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TRANSFERABLE STRESSORS IN SMALL CETACEANS: HISTORICAL STATUS, CURRENT TRENDS AND FUTURE DIRECTIONS

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Abstract Cetaceans face a wide range of natural and anthropogenic pressures that can impact on the viability of populations. Assessments of cetacean populations frequently consider single non-transferable stressors with direct effects on survival, such as fisheries bycatch, but more rarely consider stressors transmitted between animals via the food web, through close physical contact and from mother to calf. Transferable stressors can affect population dynamics via sub-lethal or lethal effects on individuals. This literature review concerns transferable stressors in small cetaceans, including their transfer routes, prevalence and effects on individuals and populations, as well as the cumulative effects of multiple stressors. We focus particularly on transferable stressors frequently affecting common small cetaceans (harbour porpoises and common, bottlenose and striped dolphins) in European waters. These stressors include harmful algal blooms, viruses (e.g. *Morbillivirus*), bacteria (e.g. *Brucella*), parasites (e.g. *Anisakis* and lungworms), organic and inorganic contaminants and microplastics. Patterns and trends in prevalence are compared across species, areas and stressors, implications for conservation are considered and knowledge gaps are identified. Further research is needed on dose–response relationships and mechanisms of stressor interactions. While available methods have permitted a better understanding of the adverse effects of transferable stressors, integration into population assessments and consequent management plans remains a challenge.

Keywords: Transference; Stressors; Dolphins; Virus; Bacteria; Parasites; Harmful Algal Blooms; Contaminants; Microplastics; Combined Effects

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Introduction

Cetacean populations face a wide range of anthropogenic threats, including fisheries interactions (especially mortality due to bycatch but also prey depletion, disturbance and displacement from foraging areas), marine pollution, climate change, habitat loss, eutrophication, disturbance and ship strikes (Harwood 2001, Avila et al. 2018, Nicol et al. 2020). To these may be added the effects of threats of natural origin such as pathogens (bacteria, viruses, fungi and parasites), the occurrence, prevalence and pathogenicity of which may also be related directly or indirectly to human activity (Johnson et al. 2009, Van Bressem et al. 2009a). In many cases, the negative effects on cetaceans are sub-lethal, e.g. compromised immune function and reduced fertility, and are reflected in individual health, growth and fecundity. In the most extreme cases, the effects could be lethal; for example, outbreaks of some pathogens such as morbillivirus can cause high and widespread mortality. In reality, multiple stressors act in combination, and the resulting effects may be additive, synergistic or antagonist.

Transferable stressors are those that can be transferred from organism to organism both within and between species, and may be of either natural or anthropogenic origin. Common routes of transfer include via the food web (prey–predator), from mother to calf via pregnancy and lactation and through close contact (with the skin, exhaled breath, body fluids, etc., during socialising, foraging in groups, mating, etc.). Transfer routes can be classified as ‘vertical’ or ‘horizontal’, although definitions could differ according to whether transfer is understood as occurring between generations or between trophic levels. Fine (1975) defined ‘vertical’ transfer as transfer across generations from mother to calf, and ‘horizontal’ transfer as transfer between individuals of the same generation. Another useful definition could refer to ‘vertical’ transfer between trophic levels and ‘horizontal’ transfer within trophic levels, with the former naturally focusing on transfers from prey to predator (and arguably also mother to calf) and the latter on transfers resulting from close contact. In this review, we will refer to the specific transfer routes, usually without reference to whether they are vertical or horizontal transfers.

The most important transfer route for many pathogens and contaminants is via trophic links. Feeding not only confers energetic and nutritional benefits, but also incurs energetic costs of prey capture and handling, associated risks of injury or predation, and facilitates exposure to transferable stressors (Ma & Li 2017). Some chemical pollutants, especially persistent organic pollutants (POPs), bioaccumulate in animal tissues, and as such, their individual level effects are also cumulative over time. They can also biomagnify as they pass through the food chain (O’Shea & Tanabe 2002). In addition, certain stressors, again notably including POPs, are maternally transmitted during pregnancy and lactation (the latter can be considered as a special case of trophic transfer, for example, in studies of diet based on stable isotopes analysis such as Borrell et al. (2016)). Understanding the transfer process for these stressors and quantifying their effects can be challenging. However, incorporating transferable stressors into food web models and population or ecosystem assessments, which usually consider only direct sources of mortality to cetaceans (e.g. bycatch and ship strikes), could help provide new insights into the status of cetacean populations and, more generally, ecosystem function. It should be noted that the development of the ‘Ecotracer’ plug-in for Ecopath with Ecosim models specifically addresses this ambition (Walters & Christensen 2018).

Our focus here is on transferable stressors affecting small cetaceans (hereafter referring to small dolphins of the family Delphinidae and to porpoises of the family Phocoenidae). Emphasis is given to European Atlantic and Mediterranean waters, as well as four of the most abundant and well-studied species in the region, namely the bottlenose dolphin (*Tursiops truncatus*), the common dolphin (*Delphinus delphis*), the striped dolphin (*Stenella coeruleoalba*) and the harbour porpoise (*Phocoena phocoena*). Cetaceans are considered sentinel species, and as such provide early warnings of existing or emerging health hazards in oceanic and coastal environments (Bossart 2011, Schwacke et al. 2014). All cetaceans in European waters are strictly protected under European Union directives, national law and international agreements. The status of cetaceans is routinely monitored and assessed, for example, following requirements of the Habitats Directive (HD) and Marine Strategy Framework Directive (MSFD), and in the context of the Common Fisheries Policy and associated Data Collection Framework (under which fishery bycatch mortality is monitored).

Bottlenose, common and striped dolphins are classified as 'least concern' at the European level by the IUCN (Genov 2023 a,b,c), with subpopulations in the Mediterranean considered as 'endangered' and 'critically endangered' (Bearzi et al. 2020, 2022 a,b, Gonzalvo & Notarbartolo Di Sciara 2021). Assessments at a country-level under the HD and MSFD generally consider the conservation status of both bottlenose and common dolphins to be poor, which is mainly due to high bycatch mortality in the case of the common dolphin. Harbour porpoises are listed as 'vulnerable' at the European level (Sharpe & Berggren 2023), and the Baltic Sea subpopulation is considered 'critically endangered' (Hammond et al. 2008). A separate IUCN assessment is currently missing for the Iberian porpoise, which forms a morphologically and genetically distinct population, likely belonging to a new subspecies (Fontaine et al. 2007, 2010, 2014, Fontaine 2016, Ben Chehida et al. 2021 a,b). This subspecies is listed as 'critically endangered' by Portugal (Torres-Pereira et al. 2023) and 'in danger of extinction' by Spain (Orden TED/1126/2020) due to its small population size and suspected high bycatch mortality. The conservation of harbour porpoises in Europe is considered to be failing despite the legislation existing to protect it (Carlén et al. 2021).

Information on stressors can also provide other kinds of ecological insights, including information on population structure, movements and feeding habits. For example, *Brucella*, and pathogens in general, may be complementary bioindicators of the ecology of the infected species and can provide information about different aspects such as the distribution, migration, diet and behaviour of marine megafauna at individual, population and ecosystem levels (Sonne et al. 2020).

The effects of single stressors, usually non-transferable, that cause direct mortality of individuals, such as fishery bycatch, on the above-mentioned species are well documented in European waters (e.g. Peltier et al. 2021, Pierce et al. 2022). However, the importance of transferable stressors is a topic that requires more attention in all cetaceans. In addition, while the effects of single stressors (e.g. exposure to polychlorinated biphenyls (PCBs)) on individuals may be well-documented, quantified and assessed, the cumulative effects of multiple stressors at the population and ecosystem levels are less well known. Even though it is challenging, integration of such effects is needed for a complete assessment of the health of populations and, ultimately, the ecosystem.

The present review focuses on gathering published information about natural and anthropogenic transferable stressors affecting small cetaceans. These transferable stressors include harmful algal blooms, viruses (e.g. morbillivirus), bacteria (e.g. *Brucella*), parasites (e.g. nematodes of the digestive and respiratory systems, namely *Anisakis* and lungworms, respectively), organic and inorganic chemical contaminants and microplastics.

We compiled information published worldwide on the transfer routes, prevalence, rates of bioaccumulation and available evidence on impacts (at individual and population levels) of these stressors. Nonetheless, we focused particularly on common small cetacean species inhabiting European and Mediterranean waters, including bottlenose dolphin, common dolphin, striped dolphin and harbour porpoise, compiling data on levels and trends for these species. We also considered the cumulative effects of multiple transferable stressors, and the cumulative effects of transferable and non-transferable stressors, as well as available methods for understanding, quantifying and predicting combined (additive, synergistic or antagonistic) effects on individuals and populations. Approaches (and possible approaches) to studying, assessing and mitigating adverse effects of the various types of stressors are described. Finally, the most important knowledge gaps are highlighted, and areas for future research are suggested.

Methodology

We initially followed the recommendations for transparent reporting of a systematic review of the available literature using Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) (Page et al. 2021). Literature was systematically identified using the academic search engines Scopus and Web of Science (WoS, all collections). A comprehensive set of search terms under the search string '(terms category Species) AND (terms category Stressor) AND (terms category Area) AND (terms category Type of study)' was used (Table 1), searching within the title, abstract and keywords in Scopus, as well as within the topic in Web of Science (WoS). The resulting list was filtered to remove less relevant articles using several exclusion criteria (Table S1). These exclusion criteria were agreed by the co-authors and tested on random subsets of papers gathered by the systematic search to ensure their efficacy. Of 1364 publications published up to and in 2022 obtained by the systematic searching, after applying the exclusion criteria and removing duplicated references, only 38.5% of these references were finally cited in this review.

It became apparent that some relevant papers known to the authors were not included following this methodology, usually because search terms appeared in the main text but not in the title, keywords or abstract. Therefore, an additional set of references was compiled based on the prior knowledge of the authors, references within papers from the systematic search and non-systematic searches, e.g. via Science Direct WoS, Scopus and Google Scholar. Based on the authors' knowledge,

Table 1 Categories and Keywords Used for the Systematic Literature Search

Category	Details
Species	'Delphinus' or 'Phocoena' or 'dolphin*' or 'porpoise*' or 'cetacean*' or 'Odontocet*' or 'Tursiops' or 'Stenella' or 'bottlenose dolphin* or 'striped dolphin*' or 'common dolphin*'
Stressor	'contaminant*' or 'pollutant*' or 'persistent organic pollutant*' or 'pah*' or 'pcb*' or 'pbde*' or 'bfr*' or 'ddt*' or 'dde*' or 'insecticid*' or 'dioxin*' or 'pcdd*' or 'pcdf*' or 'hcb*' or 'hbcd*' or 'hbde' or 'pfa*' or 'pfo*' or 'opfr*' or 'flame retardant*' or 'hfr*' or 'plastic*' or 'toxic element*' or 'trace element*' or 'heavy metal*' or 'Hg' or 'Cd' or 'Pb' or 'litter ' or 'debris' or 'plastic' or 'microplastic*' or 'mps' or 'synthetic particles' or 'fibres' or 'fragments' or 'hab' or 'harmful algal bloom*' or 'psp*' or 'shellfish poison*' or 'pathogen*' or 'virus*' or 'bacteria*' or 'parasite*' or 'brucella' or 'Escherichia coli' or 'tsd' or 'morbillivirus' or 'toxoplasma' or 'papillomavirus*' or 'respirovirus' or 'influenza' or 'arbovirus' or 'herpesvirus' or 'poxvirus' or 'adenovirus' or 'coronavirus' or 'calicivirus' or 'lobomicosis' or 'Anisakis' or 'nematode*' or 'pseudoterranova' or 'lungworm*' or 'Stenurus ' or 'Halocercus' or 'Pseudaliid*'
Area	'Europe*' or 'France' or 'Spain' or 'Portugal' or 'Netherlands' or 'United Kingdom' or 'Belgium' or 'Ireland' or 'Norway' or 'Sweden' or 'Germany' or 'Iceland' or 'Denmark' or 'Greenland' or 'England' or 'Wales' or 'Scotland' or 'Britain' or 'British Isles' or 'Slovenia' or 'Croatia' or 'Bosnia' or 'Montenegro' or 'Albania' or 'Greece' or 'Cyprus' or 'Turkey' or 'Italy' or 'Mediterranean Sea' or 'Northeast Atlantic'
Type of study	'bioaccumulation*' or 'model*' or 'framework' or 'risk*' or 'cumulative' or 'synergy*' or 'transfer*' or 'assess*' or 'impact*' or 'effect*'

All the terms of each category were included separated by 'OR', and different categories were separated by 'AND'.
In the search engines, the asterisk (*) replaces letters at the end of the keywords.

we included additional published studies from the Iberian Peninsula, as well as from new data analysis in the area.

We classified the stressors mainly according to whether their origin is usually 'natural' (e.g. harmful algal blooms, viruses – in particular Morbillivirus, bacteria – in particular *Brucella*, parasites – in particular *Anisakis* and lungworms) or anthropogenic (persistent organic pollutants, inorganic contaminants and microplastics). We focused on harbour porpoise, common, bottlenose and striped dolphins in European waters. The reviewed information was summarised by topics in the following sections:

a. Specific introduction to the groups and single stressors is provided.
b. Transmission routes and rates.
c. Levels and/or trends observed over time.
d. Effects and/or thresholds for adverse health effects.
e. Persistence and prevalence of each stressor. If documented, resistance to stressors shown by cetaceans is noted.
f. Possible reduction or mitigation measures and research needs recommended for future steps.

Then, information on the combined effects of multiple transferable stressors was compiled into the following topics:

- Introduction of combined effects and their study.
- Theoretic classification of combined effects and a generic example of possible nexus among stressors in a realistic scenario.
- Published evidences of effects resulting from the combination of two or more stressors.
- Information on interaction mechanisms between stressors.
- Summary of the proposed conceptual approaches and other methodologies for the understanding, and qualitative and quantitative assessment of the combined effects of multiple stressors on individuals, populations and ecosystems.

Transferable stressors of natural origin: pathogens and HABs

Infections with pathogens such as viruses, bacteria, fungi and parasites, as well as exposure to biotoxins, can contribute to poor health and are implicated in a substantial proportion of deaths in stranded animals (Van Bressem et al. 1999, Pearson et al. 2010, Cook et al. 2015). For example, in the Canary Islands and along the Mediterranean coast, pathologies associated with pathogens and biotoxins have been implicated in the death of most of the stranded cetaceans for which a cause of death could be established (Arbelo et al. 2013, Díaz-Delgado et al. 2018, Cuvertoret-Sanz et al. 2020). Different pathogenic organisms and biotoxins can have very different effects, and these effects may also differ between species and between sexes and life stages within a single species (Siebert et al. 2001, Ten Doeschate et al. 2017, Van Elk et al. 2019, Cunha et al. 2021, Danil et al. 2021, Dadar et al. 2022). While there is often a causal link between condition/health and pathogen burdens, the direction of this causal link is not always obvious and indeed may shift over time; poor health can be both cause and consequence of high pathogen loads (Jepson et al. 1999). Finally, while poor condition, ill health and death may have identifiable proximate causes, stressors do not act alone, which is why full necropsies, including pathological, histopathological and toxicological analyses (among others), are essential to understand the context and identify the ultimate cause(s) of death in stranded animals.

Biotoxins from harmful algal blooms (HABs)

Marine harmful algal blooms (HABs) are the result of aggregations of marine phytoplankton, such as dinoflagellates, diatoms and cyanobacteria, which produce a variety of toxins that affect marine mammals (Landsberg 2002). Strictly speaking, the origin of these toxins may have an anthropogenic component as in the cases of Anderson et al. (2002) and Glibert and Burkholder (2006). Mortality of cetaceans related to toxins from algal blooms is known from as far back as 1946, when a mortality event involving bottlenose dolphins was linked to the dinoflagellate *Gymnodinium brevis* (Gunter et al. 1948).

Some of the most common biotoxins affecting marine mammals, including small cetaceans in European waters, are brevetoxins (PbTX), domoic acid (DA), saxitoxins (STX) and β-N-methylamino-L-alanine (BMAA, a non-protein amino acid), and these will be the focus of this review. However, at a global scale, this list may be extended to include diarrhetic shellfish toxins such as okadaic acid and microcystins (Rowles et al. 2017, Broadwater et al. 2018, Danil et al. 2021) and ciguatoxins, which have been detected in monk seals (Bottein Dechraoui et al. 2011). Okadaic acid and microcystins are considered potential emerging threats that can even promote tumours, as observed in mouse skin and hepatocytes, as well as in the mucosa of the rat glandular stomach (Fujiki et al. 1988, Suganuma et al. 1988, Humpage & Falconer 1999, Valdiglesias et al. 2013). Attention should also be paid to currently uncommon in European waters but potentially emerging biotoxins, because of the known effects of climate change and human activities on the distribution of invasive algal species and optimal environmental conditions for their proliferation (Wells et al. 2015).

Transmission

Toxins produced by HABs can be transmitted to cetaceans in a variety of ways such as ingestion of contaminated prey, direct contact, inhalation of aerosolised toxins or mother to calf transfer during gestation and lactation (Bossart et al. 1998, Flewelling et al. 2005, Brodie et al. 2006, Rust et al. 2014).

Levels and trends

All the common algal toxins mentioned previously (PbTX, DA, STX and BMAA) have been detected in the focal cetacean species of this review (harbour porpoise, common dolphin, bottlenose dolphin and striped dolphin) (e.g. Twiner et al. 2012, Starr et al. 2017, Danil et al. 2021). However, to the authors' knowledge, there are few records of exposure of cetaceans to HAB biotoxins in European waters. Hall et al. (2017) found detectable DA levels in approximately 40% of the sampled individuals from 12 different cetacean species in Scotland, with concentrations in urine samples from our target species generally ranging from 0.5 to 27.5 ng/mL, with the exception of a value of almost 2500 ng/mL found in one harbour porpoise. This high concentration was similar to those found in acute cases of toxicity in urine samples of Californian sea lions (3720 ng/mL, Goldstein et al. 2008), suggesting that this harbour porpoise probably suffered neurotoxic effects. The authors concluded that exposure to DA was likely to be low, but possibly chronic in the area. Fernández et al. (2022) documented the first mass mortality of small cetaceans in Europe associated with PbTXs, affecting 12 rough-toothed dolphins (*Steno bredanensis*) in 2008 in the Canary Islands, which highlights the potential risk of brevetoxicosis to this and other small cetacean species in Europe. However, a study of harbour porpoises, common and bottlenose dolphins in the North-western Iberian Peninsula reported no evidence of exposure to BMMA (Soliño et al. 2022).

The frequency, duration and distribution of HABs are generally believed to have increased and expanded over the last few decades (e.g. van Dolah 2000, Dai et al. 2023), as suggested by the growing number of records of HABs and associated toxins registered by international databases such as HAEDAT (Harmful Algal Event Database), as well as by regional networks such as REPHY

(Observation and Surveillance Network for Phytoplankton and Hydrology in coastal waters) and REPHYTOX (Monitoring Network for Phycotoxins in marine organisms), in France. Increasing numbers of records are noticeable along both Atlantic and Mediterranean coasts of Europe (e.g. Belin et al. 2021, Hallegraeff et al. 2021, Zingone et al. 2021), notably on the west of the Iberian Peninsula, in the northeast Bay of Biscay and in the North Sea (Bresnan et al. 2021, Karlson et al. 2021). However, Hallegraeff et al. (2021) suggest that the apparent upward trend is not evident when regional monitoring effort is taken into account. Since aquaculture production has intensified over recent decades and because of concerning mortalities of farmed species associated with these toxins, subsequent HAB monitoring effort has increased (Hallegraeff et al. 2021). More consistent reporting, which accounts for monitoring effort, is needed to reliably detect changes in the frequency, intensity and the extent of HABs. Nevertheless, an increase in HABs may be expected due to factors facilitating their proliferation, such as global warming, introduction of non-indigenous species and eutrophication due to urbanisation, increasing agriculture intensity and pollution (Hallegraeff 1993, Paerl & Whitall 1999, Anderson et al. 2002, Edwards et al. 2006, Yan et al. 2017, Hallegraeff et al. 2021, Marampouti et al. 2021). Thus, exposure of cetaceans to toxins from HABs represents an increasing concern.

Effects and thresholds

Brevetoxins (PbTx) are neurotoxins produced by the dinoflagellate *Karenia brevis* (Gunter et al. 1948), which is responsible for red tide blooms. There is some evidence that other *Karenia* species may also produce PbTx (e.g. *Karenia papilionacea*) or similar molecules (Brand et al. 2012, Fowler et al. 2015). *Karenia brevis* is distributed across the Gulf of Mexico and southeast US coast, where red tides are common and blooms have occurred almost annually since 1530 (Taylor 1971), currently threatening the endemic and resident bottlenose dolphin populations in the area and causing several mass mortality events, which have occurred more frequently along the western coast of Florida (e.g. Fire et al. 2015, 2020a, Litz et al. 2014, Twiner et al. 2012). While such events are less well-known elsewhere, *K. brevis*-like species occur worldwide including in Spain, Japan and New Zealand (Hallegraeff 2014).

PbTx is a lipophilic toxin that, similar to STX, binds to voltage-gated sodium channels involved in neurotransmission (Poli et al. 1986), leading to, for example, neurological symptoms and paralysis (Broadwater et al. 2018). Additionally, PbTx is suggested to interact with immune cells, potentially modulating their functions by increasing lymphocyte proliferation and respiratory burst, which may increase susceptibility to secondary infection (Roselli et al. 2006, Gebhard et al. 2015). Brevetoxicosis symptomatology in cetaceans remains unclear, but suggested clinical signs include chuffing (explosive exhalation), respiratory tract irritation, loss of motor control, seizures and death (Landsberg 2002, Hall et al. 2017, Broadwater et al. 2018, Fire et al. 2020b). Pathological signs observed in the 12 rough-toothed dolphins stranded in the Canary Islands, which mortality was associated to brevetoxicosis as earlier described, included multisystem haemorrhages and undigested stomach contents (Fernández et al. 2022). Red tide blooms of *K. brevis* have also been linked to behavioural changes in bottlenose dolphins, probably as a result of changes in resource availability (McHugh et al. 2011). Predicting cetacean exposure to PbTx during red tide blooms, the accumulation rate in their tissues and the associated health effects remains complicated. Concentrations of *K. brevis* during red tide blooms are a weak predictor of the concentration and level of exposure to PbTx in cetaceans (Fire et al. 2021).

Domoic acid (DA) is a potent water-soluble neurotoxin produced by several species of the diatom genus *Pseudo-nitzschia*. DA binds to glutamate receptors in the vertebrate central nervous system, causing overstimulation of nerves and, consequently, potentially also excitotoxicity (Xi & Ramsdell 1996, Berman & Murray 1997). The best information on the chronic, acute and latent health effects of HAB toxins on marine mammals is available for DA, notably from stranded California sea lions (*Zalophus californianus*) during *Pseudo-nitzschia* blooms. DA toxicity causes ataxia, head weaving, scratching, seizures and coma (Gulland et al. 2002), as well as epilepsy associated with hippocampal atrophy, abnormal behaviour linked to impaired spatial navigation and memory loss, neuropathology, cardiomyopathology and eosinophilia (Ramsdell 2007, Goldstein et al. 2008, Zabka et al., 2009, Dickey-Collas et al. 2010, Buckmaster et al. 2014, Cook et al. 2015, 2018). Reproductive failure resulting from DA exposure has also been described including cases of mortality of pregnant females, abortion, in utero death, premature parturition together with developmental abnormalities (both neurological and behavioural) in surviving offspring (Brodie et al. 2006, Lefebvre et al. 2016).

Saxitoxins (STX) are water-soluble toxins that are absorbed through the intestinal mucosa and transferred by the circulatory system to tissues, except to lipophilic ones such as blubber, where this neurotoxin does not accumulate (Gerssen et al. 2010). STX are produced by dinoflagellates (*Alexandrium*, *Pyrodinium* and *Gymnodinium*) and several cyanobacteria (Pearson et al. 2010). Saxitoxins affect voltage-gated potassium, calcium and, through primarily, sodium channels and thus impede signal transmission between neurons within muscle, including heart muscle, and peripheral nerves. This may result in paralysis and cardiovascular failure (Catterall 1980, Su et al. 2004, Pearson et al. 2010). These biotoxins are known to be lethal, but the symptoms of toxicosis in marine mammals remain imprecisely known due to the difficulties in observing them. The first marine mammal mortality event related to STX affected 14 humpback whales in the northeast USA in 1980s (Geraci 1989), but STX has been detected in other marine mammal species (Twiner et al. 2012, Starr et al. 2017, Lefebvre et al. 2024), including bottlenose dolphins in eastern Florida, for which baseline levels have been proposed as a first step towards establishing reference levels for STX mortality (Fire et al. 2020a).

β-N-methylamino-L-alanine (BMAA) is a non-protein amino acid produced by cyanobacteria and diatoms. Cox et al. (2005) reported that BMAA may be produced by all known groups of cyanobacteria. BMAA has recently been detected in the brains of stranded bottlenose and common dolphins in Florida and Massachusetts, indicating that these species are susceptible to its toxicity (Davis et al. 2019, 2021). BMAA trophic transfer, biomagnification and bioaccumulation have been described in many species and are thought to occur in cetacean food chains (Jonasson et al. 2010, Mondo et al. 2012, Davis et al. 2019) although there is a lack of strong evidence and further research is needed (Lance et al. 2018, Soliño et al. 2022). Dietary consumption of BMMA has been associated with neurodegenerative diseases in humans, including amyotrophic lateral sclerosis, Parkinson's disease and Alzheimer's disease (AD) (Spencer et al. 1987, Cox et al. 2003, Bradley & Mash 2009, Nunn 2017), and has been linked to AD-like neuropathology in cetaceans (Davis et al. 2019, 2021, Vacher et al. 2022). Davis et al. (2021) observed that AD-like pathology in common dolphins progressed with increasing exposure to BMAA. However, the causal relationship between BMAA and AD-like remains unclear.

Besides the effects of toxins at an individual level, consequences for cetacean populations have also been suggested. For example, trophic transfer of toxins (mainly saxitoxins) was determined as one of the contributing factors in the decline of the critically engendered North Atlantic right whale (*Eubalaena glacialis*) (Doucette et al. 2006).

As will be apparent from some of the examples mentioned previously, algal toxins have caused several mass mortality events worldwide. Mass mortality events associated with brevetoxins have been described in bottlenose dolphins in the Gulf of Mexico and along the eastern US coast (e.g. Twiner et al. 2012), and once in rough-toothed dolphins in the Canary Islands (Fernández et al. 2022). DA was linked to large mortality events of different cetacean species in New Zealand (Bengtson Nash et al. 2017). As noted above, the first mass mortality associated with a saxitoxin exposure was recorded on Cape Cod in 1987, involving 14 humpback whales (Geraci 1989). Since then, saxitoxins have been associated with a multispecies mass mortality event involving a few belugas and harbour porpoises in the St. Lawrence estuary (Starr et al. 2017), and were probably associated with an unusual mortality event of sei whales in southern Chile (Häussermann et al. 2017).

The concentration of biotoxins in various tissues has been reported for many marine mammal species. However, knowledge about lethal doses remains limited due to a lack of data from wild populations and the difficulty and undesirability of conducting such experiments on marine mammals. The only estimate available comes from the unusual mortality event of humpback whales that occurred in 1987 in Cape Cod Bay, which was associated with STX poisoning by ingestion of contaminated mackerel (*Scomber scombrus*) at an estimated lethal daily dose of 3.2 μg STX eq. kg^{-1} BW (Geraci 1989).

Persistence, prevalence and resistance

For conducting a health risk assessment and applying it to management, it is important to consider the potential spatial and temporal mismatch between exposure to toxins and consequent effects, as well as the factors that determine such exposure. Health effects may not overlap temporally and spatially with toxin concentrations due to delayed effects, latent cases (Goldstein et al. 2008) and/or the slow elimination rate of toxins (e.g. Hinton & Ramsdell 2008), all of which hinder exposure risk assessment. Lipophilic toxins such as PbTx were estimated to persist for a several weeks in prey items of bottlenose dolphins (e.g. PbTx levels were still measurable in all tissues in striped mullet (*Mugil cephalus*) after the 8 weeks of the experiment performed by Hinton & Ramsdell 2008). Considering the levels remaining in the fish in experimental studies (such as the one mentioned above), Fire et al. (2021) proposed that a 30-day time window might reasonably represent the exposure time for cetaceans. However, the same authors concluded that the concentration of *Karenia brevis* is a weak predictor of PbTx accumulation in bottlenose dolphins, and other metrics are still needed to estimate the risk from this neurotoxin.

