence of seabass and porpoise during autumn and winter was significantly different from spring and summer (all $p < 0.05$), as well as between day and night ($p < 0.001$). Atlantic cod had a higher probability of co-occurring with porpoises during winter nights and least during autumn days (all $p < 0.001$). The probability of co-occurrence of cod and porpoise during winter nights was significantly different from

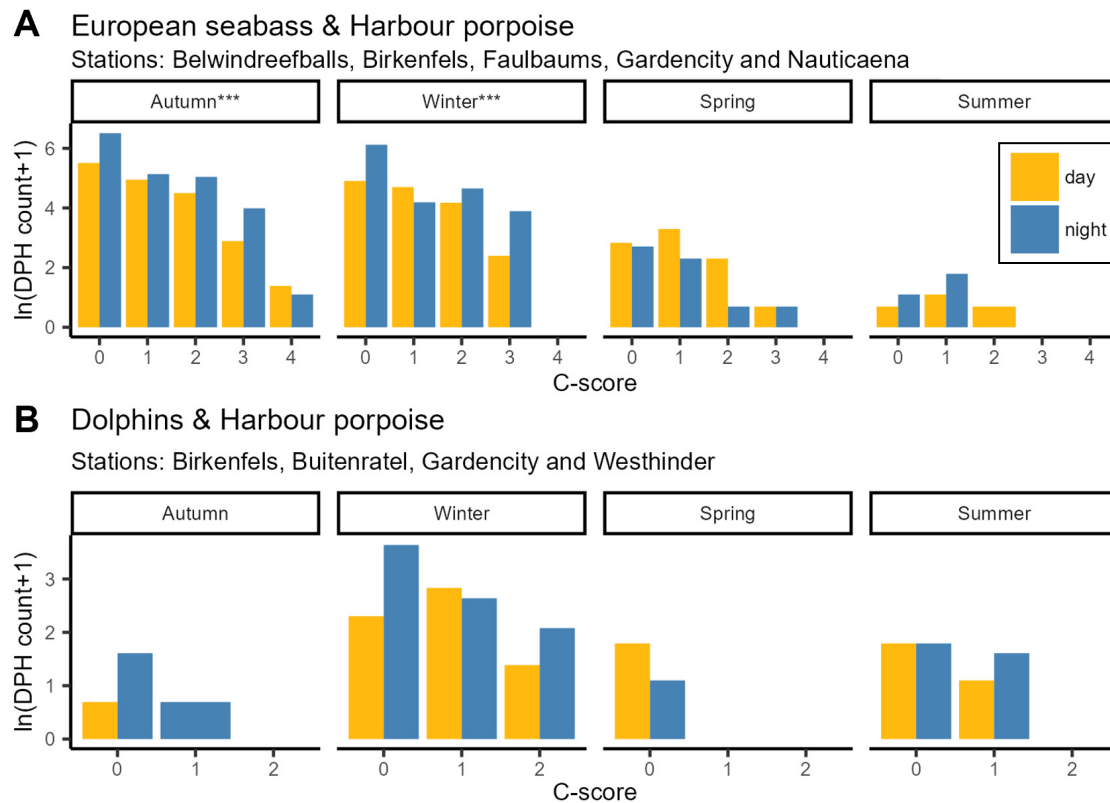


Fig. 6. Frequency of daily C-scores during daytime (yellow) and nighttime (blue) for each season for the species pairs of harbour porpoise with (A) European seabass and (B) dolphins. C-scores of the European seabass and harbour porpoise in autumn and winter during daytime were significantly different from C-scores during the night, as indicated by the asterisks (Wilcoxon rank-sum test, $p < 0.001$). Data transformation was applied on the y-axis, the count of detection-positive hours (DPH), for visual purposes, using $\ln(x + 1)$ to reduce the range of values. Stations included in the analysis, where species occurred for at least 10 h throughout the period of the data set, are mentioned

Table 3. Diel overlap coefficients (ranging from a value of 0: no overlap, to 1: complete overlap) of the 3 species pairs calculated for all stations mentioned, and diel overlap coefficients calculated per station indicated as the median [range] in the last column. For the Atlantic cod and harbour porpoise species pair, no diel overlap coefficient range is given, as only one station was considered. For dolphins and harbour porpoises, only one station (Birkenfels) had sufficient data during autumn, thus no range was also given. A value of 'NA' indicates insufficient data

