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Review

A systematic review of aquatic contamination biomarkers in seabirds and their potential for ocean health monitoring

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ABSTRACT

Seabirds are long-lived apex predators that serve as key sentinels of ocean health, integrating contaminant exposure across trophic levels. This systematic review synthesises 275 peer-reviewed studies on biomarkers of aquatic contamination in seabirds, with 124 (45.1%) published in the last decade and the earliest dating back to 1976. Most studies focused on biomarkers associated with organic contaminants (64.0%), metal(loid)s (19.6%), or both (8.0%). Blood was the predominant biological matrix (55.6%), reflecting its suitability for non-lethal monitoring, followed by liver tissue (40.7%), primarily used to assess detoxification pathways. Unlike previous reviews that focused exclusively on molecular biomarkers or synthesised the use of biomarkers across broad aquatic taxa, this study provides the first global, cross-disciplinary synthesis integrating biochemical, cellular, molecular and physiological biomarkers specifically in seabirds. Across the dataset, biomarkers of xenobiotic biotransformation were the most frequently investigated (32.0% of studies), followed by endocrine disruption (20.3%) and oxidative stress (14.9%). A key gap identified was the limited application of biomarkers in the Southern Hemisphere species. Results highlighted the need to incorporate omics approaches, such as transcriptomics and proteomics to improve understanding of sublethal toxicity of aquatic contaminants. Coupling these approaches with non-lethal sampling in ecologically diverse sentinel species and mapping of global contamination hotspots offers a path toward developing sensitive, reproducible indicators of marine environmental health. Collectively, these findings provide an evidence-based framework to guide monitoring programmes and targeted capacity building in underrepresented regions, strengthening transboundary assessment of contaminants impacts and regulatory actions in marine ecosystems.

1. Introduction

Seabirds have long lifespans and play essential roles in ecosystem functioning, particularly by transporting nutrients between marine and terrestrial environments (Linhares et al., 2024). This ecological service is especially crucial in nutrient-poor habitats, such as oceanic islands, where it contributes significantly to productivity and for the maintenance of marine biodiversity (Graham et al., 2018). However, ocean pollution poses a growing threat to hundreds of seabird species, many of which undertake complex, wide-ranging seasonal migrations across vast marine areas (Clark et al., 2023). As such, seabirds serve as important sentinels of marine environmental change and contamination (Nunes

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et al., 2022). To fully understand the consequences of ocean pollution for wild populations and the ecosystem services they provide, research must go beyond simply documenting contaminant exposure. It is essential to quantify the biological effect associated with these exposures, particularly through the use of biomarkers of aquatic contamination (Jodice et al., 2023).

Biomarkers can be defined as contaminant-induced changes in cellular or biochemical components, processes, structures, or functions that can be measured in a biological system or sample (Lomartire et al., 2021). These tools allow for the early detection of adverse effects induced by xenobiotics, defined as chemical substances that are foreign to an organism and not naturally produced through its metabolic processes (Tomkiewicz et al., 2024). Biomarkers play a critical role in supporting ecological risk assessments and informing evidence-based decision-making aimed at preventing irreversible environmental damage (Iyanagi, 2007).

Among the many biological processes affected by contaminants, biotransformation is particularly critical to understanding xenobiotic bioaccumulation, fate, and toxicity (Iyanagi, 2007). Some biomarker responses, such as cytochrome P450 enzyme activity, are strongly associated with exposure to specific contaminant classes, like polycyclic aromatic hydrocarbons (PAHs). However, their ecological relevance at the population level can be difficult to interpret (Peakall, 1992). Other responses may more directly reflect impacts on survival or reproduction but are often influenced by a wide range of environmental factors, reinforcing the need to assess multiple biomarkers from different metabolic pathways (Kreitsberg et al., 2023).

Standardising biomarker selection for long-term monitoring is fundamental for assessing ocean health and understanding the impacts of contaminants on seabird populations (King et al., 2023). However, given the variety of xenobiotic contaminants present in marine environments, environmental degradation cannot typically be evaluated using single biomarkers alone. Rather, long-term monitoring usually requires the integrated application of diverse molecular and physiological biomarkers that assess complementary aspects of organism health, in order to accurately characterise the biological effects of contamination at both individual and ecosystem levels (de Jersey et al., 2025).

Despite gaps in knowledge across diverse marine ecosystems, large quantities of emerging and persistent organic pollutants (POPs), including pesticides and pharmaceuticals, continue to be released into the environment (Rocha et al., 2018; Bastolla et al., 2022). While long-lived, high-trophic-level species such as seabirds, marine mammals, and humans, are known to bioaccumulate high concentrations of organochlorines, mercury (Hg), plastics, and other contaminants through marine diets, the sublethal effects of diffuse-source contaminants are rarely documented (Kreitsberg et al., 2023; Thiagarajan and Devarajan, 2025). This gap highlights the need for studies that assess both contaminant exposure and its sublethal biological impacts in wild populations of seabirds, to evaluate how current levels of ocean pollution may be affecting the fitness and survival of individual animals.

In summary, a pervasive current anthropogenic threat to marine biodiversity is the discharge of chemical contaminants (Tornero and Hanke, 2016; Fliedner et al., 2020) and marine debris (Deudero and Alomar, 2015; Consoli et al., 2020). Marine waters cover nearly 75% of Earth's surface and the integrity of the planet's most extensive ecosystem is being disrupted, even in remote regions like the Arctic and Antarctic, with profound implications for global biodiversity and essential ecosystem services (Bergmann et al., 2015; Bryhn et al., 2020; Karima and Shafiul Islam, 2020). In this context, tools that enable the evaluation of contaminant impacts on biodiversity, such as aquatic contamination biomarkers, have been applied to various taxonomic groups (e.g., Dias et al., 2024). Here, we systematically review biomarkers of aquatic contamination in seabirds to identify those most frequently investigated and those with the greatest potential for future application in this taxonomic group. Additionally, we aim to highlight taxonomic coverage, geographic range, contaminant classes, and metabolic pathway gaps that warrant further research on aquatic contamination effects.

Unlike previous reviews that focused exclusively on molecular biomarkers (e.g., Kreitsberg et al., 2023) or synthesised biomarker use across broad aquatic taxa without a seabird-specific perspective (Lomartire et al., 2021), this study provides the first integrated, cross-disciplinary synthesis encompassing biochemical, cellular, molecular, and physiological biomarkers specifically in seabirds worldwide. By consolidating evidence across these diverse biomarker classes, the review offers a comprehensive framework that strengthens our ability to assess homeostasis and organismal perturbations arising from exogenous chemical challenges on a global scale. To guide this synthesis, we address two overarching questions: (1) How have biomarker applications in seabirds varied across metabolic pathways, contaminant classes, tissues, and geographic regions, and what major gaps remain in global biomonitoring coverage?; and (2) What biomarkers of aquatic contamination have been studied, and how do they reflect exposure to, or toxic effects of, ocean contaminants in seabirds globally? By addressing these aspects, this review positions seabirds as model sentinel taxa for detecting contamination gradients, enhances the strategic application of biomarkers in monitoring programmes, and supports evidence-based initiatives aimed at strengthening marine environmental health and ocean conservation.

2. Materials and methods

2.1. Search strategy

To guide the formulation of the research question and the development of the search strategy for this review, the PICO framework, an acronym for *Population, Intervention, Comparison, and Outcome*, was employed as a mnemonic tool (Supplementary Table S1). Each element of the PICO framework was defined in accordance with the scope of this review to gather the most relevant information from the available scientific literature, resulting with the clearly defined research question, "*What biomarkers of aquatic contamination were studied or are currently under investigation, and how do they reflect exposure to or toxic effects of ocean pollution in seabirds globally?*".

This review applied the Search strategy to six databases: Scopus, Web of Science, PubMed (Medline), Scielo, LILACS, and Google Scholar. The structured trilingual vocabulary *DeCS – Health Sciences Descriptors*, and the English-language vocabulary *MeSH – Medical Subject Headings*, were consulted to identify official descriptors, which were combined with relevant keywords in the search strategy. Keywords used included ‘sea bird’, ‘seabird’, ‘pelagic bird’, ‘oceanic bird’, ‘seafowl’, ‘marine bird’; and ‘biomarker’, ‘biological marker’, ‘biologic marker’, ‘immune marker’, ‘immunologic marker’, ‘bioindicator’, ‘biological indicator’, ‘biological monitoring’, ‘biologic monitoring’, ‘bio monitoring’, ‘biomonitoring’, ‘biotransformation’, ‘metabolic detoxification’, ‘detoxification’, ‘oxidative stress’, ‘genotoxicity’, ‘endocrine disrupting’, ‘immunosuppression’, ‘toxic’, ‘toxicology’, ‘effect’, ‘cytotoxicity’; and ‘contamination’, ‘contaminant’, ‘contaminated’, ‘pollutant’, ‘pollution’, ‘polluted’, ‘xenobiotic’, ‘metal’, ‘metalloid’, ‘organic’. Searches also considered the plural variations of these keywords. The detailed search terms and Boolean operators used in the search strategies are provided in Supplementary Table S2. While all records retrieved from the primary databases were screened in full, the supplementary Google Scholar search was limited to the first 150 results generated for each keyword string, in accordance with established methodological guidance for searches using that platform.

Original research articles published in peer-reviewed journals and presenting data on biomarkers of aquatic contamination in seabirds, up to 1 May 2025, were included. Review articles were excluded to avoid data duplication in the analysis. However, review papers and academic theses related to the scope of this review were retained for references cross-checking against the results obtained through the primary search strategy. This complementary approach was adopted to increase comprehensiveness of the review and to identify potentially relevant publications that may have been initially overlooked.

2.2. *Publication selection process*

Inclusion and exclusion criteria were established prior to the study selection process to minimize bias, following the SYRCLE protocol (Systematic Review Centre for Laboratory Animal Experimentation, available at www.syrcle.network and www.radboudumc.nl). From a technical standpoint, no restrictions were placed on language or publication date for study inclusion. However, specific publication types that did not meet the inclusion criteria were excluded. These included review articles, methodological papers, conference abstracts, monographs, dissertations, theses, books, book chapters, reports, and records not classified as original research articles published in peer-reviewed journals. These were screened but not included in the final systematic review.

The population of interest was restricted exclusively to seabirds. Studies involving other animal groups were excluded. For the purpose of this review, seabirds were defined as bird species that rely predominantly on the marine environment for foraging and breeding throughout most of their life cycle (Harrison et al., 2021). The taxonomy adopted follows BirdLife International's classification used for the IUCN Red List (BirdLife International, 2025), using as references for this review the seabird species lists considered by Dias et al. (2019) and Harrison et al. (2021) (Supplementary Table S3). The intervention of interest involved exposure to anthropogenic contaminants; thus, studies addressing only natural contaminants or biotoxins were excluded. As for the outcomes of interest, we included studies that investigated biomarkers at the biochemical, molecular, cellular or physiological levels related to aquatic contamination. Thus, we defined the scope of this review to encompass biomarkers operating at the lower to intermediate levels of biological organisation, including molecular (e.g., gene and protein expression), biochemical (e.g., enzymatic activity), cellular (e.g., oxidative or cytotoxic damage), and physiological responses (e.g., hormones). Higher-level organismal (e.g., morphometrics, reproductive success, or body condition), ecological or demographic (e.g., population or community metrics) endpoints were intentionally excluded, as the focus of this review is on mechanistic markers of contaminant exposure and sublethal effects in seabirds.

Publication selection followed a three-tier approach (identification, screening and inclusion) based on PRISMA 2020 guidelines (Transparent Reporting of Systematic Reviews and Meta-Analyses, http://www.prisma-statement.org), and results are summarized in a flow diagram as recommended for systematic reviews, including database searches and additional records (Page et al., 2022). The screening process occurred in two stages: an initial screening of titles and abstracts, followed by full-text analysis. Both stages were independently conducted by two reviewers using the Covidence platform (https://www.covidence.org), which also facilitated the removal of duplicate records and Cohen's kappa calculations (Cohen, 1960). Inter-rater agreement was quantified using Cohen's kappa, yielding $\kappa = 0.737$ for title/abstract screening and $\kappa = 0.754$ for full-text screening, indicating substantial agreement. Disagreements were adjudicated through structured consensus discussions; when consensus could not be reached, a third reviewer provided the final decision.

2.3. *Categorization and analysis*

Data extraction from the selected publications was carried out using a standardized form developed by the authors, based on Covidence guidelines, and compiled into an Excel spreadsheet. Each publication was assigned a unique identification number, and the following information was recorded: name of the first author, year of publication, country of affiliation of the authors, gender of the first author, seabird species studied, countries where seabirds were sampled, biological materials collected, contaminants analysed (or contaminant groups), type of exposure (in vitro, in vivo, or ex vivo), reported associations between biomarker responses and contaminants, use of post-mortem samples, and whether the study was part of a long-term environmental biomonitoring program. Sampling sites were assigned to hemispheres based on their geographic location. Author affiliation countries were classified by hemisphere and World Bank income group, and each study was categorised according to hemispheric involvement (Northern-only, Southern-only, or cross-hemispheric) and income composition (high-income only, non-high-income only, or mixed-income collaboration); temporal trends were assessed using binomial generalized linear models (Tredennick et al., 2021).

International collaboration patterns were examined using chord diagrams based on author affiliation countries, in which links represent co-authorship between countries and link widths are proportional to the number of shared publications (Jiménez-Islas et al., 2024). We ran analyses and graphics using GraphPad Prism v. 10.5 and R software (R Core Team, 2023) within the RStudio v. 4.5.0 (Posit Team, 2023). Spatial visualisations and data processing were conducted using the R packages ggmap (Kahle and Wickham, 2013), ggpubr (Kassambara, 2025), rnaturalearth (Massicotte and South, 2025), sf (Pebesma, 2018), wbstats (Vargas Sepulveda, 2025) and tidyverse (Wickham et al., 2019).

Considerations were applied to certain variables assessed within publications. Regarding biological material, blood was treated as a single tissue sample category regardless of whether it was whole blood, plasma, or serum. Post-mortem samples referred to tissues collected from seabirds found dead or euthanised. Studies were classified as involving chemical analysis if they quantified contaminant concentrations in tissues or employed experimental exposures (in vivo, in vitro, or ex vivo). Studies that did not measure contaminant concentrations, but reported biomarker data relevant to aquatic contamination at a specific location were still included, as they provide valuable information for environmental biomonitoring. Studies that compared sites with varying levels of presumed contamination without measuring contaminant concentrations in seabird tissues were not classified as having conducted chemical analyses. However, studies comparing oiled versus non-oiled birds or individuals from contaminated and uncontaminated areas (e.g., oil spill versus non-impacted sites), were categorised as having a control group design, even if contaminant concentrations were not measured directly in tissues.

Biomarkers were grouped into the following categories: biotransformation, endocrine disruption, hepatic damage, oxidative stress, metal exposure and detoxification, genotoxicity, neurotoxicity, cytotoxicity, immunotoxicity, and general health parameters. To avoid conceptual ambiguity, we established explicit decision rules regarding the treatment of "general health parameters". Only studies in which physiological or haematological measures (e.g., haematocrit, leukocyte profiles, plasma metabolites) were explicitly analysed in relation to contaminant exposure or burden were classified as ecotoxicological biomarkers and included in the review. Conversely, studies reporting these parameters solely as baseline clinical descriptors, without testing associations with contaminants or contamination gradients, were excluded. Borderline cases were adjudicated based on whether the variable of interest was (i) hypothesised as mechanistically linked to contaminant effects, (ii) statistically evaluated against contaminant concentrations or exposure groups, or (iii) interpreted by the authors as indicative of contaminant-induced physiological disturbance.

3. Results and discussion

3.1. *Selected publications included in the systematic review*

A total of 4,627 potentially relevant records addressing biochemical and molecular biomarkers of aquatic contamination in seabirds were retrieved through the search strategy and compiled for screening (Fig. 1). After completing all stages of the selection process, 275 peer-reviewed articles were deemed eligible and included in this systematic review.

3.2. Historical overview and geographic distribution of publications and research topics

The number of studies investigating biomarkers of aquatic contamination in seabirds has increased substantially over the past decade, accounting for 124 publications, representing 45.1% of the 275 peer-reviewed papers included in this review. The earliest study identified was published in 1976 (Fig. 2).

The studies were conducted by authors affiliated with institutions across 37 countries. The majority of publications originated from institutions based in Canada ($n = 81$; 29.5%), the United States ($n = 68$; 24.7%), Norway ($n = 63$; 22.9%), France ($n = 38$; 13.8%), and the United Kingdom ($n = 31$; 11.3%; Fig. 3). Only three South American countries were represented among the studies included in this review, with papers from institutions in Argentina ($n = 14$; 5.1%), Chile ($n = 7$; 2.5%), and Brazil ($n = 2$; 0.7%). Analysis of author affiliations revealed a pronounced geographic and economic bias in seabird biomarker research. Most studies were authored exclusively by institutions based in the Northern Hemisphere (87.6%), whereas only 5.8% involved authors solely from the Southern Hemisphere, and 6.6% represented cross-hemispheric collaborations. In parallel, authors from high-income countries dominated publications, accounting for 89.1% of studies, while mixed-income collaborations and studies led exclusively by non-high-income countries represented 6.9% and 4.0% of publications, respectively. Despite this imbalance, the involvement of non-high-income countries increased significantly over time (binomial GLM, $\beta = 0.104 \pm 0.031$ SE, $p < 0.001$).

The diversity of countries and researchers involved in the study of biomarkers in seabirds contributes to a wide range of perspectives and scientific insights. Collaborative studies are particularly advantageous, especially given that many seabird species are migratory and move across countries and continents. The first articles authored by researchers affiliated with more than two countries on biomarkers topic were published in 2008 (Verboven et al., 2008; Verreault et al., 2008), and international collaborations have become increasingly frequent since 2010. The chord diagram (Fig. 4) illustrates patterns of international collaboration based on author affiliations, with link widths reflecting the frequency of co-authored studies among the most represented countries. This diversity in sociocultural and environmental

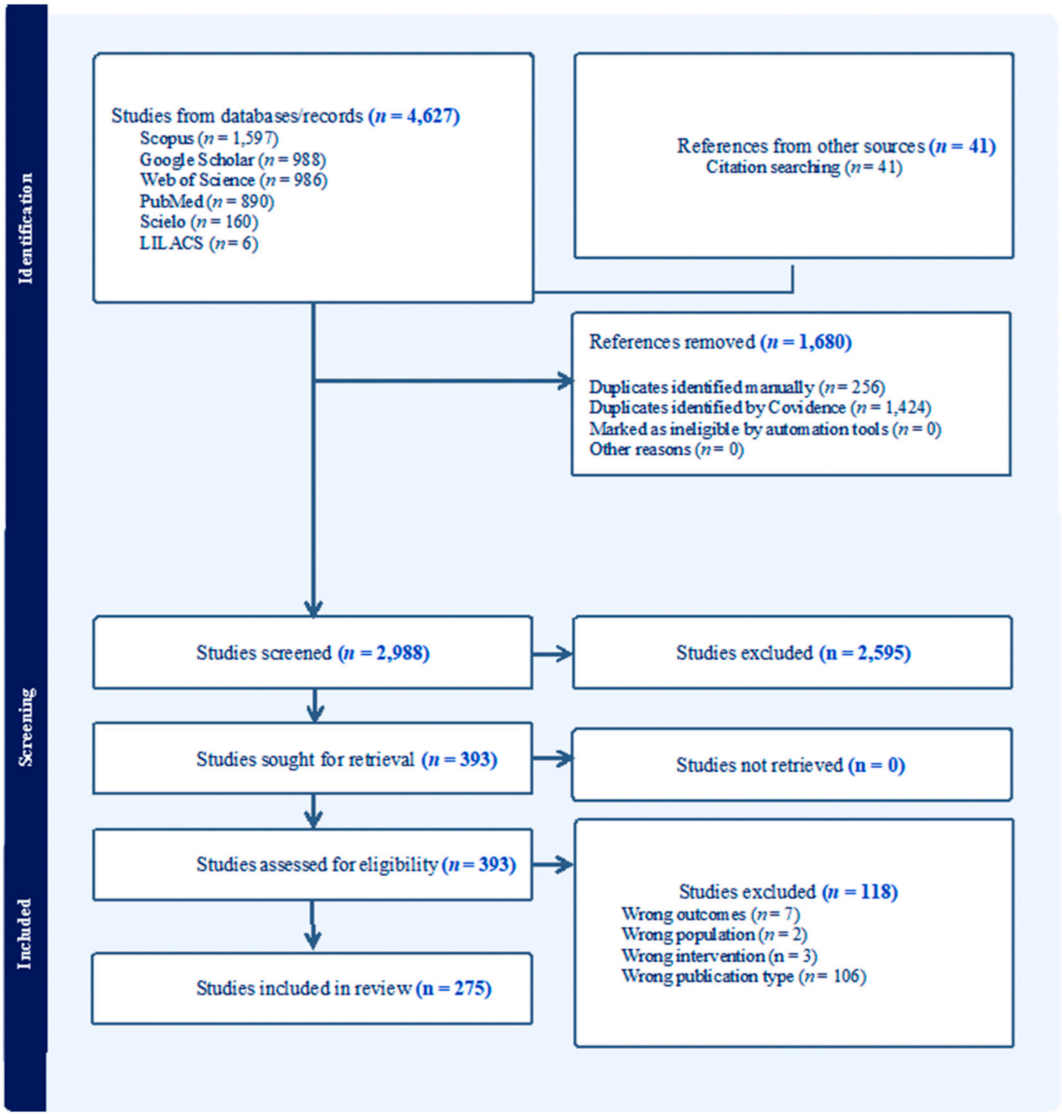

Fig. 1. Schematic summary of the study selection process, adapted from the PRISMA methodology, illustrating the three-tier approach (identification, screening and inclusion) used in this systematic review on biochemical and molecular biomarkers of aquatic contamination in seabirds, along with their respective outcomes.

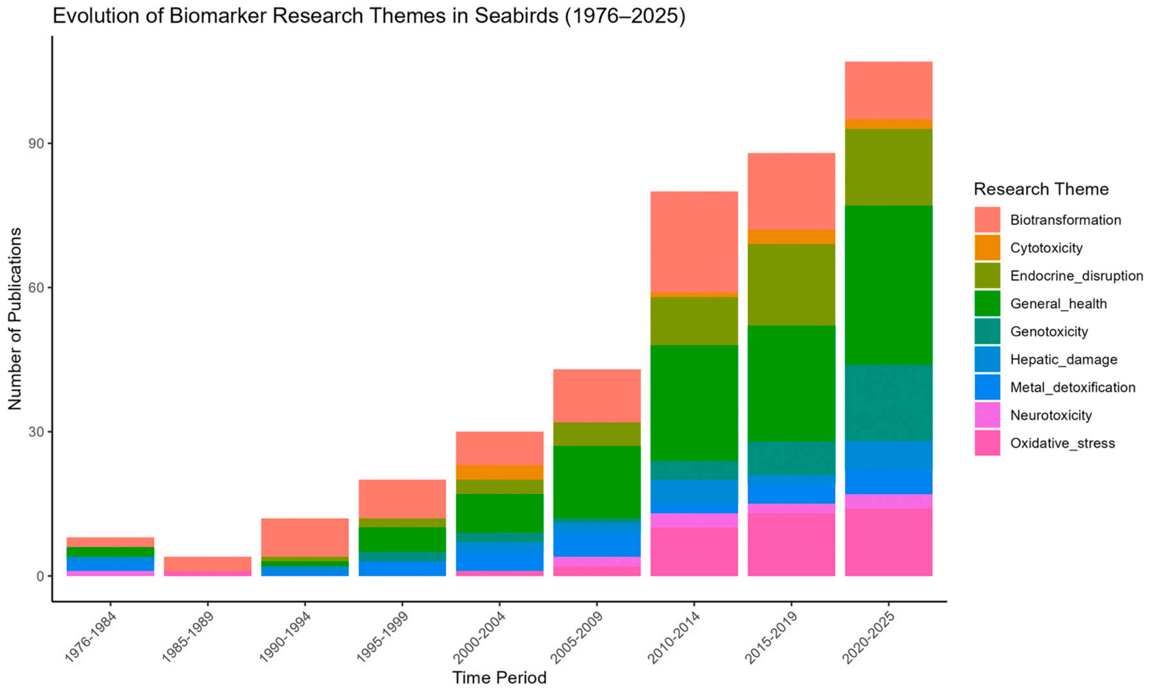

Fig. 2. Temporal distribution of publications and research theme categories on biomarkers of aquatic contamination in seabirds (1976–2025).

