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REVIEW

Understanding individual and population-level effects of plastic pollution on marine megafauna

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ABSTRACT: Plastic pollution is increasing rapidly throughout the world's oceans and is considered a major threat to marine wildlife and ecosystems. Although known to cause lethal or sub-lethal effects to vulnerable marine megafauna, population-level impacts of plastic pollution have not been thoroughly investigated. Here, we compiled and evaluated information from peer-reviewed studies that reported deleterious individual-level effects of plastic pollution on air-breathing marine megafauna (i.e. seabirds, marine mammals, and sea turtles) worldwide, highlighting those that assessed potential population-level effects. Lethal and sub-lethal individual-level effects included drowning, starvation, gastrointestinal tract damage, malnutrition, physical injury, reduced mobility, and physiological stress, resulting in reduced energy acquisition and assimilation, compromised health, reproductive impairment, and mortality. We found 47 studies published between 1969 and 2020 that considered population-level effects of plastic entanglement (n = 26), ingestion (n = 19), or both (n = 2). Of these, 7 inferred population-level effects (n = 6, entanglement; n = 1, ingestion), whereas 19 lacked evidence for effects (n = 12, entanglement; n = 6, ingestion; n = 1, both). However, no study in the past 50 yr reported direct evidence of population-level effects. Despite increased interest in and awareness of the presence of plastic pollution throughout the world's oceans, the extent and magnitude of demographic impacts on marine megafauna remains largely unassessed and therefore unknown, in contrast to well-documented effects on individuals. Addressing this major assessment gap will allow researchers and managers to compare relative effects of multiple threats—including plastic pollution—on marine megafauna populations, thus providing appropriate context for strategic conservation priority-setting.

KEY WORDS: Marine plastic · Marine debris · Population dynamics · Ingestion · Entanglement · Abandoned gear · Lost gear · Discarded gear · Ghost fishing · Marine mammal · Sea turtle · Seabird

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1. INTRODUCTION

Plastic pollution is ubiquitous throughout the world's oceans and can originate from both land- and marine-based sources, such as public littering, sewage and drainage outflows, fisheries, and shipping (Barnes et al. 2009, Ryan et al. 2009, Cózar et al. 2014, Nelms et al. 2017). Marine plastic pollution is increasing globally and accounts for up to 80% of anthropogenic waste accumulated on shorelines and in oceans (Barnes et al. 2009. Nelms et al. 2017). Today, over 5 trillion pieces of plastic, collectively weighing over

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250 000 tons, are estimated to be floating in the world's oceans (Eriksen et al. 2014).

Plastic persists in marine environments due to its chemically engineered durability, although it degrades, both physically and chemically, over time (Barnes et al. 2009, Cózar et al. 2014). Due to this persistence and increasing influx into the oceans, plastic is accumulating in a wide range of marine habitats, including shorelines, the seafloor in shallow waters as well as deep basins, and in all major ocean gyres (Barnes et al. 2009, Lebreton et al. 2012, Eriksen et al. 2014, Pham et al. 2014, Woodall et al. 2014). Due to its omnipresence, plastic pollution poses a risk to marine wildlife through ingestion, entanglement, and habitat degradation (Vegter et al. 2014).

To date, over 900 marine species have been observed interacting with plastic pollution (Vegter et al. 2014, Gall & Thompson 2015, Provencher et al. 2017, Kühn & van Franeker 2020). Air-breathing marine megafauna (i.e. seabirds, marine mammals, and sea turtles) are the taxa most commonly reported to incur effects (Kühn & van Franeker 2020), although this may be biased given that observations of effects may be most apparent for these organisms and a large number of records come from dead individuals. Plastic pollution can cause lethal individual-level effects to marine megafauna from entanglement or ingestion, but can also lead to sub-lethal individual-level effects that may influence resource acquisition, health, and reproductive output (Nelms et al. 2015, Fig. 1). Ingestion frequency has been increasing globally in seabirds and sea turtles for decades (Robards et al. 1995, Ryan et al. 2009, Teuten et al. 2009, Schuyler et al. 2014a). Estimates suggest that 99% of all seabird species and 95% of the individuals within these species may have plastic in their digestive tracts by 2050 (Wilcox et al. 2015b). More than half (52%) of the world's sea turtles are thought to have already ingested plastic material (Schuyler et al. 2016), with a predominance of microplastics (plastic particles <5 mm; Duncan et al. 2019a).