Favourable conditions for HAB growth may overlap with migrating cetaceans during certain stages of their life cycle, which could increase the risk of toxicity during vulnerable life stages. For example, southern right whales (*Eubalaena australis*) experience this overlap at the end of their calving season in the Gulf of Peninsula Valdés, where a higher concentration of copepods (DA vectors) occurs in response to spring phytoplankton blooms including (or mainly composed of) diatom producers of DA such as *Pseudo-nitzschia* (D'Agostino et al. 2017). This could explain the high mortality rate of calves of Southern right whales in this area (Rowntree et al. 2013, Wilson et al. 2016). Neonates of California sea lions showed a higher occurrence of neurological disease linked to DA when compared to older animals (24% vs. 11%) (Simeone et al. 2019).

Although a wide range of animals have developed neurotoxin resistance through gene mutations, no evidence has been found in small cetaceans. In particular, Cammen et al. (2014) found no adaptive mutations in the genes involved in the voltage-gated sodium channels to which brevetoxins bind in the bottlenose dolphins they studied.

Mitigation measures and research needs

Consistent reporting of HABs and their associated toxins is essential to detect changes in their frequency, intensity, extent and distribution. More research is necessary to enhance our understanding of the dose–response effects of different toxins on cetacean species. Further monitoring and research are needed to predict which areas in Europe experience a higher risk of HAB occurrence and which cetacean species are more susceptible to their effects.

Possible mitigation measures should focus on reducing impacts from anthropogenic activities that can alter nutrient concentrations in seawater, such as fertilisation of agricultural land with nitrates and phosphates, which consequently might facilitate the proliferation of HABs. Examples of mitigation measures include preventing excessive urbanisation, managing residual waters from agriculture and controlling ballast water discharges. Despite recent advances in detecting some of the species that cause HABs, further efforts are required to forecast these blooms and design adequate mitigation plans.

Viruses

Viral infections can compromise reproductive output and survival, with potential population-level implications. Viruses have caused large mortality events in populations of several cetacean species worldwide. The main viruses affecting cetaceans are: (1) morbilliviruses, which are able to cause mass mortality events and mainly affect the respiratory, immune and nervous systems (Domingo et al. 1990, Groch et al. 2020b); (2) poxviruses, which can cause vesicular and cutaneous lesions such as tattoo skin disease, which has been found to have a higher prevalence in juveniles (Van Bressem et al. 2009a,b); (3) herpesvirus, which have been associated with mucosal and cutaneous lesions, and occasionally with nervous system pathologies (van Elk et al. 2016); (4) papillomaviruses, which induce skin, mucosa and genital lesions such as papilloma and condylomas (Van Bressem et al. 2009a); (5) caliciviruses, which cause skin lesions (Duignan et al. 2018) and (6) influenza virus type A, which has been detected in isolated cetaceans and outbreaks of which have occurred in pinnipeds, affecting the respiratory and nervous systems (Bodewes et al. 2015).

Viruses less frequently described in cetaceans include rhabdoviruses, which affect the nervous system and have been rarely detected in cetaceans (Emelianchik et al. 2019); adenovirus, which has been associated with gastroenteritis in cetaceans (Rubio-Guerri et al. 2015); and enterovirus, hepatitis E and coronavirus (Bossart & Duignan 2018, Van Bressem et al. 1999). Recently, a new Pestivirus (*Phocoena pestivirus*, PhoPeV) was detected in harbour porpoises in the North and Baltic Sea (Jo et al. 2019, Stokholm et al. 2022).

Viruses are primarily transmitted by direct or close contact among individuals (e.g. contact with lesions, aerosols or sexual contact). Morbillivirus is apparently also transmitted from mother to calf (Bossart & Duignan 2018, Van Bressem et al. 1999).

Considering Iberian waters as an example, infections of herpesvirus have been detected in all four focal species in this review, i.e. bottlenose dolphins, striped dolphins, common dolphins and harbour porpoises (Bento et al. 2019, Vargas-Castro et al. 2020, 2021); hepatitis E has been detected in bottlenose, common and striped dolphins (Caballero-Gómez et al. 2022); poxviruses are known from common dolphins, bottlenose dolphins, striped dolphins and harbour porpoises (Sacristán et al. 2018, Vieira Jorge 2022); papillomavirus was recorded in bottlenose dolphins (Vargas-Castro et al. 2021) and morbillivirus was found in bottlenose dolphins, common dolphins, harbour porpoises and striped dolphins (Bento et al. 2016, Cuvertoret-Sanz et al. 2020, Domingo et al. 1990, Raga et al. 2008, Rubio-Guerri et al. 2018, Van Bressem et al. 2001b). No evidence has been found of infections of influenza virus, adenovirus, enterovirus, rhabdoviruses or coronavirus in these cetacean species in this area.

Morbillivirus

Cetacean morbillivirus (CeMV, genus *Morbillivirus*, family *Paramyxoviridae*, Order *Mononegavirales*) is a re-emergent pathogen; it is one of the most studied viruses of cetaceans and is considered to be a major natural cause of mortality for odontocetes and mysticetes worldwide (Van Bressem et al. 1991, Ohishi et al. 2019). The first record of morbillivirus antibodies in a marine mammal date back to 1972 when they were recorded in a Canadian ringed seal (Henderson et al. 1992), while the first confirmed epizootic episode took place in 1987, affecting hundreds of Atlantic bottlenose dolphins on the eastern coast of the United States (Lipscomb et al. 1994, Krafft et al. 1995, Taubenberger et al. 1996, Kennedy 1998). Infected cetaceans have been detected in every ocean except the Arctic (where morbillivirus has however been detected in pinnipeds and polar bears) and Antarctica. Being responsible for both endemic and epidemic fatal events, this highly contagious virus has caused several mortality outbreaks over the last 30 years (Kennedy 1998, Duignan et al. 2014, Van Bressem et al. 2014, Ohishi et al. 2019), evidently affecting cetacean population dynamics (Van Bressem et al. 1999).

CeMV has been detected in 33 cetacean species (Ohishi et al. 2019, Groch et al. 2020c; see Table S1) and six different strains have been identified. Three of them (porpoise morbillivirus – PMV, dolphin morbillivirus – DMV and pilot whale morbillivirus – PWMV) are well characterised (Domingo et al. 1990, McCullough et al. 1991, Van Bressem et al. 1991, Barrett et al. 1993, Visser et al. 1993, Taubenberger et al. 2000), while the other novel strains (Beaked whale morbillivirus – BWMV, Guiana dolphin morbillivirus – GDMV and Indo-Pacific bottlenose dolphin morbillivirus) have been relatively recently reported (West et al. 2013, Groch et al. 2014, Stephens et al. 2014, Jacob et al. 2016). Among the most common small cetacean species in European waters, infected common, bottlenose and striped dolphins have been detected in both Atlantic and Mediterranean waters, whereas positive cases in harbour porpoise have been reported only in the Atlantic, as would be expected from the distribution of this species (Frantzis et al. 2001) (Table 2).

The first cases of morbillivirus in cetaceans in Spanish waters dates from 1990 when the first epizootic outbreak took place along the coasts of Valencian Community, Catalonia and Balearic Archipelago regions, affecting thousands of striped dolphins until 1992 and spreading over the Mediterranean Sea as far as the Aegean Sea (Domingo et al. 1990, 1992, Van Bressem et al. 1991, Di Guardo et al. 1992, 1995, Aguilar & Raga 1993). A second outbreak was registered in July 2007 in the Western Mediterranean, affecting young individuals more severely, which suggests that adult striped dolphins still had some immunity to the virus and that new epizootic episodes may occur in the future (Raga et al. 2008). Since then, occasional infections of striped dolphins have been detected in the Mediterranean Sea (see Table 2).

Table 2 Cases reported in the literature of morbillivirus infections in common dolphins, bottlenose dolphins, striped dolphins and harbour porpoises in the European waters

Region	Location	Sampling Period (Positive Cases)	No. Infected Individuals/Total (Prevalence)	References
Harbor Porpoise				
NE Atl	North Sea, English Channel and UK	1989–1996 (1991–1995)	2/82 (10.89%)	Van Bressem et al. (1998)
	Northen Ireland, UK	1988	6/6 (100%)	Kennedy et al. (1991)
	England and Scotland, UK	1990	2/2 (100%)	Kennedy et al. (1992)
	British Islands, UK	1995–1999 (1996–1997)	3/116 (2.59%)	Van Bressem et al. (2001b)
	Dutch northern Sea	1989–1992 (NA)	15/37 (40.54 %)	Visser et al. (1993)
NE Atl & Baltic Sea	German Baltic and North Sea	1991–1997	65/75 (87.84%)	Müller et al. (2000)
Common Dolphin				
NE Atl	Dutch coast	1989–1992	14/22 (63.64%)	Visser et al. (1993)
	North Sea, English Channel and UK	1990–1996 (1992–1993)	2/33 (6.06%)	Van Bressem et al. (1998)
	British Islands, UK	1995–1999 (1998)	1/19 (5.26%)	Van Bressem et al. (2001b)
	Portugal	2011–2015 (2012–2013)	2/193 (10.36%)	Bento et al. (2016)
C Med	Italy	1990	1/1 (100%)	Van Bressem et al. (1993)
Bottlenose Dolphin				
NE Atl	British Islands, UK	1999	1/2 (50%)	Van Bressem et al. (2001b)
	Canary Islands, Spain	2005	1/1 (100%)	Sierra et al. (2014)
E Med	Israel	1994	Unknown	Tsur et al. (1997)

(*Continued*)

Table 2 (*Continued*) Cases reported in the literature of morbillivirus infections in common dolphins, bottlenose dolphins, striped dolphins and harbour porpoises in the European waters.

Region	Location	Sampling Period (Positive Cases)	No. Infected Individuals/Total (Prevalence)	References
C Med	Italy	1998–2014 (2012–2013)	3/7 (42.86%)	Profeta et al. (2015)
	Italy	2011	1/1 (100%)	Di Guardo et al. (2013)
	Italy	2019–2020	2/2 (100%)[a]	Giorda et al. (2022)
W Med	Iberian Peninsula, Spain	1997–1998 (1997)	1/2 (50%)	Van Bressem et al. (2001b)
	France	2007–2008 (NA)	1/3 (33.33%)	Keck et al. (2010)
Striped Dolphin				
NE Atl	Portugal	2004–2014 (2007–2014)	6/36 (16.67%)	Bento et al. (2016)
	Galicia, Spain	2004–2014 (2007–2012)	8/33 (24.24%)	Bento et al. (2016)
C Med	Italy	1990–1991 (1991)	6/14 (42.86%)	Van Bressem et al. (1993)
	Greece	1991	6/8 (75%)	Van Bressem et al. (1993)
	Italy	1991–1993 (NA)	4/16 (25%)	Di Guardo et al. (1995)
	Italy	1998–2014 (2002–2014)	18/56 (32.14%)	Profeta et al. (2015)
	Italy	2002–2014 (NA)	6/45 (13%)	Pintore et al. (2018)
	Italy	2008–2020	29/29 (100%)[a]	Giorda et al. (2022)
	Italy	2009 and 2011	3/3 (100%)	Di Guardo et al. (2013)
	Italy	2012–2018 (2017–2018)	4/8 (50%)	Garofolo et al. (2020)
	Italy	2013	Unknown	Casalone et al. (2014)
	Sicilia	2016	7/7 (100%)[a]	Mira et al. (2019)
C & W Med	Spain, Italy and Greece	1991–1992	14/14 (100%)	Visser et al. (1993)
W Med	Community of Valencia, Catalonia, Balearic Islands, Spain	1990	4/4 (100%)	Domingo et al. (1990)
	Western Mediterranean	1990	Unknown	Van Bressem et al. (1991)
	Iberian Peninsula, Spain	1997–1999 (1997–1998)	3/16 (18.75%)	Van Bressem et al. (2001b)
	Sardinia Island, Italy	2006–2011 (NA)	2/27 (7.41%)	Pennino et al. (2022)
	Spain	2007	7/10 (70%)	Raga et al. (2008)
	France	2007–2008 (NA)	9/32 (28.13%)	Keck et al. (2010)
	Community of Valencia, Spain	2010–2013 (2011–2012)	9/35 (19.4%)	Vargas-Castro et al. (2021)
	Community of Valencia, Spain	2011–2016 (2011–2015)	5/92 (5.44%)	Rubio-Guerri et al. (2018)
	Catalonia, Spain	2012–2019 (2016–2019)	13/72 (18.01%)	Cuvertoret-Sanz et al. (2020)

Information of the location, sampling period, number of infected individuals from the total analysed animals, and prevalence based on the sampling period, of each case are detailed. The year/s in which the positive cases were detected are specified between brackets if different.

[a] Case studies with non-random selection of sampled animals.

NA, Information not available; Atl, Atlantic; Med, Mediterranean; N, North; E, East; C, Central; W, West.

Transmission

CeMV can be transmitted to cetaceans via several routes and has high potential for interspecies infection (Kennedy 1998, Jo et al. 2018). CeMV is mainly transmitted via airborne particles released from the host animal that reach epithelial tissues of a susceptible individual, where it replicates and transfers into the respiratory system (Shimizu et al. 2013). Transmission from parents to offspring was suggested in the 1990s since antigens were found in reproductive organs of both male and females (Domingo et al. 1992, Kennedy et al. 1992, Schulman et al. 1997). The occurrence of maternal transfer is supported by several cases of infected foetuses (Fernández et al. 2008) and calves (Di Guardo et al. 2011, West et al. 2015, Jacob et al. 2016).

Based on the results from a self-exciting Poisson process model of the CeMV outbreak in common dolphins in the North-western Atlantic, Morris et al. (2015) suggested that infected individuals can transmit the virus for a mean of 8.3 days and up to 24 days, over a range of 220 km, mainly through local movements, and more widely by seasonal migration. The same study calculated the reproductive ratio of this virus, estimating that an average of 2.58 individuals (95% CI = 2.08–3.17) may be infected by a primary infected individual during the peak of an epidemic. Weiss et al. (2020) calculated a transmission rate of 0.27 in the southern resident killer whale community, which seems highly conservative when compared to other morbilliviruses such as measles, which can be transmitted to 90% of humans in close contact with the infected individual (Hamborsky et al. 2015).

The transmission of CeMV depends on several factors, both intrinsic and extrinsic. The susceptibility to infection is related to both the ecology of the population (e.g. habitat use, social behaviour, migration patterns, inbreeding, population size and density) and the biology of the individuals (e.g. molecular receptors and immune system) (Kennedy 1998, Van Bressem et al. 1999, Valsecchi et al. 2004, Shimizu et al. 2013, Stejskalova et al. 2017, Batley et al. 2019, Mira et al. 2019, Ohishi et al. 2019, Cloyed et al. 2021). Recently, Cunha et al. (2021) found sex- and age-related differences in the mortality rate of Guiana dolphins affected by an event linked to CeMV, suggesting that females and calves are more susceptible to this infection than (older) males.

Effects

CeMV is a pleiotropic pathogen affecting mainly the immune, respiratory and central nervous systems and, less frequently, the gastrointestinal and urinary systems (Groch et al. 2020a). Morbilliviruses initially replicate in lymphoid tissue and spread through the infection of epithelial cells (van Bressem et al. 2014). They are able to cross the hematoencephalic barrier (Sato et al. 2012), and their ability to exhibit neurovirulence depends on the immune status of the host, the presence of virus-specific receptors and the ability of the virus to spread transneuronally (Cosby et al. 2002).

The most common pathologies caused by CeMV are pneumonia, encephalitis, hepatitis, syncytia and lymphoid depletion (Di Guardo & Mazzariol 2015, Domingo et al. 1992, Kennedy 1998, Van Bressem et al. 1999, 2014). Recently, skin lesions in a fin whale were found to be associated with CeMV (Dagleish et al. 2021). Differences in pathologies among species have not been explicitly reported, but some patterns are apparent: for example, the ‘brain-only form of dolphin morbillivirus infection’ (BOFDI) mostly affects striped dolphins (*Stenella coeruleoalba*) (Di Guardo et al. 2011, Soto et al. 2011), although it was recently diagnosed in a long-finned pilot whale (*Globicephala melas*) (Wessels et al. 2021). In addition to chronic encephalitis cases detected during inter-epizootic periods, systematic infections have also been detected (e.g. Mira et al. 2019).

These pathologies can cause death, directly or indirectly. For example, due to common immunosuppressive effects, infected animals are vulnerable to secondary diseases and opportunistic pathogens (Oldstone et al. 1999, Schneider-Schaulies & Schneider-Schaulies 2009, Griffin 2010, Van Bressem et al. 2014). CeMV outbreaks can last for years, and the effects may be noticeable over at least 5 years after the epizootic, as suggested for long-finned pilot whales in the Alboran Sea (Wierucka et al. 2014) and the Strait of Gibraltar (Verborgh et al. 2019).

Persistence and prevalence

Morbilliviruses do not persist for a long time without a host, and infection is suggested to induce lifelong immunity (van Bressem et al. 2014). Therefore, the persistence of CeMV within a population depends on the size and density of that population. The only published studies relating population size with virus persistence are based on humans and other terrestrial mammals, and they apply to other viruses from the genus *Morbillivirus* such as measles virus. Black (1991) estimated that at least 300,000 humans are needed to maintain infections with measles virus. In general, areas with higher abundance and density of marine mammals are expected to be more susceptible to the spread and persistence of a CeMV epizootic. For instance, within the northeast Atlantic, the North Sea had the highest density of harbour porpoises of the regions surveyed during SCANS IV (Gilles et al. 2023), hence harbour porpoises in the North Sea might be more vulnerable area for harbour porpoises during a CeMV epizootic. On the other hand, Singer et al. (2001) showed that populations of terrestrial mammals with a larger carrying capacity had a higher probability of recovering rapidly from an epizootic event.

Wide ranges of prevalence of CeMV have been found in different cetacean populations around the world. For example, in the western Iberian Peninsula, Bento et al. (2016) estimated the prevalence of this virus in striped dolphins at 24.2% in Galician waters and 16.7% in Portuguese waters. A much lower prevalence (1%) was detected in Portugal for common dolphins. These authors suggested an endemic infection in the Eastern Atlantic population of striped dolphins, and that the virus had been actively circulating since 2007.

Mitigation measures and research needs

At present, there is no effective solution or mitigation measure to reduce or avoid CeMV impacts. Weiss et al. (2020) showed that vaccinating to induce herd immunity in a population in which the social network was based on large number of interactions and contacts between individuals, such as the case of the southern resident killer whale population in the Northeast Pacific, is unlikely to be effective. However, further research is needed to enhance our knowledge about the propagation mechanisms (transmission, susceptibility and prevalence), despite the considerable advances that have been made with the characterisation of the virus, detection techniques and understanding of its transmissibility and pathogenesis. Further research on conditions leading to outbreaks, molecular mechanisms of transmission and pathogenesis (Zinzula et al. 2022), risk assessment for the spread of infections (Weiss et al. 2020), the effects of CeMV in combination with other transferable and non-transferable stressors and methods to predict consequences for populations could also be useful to inform conservation management.

Bacteria

A large variety of bacteria is known to infect cetaceans. The frequency and intensity of infection vary depending on intrinsic factors linked to the habitat and behaviour of the cetacean species, and extrinsic factors such as the proximity to polluted areas with higher bacterial concentrations, e.g. urban areas and discharge points (Haebler & Moeller 1993, Parsons & Jefferson 2000, Wünschmann et al. 2001) or naturally higher bacterial activity, for example, as associated with algal blooms (Siebert et al. 2008).

Some of the most common bacterial agents infecting cetaceans are: (1) *Brucella ceti*, which has been associated with a wide range of clinical and pathological signs in cetaceans including infertility, abortion, osteomyelitis and neurobrucellosis, which can eventually cause the death of the animal (Guzmán-Verri et al. 2012); (2) *Vibrio* spp. (including *Vibrio alginolyticus*, *Vibrio anguillarum*, *Photobacterium damselae* subsp. *damselae* (previously *Vibrio damsela*), *Vibrio parahaemolyticus* and *Vibrio fluvialis*), which have been associated with skin lesions, septicaemia and hepatitis, but are also found in healthy individuals (Morten Tryland et al. 2018); (3) the family Pasteurellaceae (including *Actinobacillus delphinicola*, *Phocoenobacter uter* and *Actinobacillus scotiae*), for which the pathological implications are not yet clear other than a case of septicemia detected in a harbour porpoise and associated with *P. uter* (Foster et al. 1996, Morten Tryland et al. 2018); (4) *Erysipelothrix rhusiopathiae*, which was associated with bronchopneumonia in harbour porpoises in the Northeast Atlantic (Siebert et al. 2008, Melero et al. 2011, Díaz-Delgado et al. 2015); (5) *Mycobacterium* spp. infections, which affect the respiratory system and may also be associated with dermatitis and/or panniculitis (e.g. *Mycobacterium abscessus* (Clayton et al. 2012), *Mycobacterium mageritense* (Morick et al. 2008), *Mycobacterium marinum* (Bowenkamp et al. 2001) and *Mycobacterium chelonae* (Wünschmann et al. 2008)); (6) *Norcardia* spp., which produce norcardiosis and mainly affect the respiratory system, causing pneumonia, but are also associated with skin infections, osteomyelitis and granulomatous lesions in different organs of the cetacean body (Morten Tryland et al. 2018); (7) *Salmonella* spp., which may induce bronchopneumonia, severe enteritis and septicaemia (Howard et al. 1983, Foster et al. 1999, Kirkwood et al. 1997, Siebert et al. 2008); (8) *Clostridium* spp., which have been diagnosed in captive cetaceans with potentially fatal pathologies including accumulation of gas in tissues, muscle necrosis, leucocytosis and enterotoxaemia (Field 2022). Most of the bacteria mentioned above have been detected in the cetacean species covered in the present review.

Other bacteria found in the cetacean target species in the study area include: (9) *Staphylococcus aureus*, which was associated with bronchopneumonia, enteritis, myocarditis, hepatitis, nephritis, leptomeningitis and septicemia; (10) *Clostridium perfringens*, which was linked to enteritis, hepatitis and bronchopneumonia; (11) *Streptococcus* spp., which was associated with bronchopneumonia, enteritis, hepatitis, nephritis, lymphadenitis and septicemia and (12) *Escherichia coli*, which was related to bronchopneumonia, hepatitis, septicemia and lymphadenitis (Beineke et al. 2005, Siebert et al. 2008, van Elk et al. 2012). Recently, a new species in the genus *Helicobacter* has been isolated from a captive bottlenose dolphin with gastric diseases, the proposed *Helicobacter delphinicola* sp. nov. (Segawa et al. 2020).

Brucella spp. have been detected in striped dolphins and bottlenose dolphins around the Iberian Peninsula, in both Atlantic and Mediterranean waters (Van Bressem et al. 2001b, Muñoz et al. 2006, Cuvertoret-Sanz et al. 2020, Isidoro-Ayza et al. 2014). *Nocardia* spp. infection has been detected in striped dolphins in the south and east of the Iberian Peninsula (Degollada et al. 1996, Díaz-Santana et al. 2022). Soares-Castro et al. (2019) found various bacterial species in the oral microbiota of small cetaceans in the western and north-western waters of the Iberia Peninsula. *Clostridium* spp. were identified in bycaught harbour porpoises and common dolphins. Additionally, species of Pasteurellaceae such as *Phocoenobacter* spp. have been detected in striped dolphins and common dolphins dying from bycatch or disease, while *Vibrio* spp. and mycobacterial species were observed in bycaught harbour porpoises.

Brucella

This review focuses on Brucella because it is one of the most studied bacteria affecting cetaceans and causes serious health effects in individuals, including infertility, and hence also affects population dynamics.

Members of the genus *Brucella* are Gram negative bacterial pathogens belonging to the alpha-2 sub-group of the Alphaproteobacteria. *Brucella* species are non-motile and capable of surviving outside the host, although the limited available information suggests that the survival capacity depends on the environmental conditions and that marine *Brucella* species can survive up to a few weeks (Guzmán-Verri et al. 2012, Larsen et al. 2016). These generally intracellular, but also facultative-extracellular (Gorvel & Moreno 2002), bacteria are pathogens or symbionts of both animals and plants, including humans. Pseudogenisation (gene loss) in *Brucella* has been widely reported in marine mammals, particularly in dolphins, and apparently occurs more frequently in marine mammals compared to terrestrial animals. Pseudogenisation events contribute to genetic variation of these bacteria, facilitating their adaptation to different hosts (Suárez-Esquivel et al. 2017). The *Brucella* genus is composed of 12 very closely related species (they share 97%–99% of the genome), classified into classical and atypical strains, with different virulence, zoonotic potential and primary hosts. These species include *Brucella abortus*, mainly infecting bovines, bisons, camels and elks; *Brucella melitensis*, mainly infecting sheep and goats and *Brucella canis*, mainly infecting canids.

Initially, all strains affecting marine mammals were called *Brucella maris* (Jahans et al. 1997). Later, Foster et al. (2007) concluded that there were two species, named *Brucella ceti* and *Brucella pinnipedialis*, the preferred hosts of which are cetaceans and pinnipeds, respectively. The genomes for *B. ceti* and *B. pinnipedialis* have been assigned to sequence types (STs) firstly described from 9-locus multi-locus sequence typing (MLST; Whatmore et al. 2007), and then from the recognised gold standard of 21-locus multi-locus sequence analysis (MLSA, Whatmore et al. 2017). The STs are not family- or order-specific, and multiple STs can infect one individual (Curtiss et al. 2022), but pinnipeds are predominantly associated with STs 24, 25, 52, 53 and 54, while cetaceans are associated with ST 23 (mainly porpoises), ST 26 (mainly dolphins) and ST 27 (detected in both pinnipeds and cetaceans) (Whatmore et al. 2017).

Brucella was first reported in marine mammals in 1994, in both free-living and captive animals. Ross et al. (1994) reported its isolation from harbour seal (*Phoca vitulina*), harbour porpoise and common dolphin stranded along the coast of Scotland, while Ewalt et al. (1994) reported *Brucella* from an aborted foetus of a bottlenose dolphin in captivity in California. To date, *Brucella* has been isolated from marine mammals worldwide including the Arctic, Atlantic, Pacific and Antarctic Oceans (Ohishi et al. 2008, Guzmán-Verri et al. 2012, Hernández-Mora et al. 2013, Sánchez-Sarmiento et al. 2019). Most cases of infection have been reported in north Atlantic waters (Guzmán-Verri et al. 2012, Dadar et al. 2022), and an especially large number of cases have been found along the coasts of Scotland and England (Jauniaux et al. 2010). From the 93 cetacean species that might be potential hosts of *Brucella* sp. (Braulik et al., 2023), *Brucella* infection has been reported in at least 43 species sampled between 1984 and 2018 (Table S2), using both direct diagnosis techniques (methods to detect current infections such as culture, immunohistochemistry and molecular tests) and indirect diagnosis techniques (i.e. methods to detect past or current infections, such as ELISA (enzyme-linked immunosorbent assay) and RBT (Rose Bengal test)). Comparative studies suggest that some cetacean species are more susceptible to *Brucella* infections than others (e.g. Cvetnić et al. 2017); certainly, there are differences in the frequency of infection, and this pathogen has been most commonly detected in harbour porpoises, striped dolphins, Atlantic white-sided dolphins, bottlenose dolphins, common dolphins and minke whales (Table 3).

Transmission

Transmission of brucellosis among marine mammals is not yet fully elucidated. Evidence has been found that *Brucella* infection can be transmitted during sexual intercourse and through contact with aborted foetuses or placental tissues, as well as from mother to offspring (Miller et al. 1999, Hernández-Mora et al. 2008, Maquart et al. 2009, González-Barrientos et al. 2010, Guzmán-Verri et al. 2012). Lung nematodes (e.g. *Pseudalius inflexus* and *Parafilaroides decorum*) are proposed as vectors for brucellosis (Dawson et al. 2008, Perrett et al. 2004), which can be transmitted to marine mammals through the food web by feeding on contaminated intermediate fish hosts, as in the case of Californian sea lions feeding on infected coprophagous fish species such as *Girella nigricans* (Rhyan 2000, Dawson et al. 2008, Hernández-Mora et al. 2013). Other possible routes of transmission to marine mammals include contact with infected skin lesions or wounds containing parasite remains that are beginning to necrotise (Foster et al. 2002, Nymo et al. 2011) and aerosols (Corbel 2006).