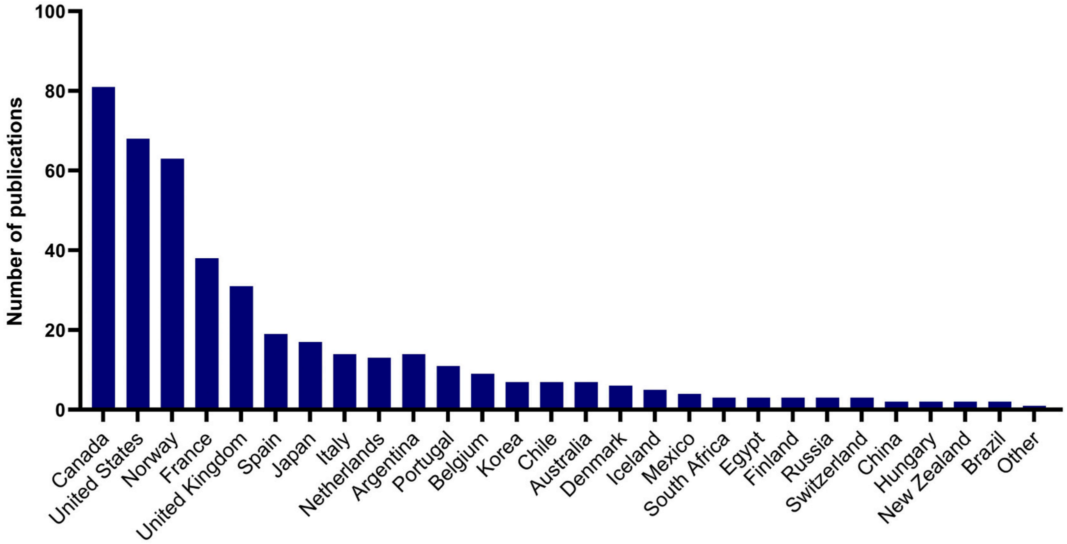

Fig. 3. Number of publications on biomarkers of aquatic contamination in seabirds by country of author affiliation. The category ‘Other’ refers to countries listed as the affiliation for only one publication and includes the United Arab Emirates, Scotland, Ireland, Malaysia, Monaco, Czech Republic, Kenya, Sweden, Thailand, and Tunisia.

contexts is also reflected in the content of the studies, which assess the effects of contamination on different species and ecosystems across the globe (Swartz et al., 2019). Nevertheless, certain regions have demonstrated a greater research effort, such as Norway, which stands out for its prominent role in monitoring the environmental impacts of contaminants on seabirds in the Arctic.

Sampling locations were predominantly situated in countries of the Northern Hemisphere, particularly Norway ($n = 57$; 20.7% of studies), Canada ($n = 57$; 20.7%), the United States ($n = 52$; 18.9%), and Japan ($n = 10$; 3.6%). Several studies were also conducted in Antarctica ($n = 18$; 6.5%), involving international collaborations among institutions from various countries (Fig. 5). In South America, sampling was considerably less frequent, with seabirds collected in Argentina ($n = 8$; 2.9%), Chile ($n = 4$; 1.5%), and Brazil ($n = 2$; 0.7%).

Considering the sampling locations, certain regions, such as the Arctic, once again stand out in the global context. Study sites in Norway alone accounted for approximately one-quarter of all publications to date, followed by a substantial number of locations sampled in Canada and the United States, with particular emphasis on the Alaskan region in the latter. In contrast, countries across Latin America, Africa, south and southeastern Asia (the highly populous China and India, for instance), contributed comparatively fewer studies, or even none. Analysing the overall proportions of studies by hemisphere, we observed that most studies (84.0%, $n = 231$) were conducted exclusively in the Northern Hemisphere, whereas only 13.5% ($n = 37$) focused solely on Southern Hemisphere sampling locations. Cross-hemispheric studies were rare,

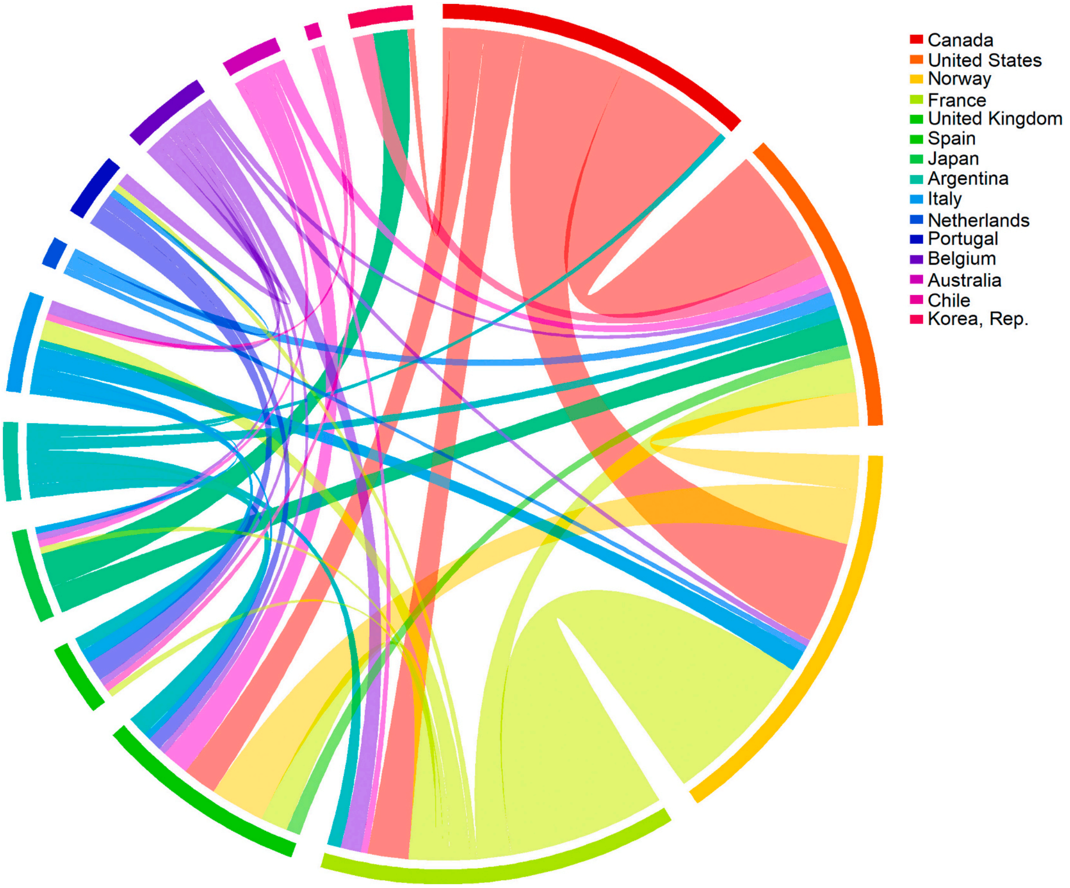

Fig. 4. Chord diagram showing international collaboration patterns among the 15 most represented countries based on author affiliations in publications on biomarkers in seabirds.

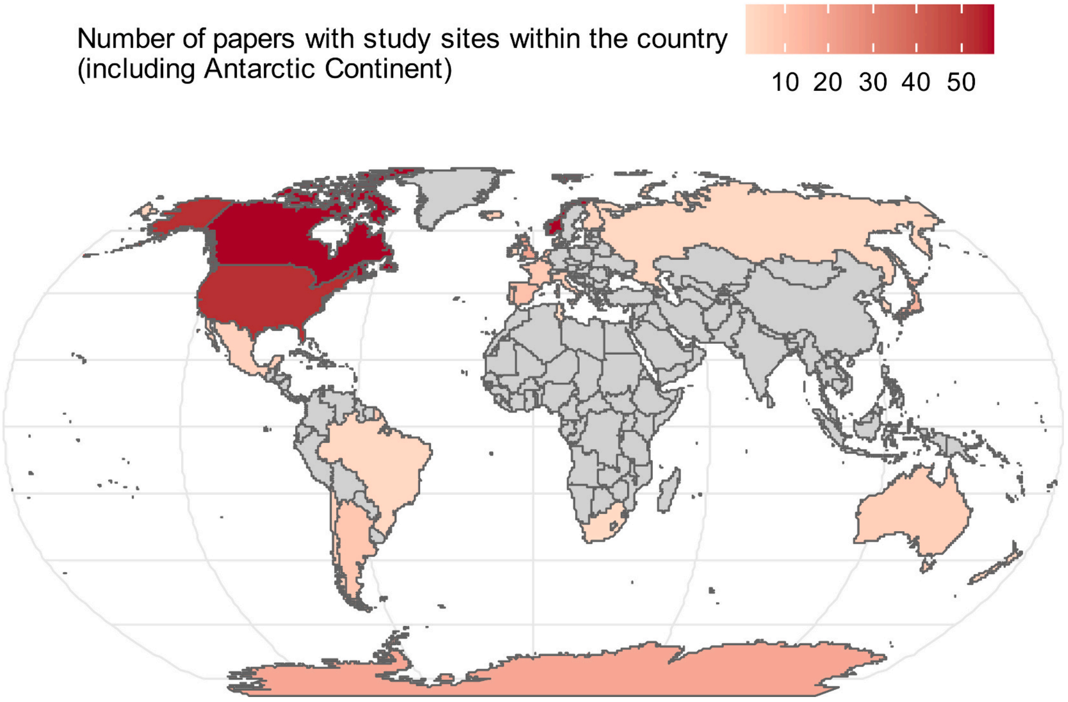

Fig. 5. Representation of each country, plus Antarctic Continent, among study sites where samples were collected and investigated in publications on biomarkers of aquatic contamination in seabirds from 1976 to 2025. The number of articles per country that included sampling locations within their territory was used to generate the figure.

accounting for only 1.1% (n =3) of the papers published. A small fraction of studies (1.5%, n = 4) could not be classified because samples were obtained offshore, involving bycatch studies. Overall, these results highlight geographic bias and a marked underrepresentation of Southern Hemisphere regions. This underscores the need for increased financial and infrastructural support to promote biomarker research in study sites within these underrepresented regions (Fig. 5).

The geographical pattern of publications on biomarkers of aquatic contamination in seabirds is closely linked to, and should be considered within, the broader political and economic context of scientific production. A well-documented disparity exists between developed and developing countries in the generation of science and technology (Karlsson et al., 2007). Westholm et al. (2004) used data from the United Nations Educational, Scientific and Cultural Organization (UNESCO) to demonstrate that developing countries contributed 42% of the global gross domestic product (GDP), yet they were responsible for only 20% of total gross expenditure on research and development. Similarly, these countries were home to 79% of the world's population but employed only 28% of the world's researchers (Westholm et al., 2004). Although these numbers represent progress compared to previous decades, the disparity remains substantial and appears to persist in recent decades, including within the field of biomarkers in seabirds.

3.3. Studied species, contaminants, and tissues

Notably, 94 of the nearly 400 extant seabird species (Dias et al., 2019; Harrison et al., 2021) have been included in studies investigating biomarkers of aquatic contamination. In 61 publications (22.2%), more than one species was investigated simultaneously. Most studies examining the effects of contamination on biomarker responses in seabirds have focused on colonial-breeding species in the Northern Hemisphere. The black-legged kittiwake (*Rissa tridactyla*; n = 27 articles; 9.8%), the

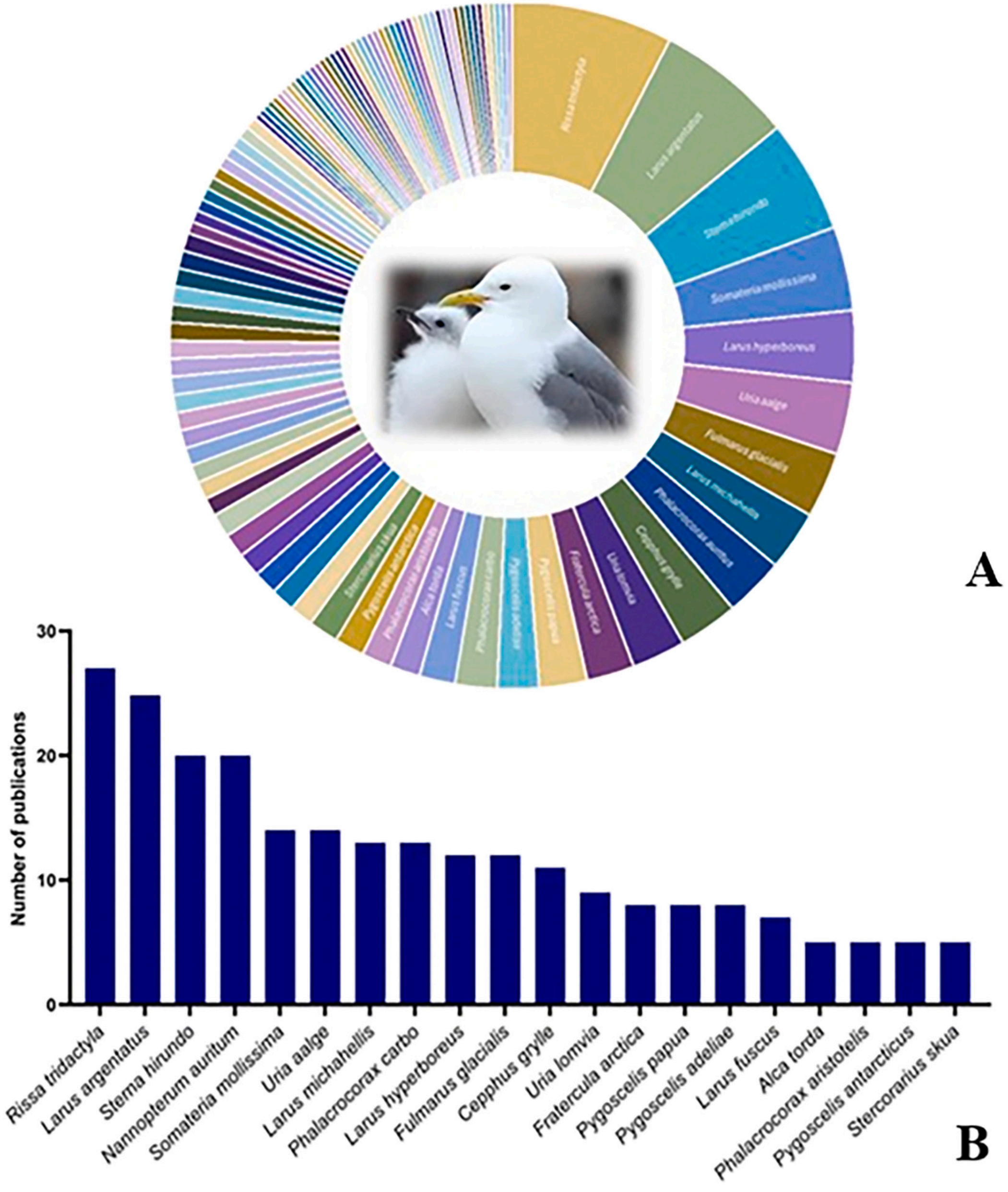

Fig. 6. Proportion (6A) of published studies considering all 94 species, and number (6B) of publications on aquatic contamination biomarkers per seabird species, depicting only those with more than 5 articles, from 1976 to 2025. The remaining species, that represented less than 5 papers each, are listed in Supplementary Table S3.

herring gull (*Larus argentatus*; $n = 27$ articles; 9.8%), and the common tern (*Sterna hirundo*; $n = 20$ articles; 7.3%) were the most frequently studied species (Fig. 6).

Most publications highlight the importance of investigating exposure to xenobiotics and associated biomarkers in a taxon-specific manner, acknowledging that species-specific foraging strategies and life-history traits can influence both contaminant sensitivity and biomarker responses. However, an analysis of the taxonomy of the 94 seabird species studied reveals a clear bias towards the order Charadriiformes (Fig. 7), which is consistent with the species richness of this group and the predominance of studies conducted in the Northern Hemisphere.

Indeed, the concentration of a contaminant at its site of action within an organism depends on the physicochemical properties of the chemical compound and the physiology of each species (toxicokinetics), which may vary according to the structural and functional peculiarities characteristic of different Orders and Families within the Class Aves (e.g., Walker, 1990). Thus, each taxonomic group may exhibit differences in the ingestion, absorption, distribution, and metabolism of contaminants across phylogenetically distant species with distinct physiologies. Once the contaminant reaches the target site, a toxicity pathway is initiated (toxicodynamics) (Walker, 1990). The resulting damage may depend on the dose and duration of exposure, the sequence of biological processes involved in maintaining homeostasis, and the organism's adaptability to chemical stressors (Sonne et al., 2020). Thus, the biological responses are modulated by species-specific particularities of the different seabird groups studied to date (Fig. 7).

Among the reviewed studies on seabird biomarkers, most investigated organic contaminants, including persistent organic pollutants (POPs), such as organochlorine pesticides (OCPs), polychlorinated biphenyls (PCBs), and polybrominated diphenyl ethers (PBDEs), as well as emerging compounds such as per- and polyfluoroalkyl substances (PFASs) ($n = 176$; 64.0%). A smaller subset focused exclusively on inorganic contaminants, primarily metals and metalloids (e.g., Hg, Pb, Cd, As, Cr) ($n = 54$; 19.6%). The remaining studies analysed both organic and inorganic contaminant groups ($n = 22$; 8.0%). Definitions and standardized terminology for contaminant classes are provided in Supplementary Table S4. The remaining studies did not investigate these contaminants ($n = 24$; 8.7%).

According to our review, most biomarker and contaminant analyses were conducted on blood and liver, with 153 (55.6%) and 112 (40.7%) publications, respectively (Fig. 8). Across biomarker classes, tissue choice strongly influenced both interpretability and feasibility of sampling. Blood-based matrices were most frequently used for biomarkers of oxidative stress, genotoxicity, immune function and endocrine disruption, reflecting their suitability for non-lethal sampling and repeated monitoring. Liver tissue predominated in studies targeting xenobiotic biotransformation pathways and metal-binding proteins, owing to its central role in detoxification processes, although its use is largely restricted to opportunistic or post-mortem sampling. Although offering a fully non-invasive alternative, feathers are primarily applied to assess metal exposure and long-term contaminant biomonitoring, but with limited resolution for short-term physiological responses. Overall, blood matrices were the most valuable non-lethal matrices to provide indicators of exposure and sublethal effects, whereas internal tissues yield higher mechanistic resolution at the cost of reduced sampling feasibility.

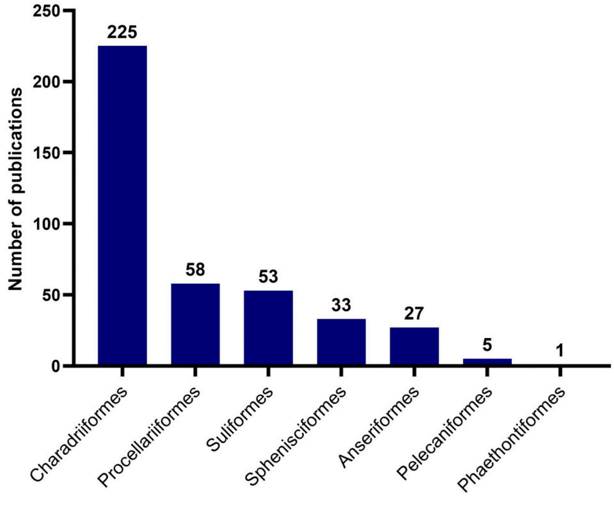

Fig. 7. Number of publications per Order in the Class Aves that have investigated biomarkers of aquatic contamination in seabirds from 1976 to 2025.

3.4. *Associations between biomarkers and contaminants*

Associations between aquatic contaminants and biomarkers in seabirds can be categorised into several functional groups. In the present review, we identified the following: biotransformation, endocrine disruption, liver damage, oxidative stress, metal exposure and detoxification, genotoxicity, neurotoxicity, cytotoxicity, immunotoxicity, and general health parameters. It is important to note that individual publications may contribute to more than one category; therefore, the total number of papers across all categories may exceed the number of unique publications ($n = 275$).

Most studies assessed contaminant-biomarker associations using correlational analyses, often conducted in natural environments with uncontrolled in situ exposure to contaminants. However, some publications reported experimental results in captivity using ex situ seabirds under controlled exposure conditions (e.g., Prichard et al., 1997; Najle et al., 2006; Pritsos et al., 2017). Studies including control groups with respect to contaminant exposure were conducted under laboratory conditions, where the control group comprised individuals not exposed to the contaminant, either through diet or dermal contact. Alternatively, some studies employed an epidemiological approach by comparing seabirds in contaminated areas with those found in reference sites located away from known contamination sources (e.g., Fossi et al., 1986; Esler et al., 2011; Franci et al., 2014). Another strategy involved selecting a group of seabirds with minimal contaminant levels as a reference group, which was then compared with birds exhibiting higher levels. Statistical analyses and mathematical modelling were employed in this case to stratify subgroups of seabirds based on contaminant concentrations and biomarkers response (e.g., Goutte et al., 2018; Sebastiano et al., 2020; Bauch et al., 2022).

3.4.1. *Xenobiotic biotransformation biomarkers*

This systematic review demonstrates that, since 1976, biomarkers of xenobiotic biotransformation have been the most extensively studied in seabirds, with 88 publications addressing this topic (32.0% of all reviewed studies). Several authors have emphasised that understanding the kinetics of xenobiotic biotransformation provides the mechanistic link and interpretative framework necessary for elucidating contaminant-induced toxicity in seabirds (Drouillard et al., 2007; Rattner et al., 2024). These insights can contribute to the development of chemical toxicodynamic models and inform long-term monitoring programmes. Additionally, the use of biotransformation system enzymes as biomarkers of contamination has been favoured due to their inducibility or inhibition in response to xenobiotic exposure (Gagné, 2014). This greater focus and relevance extend beyond seabirds, i.e. it is widely recognised across other taxonomic groups, as evidenced by pioneering studies conducted in fish (e.g., Clements et al., 1994; Luthe et al., 2002) and marine invertebrates (e.g., Boutet et al., 2004; Lüchmann et al., 2011).

