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Twelve years of acoustic monitoring reveal rising spring–autumn harbor porpoise (*Phocoena phocoena*) detection rates in the Pomeranian Bay (Baltic Sea), a transition zone between populations of concern

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Introduction: We analyzed long-term trends (2010–2021) in harbor porpoise (*Phocoena phocoena*) acoustic detections in the Pomeranian Bay (Baltic Sea) and adjacent waters east of Rügen, a transition zone between the Belt Sea and Baltic Proper populations.

Methods: Using passive acoustic monitoring (PAM) at up to 23 CPOD stations (covering an area of approximately 7,000 km^2), we quantified the percentage of porpoise-detection-positive days (*%DPD*) as an index of acoustic presence. To address uneven station coverage over time, we combined (i) a Bayesian hierarchical trend reconstruction using phenologically matched stations to bridge mid-period data gaps, and (ii) station-consistent endpoint bootstrap contrasts between an early (2010–2013) and later period (2019–2021) based on identical stations, serving as a robustness check. Generalized additive mixed models (GAMM) were used to evaluate relationships between detections and selected variables.

Results: Bootstrap contrasts provided robust evidence for strongly higher *%DPD* in spring and summer, and moderately higher *%DPD* in autumn in the later period, whereas winter patterns differed between phenology types. GAMMs indicated that potential water temperature, chlorophyll-a, and current velocity covaried with annual detections in environment-only models, but these associations weakened once temporal structure was modeled.

Discussion: The strong spring/summer increase in the period from May to October is consistent with increased seasonal occurrence of Belt Sea porpoises further east; however, changes in acoustic behavior or detectability cannot be excluded and the data do not directly quantify abundance. Our findings document increasing porpoise acoustic detection rates, except for winter, in a region facing multiple anthropogenic pressures, including shipping, offshore wind farm development, and pipeline construction.

KEYWORDS

Bayesian trend analysis, climate change, German Baltic Sea, harbor porpoise, marine mammals, passive acoustic monitoring, population shift, population trend

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Introduction

The harbor porpoise (*Phocoena phocoena* L., 1758) represents the most common cetacean species in the continental shelf waters of north-western Europe (Reid et al., 2003) and is the only cetacean species that breeds in the Baltic Sea.

The Baltic Sea is characterized by a constant outflow of brackish water in the surface layer and sporadic, wind-driven inflows of saline water near the bottom (Matthäus and Franck, 1992; Mohrholz, 2018). Water exchange with the North Atlantic is limited (Berggren, 1994; Kinze, 1994, Kinze, 1995; Berggren and Arrhenius, 1995; Benke et al., 1998). Seasonal hypoxia in deeper basins of the Baltic Proper has become increasingly common in recent decades, primarily as a consequence of eutrophication (Conley et al., 2011; Meier et al., 2019; Kõuts et al., 2021).

Our study area is located in the southernmost part of the Baltic Sea, the Pomeranian Bay (53°55'N to 54°55'N/13°25'E to 14°25'E). This shallow bay covers an area of approximately 7,000 km^2 (Figure 1), with water depths ranging from 10 to 25 m, except for two extensive sandbanks: Adlergrund in the north and Oderbank in the central bay. Two slightly deeper areas separate the Pomeranian Bay from the Arkona and Bornholm Basins to the north. The river Oder discharges a considerable runoff via several coastal lagoons into the southern bay.

The Pomeranian Bay is inhabited by two harbor porpoise populations, the western Baltic (Belt Sea) population and the Baltic Proper population (Verfuß et al., 2007; Sveegaard et al., 2010; Wiemann et al., 2010; Galatius et al., 2012; Viquerat et al., 2014; Amundin et al., 2022; Koschinski et al., 2024a, Koschinski et al., 2024b). Abundance estimates vary considerably, with only about 491 individuals (CI: 71 to 1,105) reported for the Baltic Proper population in 2011-2013 (Amundin et al., 2022) which is critically endangered (Carlén et al., 2021; Carlström et al., 2023), while the Belt Sea population exhibits much higher numbers. According to Owen et al. (2024), SCANS and Mini-SCANS surveys estimated Belt Sea abundances as follows: 1994: 51,660; 2005: 27,901; 2012: 40,475; 2016: 42,324; 2020: 17,301; 2022: 14,403, corresponding to a decline of 2.7% per year since 2005.

Large-scale acoustic monitoring and satellite telemetry data suggest that the western spatial management border for the Baltic Proper population is located west of the island of Bornholm, between Listerlandet peninsula (Sweden) and Jarosławiec (Poland), from May to October (Carlén et al., 2018), and at approximately 13°E from November to April (ICES, 2020; Sveegaard et al., 2022). The eastern border of the Belt Sea population is estimated at 13.5°E during May to October (Sveegaard et al., 2015, Sveegaard et al., 2022). Thus, both populations likely overlap in winter (Sveegaard et al., 2015, Sveegaard et al., 2022). It has been speculated that harbor porpoises of the Baltic Proper leave that area in winter to avoid sea ice (reviewed by, e.g., Teilmann and Lowry, 1996; Koschinski, 2002), leading to an eastward extension of their habitat during that season.

In the German Baltic Sea, a consistent gradient has been observed, with highest detection rates around the island of Fehmarn and lowest rates in the eastern section near the Polish border (Verfuß et al., 2007; Gallus et al., 2012; Benke et al., 2014). Within this region, acoustic detection rates peak in spring (around Fehmarn; partly also autumn/winter) and in summer/autumn

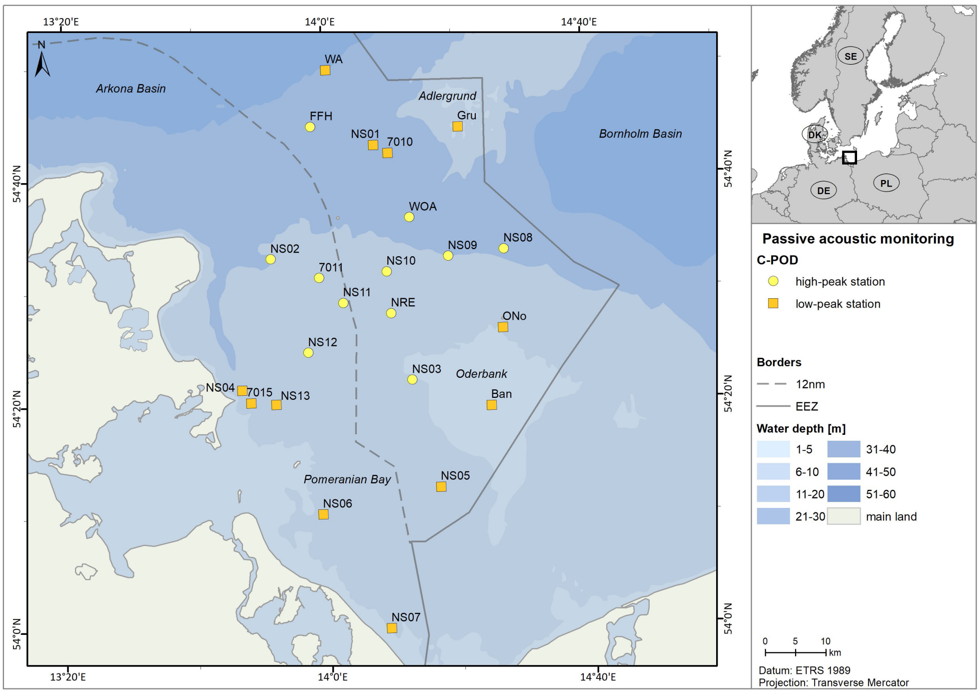

FIGURE 1
Location map showing the study area, the Pomeranian Bay in the German Baltic Sea, and the 23 CPOD positions considered in this study. Colors and shapes indicate stations with a higher summer detection peak (HPS stations: yellow circles), and those with a lower summer detection peak (LPS stations: orange squares). See Supplementary Material for phenology curves and the assignment methodology regarding both station types.