Species pair	Stations	Season	Diel overlap coefficient calculated for all stations mentioned	Diel overlap coefficients calculated per station: median [range]
Atlantic cod & harbour porpoise	Cpowerreefballs	Autumn	0.95	0.94
		Winter	0.94	0.93
		Spring	0.97	0.97
		Summer	NA	NA
European seabass & harbour porpoise	Belwindreefballs, Birkenfels, Faulbaums, Gardencity and Nauticaena	Autumn	0.95	0.83 [0.64–0.96]
		Winter	0.94	0.92 [0.49–0.92]
		Spring	0.90	0.71 [0.33–0.88]
		Summer	0.71	0.46 [0.24–0.68]
Dolphins & harbour porpoise	Birkenfels, Buitenratel, Gardencity, Westhinder	Autumn	0.74	0.5
		Winter	0.86	0.72 [0.69–0.74]
		Spring	0.62	NA
		Summer	0.76	0.51 [0.40–0.62]

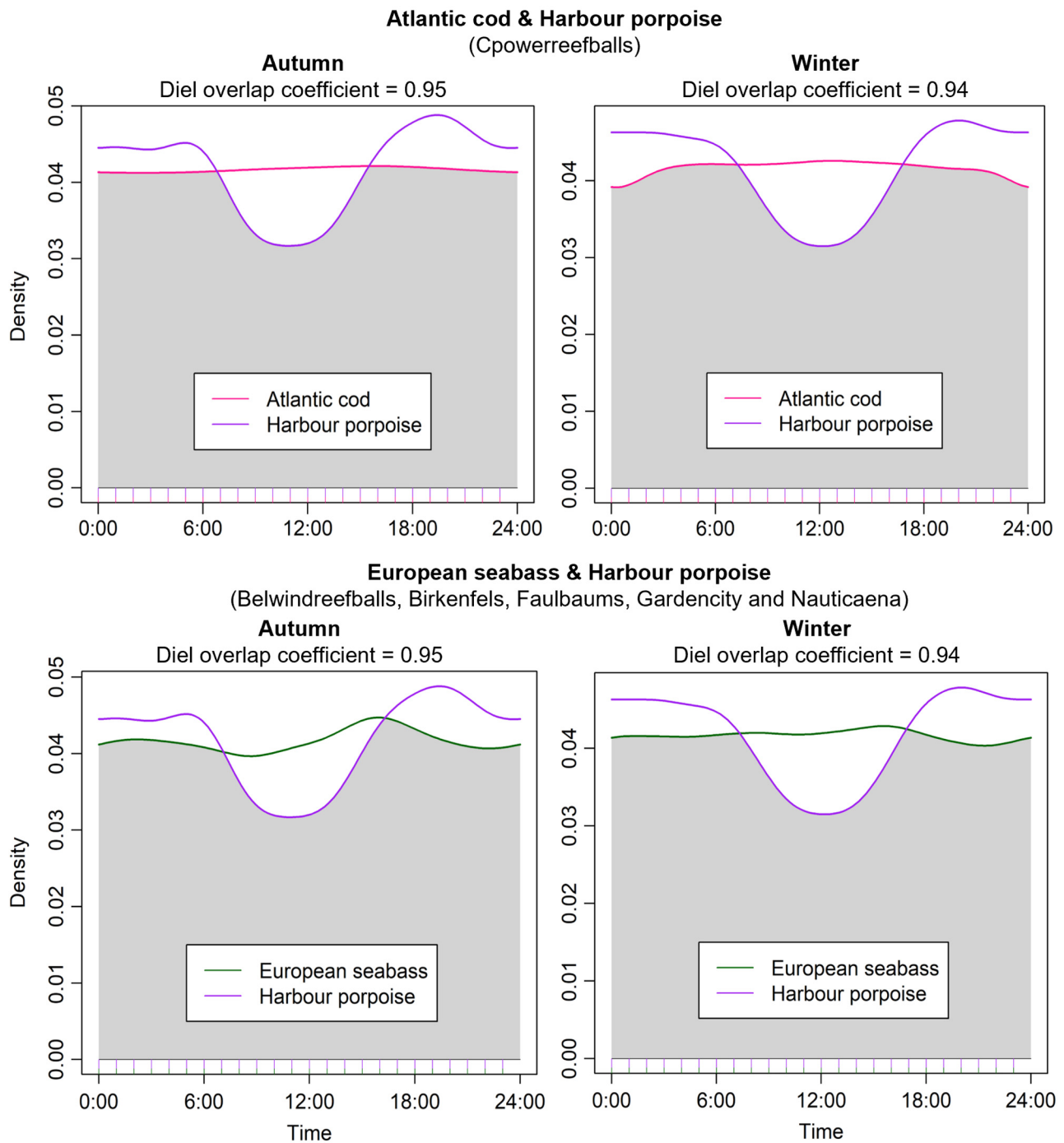


Fig. 7. Diel overlap patterns of 2 co-occurring species pairs during autumn and winter. Descriptions above each graph include the species pair, the stations included in the analysis (in parentheses), season and estimated diel overlap coefficient. Density curves at the actual times of observations of species are illustrated by the lines coloured according to the species. The area shaded grey corresponds to the coefficient of overlap, or the area under the 2 density curves for each species pair. A complete overlap equals a coefficient of 1, and no overlap equals a coefficient of 0

both autumn and spring days (all $p < 0.05$). Dolphins were predicted to have a higher probability of co-occurring with a porpoise during spring than during

winter ($p = 0.025$). Throughout all 4 seasons, there was a higher probability of dolphins co-occurring with porpoises during the night.

