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Polychlorinated biphenyls (PCBs) in marine ecosystems

A review on toxicological, physiological, and ecological factors influencing the impact of polychlorinated biphenyls on marine mammals and seabirds

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Abstract

Pollution of seawater remains one of the biggest anthropogenic threats to marine ecosystems. Eutrophication, heavy metals, plastic waste and POPs all impact marine life in various ways. Some of these forms of pollution, such as PCBs, are especially long-lasting and persistent. PCB production started around 1920 and lasted until approximately 1980. Around this time a ban on the production of PCBs was established as a result of rising environmental and health concerns, as PCBs seeped into the environment because of improper storage and disposal, leaks from technical appliances and spills. Although the dangers of biomagnification and the effects of PCBs on marine species and ecosystems are well-studied, it remains a complex topic. As PCBs continue to pose a threat to marine life, there is a need for more reliable models to predict the impact of PCBs on marine ecosystems and populations. This review is divided into three main parts; toxicology, physiology, and biomagnification, and examines what role these three components play in relation to PCB accumulation and toxicity. The PCB risk level for individual species is influenced by many factors, such as species-specific metabolic capacities and compound-specific toxicity thresholds. In addition, there are several physiological and ecological factors that influence the degree of biomagnification in a food web, such as trophic level, metabolic rate, maternal transfer, migration, feeding preferences, and habitat use. I encourage more research on toxicity thresholds, factors influencing biomagnification, and population-level effects of PCBs, in an effort to build stronger models which can aid in conservation efforts.

Introduction

Earth's marine ecosystems are under pressure of numerous anthropogenic threats. One of these threats is pollution of seawater (Halpern et al., 2008). This pollution comes in many different forms: eutrophication, heavy metal pollution, plastic pollution, and persistent organic pollutants (POPs). For instance, eutrophication is a process in which a growth limiting factor, such as nutrients, becomes overabundant as a result of human activities (Carpenter, 1981). During such events, phosphorous and nitrogen are released into the coastal environment in huge quantities, which may result in in algal blooms, eventually leading to hypoxic/anoxic environments, suffocating marine life and creating dead zones (Diaz & Rosenberg, 2008).

Furthermore, heavy metal pollution is a source of concern to marine ecosystems. In small quantities, heavy metals are essential elements for life, but many of them become toxic when exceeding a certain concentration in organisms. When substances gradually accumulate in an organism this is defined as bioaccumulation. Earth's oceans have seen a rise in the concentration of heavy metals through human input for the past centuries. These heavy metals tend to accumulate in sediments near pollution sources, which raises concerns over bioaccumulation of heavy metals in organisms adjacent to these polluted areas (Ansari, Marr, & Tariq, 2004).

Another big source of pollution are plastics, which are being produced in ever growing quantities since their discovery in the 19th century. A lot of this plastic ends up in the oceans due to accidental or intentional dumping and mismanagement of waste treatment. They pose a range of problems for marine life; from entanglement in fishing equipment to starvation of animals due to the ingestion of plastics (Barnes, Galgani, Thompson, & Barlaz, 2009). Even when broken down into smaller particles (micro- or nano-plastics), plastics can still be dangerous. These particles contain toxic additives that can leach into the environment and penetrate cell membranes as most of them are lipophilic. Besides these additives, the nanoparticles can also be contaminated by other compounds such as various POPs (Auta, Emenike, & Fauziah, 2017). Nanoparticles, due to their high surface-area-to-volume ratio, can adsorp a relatively large amount of these POPs, thus exposing organisms to these chemicals from within (da Costa, Santos, Duarte, & Rocha-Santos, 2016).

One class of POPs that is particularly relevant today due to its widespread impact on marine life are polychlorinated biphenyls (PCBs). Even though the production of PCBs has been banned for decades because of environmental and health concerns (Takasuga, Senthilkumar, Matsumura, Shiozaki, & Sakai, 2006), this class of chemicals can still be found in the oceans, as well as terrestrial environments (IARC, 2016). It is because of the properties that make it qualified for many technical appliances (chemically and thermally inert) that it degrades so slowly in the environment. Although PCBs are found at relatively low concentrations in the oceans, they are known to bioaccumulate in fatty tissues of organisms (Groom, Meffe, & Carrol, 2006). The concentrations of accumulated PCBs tend to magnify throughout the food chain, a process known as biomagnification (Campbell et al., 2015).

There are many factors that influence the extent to which PCBs impact marine life. Numerous studies have been conducted on the effects of PCBs on physiological/molecular-, individual- and population-level, but it seems that an integration of this knowledge is required to further improve conservation efforts. This essay will review existing knowledge on different factors (toxicology, physiology, and biomagnification) which might influence the impact of PCB pollution on marine life. Marine mammals and seabirds are often at the top of the food web, hence they are useful indicators for environmental pollution (Acampora,

White, Lyashevska, & O'Connor, 2017; Antoniadou et al., 2007). Therefore, this essay will focus mainly on marine mammals and seabirds. It will try to identify knowledge gaps and propose areas of interest for new research and conservation efforts.

Polychlorinated biphenyls

Chemical properties of PCBs

Polychlorinated biphenyl is a collective name for biphenyl rings in which a varying number of hydrogen atoms are substituted by chlorine atoms. The carbon positions on each ring are numbered 1-6 and 1'-6' respectively (Fig. 1). Each of the hydrogen atoms at the carbon positions can be substituted by chlorine atoms, and in total there are 209 possible PCB congeners (IARC, 2016), numbered 1 – 209 (Table A1). PCBs are compounds with exceptional chemical and thermal stability; they tend not to react with other chemicals, or under high temperatures. Breakdown or degradation in the natural environment is slow because of these properties (IARC, 2016).

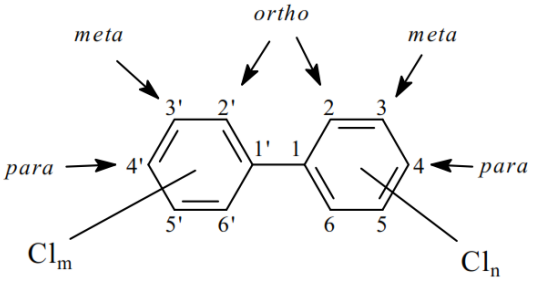

Fig. 1: Different substitution positions on the biphenyl rings numbered from 1-6 and 1'-6'. Para, meta and ortho positions are indicated.