Biotransformation is typically categorised into phases according to the type of enzymatic reaction involved (Cui and Li, 2018). Phase I and II enzymes have already been studied as potential biomarkers of aquatic contamination in seabirds. Phase I includes hydrolysis, oxidation, and

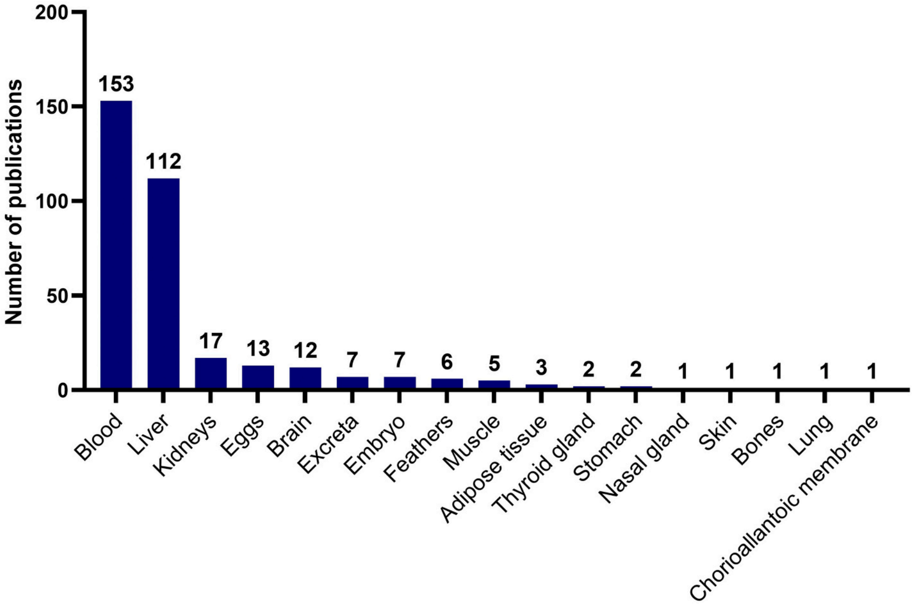

Fig. 8. Number of publications by sampled tissue for analyses of aquatic contamination biomarkers in seabirds. The numbers above bars represent the number of publications reporting results for the respective tissue.

reduction reactions, and has been investigated in seabirds through studies focusing on enzymes such as cytochrome P450s (CYPs) and aldehyde dehydrogenases (ALDs) (Table 1). Phase II has been explored in seabirds by examining conjugation reactions, primarily mediated by transferases such as glutathione S-transferases (GSTs) and UDP-glucuronosyltransferases (UGTs), which conjugate xenobiotics to molecules such as glutathione (GSH) and uridine 5′-diphosphoglucuronic acid (UDPGA), respectively. Metabolites generated through Phases I and II are subsequently excreted from the organism with the assistance of membrane efflux pumps associated with Phase III. In seabirds, Phase III has been investigated exclusively through molecular approaches, particularly focusing on gene transcription of the ATP Binding Cassette Subfamily B Member 1 (*ABCB1*) (Iyanagi, 2007; Wallace et al., 2025). Through biotransformation, lipophilic xenobiotics are converted into more polar compounds, increasing their hydrophilicity, which facilitates their elimination from cells and excretion via urine, bile, and faeces, thereby preventing toxic injury (Walker, 1990). However, the biotransformation of certain xenobiotics may also generate metabolites that are more toxic than the parent compounds, through a process known as bioactivation (van der Oost et al., 2003). Understanding these processes across the diverse groups of seabirds will undoubtedly require still further research.

In recent decades, increasing attention has been given to the transcriptional regulation of Phase I and II biotransformation enzymes by ligand-activated transcription factors, with particular emphasis on the aryl hydrocarbon receptor (AhR) (Table 1). Upon activation by agonists such as PAHs and halogenated aromatic hydrocarbons (HAHs), including polychlorinated dibenzofurans (PCDFs), polychlorinated biphenyls (PCBs), and polychlorinated dibenzo-p-dioxins (PCDDs), AhR interacts with regulatory elements of target genes (Barron et al., 2004). Studies focusing on the molecular mechanisms underlying the toxicity of these organic contaminants through AhR activation in seabirds began to emerge in 2006. In particular, comparative analyses between a model species (the domestic chicken, *Gallus gallus*) and a wild marine bird species, the common tern, investigated molecular differences in species-specific sensitivity to dioxin-like compounds and proposed the use of AhR as a biomarker of susceptibility in wildlife (Karchner et al., 2006). Subsequent studies expanded on this evidence (e.g., Farmahin et al., 2012; Nacci et al., 2016). Further research also explored the characterisation of AhR agonists in herring gull (Muusse et al., 2015), and correlations have been sought between the transcription of the *AhR* gene and the isoform of the nuclear translocator of the aryl hydrocarbon receptor (*Arnt1*) with levels of organic and inorganic contaminants in the Northern gannet, *Morus bassanus* (Champoux et al., 2020). AhR activation has been shown to modulate the transcription of several genes associated with biotransformation, including *CYP1A1*, *CYP1A2*, *NAD(P)H quinone dehydrogenase 1 (NQO1)*, *ALDH3A1*, *GSTA1* and *UGT1A6* (Larigot et al., 2018).

Among the biotransformation systems, CYP enzyme complex has been the most extensively studied biomarker in seabirds. CYP activity provides an indication of the organism's metabolic capacity and the potential for the formation of metabolites that, in some cases, may also be toxic (Walker, 1980). Investigations in seabirds have employed various assays at different cellular and molecular levels, including immunodetection, protein expression, and transcript quantification, which have demonstrated significant associations between CYP and exposure to organic contaminants (Table 1). Pioneering work by Walker (1990) provided detailed insights into the activity of various monooxygenases in avian species highlighting the central role of CYP enzymes in xenobiotic metabolism. Among the preferred substrates used in enzymatic assays, are alkoxyresorufins (such as 7-methoxyresorufin and 7-ethoxyresorufin) and 7-benzyloxyresorufin, which contain an alkyl or benzyl group linked to resorufin via an ether bond (Walker, 1990). In laboratory assays, these substrates undergo O-dealkylation or debenzylation reactions catalysed by specific CYP isoforms, producing the corresponding aldehyde (e.g., formaldehyde, acetaldehyde, or benzaldehyde) and resorufin, a fluorescent compound that can be quantified fluorimetrically. These reactions exhibit relative specificity for particular CYP isoforms (Burke et al., 1985). In humans, for example, 7-ethoxyresorufin O-deethylase (EROD) activity is predominantly catalysed by CYP1A1, whereas 7-methoxyresorufin O-deethylase (MROD) activity is mainly mediated by CYP1A2. In contrast, 7-benzyloxyresorufin O-debenzylase (BROD) activity may reflect the activity of CYP1A, CYP2B1, CYP2B2, CYP2C6, and CYP3A enzymes (Burke et al., 1985; Smith and Wilson, 2010).

In seabirds, the CYP complex has been investigated through EROD, MROD, and BROD activities (Table 1), with EROD being the most frequently applied in biomonitoring studies. Research using EROD in seabirds started in 1986, when associations between PCBs exposure and EROD activity were first explored (Fossi et al., 1986, Table 1). Since

Table 1
Biomarkers related to the xenobiotic biotransformation system in seabirds, screened from 1976 until May 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
Aldehyde oxidase	1	(↑) chlorpyrifos	*Nannopterum auritum*	(Desforges et al., 2021)
Aldrin epoxidase	3	NA	*Alca torda, Fratercula arctica*	(Ronis and Walker, 1985)
		NA	*Larus argentatus*	(Peakall et al., 1987)
		(↑) organic contaminants (oil)	*Fratercula arctica*	
		(↑) polychlorinated biphenyls (PCBs)	*Chroicocephalus ridibundus*	(Fossi et al., 1988)
Aminolevulinic Acid Synthase 1 (ALAS1)	1	(NF) inorganic contaminants (Hg, As, Cd, Pb, Se); (NF) polycyclic aromatic hydrocarbons (PAHs): 53 compounds	*Uria lomvia, Cepphus grylle*	(Zahaby et al., 2021)
Aminopyrene-N-demethylase	1	NA	*Larus argentatus, Fratercula arctica*	(Peakall et al., 1987)
ARNT: nuclear translocator of the aryl hydrocarbon receptor – isoforms 1 and 2 (*arnt1* and *arnt2*)	3	(NF) 2,3,7,8-Tetrachlorodibenzo-p-dioxin (TCDD) in treated embryos; (-) TCDD in wild embryos, young and adults (*arnt2*)	*Phalacrocorax carbo*	(Iwata et al., 2010)
		(NF) organic (PAHs), and inorganic contaminants (As, Cu, Fe, Ni, Rb, Se, V, Zn in blood; As, Ba, Cd, Cu, Fe, Mn, Mo, Pb, Rb, Se, Sn, Sr, V and Zn in feathers)	*Morus bassanus*	(Champoux et al., 2020)
		(NF) diluted bitumen - dilbit (PAC)	*Nannopterum auritum, Morus bassanus*	(Wallace et al., 2025)
Aromatic hydrocarbon hydroxylase	1	(+) PCBs; (NF) dichlorodiphenyldichloroethylene (DDE), dichloro-diphenyl-trichloroethane (DDT), dieldrin, heptachlor epoxide, oxychlordane, cis-chlordane, trans-nonachlor, toxaphene, Mirex, polychlorinated styrenes	*Sterna hirundo*	(Hoffman et al., 1993)
Aryl hydrocarbon receptor (AhR)	8	(NF) organic contaminants (TCDD and halogenated aromatic hydrocarbons (HAHs))	*Sterna hirundo*	(Karchner et al., 2006)
		NA	*Sterna hirundo*	(Farmahin et al., 2012)
		(NF) organic contaminants (dioxins, furans, and PCBs)	*Larus argentatus*	(Muusse et al., 2015)
		NA	*Sterna hirundo, Sterna dougallii*	(Nacci et al., 2016)
		(NF) organic (PAHs), and inorganic contaminants (As, Cu, Fe, Ni, Rb, Se, V, Zn in blood; and As, Ba, Cd, Cu, Fe, Mn, Mo, Pb, Rb, Se, Sn, Sr, V and Zn)	*Morus bassanus*	(Champoux et al., 2020)
		NA	*Eudyptes chrysocome, Pygoscelis papua*	(Bowen et al., 2022)
		NA	*Larus crassirostris*	(Cha et al., 2022)
		(NF) organic contaminants (PAHs, PCBs, DDTs, hexachlorobenzene (HCB), Drins, Mirex)	*Puffinus puffinus*	(Serafini et al., 2024)
Aryl hydrocarbon receptor (ahr1)	3	(NF) TCDD	*Phalacrocorax carbo*	(Iwata et al., 2010)
		(+) TCDD	*Phoebastria nigripes*	(Leena Mol et al., 2012)
		(↑) PAC	*Nannopterum auritum, Morus bassanus*	(Wallace et al., 2025)
Aryl hydrocarbon receptor (ahr2)	2	(NF) TCDD	*Phalacrocorax carbo*	(Iwata et al., 2010)
		(+) TCDD	*Phoebastria nigripes*	(Leena Mol et al., 2012)
ATP Binding Cassette Subfamily B Member 1 (abcb1)	1	(↑) PAC	*Nannopterum auritum, Morus bassanus*	(Wallace et al., 2025)
Benzo(a)pyrene 3-hydroxylase	1	NA	*Larus argentatus*	(Peakall et al., 1987)
		(↑) organic contaminants (oil)	*Fratercula arctica*	
Caffeine N-demethylation	1	(↑) PCB	*Sterna hirundo*	(Feyk et al., 2000)
Cytochrome P450 (CYP) (Western Blotting)	1	NA	*Alca tarda, Fratercula arctica, Uria aalge, Phalacrocorax aristotelis, Phalacrocorax carbo*	(Borlakoglu et al., 1990)
CYP - EROD: 7-ethoxyresorufin O-deethylase	48	(NF) PCBs	*Chroicocephalus ridibundus*	(Fossi et al., 1986)
		NA	*Larus argentatus*	(Peakall et al., 1987)
		(↑) organic contaminants (oil)	*Fratercula arctica*	
		(↑) PCBs	*Chroicocephalus ridibundus*	(Fossi et al., 1988)
		NA	*Alca torda*	(Borlakoglu et al., 1991)

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Table 1 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
		(+) 3,3',4,4'-tetrachlorobiphenyl (TCB, or PCB77)	*Somateria mollissima*	(Rozemeijer et al., 1992)
		(↑) PCBs, polychlorinated dibenzo-p-dioxins (PCDD)	*Sterna hirundo*	(Bosveld et al., 1993)
		NA	*Sterna hirundo*	(Murk et al., 1994a)
		(+) TCB	*Somateria mollissima*	(Murk et al., 1994b)
		(+) PCDDs, polychlorinated dibenzofurans (PCDFs), PCBs	*Sterna hirundo*	(Bosveld et al., 1995)
		NA	*Sterna hirundo*	(Murk et al., 1996)
		(+) PCBs	*Phalacrocorax carbo*	(Guruge and Tanabe, 1997)
		(↑) β-Naphthoflavone (BNF)	*Nannopterum auritum*	(Davis et al., 1997)
		(+) organic contaminants (PCDDs, PCDFs, PCBs, and other non-polar HAHs)	*Sterna hirundo*	(Lorenzen et al., 1997)
		(+) chlorobornanes (toxaphene®)	*Diomedea immutabilis*	(Boon et al., 1998)
		(NF) DDT, (↑) Methylcholanthrene – mimicking environmental PAHs	*Rissa tridactyla*	(Stepanova et al., 1999)
		(↑) PCBs, (+) PCBs	*Sterna hirundo*	(Bosveld et al., 2000)
		NA	*Somateria fischeri*	(Trust et al., 2000)
		(↑) CBT/10	*Sterna hirundo*	(Feyk et al., 2000)
		(+) PCBs	*Larus argentatus*	(Grasman et al., 2000)
		(+) PCB-153; (-) PCB-28e-99; (NF) Oxychlordane, p,p'-DDE, p,p'-DDT, HCB, Mirex, PCB-52, -101, -118, -138, -170 and -180	*Larus hyperboreus*	(Henriksen et al., 2000)
		(↑) organic contaminants (oil)	*Cepphus columba*	(Golet et al., 2002)
		(NF) PCBs, PCDD	*Larus argentatus*	(Kennedy et al., 2003)
		(+) PCBs	*Cepphus grylle*	(Kuzyk et al., 2003)
		(+) organic contaminants (naphthalenes, PCDDs, PCBs, DDE), (+) Hg, Cd and Pb	*Larus argentatus*	(Fox et al., 2005)
		(NF) PCBs	*Alle alle, Uria lomvia, Cepphus grylle, Rissa tridactyla*	(Borgå et al., 2005)
		(+) PCDDs, PCDFs, PCBs, dioxin-like compounds	*Phalacrocorax carbo*	(Kubota et al., 2006)
		(+) beta-hexachlorocyclohexane isomers (HCH), cis-chlordane, trans-nonachlor, Mirex, (-) HCB	*Alle alle, Uria lomvia, Cepphus grylle, Rissa tridactyla*	(Borgå et al., 2007)
		NA	*Histrionicus histrionicus*	(Esler et al., 2010)
		(↑) organic contaminants (oil)	*Histrionicus histrionicus*	(Esler and Iverson, 2010)
		(NF) PCBs, DDE	*Rissa tridactyla, Fulmarus glacialis*	(Helgason et al., 2010a)
		(+) organic contaminants (dioxin-like compounds)	*Fulmarus glacialis*	(Helgason et al., 2010b)
		(↑) TCDD (↑2,3,4,7,8- pentachlorodibenzofuran (PeCDF), (↑2,3,7,8-tetrachlorodibenzofuran (TCDF)	*Larus argentatus*	(Hervé et al., 2010)
		(NF) organic contaminants (PCDDs, PCDFs, PCBs)	*Phoebastria nigripes*	(Kubota et al., 2010)
		(↑) organic contaminants (oil)	*Larus michahellis*	(Velando et al., 2010)
		(NF) organic contaminants (OCs, PCBs, PCDDs, PCDFs, polybrominated diphenyl ethers (PBDEs), PAHs)	*Melanitta perspicillata*	(Wilson et al., 2010)
		(+) PCBs, dioxin-like compounds, SOC	*Fulmarus glacialis*	(Braune et al., 2011)
		(↑) organic contaminants (oil)	*Bucephala islandica*	(Esler et al., 2011)
		(+) organic contaminants (dioxin-like compounds)	*Phalacrocorax carbo*	(Kubota et al., 2012)
		(+) TCDD	*Phoebastria nigripes*	(Leena Mol et al., 2012)
		(+) organic contaminants (PCBs, DDTs, chlordane compounds -CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
		(NF) PBDEs, Dechlorane and its isomers	*Larus delawarensis*	(Chabot-Giguère et al., 2013)
		(+) mix of chemicals: bisphenol S (BPS), bisphenol A (BPA), tris (methylphenyl) phosphate (TMPP), tris(2-butoxyethyl) phosphate (TBOEP), triethyl phosphate (TEP), tris(2,3-dibromopropyl)	*Nannopterum auritum*	(Crump et al., 2016)

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Table 1 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
		isocyanurate (TBC), allyl 2,4,6-tribromophenyl ether (ATE), 1,2-dibromo-4-(1,2- dibromoethyl)-cyclohexane (DBE-DBCH), PCB 126, PBDE 209, tetradecabromo-1,4-diphenoxybenzene (TeDB-DiPhOBz); tris (1-chloro-2-propyl) phosphate (TCIPP), tris(1,3-dichloro-2-propyl) phosphate (TDCIPP), TCDD		
		NA	*Histrionicus histrionicus*	(Esler et al., 2016)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Alexander et al., 2017)
		(+) organic contaminants (PAHs)	*Nannopterum auritum*	(Crump et al., 2017)
		NA	*Bucephala islandica*	(Willie et al., 2017)
		(+) organohalogen flame retardant 7(OFR7)	*Nannopterum auritum*	(Pagé-Larivière et al., 2018)
		(NF) organic contaminants (PAHs, PCBs, DDTs, HCB, Drins, Mirex)	*Puffinus puffinus*	(Serafini et al., 2024)
CYP - PROD: pentoxyresorufin O-depentylase	12	NA	*Alca torda*	(Borlakoglu et al., 1991)
		(↑) CB77	*Somateria mollissima*	(Rozemeijer et al., 1992)
		(+) PCBs, (+) PCDD	*Sterna hirundo*	(Bosveld et al., 1993)
		NA	*Sterna hirundo*	(Murk et al., 1994a)
		(+) organic contaminants (PCDDs, PCDFs, PCBs)	*Sterna hirundo*	(Bosveld et al., 1995)
		(+) PCB	*Phalacrocorax carbo*	(Guruge and Tanabe, 1997)
		(↑) PCB, (+) PCB	*Sterna hirundo*	(Bosveld et al., 2000)
		(+) organic contaminants (PCDDs, PCDFs, PCBs)	*Phoebastria nigripes*	(Kubota et al., 2010)
		(NF) PCBs, DDE	*Rissa tridactyla, Fulmarus glacialis*	(Helgason et al., 2010a)
		(+) organic contaminants (dioxin-like compounds)	*Phalacrocorax carbo*	(Kubota et al., 2012)
		(NF) organic contaminants (PCBs, DDTs, CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Alexander et al., 2017)
CYP - MROD: methoxyresorufin O-demethylase	6	(↑) PCB	*Sterna hirundo*	(Bosveld et al., 2000)
		(NF) PCBs, PCDD	*Larus argentatus*	(Kennedy et al., 2003)
		(+) organic contaminants (PCDDs, PCDFs, PCBs)	*Phoebastria nigripes*	(Kubota et al., 2010)
		(NF) PCBs, DDE	*Rissa tridactyla, Fulmarus glacialis*	(Helgason et al., 2010a)
		(+) organic contaminants (dioxin-like compounds)	*Phalacrocorax carbo*	(Kubota et al., 2012)
		(NF) organic contaminants (PCBs, DDTs, CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
CYP - BROD: benzyloxyresorufin O-dealkylase	6	(NF) PCB	*Sterna hirundo*	(Bosveld et al., 2000)
		(NF) organic contaminants (PCDDs, PCDFs, PCBs)	*Phoebastria nigripes*	(Kubota et al., 2010)
		(NF) PCBs, DDE	*Rissa tridactyla, Fulmarus glacialis*	(Helgason et al., 2010a)
		(+) organic contaminants (dioxin-like compounds)	*Phalacrocorax carbo*	(Kubota et al., 2012)
		(NF) organic contaminants (PCBs, DDTs, CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Alexander et al., 2017)
CYP – ECOD: 7-ethoxycoumarin O-deethylase	1	(NF) DDT, (↑) Methylcholanthrene – mimicking environmental PAHs	*Rissa tridactyla*	(Stepanova et al., 1999)
CYP 1A1/A2 (Western Blotting)	9	(+) organic contaminants (PCDDs, PCDFs, PCBs)	*Sterna hirundo*	(Bosveld et al., 1995)
		(+) organic contaminants (PCDDs, PCDFs, PCBs and non-polar HAH)	*Sterna hirundo*	(Lorenzen et al., 1997)
		(+) PCBs	*Larus argentatus*	(Kennedy et al., 2003)
		(+) PCDDs, PCDFs, PCBs, dioxin-like compounds	*Phalacrocorax carbo*	(Kubota et al., 2006)

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Table 1 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
		(↑) PCB	*Tadorna variegata*	(Numata et al., 2008)
		(+) organic contaminants (organochlorines (OC))	*Fulmarus glacialis*	(Verreault et al., 2013)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Alexander et al., 2017)
		(+) TCDD	*Larus argentatus*	(Head and Kennedy, 2019)
		(+) Mirex, (NF) organic contaminants (PAHs, PCBs, DDTs, HCB, Drins)	*Puffinus puffinus*	(Serafini et al., 2024)
CYP1a4	18	(+) PCDDs, PCDFs, PCBs, dioxin-like compounds (DRCs): TCDF, 3,3′,4,4′-tetrachlorobiphenyl (PCB77)	*Phalacrocorax carbo*	(Kubota et al., 2006)
		(+) PCDD), furans, PCBs, 1,1,1-trichloro-2,2-bis(p-chlorophenyl) ethane and its metabolites (DOTS), HCHs, CHLs, butyltins and BPA	*Phalacrocorax carbo*	(Nakayama et al., 2006)
		(+) TCDD	*Larus argentatus*	(Head and Kennedy, 2007)
		(+) TCDD, PCB126	*Phalacrocorax carbo*	(Nakayama et al., 2008b)
		NA	*Phalacrocorax carbo*	(Kubota et al., 2008)
		(+) 2,3,7,8-TCDD; (+) 2,3,4,7,8- pentachlorodibenzofuran (PeCDF); (+) 2,3,7,8-TCDF	*Larus argentatus*	(Hervé et al., 2010)
		(+) TCDD; (↑) TCDD in embryos	*Phalacrocorax carbo*	(Iwata et al., 2010)
		(+) organohalogen flame retardants (OFRs)	*Larus argentatus*	(Porter et al., 2013)
		(NF) organic contaminants (PCBs, DDTs, CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
		(+) mix of chemicals: bisphenol S (BPS), bisphenol A (BPA), tris (methylphenyl) phosphate (TMPP), TBOEP, TEP, TBC, ATE, DBE-DBCH, PCB 126, PBDE 209, TeDB-DiPhOBz; TCIPP, TDCIPP, TCDD	*Nannopterum auritum*	(Crump et al., 2016)
		(+) organic contaminants (PAHs)	*Nannopterum auritum*	(Crump et al., 2017)
		(+) 10 OFRs	*Nannopterum auritum*	(Pagé-Larivière et al., 2018)
		(+) organic contaminants (PAHs)	*Nannopterum auritum*	(Mundy et al., 2019)
		(+) organic contaminants (PCBs, PBDEs)	*Nannopterum auritum*	(Xia et al., 2020)
		(↑) Chlorpyrifos	*Nannopterum auritum*	(Desforges et al., 2021)
		(+) perfluoroheptanoic acid (PFHpA)	*Cerorhinca monocerata*	(King et al., 2023)
		(+) PCBs	*Nannopterum auritum*	(King et al., 2025)
		(↑) diluted bitumen-dilbit (PAC)	*Nannopterum auritum*, *Morus bassanus*	(Wallace et al., 2025)
CYP1a5	14	(+) PCDDs, PCDFs, PCBs, DRCs: 2,3,7,8-TCDF, 3,3′,4,4′-tetrachlorobiphenyl (PCB77)	*Phalacrocorax carbo*	(Kubota et al., 2006)
		(+) polychlorinated dibenzo-p-dioxins (PCDD), furans, PCBs, 1,1,1-trichloro-2,2-bis(p-chlorophenyl)ethane and its metabolites (DOTS), HCHs, CHLs, butyltins and BPA	*Phalacrocorax carbo*	(Nakayama et al., 2006)
		(+) TCDD	*Larus argentatus*	(Head and Kennedy, 2007)
		NA	*Phalacrocorax carbo*	(Kubota et al., 2008)
		(+) TCDD, PCB126	*Phalacrocorax carbo*	(Nakayama et al., 2008b)
		(+) 2,3,7,8-TCDD; (+) 2,3,4,7,8-pentachlorodibenzofuran (PeCDF); (+) 2,3,7,8-tetrachlorodibenzofuran (TCDF)	*Larus argentatus*	(Hervé et al., 2010)
		(+) TCDD; (↑) TCDD in embryos	*Phalacrocorax carbo*	(Iwata et al., 2010)
		(NF) organic contaminants (PCBs, DDTs, CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
		(↑) Chlorpyrifos	*Nannopterum auritum*	(Desforges et al., 2021)
		(NF) inorganic contaminants (Hg, As, Cd, Pb, Se); (NF) PAHs: 53 compounds	*Uria lomvia*, *Cepphus grylle*	(Zahaby et al., 2021)
		(-) HCB, (+) PCBs, (NF) organic contaminants (PAHs, DDTs, Drins, Mirex)	*Puffinus puffinus*	(Serafini et al., 2024)
		(+) PCBs	*Nannopterum auritum*	(King et al., 2025)
		(↑) organic contaminants (52 polycyclic aromatic compounds - PACs)	*Cepphus grylle*	(Zahaby et al., 2025)
		(↑) diluted bitumen-dilbit (PAC)	*Nannopterum auritum*, *Morus bassanus*	(Wallace et al., 2025)