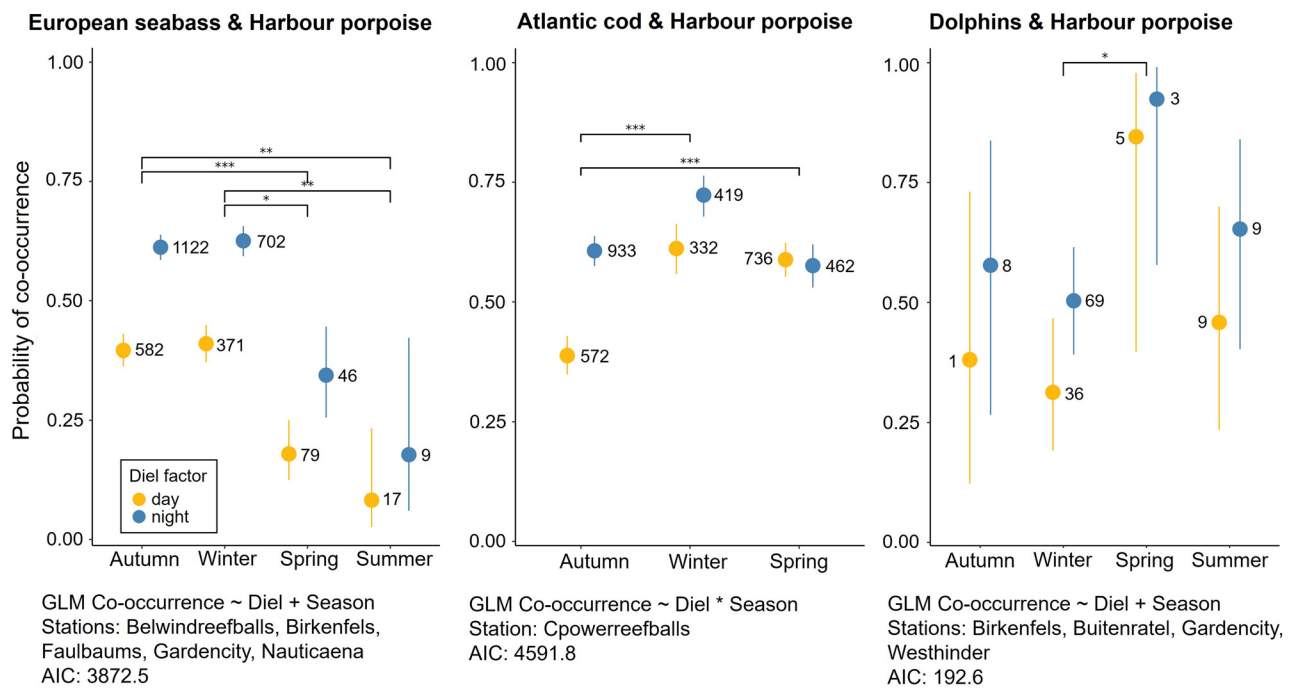


Fig. 8. Generalised linear model (GLM) results of the 3 species pairs. Numbers indicate the number of detection-positive hours (DPH) taken into account. Points indicate the predicted value of probability, while error bars show the lower and upper confidence interval. Final model used, stations taken into account (with DPH ≥ 10 h) and Akaike's information criterion (AIC) of the model are outlined in the text below the figure. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table 4. Co-occurrence backwards model selection for each species pair. Results of chi-squared test of significance ($p < 0.05$) of fixed effects and evaluation of intra-class correlation coefficient (ICC) of random effects are indicated. Random effects of models that resulted in singular fit had to be simplified and reevaluated. Calculation of ICC to evaluate the random effects was only done once the model's fixed effects were significant and if the model did not result in a singular fit, which was only the case for the European seabass and harbour porpoise model. Akaike's information criterion (AIC) of each model is also shown. Reason(s) for not selecting a model is in *italics*, enclosed in brackets. Final model selected is in **bold**. GL(M)M: generalised linear (mixed) model

GL(M)M	Fixed effects	Random effects	Singular fit	AIC
European seabass and harbour porpoise				
GLMM	Diel \times Season	(1 Station/Season)	No	3834.000
GLMM	Diel + Season	(1 Station/Season)	[Yes]	3833.600
GLMM	Diel + Season	(1 Station) [ICC = 0.013]	No	3856.600
GLM	Diel + Season	—	No	3872.500
Atlantic cod and harbour porpoise				
GLM	Diel \times Season	—	No	4591.800
Dolphins and harbour porpoise				
GLMM	Diel \times Season	(1 Station/Season)	[Yes]	194.600
GLMM	Diel + Season	(1 Station/Season)	[Yes]	194.740
GLMM	Diel + Season	(1 Station)	No	192.700
GLM	Diel \times Season + Diel + Season	—	No	191.420
GLM	Diel + Season	—	No	192.570

4. DISCUSSION

Our study serves as a demonstration of how integrating multi-sensor observations can maximize the data applicability of long-term data series, which

can be of use to perform ecosystem-based modelling or to investigate species interactions. To our knowledge, we are the first to report on the combined use of PAM and AT, 2 separate techniques that have provided continuous, long-term data