Reprinted from IARC (2016)

PCBs enter ecosystems through various pathways

The worldwide commercial production of PCBs started in the 1920's, soared in the 60's and 70's, and in most countries had stopped by the early 80's due to international bans. In this time period, an estimate of between 1 to 1.5 million tonnes of commercial PCB were produced worldwide and they were used for technical appliances as a transformer oil, coolant or hydraulic fluid. Nowadays no more PCBs are produced, but it is possible that some quantities are still in use, for instance in old technical appliances. Therefore, it is plausible that small amounts of PCB still enter the environment today. Most commercial PCBs were not made up of one congener, but rather a mixture of many congeners, and were labelled by degree of chlorination (IARC, 2016).

PCBs can end up in the environment by improper storage and disposal, leakage from technical appliances and spills. PCBs can enter the atmosphere bound to particles or in the vapour phase, as many congeners are volatile at temperatures exceeding room temperature. When equipment that uses PCBs heats up, large amounts of PCBs can be vaporized. These elevated concentrations can result in contamination of the environment, both close to and further away from the source, through precipitation like rain or snow. PCBs enter soil through industries dumping and disposing of PCBs in landfills. PCBs enter the hydrological cycle via sewage discharge, industrial effluents, urban and agricultural run-off, and precipitation. PCBs in the hydrological cycle can be either particle-bound or a solute, although they are generally poorly soluble in water and tend to accumulate in sediments (IARC, 2016).

Toxicology

Mechanism of action

PCBs are often divided into two sub-groups: non-dioxin-like PCBs (NDL-PCBs) which are mono- and ortho-substituted (Fig. 1), and dioxin-like PCBs (DL-PCBs) which mostly lack the ortho-substituted chlorine atoms. Dioxin-like compounds such as DL-PCBs are known to act through the same receptor mediated mechanism by interacting with the aryl hydrocarbon receptor (AHR). Some studies on the effects of NDL-PCBs have been conducted, but the AHR- mediated mechanism has been the most extensively studied (WHO, 2016).

The AHR-PCB receptor-ligand complex causes changes in gene expression when it is translocated to the cell nucleus, resulting in a plethora of possible effects which will be further explained under the section 'Toxic effects of PCBs'. Furthermore, the binding of DL-PBCs to the AHR mediates cytochrome P450 induction. Cytochrome P450 is a family of enzymes involved in metabolism of xenobiotics, which are chemical substances that are not naturally found in, or produced by an organism (de March, de Wit, & Muir, 1998, pp. 204–205; Giesy, Ludwig, & Tillitt, 1994, p. 253; Safe & Phil, 1990).

The metabolic index for cytochrome P450 can vary greatly between species depending on their enzyme activities. Depending on metabolic activity, PCBs may not be metabolized and can accumulate to high concentrations in tissue, likely causing toxic effects. Secondly, they may be metabolized and excreted. A third possibility is the metabolization to more biologically active and/or toxic metabolites. (de March et al., 1998, pp. 204–205) However, dioxin-like OCs such as DL-PCBs seem to be metabolized much slower, as their halogen groups prevent the cytochrome P450 enzymes from oxidizing these compounds (Poland & Knutson, 1982; Webster & Commoner, 1994, pp. 8–9)**.**

Toxicity of PCBs

The toxicity of specific PCB congeners is calculated using their Toxic Equivalency Factor (TEF). This is the relative potency of a PCB congener compared to tetrachlorodibenzo-p-dioxin (TCDD), which is the most potent of dioxin-like compounds. The potency of the mixtures of congeners relative to TCDD can be expressed as the Toxic Equivalency (TCDD-EQ or TEQ). The TEQ is the sum of the products of each congeners concentration and its corresponding TEF value (Giesy et al., 1994, pp. 255–256; Safe & Phil, 1990). The TEQ can vary greatly depending on the specific mixture of congeners.

TEQ values are used to express the No Observable Adverse Effects Level (NOAEL) and the Lowest Observable Adverse Effects Level (LOAEL). The NOAEL denotes the highest concentration at which there is no observable detrimental effect. The LOAEL denotes the lowest concentration at which there is an observable detrimental effect and is used as a toxicity threshold value for observable effects. These effects can be morphological, developmental, and physiological, and usually a specific adverse effect is used as an endpoint in studies. Many different thresholds can be found in literature. For marine mammals, toxicity thresholds ranging from 9.0 mg/kg lw (as ∑PCB) to 41 mg/kg lipid weight (as ∑PCB) have been reported (Genov et al., 2019; Jepson et al., 2016). For most fish eating birds a concentration of 7pg TEQs/g wet weight in eggs is suggested (Auman et al., 1997; Giesy et al., 1994; Guruge, Tanaka, & Tanabe, 2001). However, there is great variation in these numbers and toxicity thresholds seem to be species and endpoint specific (Giesy et al., 1994). This implies that general toxicity thresholds for certain taxonomic groups should be conservative.

Toxic effects of PCBs

As previously mentioned, PCBs manifest themselves in a myriad of ways through one common AHR-receptor mediated mechanism of action. This results in a wide range of symptoms that are associated with PCB accumulation in marine mammals and seabirds. In marine mammals, PCB accumulation is correlated with reproductive disorders such as implantation failure, sterility and premature pupping (de March et al., 1998; DeLong, Gilmartin, & Simpson, 1973; Folland et al., 2016; Jepson et al., 2016; Reijnders, 1986, 2003). PCBs are also linked to immunosuppression and hormonal disorders such as low thyroid hormone and reduced testosterone & estradiol levels. Furthermore, they are associated with morphological disorders such as skull lesions, exostosis and hermaphroditism (de March et al., 1998; Genov et al., 2019; Kannan, Blankenship, Jones, & Giesy, 2000; Reijnders, 2003; Tanabe, Iwata, & Tatsukawa, 1994).