Table 3 Cases Reported in the Literature of *Brucella* Infections in Common Dolphins, Bottlenose Dolphins, Striped Dolphins and Harbour Porpoises in the European Waters

Region	Location	Sampling Period (Positive Cases)	No. Infected Individuals/Total (Prevalence)	References
Harbour Porpoise				
NE Atl	England and Wales, UK	1989–1995 (1991–1993)	31% (11/35)	Jepson et al. (1997)
	Scotland, UK	1991–1993 (NA)	22% (4/18)[a]	Ross et al. (1994)
	Scotland, UK	1991–1999 (NA)	34% (41/119)	Patterson et al. (2000)
	Scotland, UK	1991–2001	100% (19/19)[a]	Foster et al. (2002)
	United Kingdom	1991–2004 (NA)	100% (42/42)	Dawson et al. (2008)
	Scotland, UK	1994–1995 (NA)	9% (3/35)	Foster et al. (1996)
	Cornwall, UK	1998	100% (1/1)	Dawson et al. (2004)
	Scotland, UK	2005	100% (1/1)	Dagleish et al. (2008)
	North and Baltic Sea	2005	0.62% (2/324)	Siebert et al. (2008)
	Belgium	2008	100% (1/1)	Jauniaux et al. (2010)
	Dutch coast	2008–2011 (2009–2011)	4.5% (5/112)	Maio et al. (2014)
	Southwestern Sweden	2016	100% (1/1)[a]	Neimanis et al. (2022)
	German North Sea	Unknown	0.07% (2/298)	Prenger-Berninghoff et al. (2008)
Common Dolphin				
NE Atl	England and Wales, UK	1989–1995 (1990–1993)	31% (9/29)	Jepson et al. (1997)
	Scotland, UK	1991–1993 (NA)	100%(1/1)	Ross et al. (1994)
	Scotland, UK	1991–1999 (NA)	42.9% (3/7)	Patterson et al. (2000)
	United Kingdom	1991–2004 (NA)	100% (4/4)	Dawson et al. (2008)
	Scotland, UK	1993, 1997	100% (2/2)	Foster et al. (2002)
	Cornwall, UK	2001–2008	25% (1/4)[a]	Barnett et al. (2009)
	Canary Islands, Spain	2001–2018 (2007)	33.3% (1/3)	Sierra et al. (2020)
	Cornwall, UK	2009	100% (1/1)	Davinson et al. (2013)
Bottlenose Dolphin				
NE Atl	England and Wales, UK	1898–1995 (1992)	100% (1/1)[a]	Jepson et al. (1997)
	Scotland, UK	1991–1999 (NA)	10% (1/10)	Patterson et al. (2000)
	United Kingdom	1991–2004 (NA)	100% (3/3)	Dawson et al. (2008)
	Canary Islands, Spain	2001–2018 (2005)	33.33% (1/3)	Sierra et al. (2020)
	Cornwall, UK	2004	100% (1/1)	Dawson et al. (2006)
	Southwest England	2004–2007	75% (6/8)	Davison et al. (2011)
C Med	Croatia	2015	100% (1/1)	Duvnjak et al. (2017)
	North Adriatic Sea	2015	100% (1/1)	Cvetnic et al. (2017)
W Med	Spanish Mediterranean coast	1997–1999 (NA)	50% (1/2)	Van Bressem et al. (2001b)
	Catalonia, Spain	2012	100% (1/1)	Isidoro-Ayza et al. (2014)
	Catalonia, Spain	2012–2019 (2012)	20% (1/5)	Cuvertoret-Sanz et al. (2020)

(*Continued*)

Table 3 (*Continued*) Cases Reported in the Literature of *Brucella* Infections in Common Dolphins, Bottlenose Dolphins, Striped Dolphins and Harbour Porpoises in the European Waters

Region	Location	Sampling Period (Positive Cases)	No. Infected Individuals/Total (Prevalence)	References
Striped Dolphin				
NE Atl	England and Wales, UK	1989–1995 (1992)	25% (1/4)	Jepson et al. (1997)
	Scotland, UK	1991–1999 (NA)	47.1% (4/7)	Patterson et al. (2000)
	United Kingdom	1991–2004 (NA)	100% (8/8)	Dawson et al. (2008)
	Scotland, UK	1994–1995 (NA)	100% (2/2)	Foster et al. (1996)
	Scotland, UK	1994–2002	100% (6/6)	Foster et al. (2002)
	Scotland, UK	1999	100% (3/3)	González et al. (2002)
	Canary Islands, Spain	2001–2018 (2004, 2014)	13.33% (2/15)	Sierra et al. (2020)
	Canary Islands, Spain	2004	100% (1/1)	Di Francesco et al. (2019)
	Cantabria, Spain	2004	100% (1/1)	Muñoz et al. (2006)
	Cornwall, UK	2005	100% (1/1)	Davison et al. (2009)
	Cornwall, UK	2017	16.67% (1/6)	Clear et al. (2017)
C Med	Tyrrhenian coast	2012	100% (1/1)	Alba et al. (2013)
	Apulia coast	2012	100% (2/2)	Garofolo et al. (2014)
	Italy	2012–2018	100% (8/8)	Garofolo et al. (2020)
	Italy	2012–2019	100% (8/8)	Di Francesco et al. (2019)
	Italy	2015	100% (1/1)	Grattarola et al. (2016)
W Med	Spanish Mediterranean coast	1997–1999 (NA)	12.5% (2/16)	Van Bressem et al. (2001b)
	Catalonia, Spain	2009, 2012	100% (2/2)	Isidoro-Ayza et al. (2014)
	Catalonia, Spain	2012–2019	51.7% (15/29)	Cuvertoret-Sanz et al. (2020)

Information of the location, sampling period, number of infected individuals from the total analysed animals and prevalence based on the sampling period of each case are detailed. The year/s in which the positive cases were detected are specified between brackets if different.

[a] Case studies with non-random selection of sampled animals.

NA, Information not available; Atl, Atlantic; Med, Mediterranean; N, North; E, East; C, Central; W, Western.

Effects

Brucella is responsible for brucellosis, which is a disease of special concern that is prevalent in marine mammals worldwide and able to cause zoonosis (Ewatl et al. 1994, Davison et al. 2013). In marine mammals, the sequence type ST-27 has shown particular abortive and zoonotic potential compared to the other *Brucella* genotypes (Sohn et al. 2003, McDonald et al. 2006). Despite the fact that *Brucella* has been isolated from apparently healthy individuals (e.g. Foster et al. 2002), suggesting that marine mammals can act as carriers and shedders (Guzmán-Verri et al. 2012), brucellosis can also lead to chronic diseases that can eventually cause the stranding or death of the animal (Guzmán-Verri et al. 2012).

Brucella can lead to severe clinical and pathological signs in the reproductive and nervous systems. In the reproductive system, *Brucella* causes placentitis, endometritis, abortion, orchitis and mastitis, producing chronic lesions such as abscesses with caseous necrosis and mineralisation, leading to infertility and stillbirth (Foster et al. 2002, González-Barrientos et al. 2010, Hernández-Mora et al. 2008, Miller et al. 1999, Ohishi et al. 2003, 2008). In the nervous system, *Brucella* causes neurobrucellosis and associated meningoencephalomyelitis, hyperaemia in meninges and brain, secondary hydrocephalus and fibrosis in meninges and in ventricular system (Ross et al. 1996, González et al. 2002, Hernández-Mora et al. 2008, González-Barrientos et al. 2010).

The aforementioned *Brucella*-associated lesions frequently affect multiple systems such as (1) the integumentary system, inducing subcutaneous abscesses, steatitis (Foster et al. 2002, Dawson et al. 2006, Barbieri et al. 2013) and skin ulcerations (Jauniaux et al. 2010); (2) the cardiovascular system, inducing myocarditis, pericarditis (González-Barrientos et al. 2010, Sánchez-Sarmiento et al. 2019), perivascular cuffing, fibrinoid necrosis of vessels and vasculitis (Sierra et al. 2019); (3) the musculoskeletal system, causing osteomyelitis, discospondylitis (Dagleish et al. 2007, Foster et al. 2002) and osteoarthritis (González-Barrientos et al. 2010) and (4) the reticuloendothelial system and other organs, where it causes hepatic, splenic and lymph node hyperplasia with necrosis and macrophage infiltration in the liver and spleen (Foster et al. 2002, González-Barrientos et al. 2010).

In the respiratory system, *Brucella* has been isolated from the lungs, but it has also been encountered in association with parasite infestation, making it difficult to establish a cause–effect relationship between the bacterial infection and the associated lesions (e.g. abscesses and nematodes in lungs, pneumonia, bronchopneumonia, microcalcifications, hyperaemia and leukocyte aggregates in peribronchial connective tissue (Muñoz et al. 2006, Cassle et al. 2009, González-Barrientos et al. 2010, Guzmán-Verri et al. 2012).

Occasionally, cetaceans stranded alive or found at sea in compromised conditions may present neurological symptoms of *Brucella* infection, such as weakness, tremors, reduced mobility, side swimming, lack of coordination, buoyancy problems and seizures, as has been witnessed in the cases of several striped dolphins (Isidoro-Ayza et al. 2014, Cvetnić et al. 2017, Hernández-Mora et al. 2017). However, these signs are nonspecific for *Brucella*, and they are not always present in live animals. There have been reports of infected animals that have live-stranded without exhibiting any specific symptoms of brucellosis when reaching the shore, yet test positive for *Brucella* antibodies (e.g. Muñoz et al. 2006).

Differences in pathologies associated with different *B. ceti* DNA sequence types (i.e. ST-23, 26 and 27) were explored in stranded bottlenose, common, striped, Pacific white-sided dolphins, sperm whales and harbour porpoises in the East and West US Coast and Gulf of Mexico by Curtiss et al. (2022). The authors observed that ST-26 was most commonly present in adult bottlenose and common dolphins stranded along the East coast suffering from non-suppurative meningoencephalitis. ST-27 was more frequent in the Gulf of Mexico in aborted foetuses or neonatal deaths showing signs of in utero pneumonia. Inflammation of the reproductive tract and meningoencephalitis were observed in adult bottlenose and common dolphins infected with ST-27. The former pathology was also detected in adults infected by ST-26. Pathologies associated with ST-23, including neurobrucellosis, were observed in porpoises and other species such as bottlenose dolphins.

Striped dolphins seem to be more susceptible to neurobrucellosis compared to other cetacean species (González-Barrientos et al. 2010, Guzmán-Verri et al. 2012). Meningitis, meningoencephalitis and meningoencephalomyelitis are the pathologies associated with neurobrucellosis, and they are more commonly reported in striped dolphins (Foster et al. 2002, González et al. 2002, Muñoz et al. 2006, Hernández-Mora et al. 2008, Davison et al. 2009, González-Barrientos et al. 2010, Alba et al. 2013, Isidoro-Ayza et al. 2014, Grattarola et al. 2016, Francesco et al. 2019, Garofolo et al. 2020), compared to other cetacean species such as Atlantic white-sided dolphin (Dagleish et al. 2007), common dolphin (Davison et al. 2013), harbour porpoise (Jauniaux et al. 2010), long-finned pilot whale (Davison et al. 2015), sperm whale (West et al. 2015), common bottlenose dolphin (Venn-Watson et al. 2015), Sowerby's beaked whale (Davison et al. 2021a) and minke whale (Davison et al. 2021b). Due to frequent observations of these neurobrucellosis-associated pathologies, *Brucella* infections are suspected to be a significant factor responsible for strandings and subsequent mortality of striped dolphins worldwide (González-Barrientos et al. 2010, Isidoro-Ayza et al. 2014).

Prevalence

The analysis of spatio-temporal patterns in the prevalence of *Brucella* infections in cetaceans is limited by both the lack of systematic sampling and variation in the methods used for diagnosis (e.g. Guzmán-Verri et al. 2012). Recently, a meta-regression analysis (Dadar et al. 2022) showed that, among marine mammal species, Delphinidae and Phocoenidae are the second and fourth groups, respectively, in terms of the highest prevalence of infections (39.7% and 27.2%, respectively). Spatial differences were found in the prevalence of antibodies in harbour porpoises from the eastern North Atlantic (31% in England and Wales (Jepson et al. 1997) and 33% in Scotland (Foster et al. 2002)), compared to 1.2% found in porpoises from the western North Atlantic (Bay of Fundy, Neimanis et al. 2008). Overall, higher prevalence in males (30.4%) than in females (18.6%) was found by Dadar et al. (2022) in the aquatic species considered, which included marine mammals, and infection was found in 100% of sampled aborted foetuses. The same authors found a higher prevalence in the sampled animals that stranded dead (32.3%) compared to animals that were captured alive (12.6%).

Evidence suggests that species with social structures, schooling behaviour and promiscuous mating systems, such as dusky dolphins (*Lagenorhynchus obscurus*), are more vulnerable to pathogens like *Brucella*, which may be transmitted sexually (Van Bressem et al. 2001a). A higher prevalence during the months corresponding to the calving and nursing season, and/or with higher prey availability, can be expected (Guzmán-Verri et al. 2012). This is the case of bottlenose dolphins in South Carolina, in which size group increases during spring and summer when prey abundance is higher, resulting in months when sexual activity, socialising and close contact all increase (McFee & Hopkins-Murphy 2002).

Mitigation measures and research needs

Aside from occasional successes in treating specific brucellosis lesions with antibiotics in captive dolphins (Cassle et al. 2009, 2013), no widely effective or practical treatment has been achieved for wild marine mammals. Consequently, and due to potential zoonotic risks, euthanasia has been suggested as an option to consider for live infected marine mammals (Hernández-Mora et al. 2013). To avoid human contagion from infected marine mammals, prevention measures (i.e. intense hygiene and disinfection, personal protective equipment and routine screening for *Brucella*) need to be considered in sectors handling potentially infected animals, such as rescuers, rehabilitation workers, researchers and consumer communities (Hernández-Mora et al. 2013), especially in areas inhabited by neritic marine mammal species, hence with higher chances of interaction with human populations (Guzmán-Verri et al. 2012, McFee et al. 2020).

Recommended measures for enhancing the assessment of *Brucella* infections involve standardising and validating diagnostic methods and implementing systematic *Brucella* testing (e.g. Dadar et al. 2022, Jamil et al. 2022). These measures aim to increase our understanding of the disease, the spatio-temporal trends and the impacts on population dynamics, which are particularly important for endangered species and/or populations (Hernández-Mora et al. 2013).

Identified priority research areas include: (1) the genetic mechanism of infection, (2) the influence of environmental and anthropogenic factors on *Brucella* survival, (3) the frequency and intensity of infection and (4) the effects of infection at different developmental stages of cetaceans (Di Guardo & Mazzariol 2015, Di Guardo et al. 2018, Dadar et al. 2022). Identifying the factors driving vulnerability to *Brucella* infections would allow improved assessment of the risk of infections and the effects on endangered species and populations.

Parasites

Parasites of marine mammals include a wide range of endo- and ectoparasites. As an example, more than 114 species of parasites were reported in 36 marine mammal species in just New Zealand waters (Lehnert et al. 2021). The focal cetacean species of this review are no exception to this diversity: for instance, 55 different parasite taxa have been identified infecting harbour porpoises around the world (Dzido et al. 2021) and at least 23 taxa in the case of bottlenose dolphins (Bowie 1984).

Ectoparasites reported from the focal cetacean species include crustaceans such as whale lice (Cyamidae, Amphipoda) like *Isocyamus deltobranchium*, *Isocyamus delphinii* and *Syncyamus aequus* (Lehnert et al. 2007, 2021, Martínez et al. 2008, Fraija-Fernández et al. 2017), and the sessile barnacle (Coronulidae) *Xenobalanus globicipitis* (Carrillo et al. 2015) and copepods such as *Pennella balaenopterae* (Aznar et al. 2005, Danyer et al. 2014). Hagfish (Myxini) 'bites' (Quéro et al. 2009) were also reported.

Endoparasites comprise a wide range of species. Common ones include roundworms (Nematoda) from the genera *Anisakis*, *Crassicauda*, *Halocercus*, *Stenurus*, *Pseudalius* and *Torynurus*. Flatworms (Platyhelminthes) are represented by cestodes (e.g. genera *Phyllobothrium*, *Monorygma* and *Tetrabothrius*) and trematodes (e.g. genera *Campula*, *Oschmarinella*, *Pholoter* and *Nasitrema*). Other Phyla include Acanthocephala (e.g. the thorny-headed worm *Bolbosoma* spp.), Metamonada (e.g. *Giardia intestinalis*) and Apicomplexa (e.g. *Toxoplasma gondii* and *Sarcocystis* spp.) (e.g. Abollo et al. 1998, Gibson et al. 1998, Quiñones et al. 2013, Diaz-Delgado et al. 2015, Dzido et al. 2021).

Some parasites can induce severe disease and cause the death of their cetacean hosts (Díaz-Delgado et al. 2018, Fenton et al. 2017, Terracciano et al. 2020). By affecting individual survival and reproduction, parasitism may play a role in the population dynamics of marine mammals (Raga et al. 1997, Raga et al. 2008), and high infestation levels may negatively impact cetacean populations (Dzido et al. 2021). Isolating the impact that parasites might have on marine mammals without considering their additive and synergistic effects (e.g. in combination with other pathogens and contaminants) presents methodological challenges. Vulnerability to parasite infestation may be increased, and associated pathologies may be worsened due to their interaction with other natural stressors, such as contaminants (Bull et al. 2006).

In the past 20 years, a considerable amount of research has been dedicated to parasites in the marine environment, particularly nematodes of the family Anisakidae and more specifically of the *Anisakis* genus, due to their increasing importance worldwide as the cause of a fish-borne zoonotic disease (anisakiasis) and hence a human health risk (e.g. Audicana & Kennedy 2008, Bao et al. 2017, Adroher-Auroux & Benítez-Rodríguez 2020), but also because the visible presence of large numbers of *Anisakis* in fish is an aesthetic problem for consumers, covered by food safety regulations, and hence an economic issue for stakeholders in the seafood value chain (processors, retailers, etc.) (EFSA-BIOHAZ 2010, Bao et al. 2019).

This review focuses on *Anisakis* and lungworms because they are two of the most studied parasites with the potential to cause health effects in humans and frequent relevant effects on cetaceans.

Anisakis

Anisakis is the most common genus of parasitic nematodes present in cetaceans, its occurrence being known from at least 60 species of cetaceans worldwide (Raga et al. 2018). Records of infection by *Anisakis* in our focal cetacean species date back to at least the early 1800s (e.g. Rudolphi 1809) and were continuously reported over the nineteenth century (Van Beneden 1889). The genus *Anisakis* has been widely studied as it is the main source of anisakidosis (also infrequently caused by the genus *Pseudoterranova*) (Audicana 2022).

There are currently nine identified species of the genus *Anisakis* worldwide although the taxonomy of the genus remains under revision (Mattiucci et al. 2007, 2014), all regarded as cetacean parasites (Fiorenza et al. 2020). *Anisakis simplex* (s.s.) is the main *Anisakis* species in the Northeast Atlantic (Smith & Wootten 1978, Abollo et al. 2001a, Mattiucci et al. 2018) and is considered to be a very successful parasite in this region, being the numerically dominant and most prevalent macroparasite in commercial fish stocks (Abollo et al. 2001b). This species is distributed from waters 35°N to the circumpolar waters of the Arctic Sea, including the Iberian Peninsula and the Alboran Sea in the Mediterranean (Mattiucci et al. 2014, 2017). Although cosmopolitan in distribution, *A. simplex* (s.s.) is more commonly recorded in cetaceans from colder temperate and polar waters (Davey 1971). Fourteen species of cetaceans have been identified as hosts of *A. simplex* (s.s.) worldwide (Mattiucci et al. 2018), and 12 of these in the North Atlantic (Cipriani et al. 2022).

Anisakis pegreffii is the most common *Anisakis* species in the Mediterranean Sea (Bello et al. 2021), as well as being reported in the Pacific Ocean between 30°S and 60°S (Mattiucci et al. 2018). *Anisakis pegreffii* and *A. simplex* (s.s.) occur sympatrically in the Atlantic waters of the Iberian Peninsula and the Alboran Sea in the Mediterranean (Abollo et al. 2001b, Mattiucci et al. 2005, Mattiucci et al. 2016). Worldwide, 11 cetacean species are molecularly identified as definitive hosts of *A. pegreffii*, while five of which have been reported in the NEA and five in the Mediterranean Sea (Mattiucci et al. 2018, Cipriani et al. 2022), with *Stenella coeruleoalba* and *Tursiops truncatus* being definitive host species in both regions.

Individual and syntopic infections of *A. simplex* (s.s.) and *A. pegreffii* have been reported in the NEA, including the Atlantic waters of the Iberian Peninsula, for the four cetacean species considered in this review (harbour porpoises, common, bottlenose and striped dolphins (Mattiucci et al. 2018, Cipriani et al. 2022)).

As the *Anisakis* life cycle and its routes of transmission rely on predation, its prevalence and abundance are intrinsically linked to local trophic webs. These need to be stable for the *Anisakis* life cycle to be completed (Mattiucci & Nascetti 2008, Mattiucci et al. 2017). These parasites only have one free-living period (as L3 larvae, the first post-hatching stage (Køie et al. 1995)), of 3–7 weeks, until they are ingested by small zooplanktonic crustaceans (first intermediate hosts) or die (Smith & Wootten 1978, Nagasawa 1990). Then, through predation, L3 larvae infect one or more paratenic hosts (fish and squid), and further development stops until they are eaten by cetaceans, which become their definitive hosts (Young & Lowe 1969, Smith & Wootten 1978). Once within the stomach chambers of the cetacean host, the further development of L3 larvae is triggered by an increase in temperature and a lower pH compared to fish and squid tissues (Iglesias et al. 2001), and they attach to the stomach mucosa where they develop into L4 larvae, and later into their sub-adult and sexually mature adult stages (Smith 1989, Nagasawa 1990). This process happens mainly in the forestomach or first stomach chamber of cetaceans. It appears to depend on a combination of factors, including severity of infection (Smith 1989), food availability (Gibson et al. 1998, Aznar et al. 2003), and, according to some authors, it might also serve as a mating strategy (Aznar et al. 2003, Herreras et al. 2004).

The presence of *Anisakis* in the oesophagus and other parts of the wider digestive system has been reported, but it is uncommon (Table S3). *Anisakis* females can produce over a million eggs per individual (Ugland et al. 2004), which are then excreted through the faeces of the cetaceans and thus returned to the marine environment (Young & Lowe 1969, Smith & Wootten 1978). The relationship between cetacean abundance and the amount of *Anisakis* circulating through the food web remains poorly understood.

Transmission

As with most cetacean parasites, the transmission of *Anisakis* to cetaceans is trophic, mainly through the ingestion of infected fish and squid (Raga et al. 2018). The vectors of transmission – i.e. different species prey eaten by cetaceans – vary geographically according to cetacean diet in each area. Although less common, *Anisakis* can be transmitted to small cetaceans through accidental or secondary ingestion of zooplankton such as euphausiids and copepods (Nagasawa 1990, Klimpel et al. 2004).

For example, in the Atlantic waters of the Iberian Peninsula, at least four cephalopod and 17 fish species are paratenic hosts of *A. simplex* (s.s.) and *A. pegreffii* (Abollo et al. 2001b). Prevalence of *Anisakis* in fish in this area can be up to 98.5% and 100% for blue whiting (*Micromesistius poutassou*) and European hake (*Merluccius merluccius*), respectively (Levsen et al. 2018). In this area, the main vectors of transmission of *Anisakis* spp. to common dolphin are probably these two species, as well as sardine (*Sardina pilchardus*) and mackerel (*Scomber scombrus*) (Santos et al. 2013, 2014, Marçalo et al. 2018).

In the early life stages (eggs and free L3 larvae), *Anisakis* distribution is influenced by the distribution of their (definitive) cetacean hosts, as well as environmental and oceanographic factors (Kuhn et al. (2016) and references therein). Subsequently, their distribution is mediated by the distribution of their paratenic hosts, and ultimately again by the distribution of their definitive hosts. The transmission of *Anisakis* parasites from fish to cetaceans can also be strongly influenced by anthropogenic factors. Bearzi et al. (2009) and Genov et al. (2008) observed dolphins interacting with fisheries and feeding on discards. Discarding the most heavily infected parts of the fish (i.e. the viscera) at sea could increase the rate of success of back-transmission of *Anisakis* to other paratenic and definitive hosts that feed on the discards (González et al. 2018), although the importance of this route of transmission remains to be determined.

Potential transfer routes can be inferred from data on cetacean diet composition and epidemiological data from intermediate and paratenic hosts (i.e. zooplankton, fish and cephalopods), as was done by Klimpel et al. (2004) in the Norwegian Deep. The diet of Norwegian resident harbour porpoises, which is known to differ from that in other North Atlantic areas, includes species that are considered obligatory secondary hosts of *A. simplex* (s.s.) in the area, such as pearlside (*Maurolicus muelleri*) (Klimpel et al. 2004). Other fish species important in this area for *Anisakis* transference to cetaceans, including bottlenose dolphins, are saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus*), among others (Klimpel et al. 2004).

In Argentinian waters, Berón-Vera et al. (2007) inferred *A. simplex* transference routes to common dolphins from epidemiological data on fish parasites, finding important links that greatly differ from their main prey and potentially important transmission routes in the NEA. Following a similar methodology, Romero et al. (2014) found in the same area high prevalence (83.3%) of *A. simplex* in six stranded bottlenose dolphins, but could not elucidate transfer routes, appealing for more data.

Estimating parasites burdens (as well as contaminants concentrations) that can be transferred through the food web is complicated. However, it is possible to combine information on parasites burdens (and contaminant concentrations) in prey species with information on diet and food intake of predators, to infer the amounts ingested by predators (e.g. Santos et al. 2014). Thus, combining information on common dolphin diet (blue whiting, hake, sardine and horse mackerel constitute approximately 87% of common dolphin diet in the area (Santos et al. 2013, Hernandez-Gonzalez et al. 2024), daily food consumption estimates for common dolphins (Kastelein et al. 2000) and *Anisakis* burdens in their main prey species (e.g. Levsen et al. 2018), we estimate that around 42.45 (21.28–73.12) *Anisakis* per day, or 15500 (7770–26690) per year, are transferred to common dolphins from their main prey items in Iberian Atlantic waters (Miguel López unpublished data).

Similar exercises to this one could be undertaken in those regions with available data on Anisakis in prey, diet of predators and abundance of predators. For example, in the Iberian Atlantic waters, there is existing epidemiological data for zooplankton (e.g. Gregori et al. 2015) and fish (e.g. Levsen et al. 2018, Roca-Geronès et al. 2020), alongside data on diets of harbour porpoise, common dolphin, bottlenose dolphin and striped dolphin diet data (Santos et al. 2007, 2013, 2014, Read et al. 2013, Marçalo et al. 2018, 2021, Hernandez-Gonzalez et al. 2024).

Levels and trends

Long-term studies on temporal trends of *Anisakis* abundance in cetaceans are extremely scarce. Recently, an increase of gastric ulcers caused by *Anisakis* (*A. simplex* (s.s.) and *A. pegreffii*) in cetaceans stranded was reported in Galician waters when compared to stranded animals from 2017–2018 and 1991–1996 (Pons-Bordas et al. 2020). An increase of *Anisakis* prevalence in stranded cetaceans from Portuguese waters was also recently reported by Lino et al. (2022). These changes are congruent with a reported exponential increase worldwide in *Anisakis* abundances in fish and invertebrate hosts based on a bibliographic meta-analysis of a 53-year period (1962–2015), with *Anisakis* spp. detected in the Northeast Atlantic strongly influencing this trend (Fiorenza et al. 2020).

Effects

The first record of pathological effects of *Anisakis* in marine mammals was reported by Murie and Baird (1868) in a walrus (*Odobenus rosmarus*). Early descriptions of *Anisakis* parasitism and its effects in cetaceans appear in Kikuchi et al. (1967) and Young and Lowe (1969).

Anisakis infection in cetaceans usually leads to pathologies in their digestive system, with clear consequences for the health and condition of individuals (Kirkwood et al. 1997, Gibson et al. 1998). These pathologies can include gastric and intestinal bleeding, ulcerative, fibrous and granulomatous gastritis, oesophagitis and obstructions (Geraci & St. Aubin 1987, Jaber et al. 2006, Hrabar et al. 2017) (see Table S3 for a summary).

Anisakis parasites have been suggested to get adapted to the biology of their hosts, and the hosts' immune system does not reject them (Klimpel & Palm 2011). Their effects are often chronic (Ryeng et al. 2022) and in most cases not considered directly lethal for the cetacean hosts (Baker & Martin 1992, Abollo et al. 1998, Hrabar et al. 2017). However, at least three studies have reported lethal *Anisakis* infestation events in cetaceans. Kikuchi et al. (1967) attributed the death of four dolphins in Japan to Anisakis infection, Baker (1992) diagnosed the death of a dolphin due to large gastric ulcers caused by *A. simplex* and Kirkwood et al. (1997) diagnosed the death of four porpoises (out of 234 stranded from 1990 to 1995 around the British Isles) due to severe ulcers and acute haemorrhages caused by *A. simplex*. Gastric ulcerations by *Anisakis* sp. have been reported as a secondary factor causing the death cetaceans, including 10 harbour porpoises in Swedish waters (Neimanis et al. 2022).