(Pomeranian Bay), suggesting an eastward migration of porpoises during summer (Verfuß et al., 2007; Benke et al., 2014). Based on up to ten years of passive acoustic monitoring (PAM) in the Pomeranian Bay, Gallus et al. (2012) and Benke et al. (2014) identified a secondary, less distinct winter peak. This bimodal seasonal pattern likely reflects alternating use of the Pomeranian Bay by Belt Sea and Baltic Proper porpoises. Migration results in substantial presence of Belt Sea porpoises in the Pomeranian Bay during summer/autumn and an influx of Baltic Proper animals in winter (Siebert et al., 2006; Verfuß et al., 2008; Gallus et al., 2012; Amundin, 2016).

The factors driving seasonal movements and inter-annual spatial variations in abundance of the highly opportunistic harbor porpoise are far from fully understood. Numerous studies worldwide have examined environmental factors associated with the observed dynamics in small cetacean distributions across various habitats. Depending on the methodology, as well as the spatial and temporal scale and the modeling approach, a number of variables such as hydrography, bathymetry, and prey distribution have been identified as important in explaining parts of the variation in local porpoise occurrence (MacLeod et al., 2007; Edren et al., 2010; Embling et al., 2010; Pirotta et al., 2014; Schaffeld et al., 2016; Carlén et al., 2018; Van Beest et al., 2018; Williamson et al., 2022). Natural porpoise distribution is most likely linked to prey availability, primarily fish (e.g., Sveegaard et al., 2012a, Sveegaard et al., 2012b; The Scottish Government, 2023), which in turn depends on biotic and abiotic parameters (e.g., hydrography and bathymetry; Gilles et al., 2011). Anthropogenic impacts such as shipping (Pigeault et al., 2024) or offshore wind farms (Ter Hofstede et al., 2022) may further alter natural distribution patterns.

Although reliable estimates of past population sizes are lacking, harbor porpoises were likely abundant in the inner Baltic Sea before extensive whaling in the 19th and 20th centuries (Kinze, 1995). Historical references suggest a considerable decline over the last century (Kinze, 1995; Koschinski, 2002). Today, the international recovery plan for harbor porpoises in the Baltic Sea – the Jastarnia Plan – aims to restore the Baltic Proper population to at least 80% of the carrying capacity, thereby achieving a favorable conservation status (ASCOBANS, 2016). A recent study suggests that the acoustic detection rates may be beginning to increase again, or at least that the decline has halted during May to October (Owen et al., 2021; however, that study focused on the southern Swedish part of the Baltic Proper).

In conjunction with offshore wind farm and pipeline constructions in the area, a dedicated PAM program was implemented in the German Pomeranian Bay. Data from these programs were used to assess regional trends in harbor porpoise detection rates over a decade. These data were combined with a national monitoring program conducted by the Ocean Museum Germany on behalf of the German Federal Agency for Nature Conservation (BfN). This enabled the evaluation of long-term trends in porpoise detection rates in the study area using Bayesian trend reconstruction and station-consistent endpoint bootstrap contrasts. Furthermore, the extent to which porpoise detection rates could be explained by different predictors was investigated. The potential effects of these predictors on the population dynamics in the study area are discussed. Throughout, we interpret PAM detection rates primarily as a proxy for acoustic presence rather than a direct measure of abundance.

Methods

Study design and monitoring devices

Passive acoustic monitoring (PAM) of harbor porpoises was conducted using Cetacean Porpoise Detectors (CPODs; Chelonia Limited, 2024). A CPOD is a self-contained data logger designed to continuously track ultrasonic transient sounds such as odontocete echolocation clicks. The device applies digital waveform characterization to capture click events in the 20–160 kHz frequency range, including their time of occurrence, frequency, intensity, envelope, and bandwidth (for details: see Dähne et al., 2013).

CPODs provide continuous monitoring at fine temporal resolution, complementing aerial or ship-based surveys that typically cover only a few days per year. PAM is limited to short-range detections (Todd et al., 2025: CPODs: EDR 220 m; EDA 0.153 km^2 for omnidirectional playbacks).

We quantified porpoise detections as the percentage of detection-positive days (*%DPD*; see below) and interpret this as a proxy for acoustic presence. Although tagged harbor porpoises echolocate frequently (Akamatsu et al., 2007; Wisniewska et al., 2016), PAM detection rates integrate porpoise presence, echolocation behavior and detection probability (e.g., range affected by propagation conditions and noise). Consequently, changes in *%DPD* cannot be interpreted as proportional changes in abundance without additional assumptions, and behavioral changes can affect detections (Marques et al., 2013; Nuuttila et al., 2018). Nevertheless, numerous studies have demonstrated a certain correlation between PAM detection rates and porpoise densities (Siebert and Rye, 2008; Kyhn et al., 2012; Jacobson et al., 2017; Amundin et al., 2022). Detection rates have already been used to monitor trends in Baltic Proper harbor porpoises (Owen et al., 2021).

CPODs were deployed roughly 4 m above the seafloor and operated autonomously for >12 weeks per deployment; only full days of CPOD operation were analyzed. Devices were calibrated either by the manufacturer Chelonia Ltd (stations NS01–NS13) or by the Ocean Museum Germany (other stations). Because small differences in sensitivity between calibration sources could influence absolute detection levels, we focus interpretation on temporal patterns and explicitly test endpoint differences using identical station sets (Bootstrap tests). Data were processed with CPOD.exe version 2.044 using the KERNO classifier (probability classes "high" and "moderate"). We used that classifier because we expected Belt Sea porpoises to predominate; nevertheless, classifier choice may influence detection rates if click characteristics vary in time or between populations, and we therefore applied a consistent classifier across the dataset and discuss this as a limitation. Days with excessive background noise were defined as >3 million clicks/day and/or >200 minutes/day during which the scan limit was reached; these limits were developed during numerous monitoring projects and proved to be a good compromise between on the one hand discarding those data overly influenced by background noise and on the other hand not losing too much data. These days were excluded to reduce data bias. In total, 7.5% of CPOD days were discarded based on these criteria.

Monitoring was conducted from June 2010 to December 2021 at 23 CPOD stations (Figure 1), with varying data periods. The deployment times for each CPOD are shown in Figure 2. CPOD stations "NS01" to "NS13" were deployed from 2010 to 2013 (within these: Interval 1: whole years 2011 to 2013) and again from 2018 to 2021 (Interval 2: whole years 2019 to 2021). CPOD stations "7010", "7011", "7015", "Ban", "Gru", "NRE", "ONo", and "WOA" collected data between 2010 and 2017 to varying extent (Group A: whole years 2014 to 2016). CPOD stations "FFH" and "WA" were deployed continuously from 2014 to 2020 (Group B: whole years 2017 and 2018).