In seabirds, accumulation of PCBs is linked to reproductive and developmental disorders such as eggshell thinning, reduced hatching rate, growth retardation and birth defects such as a crossed bill, dwarf appendages, brain deformities and edema. Furthermore they are associated with immunosuppression, tumors, and behavioural changes (Barron, Galbraith, & Beltman, 1995; de March et al., 1998; Giesy et al., 1994; Guruge et al., 2001; Larson et al., 1996).

Although above symptoms have been correlated to PCBs, it remains difficult to say which exact symptoms can be attributed to PCBs due to the presence of numerous different contaminants in marine ecosystems. Isolating the effects of PCBs is complicated because organisms in the wild have often been chronically exposed to relatively low concentrations of several contaminants for years (de March et al., 1998). Controlled experiments might offer a solution, but interpreting and extrapolating these results to the wild can prove difficult as not much is known about possible interactions, cumulative effects or synergism between PCBs and other contaminants in wildlife (de March et al., 1998; Giesy et al., 1994).

Physiology

Biotransformation of PCBs

Studies show that PCBs' accumulation patterns across species are quite stable compared to other contaminants like organochlorine pesticides (OCPs) and polybrominated diphenyl ethers (PBDEs) (Byun, Moon, Choi, Hwang, & Kang, 2013). This implies that PCBs are relatively more resistant to metabolic transformation compared to other pollutants (Moon et al., 2010). PCBs are known for their mostly lipophilic properties, but there is some variation between congeners. Tri- to penta-CBs have $\log K_{ow}$ values that range from 5.5 to 6.5, whereas the $\log K_{ow}$ value of hexa- to deca-CBs ranges from 6.7 to 8.26 (Byun et al., 2013). The $\log K_{ow}$ (octanol-water partition coefficient) is a coefficient that denotes the lipophilicity of a compound. The higher the coefficient, the higher the lipophilicity of the compound. (Goerke, Weber, Bornemann, Ramdohr, & Plötz, 2004; Nfon, Cousins, & Broman, 2008). The potential for bioaccumulation that each PCB congener has, is correlated with the $\log K_{ow}$(Goerke et al., 2004; Nfon et al., 2008). Although lower and higher chlorinated congeners are found together in commercial mixtures and the environment, and PCBs are relatively resistant to biotransformation, lower chlorinated PCB congeners tend to be metabolized faster than higher chlorinated congeners. As a result, higher chlorinated congeners tend to bioaccumulate to a greater extent in fatty tissue, shifting the composition of the PCB mixture to a bigger percentage of higher chlorinated, generally more toxic PCBs (ATSDR, 2000; ERASC, 2003).

The biotransformation rate of PCBs is dependent on degree of chlorination and position of chlorine substitutions on the biphenyl rings. Lower chlorinated PCB congeners display a higher rate of biotransformation because they more often lack neighbouring chlorine substitutions on ortho-meta or ortho-para positions of the biphenyl rings (Fig. 1). These free positions are favoured by cytochrome P450 mediated metabolization, whereas higher chlorinated congeners are difficult to metabolize because they usually lack these unsubstituted positions (Naso, Perrone, Ferrante, Zaccaroni, & Lucisano, 2003).

A study done on the accumulation patterns of PCBs, including fish, cephalopods, bivalves, gastropods, crustaceans and cetaceans, reports that the accumulation patterns were dominated by higher chlorinated congeners (Fig. 2), with $\log K_{ow}$ ranging between 6.7 and 7.6 (Byun et al., 2013). Another study on seabirds, revealed that the percentage of higher chlorinated PCBs increased from water, to prey, to bird egg samples, while the percentage of lower chlorinated PCBs tended to decrease (Antoniadou et al., 2007). This indeed indicates a higher capacity for the biotransformation of lower chlorinated congeners in most species, while untransformed higher chlorinated congeners bioaccumulate to a greater extent throughout the food chain.

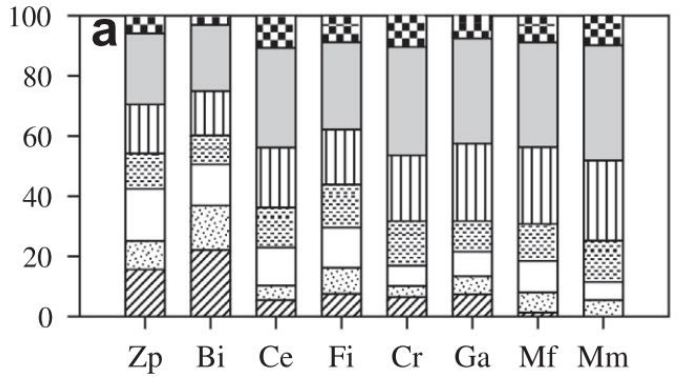

Fig. 2: Accumulation patterns of PCB congeners in a marine food web. Zp, zooplankton; Bi, bivalve; Ce, cephalopod; Fi, fish; Cr, crustacean; Ga, gastropod; Mf, female minke whale; Mm, male minke whale

Reprinted from Byun et al. (2013)

The effect of body condition on the accumulation of PCBs

In marine mammals, the body load of lipophilic pollutants strongly depends on the relative mass of blubber, and lipid mobilization results in an increase in residue levels (Aguilar & Pastor, 1999). A study on harp seals found that the PCB serum concentrations increased significantly through lipid mobilization as fat reserves were depleted (Lydersen et al., 2002). A significant negative effect of blubber on PCB blubber concentrations was found in several phocid seals, as well as Mediterranean striped dolphins (Fig. 3) (Aguilar & Pastor, 1999; Lydersen et al., 2002; J. Wolkers et al., 1998). In young Steller sea lion, the sum of PCB concentrations decreased as the biomass of pups increased. While organochlorine (OC) load increased with age, OC load showed a negative correlation to mass within the same age class (Keogh et al., 2020).

For birds, the same kind of trend can be discerned. One study showed an increase in PCB serum concentrations during incubation fast in the common eider. Females with a low body condition and high lipid metabolism showed a stronger increase in PCB concentrations (Bustnes et al., 2012). Another study on the same species reported an increase in PCB serum levels while body mass decreased during the incubation fast (Fenstad et al., 2014). In the black-legged kittiwake, blood levels of PCB-153 (one of seven indicator PCBs), increased by 2.5 times while body mass reduced (Bustnes et al., 2017). Another study on canvasbacks found an inverse relationship between declining body condition and contaminant burden (Hughes et al., 2019).

