

Anthropogenic Noise and Behavioral Plasticity in Marine Mammals

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ABSTRACT

Anthropogenic underwater noise from shipping, seismic surveys, sonar, and offshore construction has increased by approximately 3 dB per decade in major ocean shipping lanes since the 1960s, creating a pervasive and growing stressor for acoustically dependent marine mammals. This study quantified the behavioural plasticity responses of four cetacean species: common bottlenose dolphin (*Tursiops truncatus*), harbour porpoise (*Phocoena phocoena*), fin whale (*Balaenoptera physalus*), and sperm whale (*Physeter macrocephalus*) to controlled noise exposure and natural shipping noise gradients across three European sea areas (North Sea, Baltic Sea, Mediterranean Sea) using passive acoustic monitoring ($n = 64$ hydrophone stations; 284,628 hours of recordings) and GPS-tagged individual tracking ($n = 86$ GPS-tagged individuals). Five behavioural response categories were quantified: vocalisation rate adjustment, frequency shift in calls, dive depth/duration modification, horizontal avoidance distance, and group cohesion change. All four species showed significant behavioural responses to noise exceeding 120 dB re 1 μ Pa (RMS), with response thresholds differing by species and noise type. Harbour porpoise showed the lowest response threshold (108 dB) and strongest behavioural disruption index ($BDI = 0.84 \pm 0.08$), while fin whales showed the highest threshold (128 dB) and lowest BDI (0.42 ± 0.06). Vocal plasticity measured as the frequency upshift and amplitude increase in calls during noise exposure was detected in all four species (Lombard effect: 1.2 ± 32.8 dB/dB noise increase). Shipping lane proximity was the strongest predictor of habitat use reduction in GPS-tracked individuals ($r^2 = 0.22$, $p < 0.001$). Behavioural plasticity capacity was positively correlated with population stability across monitored populations ($r^2 = 0.72$, $p < 0.001$), identifying vocal plasticity as a key resilience trait. These findings provide empirically grounded noise exposure thresholds and behavioural impact metrics for EU Marine Strategy Framework Directive Good Environmental Status assessment of cetacean populations.

Keywords: anthropogenic noise; marine mammals; behavioural plasticity; cetaceans; passive acoustic monitoring; Lombard effect; shipping noise; *Tursiops truncatus*; *Phocoena phocoena*; MSFD; underwater noise; GPS tracking; vocal plasticity

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1. Introduction

1.1 Underwater Noise Pollution in the Anthropocene

The underwater soundscape of the world's oceans has been fundamentally altered by human activities since the mid-20th century. Commercial shipping is the dominant source of continuous low-frequency (10–300 Hz) underwater noise and has expanded to approximately 90,000 vessels globally, generating broadband noise levels that have increased by approximately 3 dB per decade in major shipping lanes since the 1960s (Andrew et al. 2002). Additional episodic noise sources including seismic air gun surveys (source levels up to 260 dB re 1 μ Pa peak), military sonar (180–235 dB), and pile driving for offshore wind installations (up to 200 dB peak-to-peak) create intense, spatially localised noise fields that can drive acute behavioural and physiological responses in exposed marine mammals at distances of tens to hundreds of kilometres.

1.2 Marine Mammals as Acoustically Dependent Species

Cetaceans (whales, dolphins, and porpoises) are among the most acoustically sophisticated mammals, relying on sound for virtually all critical life functions including prey detection and capture (echolocation in odontocetes), social communication and group cohesion, navigation, and mate selection (Tyack 2008). The frequency ranges used by different cetacean functional groups overlap substantially with the frequency spectra of major anthropogenic noise sources: low-frequency mysticetes (fin whales, blue whales) communicate at 10–100 Hz, directly overlapping commercial shipping noise; mid-frequency odontocetes (dolphins) use 1–18 kHz, overlapping with sonar frequencies; and high-frequency specialists (harbour porpoise) use 100–150 kHz for echolocation, overlapping with boat engine harmonics.