Bayesian trend analysis

Trend analyses were conducted at yearly resolution (whole years) and at seasonal resolution. The primary long-term comparison relies on the main station set NS01–NS13, which was deployed in both an early period (Interval 1: 2011–2013) and a late period (Interval 2: 2019–2021). To visualize and estimate a continuous time series across the full study period, the mid-period data gap (2014–2018) was bridged by adding phenologically matched stations from Groups A and B. Phenology types were identified using a UMAP (Uniform Manifold Approximation and Projection; McInnes et al., 2020) of daily seasonal curves, distinguishing stations with a pronounced summer peak (high-summer-peak stations; HPS) from stations with a weaker summer peak (low-summer-peak stations; LPS). Candidate gap stations were screened by similarity of monthly *%DPD* (*%DPD/month*) and by testing whether overall detection proportions differed between paired stations (details and resulting substitutions in Supplementary Material Section A). This gap filling is a pragmatic space-for-time substitution and could introduce bias if substituted stations differ systematically in habitat use; we therefore interpret the continuous trend reconstruction cautiously and rely primarily on station-consistent endpoint contrasts for inference (Bootstrap tests; see next section).

For phenological reasons, seasons were delineated as follows: spring (May–June; influx period), summer (July–October; generally high detection rates), autumn (November–December; efflux period), and winter (January–April; generally low detection rates). Our combined spring and summer, as well as autumn and winter correspond to the two seasonal pattern groups used by Amundin et al. (2022).

We estimated trends in *%DPD/period* (period being a whole year or season of a year) with the Bayesian hierarchical framework implemented in the R package *agTrend* version 0.17.7 (Johnson, 2017; Johnson and Fritz, 2014) in *R* version 3.6.3 (R Core Team, 2020). Observed site-level *%DPD/period* (n_{ij}) is modeled as a noisy observation of a latent site-level detection rate (N_{ij}). N_{ij} remains a detection-based index (not abundance) but represents the expected detection rate at a station and period after accounting for observation error and missing data. We retained *agTrend*'s log-normal observation model because *%DPD* is non-negative and variability is approximately multiplicative (right-skewed); modeling on the log scale ensures positive predictions and stabilizes variance. For the site sub-models, we specified a log-linear time effect (linear site models) because each site spans only about a decade and includes gaps; more flexible curve shapes would be weakly informed and risk

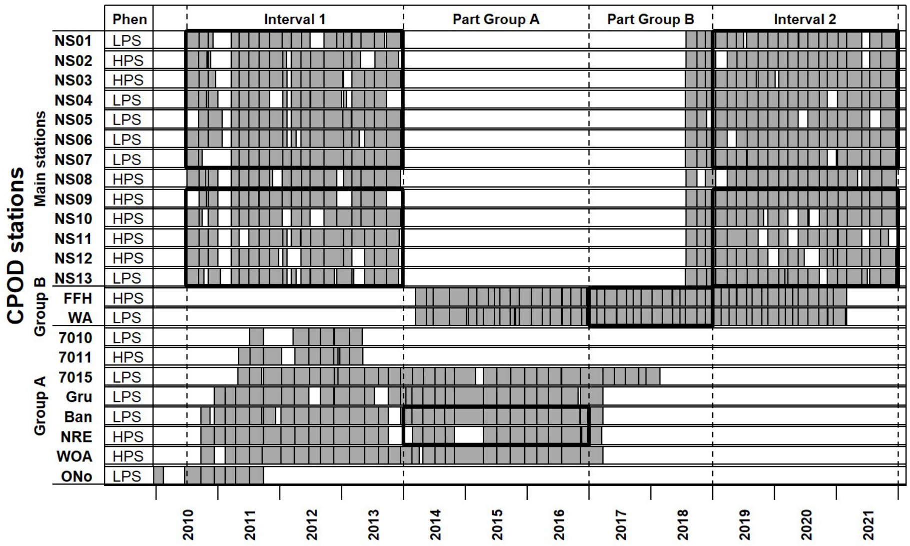

FIGURE 2
CPOD station names and deployment times, furthermore their assignment to one of three station groups (Main stations, Group A, Group B) and to one of two phenology types (Phen: LPS = low summer peak; HPS = high summer peak). Data used for Bayesian trend analyses (bold boxes) were split into four periods: Main stations: Interval 1 (2010-2013) and Interval 2 (2019-2021); gap between these two intervals filled by selected stations of Group A (Part Group A: 2014-2016) and Group B (Part Group B: 2017-2018). The selection process is given in the Supplementary Materials. Only data from Intervals 1 and 2 were used for Bootstrap tests.

overfitting, whereas the aggregated regional curve can still appear non-linear on the response scale.

agTrend augments missing site–period combinations by sampling from the posterior distribution via MCMC (e.g., Givens and Hoeting, 2005). In each MCMC iteration, latent site-level detection rates are aggregated to a regional index and the long-term trend r is summarized as the least-squares slope of the log-transformed regional index over time (Johnson and Fritz, 2014). *agTrend* was developed for abundance counts and therefore aggregates across sites by summation. Because *%DPD* is a percentage-based rate, we converted the summed index to an average detection rate by dividing by the (fixed) number of stations included in the respective model. This rescaling changes only the level of the index, not the estimated trend r, because multiplying the index by a constant factor shifts it by a constant on the log scale and therefore does not affect the time slope. We used a burn-in of 1,000 iterations and 5,000 MCMC iterations. Model equations are provided in Supplementary Material Section E.

In the resulting trend plots (Figure 3), the central estimate at each time step represents the posterior median of the aggregated *%DPD/period*, obtained from posterior predictive sampling at the site level followed by aggregation across stations. The shaded envelopes show the 95% highest posterior density credible interval (HDI) for the aggregated posterior predictive distribution at each time step. Interval widths varied through time, reflecting differences in predictive uncertainty (e.g., varying information content due to station coverage and model-based uncertainty), rather than a change in the underlying procedure.

Trendlines for full years, as well as for winter and spring, span from 2011 to 2021, while those for summer and autumn span from 2010 to 2021 as CPOD recordings began in June 2010. Therefore, not all seasons were available for individual years.

Bootstrap tests

To provide model-independent support and to evaluate robustness to station selection, we calculated non-parametric bootstrap endpoint contrasts comparing an early Interval 1 with a late Interval 2 using identical stations (NS01–NS13). Because this analysis does not rely on the gap-filled mid-period time series, it serves as a station-consistent sensitivity analysis for the observed trends. We compared *%DPD/period* between Interval 1 and Interval 2 for (i) full years (2011–2013 vs 2019–2021) and (ii) seasons, including partially sampled seasons in 2010 where applicable. For each test, 10,000 bootstrap replicates were generated by resampling with replacement within intervals, and two-sided bootstrap p-values were estimated from the empirical distribution of mean differences (Efron and Tibshirani, 1993).

Multiple testing across strata was controlled using a False Discovery Rate correction (Benjamini and Hochberg, 1995). This correction was applied separately to the full set of p-values derived from all bootstrap tests conducted within each analysis block (e.g., across all seasonal and regional panels).

All analyses were performed in R v3.6.3 (R Core Team, 2020) using *ggplot2* (Wickham, 2009), *dplyr* (Wickham et al., 2023), and *boot* (Canty and Ripley, 2019).

Generalized additive mixed model

Generalized additive mixed models (GAMM) were fitted in *mgcv* (Wood, 2015) to examine whether annual variation in porpoise detections was associated with environmental covariates, temporal structure, or both. This model type was chosen for its flexibility, as it does not require specification of a parametric form for the underlying function (Wood, 2017).

The response variable was the percentage of detection-positive days per year (*DPD_year*) per station. The geographical position of the CPOD station was included as a spatial random effect to allow inference about the entire study area, rather than being limited to the specific set of CPODs (Wood, 2017). As fixed effects, various environmental parameters were extracted for each CPOD station and time step from the Copernicus online database. These included yearly averages of daily values for surface and bottom salinity, chlorophyll-*a* concentration, mixed layer thickness, potential surface and bottom temperature, mean percentage of ice cover in the Baltic Sea (0 to 1), wind speed, surface current speed, surface current direction, and dissolved oxygen at the surface and at 20 meters depth. Variables serving as proxies for noise included among other sources, ship sonar and background noise (all detected clicks minus porpoise clicks), both derived from CPOD data.