series beneficial for ecological studies. In this study, we showed how common analyses from different co-occurrence studies could be applied to integrated PAM and AT data, and how a new layer of knowledge at a broader ecological level can be obtained when relevant techniques are combined on one platform.

4.1. Integrating PAM and AT data

When combining the 2 data types, it was important to recognize the quintessential difference in the information acquired by PAM (observations of any vocalizing dolphins and porpoises) and AT (detections of a limited number of tagged individuals). Though we opted to adapt the format of the AT (detections of individuals) to PAM data (DPH of species), we still had to account for the individual aspect of AT data. Since some species had zero to few detections at some stations, we reduced the data set to stations with a minimum number of detections of species of interest ($DPH \geq 10$). In addition, absence information had to be regarded differently: PAM would be limited to registering vocalizing cetaceans, but AT was limited by the number of tagged fish. This was illustrated by cod co-occurring with porpoise for 44.0% out of its total DPH, whereas the porpoise co-occurred with cod for only 2.4% of its total DPH. Porpoise observations were approximately 20 times higher than the fish detections, which had to be interpreted from a technical perspective rather than an ecological one.

Our data set of fish detections in the BCPAN do not thoroughly reflect the spatiotemporal pattern of habitat use by these fish species, mainly due to the spatial dispersion of the stations within a limited scale that we looked at, which is largely different from the total habitat area of migrating cod and seabass (Righton et al. 2007, De Pontual et al. 2023). Additionally, individual cod and seabass are known to exhibit residency and site fidelity within the vicinities of artificial reefs (Reubens et al. 2013, Doyle et al. 2017). For instance, 99.6% of cod detections were from Cpowerreefballs, 1 of the 2 stations next to an artificial reef in an offshore wind farm, near their release sites. In contrast to targeted telemetry studies where information of undetected fish normally holds value, our study only considered available fish detection data in a confined area (the BPNS). Therefore, our results should not be used to interpret the spatiotemporal patterns of habitat use for each fish species.