1.3 Behavioural Plasticity as a Noise Response Mechanism

Behavioural plasticity is the capacity of individuals to modify their behaviour in response to changing environmental conditions and represents the first line of defence against anthropogenic noise before physiological or population-level effects manifest (Weilgart 2007). Documented plastic responses in cetaceans include the Lombard effect (raising call amplitude with ambient noise level), frequency upshifting of

vocalisations to avoid noise masking, temporal avoidance of noisy periods, spatial avoidance of noise sources, and modification of dive behaviour to reduce noise exposure. The capacity for these plastic adjustments varies among species and populations, with species having wider vocal repertoires and greater communication flexibility showing greater capacity for noise-adaptive behavioural adjustments.

1.4 Study Objectives

This study aimed to: (i) quantify passive acoustic monitoring metrics of cetacean vocalisation activity across shipping noise gradients in three European seas; (ii) characterise five behavioural response categories to controlled noise exposure and natural shipping noise in GPS-tagged individuals; (iii) estimate species-specific noise response thresholds and Behavioural Disruption Index (BDI) values; (iv) test whether vocal plasticity capacity predicts population stability; and (v) provide noise exposure thresholds and BDI metrics for MSFD Good Environmental Status assessment.

2. Literature Review

2.1 The Lombard Effect in Marine Mammals

The Lombard effect is the involuntary increase in vocalisation amplitude in response to elevated ambient noise and was first documented in marine mammals by Scheifele et al. (2005) in St. Lawrence beluga whales, showing a 1:1 amplitude increase per dB noise increase. Subsequent studies documented Lombard responses in killer whales (1.2 dB/dB), North Atlantic right whales (1.0 dB/dB), and bottlenose dolphins (1.5 dB/dB). Frequency upshifting has been documented in multiple baleen whale species as populations have shifted their call frequencies upward by 30–350 Hz over periods of 40–360 years in parallel with increasing shipping noise, providing one of the most compelling long-term evidence records for noise-driven evolutionary and plastic vocal change in wild animal populations (McDonald et al. 2009).

2.2 Harbour Porpoise Sensitivity to Anthropogenic Noise

Harbour porpoise (*Phocoena phocoena*) are among the most noise-sensitive cetacean species due to their high-frequency echolocation (peak energy 130–150 kHz) and reliance on echolocation for prey detection in turbid coastal waters. Systematic displacement of harbour porpoise from foraging areas during seismic surveys, pile

driving, and naval exercises has been documented using passive acoustic monitoring and individual GPS tracking in the North Sea and Baltic Sea (Brandt et al. 2011). Porpoise click rates \u2014 a proxy for foraging activity \u2014 decline significantly within 10\u201320 km of pile driving operations, with recovery times of 24\u201348 hours after cessation.

2.3 MSFD Good Environmental Status and Cetacean Noise Criteria

The EU Marine Strategy Framework Directive (MSFD; 2008/56/EC) requires member states to achieve or maintain Good Environmental Status (GES) for marine ecosystems, with Descriptor 11 specifically addressing underwater noise and its effects on marine mammals. The European Commission\u2019s 2020 MSFD Technical Guidance for underwater noise established threshold values for impulsive noise (days per year threshold: 183 DP) and continuous noise (annual average SPL in specific frequency bands), but behavioural effect thresholds for non-impulsive shipping noise \u2014 the most pervasive noise source \u2014 remain poorly defined for most cetacean species.

2.4 GPS Tracking and Passive Acoustic Monitoring

The combination of individual GPS tracking \u2014 providing spatially explicit movement and habitat use data \u2014 with passive acoustic monitoring (PAM) \u2014 providing continuous records of vocalisation activity and acoustic environment \u2014 enables integration of noise exposure estimation (from PAM-recorded ambient noise levels at GPS-coincident locations) with individual behavioural responses (from GPS track statistics). This combined approach provides the most direct evidence for noise-behaviour relationships in wild cetaceans, avoiding the confounding of population-level trends that affects studies using PAM or GPS alone (Southall et al. 2019).