Above studies report relationships between a declining or lower body condition and elevated PCB concentrations. It seems that when body condition is stable, adipose tissue acts as a buffer for storing PCBs. When body condition decreases due to fasting, migration or overwintering, PCB serum and/or blubber concentrations increase because of lipid mobilization. This phenomenon of weight loss induced bioamplification can affect fitness and in some cases lead to higher mortality, as PCBs in blood serum are typically more readily available to vital organs than those stored in adipose tissue, presenting a (temporary) greater toxicological risk (Daley, Paterson, & Drouillard, 2014).

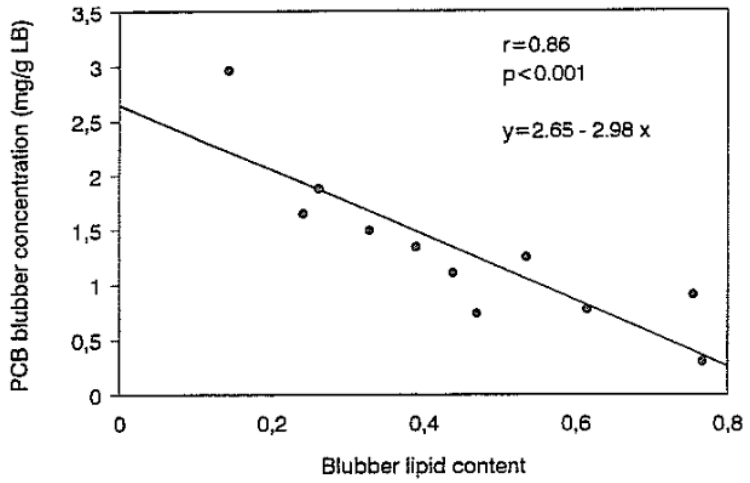

Fig. 3: A negative relationship between PCB blubber concentrations and blubber lipid content in Mediterranean striped dolphins (aged 15-19 years old)

Reprinted from Aguilar & Pastor (1999)

The effect of maternal transfer on the accumulation of PCBs

Studies among several species of marine mammals report significantly higher levels of contaminants in males as opposed to females. This difference was found in e.g. minke whales (Byun et al., 2013), harbour porpoises (Westgate, Muir, Gaskin, & Kingsley, 1997), common bottlenose dolphins (Genov et al., 2019; Wells et al., 2005), Antarctic fur seals (Brault, Goebel, Geisz, Canuel, & Dickhut, 2013), and Baikal seals (Iwata et al., 2004). Contaminants have been detected in the milk of mothers (Brault et al., 2013; Miranda Filho et al., 2009; Tanabe et al., 1994), affirming the notion that females have lower levels of contaminants due to lactational transfer of contaminants to pups (Wells et al., 2005). Although placental offloading is also a pathway of PCB elimination, transfer through lactation seems to be the more significant process for most species, as the lipid content of marine mammals' milk can be as high as 35-60% (Borgå, Fisk, Hoekstra, & Muir, 2004).

The idea of maternal offloading is further strengthened by studies reporting significant decreases in contaminant body load from nulliparous to primiparous and multiparous females (Brault et al., 2013; Genov et al., 2019; Wells et al., 2005; Westgate et al., 1997). However, one study found no significant effect of sex on PCB concentrations in ringed seals (J. Wolkers et al., 1998). It is noted that this might be since ringed seals are income breeders, meaning they continue to feed during lactation, as opposed to capital breeders which rely on built-up fat reserves. A meta-analysis on the effects of these different reproductive strategies on maternal offloading of contaminants did not find any conclusive results, possibly due to the overrepresentation of capital breeder data (Hitchcock, Varpe, Andersen, & Borgå, 2017). More data on income breeders is necessary for future research.

The effect of maternal offloading on calf survival has been studied to some extent. Model studies show that PCBs effect on calf survival, defined as the probability that a calf survives its first year, might depress population growth in several cetacean species, like the

common bottlenose dolphin, killer whale and humpback whale (Hall et al., 2006, 2018). However, one of these models showed that the effects of PCBs on immunity, mainly immunosuppression, had a bigger impact on population growth than its effects on calf survival. However, the authors noted that model predictions were limited due to parameter uncertainty (Hall et al., 2018). Another model study on killer whales around the globe predicts possible population collapse for some of the heavier contaminated populations, due to PCBs' effects on immunity and calf survival combined (Desforges et al., 2018). It seems that further research on population level effects of PCBs regarding calf survival and immunosuppression is needed to build stronger and more meaningful models.

Evidently, when it comes to birds there is no such thing as lactational transfer. However, there are other ways in which maternal transfer takes place. A study on the ring dove reports that PCBs accumulation patterns in eggs mirror the patterns found in maternal tissue rather than the patterns found in the mothers' diet, indicating transfer of contaminants from maternal tissue to eggs (Drouillard & Norstrom, 2001). In the common eider, a negative relationship between PCB-153 concentrations during incubation and clutch size is reported (Bustnes et al., 2010), strengthening the idea that contaminants can be offloaded to eggs. Evidence for excretion of PCBs to eggs has been found in several species of seabirds (Bargar, Scott, & Cobb, 2001; Caccamise, Wang, Wu, Woodward, & Li, 2012; Lemmetyinen, Rantamäki, & Karlin, 1982; Tanabe, Hidaka, & Tatsukawa, 1986). In accordance with these findings, OC serum concentrations have been reported to be higher in males than in females among a few different species of seabirds (Bustnes, Bakken, Skaare, & Erikstad, 2003; Bustnes, Fauchald, Tveraa, Helberg, & Skaare, 2008; Bustnes, Tveraa, Varpe, Henden, & Skaare, 2007). In contrast, differences in OC blood concentration between males and females seem to fluctuate in black-legged kittiwakes. In some years, no significant differences were recorded, whereas in other years a difference was found (Bustnes et al., 2017). This might be linked to poor food availability, forcing females to mobilize lipids, therefore recruiting OCs to the serum (Bustnes et al., 2008).