Models were run with and without the actual year (*year_int*) as temporal variable. The Gaussian family was chosen since GAMMs using the quasi-binomial family did not converge. Each station-year included on average 304 valid days (about 83% coverage of year days), resulting in large and comparable denominators. Residual diagnostics (QQ plots and scale-location plots of normalized residuals; see Supplementary Materials) using a Gaussian Family (identity link) showed only minor deviations from normality and constant variance (heteroscedasticity).

Collinearity among explanatory variables was assessed, and in cases of strong correlation (defined here as pairwise Spearman correlation exceeding 0.6), the biologically most meaningful variable was retained based on expert judgment (Zuur et al., 2010). To quantify multicollinearity in a regression context, variance inflation factors (VIFs) were calculated, and only variables with VIF < 3 were retained. This step yielded our core predictor set for subsequent modeling, which included: bottom salinity (*sob*), chlorophyll-*a* concentration (*chl*), potential water temperature (*thetao*: the temperature a water parcel would reach if raised adiabatically (without heat exchange) to the surface), wind speed (*wind_speed*), zonal and meridional current velocity (*uo, vo*), percentage of sonar-positive 10 minutes (*SP10M*), and background noise (*nall_minus_npos*).

The reduced set of predictors was entered into a GAMM using thin-plate shrinkage splines for each covariate. This approach applies an additional penalty to the entire smooth term, allowing uninformative effects to shrink toward zero and be effectively removed from the model (Marra and Wood, 2011; Wood, 2017). Following expert guidance (Wood, 2017) on effective degrees of freedom (edf), we applied the following decision rules:

a. edf > 1.2 and p < 0.05: retained as non-linear smooth.
b. 0.1 < edf ≤ 1.2 and p < 0.05: re-specified as linear term.
c. edf ≤ 0.1 or p ≥ 0.05: excluded from the final model.

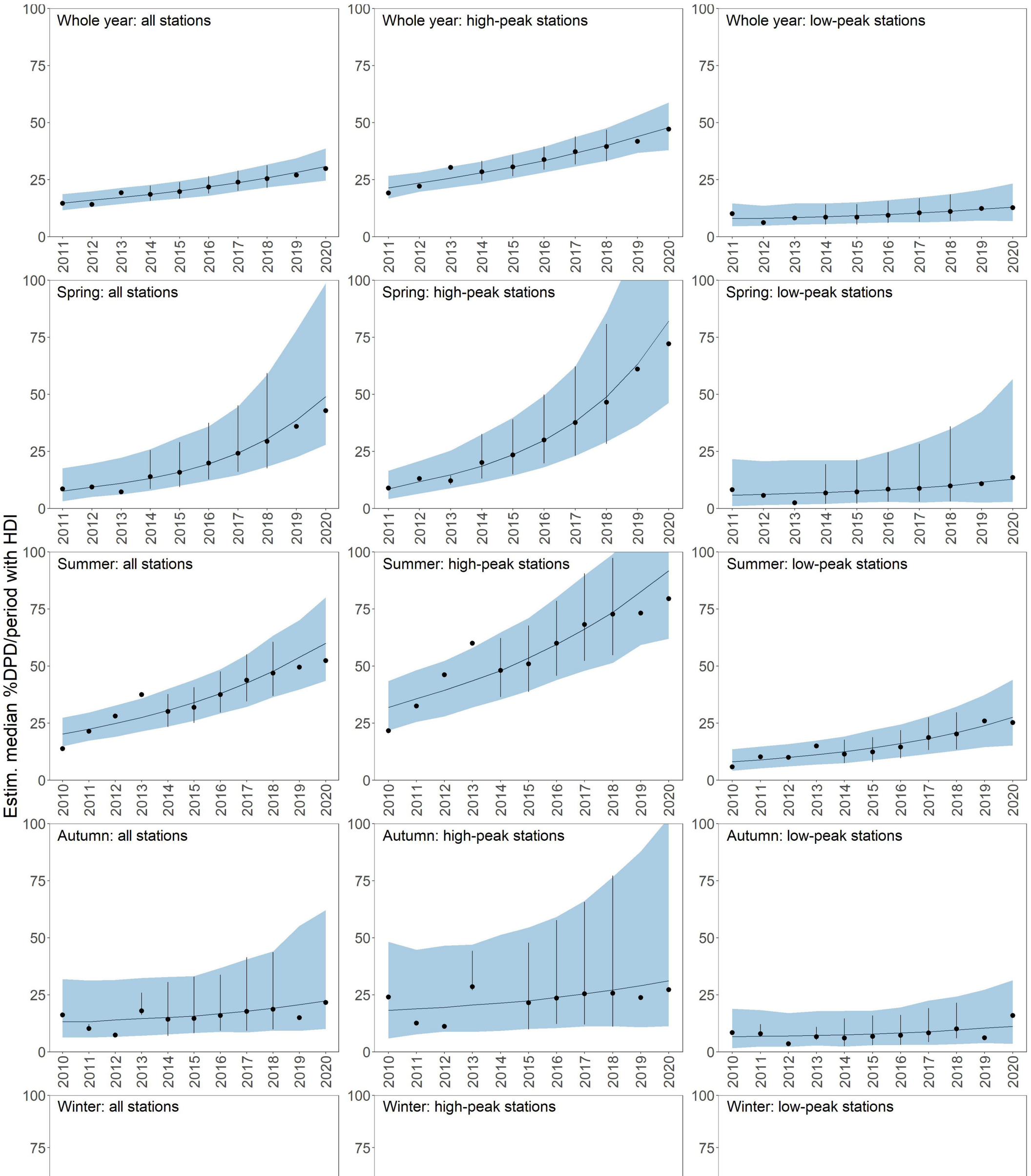

FIGURE 3
Bayesian trend analyses showing posterior summaries of aggregated *%DPD/period* for whole-year and seasonal data. Solid lines denote the posterior median; shaded envelopes represent the 95% highest density credible interval (HDI) of the aggregated posterior predictive distribution. Panels show results for all stations (left), high-peak stations (middle), and low-peak stations (right). Seasonal envelopes are color-coded (spring, green; summer, red; autumn, brown; winter, blue; whole year, gray).

This approach allowed us to systematically reduce the predictors in the model that demonstrated either a statistically robust nonlinear pattern or a parsimonious linear trend.

The final model was re-fitted using only the retained smooth and linear terms, this time without shrinkage. This ensured that effective degrees of freedom and *p*-values reflected standard REML penalization without additional shrinkage bias. Smooth terms were interpreted based on their edf and *F*-statistics, whereas linear terms were evaluated via *t*-tests on their regression coefficients. The model included a random intercept for monitoring station and accounted for within-station temporal autocorrelation via an AR(1) structure; in all models, *year_int* served as the time index for the AR(1) correlation, including models in which *year_int* was not included as a predictor.