Ulcers are the main lesions produced by *Anisakis* (Abollo et al. 1998, Hrabar et al. 2017, Pons-Bordas et al. 2020). For example, the diameter of lesions observed in small cetaceans stranded in the Iberian Peninsula range from 1 mm (open ulcer in the forestomach of a harbour porpoise, unpublished data, Figure S1) to 210 mm (hyperkeratosis area of the mucosa with associated fibrosis of the mucosa in the forestomach of a bottlenose dolphin, Pons-Bordas et al. 2020), both animals stranded in Galicia. Ulcers may appear isolated either as small discontinuity/loss of the full thickness of the tissue or wider openings with a punched-out appearance, in clusters with thickened surrounding tissue (epithelial hyperplasia) (Smith 1989, Siebert et al. 2006, Pons-Bordas et al. 2020, Lino et al. 2022), or as small multifocal openings of the tissue with intralesional nematodes. Furthermore, *A. simplex* (s.s.) has been reported to be able to induce skin lesions (granulomatous dermatitis) in harbour porpoises and bottlenose dolphins (van Beurden et al. 2015). The threshold in terms of the minimum amount of *Anisakis* individuals, which may lead to lesions in cetaceans, is still unknown and may be impossible to define, since various other factors may be involved in the pathological process, such as the immunological condition of the cetacean. Nevertheless, small ulcers associated with single attached *Anisakis* individuals have been observed in common dolphins stranded in Galicia (unpublished data).

Lesions are caused by *A nisakis* larval stages L3 and L4 attached to the gastric mucosa and submucosa, while most adults normally appear free in the cavity or superficially attached to the stomach walls (Smith 1989, Jauniaux et al. 2002, Katahira et al. 2021). Pathologies from *Anisakis* can be found in different chambers of the stomach (Alves Motta et al. 2008), although they are usually observed in the forestomach (e.g. Pons-Bordas et al. 2020), or first stomach for species with no forestomach compartment such as franciscanas and beaked whales (Kikuchi et al. 1967, Mead 1993, Aznar et al. 2003). *Anisakis* can attach and produce ulcerations in other chambers after the forestomach: the main stomach (or fundic) and the pyloric stomach (Young & Lowe 1969, Harrison et al. 1970, Hrabar et al. 2017).

Severe burdens of Anisakis feeding on the food bolus and that physically occupy a large proportion of the stomach volume may cause mild anaemia or increased risk of starvation and host debilitation, even in cases where few or non-severe ulcers are present (Gibson et al. 1998).

There are apparent differences in pathogenicity of different *Anisakis* species, with higher penetration rates for *A. simplex* (s.s.) compared to *A. pegreffii* observed in experiments with agar media (Suzuki et al. 2010), live tissue of fish (Quiazon et al. 2011) and laboratory rats (del Carmen Romero et al. 2013). Arizono et al. (2012) also reported higher *A. simplex* (s.s.) tolerance to artificial gastric conditions compared to *A. pegreffii*.

Prevalence and persistence

A growing body of research suggests that a direct relationship might exist between cetacean abundance and *Anisakis* prevalence and abundance in fish located in the same areas (Rello et al. 2009, Molina-Fernández et al. 2015, Bušelić et al. 2018, Cipriani et al. 2018, Levsen et al. 2018, Pierce et al. 2018, Roca-Geronès et al. 2020). Highly migratory fish and cetacean species acting as definitive hosts play a role in the distribution and abundance of *Anisakis* species, as well as in their population genetic structure (Cipriani et al. 2022). For example, Klimpel et al. (2004) mentioned that *A. simplex* (s.s.) transportation from the Norwegian Deep to other regions of the North Atlantic is facilitated by migrating cetaceans such as minke whales (*Balaenoptera acutorostrata).* In the Northeast Atlantic waters of the Grand Sole Bank where *A. simplex* (s.s.) is the predominant *Anisakis* species, *A. pegreffii* observations in hake were related to migratory routes of cetaceans (Mattiucci et al. 2004). In the Mediterranean waters of the Adriatic Sea, the observations of *A. simplex* (s.s.) outside this area considered outside their 'usual' habitat were related to the migratory capabilities of bottlenose dolphin, striped dolphins and bluefin tuna (Blažeković et al. 2015, Mladineo & Poljak 2014). Therefore, cetacean species or populations migrating between areas of different *Anisakis* species prevalence, such as fin whales (*Balaenoptera physalus*) migrating between Mediterranean and Atlantic waters through the Strait of Gibraltar (Gauffier et al. 2018), might be considered potential drivers of *Anisakis* distribution.

Aside from migrating animals, resident cetacean populations may also be linked to higher abundance of *Anisakis* in fish. In the 'Sanctuary for Cetaceans' of the Ligurian Sea, the high prevalence and abundance of *A. pegreffii* (the predominant species in the Mediterranean Sea) in hake has been attributed to the abundant bottlenose dolphins in the area (Mattiucci et al. 2004, 2015), which is one of the main definitive hosts of *A. pegreffii* along with common dolphin and striped dolphins (Terracciano et al. 2020). In the Balearic archipelago, Barcala et al. (2018) identified significant differences in the prevalence of *Anisakis* in paratenic hosts within areas of higher abundance of sperm whales compared to common dolphins, which also differs from other areas in the Mediterranean and could be related to the abundance of definitive hosts.

Anisakis accumulate through the trophic web: from single individuals in zooplanktonic organisms (intermediate hosts) (Klimpel et al. 2004, Gregori et al. 2015), hundreds and even thousands in larger fish (Levsen et al. 2018, Pascual et al. 2018) and up to tens of thousands in some severely infected definitive hosts depending on the cetacean species (see Table 4). Larger fish have greater probabilities of being infected by *Anisakis* parasites, and fish size is generally a good predictor for both presence and abundance (Levsen et al. 2018). A similar pattern has been detected in striped and bottlenose dolphins in the Adriatic Sea, where older individuals had significantly more *Anisakis* than the younger animals (Blažeković et al. 2015).

As far as the authors are aware, there are no published data on *Anisakis* persistence in cetaceans. McClelland (1980) experimentally infected harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) with *Pseudoterranova decipiens* parasites, detecting *P. decipiens* eggs in the faeces of grey seals 70–80 days after infection, but parasite fecundity peaked around the 50th day. Similarities between *Pseudoterranova* and *Anisakis* parasites are plausible. Iglesias et al. (2001) observed from *in vitro* experiments that *A. simplex* (s.l.) reached adult stage on average 20–60 days post infection and a maximum survival time between 111 and 158 days. Lastly, Ugland et al. (2004) reported a growth period of 30–60 days for female *Anisakis* after infecting a cetacean as larvae L3, and an egg laying period of around 7 days (the last phase of their cycle) from *in vitro* experiments of larval nematodes extracted from minke whales. After using up most of their available energy during the egg laying process, adult females die and are presumed to be excreted by the cetacean host via peristaltic movements. From these studies, an estimated persistence of infection in cetaceans of

Table 4 Cases Reported in the Literature of *Anisakis* spp. Infections in the Studied Species in European Waters (Cetacean Species, *Anisakis* spp. (Genetic Identification) and Ratio, No. Sampled Cetaceans, No. Infected Cetaceans, Prevalence, Abundance of Parasites (Mean, Range and Intensity), Location, Year, Stranded/Bycaught Cetaceans)

Region	Location	Sampling Period	Anisakis Species	Genetic Identification	Prevalence (No. Infected/Hosts)	Dominance (simplex/ pegreffii/Hybrid%)	Abundance (Average No.)	References
Harbour Porpoise								
NE Atl	Norway	2017	*Simplex*	No	43/61 (69%)	NA	NA	Ryeng et al. (2022)
	Scotland, UK	2004–2019	*Simplex*	Yes	NA	100/0/0	NA	Cipriani et al. (2022)
	Spain and Portugal	2004–2019	*Anisakis* sp.	Yes	NA	78.7/19.2/2.1	NA	Cipriani et al. (2022)
	Poland	1995–2019	*Simplex*	No	10/30 (33.3%)	NA	0–777	Dzido et al. (2021)
	Galicia	2017–2018	*Simplex*	Yes	2/3 (66.7%)	100/0/0	NA	Pons-Bordas et al. (2020)
	The Netherlands/Belgium/ Germany	2003–2016	*Simplex*	No	6/54 (11.1%)	NA	0–more than 100	van Elk et al. (2019)
	The Netherlands	2013	*Simplex*	Yes	1/1 (100%)	NA	60	van Beurden et al. (2015)
	Norway	2000	*Simplex*	No	22/25 (86%)	NA	NA	Siebert et al. (2006)
	Iceland	2000	*Simplex*	No	12/12 (100%)	NA	NA	Siebert et al. (2006)
	German North Sea	1997–2000	*Simplex*	No	9/28 (32%)	NA	NA	Lehnert et al. (2005)
	German Baltic Sea	1997–2000	*Simplex*	No	6/18 (28%)	NA	NA	Lehnert et al. (2005)
	Norway	2000	*Simplex*	No	18/22 (80%)	NA	NA	Lehnert et al. (2005)
	Nordland, Norway	1988	*Simplex*	No	11/11 (100%)	NA	NA (262)	Ugland et al. (2004)
	Danish waters	1988–1990	*Simplex*	No	35/78 (44.9%)	NA	0–3245	Herreras et al. (2004)
	Northern France and Belgium	1990–2000	*Simplex*	No	20/55 (36.36%)	NA	NA	Jauniaux et al. (2002)
	Galicia, Spain	1992–1994	*Simplex*	No	3/4 (75%)	NA	NA	Abollo et al. (1998)
	Danish waters	1988–1990	*Simplex*	No	36/70 (51%)	NA	0–2812 (369)	Herreras et al. (1997)
	Scotland, UK	1977–1983	*Simplex*	No	7/10 (70%)	NA	0–451	Smith (1989)
	England and Wales, UK	1990–1994	*Simplex*	No	103/173 (60%)	NA	NA	Gibson et al. (1998)
	Scotland, UK	1977–1984	*Simplex*	No	7/10 (70%)	NA	0–451 (113.7)	Smith (1989)
	Scotland, UK	1967–1968	*Simplex*	No	6/7 (85.7%)	NA	0–1294 (410)	Young and Lowe (1969)
	Greenland	2009	*Simplex*	No	12/20 (60%)	NA	NA	Lehnert et al. (2014)
NE Atl &	German North and Baltic Seas	1994–1996	*Simplex*	No	4/23 (17.4%)	NA	NA	Wunschimann et al. (2001)
Baltic Sea	North and Baltic Seas	1991–1996	*Simplex*	No	35/445 (7.87%)	NA	NA	Siebert et al. (2001)

Common Dolphin								
NE Atl	Spain and Portugal	2004–2019	*Anisakis* sp.	Yes	NA	67.6/29.5/2.9	NA	Cipriani et al. (2022)
	Galicia, Spain	2017–2018	*Anisakis* sp.	Yes	37/43 (86%)	50/50/0	NA	Pons-Bordas et al. (2020)
	Canary Islands, Spain	NA	*Simplex*	No	1/6 (16.7%)	NA	NA	Jaber et al. (2006)
	England and Wales, UK	1990–1994	*Simplex*	No	72/101 (71.3%)	NA	NA	Gibson et al. (1998)
	Galicia, Spain	NA	*Anisakis* sp.	Yes	NA	33.3/66.7/0	NA	Abollo et al. (2003)
	Galicia, Spain	1991–1996	*Simplex*	No	32/50 (64%)	NA	NA	Abollo et al. (1998)
Bottlenose Dolphin								
NE Atl	Spain and Portugal	2004–2019	*Anisakis* sp.	Yes	NA	33.3/77.7/0	NA	Cipriani et al. (2022)
	Galicia, Spain	2017–2018	*Simplex*	No	2/7 (28.6%)	NA	NA	Pons-Bordas et al. (2020)
	The Netherlands	2013	*Simplex*	No	1/1 (100%)	NA	100s	van Beurden et al. (2015)
	Galicia, Spain	1992–1996	*Simplex*	No	6/10 (60%)	NA	NA	Abollo et al. (1998)
	England and Wales, UK	1990–1994	*Simplex*	No	2/3 (67%)	NA	NA	Gibson et al. (1998)
C Med	Adriatic Sea, Croatia	1990–2016	*Anisakis* sp.	No	9/23 (39.1%)	NA	NA	Hrabar et al. (2017)
	Adriatic Sea, Croatia	1990–2012	*Anisakis* sp.	Yes	35/130 (26.9%)	2.56/97.44/0	0–24,032 (1187)	Blažeković et al. (2015)
	Tyrrhenian Sea	2004–2019	*Anisakis* sp.	Yes	NA	0/100/0	NA	Cipriani et al. (2022)
W Med	Sardinia, Italy	2006–2011	*Anisakis* sp.	No	1/2 (50%)	NA	NA	Pennino et al. (2022)
	Spain	1989–2008	*Anisakis* sp.	No	3/15 (20%)	NA	0-2 (0.3)	Quiñones et al. (2013)

(*Continued*)

Table 4 (*Continued*) Cases Reported in the Literature of *Anisakis* spp. Infections in the Studied Species in European Waters (Cetacean Species, *Anisakis* spp. (Genetic Identification) and Ratio, No. Sampled Cetaceans, No. Infected Cetaceans, Prevalence, Abundance of Parasites (Mean, Range and Intensity), Location, Year, Stranded/Bycaught Cetaceans)

Region	Location	Sampling Period	Anisakis Species	Genetic Identification	Prevalence (No. Infected/Hosts)	Dominance (simplex/ pegreffii/Hybrid%)	Abundance (Average No.)	References
Striped Dolphin								
NE Atl	Scotland, UK	2004–2019	*Anisakis* sp.	Yes	NA (c)	100/0/0	NA	Cipriani et al. (2022)
	Spain and Portugal	2004–2019	*Anisakis* sp.	Yes	NA (c)	81.8/18.2/0	NA	Cipriani et al. (2022)
	Canary Islands, Spain	NA	*Simplex*	No	1/11 (9.1%)	NA	NA	Jaber et al. (2006)
	Galicia, Spain	NA	*Simplex*	Yes	NA	100/0/0	NA	Abollo et al. (2003)
	Galicia, Spain	1992–1996	*Simplex*	No	3/8 (37.5%)	NA	NA	Abollo et al. (1998)
	England and Wales, UK	1990–1994	*Simplex*	No	8/14 (57%)	NA	NA	Gibson et al. (1998)
	Polish Baltic Sea	1998–1999	*Simplex*	No	1/2 (50%)	X	0–118 (59)	Rolbiecki et al. (2021)
	Galicia, Spain	2017–2018	*Simplex*	Yes	4/5 (80%)	100/0/0	NA	Pons-Bordas et al. (2020)
C Med	Adriatic Sea	2004–2019	*Anisakis* sp.	Yes	NA (c)	0/100/0	NA	Cipriani et al. (2022)
	Adriatic Sea, Croatia	1990–2016	*Anisakis* sp.	No	3/12 (23%)	NA	NA	Hrabar et al. (2017)
	Adriatic Sea, Croatia	1990–2012	*Anisakis* sp.	Yes	13/25 (52%)	2.38/97.62/0	NA (1778.05)	Blažeković et al. (2015)
W Med	Sardinia, Italy	2006–2011	*Anisakis* sp.	No	2/20 (10%)	NA	NA	Pennino et al. (2022)

NA, not available information; NA, Information not available; Atl, Atlantic; Med, Mediterranean; N, North; E, East; C, Central; W, Western.

1–2 months is expected at least for *A. simplex* (s.s.), although it could be higher and species-dependent. Furthermore, already open ulcers could facilitate reinfection and remain open by continuously ingesting prey infected with *Anisakis*.

Mitigation measures and research needs

An increase of *Anisakis* abundance in cetaceans is expected to occur, like it is happening in their intermediate and paratenic hosts (e.g. Fiorenza et al. 2020). Global warming could provoke a direct effect on *Anisakis* presence and abundance, as temperature is one of the main natural driving factors in their distribution (Kuhn et al. 2016). In the NEA, *Anisakis* species could be expected to shift northwards of the southern limits of the cold-water species *A. simplex* (s.s.). In addition, warming waters might provide a more suitable habitat for species such as *A. typica*, which has not been described infecting cetaceans in the NEA.

Aiming for a reduction in *Anisakis* infection rates and/or infection loads is complicated for both cetaceans and their prey, as they are cosmopolitan parasites and occur in all oceans. Arguably, 'natural' *Anisakis* infections are not something which could or should be managed, and only measures targeting anthropogenic 'sources' of *Anisakis* are currently possible. Plausible measures aim at reducing the so-called 'anthropogenic shortcut' (Cipriani et al. 2018) by which fish offal (i.e. the most heavily infected part of the fish) is discarded at sea. González et al. (2018) developed a tool that thermally killed *Anisakis* larvae in offal, minimising the release of potential sources of infection back to the marine environment. *Anisakis* parasites are a human health risk of increasing importance (Bao et al. 2017), as well as a socioeconomic concern (Bao et al. 2019) and biological and ecological hazard (Fiorenza et al. 2020).

Long-term and standardised monitoring is needed to obtain a clearer picture of the threat that *Anisakis* represent to cetaceans, but also of the quantitative role of the definitive hosts in maintaining the continuity of the *Anisakis* life cycle via release of their eggs in the faeces, and of the parasite life cycles and routes of infection (i.e. environmental transference), as well as on amounts transferred between trophic levels, for their incorporation into food web and ecosystem models (Pons-Bordas et al. 2020, Terracciano et al. 2020, Dzido et al. 2021, Pennino et al. 2022). Strandings represent one of the few sources of parasitological information in cetaceans, but further efforts are recommended to ensure a routine and standardised data collection on parasites, including specific reference to recording and sampling parasites in necropsy protocols. Cetacean faeces could provide information on parasite eggs in cetaceans and can be obtained from non-invasive techniques (Aznar et al. 2002; Gomes et al. 2023). Cetaceans are ultimately proxies of the overall ecosystem status, arguably also in relation to *Anisakis*. Similar to what has been suggested for human anisakiasis monitoring (Adroher-Auroux & Benítez-Rodríguez 2020), the registration of cases at European level would allow researchers and managers to assess and analyse trends at a large scale.

Lungworms

Lungworms are nematodes of the suborder Strongylida, which infect the respiratory, cardiovascular and auditory systems of marine mammals, among other vertebrates (Measures 2001). Marine mammals are particularly vulnerable to lungworm infections since they are dependent on their cardiovascular, lung and auditory capacities for foraging dives, communication and echolocation (Kijewska et al. 2003). Lungworm infections have even been responsible of disease causing the death of cetaceans (Siebert et al. 2001).

Cetaceans are infected by the family Pseudaliidae, which includes three recognised subfamilies: Pseudaliinae, Halocercinae and Stenurinae. These families include six genera, of which the most relevant to our target species are *Pseudalis*, *Halocercus*, *Stenurus* and *Torynurus*.

In odontocete cetaceans, infections of 30 species of the family Pseudaliidae have been described (Measures 2001), of which the following species infect both Phocoenidae and Delphinidae families in Europe: *Pseudalius inflexus*, *Torynurus convolutus*, *Stenurus minor* and *Stenurus auditivus*. Species that exclusively affect Phocoenidae family are *Halocercus taurica* and *Halocercus invaginatus*. Species that affect only the Delphinidae family are *Stenurus globicephalae*, *Stenurus ovatus*, *Skrjabinalius cryptocephalus*, *Skrjabinalius guevarai*, *Halocercus delphini*, *Halocercus lagenorhynchi* and *Halocercus kleinenbergi*.

The family Pseudaliidae is distributed worldwide, especially in the northern hemisphere, affecting coastal or inshore populations of odontocetes (Measures 2001, Pool et al. 2023). The first historical record of a lungworm in a cetacean was the discovery of *P. inflexus* in the bronchi, blood vessels and heart of a harbour porpoise by Schneider in 1866 (Baylis 1932).

Transmission

Despite knowledge gaps in the infection process, it is known that they are infective at their larval state L3. Based on information compiled from both marine and terrestrial lungworms, the following life cycle of lungworms in marine mammals can be elucidated: eggs containing first stage larvae in the environment are eaten by an intermediate or directly definitive host. After penetrating the intestinal wall, they are encapsulated in the serosa, where they reach the infective state (L3). This L3 larvae migrate out of the intestinal wall via the bloodstream to the respiratory and cardiovascular systems, where they mature into the infecting adult phase and reproduce. When eggs hatch into first stage larvae, they ascend passively through the bronchial tree. Once there, they are either expelled through blowhole secretions or swallowed and excreted into the aquatic environment, where they are ingested by intermediate host starting a new life cycle (Dailey 1970, Anderson 2000, Anderson et al. 2009, Lehnert et al. 2010, Reckendorf et al. 2018, Pool et al. 2020, 2021).

The duration of the life cycle of a lungworm is the duration from the ingestion of their infective stage (larvae L3) to the excretion of infective larvae by the definitive host, which in terrestrial mammals is about 4 weeks long. The incubation period between the infection of an individual by the parasite and the appearance of the first symptoms is around 3 weeks.

The main route of transmission for lungworm infections is unclear. Lungworm infection has been recorded in neonates (Dailey et al. 1991, Balbuena et al. 1994, Fauquier et al. 2009, Reckendorf et al. 2018, Pool et al. 2021), consistent with transmission from mother to calf via placental and mammary transfer, as well as in calves postlactating period when beginning to feed on invertebrate and vertebrate preys, consistent with transmission through the food web (Geraci 1978, Clausen & Andersen 1988, Reyes & Van Waerebeek 1995, Faulkner et al. 1998). Even if less likely, indirect transmission routes might also occur through the environment, such as via contaminated water, aerosol or vomit (Measures 2001). Moreover, lungworms have been suggested to serve as vectors of virus and bacteria transmission (Caldwell et al. 1968, Dawson et al. 2008).

Effects

Pseudaliids primarily inhabit the respiratory tract and cranial sinuses of odontocetes, and they can be found in the blowhole, pterygoid sinuses, cranial sinuses, bronchi, bronchioles and parenchyma. Pseudaliids can be also found in the inner and middle ear. Depending on the species, some of them may migrate through the blood vessels to the heart during their life cycle (see Dzido et al. (2021) for more references), to the pulmonary pleura (e.g. *Monorygma* spp., unpublished information) or to the mammary glands (e.g. *Crassicauda* spp., Geraci & Aubin 1987, Duignan et al. 2003, Stockin et al. 2009).

Reliable detections of lungworm infections in live cetaceans require invasive techniques or samples that are challenging to obtain like bronchoscopy and faeces and sputum (Kastelein et al. 1990, Hunt et al. 2013, Kleinertz et al. 2014), since other potential diagnostic tools such as MSP-based serological tests have not resulted suitable yet for detection in small cetaceans such as harbour porpoises (Reckendorf et al. 2021). Other signs of lungworm infections that can be observed in cetaceans during necropsy are pulmonary consolidation, enlarged and oedematous pulmonary and bronchial lymph nodes and abscesses in the airway (Measures 2001). Past lungworm presence can be suggested from calcified and encysted worms (Caldwell et al. 1968).

According to testimonials in Caldwell et al. (1968), the first non-specific symptoms recorded in cetaceans infected with lungworms were the loss of appetite and lethargy. Some clinical signs described in live cetaceans are respiratory distress, rattling or coughing sounds, expectoration of frothy mucus or mucopurulent exudate, expelled worms and altered foraging capacities (Medway & Schryver 1973, MacNeill et al. 1975, Kastelein et al. 1990, 1997); however, these symptoms are non-specific (Measures 2001, van Elk et al. 2019), and consequently, they are not always associated with lungworms.

Lungworm infections can instigate secondary bacterial infections, chronic obstructive pulmonary disease (COPD) and bronchopneumonia, which can cause severe illness and ultimately death (e.g. Jepson et al. 2000, Siebert et al. 2001, 2006, 2020, Wünschmann et al. 2001, Jauniaux et al. 2002, Lehnert et al. 2005, Pool et al. 2001). Effects on reproduction from lungworm infections have been observed in cows, including significantly reduced milk yields, fertility decline and extended calving periods (May et al. 2018). Given that, more research is needed on the effects of pseudaliids on cetaceans.

There is still a lack of understanding on the factors driving effects of lungworm infections. However, compared to other cetacean species, it has been observed that harbour porpoises seem to be particularly vulnerable to pathogeny of some lungworms such as *P. inflexus* (Van Elk et al. 2019). On one hand, several studies have observed that harbour porpoises are able to tolerate large amounts of lungworms without apparent significant health problems (e.g. Clausen & Andersen 1988, Kirkwood et al. 1997, Faulkner et al. 1998, van Elk et al. 2019, Ryeng et al. 2022). However, on the other hand, lungworm infections have been frequently associated with pneumonia, which has been a common, even the main cause of death for harbour porpoises in some regions of the Northeast Atlantic, such as in the North Sea (Siebert et al. 2001, 2006, Jauniaux et al. 2002, Lehnert et al. 2005, Van Elk et al. 2019).

Prevalence and trends

The prevalence of lungworms in odontocete cetaceans is high, and there have been reports of lungworms observations in 100% of the examined animals since early reports back to the 1960s, for example, in harbour porpoises (Andersen 1966). As earlier mentioned, it seems that harbour porpoises are particularly vulnerable to *P. inflexus*, and there are other examples suggesting phylogenetic specificity, so host preference of certain lungworms species for certain cetacean species. However, differences exist among regions, such as those that can be observed in Galicia (Spain) where only *S. minor* was observed in stranded harbour porpoises (Saldaña et al. 2022). In the Mediterranean, Pool et al. (2021) observed that *H. delphini* was more abundant and prevalent in striped and common dolphins rather than in bottlenose dolphins, Risso's dolphins (*Grampus griseus*) and long-finned pilot whales (*Globicephala melas*), while *S. ovatus* was more common in bottlenose dolphins compared to the other 4 mentioned cetaceans. In comparison, *S. globicephalae* was the only lungworm species identified in stranded long-finned pilot whales and Risso's dolphins in the Galician coast (Saldaña et al. 2022).

Despite the fact that highest prevalence of active lungworm parasitism has been reported in neonates and calves in some studies such as Fauquier et al. (2009), lungworms prevalence and infection intensity has been observed to increase with age in cetaceans (Dailey et al. 1970, Balbuena et al. 1994, Measures 2001, Siebert et al. 2001, Houde et al. 2003, Lehnert et al. 2010, Tomo et al. 2010, Ten Doeschate et al. 2017, Van Elk et al. 2019).

Regional differences in lungworm infections prevalence and severity have been observed in the Northeast Atlantic. Lungworms prevalence seems to be lower and linked to milder pathologies in harbour porpoises in northern areas such as Norway, Sweden, Iceland and Greenland, compared to the Baltic and North Sea, where severe symptoms seem more common (Jepson et al. 2000, Siebert et al. 2001, 2006, 2020, Wünschmann et al. 2001, Jauniaux et al. 2002, Lehnert et al. 2005, Reckendorf et al. 2021, Neimains et al. 2022). In the northern areas associated with less polluted waters, inflammatory lesions in harbour porpoises, especially in their respiratory tracts, and severe bacterial infections have been observed less frequently (e.g. Wünschmann et al. 2001, Siebert et al. 2006, 2009). In comparison, remarkable high rates of inflammatory lesions were recorded in harbour porpoises in the Baltic Sea (Wohlsein et al. 2019, Siebert et al. 2020), and of bronchopneumonia, often linked to nematodes infection since early 1980s and representing the most common disease of harbour porpoises in the Netherlands (van Nie 1989, Addink et al. 1995, IJsseldijk et al. 2022). These regional differences may indicate differential preference of lungworm species for host porpoise populations and/or influence of environmental conditions modulating the prey and intermediate host distribution and life cycle viability (Beineke et al. 2005, Siebert et al. 2006, 2020).

Differences over time of the prevalence of lungworm infections have been observed in some areas and parasites species. For example, in Scotland, parasitic pneumonia was a common cause of death for harbour porpoises between 2008 and 2011, but afterwards, other causes were more prevalent such as interactions with bottlenose dolphins (Brownlow 2011, Brownlow et al. 2015, 2018). In opposition, an increase in the severity of bronchopneumonia associated to lungworms has been observed in Norway (Siebert et al. 2006, Ryeng et al. 2022). The prevalence of *P. inflexus* in harbour porpoises seems to have decrease in the last decades in few regions in the Northeast Atlantic. In Germany and Belgium, *P. inflexus* was detected in 89% of the examined harbour porpoises between 1990 and 1991 (Brosens et al. 1996) and in 33% of the examined porpoises stranded in Germany in 2019 (Gabel et al. 2021). In the Baltic Sea, the prevalence in porpoises of this lungworm decreased from 88.2% between 1989 and 1995 (Rokicki et al. 1997) to 63.5% from 1995 to 2019 (Dzido et al. 2021), and in Norway from 34.4% between 1988 and 1990 (Balbuena et al. 1994) to 26% in 2017 (Ryeng et al. 2022). On the contrary, an increase in the prevalence of *S. minor* in harbour porpoises was observed in Greenland, where it rose from 86% to 95% from 1995 to 2009 (Lehnert et al. 2014). An overall increase in the prevalence of lungworm species (*H. lagenorhynchi*, *S. ovatus* and *Pharurus alatus*) was observed in common dolphins in South Australia, where prevalence varied from 14% in 1990–2004 to 63% in 2005–2006 (Tomo et al. 2010).