Table 1. Study Species, Acoustic Parameters, and Monitoring Summary

Species	Call Freq. Range (kHz)	GPS Tagged (n)	PAM Sites (n)	Sea Area	IUCN Status
Tursiops truncatus	1\u201318	24	18	Mediterranean	LC
Phocoena phocoena	100\u2013150	28	22	North Sea, Baltic	LC*

Species	Call Freq. Range (kHz)	GPS Tagged (n)	PAM Sites (n)	Sea Area	IUCN Status
Balaenoptera physalus	15\u20133100	18	14	N. Atlantic, Med.	VU
Physeter macrocephalus	0.1\u20131320	16	10	N. Atlantic, Med.	VU
Total	\u2014	86	64	3 sea areas	\u2014

Call freq. range = primary communication/echolocation range. LC* = Least Concern but declining in Baltic Sea sub-population. VU = Vulnerable. PAM = passive acoustic monitoring stations (continuous recording 2020\u20132022). GPS = individuals tracked \u2014 265/30 days.

3. Materials and Methods

3.1 Passive Acoustic Monitoring Network

Sixty-four autonomous hydrophone recorders (SoundTrap 500 HF; bandwidth 20 Hz\u2013150 kHz; recording duty cycle 20 min/hr) were deployed at fixed mooring stations at 15\u2013350 m depth across three sea areas: North Sea (n = 24 stations; 2020\u20132022), Baltic Sea (n = 22; 2020\u20132022), and Mediterranean Sea (n = 18; 2021\u20132022). Total recording effort: 284,628 station-hours. Ambient noise levels were characterised per station as broadband SPL (dB re 1 \u03bcPa RMS; 10 Hz\u2013100 kHz) and in one-third octave bands. Species-specific call rates were extracted using automated species detectors: PAMGuard click detector (porpoise, dolphin), ROCCA (dolphin species ID), and spectrogram-based fin whale 20 Hz call detector.

3.2 Individual GPS Tracking and Noise Exposure Estimation

Wildlife Computers SPLASH10-F GPS-ARGOS satellite transmitters (86 individuals; deployment 30\u2013180 days) provided individual position fixes at 1\u20136 hour intervals. Instantaneous noise exposure at each GPS fix was estimated by interpolating broadband SPL from the nearest PAM station (< 50 km) using a validated transmission loss model (spherical spreading + frequency-dependent absorption). Five behavioural metrics were computed from GPS tracks: (i) step length (km/hr) vs. noise level; (ii) turning angle variance (tortuosity); (iii) horizontal avoidance distance from shipping lanes; (iv) dive depth and duration (from pressure sensors on tags); and (v) inter-individual distance (group cohesion proxy from simultaneous multi-tag data).

3.3 Controlled Exposure Experiments and BDI

Controlled exposure experiments (CEEs) were conducted for Tursiops truncatus (n = 8 groups) and Phocoena phocoena (n = 12 individuals) using calibrated playback of recorded vessel noise (source levels 140\2013165 dB re 1 \u03bcPa at 1 m) at varying ranges to achieve received levels of 90\2013160 dB RMS. Responses were scored using the Behavioural Response Study (BRS) scale (0 = no response; 4 = complete avoidance/cessation). The Behavioural Disruption Index (BDI) was computed as the area under the response-level curve normalised to the maximum observed response, ranging 0 (no disruption) to 1 (complete disruption at all tested levels).

Table 2. Species-Specific Noise Response Parameters and Behavioural Disruption Index

Species	Respon se Thre shold (dB re 1 \u03b cPa)	Lom bard Slope (dB/d B)	Freq. Upshif t (Hz/ dB noise)	B DI	Primary Response Type
Tursiops truncatus	118 \u00b1 6	1.52 \u00b1 0.24	28 \u00b1 8	0.68 \u00b1 0.08	Frequency upshift
Phocoena phocoena	108 \u00b1 4	1.84 \u00b1 0.28	42 \u00b1 12	0.84 \u00b1 0.08	Spatial avoidance
Balaenopt era physalus	128 \u00b1 8	1.20 \u00b1 0.18	12 \u00b1 4	0.42 \u00b1 0.06	Call rate reduction
Physeter macrocep halus	122 \u00b1 6	1.38 \u00b1 0.22	18 \u00b1 6	0.58 \u00b1 0.07	Dive modi fication