The magnitude of maternal offload seems positively correlated to egg weight relative to the mothers weight (Caccamise et al., 2012; Lemmetyinen et al., 1982; Tanabe et al., 1986). However, it is likely that the degree of maternal offloading is also dependent on the reproductive strategy employed. Black-footed albatross females leave after mating but prior to egg laying, to feed and build their fat reserves. Contaminant patterns in the eggs do not mirror those found in tissue of adult specimen but seem to be from a local origin. This suggests that contaminants originate from the food ingested days before egg laying, and are not mobilized from maternal tissue (Caccamise et al., 2012).

Studies show that high levels of maternal PCBs impact viability, defined as the proportion of eggs that hatched, in several species of seabirds (Bustnes, Erikstad, Skaare, Bakken, & Mehlum, 2003; Giesy et al., 1994). Furthermore, negative relationships between OC concentrations and hatching condition of chicks have been reported (Bustnes, Erikstad, et al., 2003; Bustnes et al., 2007). Information on potential population-level effects of reduced viability and decreased hatching condition seems scarce and more research on this topic is needed.

Biomagnification

The impact of several ecological factors on the biomagnification of PCBs

For ecosystem-level PCB risk assessment, the contaminants' path and degree of magnification throughout a food web must be determined. It is generally acknowledged that

with an increase in trophic level (TL), PCBs become increasingly concentrated in the tissues of biota (Borgå, Gabrielsen, & Skaare, 2001; Borgå et al., 2012). A good example of this can be found in the killer whale, for which several ecotypes are classified within the species. Resident killer whales, residing in the coastal waters of Washington and British Columbia, feed primarily on fish, whereas transient killer whales feed predominantly on marine mammals, putting the transient killer whales at a higher trophic level (Ford et al., 1998; Herman et al., 2005; Saulitis, Matkin, Barrett-Lennard, Heise, & Ellis, 2000). The transient whales had much higher levels of PCBs than the resident whales, and in addition to that transient whales also had a higher percentage of higher chlorinated congeners in their accumulation patterns (Herman et al., 2005). This effect has been demonstrated in terrestrial (Fremlin et al., 2020), freshwater (Dietz et al., 2000) and marine food webs (Borgå et al., 2004; Dietz et al., 2000), and is usually described as biomagnification.

To quantify this magnification potential of PCBs throughout a food web, you need a biomagnification endpoint. The two most frequently encountered in food web analyses are the biomagnification factor (BMF) and the trophic magnification factor (TMF). BMFs are suited for measuring biomagnification between a specific predator and prey or single links in a food web. The BMF can be defined as the ratio of a chemical's concentration in a predator to that in its prey, and it can vary greatly between different combinations of predator and prey (Borgå et al., 2012; Franklin, 2015). Because of this, BMF might not be the best measurement for generalist predators, which hunt multiple prey species from multiple trophic levels. The TMF is a more comprehensive approach and represents an average BMF over multiple TLs or the entire food web. It is determined by calculating the regression slope of the chemical concentration and the TL of species in a food web (Borgå et al., 2012). TMF can vary greatly depending on which species are included, as there can be differences in biomagnification between specific species or groups of species. Both BMFs and TMFs are calculated with the assumption that an equilibrium between PCB concentrations of predator and prey has been reached (Borgå et al., 2004; Murray, 1998). Therefore, there are several confounding factors that must be considered when working with BMFs and TMFs.

One study on a polynyan food web (a polynya is an open water area surrounded by sea ice) demonstrated that while the TMF gave an average biomagnification factor, it overestimated BMFs for homeotherms (birds, mammals), and underestimated BMFs for poikilotherms (fish) (Fisk, Hobson, & Norstrom, 2001). Homeotherms have higher metabolic rates compared to poikilotherms, and hence a relatively greater feeding rate (Braune & Norstrom, 1989). Therefore, homeotherms have a greater uptake of contaminants through food, resulting in a potential higher rate of biomagnification than poikilotherms. This still holds true if they are feeding at a similar trophic level and are of comparable size (Borgå et al., 2012; Braune & Norstrom, 1989). Even within homeotherms, a difference in feeding rate is reflected in the BMF. Seabirds, which generally have a higher metabolic rate than mammals, were reported to have a greater BMF than ringed seals (Fisk et al., 2001), emphasizing the impact different feeding rates and energy requirements can have when calculating magnification factors.

Another factor that can result in a biased TMF is the biotransformation capacity of different species. Generally, the biotransformation capacity increases from fish to birds to mammals (Boon, Eijgenraam, Everaarts, & Duinker, 1989; Borgå et al., 2004; Kania-Korwel & Lehmler, 2016; Warner, Norstrom, Wong, & Fisk, 2005). Nevertheless, between species and depending on which PCB, this capacity can vary significantly (Borgå et al., 2004). Seabirds and most marine mammals are more proficient at metabolizing non-ortho and mono-ortho PCBs (Boon et al., 1989), whereas polar bears appear to possess a greater

capacity for metabolizing PCBs with more than one chlorine at the ortho position (Borgå et al., 2004; Norstrom, Simon, Muir, & Schweinsburg, 1988). Species-specific differences in biotransformation of PCBs were also found among seabirds. Some species, like the black-legged kittiwake, are less efficient in metabolizing PCBs than others, like the little auk. The black guillemot has difficulty metabolizing non-meta and non-para PCBs, while Brünnich's guillemot can poorly metabolize non-meta and non-para PCBs (Borgå et al., 2005).