4.2. Species co-occurrence patterns

By applying various co-occurrence analyses, we could attain information at different levels of spatial and temporal resolutions. At a seasonal resolution, we did not observe probabilities of occupancy to be higher or lower than what is expected by chance (pairwise species occupancy), while we could discern patterns of co-occurrence when using an hourly resolution (C-score and GL(M)M). The hourly resolution matrix showed greater detail of co-occurrence over time, resulting in statistically significant patterns. The methods of pairwise species occupancy (Griffith et al. 2016) and C-score (Stone & Roberts 1990, Gotelli et al. 2015) were originally designed to investigate co-occurrence through a species-by-site matrix, and therefore lacked the temporal aspect that our hourly presence–absence matrix had. However, we adapted the C-score to our hourly presence–absence matrix and obtained comparable results to the GLM. For example, both the C-score and GLM showed that the seabass and porpoise had a significantly higher probability of co-occurrence during autumn and winter nights. This temporal aspect was crucial to make the discrepancy between co-occurrence (2 species occupying the same space at the same time) and similarity in space occupancy (2 species occupying the same space at any time). The GLM, from the perspective of the species with the lowest occurrence, effectively dealt with this resolution (thus answering the question formulated as: out of the total time a seabass was observed, how much time did it co-occur with a porpoise?).

The purpose of this study was to assess the potential value of combined use of PAM and AT data, whereby we made use of already available data sets gathered in the framework of LifeWatch. Though a targeted ecological study on species co-occurrence patterns should have a study design with optimal tagging locations for the objectives in mind (e.g. closer to the PAM and AT stations), this study provided insights on the co-occurrence of cod and seabass with porpoises. The fish species were in the presence of porpoises at least one-third (seabass) to nearly half (cod) of the time they were detected. The probabilities of co-occurrence of both cod and seabass with a porpoise were found to be significantly higher at night, which was likely attributable to the patterns in occupancy. Seabass and cod were present rather continuously throughout the day, whereas porpoises were mainly present (or vocalizing) at night. Though this diel difference in co-occurrence with porpoises was found in each season for seabass, it was only evident during

autumn and winter for cod, indicating a clear seasonal interaction in their diel pattern.

Seabass and dolphins were initially expected to co-occur, since fishing effort (where one of the target species was seabass) and dolphin mortality, in addition to their dietary overlap (Spitz et al. 2013), were reported to be spatiotemporally correlated (Peltier et al. 2021). While we did not find any co-occurrence of seabass and dolphins, or of cod and seabass, which seemed to have an opposite seasonal migration pattern, it is possible that seasonal and spatial variation made the possibility of detecting co-occurrence of these species very low in addition to an insufficiently low number of tagged fish, which also largely differed over time depending on available project funding.

The co-occurrence patterns could likely be attributed to dietary overlap, as all species observed in this study were considered top predators in the BPNS whose diet included small pelagic fish such as mackerel, scads, anchovy and herring (Link & Garrison 2002, Spitz et al. 2006, 2013). Although cod was found to be one of the prey species of previously bycaught/stranded porpoises along the Belgian coast, the large size range of tagged cod (39–42.5 cm) was out of the range of the average prey length (2.5–21 cm) of porpoises based on stomach content analyses (Haelters et al. 2012). The co-occurrences of cod and porpoises observed at the wind farm, where cod exhibited residency/site fidelity (Reubens et al. 2013) and which may serve as a porpoise feeding station (Scheidat et al. 2011), were likely due to the wealth of prey available and not linked to porpoises preying on cod.

Higher probabilities of co-occurrence of cod and seabass with porpoises at night during the colder seasons could be linked to these species' patterns of diel feeding activity. Long-term echolocation diel patterns of porpoises are influenced by food availability and composition (Schaffeld et al. 2016), as they forage in deeper waters at night (Carlström 2005, Schaffeld et al. 2016), and during the colder seasons, higher food consumption is necessary for the endothermic porpoises to be able to regulate their body temperature (Haelters et al. 2012, Kastelein et al. 2018, Rojano-Donãte et al. 2018). As opportunistic feeders, their distribution can greatly reflect the distribution of their prey (Link & Garrison 2002, Santos et al. 2004). Correspondingly, crepuscular feeding behaviour was observed for Atlantic cod at the offshore wind farm (Reubens et al. 2014), and changes in swimming behaviour suggesting foraging activity during the colder seasons were observed for European seabass (Quayle et al. 2009). Further research into the potential interactions between these species, which

may exhibit seasonal avoidance or attraction towards each other, would benefit from investigating the relationship between co-occurrence and foraging behaviour from PAM data (Nuuttila et al. 2013, Todd et al. 2022), and vertical movement behaviour from AT data (Quayle et al. 2009, Reubens et al. 2014, Heerah et al. 2017).