Mitigation measures and research needs

Despite the fact that there is no recognised cure for lungworm infections in wild living cetaceans, some treatments have been applied to pinnipeds and cetaceans in aquaria and rehabilitation centres, such as the administration of the anthelmintic agent Diethylcarbamazine (Caldwell et al. 1968, Measures 2001). Usually in terrestrial mammals, a preventive approach is preferred, by means of vaccination and worming. However, measures to prevent infection or reduce its severity in wild marine mammals are not likely plausible. Future research is needed to comprehend the intricacies of lungworms transmission to cetacean definitive host and among populations, and elucidate the mechanisms linked to infectivity and pathogenesis. Dedicated investigations are advised to understand the drivers of infections of different lungworm species to different cetacean species, as well as to gather knowledge on the distribution of these lungworms that primary affect endangered cetacean species and populations. Furthermore, in-depth research on the cetacean characteristics that modulate the susceptibility to infection, such as sex or species of cetaceans, and the vulnerability to pathogenesis on their systems, such as auditory and cardiovascular, is needed. Since the respiratory system has been recommend as an indicator organ for the health status of the critically endangered population of harbour porpoises in the Baltic Sea by Siebert et al. (2020), ensuring constant and standard monitoring will be crucial for the development and implementation of this indicator.

Transferable stressors of anthropogenic origin: contaminants

It should be noted that in this review, the term ‘pollutant’ is used to define substances found in higher-than-normal concentrations due to human activity, which directly or indirectly cause adverse effects including damage to living organisms, human health or disruptions to marine activities. This definition is based on GESAMP (1990). The term ‘contaminant’, as defined by European legislation, specifically the Marine Strategy Framework Directive (Directive 2006/56/EC), refers to toxic and persistent substances liable to bioaccumulate. These substances are typically naturally occurring, but their movement or presence in the environment has been increased, either accidentally or intentionally – often, though not always, due to human activity – allowing them to enter the food chain at higher levels than would naturally occur. While all pollutants are contaminants, not all contaminants are pollutants (Chapman 2007), unless they cause harm or alter environmental conditions.

Persistent organic pollutants (POPs)

POPs are lipophilic, highly mobile, man-made and carbon-based chemicals that have been produced in large quantities and used widely (e.g. as organic solvents, pesticides, insecticides and fire retardants) (Sharma & Negi 2020). Although the usage of some compounds or formulations is banned or restricted (i.e. UNEP 2009, Stockholm Convention on Persistent Organic Pollutants 2019), POPs are of concern since they persist long term in the environment and are also subject to long-range transportation (Wania & Mackay 1996). The half-life of these compounds in seawater, which is determined by the biogeochemical processes occurring in the water column and the compound-specific properties, varies from days to years (40–60 days for POPs in marine water (EC 2003) to 2–3.4 years for hexachlorocyclohexanes (HCHs) in Antarctic seawater (Galbán-Malagón et al. 2013)). These values can be noticeably higher if the air compartment of the seawater environment is considered, since the half-life of POPs in the air is normally even longer (e.g. 5.7 years for PCBs in Antarctic seawater environment) (Dickhut et al. 2005). It should be noted that the half-life criterion for identifying a compound as persistent may vary depending on the regulatory body: UNEP,[1] UNECE[2] and EUvPvB[3] consider a POP in water persistent when its half-life is greater than 60 days, but other bodies such as CEPA[4] consider longer times (182 days) (Boethling et al. 2009). Most of these compounds are volatile and can evaporate, mainly at tropical temperatures, and global distillation or long-range atmospheric transport may occur in remote areas like the Arctic or Antarctic (Wania & Mackay 1993, Struntz et al. 2004, Wolkers et al. 2004, Lohmann et al. 2007, Garmash et al. 2013, Jepson & Law 2016, Hermanson et al. 2020, Singh & Chauhan 2021), North America and Western Europe being the major source regions identified (O’Sullivan & Sandau 2013). POPs present a high capacity to bioaccumulate and biomagnify in marine food webs (O’Shea & Tanabe 2002), and they also tend to accumulate in soils and sediments.

Most research on POPs in the marine environment and in marine mammals has focused on organo-halogenated contaminants since, on an industrial scale, they have been the most widely produced and used. These include organochlorine compounds such as PCBs (polychlorinated biphenyls), DDT (dichlorodiphenyltrichloroethane), its metabolite DDE (dichlorodiphenyldichloroethylene), CHL (chlordane), HCH (hexachlorocyclohexane), HCB (hexachlorobenzene), aldrin, dieldrin, dioxins, mirex and toxaphene. More recent concerns have been related to fluorinated compounds and perfluoroalkyl and polyfluoroalkyl substances (PFAS) (organofluorine compounds) including perfluorooctane sulfonate (PFOS), perfluorooctanoic acid (PFOA) and perfluorooctanesulfonamide (PFOSA), as well as organobromine and brominated compounds such as polybrominated diphenyl ethers (PBDEs), polybrominated biphenyls (PBBs), pentabromotoluene (PBT) and hexabromobenzene (HBB) (Taruski et al. 1975, Borrell 1993, Colborn & Smolen 1996, Kannan et al. 2002, Aguilar & Borrell 2005, Murray 2005, Houde et al. 2006b, Alonso et al. 2014, Law et al. 2014, Stohs 2014, Barón et al. 2015b, Reinke & Deck 2015, Desforges et al. 2018, Fair & Houde 2018, Pantelaki & Voutsa 2019, Sala et al. 2019, Simond et al. 2019, Stockholm Convention on Persistent Organic Pollutants 2019, Spaan et al. 2020, Andvik et al. 2021, Stockin et al. 2021).

POPs associated with plastic exposure in the marine environment are of increasing concern. Recent research has considered plasticizers such as phthalates or phthalate esters (PAEs), the dominant plasticizers for polyvinyl chloride (PVC) materials (Wadey 2003) and their relationship with the presence of (micro)plastics in marine mammals and their potential use as plastic tracers in the marine environment (Baini et al. 2017, Montoto-Martínez et al. 2021), as well as other plastic additives like bisphenols and nonylphenols (Hermabessiere et al. 2017). Organic esters such as organophosphate flame retardants (OPFRs) (organic esters of phosphoric acid-containing alkyl or aryl groups, which can be halogenated or not) have also been the subject of recent studies in cetaceans, as their production has increased as an alternative to PBDEs. These are a class of flame retardants also used as plasticizers or additives in consumer products (Sala et al. 2019).

Odontocete cetaceans occupy high trophic levels in the marine food webs, resulting in a greater exposure to POPs compared to that experienced by mysticete cetaceans or fishes (Houde et al. 2015). Cetaceans are able to biotransform some organic pollutants, which involves mixed-function oxidase enzymes, although the activity of these enzymes is higher in seals and terrestrial mammals than in cetaceans (Krahn et al. 2009, Jepson et al. 2016), but also about four times higher in odontocetes than in mysticetes (Fossi et al. 2000). However, their elimination, as well as that of their by-products, is limited, contributing to their bioaccumulation (Duinker et al. 1989, Tanabe et al. 1988, White et al. 2000).

In cetaceans, contaminant uptake primarily occurs through the diet (Aguilar et al. 1999). Given the high lipophilic characteristics of POPs, more than 90% of the total burden of these contaminants in cetaceans is concentrated in blubber (Yordy et al. 2010c). Once pollutants are stored in the lipid-rich blubber tissue, the compounds may be mobilised due to fasting or starvation, and at times during periods of intense energetic demand such as migration, pregnancy or lactation (Murphy et al. 2018). These bioenergetic bottlenecks will produce bioamplification of the contaminants as a consequence of the lipid loss and mobilisation of POPs to more sensitive tissues. This often occurs at life history stages that are most sensitive to the toxic effects of chemicals, like embryonic or juvenile development (Daley et al. 2014).

Transmission

POPs can traverse the placental membrane and can be transferred from the mother to the foetus. Nonetheless, transplacental transfer is considered to be low, for example, 4% for PCBs, 4.7% for DDT, 8.9% for HCH and 9.4% for HCB in striped dolphin (Tanabe et al. 1982); 4%–10% in the case of PCBs and DDT in long-finned pilot whale (Borrell et al. 1995). Highly halogenated biphenyls, which are more lipophilic, are less transferable from mother to foetus (Tanabe et al. 1982). Table 5 summarises the levels of organic pollutants, mainly PCBs and DDTs, which have been reported in the limited number of published mother–foetus pairs in small cetaceans (common dolphin, harbour porpoise and bottlenose dolphin). It should be noted that there have been very few experimental studies of the concentrations found in mother–foetus pairs to calculate the transmission rates (e.g. Alzieu & Duguy 1979, Storelli & Marcotrigiano 2003).

During lactation, there is a further mobilisation of POPs from the blubber of the mother to the milk (Borrell & Aguilar 2005). In cetaceans, especially the less substituted congeners or, in the case of PCBs, the less chlorinated congeners (Williams et al. 2020) are preferentially mobilised, as they are observed in higher proportions in juveniles than in adults (e.g. in harbour porpoise). Poor nutritional status in adult females can increase the off-loading into the milk (van den Heuvel-Greve et al. 2021). The off-loading percentage can vary between 70% and 88% of the mother's body load in striped dolphins, depending on the pollutant class (Tuerk et al. 2005) or between 60% and 100%

Table 5 Concentrations of Organic Pollutants Reported for Mother and Foetus Pairs in Small Cetaceans

Region	Location	Sampling Period	Sampled Tissue	Pollutants	Foetus	Mother	References	Units	Specifications
Harbour Porpoise									
NE Atl	France	1977	Placenta	tPCB	0.40	NA	Alzieu and Duguy (1979)	mg kg^{-1} tissue lyophilised	tPCB = Phenochlor DP6
				tDDT	0.11	NA			
			Blubber	tPCB	1.46	6.18			
				tDDT	0.37	1.66			
			Liver	tPCB	0.18	0.8			
				tDDT	<0.04	0.21			
			Kidney	tPCB	0.23	0.38			
				tDDT	<0.08	<8.87			
			Muscle	tPCB	0.38	0.19			
				tDDT	<0.11	<0.06			
	Ireland	2001–2004	Blubber	tPCB	1.790	3.796	Pierce et al. 2013	mg kg^{-1} lipid weight	tPCB = ∑25PCB (18,28, 31,44,47,49,52,66, 101,105,110,118,128, 138,2006) tPBDE = ∑5PBDE (47,100,99,154,153)
				tPBDE	0.171	0.354			
				tPCB	1.773	2.559			
				tPBDE	0.422	0.609			
Common Dolphin									
NE Atl	France	1977	Liver	tPCB	1.33	4.24	Alzieu and Duguy (1979)	mg kg^{-1} tissue lyophilised	tPCB = Phenochlor DP6
				tDDT	0.42	2.03			
			Kidney	tPCB	1.76	2.44			
				tDDT	<0.70	0.72			
	Ireland	2001–2004	Blubber	tPBDE	0.118	0.107	Pierce et al. 2013	mg kg^{-1} lipid weight	tPCB = ∑25PCB (18, 28, 31, 44, 47, 49, 52, 66, 101, 105, 110, 118, 128, 138, 2006)
				tPCB	1.055	0.960			
Bottlenose Dolphin									
C Med	Adriatic Sea	1996	Liver	tPCB	2.83	2.11	Storelli and Marcotrigiano (2000)	μg^{-1} lipid weight	tPCB = ∑11PCB (8, 20, 28, 35, 52, 101, 118, 138, 153, 180, 209)
				tDDT	1.63	5.80			
			Kidney	tPCB	5.08	7.89			
				tDDT	6.03	1.29			
			Uterus	tPCB	NA	3.33			
				tDDT	NA	5.83			
			Placenta	tPCB	NA	2.5			
				tDDT	NA	3.00			

Information on the Location and Time of the Sample Collection is Provided. The concentrations are arranged according to the tissues sampled and the contaminants analysed (the list of congeners of each compound is included, as well as the units). NA, Information not available; Atl, Atlantic; Med, Mediterranean; N, North; E, East; C, Central.

in long-finned pilot whales (Borrell et al. 1995). The off-loading from a mother to her first calf is of particular concern. In the case of bottlenose dolphins, Cockcroft et al. (1989) estimated that almost 80% of the pollutant load of females was passed to the first-born calf, constituting a higher risk for those individuals than to subsequent calves.

Levels and trends

POPs include a wide range of different compounds whose physico-chemical properties determine their persistence in the environment and in organisms (bioavailability), their mobility and their affinity for different tissues, among other characteristics. In cetaceans, a higher transfer efficiency has been suggested for DDTs compared to PCBs and PBDEs given the lower halogenation of the former (Tanabe et al. 1982, Borrell et al. 1995, Borrell et al. 2001, Cadieux et al. 2016). The tissue concentrations of the most common studied POPs in marine mammals are typically such that ΣPCB > ΣCHL ≈ ΣDDT ≈ ΣPFSA (Perfluoroalkyl and Polyfluoroalkyl Substances) > ΣCBZ (carbamazepine) ≈ ΣHCH ≈ ΣToxaphene ≈ ΣPFCA > ΣPBDE > HBCD (Hexabromocyclododecane) (Borrell & Aguilar 2005, 2007, Carballo et al. 2008, Law et al. 2012, Letcher et al. 2010, Shoham-Frider et al. 2009).

In cetaceans, pollutant levels are often estimated from stranded animals, but they can also be inferred from free-ranging animals (e.g. through biopsies, blow and faecal samples). Stranded animals may represent a biased proportion of the real status of the sampled population because animals with higher concentrations of POPs in their tissues may be more likely to die (Marsili et al. 2018), but also because high concentrations may be caused by a reduction in the blubber layer due to illness. In striped dolphins from the Strait of Gibraltar, stranded specimens had pollutant levels (PBDEs and MeO-PBDE) around three times higher (Barón et al. 2015a) than dolphins biopsied in the same area (Barón et al. 2015b).

The concentrations of POPs in cetaceans may be influenced by several biological and ecological factors, which could thus help explain the spatio-temporal variability and the differences in the concentration observed between species, populations, sexes and stages of development (Aguilar et al. 1999). The first of these factors, and probably the most influential, is diet. Most POPs increase in concentration as the trophic level increases, a phenomenon known as biomagnification, the extent of which depends on the POP structure, its lipophilic characteristics and degradation rate. Pollutants are metabolised and accumulated differently, which can be addressed by studying congener-specific levels and patterns of each individual (or tissue), population or species (Wolkers et al. 2004). Differences in pollutant congener profiles between individuals support the classification into different ecotypes of a species (e.g. killer whales), which are consistent with the dietary ecotype differentiation as revealed by fatty acid and stable isotope profiles (Herman et al. 2005) and can even be used as tracers to estimate other biological parameters (e.g. the lactation period) (Subramanian et al. 1988).

Continuing with the biological factors determining the POP concentrations and their variability, the metabolic processes, i.e. the ability of the organisms to assimilate, metabolise and excrete pollutants, also influence POPs load (Norstrom et al. 1992, Marsili & Focardi 1996, Borrell & Aguilar 2005a). Metabolic processes vary between cetacean species, as in the case of striped dolphins and common dolphins, which, despite their close taxonomic relationship, exhibit substantial differences in their ability to degrade PCBs by oxidative metabolism (Tanabe et al. 1988, Marsili et al. 1996, Borrell & Aguilar 2005a). Once the compounds are metabolised, usually into more water-soluble forms, they can be excreted through various mechanisms, for example, in the bile, faeces or in the urine. This latter type of excretion has been described in cetaceans for compounds such as perfluoroalkyl compounds (PFCs) (Houde et al. 2006a).

Thirdly, body size also affects POP concentrations, mainly because the process of bioaccumulation continues throughout an animal's life, but this may be modified by several size-related processes: the higher metabolic rate of smaller animals results in a higher intake of food (and hence POPs) per unit of body weight, but larger animals display a reduced activity of detoxifying enzymes. Finally, once females are mature, they can start to offload POPs to their offspring via placental transfer and lactation. Body composition is also relevant, since the relative blubber mass of an individual determines the load of lipophilic contaminants – as is nutritional status – for example, periods of high energetic demand (see section ‘Transmission’) will lead to increased lipid mobilisation and thus mobilisation of pollutants that can be metabolised, excreted or moved to other organs and tissues where they can produce negative effects. The incidence of diseases may affect POPs concentrations by reducing food intake and hence negatively affecting nutritional status, but also may have an effect by altering physiological, immune and reproductive functions.

Finally, the pollutant load depends on age, sex and reproductive status. In reproductively active females, as mentioned above, POPs are transferred to the calves through the placental membrane and lactation, which significantly reduces pollutant concentration of POPs in females, to varying degrees depending on the specific compound (Tanabe et al. 1982, Aguilar et al. 1999, Borrell et al. 2001, Borrell & Aguilar 2005b, Wells et al. 2005, Yordy et al. 2010a, Desforges et al. 2012, Cadieux et al. 2016), while POPs will continue to accumulate in males and non-fertile females (Aguilar et al. 1999, Pettersson et al. 2004, Krahn et al. 2009, Cadieux et al. 2016 and numerous other studies). The extent to which POPs are reduced in reproductively active females evidently depends on the rate of the reproduction (Aguilar et al. 1999), which in turn depends on to the life history (Yordy et al. 2010c) and reproductive strategy of the species (Tuerk et al. 2005). Over the course of an individual’s life, as is the case for body size, POPs concentrations will tend to increase with age (Aguilar et al. 1999, Krahn et al. 2009, Jepson et al. 2016, Williams et al. 2020). Table 6 lists the concentrations of organic contaminants reported in the blubber of different cetacean species in Europe by sex and maturity state (when available). Further, Figure 1 shows the identified temporal trends in the concentrations of organic pollutants.

Additionally, other ecological and external factors affect the concentrations of POPs in individuals and populations. Evidently, POPs intake depends on diet and on concentrations in prey organisms. Ultimately, geographical differences mainly reflect different background levels of environmental pollution levels. For example, the Mediterranean Sea is a partially enclosed basin with high levels of human activity on its coasts, and pollution levels in this area are considerably higher than in many other areas (Marsili et al. 2018). Thus, POPs concentrations in cetaceans will be related to home ranges, distribution and migration patterns at the basin scale (e.g. Mediterranean vs. Atlantic) (Aguilar et al. 2002, Hansen et al. 2004) – but also at the fine scale (≈ 70 km) (Litz et al. 2007). These regional differences in POPs concentrations can also be observed in the main prey species consumed by small cetaceans. For example, Bodigel et al. (2008) found that PCBs and PBDEs concentrations in hake were 1.6–13.5 times higher in the Mediterranean Sea than in the Atlantic. More recently, Moraleda et al. (2015) observed still high PCBs concentrations in hake in the Mediterranean compared to the Atlantic, but no significant differences in PAHs concentrations. Anecdotally, two main prey species of hake, namely anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), showed higher organophosphate ester (OPE) concentrations than the proper hake, indicating a low bioaccumulation of OPEs and suggesting either the volatile nature of these pollutants or their high rate of metabolisation (Sala et al. 2022).

Effects and thresholds

Negative effects of POPs are best known for DDTs and PCBs. PCBs are known to affect both the immune and reproductive systems of mammals such as cetaceans. PCB-mediated effects on reproduction and immune function can reduce the long-term viability of the populations and potentially lead to local extinctions (Jepson et al. 2016, Desforges et al. 2018). High PCB burdens are thought to be reducing the long-term viability of more of the 50% of the world’s killer whale populations (Desforges et al. 2018).

Given the numerous constraints, including legal, ethical and logistical restrictions, on conducting direct experiments to obtain dose–response functions on cetaceans, studies of the direct effects of pollutants on these species are scarce. Thus, the most common approach to predict the health effects of pollutants exposure is based on probabilistic risk assessments, which typically integrate

Table 6 Concentrations of the Most Studied Persistent Organic Pollutants Reported in Small Cetaceans in European Waters Since Records are Available

Sex/Age	Region	Location	Time Series	tPCB[a]	tPBDE	DDT	CHL	HCB	HCBD	PAEs	References
Harbour Porpoise											
Neonate	NE Atl	North Sea	1990–1998	13.7 (1)	0.13 (1)	1.9 (1)	0.15 (1)	0.14 (1)			Weijs et al. (2010)[c]
			2000–2008	16.8 (2)	0.46 (2)	1.8 [0.5–3] (2)	0.19 [0.02–0.35] (2)	0.10 [0.02–0.18] (2)			
Calf		North Sea	1990–1998	10 [8.2–11.6] (3)	2.58 [1.48–4.06] (3)	2.2 [1.9–4.7] (3)	0.25 [0.22–0.27] (3)	0.12 [0.08–0.14] (3)			Weijs et al. (2010)[c]
			2000–2008	12.8 [4–25.2] (11)	0.56 [0.23–1.46] (11)	2.4 [0.8–3.6] (11)	0.27 [0.07–0.38] (11)	0.10 [0.05–0.19] (11)			
Juvenile		North Sea	1990–1998	19.1 (1)	4.77 (1)	4.5 (1)	0.68 (1)	0.19 (1)			Weijs et al. (2010)[c]
			2000–2008	9.9 [1.1–68.2] (5)	0.49 [0.28–1.5]	1.7 [0.4–6.4] (5)	0.19 [0.07–0.55] (5)	0.14 [0.05–0.21] (5)			
Adult		North Sea	1990–1998	81.5 (1)	1.9 (1)	22.9 (1)	3.61 (1)	0.35 (1)			Weijs et al. (2010)[c]
			2000–2008	24.9 [15.3–34.5] (2)	0.43 [0.33–0.52] (2)	3.4 [2.3–4.4] (2)	0.69 [0.37–1.04] (2)	0.09 [0.08–0.09] (2)			
NA		Cardigan Bay, UK	1988	55.63 ± 29.27 (4)		13.38 ± 6.77 (4)					Morris et al. (1989)[b]
Females		Scotland, UK	2001–2003	20.32 (25.24, 31)	1.369 (1.352, 31)				0.224 (0.256, 20)		Pierce et al. (2008)
		Ireland	1990–1994	7.999 ± 3.282 [3.041–12.270] (12)		4.664 ± 1.581 [1.640–5.989] (12)					Smyth et al. (2000)
			2001–2003	10.49 (9.45, 12)	0.656 (0.492, 12)				0.296 (0.272, 7)		Pierce et al. (2008)
		France	2001–2003	27.6 (20.88, 2)	1.398 (0.939, 2)				0.153 (0.110, 2)		Pierce et al. (2008)
		Galicia, Spain	2001–2003	10.27 (7.97, 3)	0.284 (0.044, 3)				0.121 (0.037, 3)		Pierce et al. (2008)
			2004–2008	37.5 ± 30.8 (3)							Méndez-Fernandez et al. (2014)

		UK	1990–2012	13.49 [0.40–159.68] (318)				Jepson et al. (2016b)
			1991–2017	16.31 [0.46–159.68] (731)				Williams et al. (2021)
		North Sea	2001–2003	30.60 (17.99, 19)	1.056 (0.803, 19)		0.108 (0.035, 12)	Pierce et al. (2008)
Males (mature)	NE Atl & Baltic Sea	Kattegat Sea	1978–1981	40 ± 22 [17–67] (5)		98 ± 43 [35–154] (5)		Berggren et al. (1999)
			1988–1990	13 ± 5.2 [6.7–22] (10)		25 ± 20 [2.8 -61] (10)		Berggren et al. (1999)
		Norway	1988–1990	15 ± 11 [7.2–33] (8)		9.1 ± 7.4 [3.1–22] (8)		Berggren et al. (1999)
		Baltic Sea	1988–1989	46 ± 29 [14–78] (4)		116 ± 134 [20–308] (4)		Berggren et al. (1999)
		Sweden	1996	0.000241 ± 0.000021 (3)				Ishaq et al. (2000)
		Ireland	1990–1994	6.148 ± 2.802 [2.91–10.429] (6)		3.46 ± 1.132 [1.838–4.941] (6)		Smyth et al. (2000)
Males (immature)	NE Atl & Baltic Sea	Kattegat Sea	1989–1990	11 ± 5 [2.2–20] (10)		20 ± 13 [5.7–36] (10)		Berggren et al. (1999)
		Baltic Sea	1985–1993	16 ± 8 [2.9–32] (13)		15 ± 0.69 [1.5–59] (13)		Berggren et al. (1999)
Males	NE Atl	Scotland, UK	1990	33.2 (1)				Wells and Echarri (1992)
		UK	1990–2012	19.41 [0.44–150.47] (388)				Jepson et al. (2016b)

(*Continued*)

Table 6 (*Continued*) Concentrations of the Most Studied Persistent Organic Pollutants Reported in Small Cetaceans in European Waters Since Records are Available

Sex/Age	Region	Location	Time Series	tPCB[a]	tPBDE	DDT	CHL	HCB	HCBD	PAEs	References
		Iceland	1992		0.09 [0.09–0.09] (3 pools of 3–6 inds)						Rotander et al. (2012)[c]
			1997		0.08 [0.07–0.09] (3 pools of 3–6 inds)						Rotander et al. (2012)[c]
		Norway	1987–1991	23.27 [3.71–65.26] (34)		16.39 [3.22–45.09] (34)		0.62 [0.19–2.59] (34)			Kleivane et al. (1995)
			2000		0.16 [0.07–0.54] (3 pools of 3–6 inds)						Rotander et al. (2012)[c]
		Galicia, Spain	2004–2008	50.8 (1)							Méndez-Fernández et al. (2014)
Both sexes	NE Atl & Baltic Sea	Wales and England, UK	1996–1998		2.35 ± 2.01 [0.08–7.67] (59)						Law et al. (2002)
		Scotland, UK	1965–1967			21.1 [13.1–25.7]					Holden and Marsden (1967)[d]
		Iceland, Baltic Sea, North Sea & Norway	NA	5.41 ± 5.37 [0.4–26.71] (59)	0.46 ± 0.86 [0.02–4.92] (59)	0.51 ± 0.95 [0.05–7.02] (59)					Beineke et al. (2005)
		North Sea	1993–1995	17.01 [4.48–39.13] (11)		<0.0015 (11)		0.19 [0.1–0.53] (11)			Bruhn et al. (1999)
			1999		2131 (3)						Boon et al. (2002)

		Baltic Sea	1993–1995	14.91 [5.61–38.55] (18)		<0.0015 (18)	0.31 [0.14–0.92] (18)		Bruhn et al. (1999)
		Denmark	1986–1988	13.1 ± 10.47 (27)		14.94 ± 13.84 (27)			Granby and Kinze (1991)
Common Dolphin									
Females	NE Atl & W Med	France	1972–1977	122.9 ± 91.1 (12)		19.6 ± 19.0 (12)			Alzieu and Duguy (1979)
	NE Atl	Ireland	2001–2003	6.92 (6.40, 11)	0.758 (0.505, 11)			1.086 (1.137, 7)	Pierce et al. (2008)
			1990–1994	4.225 ± 5.932 [0.748–11.074] (8)		3498 ± 9.951 [0.244–12.743] (8)			Smyth et al. (2000)
		France	2001–2003	24.64 (22.93, 36)	0.61 (0.41, 36)			0.433 (0.211, 31)	Pierce et al. (2008)
		Galicia, Spain	1986	23.91 ± 17.74 [5.81–60.22] (33)		5.12 ± 3.13 [0.99–10.73] (33)			Borrell et al. (2001)
			2001–2003	19.88 (20.80, 23)	0.42 (0.18, 23)			0.19 (0.10, 23)	Pierce et al. (2008)
			2004–2008	8.7 ± 8.1 (11)					Méndez-Fernández et al. (2014)
Females (mature)	W Med	Alboran Sea	1992–1994	22.17 ± 16.92 [5.26–39.09] (2)		17.36 ± 14.48 [2.88–31.84] (2)			Borrell et al. (2001)
Females (immature)	W Med	Alboran Sea	1992–1994	25.38 ± 17.85 [5.53–69.05] (9)		25.54 ± 22.91 [4.04–86.17] (9)			Borrell et al. (2001)

(*Continued*)

Table 6 (*Continued*) Concentrations of the Most Studied Persistent Organic Pollutants Reported in Small Cetaceans in European Waters Since Records are Available