The global and pervasive nature of plastic pollution has gained substantial international attention and interest recently, both in the peer-reviewed literature and in popular media. This has included a growing number of studies documenting marine megafauna interactions with plastic pollution over the last half century (Vegter et al. 2014, Gall & Thompson 2015, Provencher et al. 2017, Kühn & van Franeker 2020), as well as visual imagery of dead or suffering animals (e.g. plastic-loaded seabird carcasses or entangled marine mammals) and their polluted habitats (e.g. oceanic 'garbage patches' or remote plastic-laden islands such as Midway Atoll). However, the effects of plastic pollution on marine megafauna populations relative to impacts of other threats have not been thoroughly investigated.

In this review, we compiled and evaluated available information from published studies that reported negative individual-level effects of plastic pollution on seabirds, marine mammals, and sea turtles worldwide, with a particular interest in highlighting studies that assessed potential population-level effects on these taxa. We conclude by discussing current knowledge gaps, recommendations for improving assessments of effects, and next phases for research and mitigation that could benefit marine megafauna.

2. METHODS

We conducted an extensive literature review to assess available information regarding population-level impacts of plastic pollution on air-breathing marine megafauna (i.e. seabirds, marine mammals, and sea turtles). Seabirds included any of the 414 species and corresponding families described by Ryan (2018), sea turtles included all 7 species, while marine mammals included cetaceans, pinnipeds (i.e.

Fig. 1. (on next page) Representative individual-level effects of plastic pollution on air-breathing marine megafauna (i.e. seabirds, marine mammals, and sea turtles) and their habitats: (A) adult humpback whale *Megaptera novaeangliae* entangled in a conglomerate of ghost fishing gear and other plastic materials, including over 22 different line types, off of Maui, Hawaii (photo: Ed Lyman, NOAA/MMHSRP permit #932-1489); (B) ringed seal *Phoca hispida* with plastic strap wrapped around its body along the coast of Alaska (photo taken by Alaska Fish and Game under ADFG research permits 358-1888 and 358-1787); (C) juvenile Kemp's ridley turtle *Lepidochelys kempii* that ingested the latex end of a toy balloon, from which the synthetic ribbon trailed from the turtle and was wrapped around its front flippers, 65 nautical miles west of Sarasota, Florida (photo: Blair Witherington); (D) great egret *Ardea alba* entangled in recreational fishing line wrapped around its neck and beak, which appeared to be inhibiting its feeding, on a Florida Atlantic beach (photo: Blair Witherington); (E) Laysan albatross chick with ingested plastic after its death at Midway Atoll National Wildlife Refuge (photo: John Klavitter, USFWS); (F) olive ridley turtles *Lepidochelys olivacea* entangled at the surface in a conglomerate of ghost fishing gear in the Maldives, where turtles frequently become entangled in a single conglomerate of derelict gear (photo: Dave Bretherton/Olive Ridley Project); and (G) surface convergence front 'weedlines' in the northern Gulf of Mexico, which provide important oceanic habitat for marine megafauna, with accumulated *Sargassum* algae and a typical plastic load (photo: Blair Witherington)


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sea lions, seals, and walruses), sirenians (i.e. manatees and dugongs), sea otters, and polar bears. We searched ISI Web of Knowledge for articles published between 1969 and 2020 (last search was conducted on 7 February 2020) for the terms population, plastic, litter, debris, and ingest/entangle. Alongside each search term, we also incorporated the relevant taxon of interest, including marine mammal, cetacean, whale, dolphin, porpoise, seal, sea lion, walrus, dugong, manatee, sea cow, sea otter, turtle, seabird, and marine bird. Standard searches were augmented by the global database 'LITTERBASE' (https://litterbase.awi.de/). Papers were further filtered for the words 'population' and 'demography', to determine whether the authors attempted to assess the effects of plastic pollution on marine megafauna populations. Although we did not include grey literature, we are confident that our literature review represents the current state of peer-reviewed knowledge regarding marine plastic interactions in these taxa.