4.3. The value of multi-sensor observations to EBM

One challenging aspect of EBM is the consideration of cumulative impacts and the interdependent nature of ecosystems (Rosenberg & McLeod 2005, Curtin & Prellezo 2010). Defined as a strategy to address this challenge, an integrated approach is central to EBM in achieving conservation and sustainability (UN Convention for Biological Diversity 2000). An integrated management approach can greatly benefit from an integrated observation approach, as provided by large-scale multi-sensor observation networks. Multi-sensor observations integrated across time and space may bridge knowledge gaps in ecosystem dynamics, one aspect of which is species co-occurrence.

The combination of PAM and AT in this study was first driven by practical considerations: the multi-use platform proved to be an efficient mooring design which can fit both a C-POD and a VR2AR acoustic receiver equipped with an acoustic release system (Goossens et al. 2020). Through this opportunistic application of the technologies, we gathered a data set of 3 years with a median of 23 898 and 17 868 h of AT and PAM data, respectively, at 10 stations. This type of continuous long-term data set at such high temporal resolution is rare for co-occurrence studies, which require large data sets but generally rely on data from sparse/discontinuous sampling periods (Mackenzie et al. 2004, Lamothe et al. 2019, Blanchet et al. 2020).

Mooring scientific instruments together made for time- and cost-efficient deployments and generated multiple data sets that were spatiotemporally synchronized. Aside from the C-POD and acoustic receiver, moorings could be fitted with other scientific equipment such as the SoundTrap hydrophone (Ocean Instruments NZ), Wide Band Autonomous Transceiver scientific echosounder system (Kongsberg Maritime) and an acoustic Doppler current profiler (Teledyne Marine) (Goossens et al. 2020). With the current development of large-scale networks of acoustic instruments (Mellinger et al. 2007, Risch et al. 2014, Abecasis et al. 2018, Reubens et al. 2019), the

combination of different acoustic technologies would further expand data applicability. The resulting long-term, high-resolution data sets could significantly contribute to other co-occurrence studies relying on sightings, strandings, catch and fishery observer data (e.g. Escalle et al. 2016, Pulver et al. 2016, Lamothe et al. 2019, Peltier et al. 2021), for which continuous sampling would not be possible. To better account for spatiotemporal autocorrelation and error, more complex statistical analyses could be applied, such as the Integrated Nested Laplace Approximation for Bayesian inference (Martino & Riebler 2020) and models that consider imperfect detection and site characteristics (Mackenzie et al. 2004). This would contribute to identify multispecies hotspots, to understand species interactions, to inform on habitat function at a community level and to register distributional shifts due to global and ecosystem changes (Ward et al. 2015, Brownscombe et al. 2022).

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Appendix

Table A1. Overview of analyses in hourly, monthly or seasonal temporal resolutions, with spatial resolutions of either the Belgian cetacean passive acoustic network (BCPAN) as a whole or per station. Publications listed serve as examples, but this list is not exhaustive

Analysis	Occupancy/ co-occurrence	Temporal resolution	Spatial resolution	Description	Application in other publications
Pairwise species monthly occupancy	Occupancy	Monthly	BCPAN	Probability of 2 species both occurring in the same month based on the number of stations they occupied within that month	Pulver et al. (2016), Noor et al. (2017)
Co-occurrence percentage	Co-occurrence	Hourly	Station	Percentage of solitary hours (or no other species detected) and hours of co-occurrence with other species	Bauer et al. (2015)
C-score	Co-occurrence	Hourly	BCPAN (stations with at least 10 DPH of both species)	A measurement of aggregation of 2 species based on the number of stations of co-occurrence per hour	Kamilar & Ledogar (2011), Ramos et al. (2019)
Diel overlap	Occupancy	Seasonal	BCPAN (stations with at least 10 DPH of both species)	Extent of overlap of the species' seasonal diel patterns	Noor et al. (2017), Gracanic & Mikac (2022)
Co-occurrence modelling: logistic regression	Co-occurrence	Hourly	Station (with at least 10 DPH of both species)	Probability of a species, if present at a certain station, co-occurring with another species	Mackenzie et al. (2004), Sebastián-González et al. (2010)

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