Additionally, migration events can throw off the accuracy of TMFs. For example, many species of mammals and birds are migrating to arctic ecosystems in the summer (Borgå et al., 2004) to forage for lipid-rich prey items (Murray, 1998). As the arctic habitats are likely less contaminated than the more southern, temperate ecosystems (Fisk et al., 2001), it is likely that these organisms aren't exposed to the same PCB concentrations and patterns throughout the year. This may generate inaccurate calculations of TMFs because as discussed earlier, TMFs assume that a steady state between the concentrations of PCBs of predator and prey has been achieved (Borgå et al., 2004). A good example is a population of black-legged kittiwakes from North America, which migrates to the Canadian Arctic in summer to breed. PCB concentrations were found to be much higher in this species as compared to other species of seabird that were of a comparable trophic level, but year-round residents of the Arctic such as the black guillemot (Buckman et al., 2004). In the Antarctic, contaminant concentrations in migrating species of seabird, such as the brown skua and South polar skua, were reported to be higher than those in resident birds such as the Adèlie and Emperor penguin (Corsolini, Borghesi, Ademollo, & Focardi, 2011). Similar processes occur within certain migratory or non-sedentary marine mammals, like the harbour porpoises that reside in and migrate between the North Sea and the Baltic Sea. Several cases were reported where the PCB/DDT ratio in blubber of harbour porpoises that washed up on the German shore were more similar to the PCB/DDT ratios samples from the Baltic Sea (Vetter, Luckasa, Heidemann, & Skírnisson, 1996).

Furthermore, individual feeding preferences can distort the calculation of magnification factors. In walrus, evidence for individual prey selection has been found in populations from the Eastern Hudson Bay, Canada, and in one from Svalbard, Norway. A large variation in PCB levels was found within both groups. Individuals with elevated PCB concentrations also displayed greater proportions of higher chlorinated, more persistent PCBs. This suggests they are feeding on a higher trophic level than their peers, foraging not only for molluscs but also incorporating seals into their diet. (Muir et al., 1995; H. Wolkers et al., 2006). This effect is also seen in some species of seabird, which occasionally forage on offal and cadavers of marine mammals (Fisk et al., 2001; Renaud & McLaren, 1982). Their OC concentrations exceeded the expected levels based on $\delta^{15}N$ values. $\delta^{15}N$ is a value used for determining an organisms trophic level with the use of stable isotopes, where a higher $\delta^{15}N$ value indicates a higher trophic level (Buckman et al., 2004). This demonstrates that these subtle shifts in diet can skew biomagnification endpoints, as these feeding preferences do not always show up in stable isotope analysis but can still heighten PCB concentrations.

Lastly, habitat selection can result in varying PCB concentrations, thus possibly distorting BMF and TMF calculations. This can happen through prey that was locally contaminated (Borgå et al., 2004; Brown et al., 2015). For instance, in Labrador ringed seals from four different marine inlets, a difference in PCB concentrations and accumulation patterns could be explained by local prey contamination resulting from differences in contamination between inlets, rather than individual feeding preferences (Brown et al., 2015).

Although trophic level seems to be the major factor in explaining PCB dynamics and concentrations for seabirds and mammals (Borgå et al., 2004), it is important that the aforementioned confounding factors are taken into account when modelling population-level effects on these species.

Conclusions

Polychlorinated biphenyls are pollutants that still give rise to concern regarding their effects on marine ecosystems. Because of their chemically and thermally inert nature they are persistent in the environment, even decades after their production was banned. Thanks to their lipophilic nature and resistance to metabolic transformation, they bioaccumulate in the tissue of organisms. Toxicity thresholds seem to be species and endpoint specific. However, because of ethical and practical constraints, thresholds for many species of marine mammals remain unaccounted for. Nevertheless, many lab controlled- and field studies correlate accumulation of PCBs with detrimental effects on health, immunity, and reproductive potential of marine mammals and seabirds. However, as numerous contaminants often exist simultaneously in the environment, it remains challenging to pinpoint the exact effects of chronic PCB exposure. Most species are more capable of metabolizing lower chlorinated PCBs than the generally more toxic higher chlorinated congeners. Therefore, these more toxic PCBs tend to be overrepresented in organisms higher up the food chain when compared to their ratio in commercially produced mixtures. Furthermore, seasonal fat loss or a declining body condition seems to elevate circulating PCB concentrations in both marine mammals and seabirds which may in turn affect fitness. Maternal transfer on the other hand, seems to decrease the PCB concentrations in females of some species of marine mammals and seabirds. Although this may alleviate some effects of PCBs on the mother, the transfer of PCBs from mother to offspring could negatively affect offspring survival. A few model studies on offspring survival have been conducted, but conclusive results remain scarce, hence more research into this topic is essential for understanding population-level effects. When modelling population-level effects of PCBs it is necessary to have insight into the biomagnification of these compounds. Generally, PCBs tend to be biomagnified throughout the food web. As marine mammals and seabirds inhabit high trophic levels, they are excellent bioindicators that can give insight into the health of a food web. Factors, besides trophic level, reported to influence the biomagnification of PCBs are maternal transfer, metabolic rate, biotransformation capacities, migration, feeding preferences and habitat use, and these should be considered in a model-based approach. More data on the effect of these factors on PCB accumulation and magnification, as well as a more comprehensive database on species-specific toxicity thresholds is needed, as it would enable more reliable models of PCBs effects on population dynamics to be built. This is crucial for future risk assessment and conservation efforts, as marine top predators are generally at the highest risk of PCB toxicity and are at the same time of great importance for ecosystem stability, because they are often keystone species. It is therefore of utmost importance that these species are protected to the best of our efforts.

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Appendix A: Table of PCB congeners