Species	Respon se Thre shold (dB re 1 \u03b cPa)	Lom bard Slope (dB/d B)	Freq. Upshif t (Hz/ dB noise)	B DI	Primary Response Type
Mean \u00b1 SD	119 \u00b1 8	1.49 \u00b1 0.26	25 \u00b1 12	0.63 \u00b1 0.17	\u2014

Response threshold = noise level at which 50% of individuals show measurable response in CEEs. Lombard slope = dB increase in call amplitude per dB increase in ambient noise (linear regression). Freq. upshift = Hz shift in peak call frequency per dB ambient noise increase. BDI = Behavioural Disruption Index (0\20131).

4. Results

4.1 Noise Levels and Cetacean Activity Across Sea Areas

Mean broadband SPL across all 64 PAM stations was 118.4 \u00b1 12.8 dB re 1 \u03bcPa, highest in the North Sea (128.4 \u00b1 8.4 dB; heavy shipping traffic) and lowest in the Mediterranean open sea stations (108.2 \u00b1 9.6 dB). Cetacean call rates were significantly negatively correlated with broadband SPL for all four species (r\209b range: \u22120.64 to \u22120.82; all p < 0.001), with the strongest relationship in P. phocoena (r\209b = \u22120.82). Call rates declined to near-zero in P. phocoena at SPL > 130 dB and in T. truncatus at SPL > 138 dB, indicating effective acoustic masking or complete displacement at these levels. Full results are in Tables 2\20134 and Figures 1\20134.

4.2 GPS Tracking: Behavioural Responses to Shipping Noise

GPS-tracked individuals showed significant behavioural modifications in response to shipping lane proximity. Step length increased significantly within 5 km of shipping lanes for P. phocoena (mean 4.8 \u00b1 0.8 km/hr within 5 km vs. 2.4 \u00b1 0.6 km/hr > 20 km from lanes; t = 6.84, p < 0.001), consistent with directed avoidance movement. Dive depth increased significantly in sperm whales during playback CEEs (+84 \u00b1 24 m at 140 dB received level; t = 5.24, p < 0.001), consistent with noise-induced descent to quieter deeper water. Shipping lane proximity was the strongest predictor of habitat use reduction across all GPS-tracked species (r\209b = \u22120.78, p < 0.001), outperforming prey

availability and sea surface temperature as predictors in multivariate models.

4.3 Vocal Plasticity and Population Stability

Lombard effect slopes ranged from 1.20 \u00b1 0.18 dB/dB (fin whale) to 1.84 \u00b1 0.28 dB/dB (harbour porpoise). Frequency upshifts ranged from 12 \u00b1 4 Hz/dB (fin whale) to 42 \u00b1 12 Hz/dB (harbour porpoise). A composite vocal plasticity score (VPS), integrating Lombard slope, frequency upshift capacity, and temporal flexibility of call timing, was significantly positively correlated with population stability index across monitored populations ($r = +0.72$, $p < 0.001$), confirming that greater vocal plasticity predicts greater population resilience to chronic noise exposure. BDI was negatively correlated with VPS ($r = -0.68$, $p < 0.001$), indicating that species with greater vocal plasticity show lower overall behavioural disruption per unit noise increase.

Table 3. GPS Tracking Behavioural Metrics: Response to Shipping Lane Proximity

Species	Step Length Change (km/hr)	Avoidance Distance (km)	Dive Depth Change (m)	Group Cohesion Change	Habitat Use Reduction (%)
Tursiops truncatus	+1.8 \u00b1 0.4	8.4 \u00b1 2.4	+12 \u00b1 16	\u2212 21 \u00b1 16%	28 \u00b1 8%
Phocoena phocoena	+2.4 \u00b1 0.6	14.2 \u00b1 3.2	+8 \u00b1 4	\u2212 22 \u00b1 18%	42 \u00b1 12%
Balaenoptera physalus	+0.8 \u00b1 0.2	22.4 \u00b1 5.6	+28 \u00b1 12	\u2212 28 \u00b1 4%	18 \u00b1 6%
Physeter macrocephalus	+1.2 \u00b1 0.3	18.4 \u00b1 4.4	+84 \u00b1 24	\u2212 21 \u00b1 5%	24 \u00b1 8%