To evaluate whether the identified environmental predictors reflected an independent ecological relationship or merely captured a shared long-term trend over years, we applied two complementary strategies:

a. Models without vs. with a year smoother (Models A and B): To evaluate whether environmental covariates explained variation in detection rates beyond the long-term temporal increase, we fitted two GAMMs with identical random-effects and autocorrelation structure and the same environmental predictor set, differing only in whether a smooth term for *year_int* was included (Model A: environment only; Model B: environment + s(*year_int*)). Because *year_int* and temporally trending environmental covariates can share low-frequency structure, term-wise significance can change simply because the model reallocates shared signal between correlated predictors. Therefore, in addition to reporting term-wise tests, we quantified the unique contribution of the temporal term and the environmental predictor set using likelihood-based model comparisons. For this purpose, Models A and B, as well as a reduced year-only model (Model Y: *DPD_year* ~ s(*year_int*)), were refitted using maximum likelihood (ML) and compared using AIC and likelihood ratio tests (LRT). ML refits were used solely for model comparison; all effect estimates, smooth shapes, and diagnostic checks are reported from the REML fits.
b. Detrending via residuals prior to modeling (Model C): As a complementary diagnostic to evaluate whether environment–detection relationships persisted beyond shared temporal structure, we applied a residual-detrending approach (Van de Pol and Wright, 2009; Wood, 2017). For each environmental predictor retained in Model A, we fitted a GAMM with *year_int* as the explanatory variable (and the same station structure where applicable) and extracted residuals as detrended covariates (prefixed *res_*). We then refitted the GAMM including s(*year_int*) together with these detrended predictors, while keeping the same random-intercept and AR (1) correlation structure as in Models A and B. This procedure tests whether interannual deviations in environmental conditions (i.e., variation not explained by the shared long-term trend) explain additional variation in detection rates. Model C was fitted by REML, consistent with the primary analyses; ML refits were used only for the nested model comparisons described above.

Results

Long-term trends and bootstrap testing

Bayesian trend analysis (Figure 3) indicated a clear long-term increase in overall annual harbor porpoise detection rates (*%DPD/period*, with *period* referring to either year or season) from 2010/11 to 2021 in the Pomeranian Bay. The upward pattern was most pronounced in spring (May to June) and summer (July to October), and was evident both for HPS and LPS. Autumn (November to December) also showed an increase, particularly at HPS, whereas in winter (January to April), when animals of the Baltic Proper might reach the region, HPS showed no clear trend and LPS a declining trend.

To evaluate whether the inferred spring–autumn increase depended on the gap-filling station selection used in the Bayesian reconstruction (2014–2018), we conducted station-consistent endpoint bootstrap contrasts using only the stations deployed in both main intervals (NS01–NS13). Because these tests compare Interval 1 and Interval 2 directly and do not use mid-period augmentation, they serve as a robustness check for station selection and gap filling of the Bayesian trend analysis. In accordance with the trend lines, the most pronounced increase in detection rates occurred in spring, where detection rates at HPS rose more than sixfold during Interval 2 (2019 to 2021) compared to Interval 1 (for spring and winter: 2011 to 2013) (Table 1). In summer, detection rates approximately doubled over the study period, while autumn showed a nearly 1.5-fold increase (Interval 1 for these two seasons: 2010 to 2013). Especially in spring, the positive trend was stronger at HPS than at LPS.

Overall, the highest porpoise detection rates were modeled for summer 2019 to 2021 at HPS, reaching approximately 76%*DPD/period*. In contrast, the lowest rates were recorded during winter 2019 to 2021 at LPS, with values around 2%*DPD/period*. In the earlier years of Interval 1 (2011 to 2013), detection rates in spring resembled those observed in winter. However, in Interval 2 (2019 to 2021), spring detection rates approached summer levels.

Generalized additive mixed models

To assess whether annual variation in porpoise detections was better described by environmental covariates, a temporal smoother, or both, we compared three GAMMs (Models A to C; Table 2; Figures 4, 5; Supplementary Figure 8). Model A included only the selected environmental predictors, Model B added a smooth for year (*year_int*), and Model C used detrended versions of the environmental predictors as a diagnostic of shared temporal structure.

Model A (environmentals only; Figure 4): Shrinkage selection retained potential temperature (*thetao*; smooth), chlorophyll-*a* (*chl*; linear), and meridional current velocity (*vo*; linear). All three terms were supported in this environment-only model (Table 2; s(*thetao*) $p = 1.42\times10^{-6}$; *chl* $p = 0.035$; *vo* $p = 0.0218$), and the model explained 46.6% of the variance in *DPD_year* (adj. $R^2 = 0.466$).

Model B (environmentals + year; Figure 5): Adding a smooth for *year_int* yielded an adjusted R^2 of 0.378 and the year smooth was strongly supported (Table 2; s(*year_int*) $p = 0.000841$). In this model, *thetao, chl*, and *vo* were not statistically distinguishable from zero at the 0.05 level (Table 2; s(*thetao*) $p = 0.080$; *chl* $p = 0.194$; *vo* $p = 0.320$). This pattern is consistent with substantial shared low-frequency temporal structure between detections and the environmental covariates, such that their individual contributions are difficult to separate from time in this dataset.

Model C (detrended predictors + year; diagnostic; Supplementary Figure 8): When the long-term temporal

TABLE 1 **Results of two-sided bootstrap tests (see Methods) comparing the percentage of detection-positive days (*%DPD/period*) between Interval 1 [2010 (in some cases 2011) to 2013] and Interval 2 (2019 to 2021).**

Period	Phenology type	*%DPD/period* median interval 1	*%DPD/period* median interval 2	Change in interval 2 (interval 1 = 100%)	Trend level	Significance (after FDR correction)
Whole year	overall	16	28	175	+	***
	HPS	24	44	183	+	***
	LPS	7.9	12	152	+	***
Winter (Jan-Apr)	overall	5.7	4.1	72	–	ns
	HPS	4.9	6.5	133	+	ns
	LPS	6.5	2.0	31	- -	***
Spring (May-Jun)	overall	7.4	38	514	+++	***
	HPS	9.7	66	680	+++	***
	LPS	5.4	10	185	+	***
Summer (Jul-Oct)	overall	25	50	200	+	***
	HPS	41	76	185	+	***
	LPS	10	26	260	++	***
Autumn (Nov-Dec)	overall	12	17	142	+	*
	HPS	17	26	153	+	*
	LPS	6.4	8.7	136	+	ns

Data were analyzed for whole years and individual seasons, and for HPS, LPS, and all stations. Shown are the medians of detection rates in each interval, the percent change, and the significance level after Benjamini-Hochberg false-discovery rate (FDR) correction (Benjamini and Hochberg, 1995). Significance codes: *p < 0.05; **p < 0.01; ***p < 0.001 (two-sided). Trend levels: - - -, <25% (= reduction to less than a quarter); - -, 25-50%; -, 51-90%; 0: 91-110%; +, 111-200%; ++, 201-400%; +++, >400% (= more than 4-fold increase).

TABLE 2 **Parameter estimates for GAMMs Models A–C fitted to annual porpoise detection rates (*DPD_year*; Gaussian family with identity link).**

Model	Component	Term	Estim.	SE	Statistic	Type	p-value	edf	Ref df
A	Parametric	(Intercept)	31.013	4.768	6.505	t	6.87e-09		
A	Parametric	*chl*	-3.940	1.838	-2.143	t	0.035		
A	Parametric	*vo*	-156.535	66.849	-2.342	t	0.022		
A	Smooth	s(*thetao*)			12.870	F	1.42e-06	1.296	2
B	Parametric	(Intercept)	26.514	4.908	5.402	t	7.03e-07		
B	Parametric	*chl*	-2.441	1.862	-1.311	t	0.194		
B	Parametric	*vo*	-70.072	70.038	-1.000	t	0.320		
B	Smooth	s(*year_int*)			4.402	F	8.41e-04	1.001	2
B	Smooth	s(*thetao*)			0.935	F	0.080	0.686	2
C	Parametric	(Intercept)	20.038	2.397	8.359	t	2.00e-12		
C	Parametric	*res_chl*	-2.226	1.859	-1.198	t	0.235		
C	Parametric	*res_vo*	-53.589	69.939	-0.766	t	0.446		
C	Smooth	s(*year_int*)			13.359	F	8.95e-07	1.148	2
C	Smooth	s(*res_thetao*)			0.426	F	0.177	0.465	2
Model	Summary						Adj R2	Sc. est.	n
A	Model summ.						0.466	65.609	82
B	Model summ.						0.378	66.075	82
C	Model summ.						0.357	66.917	82

Parametric terms are reported with estimates, standard errors (SE), t-statistics, and p-values. Smooth terms are reported with approximate F-statistics, p-values, and effective degrees of freedom (edf; with reference degrees of freedom, Ref df). Model summaries include adjusted R^2, residual scale estimate (Sc. est.), and sample size n.