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Table 1 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
CYP1b1	1	(NF) diluted bitumen-dilbit (PAC)	*Nannopterum auritum, Morus bassanus*	(Wallace et al., 2025)
CYP3a37	6	(+) OFRs	*Larus argentatus*	(Porter et al., 2013)
		(NF) organic contaminants (PCBs, DDTs, CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
		(+) organic contaminants (PCBs, PBDEs)	*Nannopterum auritum*	(Xia et al., 2020)
		(+) replacement compounds to bisphenol A (BPA): 4,4′-propane-2,2-diyl) diphenol - BPA, bis 4-hydroxyphenyl methane - BPF, bis 3-allyl-4-hydroxyphenyl sulfone - TGSH, 7-bis 4-hydroxyphenylthio-3,5-dioxaheptane - DD-70, 2,2-bis 4-hydroxyphenyl), hexafluoropropane- BPAF, 4-hydroxyphenyl 4-isoprooxyphenylsulfone - BPSIP	*Nannopterum auritum*	(Sharin et al., 2021)
		(NF) inorganic contaminants (Hg, As, Cd, Pb, Se); (NF) PAHS: 53 compounds	*Uria lomvia, Cepphus grylle*	(Zahaby et al., 2021)
		(+) tHg	*Cerorhinca monocerata*	(King et al., 2023)
CYP 2B1/2 (Western Blotting)	1	(+) organic contaminants (PCDDs, PCDFs, PCBs)	*Sterna hirundo*	(Bosveld et al., 1995)
CYP2B/3A-like: 6β-hydroxylation of testosterone	3	(NF) Oxichlordane, p,p'-DDE, p,p'-DDT, HCB, Mirex, PCB-28, -52, -99, -101, -118, -138, -153, -170 and -180	*Larus hyperboreus*	(Henriksen et al., 2000)
		(NF) PCBs	*Alle alle, Uria lomvia, Cepphus grille, Rissa tridactyla*	(Borgå et al., 2005)
		(NF) beta-HCH, cis-chlordane, trans-Nonachlor, Mirex, HCB	*Alle alle, Uria lomvia, Cepphus grille, Rissa tridactyla*	(Borgå et al., 2007)
CYP2B: testosterone hydroxylation to androstenedione	1	(-) PCBs	*Rissa tridactyla, Fulmarus glacialis*	(Helgason et al., 2010a)
CYP2C45	1	(-) PCBs, dichlorodiphenyltrichloroethane (DDT), PFOS, perfluorononanoic acid (PFNA), PFOSA, dioxins	*Phalacrocorax carbo*	(Kubota et al., 2011)
CYP2E1	1	(↑) DDT, HCB and PCDD/F	*Larus dominicanus*	(Numata et al., 2008)
CYP2J25	1	(-) PCBs, dichlorodiphenyltrichloroethane (DDT), perfluorooctanesulfonic acid (PFOS), perfluorononanoic acid (PFNA), perfluorooctanesulfonamide (PFOSA), dioxins	*Phalacrocorax carbo*	(Kubota et al., 2011)
Epoxide hydrolase (EH)	1	NA	*Larus argentatus, Fratercula arctica*	(Peakall et al., 1987)
Glutathione S-transferase (GST)	10	NA	*Alca torda*	(Borlakoglu et al., 1991)
		(NF) DDE, DDT, dieldrin, heptachlor epoxide, oxychlordane, cis-chlordane, trans-nonachlor, toxaphene, Mirex, polychlorinated styrenes and PCBs	*Sterna hirundo*	(Hoffman et al., 1993)
		(NF) DDT, (↑) Methylcholanthrene – mimicking environmental PAHs	*Rissa tridactyla*	(Stepanova et al., 1999)
		(NF) PCBs, DDE	*Rissa tridactyla, Fulmarus glacialis*	(Helgason et al., 2010a)
		(-) MeHg	*Leucophaeus atricilla*	(Jenko et al., 2012)
		(+) Cd, (-) Zn, (NF) other inorganic contaminants	*Chroicocephalus genei*	(Espín et al., 2016)
		NA	*Larus fuscus*	(Santos et al., 2019)
		(+) Triclosan	*Larus michahellis*	(Possenti et al., 2019)
		(NF) Cd, Pb, Zn	*Ardenna gravis*	(Hernández-Moreno et al., 2021)
		(-) Mirex, (+) Drins, (NF) organic contaminants (PAHs, PCBs, DDTs, HCB)	*Puffinus puffinus*	(Serafini et al., 2024)
GST	1	(NF) organic contaminants (PCBs, DDTs, CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
O-Hexyl O-2,5-dichlorophenyl phosphoramidate (HDCPase)	1	(↑) Cu2+, Zn2+	*Sula leucogaster, Fregata magnificens, Sula nebouxii, Sula dactylatra, Sula sula*	(Monroy-Noyola et al., 2019)
Hepatic microsomal monooxygenases	1	(NF) PCB	*Alca torda, Fratercula arctica*	(Knight and Walker, 1982)
Hexachlorocyclohexane epoxide (HCE) hydroxylase	1	NA	*Alca torda, Fratercula arctica*	(Ronis and Walker, 1985)
hif1α, and *vegfα*	1	(NF) diluted bitumen - dilbit (PAC) concentrations	*Nannopterum auritum, Morus bassanus*	(Wallace et al., 2025)
Methionine adenosyltransferase I, alpha (MAT1A)	1	(↑) Methylmercury (MeHg)	*Leucophaeus atricilla*	(Jenko et al., 2012)
NADPH-cytochrome c reductase	1	(+) PCBs	*Chroicocephalus ridibundus*	(Fossi et al., 1988)
NADH- ferricyanide reductase	1	(+) PCBs	*Chroicocephalus ridibundus*	(Fossi et al., 1988)

(*continued on next page*)

Table 1 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
Protein-bound sulfhydryl (PBSH)	1	(-) MeHg	*Leucophaeus atricilla*	(Jenko et al., 2012)
Thyroxine UDP-glucuronosyltransferases (T4-UGT)	1	(NF) PHAH - polyhalogenated aromatic hydrocarbons: PCBs, PCDFs and PCDDs	*Sterna hirundo*	(Murk et al., 1994b)
Uridine diphosphate glucuronosyltransferases (UGTs)	4	NA	*Larus argentatus*, *Uria aalge*	(Peakall et al., 1987)
		(↑) organic contaminants (oil)	*Fratercula arctica*	(Peakall et al., 1987)
		(NF) DDT, (↑) Methylcholanthrene – mimicking environmental PAHs	*Rissa tridactyla*	(Stepanova et al., 1999)
		(NF) PCBs, DDE	*Rissa tridactyla, Fulmarus glacialis*	(Helgason et al., 2010a)
		NA	*Spheniscus humboldti*	(Kawai et al., 2019)
UGT1 (*UGT1, UGT1A1, UGT1A9, UGT1E*)	7	(+) OFRs	*Larus argentatus*	(Porter et al., 2013)
		(NF) organic contaminants (PCBs, DDTs, CHLs, PBDEs)	*Larus argentatus*	(Routti et al., 2013)
		(+) mix of chemicals: BPS, BPA, TMPP, TBOEP, TEP, TBC, ATE, DBE-DBCH, PCB 126, PBDE 209, TeDB-DiPhOBz; TCIPP, TDCIPP, TCDD	*Nannopterum auritum*	(Crump et al., 2016)
		NA	*Spheniscus humboldti*	(Kawai et al., 2019)
		(+) organic contaminants (PAHs)	*Nannopterum auritum*	(Mundy et al., 2019)
		(+) dechlorane plus	*Fulmarus glacialis*	(Mortensen et al., 2022)
		(-) HCB, (+) PCBs, (NF) organic contaminants (PAHs, DDTs, drins, Mirex)	*Puffinus puffinus*	(Serafini et al., 2024)
UDP galactose 4 epimerase	1	(↓) Chlorpyrifos	*Nannopterum auritum*	(Desforges et al., 2021)

then, EROD activity, catalysed by isoenzymes of the CYP1A subfamily and induced by persistent organic pollutants (POPs) with affinity for the AhR (Knutson and Poland, 1982; Peakall, 1992), has become the most extensively studied biomarker in seabirds, quantified in 17.5% of the total analysed papers ($n = 48$). Other CYP substrates have also been widely used over recent decades to further characterise the biotransformation potential in seabirds (Helgason et al., 2010a). Among these, notable examples include pentoxyresorufin O-dealkylase (PROD; $n = 12$; 4.4%), BROD ($n = 6$; 2.2%), and MROD ($n = 6$; 2.2%) (Table 1).

While CYP1A is the most investigated isoform in ecotoxicological studies, other CYP families such as CYP2 and CYP3 have also received attention in seabirds (Table 1). Although 18 CYP families are known in humans, comprising a total of 41 subfamilies (Nebert et al., 2013), we still lack knowledge on a detailed description of CYP families for seabirds. In mammals, CYP1, CYP2, CYP3, and CYP4 families are responsible for xenobiotic metabolism and are highly inducible. The remaining CYPs primarily function in the metabolism of endogenous compounds and are either not inducible or only weakly inducible by contaminants (Nebert et al., 2013). Together, CYP1, CYP2, and CYP3 enzymes constitute 70% of the total hepatic CYP content in humans and are responsible for the metabolism of 90% of xenobiotics (Esteves et al., 2021). Although the roles of CYP isoforms are evolutionarily conserved, interspecies differences in CYP1, CYP2, and CYP3 genes between birds and mammals may be relevant for their extrapolation in toxicological studies (Watanabe et al., 2013). Thus, detailed characterisation of the physiological and functional properties of these isoforms in seabirds is essential (Watanabe et al., 2013).

In seabirds, studies on CYP2B isoforms (particularly CYP2B6) have sought to understand their role in testosterone metabolism, considering their involvement in 16α-hydroxylation and other hydroxylation sites (Helgason et al., 2010a). Hydroxylated testosterone metabolites reflect the activities of a variety of CYP proteins, including those from the CYP2 and CYP3 families (Paolini et al., 1997). In black-legged kittiwakes, a negative correlation was found between androstenedione and OH-PCB 146, suggesting that parent PCBs were metabolized to OH-PCB 146 via CYP2B mediated hydroxylation, representing the only significant correlation observed in seabirds to date (Helgason et al., 2010a). As an illustrative example for class Aves, in great blue herons (*Ardea herodias*), exposure to environmentally relevant levels of tetrachlorodibenzo-p-dioxin (TCDD) increased testosterone hydroxylation activities at the 2β-, 6β-, and 15α-positions in captive female (Sanderson et al., 1997). However, CYP2B enzymes generally exhibit lower activity in 6β-hydroxylation compared to CYP3A. This is notable because testosterone 6β-hydroxylation is a widely marker of CYP3A activity, given its role in the hepatic metabolism of a broad range of substances, including steroid hormones and xenobiotics (Borgå et al., 2007). Alterations in testosterone hydroxylation may affect steroid hormone homeostasis and impair reproductive function, highlighting the importance of further investigating this pathway in seabirds, an area still underexplored ($n = 4$; 1.5% of papers reviewed).

Regarding Phase II biotransformation and the conjugating enzymes involved, GST activity has been assessed as a biomarker in ecotoxicological studies involving seabirds ($n = 11$ papers; 4.0%), showing associations with both organic and inorganic contaminants (Table 1, definitions on Table S4). Since 2012, protein expression and transcript levels of different GST isoforms have also been investigated in seabird species (e.g., Routti et al., 2013). GST is a key phase II detoxification enzyme that facilitates the conjugation of xenobiotic metabolites, such as hydroxylated PCBs, enhancing their excretion and reducing their toxic potential in target tissues, as the liver (Helgason et al., 2010a). In seabirds, GST activity has been shown to respond dynamically to contaminant exposure, such as to cadmium (Cd), zinc (Zn), mercury (Hg) and organochlorine pesticides (e.g., drins and mirex, Table S4), serving as a biomarker in ecotoxicological assessments (Jenko et al., 2012; Espín et al., 2016; Serafini et al., 2024). Likewise, UGTs were assessed in seabirds within 11 studies (4.0%) and are considered a critical phase II biotransformation enzymes in birds, catalysing the conjugation of polar metabolites such as phenols and quinoles, especially those derived from polycyclic aromatic hydrocarbons (Table S4), thereby enhancing their solubility and excretion (Kawai et al., 2019). In seabirds, UGT1 has been linked to xenobiotic metabolism pathways regulated by the AhR signalling cascade, and transcripts association with organic contaminants suggested its potential as a biomarker of xenobiotic-induced metabolic disruption (e.g., Mundy et al., 2019; Mortensen et al., 2022; Serafini et al., 2024). Furthermore, recent insights into the evolutionary relationships of UGT1 genes suggest that these isoforms may have specifically evolved to metabolize exogenous compounds, reinforcing their functional importance in detoxification pathways in wildlife exposed to environmental contaminants (Kreitsberg et al., 2023).

3.4.2. *Biomarkers related to endocrine disruption*

Our review identified 56 articles addressing relationships between environmental contaminants and endocrine mechanisms in seabirds, representing 20.3% of all reviewed publications. Despite recent interest, research in this area remains limited, particularly considering the small proportion of species and environments studied. There is a clear need to expand this field of investigation, especially in light of the increasing presence of endocrine-disrupting compounds (EDCs) in aquatic environments. EDCs are defined as exogenous substances or mixtures that interfere with the function of the endocrine system and consequently cause adverse health effects in organisms, their offspring, or (sub)populations exposed (Encarnação et al., 2019). Among EDCs, particular attention has been given to PCBs, polybrominated diphenyl ethers (PBDEs), organochlorine pesticides (OCs), bisphenol A (BPA), and phthalates, due to their potential to impact both health and ecosystems. Seabirds frequently exhibit elevated levels of these contaminants in their tissues compared to terrestrial birds or even humans (e.g., Taniguchi et al., 2016; Vanstreels et al., 2023).

In seabirds, reviewed articles showed that usually a stress response involves the release of corticosterone (CORT), which is typically accompanied by a reduction in circulating levels of prolactin, an anterior pituitary hormone widely involved in the regulation of parental care (Groscolas et al., 2008; Tartu et al., 2013). Glucocorticoids, such as CORT, are hormones involved in a wide range of physiological processes, including reproduction, behaviour, stress adaptation, and even modulation of the immune system (Wingfield and Sapolsky, 2003). More specifically, the release of CORT, mediated by the hypothalamic-pituitary-adrenal axis during stressful events, triggers physiological and behavioural adjustments, redirecting energy investment from reproduction towards self-preservation and survival (Wingfield and Sapolsky, 2003).

In seabirds, CORT is the most frequently assessed biomarker of endocrine disruption ($n = 19$ articles; 6.9%) (Table 2). Bourgeon et al. (2012), investigated stress induced by xenobiotics in great skua (*Stercorarius skua*) by measuring CORT in feathers and observed that increasing concentrations of PBDEs were associated with reduced hormone levels. Feather CORT represents an integrated, long-term measure of stress physiology, reflecting both baseline and induced hormone levels (Lattin et al., 2011). However, the effect of organic contaminants on endocrine biomarkers may be context-dependent, and may be influenced by ecological factors such as food availability and/or climatic conditions (Bourgeon et al., 2012). Furthermore, elevated levels of CORT have been associated with immunosuppression (Råberg et al., 1998) and oxidative stress in seabirds (Costantini et al., 2008), emphasizing its role as a modulator of both endocrine and immune responses.

Endocrine disruption biomarkers related to thyroid activity ranked second among the most studied in seabirds, with particular emphasis on plasma levels of total thyroxine (TT4; $n = 16$ articles, 5.8%), total triiodothyronine (TT3; $n = 18$ articles, 6.5%), free thyroxine (FT4; $n = 9$ articles, 3.3%), free triiodothyronine (FT3; $n = 8$ articles, 2.9%), as well as analyses of the TT3:TT4 ($n = 2$ articles, 0.7%) and TT4:TT3 ratios ($n = 4$ articles, 1.5%), and the TT3:FT3 and TT4:FT4 ratios ($n = 1$ article each, 0.4%) (Table 2). Early investigations, such as Nøst et al. (2012) reported positive correlations between perfluorinated compounds (PFAS) and TT4, as well as between TT3 and PCBs, DDE, ΣCHLs, and ΣDDTs. Similarly, Ask et al. (2020) found positive correlations between PFAS exposure and both TT4 and TT3 (Table 2). The ratio between TT4 and TT3 has been considered a sensitive indicator of contaminant exposure in other taxonomic groups, such as seals and polar bears (*Ursus maritimus*), as chemical contaminants like PCBs can alter this balance through direct action on the thyroid gland (Rattner et al., 1984; Braathen et al., 2004; Grønnestad et al., 2018). This alteration occurs through interference with transport proteins (e.g., transthyretin or albumin) inhibition of peripheral conversion of TT4 to TT3 by deiodinases, or enhanced glucuronidation (Rattner et al., 1984). Since 2008, some studies have also addressed gene transcription levels related to thyroid function in response to contaminants. Among these, notable investigations include those focusing on genes such as *transthyretin* (*TTR*), *iodothyronine deiodinases type 1* and *type 2* (*DIO1* and *DIO2*) (Mortensen et al., 2022), and *thyroid hormone receptor alpha* (*TRα*) and *beta* (*TRβ*) (Crump et al., 2008).

Prolactin has also been analysed as a biomarker of endocrine disruption in eight studies involving seabirds (2.9% of all papers). Significant reductions in prolactin levels were observed as a response to mercury (Hg) (Smith et al., 2023) and PBDE contamination in seabirds (Verreault et al., 2008). For example, in male Glaucous gull (*Larus hyperboreus*) baseline prolactin levels and their decline following a restraint protocol of the sampled bird were negatively associated with plasma concentrations of organochlorine compounds (OCs), PCBs, brominated flame retardants, and their metabolites, although significant effects were observed only for PBDEs (Verreault et al., 2008). However, some studies did not find a clear or significant relationship between circulating prolactin levels and organic or inorganic contaminants in seabirds (Table 2). Prolactin secreted by the anterior pituitary is responsible for stimulating parental behaviours, such as chick provisioning and egg incubation (Buntin et al., 1996). However, its levels have been shown to decrease in response to acute stress (Chastel et al., 2005). The limited proportion of studies employing this important biomarker drew particular attention in the present review.

Other endocrine disruption biomarkers investigated in more than one publication include reproductive hormones such as testosterone, estradiol, and luteinising hormone. However, considering the potential relevance and importance of this topic, studies investigating the extent to which the endocrine activity of seabirds is affected by contaminants remain limited (Table 2).

3.4.3. *Biomarkers of hepatic damage*

Most studies on biomarkers of hepatic damage assessed multiple biomarkers simultaneously. In seabirds, these investigations were predominantly correlational, although some controlled experiments have also been conducted (Table 3). The liver was the tissue of choice in 112 of the 275 articles included in this review (40.7%), likely reflecting its central role in xenobiotic metabolism and detoxification. Hepatic tissue analysis may serve multiple investigative purposes and does not necessarily involve biomarkers specifically indicative of hepatotoxicity. However, when considering only studies focused on hepatic damage, a total of 19 articles addressed this topic, representing merely 6.9% of the overall publications. Studies on hepatic damage biomarkers in seabirds primarily measured the activities of enzymes such as aspartate aminotransferase (AST), alanine aminotransferase (ALT), alkaline phosphatase (ALP), and γ-glutamyl transpeptidase (GGT), as well as total bilirubin and bile acid content. These biomarkers were mostly measured in blood samples, but related to hepatic function (e.g., Tamber et al., 2023).