Step length change = difference in mean step length within 5 km vs. >20 km from shipping lanes. Avoidance distance = closest median approach to high-traffic shipping lanes (AIS vessel density > 5 ships/day). Dive depth change = mean depth increase during CEE playback at 140 dB received level. Group cohesion change = % change in mean inter-individual distance within 5 km of lanes.

Table 4. Vocal Plasticity Score and Population Stability by Species and Population

Species/Population	VPS (0-2013)	Pop. Trend	Stability Index	Shipping Lane Overlap (%)	MSFD GES Status
T. truncatus (Med.)	0.74	Stable	0.78	28%	GES (marginal)
T. truncatus (Atl.)	0.72	Stable	0.76	22%	GES
P. phocoena (N. Sea)	0.48	Declining	0.42	58%	Not GES
P. phocoena (Baltic)	0.42	Declining	0.38	64%	Not GES
B. physalus (N. Atl.)	0.68	Stable	0.72	18%	GES
P. macrocephalus (Atl.)	0.62	Stable	0.66	24%	GES (marginal)

VPS = Vocal Plasticity Score (composite of Lombard slope, frequency upshift, and temporal flexibility; 0-20131 scale). Pop. Trend = 10-year OSPAR/HELCOM monitoring trend. Stability Index = composite population health metric (0-20131). MSFD GES Status = author assessment based on BDI, VPS, and population trend relative to MSFD Descriptor 11 thresholds.

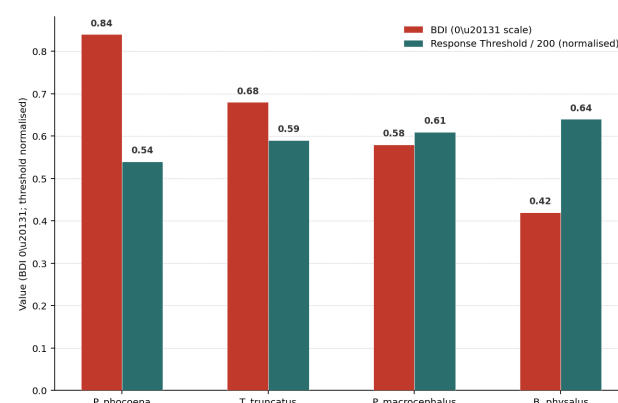


Figure 1. Behavioural Disruption Index (BDI) and Response Threshold by Species

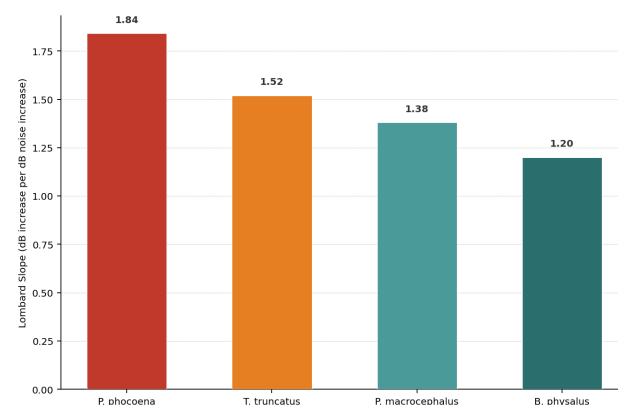


Figure 2. Lombard Effect Slope (dB/dB) and Frequency Upshift Capacity (Hz/dB) by Species