IUPAC name	BZ congener number
Biphenyl	0
2-Chlorobiphenyl	1
3-Chlorobiphenyl	2
4-Chlorobiphenyl	3
2,2'-Dichlorobiphenyl	4
2,3-Dichlorobiphenyl	5
2,3'-Dichlorobiphenyl	6
2,4-Dichlorobiphenyl	7
2,4'-Dichlorobiphenyl	8
2,5-Dichlorobiphenyl	9
2,6-Dichlorobiphenyl	10
3,3'-Dichlorobiphenyl	11
3,4-Dichlorobiphenyl	12
3,4'-Dichlorobiphenyl	13
3,5-Dichlorobiphenyl	14
4,4'-Dichlorobiphenyl	15
2,2',3-Trichlorobiphenyl	16
2,2',4-Trichlorobiphenyl	17
2,2',5-Trichlorobiphenyl	18
2,2',6-Trichlorobiphenyl	19
2,3,3'-Trichlorobiphenyl	20
2,3,4-Trichlorobiphenyl	21
2,3,4'-Trichlorobiphenyl	22
2,3,5-Trichlorobiphenyl	23
2,3,6-Trichlorobiphenyl	24
2,3',4-Trichlorobiphenyl	25
2,3',5-Trichlorobiphenyl	26
2,3',6-Trichlorobiphenyl	27
2,4,4'-Trichlorobiphenyl	28
2,4,5-Trichlorobiphenyl	29
2,4,6-Trichlorobiphenyl	30
2,4',5-Trichlorobiphenyl	31
2,4',6-Trichlorobiphenyl	32
2,3',4'-Trichlorobiphenyl	33
2,3',5'-Trichlorobiphenyl	34
3,3',4-Trichlorobiphenyl	35
3,3',5-Trichlorobiphenyl	36
3,4,4'-Trichlorobiphenyl	37
3,4,5-Trichlorobiphenyl	38
3,4',5-Trichlorobiphenyl	39
2,2',3,3'-Tetrachlorobiphenyl	40
2,2',3,4-Tetrachlorobiphenyl	41
2,2',3,4'-Tetrachlorobiphenyl	42
2,2',3,5-Tetrachlorobiphenyl	43
2,2',3,5'-Tetrachlorobiphenyl	44
2,2',3,6-Tetrachlorobiphenyl	45
2,2',3,6'-Tetrachlorobiphenyl	46
2,2',4,4'-Tetrachlorobiphenyl	47

Table A1: PCB congeners with their IUPAC name and sorted on BZ congener number

Adapted from IARC (2016)

2,2',4,5-Tetrachlorobiphenyl	48
2,2',4,5'-Tetrachlorobiphenyl	49
2,2',4,6-Tetrachlorobiphenyl	50
2,2',4,6'-Tetrachlorobiphenyl	51
2,2',5,5'-Tetrachlorobiphenyl	52
2,2',5,6'-Tetrachlorobiphenyl	53
2,2',6,6'-Tetrachlorobiphenyl	54
2,3,3',4-Tetrachlorobiphenyl	55
2,3,3',4'-Tetrachlorobiphenyl	56
2,3,3',5-Tetrachlorobiphenyl	57
2,3,3',5'-Tetrachlorobiphenyl	58
2,3,3',6-Tetrachlorobiphenyl	59
2,3,4,4'-Tetrachlorobiphenyl	60
2,3,4,5-Tetrachlorobiphenyl	61
2,3,4,6-Tetrachlorobiphenyl	62
2,3,4',5-Tetrachlorobiphenyl	63
2,3,4',6-Tetrachlorobiphenyl	64
2,3,5,6-Tetrachlorobiphenyl	65
2,3',4,4'-Tetrachlorobiphenyl	66
2,3',4,5-Tetrachlorobiphenyl	67
2,3',4,5'-Tetrachlorobiphenyl	68
2,3',4,6-Tetrachlorobiphenyl	69
2,3',4',5-Tetrachlorobiphenyl	70
2,3',4',6-Tetrachlorobiphenyl	71
2,3',5,5'-Tetrachlorobiphenyl	72
2,3',5',6-Tetrachlorobiphenyl	73
2,4,4',5-Tetrachlorobiphenyl	74
2,4,4',6-Tetrachlorobiphenyl	75
2,3',4',5'-Tetrachlorobiphenyl	76
3,3',4,4'-Tetrachlorobiphenyl	77
3,3',4,5-Tetrachlorobiphenyl	78
3,3',4,5'-Tetrachlorobiphenyl	79
3,3',5,5'-Tetrachlorobiphenyl	80
3,4,4',5-Tetrachlorobiphenyl	81
2,2',3,3',4-Pentachlorobiphenyl	82
2,2',3,3',5-Pentachlorobiphenyl	83
2,2',3,3',6-Pentachlorobiphenyl	84
2,2',3,4,4'-Pentachlorobiphenyl	85
2,2',3,4,5-Pentachlorobiphenyl	86
2,2',3,4,5'-Pentachlorobiphenyl	87
2,2',3,4,6-Pentachlorobiphenyl	88
2,2',3,4,6'-Pentachlorobiphenyl	89
2,2',3,4',5-Pentachlorobiphenyl	90
2,2',3,4',6-Pentachlorobiphenyl	91
2,2',3,5,5'-Pentachlorobiphenyl	92
2,2',3,5,6-Pentachlorobiphenyl	93
2,2',3,5,6'-Pentachlorobiphenyl	94
2,2',3,5',6-Pentachlorobiphenyl	95
2,2',3,6,6'-Pentachlorobiphenyl	96
2,2',3,4',5'-Pentachlorobiphenyl	97
2,2',3,4',6'-Pentachlorobiphenyl	98
2,2',4,4',5-Pentachlorobiphenyl	99
2,2',4,4',6-Pentachlorobiphenyl	100