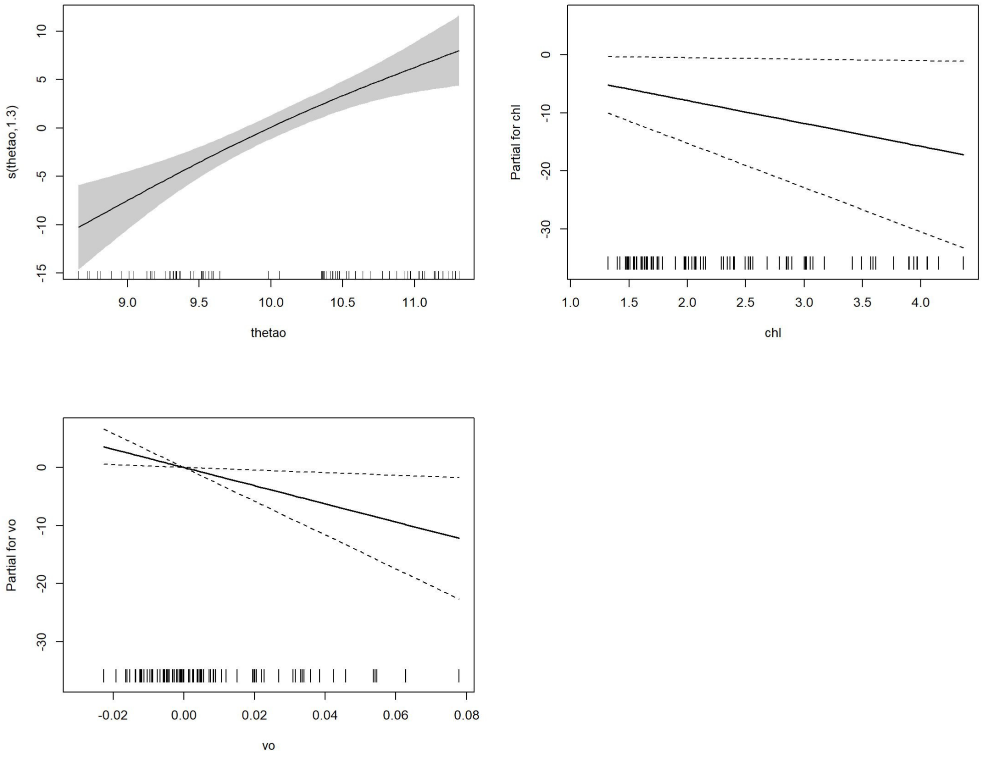

FIGURE 4
Partial effects (partial contribution of the term to the fitted values: centered, conditional on the other terms) from Model A (environmentals-only GAMM). The model included a smooth term for potential temperature (*thetao*) and linear terms for chlorophyll-*a* (*chl*) and meridional current velocity (*vo*). Solid lines show estimated partial effects on the response scale (centered), with uncertainty shown as 95% confidence intervals (shaded for smooth terms; dashed ±2 SE for linear terms). Rug marks indicate the distribution of covariate values.

component was first removed from each environmental predictor and the model refitted with *year_int*, the detrended predictors were not supported (Table 2; s(*res_thetao*) p = 0.177; *res_chl* p = 0.235; *res_vo* p = 0.446), whereas the year smooth remained strongly supported ($p = 8.95\times10^{-7}$). This outcome supports the interpretation that the associations in Model A largely reflect shared long-term structure between detections and environmental covariates rather than year-to-year deviations around the trend.

Model comparison using ML fits (Supplementary Table 2): To quantify the unique contribution of the temporal smoother versus the environmental predictor set (given their shared low-frequency structure), we refitted Model A (environment only), Model B (environment + s(*year_int*)), and a reduced year-only model (Model Y: s(*year_int*) only) using maximum likelihood. Model B differed little from Model A (AIC 583.1 vs 584.1; likelihood-ratio test L.Ratio = 3.04, p = 0.081), indicating only marginal support for adding the year smoother beyond the environmental terms. Conversely, adding environmental predictors to the year-only model did not improve fit (Model B vs Model Y: L.Ratio = 1.84, p = 0.605) and increased AIC (583.1 vs 578.9), indicating that once the long-term temporal component is modeled explicitly, the retained environmental covariates add little additional explanatory power. Concurvity diagnostics further indicated substantial overlap between s(*year_int*) and s(*thetao*), consistent with shared temporal structure.

Discussion

Harbor porpoise trend in acoustic detections

From 2010/11 to 2021, we observed an overall increase in harbor porpoise CPOD detections in the Pomeranian Bay, driven primarily by higher detection rates in spring and summer (May–October), with the most pronounced rise in late spring/early summer (May–June). Detection rates in autumn (November–December) increased more moderately, whereas winter (January–April) showed no uniform signal across phenology types: the HPS station group showed no clear winter trend, while the LPS group tended to decline. Detection rates in winter, when animals of the Baltic Proper might reach the region, were generally low. Overall, detection rates likely reflect a mixture of animals and behaviors, limiting strong ecological inference.

Our primary evidence for long-term change in spring–autumn detections is the station-consistent endpoint bootstrap analysis. By contrasting Interval 1 (2010/11–2013) with Interval 2 (2019–2021) using the identical set of consistently calibrated stations (NS01–NS13), the bootstrap tests indicate that *%DPD/period* in Interval 2 was substantially higher than in Interval 1 in spring and summer, and moderately higher in autumn (Table 1). Because this comparison uses the same stations in both periods and does not require any