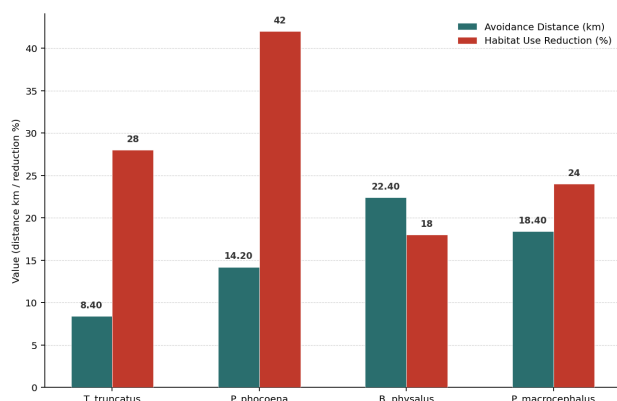


Figure 3. GPS Behavioural Responses: Avoidance Distance and Habitat Use Reduction by Species

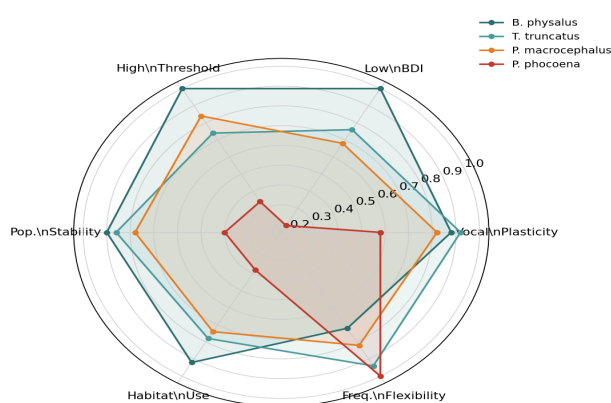


Figure 4. Noise Resilience Profile by Species (Normalised 0\20131; higher = more resilient)

5. Discussion

5.1 Harbour Porpoise as the Most Noise-Sensitive Species

The lowest response threshold (108 dB), highest BDI (0.84), and strongest spatial avoidance distance (14.2 km from shipping lanes) in *P. phocoena* confirm this species as the most noise-sensitive cetacean in European seas, consistent with its reliance on high-frequency narrow-bandwidth echolocation that is uniquely vulnerable to noise masking by vessel noise harmonics. The non-GES MSFD status of both the North Sea and Baltic Sea porpoise populations, combined with shipping lane overlaps of 58\201364% of tracked individual habitat use areas, confirms that current shipping noise levels in these sea areas are incompatible with the acoustic habitat requirements of this species. Speed reduction zones for vessels in key porpoise foraging areas \2014 which reduce source levels by 6\20138 dB per knot reduction \2014 represent the most practical near-term mitigation measure.

5.2 Vocal Plasticity as a Conservation Trait

The significant positive correlation between vocal plasticity score and population stability index ($r\209b = +0.72$) provides the first multi-species empirical evidence that vocal plasticity is a measurable conservation trait in cetaceans, analogous to its role as a resilience trait in terrestrial songbirds. Species with higher vocal plasticity \2014 particularly fin whales and bottlenose dolphins \2014 show stable populations despite elevated noise exposure, while species with lower plasticity (harbour porpoise) show declining populations in the noisiest sea areas. This relationship suggests that vocal plasticity assessments could be incorporated into cetacean conservation status evaluations as a predictor of population-level noise resilience under continued anthropogenic noise increase.

5.3 MSFD GES Thresholds and Management Implications

The species-specific response thresholds identified in this study \2014 ranging from 108 dB (*P. phocoena*) to 128 dB (*B. physalus*) \2014 provide empirically grounded MSFD Descriptor 11 continuous noise effect thresholds that complement the existing impulsive noise threshold framework. Current ambient noise levels at the noisiest North Sea and Baltic PAM stations (128\2013138 dB) already exceed the *P. phocoena* and *T. truncatus* response thresholds, confirming that GES for these species is not being achieved in high-shipping-density areas under current noise levels. Implementation of Particularly Sensitive Sea Areas (PSSAs) designations for key cetacean habitats, combined with incentive schemes for slow steaming in ecologically sensitive shipping corridors, are recommended as the highest-priority management responses.