Sex/Age	Region	Location	Time Series	tPCB[a]	tPBDE	DDT	CHL	HCB	HCBD	PAEs	References
Males	NE Atl	Ireland	1990–1994	8.945 ± 5.945 [1.555–15.883] (8)		9.444 ± 6.812 [2.385–15.115] (8)					Smyth et al. (2000)
		Galicia, Spain	1986	37.85 ± 18.99 [9.24–86.24] (33)		9.51 ± 4.17 [2.00–20.89] (33)					Borrell et al. (2001)
			2004–2008	38.9 ± 22.2 (8)							Méndez-Fernández et al. (2014)
	C Med	Adriatic Sea	2004	138.1 (1)		105.9 (1)		0.4 (1)			Lazar et al. (2012)
	W Med	France	1972–1977			73.5 (12)[b]					Alzieu and Duguy (1979)
Males (mature)	W Med	Alboran Sea	1992–1994	88.26 ± 37.74 [36.06–124.03] (3)		118.68 ± 54.76 [41.81–165.26] (3)					Borrell et al. (2001)
Males (immature)	W Med	Alboran Sea	1992–1994	20.42 ± 7.71 [7.70–29.39] (8)		19.27 ± 6.57 [7.98–28.21] (8)					Borrell et al. (2001)
Both sexes	NE Atl	Galicia, Spain	1984	31.11 ± 18.19 [8.14–71.86] (54)		15.54 ± 8.47 [5.46–39.73] (54)					Borrell et al. (2001)
	W Med	Alboran Sea	2004–2011		1 [0.09–2.04] (10)						Barón et al. (2015b)
Bottlenose Dolphin											
Female	W Med	Spain	1978–2002	286.61 ± 274.59 [23–1377.2] (36)		125.80 ± 128.46 [6.5–548.8] (35)		1.06 ± 1.18 [0–5.2] (27)			Borrell and Aguilar (2007)

	C Med	Tyrrhenian and Adriatic Sea	1987–1992	33323 [200–139854] (8)		9270 [515–46144] (8)		378 [32–950] (8)		Marsili and Focardi (1997)[b]
		Adriatic Sea	1992	1000 ± 750 (7)		330 ± 390 (7)				Corsolini et al. (1995)
	NE Atl	Cardigan Bay, UK	NA	16.5 (1)						Wells and Echarri (1992)
Female (Calf)	NE Atl	Scotland, UK	1988	290 (1)		150 (1)				Morris et al. (1989)[b]
Males	NE Atl	Canary Islands, Spain	1993–2001	12.74 ± 9.79 (7)			1.26 ± 1.18 (7)	0.043 ± 0.030 (7)		Carballo et al. (2008)
		Ireland	2000	23.9 ± 20.8 (6)		3.17± 4.22 (6)	0.55 ± 0.5 (6)	0.04 ± 0.035 (6)		Berrow et al. (2002)
	C Med	Adriatic Sea	1999–2000	32.71 ± 16.95 [7.26–56.96] (9)						Storelli and Marcotrigiano (2003)
No sex	C Med	Ligurian Sea	2014						29,156 (1)[b]	Baini et al. (2017)
Both sexes	C Med	Tyrrhenian, Adriatic and Ligurian	1990–1992		0.24 [0.07–0.52] (4)					Petterson et al. (2004)
		Adriatic Sea	2000–2005	97 ± 133 [2–494] (13)		47 ± 75 [0.4–279] (13)				Romanić et al. (2014)
		Ligurian Sea	2007–2009	367.9 (9)		143.7 (9)				Lauriano et al. (2014)

(*Continued*)

Table 6 (*Continued*) Concentrations of the Most Studied Persistent Organic Pollutants Reported in Small Cetaceans in European Waters Since Records are Available

Sex/Age	Region	Location	Time Series	tPCB[a]	tPBDE	DDT	CHL	HCB	HCBD	PAEs	References
	W Med	Alboran Sea	2004–2011		0.85 (1)						Barón et al. (2015b)
		Catalonia, Spain	1994–2002	161. 23 ± 84.76 (14)		52.82 ± 28.91 (14)		0.62 ± 0.34 (14)			Borrell et al. (2006)
		Community of Valencia, Spain	1994–2000	174.35 ± 114.30 (15)		66.31 ± 40.13 (15)		0.58 ± 0.31 (15)			Borrell et al. (2006)
		Balearic Islands, Spain	1997–2001	117.34 ± 104.10 (8)		64.63 ± 40.13 (8)		0.52 ± 0.38 (8)			Borrell et al. (2006)
	NE Atl	Portugal	1995–2000	75.31 ± 39.45 (7)		31.03 ± 20.04 (7)		0.38 ± 0.2 (7)			Borrell et al. (2006)
		Huelva, Spain	2000–2001	182.58 ± 90.76 (5)		113.95 ± 39.98 (5)		0.32 ± 0.11 (5)			Borrell et al. (2006)
Striped Dolphin											
Females	W Med	France	2007–2009	45.32 ± 45.69 (13)		13.79 ± 13.62 (13)					Wafo et al. (2012)
Males	W Med	France	2007–2009	57.72 ± 41.90 (19)		14.38 ± 7.40 (19)					Wafo et al. (2012)
Both sexes	NE Atl	Cardigan Bay, UK	1988	21.5 (1)		49 (1)					Morris et al. (1989)[b]
	NE Atl & W Med	France	1972–1977	266.9 ± 250.7 (8)		70.9 ± 68.7 (8)					Alzieu and Duguy (1979)[b]
	W Med	France	2007–2009	57.34 ± 46.23 (37)		15.99 ± 13.27 (37)					Wafo et al. (2012)

Spain	1987–2002	199 ± 150 (186)		114 ± 103 (183)	Aguilar and Borrell (2005)
	1990	393 ± 202 [94–670] (10)		139 ± 84 [22–230] (10)	Kannan et al. (1993)
	1990–1992	855.9 ± 569 (30)			Borrell et al. (1996)
Catalonia, Community of Valencia and Balearic Islands	2004–2009	45.60 ± 36.60 [7.33–152.54] (28)		49.91 ± 55.23 [5.65–258.16] (28)	Castrillón et al. (2010)
Alboran Sea	2004–2011		0.94 [0.01–2.25] (11)		Barón et al. (2015b)
Spain	1992–1994	68 ± 39 (24)		79 ± 47 (24)	Borrell and Aguilar (2005a)
France				344.2 (8)	Alzieu and Duguy (1979)
	2000–2003	69,98 [43.83–110.34] (3)		4.04 [2.71–6.66] (3)	Wafo et al. (2005)
	2010–2016	21.06 [5.24–71.91] (45)		10.78 [1.24–38.72] (45)	Dron et al. (2022)

(*Continued*)

Table 6 (*Continued*) Concentrations of the Most Studied Persistent Organic Pollutants Reported in Small Cetaceans in European Waters Since Records are Available

Sex/Age	Region	Location	Time Series	tPCB[a]	tPBDE	DDT	CHL	HCB	HCBD	PAEs	References
	C Med	Tyrrhenian, Adriatic and Ligurian Sea	1988–1994	78.86 ± 139.19 [9.20–573.26] (24)		41.90 ± 88.94 [4.91–349.96] (24)					Marsili et al. (1997)
			1990–1992		3.62 [0.73–8.13] (5)						Petterson et al. (2004)
		Tyrrhenian and Ligurian Sea	1989–1990	35.59 ± 47.75 [7.2–89.6] (3)							Reich et al. (1999)
		Ligurian Sea	1990–1993	[46.8–86.0] (24)		[23.6–63.5] (24)					Marsili et al. (1996)[b]
			2007–2009	139.9 (15)		92.9 (15)					Lauriano et al. (2014)
			2014							26,212 (1)	Baini et al. (2017)[b]
		Tyrrhenian Sea	2002	13.23 ± 6.35 [3.01–22.71] (9)		10.04 ± 5.31 [2.19–18.17] (9)		0.07 ± 0.09 [0.01–0.31] (9)			Fossi et al. (2004)
		Adriatic Sea	1999–2004	21.99 ± 20.31 [1.14–69.82] (17)							Storelli et al. (2012)

Information is provided by species (on bottlenose dolphin, common dolphin, striped dolphin and harbour porpoise), sex and maturity state (when available), sampling area and time series. The table shows the Concentrations of PCB, PBDE, DDT, CHL, HCB, HCBD and PAEs in blubber, describing their mean value ± standard deviation, range between square brackets and the number of samples between brackets.

[a] The total number of congeners of each compound studied in the different studies may vary, so in Table S5, it is specified which congeners are reported in each study, if available in the published literature.

[b] The units are µg g^{-1} w.w. (Morris et al. 1989), ng g^{-1} d.w. (Marsili & Focardi 1996, Baini et al. 2017), mg kg^{-1} lyophilised d.w. (Alzieu & Duguy 1979) and µg g^{-1} d.w. (Marsili et al. 1996, Marsili & Focardi 1997, Fossi et al. 2004).

[c] Values provided are the median values, not the mean.

[d] The units are ppm.

NA, Not available.

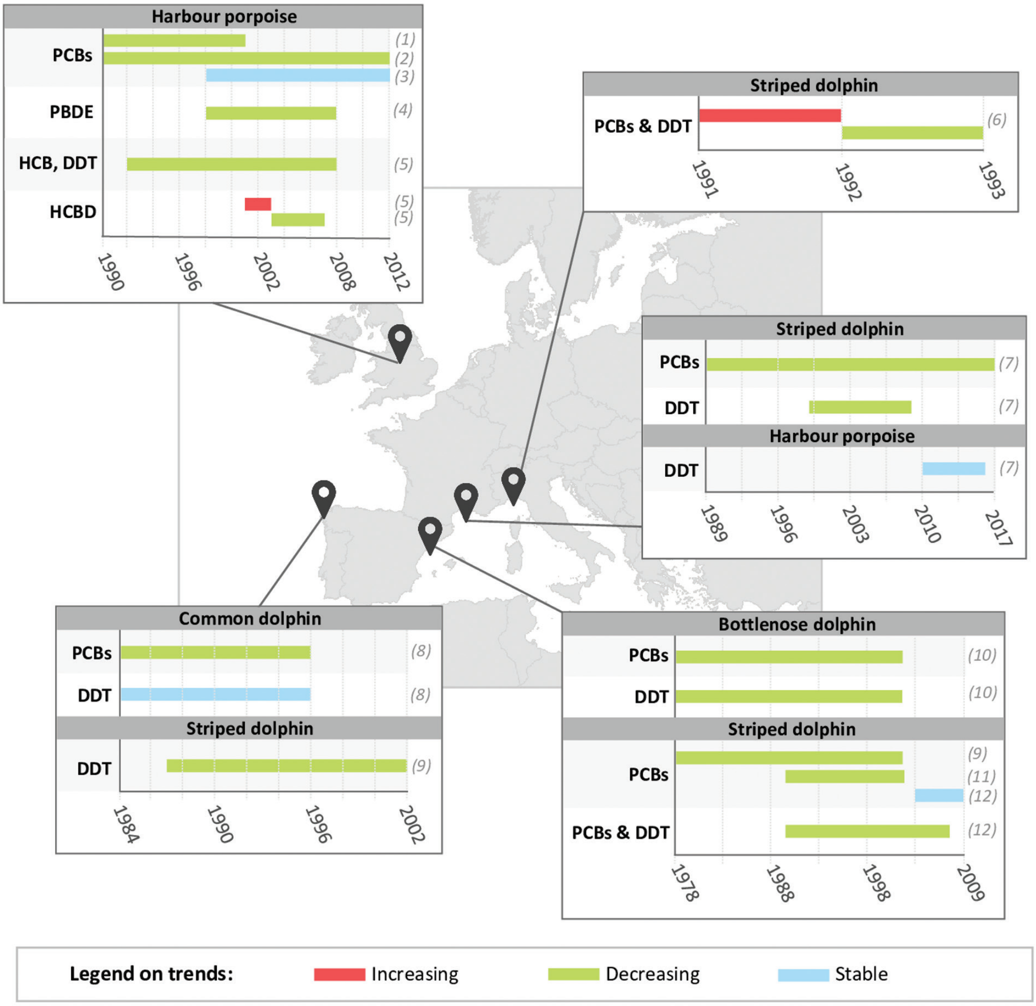

Figure 1 Graphs of the overall trends in concentrations (red = increasing trend, green = decreasing trend, blue = stable trend) of several persistent organic pollutants in the small cetacean species studied, represented by horizontal bars, by compound, by area and by time series. Numbers in brackets to the right of each horizontal bar indicate the reference of the corresponding study: (1) Jepson et al. (2005); (2) Jepson and Law (2016); (3) Jepson et al. (2016a); (4) Law et al. (2010); (5) Law et al. (2012); (6) Marsili and Focardi (1996); (7) Dron et al. (2022); (8) Borrell et al. (2001); (9) Aguilar and Borrell (2005); (10) Aguilar and Borrell (2007); (11) Castrillón et al. (2010); (12) Jepson et al. (2016b).

pollutant concentrations observed in a sample of animals from a population of cetaceans (often stranded animals) and a surrogate dose–response relationship based on other mammals (e.g. mink) (Kannan et al. 2000, Schwacke et al. 2009). Various threshold concentrations of PCBs for effects on reproduction have been proposed (see Table 7).

Specific effects on immune function have been identified from *in vitro* studies: a significant negative correlation between PCB concentrations and lymphocyte proliferative responses to mitogen stimulation was found for bottlenose dolphins (Lahvis et al. 1995), and splenocyte proliferative responses in beluga (*Delphinapterus leucas*) leukocytes were significantly reduced after exposure to mixtures of PCB and DDT (Guise et al. 1998). Beineke et al. (1995) found that PCB and PBDE

Table 7 Organic Pollutants Threshold Levels Proposed in the Literature for the Cetacean Species of Concern for this Review and Brief Description of the Associated Health Effects or Response of Cetaceans

Contaminant	Species	Threshold	Effect/Response	References
PCB	Bottlenose dolphin	700 ng g^{-1} w.w.	Immune system: 50% reduced proliferative response of lymphocytes	Lahvis et al. (1995)
		0.14 ± 0.25 ppm[a]	Immune system: Reduced lymphocyte proliferation	Desforges et al. (2016)
		14.8 µg g^{-1} l.w. (Σ15PCBs)	Reproductive effects (based on a fitted dose–response model, probabilistic risk assessment of reproductive effects)	Schwacke et al. (2002)
4,4′-DDE and PCB138 (antiestrogenic contaminant)	Bottlenose dolphin	20 µmol L^{-1}[a]	Reproductive effects: Estrogenic effects	Yordy et al. (2010a)
OHC	Harbour porpoise	1 ppm	Higher risk of deleterious effect on health	Letcher et al. (2010)

In the case of threshold values for PCBs, it should be noted that most studies report threshold values for the total sum of PCB congeners, without these necessarily being the same. Contaminant concentration is also measured in different units.

[a] Indicates that the threshold has been established from dose–response relationships or bioassays.

concentrations were significantly correlated with thymic atrophy and splenic depletion in harbour porpoise in German and *Baltic* Seas.

PCBs contamination reduces the reproductive capacity of cetaceans, through diverse mechanisms like direct reproductive dysfunction or calf survival capacity (Hall et al. 2018), as evidenced by population declines observed in numerous cetacean populations that have been studied extensively such as the beluga whale population of St. Lawrence (Martineau et al. 1987, De Guise et al. 1995), the Northeast Atlantic populations of harbour porpoises and killer whales and the western Mediterranean population of striped dolphins (Desforges et al. 2018, Jepson et al. 2016). Nonetheless, it is not always possible to link PCB exposure directly or in isolation to population declines.

Various pathologies have been associated with PCBs, mainly in females, resulting from the exposure to these contaminants although there are other confounding factors that are difficult in the distinction of these effects (Murphy et al. 2018). Reproductive disorders in female cetaceans associated with high concentrations of PCBs described in the literature include cancer (ovarian tumours and adenocarcinomas) (Martineau et al. 2002), hermaphroditism (De Guise et al. 1994), ovarian luteinized cysts that may lead to abortions (Munson et al. 1998), other tumours (cervix squamous cell carcinoma and leiomyoma) but also some lesions and infections of the reproductive tract like papilloma-like lesions, endometritis and vaginal plaques (Murphy et al. 2015). It has been shown through causal relationship studies that high concentrations of PCBs in common dolphins do not inhibit ovulation, conception or foetal implantation but do inhibit foetal or neonatal survival (Murphy et al. 2015). This effect, which is after all the result of numerous dysfunctions of the reproductive system and gestational development, has also been described in harbour porpoises (Murphy et al. 2015), bottlenose dolphins (Schwake et al. 2002) and beluga whales (De Guise et al. 1995).

Reproductive effects in males are less well known, but generally exposure to high concentrations of PCBs has been associated to a general reduction in fertility in male harbour porpoises of UK (Williams et al. 2020), reflected for example through reduced testes weights, which are correlated with sperm production (Williams et al. 2021). Due to maternal transfer, high PCB concentrations can reduce foetal and neonatal survival in common dolphins, although subsequent calves may benefit from the mother having a reduced PCBs load. Murphy et al. (2018) observed that some previously gravid resting females had not successfully offloaded their pollutants burdens and had high PCB burdens (17.2–93.68 μg g^{-1} l.w. (lipid weight)). Some females with PCB concentrations above the threshold for the onset of adverse health effects were still able to ovulate, conceive and successfully implant the foetus (Murphy 2010, Murphy et al. 2018).

PAHs are thought to have immunosuppressive and immunotoxic effects. PAHs have been associated with severe lung disease in bottlenose dolphins in the Gulf of Mexico, after an oil spill (Schwacke et al. 2014). Another study in the Canary Islands detected the presence of these compounds in bottlenose dolphins, but their impact on the individuals and population remains poorly known (García-Alvarez et al. 2014). Immunotoxic effects have been reported in beluga whales, reflecting to toxic effects of planar halogenated aromatic hydrocarbons (PHAHs) (which is four times higher than in humans) and the high binding affinity of beluga AHR[5] with PHAHs (Jensen & Hahn 2001).

PFOS can cause mutagenic alterations of gene expression in primary bottlenose dolphin cell cultures (Mollenhauer et al. 2009). Other effects of PFAS on wild-ranging bottlenose dolphins include immune, hematopoietic, renal and hepatic dysfunctions when exposed to high PFAS burdens (Fair et al. 2013).

Phthalates are endocrine disruptors, and transactivation results of thyroid hormone and glucocorticoid receptor have been reported for phthalates in several mammalian species such as whales and polar bears. Given that the ligand binding domains of the receptors are identical in whales and killer whales, belugas, polar bears and humans, these effects could be also considered in those species (Routti et al. 2021).

Thresholds provide a benchmark for assessing pollutant exposure and its biological significance, and they represent exposure or dose limits values below which adverse health effects are not expected (Jepson et al. 2005, Murphy et al. 2015). Generally, when we refer to adverse health effects, it means toxicity, that is to say, pathology or functional impairment (Zoeller et al. 2014). Controversy surrounds the use of thresholds since not all individuals are equally sensitive to a particular dose, and therefore, a graduated response is expected in the form of an exposure–response relationship (Zoeller et al. 2014). Due to the difficulty in establishing exposure–response relationships, the majority of threshold values proposed for cetaceans are often based on studies conducted on surrogate species such as mice and mink.

Thresholds may vary during critical periods for organisms like development or migration (Borrell & Aguilar 2005b). Confounding factors and other stressors that act in combination with pollutants and can lead to additive, synergistic or antagonistic effects should be considered. Because of this, identifying chronic and sub-lethal responses to specific pollutants is challenging, particularly when adverse responses have delayed latent effects.

Threshold values are best known for PCBs. However, the interpretation of these thresholds may be complicated not only due to the evidence coming from other mammal species but also due to them being based on different combinations of PCB congeners and a lack of clarity about the relationship between the concentration of PCBs in blubber and the total PCB burden. The already proposed thresholds for organic contaminants that can be applied to the cetacean species of concern for this review (among other odontocete cetaceans) are described in Table 7.

Other more general thresholds for POPs in marine mammals have also been proposed. For example, the most commonly applied thresholds for assessing PCB contamination in marine mammal studies, for unspecified effects, are a lower bound of 9 mg kg^{-1} l.w. and an upper bound of 41 mg kg^{-1} l.w. (studied on seals, Helle 1976, Jepson et al. 2016), with a proposed intermediate toxicity equivalent (TEQ) of 17 mg kg^{-1} l.w. (studied in the blubber and blood of otters, seals and dolphins) (Kannan et al. 2000). These threshold values for total PCBs were also proposed by OSPAR to perform the preliminary status assessment of PCB toxicity, in the framework of the newly proposed 'Pilot Assessment of Status and Trends of Persistent Chemicals in Marine Mammals' (Pinzone et al. 2022).

Another example would be the threshold established for OHC[6] in several arctic cetacean species namely bowhead whale (*Balaena mysticetus*), beluga whale and ringed seal (*Pusa hispida*), which could be considered an indicator of higher risk of a deleterious effect on health, through complex and/or combined modes of action, is 1 ppm in any target tissue (Letcher et al. 2010).

Despite efforts to reduce PCBs levels in the environment, and the already observed decreasing trends in some European regions, concentrations observed in cetaceans are still commonly above thresholds at which adverse health effects such as reproductive impairment would be expected. For example, PCB concentrations in blubber of 92% (12 out of 13) of male adult harbour porpoises stranded or bycaught in the North Sea between 2006 and 2019 exceed the toxic threshold of 9mg kg^{-1} l.w. (van den Heuvel-Greve et al. 2021).

Mitigation measures and research needs

Several international and regional agreements aim to manage or ban the use of some POPs and other hazardous substances or wastes, including the Stockholm Convention, Rotterdam Convention, Basel Convention, UNECE Conventions (United Nations Economic Commission for Europe) and MARPOL (International Convention for the Prevention of Pollution from Ships). Nonetheless, based on the latest assessments, many countries will not achieve the agreed targets (e.g. under the Stockholm Convention), for example, in terms of production, use and control of these compounds (Law & Jepson 2017, Desforges et al. 2018).

Evidence from long-term studies indicates that PCB levels are decreasing in some cetacean populations and in their main prey species. For example, decreasing trends of PCB concentrations have been observed in harbour porpoise in the UK (Williams et al. 2020) and in herring in the Baltic Proper (Danielsson et al. 2020), in sardine, anchovy and bogue in the Mediterranean (Bartalini et al. 2020), as well as of DDTs, HCH, HCB and *trans*-nonachlor TNC in cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) from the Barents Sea, although the declining rate in this area has slowed down since 2000. Nevertheless, the persistence of these chemicals means that the decline is slow.

There is no realistic way to directly reduce POP concentrations in cetaceans. Where bioaccumulation of POPs threatens populations, either in isolation or in combination with other threats, the best option is to reduce those other threats that can be reduced. The assessment and implementation of measures to reduce the use and waste management of certain POPs could reduce their levels in the environment.

The need for standardised reporting should be addressed. Chlorinated biphenyls found in marine mammals and fishes are similar, being dominated by congeners 138, 153 and 158. ICES proposed a group of 7 CBs congeners (IUPAC numbers 28, 52, 101, 118, 138, 153, 180) as an indicator of pollution levels, which are usually found in higher concentrations in technical mixtures and present a wide chlorination range (Webster et al. 2013). Thus, employing the standardised reporting proposed by ICES and recommended for monitoring by the European Union Community Bureau of Reference, which in addition has been part of the OSPAR Coordinated Environmental Monitoring Programme (CEMP) since 1998, will ease comparisons between areas, species, populations and even individuals (Jepson et al. 2005).

Regular monitoring and reporting should be established, which is already required by some legislations, and it has been proposed by OSPAR QSR2023 ('Pilot assessment of status and trends of Persistent Chemicals in marine mammals' (Pinzone et al. 2022)) and the Marine Strategy Framework Directive (MSFD) (Directive 2008/56/EC).

Whenever possible, comprehensive congener-specific analysis should be performed to investigate and understand contamination sources, fate, transport and bioaccumulation mechanisms (Megson et al. 2019). Although the health risks of organic contaminants, especially PCBs, have long been known (DHEW Committee 1978) leading to the implementation of strict bans and regulations (e.g. Stockholm Convention), the real threat now lies in unintended or accidental sources of PCBs (Vorkamp 2016, Hermanson et al. 2020). In fact, non-Aroclor PCBs or other non-commercial mixtures of PCBs are becoming more important in the environment due to weathering and fractionation processes (Megson et al. 2019). Recent studies on the PCBs profiles in several cetacean species stranded in the UK identified PCB profiles that do not fit the commercial Aroclor signatures, but that indicated patterns of congeners that are resistant to biotransformation and elimination (Megson et al. 2022). Moreover, the profiles of some individuals of sei whale (*Balaenoptera borealis*) included lighter PCB congeners (e.g. PCB 11), suggesting atmospheric deposition, instead of terrestrial discharges, as the main source of exposure (Megson et al. 2022).

Dose–response studies or, alternatively, probabilistic risk assessments should be conducted to better understand the effects on cetaceans. Currently, this kind of analysis is scarce (Schwacke et al. 2009) since carrying out pollutant assessments in cetaceans presents numerous logistical problems due to their wide-ranging distribution and the inaccessibility of their habitat, as well as the several national and international regulations protecting these species, difficult samples collection and results interpretation.

Inorganic contaminants

Inorganic contaminants are a broad group of elements and compounds that include toxic metals such as heavy metals, trace elements, mineral acids, inorganic salts, sulphates, nitrides, nitrates, nitrites, fluorine compounds and cyanides that occur mainly in the form of dissolved anions and cations (Wasewar et al. 2020, Gogoi et al. 2021). Some inorganic contaminants are present naturally in the earth crust (rocks, volcanoes and soils) and can enter the marine environment due to weathering and erosion. However, anthropogenic activities have significantly altered the natural cycles and concentrations in the environment of these contaminants of natural origin (Vitousek et al. 1997). Consequently, anthropic sources (industrial usage, mining, fuel production, combustion of leaded petrol, smelting and untreated effluent discharges) (Mishra et al. 2019, Sharma & Negi 2020, Méndez-Fernandez et al. 2022) are the primary contributors to the contamination caused by natural elements, which may be the only source of contaminants in certain environments or systems.

Heavy metals are a group of 53 elements, of the 90 naturally occurring elements, with a high relative density and atomic weight, most of which belong to the transition group of the periodic table (e.g. cadmium (Cd), mercury (Hg) and chromium (Cr)). Metalloids, such as arsenic (As) and the naturally occurring actinide and lanthanide elements, are also considered as heavy metals (Rahman & Singh 2019). They are not biodegradable and may persist in the environment for long periods of time, which makes these elements a great concern for the future (Wu et al. 2010). Although the major proportion of these elements are present in the environment as inactive minerals, they become toxic when made bioavailable and/or soluble in water (which is mostly due to anthropogenic causes, but also includes some natural processes) because they might interact with biological organisms (Rahman & Singh 2019). The danger of these elements lies in their ability to bind to a wide variety of functional groups in biomolecules, such as carboxylic acid, amino acid and sulphur-containing groups. As a result, they can bind to proteins and enzymes and alter their functions. In addition, they can precipitate or promote the decomposition of phosphate biomolecules (Shmeis 2022).

Numerous metals (iron (Fe), cobalt (Co), copper (Cu), selenium (Se), manganese (Mn), zinc (Zn) and molybdenum (Mo)) are essential for the organisms or for their metabolic activity (micronutrients) at low concentrations (Peralta-Videa et al. 2009). Nevertheless, if metal concentrations exceed a certain threshold, adverse health effects may result (Ali et al. 2019), even compromising survival (Méndez-Fernández et al. 2022). There are some heavy metals such as Cd, lead (Pb), Hg and Cr known to cause adverse health effects, but without a known threshold value for these effects, or for which a threshold cannot be established, and are therefore described as the most problematic elements. These are also considered as priority elements with toxicological profile by several organisations (AMAP[7]/UNEP[8] 2013; ATSDR[9] 2015). Of particular concern are Hg and Cd, which do not have any physiological function and are toxic for mammals even at very low concentrations (Wren et al. 1995, Machovsky-Capuska et al. 2020). Hg can also be found in the environment in its methylated form, methylmercury (MeHg), which makes it more soluble than its inorganic form and therefore more bioavailable.

Marine mammals usually present higher concentrations of these elements in their tissues than are found in the marine environment in which they live. For example, 58.4 pg L^{-1} of MeHg were recorded in seawater from the northwest Atlantic, versus 325.8 ng g^{-1} w.w. detected in harbour porpoise, representing a biomagnification factor between 16 and 22 (Harding et al. 2018). This reflects the prolonged biological half-life of these elements (e.g. Hg ≈ 10 years and Cd ≈ 10–30 years) and therefore their potential to bioaccumulate, as well as the influence of the life history and ecological characteristics of marine mammals (i.e. apex predators and long-lived species, presenting age- and size-related accumulation (Cecílio et al. 2006, Durante et al. 2020)).