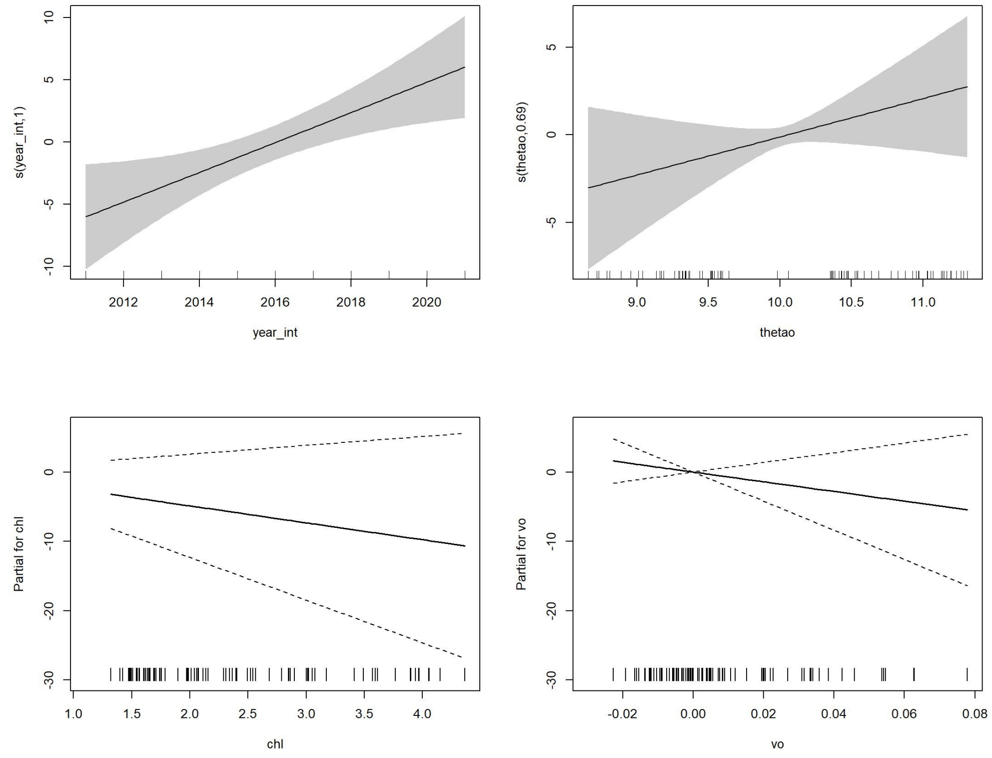

FIGURE 5

Partial effects (partial contribution of the term to the fitted values: centered, conditional on the other terms) from Model B (environmentals + temporal smoother). Model B included the same environmental predictors as Model A and additionally a smooth term for *year_int*. Uncertainty is shown as 95% confidence intervals (shaded for smooth terms; dashed ±2 SE for linear terms). After including *year_int*, the environmental terms were reduced in magnitude and were not statistically distinguishable from zero (Table 2), indicating shared temporal structure between the covariates and long-term detection changes.

augmentation of the mid-period gap (2014–2018), it serves as a robustness (sensitivity) check against the concern that inferred long-term trends could be driven by station selection during the gap-filled years. At the same time, endpoint contrasts cannot resolve whether detection rates fluctuated strongly within 2014–2018 or identify when within the decade the increase occurred; yet they clearly demonstrate that detections in the late period were markedly higher in spring–autumn than in the early period.

The Bayesian trend reconstruction provides a complementary, model-based description of how detection rates could have developed across the full period, including the mid-period gap, and it helps quantify uncertainty in the reconstructed time series. However, because it uses gap-filling and distributional assumptions, we interpret the Bayesian trend estimates primarily as a continuous reconstruction consistent with the station-consistent bootstrap evidence, rather than as stand-alone proof of the temporal trajectory during 2014–2018.

Putting our results into context, earlier abundance surveys in the Kattegat, Belt Seas, and western Baltic have produced variable density estimates without a consistent directional change from 2005 to 2016 (Sveegaard et al., 2013; Viquerat et al., 2014; Hammond et al., 2002, Hammond et al., 2013, Hammond et al., 2021; Gilles et al., 2023, Gilles et al., 2025). More recent assessments even suggest that the Belt Sea population may not have increased, with a non-significant decline reported by Sveegaard et al. (2022) and a statistically weak but concerning negative trend proposed by Owen et al. (2024). In German Baltic waters, Benke et al. (2014) reported low T-POD detection rates in the Pomeranian Bay until 2007 followed by an increase until 2012; our study suggests that elevated detection rates, particularly in spring and summer, likely continued at least until 2021. PAM results from waters around Bornholm also indicate increasing summer detections across the broader region (WSP and BioConsult SH, 2024). Taken together, these findings strengthen the case that the spring–autumn increase in detections in the Pomeranian Bay is real and persistent, while they also caution against interpreting it as evidence of a general increase in Belt Sea abundance.

Is the spring–autumn increase consistent with a distributional shift?

Within the broader regional gradient, several lines of evidence suggest that summer detections in the Pomeranian Bay are predominantly associated with animals from the Belt Sea population (Gallus et al., 2012; Benke et al., 2014). Benke et al. (2014) reported that from 2002 to 2012 approximately 94% of detection-positive days per month occurred near Fehmarn, whereas only ~4% occurred in the Pomeranian Bay, with the latter value already increasing through time. They further described a longitudinal shift in seasonal timing, with detections peaking from spring to autumn in the west but only from late summer to early autumn in the east, consistent with an eastward seasonal movement. Our results indicate that this seasonal pattern now begins earlier and extends farther east, given the strong spring and summer increases at stations between ~13.8°E and 14.5°E.

Sveegaard et al. (2015) found that between May and September porpoise density declined sharply east of 13.5°E, implying that only a small fraction of Belt Sea animals crossed this line during summer. If the high spring–summer detections observed in 2019–2021 in the Pomeranian Bay mainly originate from the Belt Sea population (rather than the Critically Endangered Baltic Proper population, which may occur in the region mainly in winter), then one plausible hypothesis is that the effective summer boundary reported by Sveegaard et al. (2015) has shifted eastward since 2010, as also discussed by Koschinski et al. (2024a). This interpretation is consistent with broader indications of spatial redistribution in the southwestern Baltic Sea: a southeastward expansion of the Belt Sea population since the late 1990s has been reported west of our study area (Van Beest et al., 2025), and habitat suitability shifts can change the importance of protected areas over time (Van Beest et al., 2018). However, our data do not directly distinguish between redistribution, changes in local density, or changes in acoustic behavior. Therefore, a distributional shift should be treated as a working hypothesis rather than a demonstrated mechanism, and it requires further testing with complementary information (e.g., telemetry, genetic assignment, or integrated visual–acoustic survey designs).

The contrasting winter patterns between phenology types are potentially relevant in this context. Winter detections were generally low and may include animals from the Baltic Proper population, which complicates interpretation. The declining winter trend at LPS sites could reflect changes in winter occurrence, shifts in seasonal movements, local habitat use, or behavioral/detectability effects rather than a change in abundance. Given these uncertainties, we refrain from large-scale inference from winter trends and instead highlight winter heterogeneity as a target for future studies.

Environmental covariates: covariance with time rather than demonstrated drivers

Harbor porpoise habitat selection is often linked to prey availability (Stedt et al., 2024), but since prey data are rarely available at sufficient resolution environmental covariates are frequently used as proxies (Gilles et al., 2011; Sveegaard et al., 2012a, Sveegaard et al., 2012b; Booth et al., 2013). Although prey-driven explanations are biologically plausible (Read and Westgate, 1997), they are difficult to test directly because prey data are often unavailable at appropriate scales (Santos and Pierce, 2003), which was also the case for our study. We therefore evaluated environmental parameters that could plausibly covary with prey and habitat conditions (e.g., temperature, oxygen, chlorophyll-*a*, and currents).

Our GAMM results underscore an important interpretive distinction. When fitting a model with only environmental predictors, potential water temperature, chlorophyll-*a* concentration, and meridional current velocity were significant correlates of annual detection rates, similar to correlations discussed for the region by Gallus et al. (2012) and Benke et al. (2014), and for the Baltic Proper population by Carlén et al. (2018). However, after including a smooth term for year, these environmental effects were strongly attenuated and no longer independently supported. This pattern indicates substantial temporal confounding: the environmental predictors and detection rates share long-term trajectories, and the models cannot separate their contributions at annual resolution. Accordingly, we interpret these relationships as covariance with long-term change rather than evidence of causal drivers, and we avoid inferring mechanisms without independent corroboration.