2,2',4,5,5'-Pentachlorobiphenyl	101
2,2',4,5,6'-Pentachlorobiphenyl	102
2,2',4,5',6-Pentachlorobiphenyl	103
2,2',4,6,6'-Pentachlorobiphenyl	104
2,3,3',4,4'-Pentachlorobiphenyl	105
2,3,3',4,5-Pentachlorobiphenyl	106
2,3,3',4',5-Pentachlorobiphenyl	107
2,3,3',4,5'-Pentachlorobiphenyl	108
2,3,3',4,6-Pentachlorobiphenyl	109
2,3,3',4',6-Pentachlorobiphenyl	110
2,3,3',5,5'-Pentachlorobiphenyl	111
2,3,3',5,6-Pentachlorobiphenyl	112
2,3,3',5',6-Pentachlorobiphenyl	113
2,3,4,4',5-Pentachlorobiphenyl	114
2,3,4,4',6-Pentachlorobiphenyl	115
2,3,4,5,6-Pentachlorobiphenyl	116
2,3,4',5,6-Pentachlorobiphenyl	117
2,3',4,4',5-Pentachlorobiphenyl	118
2,3',4,4',6-Pentachlorobiphenyl	119
2,3',4,5,5'-Pentachlorobiphenyl	120
2,3',4,5',6-Pentachlorobiphenyl	121
2,3,3',4',5'-Pentachlorobiphenyl	122
2,3',4,4',5'-Pentachlorobiphenyl	123
2,3',4',5,5'-Pentachlorobiphenyl	124
2,3',4',5',6-Pentachlorobiphenyl	125
3,3',4,4',5-Pentachlorobiphenyl	126
3,3',4,5,5'-Pentachlorobiphenyl	127
2,2',3,3',4,4'-Hexachlorobiphenyl	128
2,2',3,3',4,5-Hexachlorobiphenyl	129
2,2',3,3',4,5'-Hexachlorobiphenyl	130
2,2',3,3',4,6-Hexachlorobiphenyl	131
2,2',3,3',4,6'-Hexachlorobiphenyl	132
2,2',3,3',5,5'-Hexachlorobiphenyl	133
2,2',3,3',5,6-Hexachlorobiphenyl	134
2,2',3,3',5,6'-Hexachlorobiphenyl	135
2,2',3,3',6,6'-Hexachlorobiphenyl	136
2,2',3,4,4',5-Hexachlorobiphenyl	137
2,2',3,4,4',5'-Hexachlorobiphenyl	138
2,2',3,4,4',6-Hexachlorobiphenyl	139
2,2',3,4,4',6'-Hexachlorobiphenyl	140
2,2',3,4,5,5'-Hexachlorobiphenyl	141
2,2',3,4,5,6-Hexachlorobiphenyl	142
2,2',3,4,5,6'-Hexachlorobiphenyl	143
2,2',3,4,5',6-Hexachlorobiphenyl	144
2,2',3,4,6,6'-Hexachlorobiphenyl	145
2,2',3,4',5,5'-Hexachlorobiphenyl	146
2,2',3,4',5,6-Hexachlorobiphenyl	147
2,2',3,4',5,6'-Hexachlorobiphenyl	148
2,2',3,4',5',6-Hexachlorobiphenyl	149
2,2',3,4',6,6'-Hexachlorobiphenyl	150
2,2',3,5,5',6-Hexachlorobiphenyl	151
2,2',3,5,6,6'-Hexachlorobiphenyl	152
2,2',4,4',5,5'-Hexachlorobiphenyl	153

2,2',4,4',5,6'-Hexachlorobiphenyl	154
2,2',4,4',6,6'-Hexachlorobiphenyl	155
2,3,3',4,4',5-Hexachlorobiphenyl	156
2,3,3',4,4',5'-Hexachlorobiphenyl	157
2,3,3',4,4',6-Hexachlorobiphenyl	158
2,3,3',4,5,5'-Hexachlorobiphenyl	159
2,3,3',4,5,6-Hexachlorobiphenyl	160
2,3,3',4,5',6-Hexachlorobiphenyl	161
2,3,3',4',5,5'-Hexachlorobiphenyl	162
2,3,3',4',5,6-Hexachlorobiphenyl	163
2,3,3',4',5',6-Hexachlorobiphenyl	164
2,3,3',5,5',6-Hexachlorobiphenyl	165
2,3,4,4',5,6-Hexachlorobiphenyl	166
2,3',4,4',5,5'-Hexachlorobiphenyl	167
2,3',4,4',5',6-Hexachlorobiphenyl	168
3,3',4,4',5,5'-Hexachlorobiphenyl	169
2,2',3,3',4,4',5-Heptachlorobiphenyl	170
2,2',3,3',4,4',6-Heptachlorobiphenyl	171
2,2',3,3',4,5,5'-Heptachlorobiphenyl	172
2,2',3,3',4,5,6-Heptachlorobiphenyl	173
2,2',3,3',4,5,6'-Heptachlorobiphenyl	174
2,2',3,3',4,5',6-Heptachlorobiphenyl	175
2,2',3,3',4,6,6'-Heptachlorobiphenyl	176
2,2',3,3',4,5',6'-Heptachlorobiphenyl	177
2,2',3,3',5,5',6-Heptachlorobiphenyl	178
2,2',3,3',5,6,6'-Heptachlorobiphenyl	179
2,2',3,4,4',5,5'-Heptachlorobiphenyl	180
2,2',3,4,4',5,6-Heptachlorobiphenyl	181
2,2',3,4,4',5,6'-Heptachlorobiphenyl	182
2,2',3,4,4',5',6-Heptachlorobiphenyl	183
2,2',3,4,4',6,6'-Heptachlorobiphenyl	184
2,2',3,4,5,5',6-Heptachlorobiphenyl	185
2,2',3,4,5,6,6'-Heptachlorobiphenyl	186
2,2',3,4',5,5',6-Heptachlorobiphenyl	187
2,2',3,4',5,6,6'-Heptachlorobiphenyl	188
2,3,3',4,4',5,5'-Heptachlorobiphenyl	189
2,3,3',4,4',5,6-Heptachlorobiphenyl	190
2,3,3',4,4',5',6-Heptachlorobiphenyl	191
2,3,3',4,5,5',6-Heptachlorobiphenyl	192
2,3,3',4',5,5',6-Heptachlorobiphenyl	193
2,2',3,3',4,4',5,5'-Octachlorobiphenyl	194
2,2',3,3',4,4',5,6-Octachlorobiphenyl	195
2,2',3,3',4,4',5,6'-Octachlorobiphenyl	196
2,2',3,3',4,4',6,6'-Octachlorobiphenyl	197
2,2',3,3',4,5,5',6-Octachlorobiphenyl	198
2,2',3,3',4,5,5',6'-Octachlorobiphenyl	199
2,2',3,3',4,5,6,6'-Octachlorobiphenyl	200
2,2',3,3',4,5',6,6'-Octachlorobiphenyl	201
2,2',3,3',5,5',6,6'-Octachlorobiphenyl	202
2,2',3,4,4',5,5',6-Octachlorobiphenyl	203
2,2',3,4,4',5,6,6'-Octachlorobiphenyl	204
2,3,3',4,4',5,5',6-Octachlorobiphenyl	205
2,2',3,3',4,4',5,5',6-	206

Nonachlorobiphenyl	
2,2',3,3',4,4',5,6,6'-Nonachlorobiphenyl	207
2,2',3,3',4,5,5',6,6'-Nonachlorobiphenyl	208
Decachlorobiphenyl	209