Among the identified correlations, exposure to organic contaminants was positively correlated with ALT activities (chlordanes – CHLs, PBDEs, and trimethyltin – TMT) and GGT activities (PCBs, HCHs, HCB, CHLs) in a study of the great skua (Sonne et al., 2013). For ALP, an experimental study with double-crested cormorant (*Nannopterum auritum*) reported elevated enzyme activity following oil ingestion (Dean et al., 2017a). The same authors observed decreases in albumin, total proteins, cholesterol, ALT, AST, and GGT in response to oil exposure under controlled conditions (Dean et al., 2017a; Dean et al., 2017b). Despite

Table 2

Biomarkers related to endocrine disruption in seabirds, screened between 1976 and 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
Androgen receptor AR	1	NA	*Phalacrocorax carbo*, *Haliaeetus pelagicus*	(Misaki et al., 2015)
Androstenedione	2	(NF) PCBs,	*Sterna hirundo*	(French et al., 2001)
		(NF) PFAS	*Rissa tridactyla*	(Jouanneau et al., 2023)
Corticosterone (CORT)	16	(↑) organic contaminants (oil) - females	*Spheniscus magellanicus*	(Fowler et al., 1995)
		(+) Cd, (-) Se	*Somateria mollissima*	(Wayland et al., 2002)
		(-) PBDEs	*Stercorarius skua*	(Bourgeon et al., 2012)
		NA	*Pygoscelis papua*	(Barbosa et al., 2013)
		(NF) organic contaminants (PAHs)	*Morus bassanus*	(Franci et al., 2014)
		(NF) organic contaminants (PCBs, pesticides: HCB,p,p′-DDE, CHL)	*Rissa tridactyla*	(Tartu et al., 2014a)
		(+) PCBs, (NF) OCPs, (NF) Hg	*Rissa tridactyla*	(Tartu et al., 2015b)
		(+) PCBs	*Stercorarius maccormicki*, *Daption capense*, *Diomedea exulans*, *Pagodroma nivea*, *Rissa tridactyla*, *Somateria molissima*	(Tartu et al., 2015c)
		(-) Σ7PCBs	*Larus hyperboreus*	(Tartu et al., 2015c)
		(NF) Hg	*Rissa tridactyla*	(Tartu et al., 2016)
		(NF) organic contaminants (oiled birds)	*Eudyptula minor*	(Chilvers et al., 2016)
		(-) Hg; (NF) Pb	*Somateria mollissima*	(Provencher et al., 2016)
		NA	*Morus bassanus*	(Fairhurst et al., 2017)
		(NF) organic contaminants (PCBs, DDTs, CHL, HCB, Mirex)	*Stercorarius maccormicki*	(Goutte et al., 2018)
		(↑) organic and inorganic contaminants (oil spill)	*Morus bassanus*	(Champoux et al., 2020)
		(NF) organic contaminants (PAHs)	*Pelecanus occidentalis*	(Jodice et al., 2023)
		(NF) PFAS	*Rissa tridactyla*	(Jouanneau et al., 2023)
Corticosterone – post-stress induction	3	(+) PCBs	*Rissa tridactyla*	(Tartu et al., 2014a)
		(-) PCBs (males)	*Stercorarius maccormicki*, *Daption capense*, *Diomedea exulans*, *Larus hyperboreus*, *Pagodroma nivea*, *Rissa tridactyla*, *Somateria mollissima*	(Tartu et al., 2015c)
		(+) organic contaminants (POPs)	*Pagodroma nivea*	(Tartu et al., 2015a)
Deiodinases 1	2	(-) PBDE (Σocta-BDE, BDE-201, BDE-197/BDE-204)	*Larus delawarensis*	(François et al., 2016)
		(+) PBDE; (-) pentabromoethylbenzene (PBEB)	*Fulmarus glacialis*	(Mortensen et al., 2022)
Deiodinases 1 (D1)	3	(-) BDE-209: Σnona + octa + hepta-BDE, BDE-209: ∑octa-BDE, BDE-209: ∑hepta-BDE, BDE-209:∑nona-BDE; (↓) PBDE in females	*Larus delawarensis*	(François et al., 2016)
		(+) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
		(NF) PBDEs, other flame retardants (PBEB, dechlorane 602, dechlorane plus)	*Fulmarus glacialis*	(Mortensen et al., 2022)
Deiodinases 2 (D2)	2	(NF) PBDEs, other flame retardants (PBEB, dechlorane 602, dechlorane plus)	*Fulmarus glacialis*	(Mortensen et al., 2022)
		(+) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
		(+) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
Deiodinases 3 (D3)	2	(-) brominated flame retardants (BFR): e.g.,PBDEs; HOCs: e.g.,PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)

(*continued on next page*)

Table 2 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
		(+) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
Estradiol	4	(↓) organic contaminants (oil, females)	*Spheniscus magellanicus*	(Fowler et al., 1995)
		(NF) PCBs,	*Sterna hirundo*	(French et al., 2001)
		(-) organic contaminants (α-HBCD, ΣPBDE, ΣPCB, Mirex, ΣDDT)	*Larus hyperboreus*	(Verboven et al., 2008)
		(NF) organic (PAHs), and inorganic contaminants (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn)	*Morus bassanus*	(Champoux et al., 2020)
Estrogen Receptor alpha and beta (Erα and Erβ)	1	(+) bisphenol-A (BPA), bisphenol-S (BPS), 4-octylphenol (4-OP), benzyl butyl phthalate (BBP), (-) tetrabromobisphenol-A (TBBPA), 2,5,2 ′,5′ tetrachloro-biphenyl (PCB-52), 2,2′ , 3,4,4′ ,5′-hexachlorobiphenyl (PCB-138)	*Fulmarus glacialis*	(Van Hassel et al., 2025)
Estrogen Receptor 1 (ESR1)	1	(-) HCB, (+) Mirex, (NF) organic contaminants (PAHs, PCBs, DDTs, HCB, Drins)	*Puffinus puffinus*	(Serafini et al., 2024)
Free triiodothyronine (FT3)	8	(NF) organic contaminants (PDDT, PCHL, PPCB, PCBs, DDTs, CHLs, PBDEs, MeO-PBDEs, OH-PCBs/PBDEs)	*Larus hyperboreus*	(Verreault et al., 2007)
		(NF) organic contaminants	*Fulmarus glacialis*	(Helgason et al., 2010b)
		(NF) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
		(+) PFOS; (-) organohalogen contaminants (OHCs) - females	*Larus hyperboreus*	(Melnes et al., 2017)
		(NF) organic contaminants	*Rissa tridactyla*	(Svendsen et al., 2018)
		(NF) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
		(NF) organic (HPAs), inorganic contaminants (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn)	*Morus bassanus*	(Champoux et al., 2020)
		(+) PFAAs - PFOS, PFNA, PFDA, PFDoA, PFTeDA, ∑PFCA7, ∑PFAA	*Uria lomvia*	(Choy et al., 2022)
Free thyroxine (FT4)	9	(NF) organic contaminants (PAHs, PCBs, PCDFs, PCDDs)	*Sterna hirundo*	(Murk et al., 1994b)
		(NF) organic contaminants (PDDT, PCHL, PPCB, PCBs, DDTs, CHLs, PBDEs, MeO-PBDEs, OH-PCBs/PBDEs)	*Larus hyperboreus*	(Verreault et al., 2007)
		(NF) organic contaminants	*Fulmarus glacialis*	(Helgason et al., 2010b)
		(NF) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
		(-) organic contaminants - organohalogenated (OHCs) – females	*Larus hyperboreus*	(Melnes et al., 2017)
		(-) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
		(NF) organic (PAHs), inorganic contaminants (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn)	*Morus bassanus*	(Champoux et al., 2020)
		(NF) PBDEs, other flame retardants (PBEB, dechlorane 602, dechlorane plus)	*Fulmarus glacialis*	(Mortensen et al., 2022)
		(NF) perfluoroalquil acids (PFAAs) - PFOS, PFNA, PFDA, PFDoA, PFTeDA, ∑PFCA7, ∑PFAA	*Uria lomvia*	(Choy et al., 2022)
Glucocorticoid metabolites (ufGCM)	1	NA	*Spheniscus demersus*	(Scheun et al., 2021)
Luteinizing hormone (LH)	3	(↓) organic contaminants (oil)	*Spheniscus magellanicus*	(Fowler et al., 1995)
		(+) Hg (females); (-) (Hg; males)	*Rissa tridactyla*	(Tartu et al., 2013)
		(-) Hg (age class =< 23 years)	*Pagodroma nivea*	(Tartu et al., 2014b)
Progesterone	1	(NF) organic contaminants (oil)	*Spheniscus magellanicus*	(Fowler et al., 1995)
Prolactin (PRL)	8	(-) organic contaminants (PBDE; males)	*Larus hyperboreus*	(Verreault et al., 2008)
		(NF) organic contaminants (PAHs)	*Morus bassanus*	(Franci et al., 2014)
		(-) Hg (males); (NF) Hg (females)	*Rissa tridactyla*	(Tartu et al., 2016)
		(-) Hg (males)	*Pagodroma nivea*	(Tartu et al., 2015a)
		(NF) organic contaminants (oxychlordane, PFAs), (NF) Hg	*Rissa tridactyla*	(Blévin et al., 2018)
		(NF) organic contaminants (PCBs, DDTs, CHL, HCB, Mirex)	*Stercorarius maccormicki*	(Goutte et al., 2018)
		(NF) Hg	*Pterodroma macroptera, Ardenna carneipes*	(Gilmour et al., 2019)

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Table 2 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
		(-) Hg	*Somateria mollissima*	(Smith et al., 2023)
Sodium iodide symporter	2	(+) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
		(+) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
Sulfotransferase family 1E member 1 - (SULT1e1)	1	(NF) organic contaminants (52 polycyclic aromatic compounds - PACs)	*Cepphus grylle*	(Zahaby et al., 2025)
Testosterone	7	(↓) organic contaminants (oil)	*Spheniscus magellanicus*	(Fowler et al., 1995)
		(NF) PCBs (hidroxitestosterone)	*Sterna hirundo*	(Bosveld et al., 2000)
		(NF) PCBs	*Sterna hirundo*	(French et al., 2001)
		(+) organic contaminants (α-HBCD, ΣPBDE, ΣPCB, Mirex, ΣDDT)	*Larus hyperboreus*	(Verboven et al., 2008)
		(NF) Hg	*Rissa tridactyla*	(Tartu et al., 2013)
		(NF) organic (PAHs), inorganic contaminants (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn)	*Morus bassanus*	(Champoux et al., 2020)
		(+) PFAS, PFNA, PFDcA, PFUnA (testosterone), (NF) PFAS (DHT)	*Rissa tridactyla*	(Jouanneau et al., 2023)
Thyroglobulin (in the thyroid gland)	1	(+) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
Thyroid hormone receptor alpha (TR α)	4	NA	*Larus argentatus*	(Crump et al., 2008)
		NA	*Eudyptes chrysocome, Pygoscelis papua*	(Bowen et al., 2022)
		(+) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
		(NF) PBDEs, other flame retardants (PBEB, dechlorane 602, dechlorane plus)	*Fulmarus glacialis*	(Mortensen et al., 2022)
Thyroid hormone receptor beta (TR β)	2	(↑) T3, in 0.03 and 0.3 nM	*Larus argentatus*	(Crump et al., 2008)
		(+) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
Thyroid hormone responsive spot-14 (THRSP)	3	(↓) Chlorpyrifos, depending on the dose	*Nannopterum auritum*	(Desforges et al., 2021)
		(NF) inorganic contaminants (Hg, As, Cd, Pb, Se), organic contaminants (53 polycyclic aromatic compounds analysed)	*Cepphus grylle*	(Zahaby et al., 2021)
		(↑) organic contaminants (52 polycyclic aromatic compounds - PACs)	*Cepphus grylle*	(Zahaby et al., 2025)
Thyroid Hormones hepatic transporter - *ATP-binding cassette sub-family C member 2 (ABCC2)*	1	(+) PBDE	*Fulmarus glacialis*	(Mortensen et al., 2022)
Thyroid peroxidase	1	(-) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
Thyroid-stimulating hormone (TSH)	1	(-) PAHs (oiled birds)	*Uria aalge*	(Troisi et al., 2016)
Total triiodothyronine (TT3)	18	(NF) organic contaminants (PAHs, PCBs, PCDFs, PCDDs)	*Sterna hirundo*	(Murk et al., 1994b)
		NA	*Sterna hirundo*	(Murk et al., 1996)
		(NF) organic contaminants (PDDT, PCHL, PPCB, PCBs, DDTs, CHLs, PBDEs, MeO-PBDEs, OH-PCBs/PBDEs)	*Larus hyperboreus*	(Verreault et al., 2007)
		(NF) organic contaminants	*Fulmarus glacialis*	(Helgason et al., 2010b)
		(-) p,p'-DDD; (NF) organic contaminants (PCBs, organochlorines pesticides)	*Fulmarus glacialis*	(Braune et al., 2011)
		(+) organic contaminants (PCBs, DDE, ΣCHLs, ΣDDTs)	*Rissa tridactyla*	(Nøst et al., 2012)
		(NF) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
		(-) chlordanes; (NF) Hg; PCBs, p,p′-DDE, β-HCH, HCB, PFOSlin, PFNA, PFDcA, PFUnA, PFDoA, PFTrA	*Rissa tridactyla*	(Blévin et al., 2017a)
		(NF) organic contaminants	*Rissa tridactyla*	(Svendsen et al., 2018)
		(NF) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
		(+) organic contaminants (PAHs)	*Morus bassanus*	(Champoux et al., 2020)
		(NF) PBDEs, other flame retardants (PBEB, dechlorane 602, dechlorane plus)	*Fulmarus glacialis*	(Mortensen et al., 2022)
		(+) PFAS	*Rissa tridactyla*	(Ask et al., 2020)

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Table 2 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
		(+) PFAS (PFUnDA, PFDoDA, PFTrDA, PFTeDA, Br-PFOS) – females	*Larus marinus*	(Sebastiano et al., 2021)
		(-) PFAAs - PFOS, PFNA, PFDA, PFDoA, PFTeDA, ∑PFCA7, ∑PFAA	*Uria lomvia*	(Choy et al., 2022)
		(-) PFDA and PFDoDA (males); (+) PFTeDA (females); (NF) PFDA, PFDoDA (females); (NF) PFTeDA (males); (NF) PFNA, PFUnDA, PFTrDA, PFHxS, L-PFGpS, Br-PFOS, L-PFOS	*Larus argentatus*	(Sebastiano et al., 2023)
		(+) PFDoDA; (NF) PFNA, PFDA, PFUnDA, PFTrDA, PFTeDA, PFHxS, L-PFHpS, Br-PFOS, L-PFOS	*Larus marinus*	(Sebastiano et al., 2023)
		(+) PFTrDA; (NF) PFNA, PFDA, PFUnDA, PFDoDA, PFTeDA, PFHxS, L-PFHpS, Br-PFOS, L-PFOS	*Larus fuscus*	(Sebastiano et al., 2023)
		(NF) PFAS	*Rissa tridactyla*	(Jouanneau et al., 2023)
		(+) PFAS (linPFOS, PFUnDA, PFDoDA, PFTrDA, ΣPFOS, ΣPFSA, ΣPFAS)	*Sterna paradisaea*	(Aune et al., 2024)
Total thyroxine (TT4)	16	(NF) PAHs, PCBs, PCDFs, PCDDs	*Sterna hirundo*	(Murk et al., 1994b)
		NA	*Sterna hirundo*	(Murk et al., 1996)
		(+) PCBs	*Sterna hirundo*	(Bosveld et al., 2000)
		(NF) organic contaminants (PDDT, PCHL, PPCB, PCBs, DDTs, CHLs, PBDEs, MeO-PBDEs, OH-PCBs/PBDEs)	*Larus hyperboreus*	(Verreault et al., 2007)
		(NF) organic contaminants	*Fulmarus glacialis*	(Helgason et al., 2010b)
		(+) perfluorinated compounds (PFCs)	*Rissa tridactyla, Fulmarus glacialis*	(Nøst et al., 2012)
		(+) organic contaminants (ΣPCB, ΣPCDD, ΣPCDF)	*Fulmarus glacialis*	(Verreault et al., 2013)
		(+) brominated flame retardants (BFR): e.g., PBDEs; HOCs: e.g., PCBs, DDT, HCB	*Larus delawarensis*	(Técher et al., 2016)
		(NF) Hg; (NF) organic contaminants (oxychlordane, trans- and cis-nonachlor, PCBs, p,p′-DDE, β-HCH, HCB, PFOSlin, PFNA, PFDcA, PFUnA, PFDoA, PFTrA)	*Rissa tridactyla*	(Blévin et al., 2017a)
		(-) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
		(NF) organic (HPAs), inorganic contaminants (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn); ↑ (oil)	*Morus bassanus*	(Champoux et al., 2020)
		(NF) PBDEs, other flame retardants (PBEB, dechlorane 602, dechlorane plus)	*Fulmarus glacialis*	(Mortensen et al., 2022)
		(+) PFAS	*Rissa tridactyla*	(Ask et al., 2020)
		(+) organic contaminants (PFAAs, PFOA)	*Uria lomvia*	(Choy et al., 2022)
		(NF) PFAS	*Rissa tridactyla*	(Jouanneau et al., 2023)
		(NF) PFAS	*Sterna paradisaea*	(Aune et al., 2024)
Transcription of multiple genes related to the endocrine system (*IGF1, AKT1*, *NCOA3*, *THRSP*)	1	(NF) Hg, As, Cd, Pb, Se, 53 PACs	*Uria lomvia, Cepphus grylle*	(Zahaby et al., 2021)
Transcription of multiple genes related to the endocrine system (*type II iodothyronine* 5#*-deiodinase D2 and D3, transthyretin (TTR), myelin basic protein, neurogranin (RC3), octamer motif–binding factor (Oct-1)*)	1	(NF) perfluoroalkyl compounds (PFCs), (+) perfluoroalkyl compounds (PFCs) for neurogranin (RC3), octamer motif-binding factor (Oct-1)	*Larus argentatus*	(Vongphachan et al., 2011)
Transthyretin (TTR)	5	(↓) DE-71; (↓) T3	*Larus argentatus*	(Crump et al., 2008)
		(NF) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
		(NF) PBDEs, other flame retardants (PBEB, dechlorane 602, dechlorane plus)	*Fulmarus glacialis*	(Mortensen et al., 2022)
		(NF) inorganic contaminants (Hg, As, Cd, Pb, Se), 53 polycyclic aromatic compounds - PACs)	*Uria lomvia, Cepphus grylle*	(Zahaby et al., 2021)
		(↑) organic contaminants (52 polycyclic aromatic compounds - PACs)	*Cepphus grylle*	(Zahaby et al., 2025)
TT3:FT3	1	(-) PCB 28, 138, 187, ΣPBDE	*Rissa tridactyla*	(Svendsen et al., 2018)
TT4:FT4	1	(+) dechlorane plus, (-) pentabromoethylbenzene (PBEB)	*Fulmarus glacialis*	(Mortensen et al., 2022)
TT3:TT4	2	(NF) PFAS	*Rissa tridactyla*	(Jouanneau et al., 2023)
		(-) perfluoroalkyl acids (PFAAs) - PFOA and PFTeDA, (+) PFOS, PFDA, PFDoA, PFTeDA, ΣPFCA7, ΣPFAA	*Uria lomvia*	(Choy et al., 2022)

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Table 2 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
TT4:TT3	4	(+) p,p'-DDD, Mirex, (NF) PCBs, organochlorines pesticides	*Fulmarus glacialis*	(Braune et al., 2011)
		(+) organic contaminants (ΣPCB, ΣPCDD, ΣPCDF)	*Fulmarus glacialis*	(Verreault et al., 2013)
		(-) halogenated flame retardants (HFRs, PBDEs)	*Larus delawarensis*	(Técher et al., 2018)
		(NF) PFAS	*Sterna paradisaea*	(Aune et al., 2024)

Table 3
Biomarkers related to hepatic damage in seabirds, screened in papers published between 1976 and 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
Alanine aminotransferase (ALT)	6	(↑) trimethyltin (TMT)	*Pygoscelis papua*	(Najle et al., 2006)
		(+) organic contaminants (CHLs, PBDEs)	*Stercorarius skua*	(Sonne et al., 2013)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017b)
		(NF) organic (HPAs), and inorganic contaminants (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn)	*Morus bassanus*	(Champoux et al., 2020)
		(NF) Hg	*Somateria mollissima*	(Ma et al., 2020)
		(+) THg	*Stercorarius antarcticus*	(Ibañez et al., 2024)
Alkaline phosphatase (ALP)	5	(↓) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(NF) organic contaminants	*Stercorarius skua*	(Sonne et al., 2013)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017b)
		(+) organic contaminants (naphthalene, biphenyl)	*Morus bassanus*	(Champoux et al., 2020)
		(NF) Hg	*Somateria mollissima*	(Ma et al., 2020)
Aspartate aminotransferase (AST)	11	(↑) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(↑) organic contaminants (oil)	*Cepphus columba*	(Golet et al., 2002)
		(↑) trimethyltin (TMT)	*Pygoscelis papua*	(Najle et al., 2006)
		(↑) ∑PAHs, (+) organic contaminants (oil)	*Larus michahellis*	(Alonso-Alvarez et al., 2007)
		NA	*Larus michahellis*	(Pérez et al., 2010)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017a)
		(NF) organic contaminants (oil)	*Nannopterum auritum*, *Leucophaeus atricilla*	(Dean et al., 2017b)
		(NF) organic (HPAs), and inorganic (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn) contaminants	*Morus bassanus*	(Champoux et al., 2020)
		(NF) THg	*Stercorarius antarcticus*	(Ibañez et al., 2024)
		(NF) organic contaminants (PAHs)	*Pelecanus occidentalis*	(Jodice et al., 2023)
		NA	*Cerorhinca monocerata*	(Lee et al., 2024)
Bile acids	5	(NF) organic contaminants	*Cepphus columba*	(Seiser et al., 2000)
		(NF) organic contaminants	*Stercorarius skua*	(Sonne et al., 2013)
		(NF) Hg	*Somateria mollissima*	(Ma et al., 2020)
		(NF) organic and inorganic contaminants	*Uria lomvia*	(Sarma et al., 2022)
		(-) Cd, Hg (taurocholic acid, deoxycholic acid, taurochenodeoxycholate, taurodeoxycholic acid); (NF) organic contaminants	*Cepphus grylle*	(Sarma et al., 2022)
Bilirubin	1	(+) organic contaminants (HCHs, PBDEs)	*Stercorarius skua*	(Sonne et al., 2013)
Hemosiderosis	1	(+) organic contaminants (oil)	*Uria aalge*, *U. lomvia*, *Clangula hyemalis*	(Khan and Nag, 1993)
Ornithine carbamoyltransferase (OCT)	1	(+) organic contaminants (oil)	*Cepphus grylle*	(Peakall et al., 1980)
γ- glutamyl transferase (GGT)	8	(↓) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(↑) ∑PAHs (adult females), (+) organic contaminants (∑PAHs - nestlings)	*Larus michahellis*	(Alonso-Alvarez et al., 2007)
		(-) Hg	*Sterna forsteri*, *Hydroprogne caspia*	(Hoffman et al., 2011)
		(+) organic contaminants (PCBs, HCHs, HCB, CHLs)	*Stercorarius skua*	(Sonne et al., 2013)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017a)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017b)
		(NF) organic (PAHs), inorganic (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn) contaminants	*Morus bassanus*	(Champoux et al., 2020)
		(NF) Hg	*Somateria mollissima*	(Ma et al., 2020)

these findings, only 1.8% ($n = 5$) of the reviewed articles addressed ALP and only 2.2% ($n = 6$) ALT as biomarkers of hepatic damage in seabirds associated with contaminants. However, AST and GGT were studied in nearly twice as many publications ($n = 11$; 4.0% and $n = 8$; 2.9%, respectively). Interpretation of hepatic damage biomarkers in seabirds is constrained by the limited availability of validated, species-specific clinical reference ranges (e.g., Lee et al., 2024). Consequently, most reviewed studies relied on relative differences among exposure groups, temporal comparisons, or contrasts with reference populations rather than absolute diagnostic thresholds. Enzyme activities such as AST and ALT are commonly interpreted as indicators of hepatocellular injury, whereas ALP and GGT are used more cautiously as markers of biliary dysfunction or cholestasis, but due to wide distribution their single estimation lacks specificity (Anand and Mallick, 2019). Where reported, enzymes quantification was performed using either wet-chemistry spectrophotometric assays or dry-chemistry automated platforms, with methodological heterogeneity further limiting cross-study comparability (Table 3). Overall, our review brings studies focusing on hepatic biomarkers in seabirds as indicators of sublethal tissue damage within an ecotoxicological framework, rather than clinical diagnostic endpoints.

Bilirubin showed a positive correlation with organic contaminants (HCHs and PBDEs) in seabirds, although assessed only in the great skua (Sonne et al., 2013). According to Tamber et al. (2023), increased serum ALP activity indicates injury to the canalicular membrane or biliary epithelial cells, while elevated total bilirubin serves as an indicator of hepatobiliary damage and overall liver function in humans. Furthermore, increased GGT activity is a marker of hepatobiliary injury, particularly cholestasis and biliary effects. The authors also associate elevated serum AST or ALT activities with hepatocellular necrosis (Tamber et al., 2023).

Another enzyme, ornithine carbamoyltransferase (OCT, or ornithine transcarbamylase), involved in nitrogen metabolism, showed a positive correlation with oil in black guillemot (*Cepphus grille*) (Peakall et al., 1980; Imoto et al., 2022). Additionally, one study found a positive association in three bird species (*Uria aalge*, *Uria lomvia*, *Clangula hyemalis*), between crude oil and haemosiderosis that is, the excessive accumulation of intracellular haemosiderin (Khan and Nag, 1993). Haemosiderin is an iron-containing complex derived from the degradation of haemoglobin, which accumulates in macrophages of the reticuloendothelial system and other tissues (Bulte et al., 1997).

3.4.4. *Biomarkers of oxidative stress*

Since 2001, numerous studies have investigated biomarkers of oxidative stress in seabirds, reflecting the importance attributed to these processes in ecotoxicological assessments ($n = 41$; 14.9%) (Table 4). Exposure to environmental contaminants can disrupt the balance between reactive oxygen species (ROS) production and antioxidant defence mechanisms, resulting in oxidative stress. The antioxidant defence system comprises both enzymatic and non-enzymatic components responsible for the elimination of ROS, including superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPx), and reduced glutathione (GSH) (Hoffman et al., 2011).