Even under this cautious framing, it remains useful to consider plausible ecological pathways that could link environmental change to detections. For example, chlorophyll-*a* is often used as a proxy for primary productivity. Sprat and herring are pelagic planktivorous species (Casini et al., 2004), and zooplankton production can depend on phytoplankton dynamics (Bunker and Hirst, 2004), which could plausibly connect productivity to prey availability and porpoise occurrence. At the same time, a negative chlorophyll-*a* association (as in our environment-only model) does not necessarily imply fewer porpoises: if higher productivity increases prey encounter rates, porpoises may reduce active searching/echolocation effort, producing fewer detections at similar densities. Meridional currents may also influence prey transport and aggregation, affecting foraging opportunities, but these remain hypotheses that require finer-scale data.

Eutrophication and oxygen depletion provide another example of a long-term process that could alter prey distribution and thus porpoise detections. Nutrient influx from rivers can promote eutrophication (Conley et al., 2011; Kõuts et al., 2021) and contribute to hypoxia with negative ecosystem consequences (HELCOM, 2023c, HELCOM, 2023a). Bottom water hypoxia affects benthic habitats (Carstensen et al., 2014) and has expanded in many parts of the Baltic Sea (e.g., Bergen et al., 2018; Savchuk, 2018), although shallow waters such as the Pomeranian Bay may be less affected (HELCOM, 2023b). Oxygen was not a significant predictor in our models, but hypoxia elsewhere could contribute to redistribution of demersal fish (Hinrichsen et al., 2011; Schaber et al., 2012) and thus indirectly influence porpoise distribution. For example, the distributional center of herring shifted into the Arkona Sea during years with salty inflows that alleviated hypoxia (Miethe et al., 2014). Such processes could, in principle, shift prey and predators toward the comparatively shallow Pomeranian Bay.

Water temperature deserves particular attention because warming is a defining feature of long-term change in the Baltic Sea and is tightly aligned with time in our models. Temperatures increased by approximately 0.5–1.5 °C between 2010 and 2021 in waters surrounding our study area (Skjevik et al., 2022), and bottom temperatures have risen markedly over longer periods in the northern Baltic Sea (Kankaanpää et al., 2023). Warming can have cascading effects across trophic levels and marine mammals (MacKenzie et al., 2007; Nyman, 2015; Horn et al., 2016; Polte et al., 2021; Meier et al., 2022) and may influence prey distributions and phenology. In the Sound, prey and porpoise distributions covaried seasonally (Sveegaard et al., 2012a), and herring abundance has been linked to predator distributions (Sveegaard et al., 2012b). Several key prey species in the southern Baltic may correlate with water temperature and salinity (Akimova et al., 2016; Andreasen et al., 2017), while herring reproductive success can decline during mild winters (Polte et al., 2021). Such dynamic abiotic conditions may therefore influence fine-scale porpoise movements (Van Beest et al., 2018). Nonetheless, because warming and other long-term environmental trends are so closely aligned with time, their apparent effects are largely absorbed by the temporal smoother in our GAMMs, consistent with broader evidence that climate-driven warming acts as a pervasive background process shaping marine life (Poloczanska et al., 2013).

Anthropogenic pressures and detectability

Beyond ecosystem change, the Pomeranian Bay is a high-use area with multiple anthropogenic pressures, including shipping, fishing, and the installation of offshore infrastructure. As noted above, anthropogenic noise is common in the region (Mustonen et al., 2019) and can influence porpoise behavior and detectability at short time scales (Erbe et al., 2018; HELCOM, 2019). Offshore wind farm construction can generate impulsive noise (Stöber and Thomsen, 2019), and the Nord Stream pipelines were installed through the area during our study period. While such factors may not emerge as predictors in annual-scale GAMMs, they could contribute to localized or episodic changes in detection rates and should be evaluated using higher-resolution analyses where possible.

Methodological considerations

A central limitation of PAM time series is that detection rates quantify acoustic detections rather than abundance. Detection rates are influenced by porpoise presence within detection range, but also by detectability (e.g., propagation conditions and masking) and by acoustic behavior (e.g., changes in clicking/foraging effort). Consequently, increases in detection rates cannot under all circumstances be interpreted as proportional changes in density or abundance without additional assumptions or auxiliary data. This is particularly relevant when discussing ecological mechanisms: for example, changes in prey availability could plausibly alter foraging effort and thus the rate of echolocation clicks, changing detection rates even if local density remained similar.

Short-term changes in detectability may be driven by acoustic background noise, which can mask porpoise signals and varies with both natural and anthropogenic processes. Although CPOD-measured noise was not a significant predictor at annual resolution in our GAMMs, noise was present in the area and can influence detections on shorter time scales, including noise generated at the device (e.g., chain clatter) (Clausen et al., 2018), shipping and other human activities (Erbe et al., 2018; HELCOM, 2019), and the spatially and temporally variable ambient soundscape of the Baltic Sea (Mustonen et al., 2019). Construction activities (e.g., offshore wind farms, pipelines) can also generate intense noise (Stöber and Thomsen, 2019). Such processes may affect detection probability at time scales that our annual models cannot resolve, reinforcing the need for cautious interpretation of long-term detection trends.

Statistically, our long-term inference rests on combining complementary approaches. The Bayesian trend analysis applied here (Johnson and Fritz, 2014) is designed to estimate trends in aggregated time series while propagating uncertainty, which is valuable when station operation is incomplete over time. However, because mid-period years required augmentation using phenology-matched station groups, we treat the Bayesian reconstruction as conditional on those design choices and emphasize the station-consistent endpoint bootstrap contrasts as a key robustness check for the spring–autumn increase. This combined interpretation follows the strengths and limitations of each approach: the bootstrap tests are model-independent but cannot resolve intermediate variability, whereas the Bayesian model provides a continuous reconstruction but relies on gap-filling and assumptions.

The dataset spans more than a decade, which is a major strength given that detecting population trends in long-lived species typically requires long monitoring periods (White, 2019). Ideally, trend monitoring would be based on randomized survey designs and consistent station deployment, but such designs are often infeasible when data are collected across multiple projects. Consequently, caution is required when translating acoustic detection trends into conservation conclusions. Nevertheless, the underlying trend estimation framework has proven useful in other contexts, including aerial surveys assessing harbor porpoise trends in the North Sea and Belt Sea (Nachtsheim et al., 2021; Owen et al., 2024). For PAM data, the approach has so far mainly been applied in a public research report on porpoise trends in the German Bight (Rose et al., 2025). The strong and seasonally structured increase documented here therefore provides an important long-term signal from a key transition zone between populations of conservation concern.

Conclusion

Using twelve years of PAM data, we document a marked increase in harbor porpoise acoustic detection rates in the Pomeranian Bay from spring through autumn, supported by station-consistent endpoint bootstrap contrasts and by a Bayesian trend reconstruction. Winter trends were heterogeneous across station phenology types. Because PAM-derived detection rates integrate presence, behavior and detectability, but are not a direct estimate of abundance, our results are best interpreted as an increase in acoustic presence, consistent with increased seasonal occurrence of Belt Sea porpoises further east.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because of indirect study of acoustical signals, no animal contact.

Author contributions

AR: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. JV: Methodology, Project administration, Writing – review & editing. RV: Methodology, Writing – review & editing. AS: Investigation, Methodology, Project administration, Visualization, Writing – review & editing. VK: Data curation, Resources, Writing – review & editing. AG: Data curation, Resources, Writing – review & editing. MD: Data curation, Funding acquisition, Investigation, Methodology, Resources, Validation, Writing – review & editing. AD: Funding acquisition, Investigation, Project administration, Writing – review & editing.

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Conflict of interest

Authors AR, JV, RV, AS, VK, and AD were employed by company BioConsult SH GmbH & Co. KG.

The remaining author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2026.1839791/full#supplementary-material

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