In cetaceans, the main source of exposure to inorganic contaminants is the trophic route (ingestion) rather than direct contact with the environment, even in highly polluted habitats (Aguilar et al. 1999, Ramos & González-Solís 2012, Méndez-Fernández et al. 2022), although there are also several other pathways for trace element intake (respiration/inhalation, absorption through the skin/dermal exposure and transference through placenta or lactation) (Hall et al. 1997, Ferreira et al. 2016). Therefore, the variation in their concentration, between individuals, populations and between species, is closely related to age and size, food intake, metabolic rate (which is in turn influenced by the weight of the animals and their migration or physiological status such as fasting) and feeding areas, as well as other biological factors such as sex, reproductive status or the tissue considered (Das et al. 2002, Machovsky-Capuska et al. 2020, Méndez-Fernández et al. 2022). The concentrations of inorganic contaminants vary greatly between species, especially those of non-essential metals such as Cd and Hg (Das et al. 2002).

Since cetaceans have a limited capacity to metabolise, eliminate and/or excrete some of these elements, they are generally sequestered in tissues (Monk et al. 2014). Trace elements and heavy metals distribute differently in tissues (or their target tissues differ) depending on their physicochemical characteristics (Lahaye et al. 2006, Machovsky-Capuska et al. 2020). Metabolically active tissues such as liver and kidneys accumulate heavy metals more rapidly than other tissues such as skin and muscles (Ali et al. 2019). It is most common for metals to concentrate in soft tissues, although some (like Zn and Pb) concentrate in bones and skin (Leonzio et al. 1992, Caurant et al. 1996, Bowles 1999, López-Berenguer et al. 2020). Differently, concentrations of Hg are higher in liver (unlike in terrestrial animals) (Caurant et al. 1996, Das et al. 2002, Kershaw & Hall 2019) and concentrations of Cd are higher in kidney (Wagemann & Muir 1984, Machovsky et al. 2020). For further information on tissue specificity and distribution of heavy metals and trace elements in cetaceans, see Bowles (1999) and Das et al. (2002).

Transmission

The main route by which heavy metals enter cetaceans is through their diet. For example, Hg is transferred to cetaceans mainly in its organic form, methylmercury, from the tissues of preys mainly fish species (Svensson et al. 1992, Das et al. 2002, Bustamante et al. 2006, Kershaw & Hall 2019).

The only mechanism by which inorganic contaminants are transferred among cetaceans is from mother to calf through the placenta or milk during lactation (Wagemann et al. 1988). Due to the serious physiological effects that these metals can have on foetuses, such as developmental alterations and even foetal death, this transfer mechanism is of particular concern (Kershaw & Hall 2019). Transfer of some elements such as Cu, Co, Pb, Ni and Fe from mother to calf through the placenta membrane has been reported (Underwood 1977, Wagemann et al. 1988, Law 1996, Das et al. 2002, Yang et al. 2004, Lahaye et al. 2007). Consequently, it is to be expected that the concentrations of some metals in mature females will decrease significantly as gestation progresses (Das et al. 2002). In contrast, transplacental transfer of other elements such as Cd appears to be very limited, as the concentrations of Cd reported in foetal kidneys are extremely low compared with those of the mother (Honda et al. 1981, Wagemann et al. 1988, Law et al. 1992, Caurant et al. 1994, Yang et al. 2004). Likewise, Hg can be transferred through the placenta, especially in its methylated form, MeHg, but several studies have indicated that the transfer is very limited (Honda et al. 1981, Law et al. 1992, Caurant et al. 1993, Lahaye et al. 2007). Additionally, Hg transfer through milk has also been shown to be negligible (Honda et al. 1986).

Levels and trends

Individual's contaminant level variability is related to several biological and ecological factors, including their species, age, sex, diet, geographic location, the type of tissue being examined (Caurant et al. 1994, Das et al. 2002) and the properties of their metallothioneins. In addition, it is also dependent on the characteristics of the contaminant, possible metal–metal interactions and even other anthropogenic influences.

Early stages of the development of marine mammals are characterised by certain elements that are found at exceptionally high concentrations. For example, significant high concentrations of Cu and Zn, both of which are essential elements, have been reported in neonates and very young animals (Underwood 1977, Wagemann et al. 1998, Caurant et al. 1994, Yang et al. 2004). Bioaccumulation during gestation, coupled with a very low excretion rate of these metals by the foetus or newborn, could be a contributing factor to the high concentrations described (Lahaye et al. 2007), as well as specific requirements of their tissues, which are undergoing rapid growth and differentiation (Wagemann et al. 1998, Das et al. 2002). Regardless of the species or tissue, the most common elements exhibit trends related with age or length, a descriptor commonly associated with age that can therefore be used synonymously. As a general rule, increasing age is associated with higher concentrations of Hg, Se, Cd, Mn and Pb (Bowles 1999, Das et al. 2002, Lahaye et al. 2006, Bellante et al. 2009, Borrell et al. 2014, Wafo et al. 2014, Ferreira et al. 2016), while there is an age-related decrease in the concentrations of Cr, Cu, Fe, Ni and Zn (Eisler 1984, López-Berenguer et al. 2020). There are however some tissue and element exceptions, such as the decrease in mercury concentrations with age in all tissues except the brain, where they present an inverse correlation (Reed et al. 2015, López-Berenguer et al. 2020).

Diet is one of the main factors determining inorganic contaminants levels in cetaceans, as the main input of these contaminants is via the diet (Aguilar et al. 1999). Thus, depending on the dietary preferences of different cetacean species and their trophic position, contaminant concentrations will vary accordingly given the biomagnification capacity of these elements. For example, mysticete cetaceans generally will show lower concentrations of inorganic contaminants than odontocetes and pinnipeds (Das et al. 2002). Furthermore, physiological changes associated with temporary dietary changes (i.e. pregnancy, lactation or migration) will also affect inorganic contaminant concentrations (Caurant et al. 1996, López-Berenguer et al. 2020). Species whose diet consists mainly of fish will present higher concentrations of Hg because of its biomagnification through the food web, when available as MeHg (Svensson et al. 1992, Nakagawa et al. 1997, Das et al. 2002). Cd concentrations in cetacean tissues are also considered to be diet-related (Aguilar et al. 1999) and the main source is cephalopods given their high Cd levels in the viscera and the presence of the element in bioavailable forms in them (Honda & Tatsukawa 1983, Miles & Hills 1994, Bustamante et al. 2002, Das et al. 2002, Lahaye et al. 2007). Therefore, Cd concentrations may be indicators of dietary preferences and/or changes. Teuthophagous cetaceans will present higher concentrations of Cd. For example, in harbour porpoises of the Northeast Atlantic, a population-scale dietary change has been described based on increasing renal Cd concentrations with a south-north gradient, characterising an increase in cephalopod consumption with latitude (Lahaye et al. 2007). Inorganic contaminants are accumulated in tissues according to their intake, but their retention rate may differ, for example, between males and females due to differences in hormone metabolism (Caurant et al. 1994).

Sex is also considered a determining factor of levels of inorganic contaminants in cetaceans. Further investigation of this factor is needed, or confounding factors actors need to be properly addressed, as the results of different studies vary. Some studies have found no significant differences between sexes in Hg concentration (Borrell et al. 2014, Ferreira et al. 2016), while others have found significant differences in Hg and other metal concentrations (Caurant et al. 1994, Capelli et al. 2000, Cardellicchio et al. 2002). According to consensus, the reproductive status of females can have a significant impact on the concentrations of some metals. In mature females, the concentration of Fe, Co, Pb and Ni decreases as the gestation progresses due to mother–calf transference. Elevated Hg concentrations have been reported in pregnant and lactating female pilot whales (Caurant et al. 1996), according to the authors, possibly due to differences in diet associated with their physiological state or a decrease in detoxifying capacity.

Lastly, the distribution and geographical location of cetaceans also plays a crucial role in their inorganic contaminant concentrations in relation to the basal or natural levels of these elements in the area of distribution. For example, given the geological characteristics of the Mediterranean basin (semi-enclosed basin with intense anthropogenic pressure), Hg levels are higher in this area, which may lead to the assumption that the high Hg concentrations observed in Mediterranean dolphins, compared to Atlantic dolphins, are of natural origin due to basal levels in the basin (Andre et al. 1991, Das et al. 2002). Regional differences have been also observed in cetaceans' prey species, such as hake, which showed higher Pb and Cd in the Mediterranean (9.54 ± 2.69 μg kg^{-1} w.w. and 2.21 ± 0.26 μg kg^{-1} w.w., respectively) compared to the Atlantic (3.90 ± 0.4 μg kg^{-1} w.w. and 1.7 ± 1.01 μg kg^{-1} w.w.) (Celik et al. 2004), as well as horse mackerel, which showed a difference in Hg concentrations of two orders of magnitude between Mediterranean (680 μg kg^{-1} w.w., Storelli et al. 2006; 307 ± 317 d.w., Chouvelin et al. 2014; 350 μg kg^{-1} w.w., Capodiferro et al. 2022) and the contiguous Atlantic waters of Portugal (1.9 μg kg^{-1} w.w., da Silva et al. 2020). Habitat depth has also been demonstrated to have an important influence on elements concentrations. For example, it has been proved that the concentration of Hg increases as the feeding depth of the cetacean prey increases (Koenig et al. 2013, Borrell et al. 2014). Table 8 lists the concentrations of inorganic contaminants reported in the tissues of different cetacean species in Europe by sex and maturity state (when available). Further, Figure 2 shows the identified temporal trends in the concentrations of inorganic contaminants.

Effects and thresholds

Inorganic contaminants have varying effects on the organisms depending on the metal speciation, concentration, bioavailability and other factors, such as the time of exposure and the physiological characteristics of the individuals. As described in the introduction of this section, organic conformations are generally the most toxic because of their increased fat solubility, which enables these elements a greater potential to move into different tissues of the organisms. For example, organic forms are able to cross the blood–brain barrier, which enables these elements to penetrate the brain, where they may have numerous neurotoxic effects (Carpenter 2001, López-Berenguer et al. 2020). Additionally, since some inorganic contaminants or trace elements have biological functions, their excess or deficiency can have serious health consequences (Hansen et al. 2016), but given the difficulties of fitting dose–response curves for these contaminants in cetaceans, there is little information on this.

Most of the effects described for heavy metals in general focus on the immune response, although again, depending on the metal and exposure, they are known to affect numerous tissues and systems. Heavy metals exposure may result in an immunosuppression or immunoenhancement, producing chronic inflammatory processes that lead to hypersensitivity and autoimmunity (Lynes et al. 2006, Kakuschke & Prange 2007). For example, immunosuppression has been described for toxic heavy metals like Pb and Cd, while an exacerbated immune response has been described for Hg and Be, producing autoimmune diseases (Cámara Pellissó et al. 2008). Other effects described

Table 8 Concentrations of the Most Studied Inorganic Contaminants Reported in Small Cetaceans in European Waters Since Records Are Available

Region	Location (Maturity State)	Period	Tissue	Inorganic Contaminant: Hg	Cd	Pb	Se	References
Harbour Porpoise								
NE Atl	Bay of Biscay	2009–2012	Liver	13.05 ± 19.43 [0.61–65.25] (105)[a]	0.15 ± 0.15 [<0.01[b]–0.44] (105)[a]		6.96 ± 8.99 [0.58–30.74] (105)[a]	Mahfouz et al. (2014)
			Kidney		0.67 ± 0.62 [<0.01[b]–1.92] (105)[a]		2.88 ± 1.44 [0.72–5.52] (105)[a]	
			Muscle					
	Portugal	2005–2013	Liver	20.8 ± 4.68 [0.25–102.37] (42)	0.15 ± 0.03 [0.00–0.63] (42)	0.07 ± 0.32 [0.02–0.20] (42)	11.50 ± 2.34 [0.75–49.46] (42)	Ferreira et al. (2016)
			Kidney	2.66 ± 0.29 [0.25–7.88] (42)	0.41 ± 0.06 [0.01–1.16] (42)	0.05 ± 0.01 [0.01–0.17] (42)	3.78 ± 0.32 [0.81–8.48] (42)	
			Muscle	1.82 ± 0.20 [0.32–5.07] (42)	0.01 ± 0.00 [0.00–0.01] (42)	0.02 ± 0.00 [0.00–0.12] (42)	0.44 ± 0.03 [0.20–0.99] (42)	
	France	2004–2015	Liver	42.9 ± 59.7 (36)	2.64 ± 2.39 (35)	0.061 ± 0.036 (31)	21.0 ± 25.3 (36)	Méndez-Fernández et al. (2022)
			Kidney					
			Muscle					
	Galicia, Spain	2004–2008	Liver	31.0 ± 59.5 (19)	8.3 ± 8.4 (19)	< 0.07 (19)	16.9 ± 30.1 (19)	Méndez-Fernández et al. (2014)
			Kidney	2.7 ± 1.9 (19)	30.0 ± 26.9 (19)	< 0.07 (19)	2.9 ± 1.6 (19)	
			Muscle					
	North Sea & Kattegat Sea	1987–1990	Liver	6.2 (17)				Joiris et al. (1991)
			Kidney	5.7 (17)				
			Muscle	3.07 (17)				
Common Dolphin								
NE Atl	France	2001–2017	Liver	28.6 ± 43.2 (201)		0.035 ± 0.03 (201)	26.7 ± 36.2 (201)	Méndez-Fernández et al. (2022)
			Kidney		5.18 ± 7.66 (201)			
			Muscle					
	Portugal	2009–2013	Liver	16.7 ± 2.9 [0.5–66.0] (36)	0.4 ± 0.06 [0.00–2.08] (36)	0.02 ± 0.00 [0.01–0.04] (36)	7.4 ± 1.01 [1.3–26.7] (36)	Monteiro et al. (2016)
			Kidney	2.1 ± 0.2 [0.2–4.9] (36)	2.3 ± 0.3 [0.00–8.0] (36)	0.02 ± 0.00 [0.00–0.07] (36)	4.0 ± 0.2 [1.1–7.8] (36)	

(*Continued*)

Table 8 (*Continued*) Concentrations of the Most Studied Inorganic Contaminants Reported in Small Cetaceans in European Waters Since Records Are Available

Region	Location (Maturity State)	Period	Tissue	Inorganic Contaminant				References
				Hg	Cd	Pb	Se	
			Muscle	0.9 ± 0.08 [0.1–1.8] (36)	0.01 ± 0.00 [0.00–0.06] (36)	0.01 ± 0.00 [0.00–0.06] (36)	0.8 ± 0.05 [0.3–1.4] (36)	
	Portugal	1995–1998	Liver	11.0 ± 18.3 (24)	2.5 (1)			Zhou et al. (2001)
			Kidney	1.63 ± 1.44 (24)	0.55 ± 0.32 (4)			
			Muscle	0.80 ± 0.70 (24)				
	Galicia, Spain	2004–2008	Liver	10.4 ± 31.8 (114)	0.4 ± 0.5 (114)	< 0.07[b] (114)	5.0 ± 5.8 (114)	Méndez-Fernández et al. (2014)
			Kidney	1.6 ± 2.1 (114)	2.3 ± 2.7 (114)	< 0.07[b] (114)	2.7 ± 1.1 (114)	
			Muscle					
	Bay of Biscay	1977–1990	Liver	216 ± 204 (29)	11 ± 26 (29)			Holsbeek et al. (1998)
			Kidney	25 ± 34 (29)	14 ± 22 (29)			
			Muscle	12 ± 7 (29)	0.5 ± 1.2 (29)			
Bottlenose Dolphin								
NE Atl	Portugal	2005–2013	Liver	131.486, 30.306 [2.267–524.282] (25)	0.811, 0.180 [0.004–2.682] (25)	0.087, 0.016 [0.006–0.312] (25)	42.844, 8.950 [1.114–143.416] (25)	Monteiro et al. (2016)
			Kidney	13.812, 2.439 [0.704–49.470] (25)	2.412, 0.555 [0.005–9.030] (25)	0.028, 0.006 [0.002–0.105] (25)	5.589, 0.619 [0.755–11.875] (25)	
			Muscle	4.442, 1.102 [0.523–26.906] (25)	0.027, 0.067 [0.002–0.106] (25)	0.041, 0.011 [0.003–0.223] (25)	0.961, 0.232 [0.337–5.983] (25)	
	Galicia, Spain and Portugal	2004–2008	Liver	19.1 ± 22.4 (8)	1.2 ± 2.9 (8)	< 0.07[b] (8)	10.8 ± 13.0 (8)	Méndez-Ferrnández et al. (2014b)
			Kidney	8.4 ± 7.2 (6)	5.7 ± 13.8 (6)	< 0.07[b] (6)	4.6 ± 3.1 (6)	
			Muscle					
	Cardigan Bay	1988	Liver		<0.06 (1)			Morris et al. (1989)
			Kidney					
			Muscle	<10 (1)		<0.6 (1)		
C Med	Adriatic Sea	1996–1997	Liver	393.36 ± 1.32 (1)				Storelli and Marcotrigiano (2000)
			Kidney	34.58 ± 1.8 (1)				
			Muscle					

Striped Dolphin								
NE Atl	Portugal	2005–2014	Liver	39.7 ± 10. 5 [1.0–237.3] (31)	3.4 ± 0.6 [0.0–14.7] (31)	0.0 ± 0.0 [0.0–0.1] (31)	13.4 ± 2.9 [1.1–65.4] (31)	Monteiro et al. (2020)
			Kidney	4.9 ± 0.5 [0.7–11.0] (31)	19.3 ± 2.8 [0.1–69.3] (31)	0.0 ± 0.0 [0.0–0.2] (31)	4.5 ± 0.2 [1.1–7.7] (31)	
			Muscle	2.4 ± 0.5 [0.3–18.2] (31)	0.1 ± 0.0 [0.0–0.4] (31)	0.0 ± 0.0 [0.0–0.2] (31)	1.0 ± 0.2 [0.4–5.3] (31)	
	Bay of Biscay	1972–1980	Liver	51.64 ± 29.4 [1.2–87] (8)				Andre et al. (1991)
			Kidney	7.33 ± 4.92 [2.6–15] (7)				
			Muscle	3.75 ± 3.71 [1.5–12] (7)				
	Bay of Biscay (immature)	1999–2004	Liver	6.5 ± 6 [1.2–24.1] (12)				Lahaye et al. (2006)
			Kidney		10.6 ± 9.0 [2.1–30.8] (12)			
			Muscle					
	Bay of Biscay (mature)	1999–2004	Liver	138 ± 92 [6.4–317] (6)				Lahaye et al. (2006)
			Kidney		12.9 ± 10.8 [0.29–40.2] (6)			
			Muscle					
	Bay of Biscay (mature)	1993	Liver					Das et al. (2000)
			Kidney		17 ± 15 [0.2–51] (23)			
			Muscle					
	Cardigan Bay	1988	Liver					Morris et al. (1989)
			Kidney					
			Muscle	<0.5 (1)	<0.06 (1)	<0.6 (1)		

(*Continued*)

Table 8 (*Continued*) Concentrations of the Most Studied Inorganic Contaminants Reported in Small Cetaceans in European Waters Since Records Are Available

Region	Location (Maturity State)	Period	Tissue	Inorganic Contaminant: Hg	Cd	Pb	Se	References
	W Med	1972–1980	Liver	355.8 ± 369.4 [1.2–1544.0] (25)				Andre et al. (1991)
W Med			Kidney	30.4 ± 34.0 [1.4–178.9] (27)				
			Muscle	28.3 ± 29.3 [1.0–81.2] (13)				
		1990–1993	Liver	321.43 ± 261.31 (23)				Borrell et al. (2014)
			Kidney	16.11 ± 10.17 (23)				
			Muscle					
		2007–2009	Liver	185.48 ± 197.21 (30)				
			Kidney	13.43 ± 11.72 (30)				
			Muscle					
	France	1988–1990	Liver	193.84 [19.72–658.76] (13)[a]				Augier et al. (1993)
			Kidney	20.93 [3.43–81.91] (13)[a]				
			Muscle	44.8 [7.4–155.4] (13)				
	France	2002–2009	Liver	149.12 ± 261.89 [2.87–1558.46] (55)[a]	0.89 ± 0.96 [0.01–3.31] (55)[a]		61.39 ± 115.59 [0.41–681.5] (55)[a]	Wafo et al. (2014)
			Kidney	17.95 ± 18.33 [1.56–77.72] (55)[a]	2.47 ± 2.78 [0.01–10.92] (55)[a]		6.89 ± 6.31 [0.72–29.16] (55)[a]	
			Muscle	26.4 ± 35.5 [3.1–133] (55)[a]	0.1 ± 0.1 [0.01–11.4] (55)		11 ± 14.7 [1.1–61.7] (55)	
C Med	Tyrrhenian Sea	2002	Skin	6.15 ± 1.58 [3.92–8.38] (9)	0.04 ± 0.02 [0.02–0.09] (9)	0.61 ± 0.48 [0.19–1.49] (9)		Fossi et al. (2004)

Information is provided by species (on bottlenose dolphin, common dolphin, striped dolphin and harbour porpoise), sex and maturity state (when available), sampling area and time series. Contaminant concentrations are expressed in μg g^{-1} w.w. The table shows the concentrations of Hg, Cd, Pb and Se in various tissues, describing their mean value ± standard deviation, range between square brackets and the number of samples between brackets.

[a] Concentrations that have been converted into wet weight following the conversion factors proposed by the authors of each study.

[b] Heavy metal concentration was lower than specified number in the corresponding cell, which is the minimum concentration measured by the instrument.

NA, Not available.

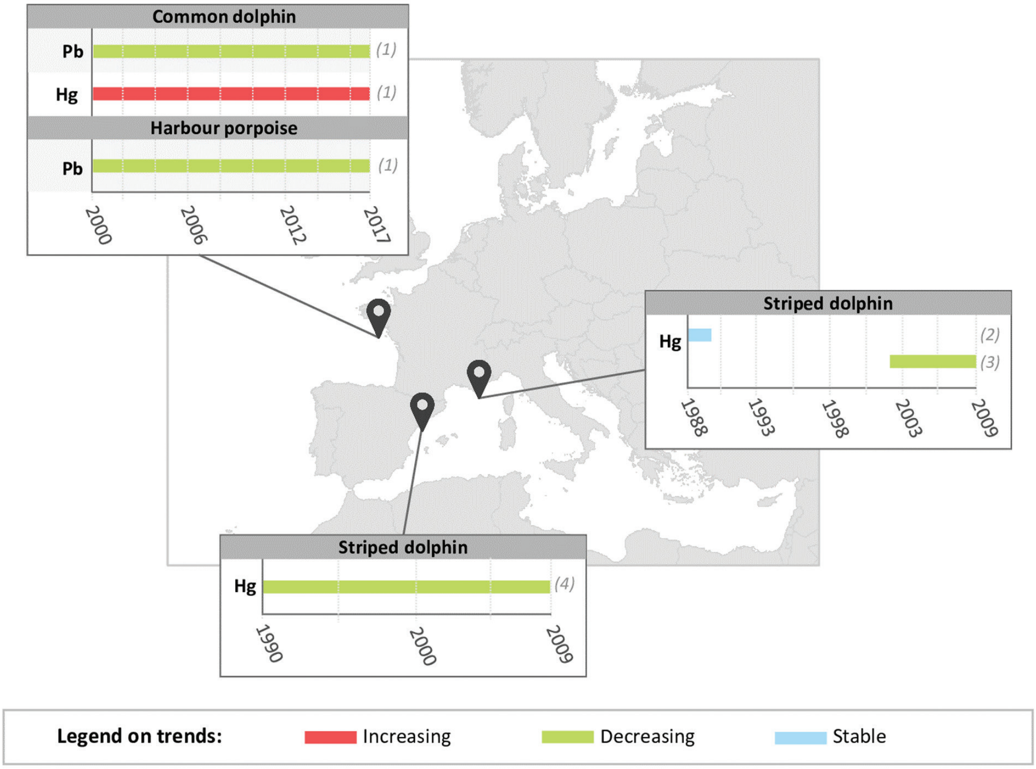

Figure 2 Graphs of the overall trends in concentrations (red = increasing trend, green = decreasing trend and blue = stable trend) of inorganic contaminants in the small cetacean species studied, represented by horizontal bars, by compound, by area and by time series. Numbers in brackets to the right of each horizontal bar indicate the reference of the corresponding study: (1) Méndez-Fernández et al. (2022); (2) Augier et al. (1993); (3) Wafo et al. (2014); (4) Borrell et al. (2014).

for heavy metals in odontocetes in the literature include hepatic damage (e.g. from Pb intoxication (Law et al. 1991, Rawson et al. 1993, 1995, Shlosberg et al. 1997); renal damage (WHO 1992, Dietz et al. 1998, Das et al. 2002, Lavery et al. 2009); genetic alterations (Lynes et al. 2006, Mollenhauen et al. 2009) and neurotoxicity (Kershaw & Hall 2019, López-Berenguer et al. 2020)).

Hg is one of the most widely studied heavy metals in the literature and its contamination seems to be a major problem for odontocete cetaceans compared to other marine mammal groups, as Hg concentrations observed, for example, in belugas' brain tissue are an order of magnitude higher than those registered in other marine mammals of the area like polar bears and seals (Lemes et al. 2011). Although the highest Hg concentrations are registered in the liver due to Hg detoxification processes occurring in this tissue, the target organ of Hg is brain where it produces the most serious effects. The main physiological effect associated with this element is neurotoxicity (Dietz et al. 2013, Kerwshaw & Hall 2019, López-Berenguer et al. 2020). In the liver, Hg can also produce negative effects such as hepatic processes disruption and development of lesions characteristics of Hg exposure (Law et al. 1991, Rawson et al. 1993) and other mild pathologies such as fatty liver (Rawson et al. 1995). Hepatoxicity and kidney damage of Hg are species-specific and depend on the formation of mercury–selenium complexes (mercury selenide, Hg-Se), which reduce Hg toxicity by binding selenium to free forms of Hg but can lead to selenium deficiency for other enzymes that protect from the oxidative damage caused by Hg of each species or individuals (Kerwshaw

Table 9 Inorganic Contaminants Threshold Levels Proposed in the Literature for the Cetacean Species of Concern for this Review and Brief Description of the Associated Health Effects or Response of Cetaceans

Contaminant	Species	Threshold	Effect/Response	References
Hg	Marine mammals	60 μg g^{-1} w.w.	Hepatic damage	Law (1996)
	Bottlenose dolphin	600 mg for a 300 kg individual	Mild fatty liver	Rawson et al. (1995)
	Bottlenose dolphin	449 μg g^{-1} w.w.	Hepatic and kidney lesions	Rawson et al. (1993)
	Bottlenose dolphin[a]	0.21 ± 0.065 ppm	Immunosuppressive effects – Reduced lymphocyte proliferation	Desforges et al. (2016)
	Bottlenose dolphin[a]	1 mg L^{-1}	Immunosuppressive effects – Reduced lymphocyte proliferation	Cámare Pellissó et al. (2008)
MeHg	Bottlenose dolphin[b]	1 ppm	Gene expression changes	Mollenhauer et al. (2009)
Cd	Mammals	800 μg g^{-1} d.w. (or 200 μg g^{-1} w.w.)	Kidney damage (for mammal species, not registered in marine mammals in which concentrations are high, suggesting efficient detoxification mechanisms) (Dietz et al. 1998)	WHO (1992), Das et al. (2002)
	Bottlenose dolphin[a]	2.44 ± 0.38 ppm	Immunosuppressive effects – Reduced lymphocyte proliferation	Desforges et al. (2016)
	Bottlenose dolphin[a]	10 mg L^{-1}	Immunosuppressive effects – Reduced lymphocyte proliferation	Cámara Pellissó et al. (2008)
Pb	Bottlenose dolphin[a]	50 mg L^{-1}	Immunosuppressive effects – Reduced lymphocyte proliferation	Cámara Pellissó et al. (2008)

[a] Indicates that the threshold has been established from dose–response bioassays.
[b] From skin cell cultures.

& Hall 2019). Other effects have also including those related to climate change (Van of genetic alterations (in the form of MeHg), due to changes in gene expression (Mollenhauer et al. 2009), and immunosuppressive effects such as reduced lymphocyte proliferation (Desforges et al. 2016), resulting among others in a higher prevalence of parasitic infections and pneumonia (Siebert et al. 1999, Bennet et al. 2001).

As mentioned previously, due to the lack of precise knowledge about the physiology of cetacean species and the biological role that some inorganic elements play, few studies have been able to establish threshold values above which negative effects of metal exposure are expected.

The already proposed thresholds for the most commonly reported inorganic contaminants that can be applied to the cetacean species of concern for this review, among other odontocete cetaceans, are described in Table 9.

Mitigation measures and research needs

In August 2017, the 'Minamata Convention on Mercury' was ratified by 91 countries, with the aim of reducing global emissions and thus protecting human health and the environment (Selin et al. 2018). In the Convention, it was agreed to continuously monitor Hg in the marine environment to determine whether new measures are efficient in reducing the uptake and impact of Hg on marine food chains (Kershaw & Hall 2019).