Lipid peroxidation has been one of the most frequently used biomarkers of oxidative stress ($n = 19$ articles, 6.9%). This process indicates oxidative damage when pro-oxidant events overwhelm the organism's antioxidant defences. The breakdown of polyunsaturated fatty acids leads to the formation of malondialdehyde (MDA) and 4-hydroxynonenals, and their quantification, most commonly assessed using the thiobarbituric acid reactive substances (TBARS) assay, is widely recognised as an indicator of lipid peroxidation, typically expressed as nmol MDA per mg of protein (Pritsos et al., 2017; Veríssimo et al., 2024b). Increased lipid peroxidation has been reported in response to exposure of organic contaminants (i.e., crude oil and triclosan, definitions on Table S4) in Magellanic penguins (*Spheniscus magellanicus*) and yellow-legged gulls (*Larus michahellis*) (Romero et al., 2015; Possenti et al., 2019). Positive correlations with lipid peroxidation were also observed with mercury (Hg) in two tern species (*Sterna forsteri* and *Hydroprogne caspia*) (Hoffman et al., 2011), and with dicyclohexyl phthalate (DCHP) in herring gulls, considered as a plastic-related chemical (Table S4) (Allen et al., 2021).

Among the antioxidant enzymes, SOD is the most studied in seabirds, with 14 publications reporting SOD activity in liver and/or blood (Table 4). Two of these studies reported a negative association between SOD activity in liver homogenates and petroleum-related contaminants (Horak et al., 2017; Pritsos et al., 2017), whereas a positive association was found between SOD activity in blood and inorganic mercury (Hg), as well as the organochlorines β-HCH and HCB (Espín et al., 2016; Costantini et al., 2019). Catalase (CAT) was assessed in nine publications, which yielded conflicting outcomes. While one study reported a negative correlation between CAT activity in liver homogenates and PCB levels in herring gulls (Hegseth et al., 2011a), another documented a positive association between CAT activity in liver homogenates and PCBs and iron in three seabird species (Hegseth et al., 2011b). The remaining studies found no association between CAT and the contaminants measured or detected no significant differences across exposure categories (Table 4). Regarding GPx, negative associations were observed with organic contaminants and Hg, whereas selenium (Se) was positively related with the enzyme activity measured in blood samples (Franson et al., 2011) (Table 4). Hegseth et al. (2011b) differentiated two isoforms of GPx and reported a positive association between the selenium-dependent isoform measured in liver homogenates and PCBs levels in contaminated seabirds.

The role of the endogenous GSH as a biomarker of aquatic contamination in seabirds was evaluated in 10 studies, with four reporting positive associations found for both organic and inorganic contaminants (Espín et al., 2016; Dean et al., 2017a; Horak et al., 2017; Pritsos et al., 2017). Some studies also addressed the analysis of oxidised glutathione (GSSG) ($n = 7$; 2.5%) and the GSH:GSSG ratio ($n = 5$; 1.8%; Table 4). Total glutathione (tGSH) was investigated in five studies, with three reporting a positive association between organic contaminants and tGSH measured in blood and or liver (Dean et al., 2017a; Horak et al., 2017; Pritsos et al., 2017). GSH plays a crucial role in preventing cellular damage mediated by ROS. Together with SOD, which converts superoxide anions into hydrogen peroxide (H_2O_2), GPx catalyses the conversion of H_2O_2 into water. As a consequence of this reaction, GSH is oxidised to glutathione disulfide (GSSG). Thus, GSH acts as a cofactor in the elimination of toxic radicals from the organism. During oxidative stress, GSH levels decrease while GSSG concentration increases, potentially influencing signal transduction by stimulating activation of the transcription factor NF-κB (Federici et al., 2024). These mechanisms have only begun to be investigated in seabirds from the 2010s onwards, and much remains to be elucidated.

3.4.5. *Biomarkers of metal and metalloid exposure and detoxification*

Several studies included in the present review have been documented metallothioneins (MTs) in the liver and/or kidneys of various seabird species, including *Oceanodroma leucorhoa*, *Fratercula arctica*, *Nannopterum auritum*, *Larus argentatus*, *Chroicocephalus ridibundus*, *Fulmarus glacialis*, *Uria aalge*, *Rissa tridactyla*, and *Melanitta nigra* (Osborn, 1978; Elliott et al., 1992; Wenzel et al., 1996). MTs are low molecular weight, soluble proteins characterised by their thermal stability, high cysteine content, and absence of aromatic amino acids (Hamer, 1986). They play essential roles in the transport and storage of metal(oid)s, as well as in minimising the toxic effects of certain metals by sequestering and reducing free metal ions (Hamilton and Mehrle, 1986; Vallee, 1995; Roesijadi, 1996). Since their discovery in 1957, the presence of MTs has been confirmed in numerous animals and proposed as a biomarker of metal contamination (Hamza-Chaffai et al., 1997).

MTs in seabirds have been studied since 1978 ($n = 20$ articles; 7.3%), with the majority of publications reporting positive correlations with metals, particularly with Zn, Cu, Cd and Hg (Table 5). Quantification of MTs and their relationship with metal(oid)s levels provides valuable insight into the behaviour of these elements within organisms. For this reason, MTs are considered classical biomarkers related to the detoxification of non-essential metals (such as Cd, Hg and Pb) and the regulation of essential metals (such as Cu and Zn). Moreover, they are also known for their antioxidant functions (Hamza-Chaffai et al., 1997; Lomartire et al., 2021).

In addition, the role of selenonein in metal detoxification in seabirds

Table 4

Biomarkers related to oxidative stress in seabirds, screened in studies published between 1976 and 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
Catalase (CAT)	8	(+) PCBs, Fe	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(-) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
		NA	*Spheniscus magellanicus*	(Carabajal et al., 2016)
		NA	*Fregata magnificens*	(Sebastiano et al., 2017)
		NA	*Larus fuscus*	(Santos et al., 2019)
		NA	*Sterna hirundo*	(Oudi et al., 2019)
		(NF) Hg	*Puffinus opisthomelas*	(Soldatini et al., 2020)
		(NF) Cd, Pb, Zn	*Ardenna gravis*	(Hernández-Moreno et al., 2021)
Cytochrome c oxidase – subunit I (COI)	1	(↑) MeHg	*Leucophaeus atricilla*	(Jenko et al., 2012)
Ferric Reducing Antioxidant Capacity of Erythrocytes (non-enzymatic antioxidant capacity) - FRAE	1	(-) Hg	*Puffinus opisthomelas*	(Soldatini et al., 2020)
Glucose-6-phosphate dehydrogenase (G-6-PDH)	2	(+) Hg	*Sterna forsteri, Hydroprogne caspia*	(Hoffman et al., 2011)
		(+) MeHg	*Leucophaeus atricilla*	(Jenko et al., 2012)
GSSG reductase	1	(-) Hg	*Sterna forsteri, Hydroprogne caspia*	(Hoffman et al., 2011)
Glutathione disulfide (oxidised glutathione) (GSSG)	7	(NF) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
		(+) Hg	*Sterna forsteri, Hydroprogne caspia*	(Hoffman et al., 2011)
		(NF) organic contaminants (PBDE, DE-71)	*Sterna hirundo*	(Rattner et al., 2013)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017b)
		(+) organic contaminants (oil)	*Leucophaeus atricilla*	(Horak et al., 2017)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Pritsos et al., 2017)
		NA	*Fregata magnificens*	(Sebastiano et al., 2017)
Glutathione peroxidase (GPx)	9	(-) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
		(+) Se	*Clangula hyemalis*	(Franson et al., 2011)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Pritsos et al., 2017)
		NA	*Fregata magnificens*	(Sebastiano et al., 2017)
		(NF) organic contaminants (PCBs, OCPs, PBDEs)	*Calonectris diomedea*	(Costantini et al., 2017)
		(-) Hg	*Calonectris diomedea*	(Costantini et al., 2020)
		(-) Hg	*Puffinus opisthomelas*	(Soldatini et al., 2020)
		(+) PBDE, MeO-BDEs	*Larus michahellis, Ichthyaetus audouinii*	(Veríssimo et al., 2024b)
		(↑) PBDE - polybrominated diphenyl ethers - BDE99 (plasticizer)	*Larus michahellis, Larus fuscus*	(Veríssimo et al., 2024a)
GPx – Se dependent	1	(+) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
GPx – Se independent	1	(-) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
GPX1	2	(+) PFCs; DRCs	*Phalacrocorax carbo*	(Nakayama et al., 2008a)
		(NF) THg, methyl mercury (MeHg)	*Nannopterum auritum*	(Gibson et al., 2014)
GPX3 - extracellular glutathione peroxidase 3 detectable in the plasma (proteomics)	1	(-) plastic ingestion	*Ardenna carneipes*	(de Jersey et al., 2025)

(*continued on next page*)

Table 4 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
GPX3	1	(-) polychlorinated dibenzo-p-dioxins (PCDD), furans, PCBs, 1,1,1-trichloro-2,2- bis(p-chlorophenyl) ethane and its metabolites (DOTS), hexachlorocyclohexane isomers (HCHs), chlordane compounds (CHLs), butyltins and BPA	*Phalacrocorax carbo*	(Nakayama et al., 2006)
		(+) THg, methyl mercury (MeHg)	*Nannopterum auritum*	(Gibson et al., 2014)
Glutathione reductase (GR)	3	(NF) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(NF) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
		(NF) Se	*Clangula hyemalis*	(Franson et al., 2011)
Glutathione S-transferase alpha 3 (GSTA3)	1	(+) PFCs; DRCs	*Phalacrocorax carbo*	(Nakayama et al., 2008a)
Glutathione S- transferase μ (GSTM)	1	(-) polychlorinated dibenzo-p-dioxins (PCDD), furans, PCBs, 1,1,1-trichloro-2,2- bis(p-chlorophenyl)ethane and its metabolites (DOTS), hexachlorocyclohexane isomers (HCHs), chlordane compounds (CHLs), butyltins, BPA	*Phalacrocorax carbo*	(Nakayama et al., 2006)
GSTM3	1	(+) THg, methyl mercury (MeHg)	*Nannopterum auritum*	(Gibson et al., 2014)
		(↑) organic contaminants (52 polycyclic aromatic compounds - PACs)	*Cepphus grylle*	(Zahaby et al., 2025)
Glutathione Specific Gamma-Glutamylcyclotransferase 1 (Chac1)	1	(↓) Chlorpyrifos	*Nannopterum auritum*	(Desforges et al., 2021)
Lipid peroxidation	19	(+) Hg	*Sterna forsteri, Hydroprogne caspia*	(Hoffman et al., 2011)
		(NF) organic contaminants (PBDE, DE-71)	*Sterna hirundo*	(Rattner et al., 2013)
		(↑) organic contaminants (oil)	*Spheniscus magelanicus*	(Romero et al., 2015)
		NA	*Spheniscus magellanicus*	(Carabajal et al., 2016)
		(NF) organic contaminants (oil)	*Nannopterum auritum, Leucophaeus atricilla*	(Dean et al., 2017b)
		(NF) organic contaminants (oil)	*Nannopterum auritum*	(Pritsos et al., 2017)
		NA	*Fregata magnificens*	(Sebastiano et al., 2017)
		NA	*Sterna hirundo*	(Oudi et al., 2019)
		(↑) Triclosan	*Larus michahellis*	(Possenti et al., 2019)
		(NF) inorganic contaminants (Al, As, Pb, Cd, Cr, Fe, Cu, Mn, Ni, Hg, Se, Ag e Zn)	*Larus michahellis, Ichthyaetus audouinii*	(Laranjeiro et al., 2020)
		(-) Hg	*Larus fuscus*	(Santos et al., 2020)
		(NF) Hg	*Puffinus opisthomelas*	(Soldatini et al., 2020)
		(+) dicyclohexyl phthalate (DCHP)	*Larus argentatus*	(Allen et al., 2021)
		(NF) inorganic contaminants (e.g., As, Cd, Hg, Pb, Sr)	*Calonectris borealis*	(Laranjeiro et al., 2021)
		(NF) ΣHOC and metals	*Rissa tridactyla, Fulmarus glacialis*	(Hegseth et al., 2011c)
		(+) ΣHOC	*Larus argentatus*	(Hegseth et al., 2011c)
		(NF) organic contaminants (ΣHOC)	*Larus argentatus*	(Hegseth et al., 2014)
		(NF) Cd, Pb, Zn	*Ardenna gravis*	(Hernández-Moreno et al., 2021)
		(-) PBDE, MeO-BDEs	*Larus michahellis, Ichthyaetus audouinii*	(Veríssimo et al., 2024b)
Oxidative Stress Index (OSI)	2	(-) organic contaminants (organochlorines - OCs and flame retardants - PBDEs)	*Stercorarius skua*	(Bourgeon et al., 2012)
		NA	*Larus atlanticus*	(García et al., 2023)
Peroxiredoxin 4 (PRDX4)	1	NA	*Eudyptes chrysocome, Pygoscelis papua*	(Bowen et al., 2022)
Peroxiredoxin 6 (PRDX6)	1	NA	*Eudyptes chrysocome, Pygoscelis papua*	(Bowen et al., 2022)
Plasma total oxidant status (TOS)	1	(-) organic contaminants (PCBs and PBDEs)	*Stercorarius skua*	(Bourgeon et al., 2012)

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Table 4 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
Protein-bound thiols (PBSH)	1	(-) Hg	*Sterna forsteri, Hydroprogne caspia*	(Hoffman et al., 2011)
Protein carbonyls	3	NA	*Fregata magnificens*	(Sebastiano et al., 2017)
		(+) PFAs, PFFA	*Rissa tridactyla*	(Costantini et al., 2019)
		(+) Hg	*Calonectris diomedea*	(Costantini et al., 2020)
Reactive oxygen metabolites (d-ROM)	6	(NF) organic contaminants (PCBs, OCPs, PBDEs)	*Calonectris diomedea*	(Costantini et al., 2017)
		(NF) organic contaminants; (NF) Hg	*Cepphus grylle mandtii*	(Eckbo et al., 2019)
		(NF) inorganic contaminants (Al, As, Pb, Cd, Cr, Fe, Cu, Mn, Ni, Hg, Se, Ag, Zn)	*Larus michahellis, Ichthyaetus audouinii*	(Laranjeiro et al., 2020)
		(NF) inorganic contaminants (e.g., As, Cd, Hg, Pb, Sr)	*Calonectris borealis*	(Laranjeiro et al., 2021)
		NA	*Larus atlanticus*	(García et al., 2023)
		(NF) PBDE - polybrominated diphenyl ethers - BDE99 (plasticizer)	*Larus michahellis,* *Larus fuscus*	(Veríssimo et al., 2024a)
Reactive oxygen species (ROS)	1	(↑) Triclosan	*Larus michahellis*	(Possenti et al., 2019)
Reduced glutathione (GSH)	10	(NF) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(NF) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
		(-) Hg	*Sterna forsteri, Hydroprogne caspia*	(Hoffman et al., 2011)
		(NF) organic contaminants (PBDE, DE-71)	*Sterna hirundo*	(Rattner et al., 2013)
		(+) Cu, Zn, Pb	*Chroicocephalus genei, Ichthyaetus audouinii*	(Espín et al., 2016)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017b)
		(+) organic contaminants (oil)	*Leucophaeus atricilla*	(Horak et al., 2017)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Pritsos et al., 2017)
		NA	*Fregata magnificens*	(Sebastiano et al., 2017)
		(NF) Cd, Pb, Zn	*Ardenna gravis*	(Hernández-Moreno et al., 2021)
rGSH:GSSG	4	(NF) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(NF) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
		(-) organic contaminants (oil)	*Leucophaeus atricilla*	(Horak et al., 2017)
		NA	*Fregata magnificens*	(Sebastiano et al., 2017)
GSSG:GSH	1	(+) Hg	*Sterna forsteri, Hydroprogne caspia*	(Hoffman et al., 2011)
Superoxide dismutase (SOD)	10	(NF) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(NF) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
		(+) Hg; (-) Zn; (NF) other inorganic contaminants	*Chroicocephalus genei*	(Espín et al., 2016)
		(+) β-HCH, HCB (females)	*Calonectris diomedea*	(Costantini et al., 2017)
		(NF) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017b)
		(-) organic contaminants (oil)	*Leucophaeus atricilla*	(Horak et al., 2017)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Pritsos et al., 2017)
		NA	*Fregata magnificens*	(Sebastiano et al., 2017)
		NA inorganic contaminants	*Sterna hirundo*	(Oudi et al., 2019)
		(NF) Hg	*Puffinus opisthomelas*	(Soldatini et al., 2020)
Cu/Zn superoxide dismutase 1 (SOD1)	4	(-) polychlorinated dibenzo-p-dioxins (PCDD), furans, PCBs, 1,1,1-trichloro-2,2-bis(p-chlorophenyl)ethane and its metabolites	*Phalacrocorax carbo*	(Nakayama et al., 2006)

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Table 4 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
		(DOTS), hexachlorocyclohexane isomers (HCHs), chlordane compounds (CHLs), butyltins, BPA		
		(NF) THg, methyl mercury (Me–Hg)	*Nannopterum auritum*	(Gibson et al., 2014)
		(+) plastic ingestion	*Ardenna carneipes*	(de Jersey et al., 2025)
		(↑) diluted bitumen - dilbit (PAC)	*Nannopterum auritum, Morus bassanus*	(Wallace et al., 2025)
Total glutathione (tGSH)	5	(NF) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(NF) organic and inorganic contaminants	*Somateria mollissima*	(Fenstad et al., 2016a)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017b)
		(+) organic contaminants (oil)	*Leucophaeus atricilla*	(Horak et al., 2017)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Pritsos et al., 2017)
Total Oxyradical Scavenging Capacity (TOSC) – HNOOH	2	(-) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(NF) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
Total Oxyradical Scavenging Capacity (TOSC) – OH	2	(+) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(NF) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
Total Oxyradical Scavenging Capacity (TOSC) – ROO	3	NA	*Pygoscelis adeliae, Aptenodytes forsteri, Stercorarius maccormicki, Pagodroma nivea*	(Corsolini et al., 2001)
		(-) PCBs	*Rissa tridactyla, Fulmarus glacialis, Larus argentatus*	(Hegseth et al., 2011b)
		(-) PCBs	*Larus argentatus*	(Hegseth et al., 2011a)
Total plasma antioxidant status (TAS) or capacity (TAC)	11	(+) organic contaminants (PCBs)	*Stercorarius skua*	(Bourgeon et al., 2012)
		(+) PCB 28, 52, 99, 101, 105, 118, 138, 153, 180, 183, 187, 194; p, p'-DDE, HCH, Mirex, HCB	*Somateria mollissima*	(Fenstad et al., 2016a)
		(+) oxychlordane (OxC)	*Calonectris diomedea*	(Costantini et al., 2017)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Pritsos et al., 2017)
		NA	*Fregata magnificens*	(Sebastiano et al., 2017)
		(NF) organic contaminants, (NF) Hg	*Cepphus grylle mandtii*	(Eckbo et al., 2019)
		(-) PFAs, PFFA	*Rissa tridactyla*	(Costantini et al., 2019)
		(-) Hg	*Calonectris diomedea*	(Costantini et al., 2020)
		(NF) inorganic contaminants (Al, As, Pb, Cd, Cr, Fe, Cu, Mn, Ni, Hg, Se, Ag, Zn)	*Larus michahellis, Ichthyaetus audouinii*	(Laranjeiro et al., 2020)
		(NF) inorganic contaminants (e.g., As, Cd, Hg, Pb, Sr)	*Calonectris borealis*	(Laranjeiro et al., 2021)
		NA	*Larus atlanticus*	(García et al., 2023)
		(NF) PBDE, MeO-BDEs	*Larus michahellis, Ichthyaetus audouinii*	(Veríssimo et al., 2024b)
		(NF) PBDE - polybrominated diphenyl ethers - BDE99 (plasticizer)	*Larus michahellis, Larus fuscus*	(Veríssimo et al., 2024a)
Total reduced thiols (TSH)	1	(-) Hg	*Sterna forsteri, Hydroprogne caspia*	(Hoffman et al., 2011)
Transcription of multiple genes related to oxidative stress (*GPX3, GSTM3*)	1	(NF) inorganic contaminants (Hg, As, Cd, Pb, Se), and 53 PACs	*Uria lomvia, Cepphus grylle*	(Zahaby et al., 2021)

was studied by Hanafi et al. (2022), who demonstrated a negative correlation with Hg and a positive correlation with selenium (Se). Furthermore, transcriptional studies of the *Selenoprotein P* gene (*sepp1*) showed positive associations with Hg in rhinoceros auklet (*Cerorhinca monocerata*) (King et al., 2023). A positive correlation was also observed between hepatic Se concentrations and levels of Hg and MeHg in giant-petrels (*Macronectes halli* and *M. giganteus*) and Magellanic penguins (Kehrig et al., 2015; Manceau et al., 2021).

3.4.6. *Biomarkers of genotoxicity*

Due to the scarcity of studies on genotoxicity in most seabird species, little is known on baseline levels of DNA damage, sensitivity to genotoxic substances, DNA repair capacity, and the relationship between contaminant exposure and DNA damage. On the other hand, there has been a growing interest in this topic, with 32 articles addressing genotoxicity (11.6% of the total), reflecting the importance of DNA integrity and maintenance for cellular and tissue functions. Many contaminants to which seabirds have been exposed are genotoxic and may compromise

Table 5
Biomarkers related to metal exposure and detoxification in seabirds, screened in studies published between 1976 and 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
Metallothionein (MT)	17	(+) Zn, Cd; (NF) Hg	*Fulmarus glacialis*	(Osborn, 1978)
		(+) Zn, Hg, Cd	*Stercorarius skua*	(Hutton, 1981)
		(+) Cd; (NF) Hg	*Oceanodroma leucorhoa, Larus argentatus*	(Elliott et al., 1992)
		(+) Cd, Hg	*Fratercula arctica*	(Elliott et al., 1992)
		(NF) Cd, Hg	*Nannopterum auritum*	(Elliott et al., 1992)
		(+) Cu, Zn; (NF) Cd	*Uria aalge*	(Bouquegneau et al., 1996)
		(+) Cd, Zn, Cu; (NF) Hg	*Larus fuscus*	(Stewart et al., 1996)
		(+) Cd, Zn, Cu (kidney); (+) Zn (liver)	*Calonectris diomedea*	(Stewart and et al., 1996)
		(+) Cd	*Cerorhinca monocerata, Ptychoramphus aleuticus, Synthliboramphus antiquus*	(Elliott and Scheuhammer, 1997)
		(+) Cd, Cu, Zn	*Somateria fischeri*	(Trust et al., 2000)
		(+) Zn, Cu; (NF) Cd	*Uria aalge*	(Debacker et al., 2001)
		(+) Cd, Zn, Cu	*Melanitta perspicillata*	(Barjaktarovic et al., 2002)
		(+) Zn, Cu, Cd, Hg	*Phoebastria nigripes*	(Ikemoto et al., 2004)
		(+) Cu, Zn; (NF) Cd	*Phalacrocorax carbo*	(Nam et al., 2005)
		(NF) Cd, Zn, Cu	*Larus hyperboreus, Cepphus grylle*	(Braune and Scheuhammer, 2008)
		(+) Cd, Zn; (NF) Cu	*Rissa tridactyla, Uria lomvia*	(Braune and Scheuhammer, 2008)
		(+) Cd; (NF) Cu, Zn	*Fulmarus glacialis*	(Braune and Scheuhammer, 2008)
		(+) Hg, (-) Se	*Melanitta perspicillata*	(Elliott et al., 2007)
		(+) Cd, Cu, Hg, Zn	*Pterodroma baraui, Puffinus lherminieri, Phaethon lepturus*	(Kojadinovic et al., 2007)
		(+) Cd, Pb, Hg total, Hg_{inorg}; (NF), MeHg	*Spheniscus magellanicus*	(Kehrig et al., 2015)
		(+) Cd > Zn > Hg > Cu > Se; (-) Se:Hg	*Rissa tridactyla*	(Øverjordet et al., 2015)
		(+) Cu, Zn	*Spheniscus magellanicus*	(Romero et al., 2015)
Metallothionein (MT)	3	NA	*Larus crassirostris*	(Kim et al., 2013)
		(NF) organic (PAHs), and inorganic contaminants (As, Cu, Fe, Ni, Rb, Se, V, Zn in blood; and As, Ba, Cd, Cu, Fe, Mn, Mo, Pb, Rb, Se, Sn, Sr, V, Zn in feathers)	*Morus bassanus*	(Champoux et al., 2020)
		(NF) Hg, As, Cd, Pb, Se and 53 polycyclic aromatic compounds	*Uria lomvia, Cepphus grylle*	(Zahaby et al., 2021)
Selenium (Se) – hepatic concentration	2	(+) Hg	*Macronectes halli, M. giganteus*	(Manceau et al., 2021)
		(+) MeHg; (+) Cd, Pb, Hg	*Spheniscus magellanicus*	(Kehrig et al., 2015)
Selenoneine	1	(-) Hg, (+) Se	*Macronectes* spp.	(Hanafi et al., 2022)
Selenoprotein P (sepp1)	1	(+) Hg	*Cerorhinca monocerata*	(King et al., 2023)

the genome through the production of ROS, DNA strand breaks, and impairment of DNA repair mechanisms (Marabini et al., 2011). Such genotoxic effects may lead to cell death, chromosomal aberrations, and mutations, resulting in adverse outcomes such as cancer, accelerated ageing, reproductive impairment, and developmental malformations (Fernandez et al., 2021). Several cellular mechanisms protect DNA, including antioxidant and repair systems, the effectiveness of which depends on individual factors such as energy expenditure, health status, and dietary antioxidant intake (Carravieri et al., 2023).