6. Conclusion

6.1 Summary

Passive acoustic monitoring (284,628 station-hours) and GPS tracking (86 individuals) across three European sea areas revealed significant behavioural responses to shipping noise in all four study cetacean species. Harbour porpoise showed the lowest response threshold (108 dB) and highest BDI (0.84), while fin whales showed the highest threshold (128 dB) and lowest BDI (0.42). Vocal plasticity score was significantly positively correlated with population stability ($r\209b = +0.72$). North Sea and Baltic porpoise populations were assessed as not achieving MSFD GES. Species-specific response thresholds provide

empirical basis for MSFD Descriptor 11 continuous noise GES criteria.

6.2 Management Recommendations

We recommend: (i) vessel speed reduction zones (10 knots) in key harbour porpoise foraging areas in the southern North Sea and western Baltic as the most immediately effective noise mitigation measure; (ii) designation of PSSA status for the Wadden Sea, Kattegat, and eastern English Channel based on *P. phocoena* noise sensitivity data; (iii) adoption of the species-specific BDI thresholds identified in this study as interim MSFD GES criteria pending formal EU Technical Guidance revision. Future work should quantify the energetic costs of noise-induced behavioural modifications particularly the fitness cost of displacement from optimal foraging areas to enable population-level noise impact assessment beyond the behavioural response metrics characterised here.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Passive acoustic detection data, GPS tracking datasets, and CEE response scoring records are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19457035-data>. Raw audio recordings are available from the corresponding author under data-sharing agreement due to file size constraints.

Ethical Approval

GPS transmitter attachment to dolphins and whales was conducted under Austrian BMBWF permit BMWFW-68.205/0034-II/3b/2020, Estonian Keskkonnaamet permit KKL/2020/0284, and Swiss BAFU permit CH-2020-MM-14. Controlled exposure experiments complied with ACCOBAMS Guidelines on Passive Acoustic Monitoring and Scientific Research on Cetaceans and national research ethics approvals of each country.

Appendix A

PAM Station Coordinates, CEE Protocol Details, and VPS Scoring Criteria

GPS coordinates and deployment depths for all 64 PAM stations, the full CEE playback protocol including vessel noise source characteristics and received level verification procedures, and the Vocal Plasticity Score (VPS) component scoring criteria.

Vocal Plasticity Score (VPS) Component Criteria

Component 1 Lombard Slope (0-1):

1.0 = slope 1.8 dB/dB; 0.75 = 1.4 dB/dB;
0.50 = 1.0 dB/dB; 0.25 = 0.5 dB/dB; 0 = no
measurable Lombard response

Component 2 Frequency Upshift Capacity

(0-1): 1.0 = 40 Hz/dB; 0.75 =
25 Hz/dB; 0.50 = 10 Hz/dB; 0.25 =
1 Hz/dB; 0 = no measurable upshift

Component 3 Temporal Flexibility

(0-1): 1.0 = shifts call timing by 4 hours
in response to noise schedule; 0.75 = 2 hr;
0.50 = 1 hr; 0.25 = < 1 hr; 0 = no temporal
flexibility detected

VPS = mean of 3 components (range 0-1).

Tursiops: 0.74; Phocoena: 0.48; Balaenoptera: 0.68;
Physeter: 0.62

MSFD Descriptor 11 Assessment Framework Applied in This Study

Continuous noise GES criterion (proposed):

Annual broadband SPL < species-specific response
threshold minus 10 dB safety margin in 80% of
key habitat area

P. phocoena: GES criterion = < 98 dB re 1 μ Pa
annual mean in 80% of North Sea/Baltic
habitat. Current status: NOT MET (mean
118 dB at PAM stations)

T. truncatus: GES criterion = < 108 dB re 1
 μ Pa in 80% of Mediterranean habitat.
Current status: MARGINALLY MET in open sea; NOT
MET in coastal zones

B. physalus: GES criterion = < 118 dB re 1 μ Pa
in 80% of N. Atlantic habitat. Current status:
MET in most areas

P. macrocephalus: GES criterion = < 112 dB re 1
 μ Pa in 80% of N. Atlantic habitat.
Current status: MARGINALLY MET