Other regional and international agreements that aim to regulate and control the problem of mass discharge of toxic heavy metals include the Restriction of Hazardous Substance Directive (2003), which has banned the use of Cd, Cr, Hg and Pb in the manufacturing of electric equipment in the EU member states.

A possible mitigation measure for Hg might be to maintain an adequate Se status in animals from regions with an elevated Hg exposure, in order to mitigate its toxicity (Kershaw & Hall 2019). Furthermore, through the reporting of both Hg and Se concentrations in tandem, a better assessment of cetacean health can be performed. Unfortunately, no individual remediation method has been developed or identified, which may be universally effective and applicable for complete detoxification of heavy metals and other inorganic contaminants (Rahnan & Singh 2019).

Microplastics

Plastics, which constitute around 60%–80% of the marine debris, are known to have negative physical impacts on marine mammals in seas and oceans all over the world (Panti et al. 2019), mainly through entanglement (Baulch & Perry 2014, Fossi et al. 2018) and ingestion (De Stephanis et al. 2013, Alexiadou 2019), which can result in drowning, strangulation, suffocation and/or starvation (Fossi et al. 2018). However, one area of particular concern is the exposure of marine mammals to microplastics, since these plastics of less than 5 mm in length can not only leach out plastics additives during their fragmentation (e.g. pigments, Brominated Flame Retardants – BFR, Polybrominated Diphenyl Ethers – PBDE, phthalates, nonylphenol – NP and Bisphenol A – BPA) (Koelmans et al. 2014, Hermabessiere et al. 2017), but they are also able to adsorb contaminants from the marine environment (e.g. heavy metals, antibiotics, pesticides – DDTs, Persistent Organic Pollutants – POPs and Polycyclic Aromatic Hydrocarbons - PAHs). The four most common types of microplastics in the marine environment are polyethylene (PE), polypropylene (PP), polystyrene (PS) and polyvinyl chloride (PVC) (Endo et al. 2005), and their density, along with the size, ageing, colour and shape, are important factors in determining the absorption and concentration levels of chemicals (Hirai et al. 2011, Heskett et al. 2012, Rochman et al. 2013, Wang et al. 2018). Furthermore, microplastics also have the potential to act as vectors of pathogens (e.g. diatoms, coccolithophores, bryozoans, dinoflagellates, cyanobacteria, fungi and bacteria) (Zettler et al. 2013, Eich et al. 2015, De Tender et al. 2015, Queró & Luna 2017) aside from sorbed chemicals (Koelmans et al. 2016, Kedzierski et al. 2018, Alava 2020, Meaza et al. 2021).

Transmission

Marine mammals are exposed to microplastics mainly through ingestion (Lusher 2015), and, depending on the feeding strategy used by marine mammals, microplastics can be ingested directly from the seawater by filter-feeders (e.g. whales) (Besseling et al. 2015, Germanov et al. 2018, Burkhardt-Holm & N'Guyen 2019) or indirectly by raptorial-feeders (e.g. dolphins and seals) through consumption of contaminated prey (i.e. trophic transfer) (Hernandez-Gonzalez et al. 2018, Lusher et al. 2018, Nelms et al. 2019, Ugwu et al. 2021). Another possible route of microplastic uptake by marine mammals could be the inhalation of atmospheric microplastics, although the extent to which this occurs is currently unknown (Fossi et al. 2018).

Effects

It has been found that the average number of microplastics in the digestive tracts of marine mammals worldwide ranged from 3 to 88 microplastic items per individual, with blue being the most common colour reported and fibres being the predominant particle shape for the majority of studies (Kühn & van Franeker 2020, Meaza et al. 2021, Zantis et al. 2021). Due to the small size (from 0.1 to 5 mm) and the low quantities of microplastics found in several marine mammal species, it is unlikely that they cause physical harm to the gastrointestinal tracts (e.g. mechanical obstruction or injuries).

However, gut conditions such as temperature and pH facilitate the desorption of sorbed contaminants, increasing their bioavailability (Bakir et al. 2014). Therefore, microplastics could contribute to chronic exposure to high concentrations of biologically active toxic contaminants and associated adverse health effects for individuals such as endocrine disruption, reproductive disorders, immune system suppression and carcinogenesis, among others (Miller et al. 2020, Nabi et al. 2022).

As the physical effects of microplastics are apparently not relevant in the gastrointestinal tracts of marine mammals, no threshold values for microplastics concentrations have been set to date. The effects and threshold values of persistent organic and inorganic contaminants that may be associated with microplastics are described in Sections Persistent organic pollutants (POPs) and Inorganic contaminants.

Mitigation measures and research needs

Microplastics have become almost ubiquitous in marine organisms, but their relative importance as vectors of contaminants remains the subject of speculation since marine organisms are also exposed to contaminants from the environment via other routes (i.e. water, air, sediment and food) (Ziccardi et al. 2016, Burns & Boxall 2018). In fact, it has been proposed that the transference of organic contaminants into biological organisms by dietary microplastics may be small or limited compared to the natural routes of exposure (Gouin et al. 2011, Beckingham & Ghosh 2017, Lohmann 2017).

Modelling of bioaccumulation and biomagnification of contaminants in tissues accounting for release rates of contaminants from ingested microplastics could provide useful insights (Bakir et al. 2014). This might permit predictions of contaminant concentrations in the tissues of organisms following ingestion of microplastics and inform the investigation of any related toxicological effects.

Pollution of microplastics is a global issue as they are a significant stressor in all marine environments and a hazard to organisms. Removing microplastics completely from the marine environment is almost impossible because of the small size, large quantities and variety of forms of plastic particles. However, it may be possible to decrease the entry of microplastics into the marine environment if the original sources (and classes) of microplastics pollution can be identified. In addition, stringent policies are required at various levels (local, regional, national and international) to mitigate microplastics pollution and, equally importantly, effective implementation. Current strategies include restrictions on plastic production and use, changing human behaviour through environmental education (i.e. raising public awareness), proper disposal of wastes (i.e. circular economy reduce-reuse-recycle), promotion of beach clean-up programmes and biotechnology (e.g. development of new biodegradable materials, implementing the use of bacteria to degrade plastic polymers) (Wu et al. 2016, Auta et al. 2017, Ogunola et al. 2018, Chaukura et al. 2021, Mallik et al. 2021, Onyena et al. 2021). It is presently doubtful that such approaches are making a significant difference.

Combined effects of multiple transferable threats

Introduction of combined effects and their study

In the real world, multiple stressors simultaneously affect organisms. Numerous studies have demonstrated the effects of individual stressors on cetaceans and provided information on the intensities of multiple stressors (e.g. contaminant concentrations and parasite burdens). However, few studies have described the interrelationships among stressors, receptors and their mechanisms of interaction. Several kinds of barriers to this type of study exist, including the potentially high complexity of the interactions to be studied, but also the difficulty of obtaining data and the need to transcend discipline boundaries.

There exist many possible stressor combinations that operate concurrently across multiple organisation levels (i.e. individual, population, etc.), under potentially complex relationships modulated by confounding factors. The behavioural and physiological changes in individuals and consequent effects on populations, including shifts in life history traits and population trends, also depend on their resilience – their capacity to compensate for the consequences of and recover from disturbances (Lusseau 2014, Nattrass & Lusseau 2016).

Limitations in studying combined effects can arise from the difficulty of detecting them, which depends on the timing and sequence of exposure to stressors, as well as the duration and type of effects, whether acute or chronic, immediate or delayed, simultaneous or sequential (Bender et al. 1984, Crain et al. 2008). In some cases, exposure intervals may be brief and will not necessarily coincide with the periods available for observing their effects (Pirotta et al. 2022). Moreover, there may be potential future indirect or cascading effects to consider (Segner et al. 2014, Orr et al. 2020, Wilson et al. 2020). The potential for some stressors to be bioaccumulated and the developmental stages of the affected organisms also require consideration (Orr et al. 2020).

Most studies have examined non-transferable stressors that are also direct sources of mortality, such as bycatch and ship collisions, or those with observable effects on behaviour, such as disturbance due to whale watching, rather than transferable stressors. Where a direct link to mortality is not observed, most of the proposed relationships between exposure to stressors and subsequent outcomes are circumstantial and context-specific.

In some species, dose–response relationships between stressors and animals can be tested through experiments, and recent research based on experiments involving multiple stressors has increased, as highlighted by Gunderson et al (2016). However, conducting experiments on protected and charismatic cetaceans is impractical due to the challenges posed by the inaccessibility and complexity of cetacean habitat, as well as legal and ethical considerations, apart from the large number of potential scenarios that would need to be tested when considering multiple stressors (Lundstedt et al. 1998, Côte et al. 2016, Katzir et al. 2019). We can nevertheless draw inferences from comparisons of behaviour, indicators of health, condition, fecundity and/or survival, between individuals and populations thought to have experienced different levels of stressor exposure. We can also make inferences based on studies of other more accessible and/or less protected species.

The challenges of studying multiple stressors also relate to the wide variety of disciplines involved (e.g. toxicology, physiology, ecology, epidemiology and pharmacology), the diverse conceptual approaches and intrinsic limitations in research methods. Science compartmentalisation is a common issue that leads to gaps in cross-disciplinary knowledge and inconsistencies in the terminology, which hinder the sharing of interdisciplinary knowledge and, eventually, the development of a unified and integrative approach. Additionally, the exponentially growing number of published studies and the limited resources available within research groups complicate the study of multiple stressors. These issues have been previously identified by several authors such as Côte et al. (2016), Hague et al. (2022), Orr et al. (2020) and Pirotta et al. (2022).

In general, knowledge is lacking on the mechanisms that govern and modulate the interactions of multiple stressors, and the resulting combined effects. There is also a lack of ecological understanding of the consequences of stressors that cetacean individuals and populations face in the real world. Finally, the integration of combined impacts of multiple stressors into impact assessments and management plans is presently difficult or impossible. At best, it is complicated by the wide confidence intervals around the identified relationships (Burris & Canter 1997, Kroeker et al. 2017), and at worst, we would need to operationalise pure speculation.

Despite all the associated challenges, it is crucial to comprehend and assess the combined effects that could affect individuals and populations. Accounting for them within impact assessments and protection strategies for vulnerable species continues to be a priority.

In this section, we establish the context by introducing the theory of combined effects and presenting a general example. We then (1) summarise the published research on interactions and effects of multiple transferable stressors, focused on small cetacean species in European seas, (2) provide information on the (few) described mechanisms that underlie the interactions among stressors, (3) describe the available statistical and mathematical techniques for modelling the impacts of multiple stressors on the trajectory of cetacean populations and (4) offer recommendations for future research.

Classification of combined effects and a generic example

The combined effects resulting from multiple stressors are typically classified as additive, where the resulting impact is the sum of the individual effects of each stressor, or synergistic or antagonistic, where the final effect differs from the sum of the individual effects because some stressors exacerbate or mitigate the effects of others (Folt et al. 1999, Crain et al. 2008, Piggott et al. 2015, Schäfer & Piggott 2018). As is the case for effects of single stressors, the combined effects will depend on the nature and intensity of the stressors (e.g. infection intensity), the receptors (e.g. sensitivity and resilience, conditioned by species, sex, age and health condition), how the latter respond to the former (e.g. dose–response relationships) and the mechanisms underlying the response (Folt et al. 1999, Piggott et al. 2015, Gunderson et al. 2016, Nattrass & Lusseau 2016, Pirotta et al. 2022). In addition, various confounding factors, which are not stressors themselves, can modulate the underlying relationship. For instance, a compromised immune response (regardless of whether caused by a stressor or a confounding factor) will render animals more susceptible to infections. Therefore, various external confounding factors, such as environmental conditions, and internal cofounding factors, such as developmental stage of organisms, may directly or indirectly modulate the association between multiple stressors and their effects on individual health and population status.

For example, the effects of a CeMV episode on a cetacean population are determined by various factors, including the intensity and virulence of the CeMV, the density and susceptibility of the cetacean population, other stressors acting simultaneously and the interacting mechanisms. Other stressors simultaneously affecting the population could include: chemical contaminants that have potential to bioaccumulate, notably POPs, such as DDTs and/or PCBs (Aguilar & Borrell 1994, Mazzariol et al. 2012, Lauriano et al. 2014, Verborgh et al. 2019, Dron et al. 2022), and toxic elements (Manhães et al. 2021); habitat loss and degradation (Van Bressem et al. 1999); stress and/or injury and/or death linked to interactions with vessels, such as whale-watching encounters, disturbance from high levels of maritime traffic, fishery bycatch and collisions with vessels (Van Bressem et al. 2009a, Verborgh et al. 2019); and reduced prey availability (Aguilar & Raga 1993, Van Bressem et al. 2009a).

The exposure of cetacean individuals and populations to stressors, as well as their susceptibility to pathogenic effects, is modulated not only by individual characteristics (e.g. age, reproductive status and health status) and population characteristics (e.g. species susceptibility, age and sex distribution) but also by the environmental conditions such as sea surface temperature and primary productivity, including those related to climate change (Van Bressem et al. 2009a, Burge et al. 2014, Kemper et al. 2016, VanWormer et al. 2019, Sanderson & Alexander 2020).

Published evidence of combined effects

In the following paragraphs, we have summarised the effects described in the literature for multiple stressors acting in combination in cetacean species in European waters. Due to the significant amount of literature available on POPs, most published information on combined effects relates to this stressor in combination with others. Given the effects of PCBs on the immune system, higher concentrations of PCBs tend to be associated with increased mortality from infectious diseases.

Possible combined effects of high concentrations of PCBs and infectious diseases have been described in relation to morbillivirus infections, particularly in Mediterranean striped dolphins (e.g. Kannan et al. 1993, Aguilar & Borrell 1994, Borrell et al. 1996) and in bottlenose dolphins infected with *Brucella ceti* and exhibiting high PCB concentrations in England (Davison et al. 2011). Comparison of harbour porpoise populations living in more polluted waters, such as those of the German North and Baltic seas, with those living in less polluted regions, has shown a higher incidence of severe bacterial infections, as well as associated flora changes and lesions, when background pollutant levels are higher, again demonstrating the possible combined effects of these stressors (Wünschmann et al. 2001, Siebert et al. 2008).

Moreover, a higher prevalence of ectoparasites was observed in striped dolphins infected with morbillivirus in the Mediterranean, some of which had also high PCB levels (Aznar et al. 2005). (Wünschmann et al. 2001, Siebert et al. 2008). PCB concentrations were also positively associated with nematode prevalence in harbour porpoises (Bull et al. 2006) and bottlenose dolphins (Kuehl et al. 1991), although the highest nematode burdens were not necessarily linked to the highest PCB levels. Nematode burdens also depend on diet, host size and geographic location. In fish, the relationship between these factors is generally well-known (e.g. Levsen et al. 2018), while geographical patterns in *Anisakis* burdens of fish are also reflected in cetaceans (Table 4), as are effects of host size and age to some extent. However, long-term and large-scale studies, e.g. at European level, are lacking. Significant positive relationships between nematode infections and DDT concentrations have been observed in cetaceans, such as Indo-Pacific finless porpoises (Gui et al. 2018).

Higher heavy metal concentrations, particularly Hg, Se, Hg:Se, Zn and Cd, were found in harbour porpoises that died from various types of diseases in Northern and Western Europe, namely parasitic respiratory infections, pneumonia, emaciation and non-specific infectious diseases (Siebert et al. 1999, Bennett et al. 2001, Das et al. 2004, Pierce et al. 2008, Mahfouz et al. 2014, Ferreira et al. 2016). Conversely, higher parasitic infestations in harbour porpoises were associated with lower levels of Zn, As and Ni along continental Portugal (Ferreira et al. 2016).

Combined effects can also occur due to related or similar stressors, such as pathogens. Co-infections of *Morbillivirus*, *Brucella*, *Toxoplasma gondii* and other pathogens have been reported in European waters in striped dolphins (e.g. Profeta et al. 2015, Grattarola et al. 2016, Pintore et al. 2018, Di Francesco et al. 2019, Cuvertoret-Sanz et al. 2020, Garofolo et al. 2020, Vargas-Castro et al. 2021), bottlenose dolphins (e.g. Profeta et al. 2015, Vargas-Castro et al. 2021, Sierra et al. 2014) and harbour porpoises (e.g. Siebert et al. 2001). Examples of co-infections in other cetacean species outside Europe of the three pathogens just mentioned (e.g. in belugas in the Black Sea (Alekseev et al. 2009), in Guiana dolphins in Brazil (Cunha et al. 2021)), include the first case of co-infection with *Morbillivirus* and *Brucella* detected in a sperm whale neonate in Hawaii, indicating in utero transmission of these two pathogens (West et al. 2015).

Different biotoxins arising from HABs can co-occur, although their combined effects are not clearly understood. Exposure to biotoxins from HABs has been linked to an increased susceptibility to secondary pathogenic infections (Gebhard et al. 2015); for example, saxitoxins and brevetoxins exposure were associated with phocine distemper virus infection in harbour seals (*Phoca vitulina*) (Bogomolni et al. 2016) and with *Morbillivirus* outbreaks in bottlenose dolphins, respectively (Fire et al. 2015, Flewelling et al. 2005, Twiner et al. 2012). Synergistic effects of HAB toxins and pollutants, such as for BMMA and MeHg (Rush et al. 2012), may augment Alzheimer's-like neuropathology in common dolphins (Davis et al. 2021).

Non-transferable stressors such as climate change, anthropogenic noise, bycatch or ship collision interact with transferable stressors inducing combined effects. Climate change itself encompasses a wide range of stressors, and even if the underlying mechanisms are not always clear, climate change may induce increases in pathogen prevalence (e.g. Brucella, Dadar et al. (2022)), the northern geographic range and duration of HAB blooms (e.g. Anderson et al. 2022, Lefebvre et al. 2002) and contaminant levels in high- and mid-trophic predators (e.g. PCBs and MeHg, Alava et al. (2018)). Therefore, when investigating, modelling or predicting the combined effects of various stressors on organisms and populations, consideration must also be given to all the other potential stressors, transferable or otherwise.

Interaction mechanisms

While we are far from fully understanding the mechanisms by which different stressors interact, some potential interaction mechanisms have been identified, albeit often (not always) between multiple stressors within the same general category (e.g. between different POPs).

It is understood that certain combinations of POPs can interact, heighten toxicity and produce diverse effects on individuals, not necessarily detrimental to health. For example, Yordy et al. (2010a) found that the exposure to a combination of four persistent organic pollutants, namely 4,4′-DDE, *trans*-nonachlor, PCB 138 and PCB 180, can increase the oestrogenic capacity of bottlenose dolphins. Mongillo et al. (2016) concluded that interactive effects of multiple chemicals that might be plausible in cetaceans include "enhancing developmental neurobehavioral defects, inducing protein and mRNA expression, reducing learning and memory, and enhancing neurotoxicity and cytogenotoxicity", all of which have been described for rats and humans.

In the case of immunotoxic and neurotoxic POPs such as dioxins and dioxin-like compounds (DLCs), it is known that they bioaccumulate in top predators like cetaceans to a degree which depends on the dietary preferences and prey availability (Fossi et al. 2013, Van Bressem et al. 2009a). These pollutants trigger apoptosis, or death, of human neuronal cells (Morales-Hernández et al. 2012), which has been suggested to be followed by a compensatory increase in the expression of the cellular prion protein (PrPC), which possesses anti-apoptotic properties (Aguzzi et al. 2008). This process potentially facilitates the colonisation and replication of *B. ceti* bacteria within brain cells, establishing a plausible connection between dioxins and DLCs in cetacean tissues and neurobrucellosis (Di Guardo & Mazzariol 2015).

Heavy metals may interact with each other and produce synergetic or antagonistic effects in their accumulation and toxicity. In particular, there is competition between elements for binding sites such as metallothioneins (Caurant et al. 1994). Cu and Cd present an interaction for a binding protein, since the same metallothionein regulates Cu homeostasis and Cd sequestration, which is reflected as a negative correlation between amounts of these two elements (Caurant et al. 1994, Hansen et al. 2016). The same kind of competitive interaction for cadmium-binding proteins has been described for zinc (Wagemann et al. 1988, Das et al. 2000), although the negative relationship between Zn and Cd concentrations has not always proved to be significant in cetacean studies (Lahaye et al. 2007). Metabolic interference may also occur between elements, such as the As–Cd and As–Se pairs, whose metabolic pathways are very similar; interactions within each of these pairs have been observed in determining toxic effects (Chappuis 1991). Some elements may function as modifiers of the toxicity of other elements. The most important case of this modification is Se, which binds to numerous elements (Hg, Cd, Pb, Pt, Ag, Sn) and forms selenides, which are metabolically inactive compounds (Caurant et al. 1994, Mackey et al. 2003) and play an important role in detoxification. In cetacean studies, the most frequently reported interaction of Se is that with Hg or MeHg. These two elements have a high affinity and their binding produces mercuric selenide crystals that are stored in the liver. Therefore, studies usually report strong positive correlations between the concentrations of these elements (Das et al. 2002, Lahaye et al. 2007, Yang et al. 2007, Hansen et al. 2016). This detoxifying activity of Se nevertheless has consequences: the depletion of bioavailable Se, which has other biological functions in the formation and activity of selenoenzymes, may occur, leading to the inhibition of some inflammatory mechanisms (Ralston et al. 2012, Hansen et al. 2016, Kershaw & Hall 2019).

Conceptual approaches and beyond

In the literature, two main types of conceptual approaches to the study of multiple stressors can be found: (1) receptor-focused and (2) stressor-focused approaches. The former category includes approaches that seek to address a wide range of receptor organisms and levels of organisation, as well as the various possible direct, indirect and even cascading responses within the food chain (e.g. Segner et al. 2014). This category also includes approaches focusing on the interaction mechanisms and ecological scales at which stressors act (Simmons et al. 2021). The last receptor-focused approach included in this review is the 'ECUME' risk-based approach, which aims to identify which stressors, receptors and impact pathways should be set as priorities for management or further research (Brignon et al. 2022). The stressor-focused approaches include those aiming to categorise stressors according to their nature, properties and traits (Rillig et al. 2021).

A range of analytical tools has been developed to understand and quantify the effects of multiple stressors across organisational levels. These can be categorised as data-driven or process driven and at least some are inherently cross-disciplinary (e.g. Pirotta et al. 2022). Examples of these tools include visualisation of co-occurring threats in an ecosystem and their interactions, as schematic webs (Geary et al. 2019), multiscale and multi-stressor structural equation models (e.g. Villeneuve et al. 2018), Bayesian Belief Networks (e.g. Molina-Navarro et al. 2020), Pathways of Effects and Population Viability Analysis (e.g. Murray et al. 2021), Population Consequences of Disturbance (PCoD) (National Research Council 2005, New et al. 2014, Pirotta et al. 2018), interim Population Consequences of Disturbance (iPCoD) (Harwood et al. 2014, King et al. 2015) and Population Consequences of Multiple Stressors (PCoMS) (National Academies 2017) frameworks.

Selecting the most appropriate method for analysing and predicting the effects of multiple stressors remains a critical and potentially difficult step, particularly where experimental manipulations are prohibitive, and, in the absence of guidance, it is tempting to suggest comparing the outcomes from a range of approaches (data permitting). In an attempt to facilitate and guide the selection of the most appropriate method, Pirotta et al. (2022) put forward a conceptual framework that evaluates different existing approaches to understanding combined effects, considering the assumptions made about the underlying mechanisms, the management objectives and the predictive requirements needed to attain them. Irrespective of the analytical method employed, uncertainties are numerous and inevitable. In order to account for this variability, Simmons et al. (2021) advocated the adoption of an ensemble modelling approach accounting for different sources of uncertainty when predicting the combined effects of multiple stressors. Such approaches have been favoured in other contexts, e.g. for habitat modelling, but we would urge caution. By essentially bypassing the need for concern about the mechanistic assumptions underlying each component model, ensemble models could be seen as either overcoming or potentially compounding the limitations of all the component models – and, if nothing else, perhaps represent an apt metaphor for the problem they seek to solve!

To sum up, understanding of the combined effects of multiple stressors (transferable and non-transferable) is crucial both to elucidate the nature and ecological significance of those effects (at individual, population and ecosystem levels) and to permit us to manage what can be managed (given that the impacts of some stressors are essentially unmanageable, such as those of persistent legacy contaminants). Further efforts are thus needed to develop and implement standardised long-term monitoring programmes that ensure the consistent collection of relevant data, to provide a stronger base for subsequent analysis and modelling and to develop improved conceptual frameworks, methods and models to describe and quantify the combined effects of multiple transferable stressors, in ways that capture the underlying processes, provide scalability of results to larger or different ecosystems, account for spatio-temporal variability, can incorporate expert knowledge and which facilitate subsequent management. However, perhaps above all, we need further work to test and validate existing approaches under real-world scenarios.

Conclusions

The literature reviewed has shown differences between small cetacean species and between regions in terms of the prevalence and intensity of exposure to stressors, and trends therein. The review also reflected disparities in monitoring programmes, approaches to setting and implementing thresholds, mitigation actions and the legislation which supports them, as well as the differences in the amount of research conducted on different transferable stressors. Some cetacean species are apparently more affected by certain stressors, which might be related to higher exposure, susceptibility or vulnerability. For example, striped dolphins in the Mediterranean Sea appear to be particularly susceptible to Morbillivirus infection, while harbour porpoises are susceptible to *Pseudalius inflexus* infestation. Of special concern are those regions where stressor prevalence and intensity are high (e.g. highly polluted areas) and/or which provide a home for endangered species or populations (e.g. the harbour porpoise population in the Baltic Sea Proper).

Declining trends have been detected for some transferable stressors such as POPs, even if concentrations are not yet below thresholds for adverse health effects, which gives us some basis for optimism. On the contrary, there have been reported increasing trends for other contaminants and other transferable stressors such as HABs. There is a general lack of long-term monitoring programmes that would allow us to detect trends in impacts, as well as a common feeling within the scientific community that management authorities and policymakers need to engage more with these issues.

Current research remains more focused on non-transferable stressors causing direct mortality of cetaceans, the effects of which are known to be important and which are arguably easier to quantify and mitigate compared to transferable stressors. In relation to transferable stressors, many challenges remain, including establishing cause–effect relationships between stressors and the outcomes seen in the receptor, understanding how sub-lethal impacts of transferable stressors interact with those of non-transferable stressors and accounting for numerous natural confounding factors.

Although this is perhaps a counterintuitive message, given the uncertainties in our understanding of transferable stressors and their cumulative effects, in the short-term, it is crucial to ensure that we adequately manage those threats to small cetaceans that can already be managed, primarily those due to the non-transferrable stressors. It is also critical that we address knowledge gaps in the context of responding and adapting to climate change, biodiversity loss and the growing human population.

Further efforts are needed to fill knowledge gaps on the sub-lethal impacts of transferable stressors, which may compromise individual health and thus affect population recruitment and mortality rates. More research is needed to quantify the amounts transferred (e.g. *Anisakis* from prey to predator, or PCBs from mother to calf) and to understand the mechanisms by which multiple stressors interact and generate cumulative impacts. Further steps are needed to develop modelling tools that account for multiple stressors of different types, ensuring that they are ecologically meaningful, and to implement them in ecosystem assessments.

While all threats to protected, endangered or vulnerable species deserve attention, priority may be given according to (1) their potential to cause lethal effects, epizootic and mass mortality events, such as pathogens and biotoxins like viruses or HABs, (2) increases in prevalence and/or intensity, such as seen in some parasites and contaminants, and (3) their emergence in new areas, for example as a consequence of climate change.

At present, there are no viable solutions available to eliminate transferable stressors, but mitigation and reduction measures should focus on their sources and on anthropogenic activities that exacerbate their effects (e.g. human activities' contribution to accelerate climate change).

As discussed by Santos and Pierce (2015) in relation to the MSFD, environmental legislation usually encapsulates our best intentions but struggles to deliver the intended solutions, as monitoring is prioritised over measures, the thresholds needed to trigger actions are endlessly debated, targets invariably end up looking more like the *status quo* than anything more ambitious and measures suffer from incomplete implementation and lack of enforcement. Such issues reflect the mindsets of the stakeholders involved, including scientists, managers and policymakers. If this is already challenging in relation to non-transferable stressors, like fishery bycatch, it is arguably more so for transferable stressors, whose effects are often slow acting, indirect, cumulative and poorly understood. Nevertheless, these are threats to which we must give urgent attention.

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Notes

1 UNEP: United Nations Environment Programme.
2 UNECE: United Nations Economic Commission for Europe.
3 EUvPvB: European Union Very Persistent, Very Bioaccumulative Compounds.
4 CEPA: Canadian Environmental Protection Act.
5 AHRs: Aryl hydrocarbon receptor protein that regulates CYP induction.
6 OHC: Organohalogen Contaminants.
7 AMAP: Arctic Monitoring and Assessment Programme.
8 ATSDR: Agency for Toxic Substances and Disease Registry (USA).

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