A considerable proportion of the publications on seabird genotoxicity has focused on the effects of contaminants on telomere length ($n =$ 7 articles; 2.5% of the total; Table 6), highlighting an important gap in current knowledge. Telomeres are non-coding, repetitive DNA sequences located at the ends of chromosomes, playing a crucial role in safeguarding genome integrity (Blackburn, 2005). These sequences shorten with each cell division and are susceptible to environmental stressors (Angelier et al., 2018). Overall, exposure to organic contaminants has been negatively correlated with telomere length, with the exception of PFAS and PFOS (Table 6). For inorganic contaminants, a negative correlation between Hg and telomere length has so far been observed in Cory's shearwater (*Calonectris borealis*) (Bauch et al., 2022).

Other genotoxicity biomarkers have also been used in seabirds, including direct analyses of DNA damage. Analyses of DNA strand breaks was assessed in seven studies (Table 6), and revealed positive associations with organic contaminants (Fenstad et al., 2014; Keilen et al., 2022) and with the inorganic Hg (Fenstad et al., 2016b). The comet assay (single-cell gel electrophoresis) is a widely applied method in eco-genotoxicology, and quantifies DNA strand breaks using parameters such as the percentage of DNA in the comet tail (%DNA in tail) and tail moment, which reflect the extent of DNA migration during electrophoresis (Azqueta and Collins, 2013). Other studies investigated intracellular variations in DNA content, expressed as the **h**alf-**p**eak **co**efficient of **v**ariation (HPCV), as well as the relative length of nuclear DNA strands isolated from compacted erythrocytes; **m**edian **m**olecular **l**ength (MML), the frequency of micronucleated erythrocytes (MNE), and nuclear abnormalities in erythrocytes (Table 6). Erythrocyte nuclear abnormalities (ENAs), in turn, have received considerable attention for their methodological development, addressed in 11 publications. However, only five of these detected direct associations with contaminants, and just two reported an increase in ENAs in response to Hg and/or PFAS/PFOS exposure (Santos et al., 2020; Wells et al., 2024).

Across all genotoxicity endpoints reviewed, blood was the exclusive biological matrix used, including whole blood, erythrocytes, or isolated blood cells, reflecting its suitability for non-lethal sampling in seabirds. Importantly, the assays applied capture distinct levels of genomic damage, with telomere length reflecting cumulative and long-term cellular stress, comet assay metrics indicating recent DNA strand breakage, and erythrocytic nuclear abnormalities (including

Table 6

Biomarkers related to genotoxicity in seabirds, screened in studies published between 1976 and 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/−, ↑/↓)	Species	Reference
DNA damage – alkaline DNA precipitation assay	1	(NF) inorganic contaminants (e.g., As, Cd, Hg, Pb, Sr)	*Calonectris borealis*	(Laranjeiro et al., 2021)
DNA damage – double-strand breaks / comet assay	7	NA	*Thalasseus maximus*	(Maness and Emslie, 2001)
		(+) organic contaminants (POPs, DDE, PCB 180)	*Somateria mollissima*	(Fenstad et al., 2014)
		(+) Hg	*Somateria mollissima*	(Fenstad et al., 2016b)
		(NF) organic contaminants (PCBs, OCPs, PFAS, PBDEs)	*Somateria mollissima*, *Cepphus grylle*, *Rissa tridactyla*, *Larus hyperboreus*, *Stercorarius parasiticus*, *S. skua*	(Haarr et al., 2018)
		(NF) organic (PAHs), and inorganic (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn) contaminants	*Morus bassanus*	(Champoux et al., 2020)
		(NF) inorganic contaminants (Al, As, Pb, Cd, Cr, Fe, Cu, Mn, Ni, Hg, Se, Ag, Zn)	*Ichthyaetus audouinii*, *Larus michahellis*	(Laranjeiro et al., 2020)
		(↑) hydrogen peroxide following environmental exposure to PBDEs and PCBs	*Larus argentatus*	(Keilen et al., 2022)
DNA repair and cellular apoptosis gene transcription: *P53R2, BAX, GADD45α*	1	(+) organic contaminants (PAHs)	*Nannopterum auritum*	(Wallace et al., 2018)
Erythrocyte nuclear abnormalities (ENAs)	11	NA	*Pygoscelis papua*	(Barbosa et al., 2013)
		NA	*Pygoscelis adeliae*, *P. antarcticus*, *P. papua*	(de Mas et al., 2015)
		NA	*Pygoscelis papua*, *P. adeliae*	(D'Amico et al., 2016)
		NA	*Pygoscelis adeliae*	(Olmastroni et al., 2019)
		(↑) Hg	*Larus fuscus*	(Santos et al., 2020)
		NA	*Larus dominicanus*	(Frixione et al., 2022)
		NA	*Larus dominicanus*	(Frixione et al., 2024)
		(NF) Hg	*Pygoscelis adeliae*	(Olmastroni et al., 2024)
		(NF) inorganic contaminants (Hg, Se, As, Cd, Co, Cr, Cu, Fe, Hg, Mn, Ni, Pb, Sn, Sr, Zn)	*Larus michahellis*, *Ichthyaetus audouinii*, *Calonectris borealis*	(dos Santos et al., 2024)
		(NF) PBDE, MeO-BDEs	*Larus michahellis*, *Ichthyaetus audouinii*	(Veríssimo et al., 2024b)
		(+) PFAS, PFOS	*Eudyptula minor*	(Wells et al., 2024)
Frequency of micronucleated erythrocytes (MNE)	6	NA	*Pygoscelis adeliae*, *P. antarcticus*, *P. papua*	(de Mas et al., 2015)
		NA	*Sterna hirundo*	(Oudi et al., 2019)
		(NF) organic contaminants (OCPs)	*Sula nebouxii*	(Piña-Ortiz et al., 2021)
		NA	*Larus dominicanus*	(Frixione et al., 2022)
		(NF) inorganic contaminants (Hg, Cd)	*Sula nebouxii*, *S. leucogaster*, *Nannopterum auritum*, *Fregata magnificens*, *Pelecanus occidentalis*, *Thalasseus maximus*, *Leucophaeus atricilla*, *Larus heermanni*	(Ceyca-Contreras et al., 2023)
		(NF) Hg	*Pygoscelis adeliae*	(Olmastroni et al., 2024)
Intracellular variation in DNA content – half peak coefficient of variation (HPCV)	1	NA	*Somateria mollissima*	(Matson et al., 2004)
Median molecular length (MML) = relative length of nuclear DNA strands isolated from condensed erythrocytes	1	(-) organic contaminants (naphthalene, PCDDs), (-) inorganic contaminants (Hg, Pb)	*Larus argentatus*	(Fox et al., 2005)
Micronucleated polychromatic erythrocytes (MNPCE)	1	(NF) inorganic contaminants (Hg, Cd)	*Sula nebouxii*, *S. leucogaster*, *Nannopterum auritum*, *Fregata magnificens*, *Pelecanus occidentalis*, *Thalasseus maximus*, *Leucophaeus atricilla*, *Larus heermanni*	(Ceyca-Contreras et al., 2023)
Minisatellite loci mutations	2	NA	*Nannopterum auritum*	(King et al., 2014)
		NA	*Larus argentatus*	(Yauk and Quinn, 1999)
Mutagenicity test using the Ames assay with *Salmonella* microsomes	1	(NF) DDT; (NF) Methylcholanthrene – mimicking environmental PAHs	*Rissa tridactyla*	(Stepanova et al., 1999)

(*continued on next page*)

Table 6 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/−, ↑/↓)	Species	Reference
O-6-methylguanine-DNA methyltransferase (MGMT)		(NF) organic contaminants (52 polycyclic aromatic compounds - PACs)	*Cepphus grylle*	(Zahaby et al., 2025)
Relative telomere length	7	(-) organic contaminants (POPs - oxychlordane)	*Rissa tridactyla*	(Blévin et al., 2016)
		(+) PFAS	*Rissa tridactyla*	(Blévin et al., 2017b)
		(-) organic contaminants (pesticides), (NF) Hg	*Cepphus grylle mandtii*	(Eckbo et al., 2019)
		(+) PFAS (PFNA, PFTeDA)	*Larus hyperboreus*	(Sebastiano et al., 2020)
		(-) Hg	*Calonectris borealis*	(Bauch et al., 2022)
		(NF) Hg	*Alle alle*	(Carravieri et al., 2023)
		(NF) PFNA, PFDA, PFUnDA, PFDoDA, PFTrDA, PFTeDA, PFHxS, L-PFHpS, Br-PFOS, L-PFOS	*Larus argentatus, L. marinus, L. fuscus*	(Sebastiano et al., 2023)
		(+) L-PFOS; (NF) PFNA, PFDA, PFUnDA, PFDoDA, PFTrDA, PFTeDA, PFHxS, L-PFHpS, Br-PFOS	*Larus michahellis*	(Sebastiano et al., 2023)
8-hydroxy-2'-deoxyguanosine (8-OH-dG) = evidence of oxidative DNA damage	1	↑ PBDE-71	*Sterna hirundo*	(Rattner et al., 2013)

micronuclei), as well as HPCV and MML, providing integrative indicators of chromosomal damage. Despite their complementary nature, considerable heterogeneity in assay protocols and reporting metrics was evident across studies (Table 6). This underscores the need for greater standardization of genotoxicity assays and endpoints to improve comparability across colonies, species, and sampling years.

3.4.7. Biomarkers of neurotoxicity

The activities of the enzymes butyrylcholinesterase (BuChE) and acetylcholinesterase (AChE) were the most commonly used biomarkers to assess neurotoxicity in seabirds, but reported in only 3 (1.1%) and 6 (2.2%) studies, respectively (Table 7). Inhibition of these enzymes is a reliable indicative of exposure to neurotoxic contaminants, such as organophosphate and carbamate pesticides (Oropesa et al., 2007). AChE hydrolyses acetylcholine into acetate and choline, thereby regulating neurotransmitter levels and preventing continuous stimulation at cholinergic synapses. BuChE, in turn, plays a protective role by hydrolysing compounds that could inhibit AChE activity (Santos et al., 2019).

Neurotoxicity refers to the direct or indirect effects of chemical substances that impair the nervous system and can be assessed using traditional biomarkers such as AChE and BuChE activities, as well as more recently through omics-based tools like proteomics. In this context, the detection of circulating proteins such as brain-derived neurotrophic factor (BDNF), microtubule-associated protein 1A (MAP1A), and growth-associated protein 43 (GAP43) has been indicative of neurotoxic effects related to plastic ingestion in flesh-footed shearwater (*Ardenna carneipes*) (de Jersey et al., 2025).

Certain chemical compounds exert direct effects on neurons, while others interfere with metabolic processes that are critical for the proper functioning of the nervous system. Some contaminants may impair neural function, whereas others may induce developmental disturbances or cause damage to the adult nervous system (Vellingiri et al., 2022). In addition to the detection of neurotoxic effects through the inhibition of cholinesterases caused by organophosphates and carbamates, exposure to these compounds can be assessed using dialkyl phosphate (DAP) metabolites measured in biological samples; however, these metabolites should be interpreted with caution due to their limited specificity to parent organophosphates and evidence that toxicologically irrelevant DAPs may occur in the environment, necessitating careful consideration of exposure context and levels (Sudakin and Stone, 2011). Moreover, neurotoxicity can also result from changes in sodium channels in neuronal membranes by compounds such as pyrethroids and organochlorines (Colosio et al., 2003).

3.4.8. Biomarkers of cytotoxicity

In seabirds, lactate dehydrogenase (LDH) measurement has been investigated as a biomarker of cytotoxicity caused by aquatic contamination in six studies; however, only two demonstrated significant associations between LDH and organic contaminants, specifically petroleum-derived compounds (Table 8). Golet et al. (2002) observed a positive variation in LDH levels in pigeon guillemot (*Cepphus columba*) from areas exposed to oil spills compared to levels in the same species from uncontaminated areas. Meanwhile, Santos et al. (2019) quantified variation in activity of LDH with the focus on standardising methods to determine plasma biomarker levels and non-lethally monitor the effects of environmental contamination throughout the life cycle of lesser black-backed gull (*Larus fuscus*). LDH is a key enzyme in carbohydrate metabolism, catalysing the reversible conversion of lactate to pyruvate (Diamantino et al., 2001). LDH occurs as multiple isoenzymes with differing tissue distributions; however, most ecotoxicological studies focus on total LDH activity, without resolving isoenzyme profiles or temperature sensitivity of enzyme activity (Bojarski et al., 2025). In birds, LDH plasma activity provides an indication of tissue and/or organ damage, particularly in the liver, and is recognised as a marker of cell death (Barata et al., 2010). Moreover, LDH measurements should be interpreted cautiously in ecotoxicological contexts, particularly when comparing across species, seasons, or studies with differing analytical protocols (Klein et al., 2020). Endogenous and/or exogenous effect of contaminants resulting in cell death in seabirds is thus best assessed using LDH in combination with complementary biochemical or cellular biomarkers.

Six other articles explored cytotoxicity in seabirds, evaluating lysosomal membrane stability (2 studies), neutral lipid content (2 studies), and lipofuscin accumulation (2 studies), among other parameters considered potentially indicative of cellular stress or death (Hegseth et al., 2011c; Hegseth et al., 2014; Table 8).

3.4.9. Biomarkers related to the immune system

Immune function impairment has been recognised as a potential biomarker for examining the impacts of contaminant exposure in seabirds. Among immune-related biomarkers, Smits and Williams (1999) associated an elevated heterophil-to-lymphocyte (H:L) ratio with immunosuppression. Since then, this ratio has been assessed in seabirds as a potential biomarker of ecotoxicity ($n = 17$ articles; 6.2%) (Table 9).

Table 7

Biomarkers related to neurotoxicity in seabirds, screened in studies published between 1976 and 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/−, ↑/↓)	Species	Reference
Acetylcholinesterase (AChE)	6	(↓) organic contaminants (oil)	*Uria aalge*, *Alca torda*	(Oropesa et al., 2007)
		NA	*Morus bassanus*	(Santos et al., 2012)
		NA	*Larus michahellis*	(Morcillo et al., 2018)
		NA	*Larus fuscus*	(Santos et al., 2019)
		(↓) PBDE - polybrominated diphenyl ethers - BDE99 (plasticizer)	*Larus michahellis*, *L. fuscus*	(Veríssimo et al., 2024a)
		(-) PBDE, MeO-BDEs	*Larus michahellis*, *Ichthyaetus audouinii*	(Veríssimo et al., 2024b)
Brain- derived neurotrophic factor (BDNF)/ proteomic	1	(-) plastic ingestion	*Ardenna carneipes*	(de Jersey et al., 2025)
Butyrylcholinesterase (BChE)	3	NA	*Morus bassanus*	(Santos et al., 2012)
		NA	*Larus michahellis*	(Morcillo et al., 2018)
		NA	*Larus fuscus*	(Santos et al., 2019)
Carboxylesterase (CbE)	1	NA	*Larus michahellis*	(Morcillo et al., 2018)
Cholinesterase (ChE)	2	(NF) organic contaminants (oil)	*Cepphus grylle*	(Peakall et al., 1980)
		(↓) PBDE - polybrominated diphenyl ethers - BDE99 (plasticizer)	*Larus michahellis*, *L. fuscus*	(Veríssimo et al., 2024a)
Embryonic neuronal damage (HGEN)	1	(↓) cell viability following exposure to DE-71	*Larus argentatus*	(Crump et al., 2008)
Growth-associated protein 43 (GAP43)/proteomic	1	(+) plastic ingestion	*Ardenna carneipes*	(de Jersey et al., 2025)
Microtubule-associated protein 1A (MAP1A)/ proteomic	1	(+) plastic ingestion	*Ardenna carneipes*	(de Jersey et al., 2025)
N-methyl-D-aspartate (NMDA) glutamate receptor	1	(NF) MeHg	*Uria lomvia*, *Sterna paradisaea*	(Braune et al., 2012)
Muscarinic acetylcholine receptor (mACh)	1	(NF) MeHg	*Uria lomvia*, *Sterna paradisaea*	(Braune et al., 2012)
Propionylthiocholine iodide (PrSCh)	1	NA	*Morus bassanus*	(Santos et al., 2012)

However, positive associations with organic contaminants were significant in only four studies (Finkelstein et al., 2007; Jara-Carrasco et al., 2015; Champoux et al., 2020; Veríssimo et al., 2024b). The limited number of significant correlations may indicate the non-specific stress response, which can be triggered by diverse factors such as infections, environmental changes, toxin exposure, handling-time during biological sample collection, or the bird's age class (Smits and Williams, 1999).

In male eider ducks (*Somateria mollissima*), the H:L ratio was inversely correlated with hepatic Se levels (Wayland et al., 2002), suggesting a potential mitigating effect of this element on immunosuppression caused by chronic stress in birds. However, although the H:L ratio is a useful tool for assessing stress and immunotoxicity in avian species, it should be interpreted alongside other haematological parameters and biomarkers. Evidence showed also that the developmental stage of the birds should be considered to provide a more robust interpretation of the results.

In addition to H:L ratio analyses, immunoglobulins levels in plasma samples have been investigated in seabirds, in special γ-globulins (Igγ; Table 9), which demonstrated a negative association with organic contaminants (oil, PCBs, β-endosulfan) (Sagerup et al., 2014; Dean et al. 2017b; Jara et al., 2018). Leukocyte counts, assessed in 17 studies, showed positive significant increases in response to contaminants such as DDE, organochlorines (OCs), highly persistent pollutants (HPPs), and oil in four of these studies (Table 9). As multiple contaminants can alter immune function, immunological dysfunction may be observed in the absence of other clinical signs of toxicity, with detrimental implications for individual health (Grasman, 2002; Kataoka and Kashiwada, 2021). Consequently, immune function has been widely used to assess contaminant effects in wild birds (Grasman and Fox, 2001; Fair et al., 2003). Indeed, recent studies have revealed that contaminant-induced inhibition of immune responses can compromise individual fitness, reducing long-term survival (Hasselquist and Nilsson, 2012; Nelson-Flower et al., 2023). For decades, evidence has suggested that alterations in the immune system, which affect disease susceptibility, provide sensitive and early indicators of the toxic effects of contaminants (Fairbrother et al., 2004). Immunological disruption induced by contaminants may contribute to disease outbreaks, particularly in species that breed in large colonies and are thus more prone to transmission among physically proximate individuals. The vulnerability of large colonies to infectious disease impact is exemplified by outbreaks of highly pathogenic avian influenza, which have caused devastating consequences in numerous colonies of marine mammals and albatrosses (Banyard et al., 2024). Therefore, despite the lack of specificity of some immune-related biomarkers to particular contaminants, indirect monitoring of avian health remains important, specially within the One Health framework, providing a more holistic assessment of the health status of seabirds and their ecosystems.

3.4.10. Biomarkers of general animal health

Reference values of biomarkers for assessing general health status are scarce for most seabird species. The reviewed studies highlighted the importance of establishing baseline values, in addition to recognising the substantial interspecific variation observed among taxa (e.g., Finkelstein et al., 2007). Table S5 display the associations between aquatic contaminants and parameters of general health, considered as potential ecotoxicological biomarkers. As in mammals, blood biochemistry is widely used in both domestic and wild birds to monitor organ systems and homeostasis, providing an overview of individual health (Maceda-Veiga et al., 2015; Ma et al., 2020). Beyond haematological parameters, 41 publications addressed the assessment of electrolytes, proteins, and biochemical profiles in plasma and/or serum, with these parameters serving as indicators of the health status of individuals. Additionally, some studies have associated these parameters with adverse effects of contaminants (Supplementary Table S5).

Porphyrins levels were investigated in nine studies (3.3%) as another parameter of health status of seabirds. Disturbances in the heme biosynthesis pathway can lead to elevated levels of highly carboxylated porphyrins (HCP) in the liver (Marks, 1985). In free-living birds, exposure to persistent organic pollutants (POPs) is the only known cause of increased HCP (Fox et al., 1988; Kennedy et al., 1998). The toxic effects

Table 8

Biomarkers related to cytotoxicity in seabirds, screened in studies published between 1976 and 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/-, ↑/↓)	Species	Reference
Cell viability determination (cell culture)	1	(-) mix of chemicals: bisphenol S (BPS), bisphenol A (BPA), tris (methylphenyl) phosphate (TMPP), tris(2-butoxyethyl) phosphate (TBOEP), triethyl phosphate (TEP), tris(2,3-dibromopropyl) isocyanurate (TBC), allyl 2,4,6-tribromophenyl ether (ATE), 1,2-dibromo-4-(1,2- dibromoethyl)-cyclohexane (DBE-DBCH), PCB 126, BDE 209, tetradecabromo-1,4-diphenoxybenzene (TeDB-DiPhOBz); tris (1-chloro-2-propyl) phosphate (TCIPP), tris(1,3-dichloro-2-propyl) phosphate (TDCIPP), TCDD	*Nannopterum auritum*	(Crump et al., 2016)
Lactate dehydrogenase (LDH)	6	(NF) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(↑) organic contaminants (oil)	*Cepphus columba*	(Golet et al., 2002)
		(NF) organic contaminants (oil)	*Nannopterum auritum*, *Leucophaeus atricilla*	(Dean et al., 2017b)
		NA	*Larus fuscus*	(Santos et al., 2019)
		(NF) organic (PAHs), inorganic contaminants (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn)	*Morus bassanus*	(Champoux et al., 2020)
		(+) plastic ingestion	*Ardenna carneipes*	(de Jersey et al., 2025)
Lipofuscin	2	(NF) ΣHOC; (+) Cr, Cd, Pb	*Rissa tridactyla*, *Larus argentatus*, *Fulmarus glacialis*	(Hegseth et al., 2011c)
		(↑) ΣHOC	*Larus argentatus*	(Hegseth et al., 2014)
Lysosomal membrane stability	2	(NF) ΣHOC, inorganic contaminants (metals only)	*Rissa tridactyla*, *Larus argentatus*, *Fulmarus glacialis*	(Hegseth et al., 2011c)
		(↓) ΣHOC	*Larus argentatus*	(Hegseth et al., 2014)
Neutral lipids	2	(NF) ΣHOC, inorganic contaminants (metals)	*Rissa tridactyla*, *Larus argentatus*, *Fulmarus glacialis*	(Hegseth et al., 2011c)
		(↓) ΣHOC	*Larus argentatus*	(Hegseth et al., 2014)
Plasma glyceraldehyde- 3- phosphate dehydrogenase (GAPDH), and high mobility group box 1 (HMGB1)/proteomics	1	(+) plastic ingestion	*Ardenna carneipes*	(de Jersey et al., 2025)
Platelet-derived growth factor receptor β (PDGFRβ)	1	(+) plastic ingestion	*Ardenna carneipes*	(de Jersey et al., 2025)

of environmental contaminants on porphyrin metabolism were first observed in humans in the 1960s following episodes of acute intoxication with dioxins (Bleiberg et al., 1964) and hexachlorobenzene (Cam and Nigogosyan, 1963). Different classes of environmental contaminants can interfere with heme biosynthesis in various ways, either through direct interference with enzymes of the biosynthetic pathway or by increasing the oxidation rate of intermediate porphyrinogens, causing alterations in the profile of accumulated or excreted porphyrins (Marks, 1985). Porphyrins can be detected in different biological materials even at very low concentrations and have therefore been proposed as sensitive biomarkers of exposure to both organic and inorganic contaminants in seabirds (Celis et al., 2014; Pérez de Vargas et al., 2020) (Table S5).

Vitamin levels have also been evaluated as indicators of general health in response to contaminant exposures in seabirds (Table S5). Alterations in vitamin concentrations may indicate metabolic imbalances resulting from exposure to environmental contaminants across various physiological systems (Zhou et al., 2024). Between the most studied, vitamin A is stored primarily in the form of retinyl palmitate. Although the mechanisms underlying the disruption of vitamin A homeostasis are not yet fully understood, studies in seabirds have demonstrated that retinol levels may be negatively correlated with PCB concentrations (e.g., Kuzyk et al., 2003; Murvoll et al., 2006; Verreault et al., 2013). Similar patterns of negative correlation have also been observed for α-tocopherol (vitamin E) and organic contaminants (Murvoll et al., 2006; Miljeteig et al., 2012; Allen et al., 2021). Both vitamins A and E play essential roles in maintaining physiological homeostasis, particularly in energy metabolism, immune function, and antioxidant defence (Murvoll et al., 2006). However, several POPs can interfere with vitamin A (retinol) homeostasis in animals (Nilsson and Håkansson, 2002), supporting the use of vitamin levels as health biomarkers.

More recently, the application of omics technologies to assess general health status in seabirds has begun to be explored and may help to overcome intrinsic limitations associated with the evaluation of broader and less specific parameters. Health diagnostics of wildlife have historically relied on the assessment of select serum biomarkers and the identification of contaminant or pathogen burdens within specific tissues as indicators of the extent of injury. However, these approaches fail to capture the physiological response of the individual to stressors, thereby restricting the scope of interpretation. Gene-based health diagnostics offer an opportunity for an alternative, whole-system, or holistic assessment of health, not only in individuals or populations but potentially at the ecosystem level (Bowen et al., 2022; de Jersey et al., 2025).

Table 9
Biomarkers related to the immune system in seabirds, screened in studies published between 1976 and 2025. The number of articles (*n*) that investigated each biomarker is shown. Associations between biomarkers and contaminants are represented by positive (+) or negative (−) correlations, or by increases (↑) or decreases (↓) in biomarker levels compared to a control group. NF (Not Found) indicates the absence of significant associations between biomarkers and contaminants, while NA (Not Applicable) refers to articles that did not directly investigate associations between biomarkers and contaminants. Gene names are presented in italics.

Biomarker	*n*	Association with contaminant(s) (+/−, ↑/↓)	Species	Reference
Albumin:globulin ratio	6	(NF) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(NF) organic contaminants (oil)	*Nannopterum auritum, Leucophaeus atricilla*	(Dean et al., 2017b)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017a)
		(+) organic (C2-Benzo[a]anth/Chry, 2,6-Dimethyl naph), (NF) PAHs, inorganic (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn) contaminants	*Morus bassanus*	(Champoux et al., 2020)
		NA	*Larus atlanticus*	(García et al., 2023)
		NA	*Cerorhinca monocerata*	(Lee et al., 2024)
Antibody response to diphtheria toxoid	1	(-) organic contaminants (HCB, oxichlordane)	*Larus hyperboreus*	(Bustnes et al., 2004)
Heterophil:lymphocyte ratio (H:L)	17	(-) Se	*Somateria mollissima*	(Wayland et al., 2002)
		(+) organic (organochlorines), (NF), inorganic (Ag, Cd, Sn, Pb, Cr, Ni, Cu, Zn, As, Se, Hg total) contaminants	*Phoebastria nigripes*	(Finkelstein et al., 2007)
		(NF) PCBs, OCs	*Fulmarus glacialis*	(Mallory et al., 2007)
		(NF) organic contaminants (OCs, PCBs, PCDDs, PCDFs, PBDEs, PAHs)	*Melanitta perspicillata*	(Wilson et al., 2010)
		NA	*Pygoscelis papua*	(Barbosa et al., 2013)
		(+) organic contaminants (DDTs, PCBs); (NF) HCB, α-endosulfan, β-endosulfan	*Pygoscelis antarcticus*	(Jara-Carrasco et al., 2015)
		NA	*Spheniscus magellanicus*	(Carabajal et al., 2016)
		NA	*Pygoscelis papua, P. adeliae*	(D'Amico et al., 2016)
		NA	*Pygoscelis adeliae*	(Olmastroni et al., 2019)
		(-) organic (PAHs); (NF) inorganic (As, Ba, Cd, Cu, Fe, Mn, Mo, Ni, Pb, Rb, Se, Sn, Sr, V, Zn) contaminants	*Morus bassanus*	(Champoux et al., 2020)
		(NF) organic contaminants (OCP)	*Sula nebouxii*	(Piña-Ortiz et al., 2021)
		NA	*Larus atlanticus*	(García et al., 2023)
		(NF) organic contaminants (PAHs)	*Pelecanus occidentalis*	(Jodice et al., 2023)
		(NF) Hg	*Pygoscelis adelia*	(Olmastroni et al., 2024)
		(NF) Inorganic contaminants (Hg, Se, As, Cd, Co, Cr, Cu, Fe, Hg, Mn, Ni, Pb, Sn, Sr, Zn)	*Larus michahellis, Ichthyaetus audouinii, Calonectris borealis*	(dos Santos et al., 2024)
		(-) PBDE, MeO-BDEs	*Larus michahellis, Ichthyaetus audouinii*	(Veríssimo et al., 2024b)
		(NF) PFAS, PFOS	*Eudyptula minor*	(Wells et al., 2024)
IgG titres	1	(+) organic contaminants (PCBs, DDE)	*Sterna caspia*	(Grasman and Fox, 2001)
Interleukin 16 (IL16)	1	(NF) organic contaminants (52 polycyclic aromatic compounds - PACs)	*Cepphus grylle*	(Zahaby et al., 2025)
Lymphocyte proliferation - cell culture	2	(NF) PCBs, PCDD, TCDD	*Larus argentatus*	(Grasman et al., 2013)
		(NF) organic contaminants (crude oil and photoactivated oil exposure)	*Uria aalge,* *Fratercula cirrhata,* *F. corniculata*	(Counihan et al., 2023)
Macrophage activity and hydrogen peroxide production - cell culture exposed to oil	1	(↑) organic contaminants (crude oil and photoactivated oil exposure)	*Uria aalge, Fratercula cirrhata, F. corniculata*	(Counihan et al., 2023)
Macrophage phagocytosis	1	(-) Hg, (NF) organic (PCBs, DDTs, Chlordanes, HCB), (NF) inorganic (Ag, Cd, Pb, Cr, Ni, Zn, As, Se) contaminants	*Phoebastria nigripes*	(Finkelstein et al., 2007)
Macrophage phagocytosis (cell culture)	1	(↓) organic contaminants (crude oil and photoactivated oil exposure)	*Uria aalge, Fratercula cirrhata, F. corniculata*	(Counihan et al., 2023)
Mitogen-induced T lymphocyte proliferation	1	(+) organic (organochlorines), (NF) inorganic (Ag, Cd, Sn, Pb, Cr, Ni, Cu, Zn, As, Se, Hg total) contaminants	*Phoebastria nigripes*	(Finkelstein et al., 2007)
Phytohemagglutinin (PHA) skin response	2	(-) organic contaminants (PCBs, DDE)	*Sterna caspia*	(Grasman and Fox, 2001)
		(-) PCBs, PCDD, TCDD	*Larus argentatus*	(Grasman et al., 2013)

(*continued on next page*)

Table 9 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/−, ↑/↓)	Species	Reference
Total antibody titres (IgM + IgG)	1	(+) organic contaminants (PCBs, DDE)	*Sterna caspia*	(Grasman and Fox, 2001)
Total leucocytes (hemogram - white blood cell count)	17	(+) p,p'-DDE	*Larus argentatus*	(Grasman et al., 2000)
		(NF) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(NF) organic contaminants (PCBs, 21 pesticides)	*Sterna caspia*	(Grasman and Fox, 2001)
		(+) OCs	*Larus hyperboreus*	(Bustnes et al., 2004)
		(NF) PCB-99, -118, -138, -153, -170, -180, HCB, β-HCH, oxyilordan, p,p'-DDE	*Larus marinus*	(Bustnes et al., 2007)
		(NF) organic (PCBs, DDTs, Chlordanes, HCB), (NF) inorganic (Ag, Cd, Sn, Pb, Cr, Ni, Cu, Zn, As, Se, Hg total) contaminants	*Phoebastria nigripes*	(Finkelstein et al., 2007)
		(+) organic contaminants (oil)	*Sterna hirundo*	(Nisbet et al., 2015)
		NA	*Spheniscus magellanicus*	(Carabajal et al., 2016)
		NA	*Pygoscelis papua, P. adeliae*	(D'Amico et al., 2016)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017b)
		NA	*Pygoscelis adeliae*	(Olmastroni et al., 2019)
		(+) organic (PAHs), (NF) inorganic (As, Cu, Fe, Ni, Rb, Se, V, Zn in blood; As, Ba, Cd, Cu, Fe, Mn, Mo, Pb, Rb, Se, Sn, Sr, V, Zn in feathers) contaminants	*Morus bassanus*	(Champoux et al., 2020)
		NA	*Larus atlanticus*	(García et al., 2023)
		(NF) Hg	*Pygoscelis adeliae*	(Olmastroni et al., 2024)
		(NF) inorganic contaminants (Hg, Se, As, Cd, Co, Cr, Cu, Fe, Hg, Mn, Ni, Pb, Sn, Sr, Zn)	*Larus michahellis, Ichthyaetus audouinii, Calonectris borealis*	(dos Santos et al., 2024)
		(-) PBDE, MeO-BDEs	*Larus michahellis, Ichthyaetus audouinii*	(Veríssimo et al., 2024b)
		(NF) PFAS, PFOS	*Eudyptula minor*	(Wells et al., 2024)
α-1-Globulins	5	(NF) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(↑) aviation fuel – JP-1, Polar Diesel	*Pygoscelis adeliae*	(Najle et al., 2006)
		(↑) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017a)
		(NF) organic contaminants (oil)	*Nannopterum auritum, Leucophaeus atricilla*	(Dean et al., 2017b)
		NA	*Cerorhinca monocerata*	(Lee et al., 2024)
α-2-Globulins	5	(NF) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(↑) aviation fuel – JP-1, polar diesel	*Pygoscelis adeliae*	(Najle et al., 2006)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017a)
		(↓) organic contaminants (oil)	*Nannopterum auritum, Leucophaeus atricilla*	(Dean et al., 2017b)
		NA	*Cerorhinca monocerata*	(Lee et al., 2024)
β-Globulins	5	(NF) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(↑) trimethyltin (TMT)	*Pygoscelis papua*	(Najle et al., 2006)
		(↓) aviation fuel – JP-1, polar diesel	*Pygoscelis adeliae*	(Najle et al., 2006)
		(NF) organic contaminants (oil)	*Nannopterum auritum, Leucophaeus atricilla*	(Dean et al., 2017b)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017a)
		NA	*Cerorhinca monocerata*	(Lee et al., 2024)
γ-globulins (gamma-globulins)	12	(NF) organic contaminants (oil)	*Cepphus columba*	(Seiser et al., 2000)
		(↓) aviation fuel – JP-1, Polar Diesel	*Pygoscelis adeliae*	(Najle et al., 2006)
		(NF) organic contaminants (PCBs, PBDEs)	*Stercorarius skua*	(Bourgeon et al., 2012)
		NA	*Pygoscelis adeliae, P. antarctica, P. papua*	(Larsen et al., 2012)

(*continued on next page*)

Table 9 (*continued*)

Biomarker	*n*	Association with contaminant(s) (+/−, ↑/↓)	Species	Reference
		NA	*Pygoscelis papua*	(Barbosa et al., 2013)
		(NF) HCB, oxychlordane, p,p'-DDE, PCB-28, -99, -101, -118, -138, -153, -170, -180, PBDE-47, -99, -100, -153, -154	*Rissa tridactyla*	(Sagerup et al., 2014)
		(-) PCB-170, -180 in males; (NF) HCB, oxychlordane, p,p'-DDE, PCB-28, -99, -101, -118, -138, -153, PBDE-47, -99, -100, -153, -154 in males; (+) HCB, oxychlordane, PCB-28,-99, -170, -180 in females; (NF) p,p'-DDE, PCB-101, -118, -138, -153; PBDE-47, -99, -100, -153 in females	*Fratercula arctica*	(Sagerup et al., 2014)
		(NF) inorganic contaminants (Hg, Pb)	*Somateria mollissima*	(Provencher et al., 2016)
		(NF) organic contaminants (oil)	*Nannopterum auritum*, *Leucophaeus atricilla*	(Dean et al., 2017b)
		(↓) organic contaminants (oil)	*Nannopterum auritum*	(Dean et al., 2017a)
		(-) PCB-138, PCB-180, β-endosulfan	*Pygoscelis antarcticus*	(Jara et al., 2018)
		(-) THg	*Stercorarius antarcticus*	(Ibañez et al., 2024)
		NA	*Cerorhinca monocerata*	(Lee et al., 2024)

3.5. *Critical analysis of gaps in the use of biomarkers in seabirds*

Considering the publications reviewed herein, it is noteworthy that seabirds are excellent models for assessing the status of marine ecosystems, owing to their long lifespans, wide geographic distribution, and position as apex predators within the trophic chain (Burger and Gochfeld, 2004). These characteristics render them highly susceptible to the processes of bioaccumulation and biomagnification of contaminants along the food web (Lima et al., 2023). However, it is important to emphasise that seabirds do not constitute a homogeneous group regarding geographic distribution, habitat use, exposure pathways, and susceptibility to contaminants. There is increasing evidence of interspecific variation in tolerance, metabolism, and bioaccumulation of xenobiotics, which may reflect evolutionary, ecological, and physiological differences. Coastal species, for example, tend to have greater contact with urban and industrial contaminants, whereas pelagic and oceanic species may be more vulnerable to contaminants transported over long distances by currents and to the ingestion of microplastics. Nonetheless, there is a clear bias in the existing bibliography, which is concentrated on a few emblematic species in detriment of other, less-represented orders, such as many threatened Procellariiformes, Sphenisciformes, tropical seabirds, or other species from the Southern Hemisphere.

The impact of pollution from diffuse sources in the marine environment is difficult to comprehend, as global contaminants are generally ubiquitous and found at elevated concentrations in marine predators with extensive foraging ranges (Zhang et al., 2024). Seabirds, in turn, are exposed to a wide variety of xenobiotics, including complex mixtures of organic contaminants, metal(loid)s, nano-, micro- and macroplastics, and emerging contaminants, originating from multiple anthropogenic sources that converge in the marine environment. Although pollution is recognised as one of the main threats to the conservation of global marine avifauna, studies aimed at characterising the biological responses of these species to chemical exposure remain scarce and unevenly distributed across taxonomic groups and oceanic regions. Based on the results of this review, a significant lack of studies on biomarkers in seabirds from the Global South was identified, with migratory species present in Southern Hemisphere countries being investigated far less intensively than other species in the Northern Hemisphere. In Latin America and Africa, qualitative and quantitative determination of contaminant concentrations in seabirds currently predominate (e.g., Lima et al., 2023), while few studies have been conducted to more precisely assess the toxic effects of these contaminants (Lomartire et al., 2021; Kreitsberg et al., 2023). Reducing the geographic imbalance in seabird biomonitoring will require coordinated international efforts that integrate capacity building, open data-sharing practices, and equitable research partnerships (Ruelas-Inzunza et al., 2023). These strategies are particularly critical for translating biomarker evidence into effective conservation actions in regions where marine pollution pressures are intensifying but empirical data remain scarce.

Nonetheless, to address the growing problem of environmental pollution, the use of biomarkers of exposure and effects of aquatic contamination has proven promising over recent decades, with an increasing number of studies involving seabirds. The investigation of these biomarkers may represent an efficient and cost-effective approach to identifying early signs of adverse effects of pollutants on the health of populations and their environments (e.g., Zahaby et al., 2021; Rattner et al., 2024). Across biomarker classes in our review, tissue choice critically shaped both interpretability and feasibility, with blood-based matrices emerging as the most informative non-lethal option for monitoring oxidative stress, immune function and endocrine disruption biomarker responses. Liver samples provide higher mechanistic resolution for detoxification pathways, largely in post-mortem contexts, and feathers offering a non-invasive matrix for long-term exposure and limited sensitivity to short-term effects.

For decades, the biotransformation system in response to environmental contamination has stood out as one of the most extensively studied biomarkers in seabirds, particularly the enzymes of the cytochrome P450 complex. However, over the years, pathways related to homeostasis have increasingly been incorporated, which may deepen the understanding of contaminant effects on the health of these animals and reveal differences in vulnerability among species, sexes, and age classes. Publications analysed indicate that results can vary considerably depending on the biomarkers selected, species, sex, age, seasonality, and the chemical contaminant, whether jointly or individually (e.g., Helgason et al., 2010a; Routti et al., 2013). However, results obtained from animals sampled in natural environments tend to exhibit complex variations influenced by multiple environmental and ecological factors that may interact with one another (Kreitsberg et al., 2023).

With recent advances in molecular studies and available technologies, the application of omics methods, such as transcriptomic and proteomic techniques is a strategy that substantially accelerates the identification of biomarkers of exposure, effect, and/or susceptibility. Transcriptomic studies, for example, enable the identification of coding genes across different species by assessing differentially transcribed genes among individuals exposed to varying levels of environmental contamination (e.g., Piazza et al., 2024). Thus, it becomes feasible to estimate homeostasis and transcriptional alterations resulting from exogenous challenges on a broader scale (Kreitsberg et al., 2023), which can be valuable for biomonitoring and regulatory decision-making

(Serafini et al., 2024).

Conversely, over the past decades, there has been a shift in the focus of research related to biomarkers in seabirds and specific contaminants. While classical contaminants such as persistent organic pollutants, including PCBs and organochlorine pesticides, dominated early studies, biomarker research has progressively turned towards emerging contaminants, such as perfluoroalkyl substances, brominated flame retardants, pharmaceuticals and personal care products, as well as plastics in their various forms (nano, micro, meso and macroplastics, and their additives). Concurrently, contaminants derived from the petroleum industry and mining continue to be of significant concern in certain regions. Therefore, the next recommended step following this systematic review is to integrate biomarker effect studies with mapping of critical areas with known contamination histories from specific sources (e.g., urban plumes, plastic accumulation zones, petroleum extraction sites, active mining regions). Such broader mapping efforts may serve as a starting point for planning biomarker studies aimed at assessing population-level impacts and elucidating mechanisms of toxicity (e.g., Clark et al., 2023).

In a scenario involving multiple variables and complexity not comparable to experimental studies, linear statistical analyses, which have been used for decades, may not be adequate when considering more comprehensive datasets that relate contaminants, biomarkers, and biological and ecological variables affecting organism health in natural environments. Indeed, for about a decade, it has been recognised that relationships between contaminants and biological responses frequently follow non-linear patterns within the field of ecotoxicology (e.g., Serafini et al., 2024). In this context, statistical models, such as Generalised Linear Models (GLMs), Generalized Additive Models (GAMs), and other approaches, stand out as particularly useful tools for ecotoxicological studies, as they enable the simultaneous evaluation of non-linear and complex relationships among multiple dependent and independent variables (Tredennick et al., 2021). Although the present systematic review assessed measured values from a suit of studies, we concluded that the effect size, via meta-analysis, could not be performed given the limited number of studies per taxonomic group and the substantial potential for variation. While meta-analytical studies are common in clinical medicine, this article establishes the foundations, the compilation of initial data, from which such an analysis could eventually emerge, as gaps are progressively filled and more studies per species and biomarker become available to allow such comparisons.

In this regard, advances in sampling techniques would be fundamental to linking biomarkers with the impacts of diffuse contaminants in the environment over time, providing critical support for more precautionary decision-making by managers and environmental agencies. Research in ecological settings should prioritise methods that investigate the sublethal effects of contaminants on the health of seabirds, preferably employing biomarkers assessed through non-lethal approaches. This would enable early interventions, as many impacts manifest only in the long term, including transgenerational effects. However, it is crucial that these findings are connected to regulatory frameworks, as monitoring such effects can underpin guidelines and environmental management at regional, national, and even global scales, taking into account the migratory patterns of many seabird species.

4. Conclusions

Our review documents a broad range of biomarkers of exposure and effect to anthropogenic chemical contaminants in seabirds worldwide. Although some of the studies addressed point-source oil spills or areas with higher contamination than others, pollution from diffuse sources is currently the foremost international concern, particularly in regions where seabirds and humans may be at risk due to contamination of the marine food web.

Based on the results and insights from this review, we propose that future studies prioritise an integrated approach to environmental risk assessment and seabird conservation, emphasising the use of aquatic contamination biomarkers for biomonitoring in order to inform public policies, guide management strategies, and identify priority substances for environmental regulation. In this context, it becomes essential to promote regionally and taxonomically comprehensive studies, with a focus on sentinel species that reflect different ecological strategies and risk profiles. The integration of omics tools, bioaccumulation metrics, and demographic data over the long term may enable the identification of sensitive and reproducible biological responses, thereby facilitating the development of robust environmental health indicators tailored to the global marine context. Moreover, recent advances in functional genomics offer promising opportunities to unravel adaptive mechanisms and long-term pollution effects on marine biodiversity.

The pronounced hemispheric bias observed in sampling locations highlights the need for strategic capacity building in the Southern Hemisphere, where seabirds are increasingly exposed to anthropogenic pressures yet remain underrepresented in biomarkers research. Strengthening regional expertise and promoting standardized protocols will be essential to reduce geographic disparities and support globally comparable assessments of marine contamination effects.

Finally, based on the evidence synthesised in this review, we propose the following priorities for policy makers and marine monitoring programmes over the next 1–3 years: (1) adopt core biomarker panels aligned with monitoring objectives, prioritising xenobiotic biotransformation and metal detoxification (e.g., CYP1A, MTs), endocrine disruption (e.g., CORT, thyroid hormones, *ESR*), and immune function (e.g., H:L ratio and immunoglobulins) as complementary indicators of exposure and sublethal effects; (2) prioritise non-lethal, blood-based sampling protocols to enable repeated assessments across seasons and years, while maintaining opportunistic use of internal tissues (liver) to support mechanistic interpretation where ethically and logistically feasible; and (3) strategically expand biomonitoring to underrepresented regions and species, particularly in the Southern Hemisphere, through capacity building, harmonised protocols, and open data-sharing frameworks that facilitate comparability across colonies, jurisdictions, and time.

CRediT authorship contribution statement

Patricia Pereira Serafini: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Vera Helena Vidal Dias:** Writing – review & editing, Software, Methodology, Data curation, Conceptualization. **Daína Lima:** Writing – review & editing, Methodology, Formal analysis. **Deivid Medeiros da Costa:** Writing – review & editing, Methodology, Formal analysis. **Guilherme de Espindola da Silveira:** Writing – review & editing, Methodology, Formal analysis. **Marcia Eduarda Geraldo:** Writing – review & editing, Methodology, Formal analysis. **Vanessa Schadeck Deconto:** Writing – review & editing, Methodology, Formal analysis. **Leandro Bugoni:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Afonso Celso Dias Bainy:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Karim Hahn Lüchmann:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2026.119234.

Data availability

Data will be made available on request.

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