Each published study was evaluated and filtered to remove cases where plastic pollution was not addressed independently from other threats or if the study was a review that lacked original data. We considered entanglement in derelict gear, but not entanglement in active fishing gear (i.e. bycatch). Data were collated based on the lowest taxonomic group, interaction type (i.e. entanglement and/or ingestion), individual effect (i.e. lethal or sub-lethal), location of interaction (i.e. ocean region), and number of individuals impacted (Dataset S1 in the Supplement at www.int-res.com/articles/suppl/n043p234_supp.xlsx). Effects were classified as 'lethal' if an animal's cause of death was due to an interaction with plastic; all other effects were considered 'sub-lethal'.

We partitioned population-level assessments into 4 categories: (1) direct effects, i.e. the study provided direct evidence of population-level effects; (2) inferred effects, i.e. the study inferred population-level effects based on mortality rates or estimates, or pervasive sub-lethal individual-level effects that were likely to lead to decreased population size or growth, such as reduced reproductive output relative to the current population status (e.g. van der Hoop et al. 2017; see Table 1); (3) lacking evidence for effects, i.e. the study found no evidence for a population-level effect (e.g. Votier et al. 2011; see Table 1), and; (4) more data needed, i.e. the study concluded that there was insufficient evidence to determine if plastic pollution caused a population-level effect (e.g. Brandão et al. 2011, Dataset S1).

3. OVERVIEW OF DOCUMENTED INDIVIDUAL-LEVEL EFFECTS OF PLASTIC POLLUTION ON MARINE MEGAFAUNA

Understanding how plastic pollution affects individuals is a first step toward assessing population-level impacts (Browne et al. 2015). In this section we highlight the various pathways described in the literature by which marine megafauna interact with plastic pollution, and discuss their resulting individual-level effects.

3.1. Entanglement

Marine megafauna can become entangled in plastic pollution including fibrous material, line, rope, packing bands, netting, and other packaging material. Animals may be attracted to plastic material in several ways, including (1) by curiosity or naivety (especially in immature animals); (2) to use as a resting platform, source of shelter, or nesting material; (3) to seek prey that is entangled in or attracted/attached to the material (Matsuoka et al. 2005, Gregory 2009, Jensen et al. 2013, Duncan et al. 2017, Grant et al. 2018); or (4) by the odor of biofouled plastic, which may be mistaken for food (Pfaller et al. 2020). Compared to other plastic items, ghost or derelict fishing gear (i.e. gear that is abandoned, lost, or discarded) such as nets, pots, traps, lines, and buoys, is widely recognized as a major source of mortality in marine megafauna (Wilcox et al. 2016, Duncan et al. 2017).

3.2. Physical injury and illness

Entanglement in plastic pollution can lead to physical injuries that include lacerations, constriction (i.e. flesh clearly drawn in by impacting material, such as packing bands or monofilament line, which puts enough pressure on the animal's skin to impede blood or air flow; Allen et al. 2012), severe sclerosis, loss of limbs, and difficulty breathing if the airway becomes restricted (Snoddy et al. 2009, Vegter et al. 2014). The animal may starve, drown, or be unable to escape predators or hazards if the entangled material hampers movement (Gregory 2009, Barreiros & Raykov 2014, Vegter et al. 2014, Nelms et al. 2015). Marine megafauna entangled in plastic ropes, lines, and floats may develop systemic infections and chronic debilitation from extensive tissue damage (Cassoff et al. 2011), and pinnipeds have been known to insert their heads through plastic packing bands, which can eventually lead to severed blood vessels (Fowler 1987). Entanglement of seabirds, both at sea and at terrestrial breeding sites, may reduce their flying and foraging efficiency (Derraik 2002, Voltier et al. 2011).

3.3. Physiological stress

Entanglement in plastic pollution can lead to severe physiological stress, inhibiting diving and resulting in increased hydrodynamic drag (Ceccarelli 2009, Macfayden et al. 2009, Gilardi et al. 2010, van der Hoop et al. 2014, Wilcox et al. 2015a). It is estimated that an entangled North Atlantic right whale *Eubalaena glacialis* incurred an increase in average locomotory power requirements of 70.5% when entangled in plastic rope (van der Hoop et al. 2014), while energy requirements for a California sea lion *Zalophus californianus* entangled in plastic netting increased 4 fold (Feldkamp 1985). In laboratory experiments, entangled fur seals reduced swimming time by 75%, increased resting by 138%, and increased their mean energy expenditure by 112% (Feldkamp et al. 1989). Several studies have shown that sea turtles entangled in active fishing gear for as little as 30 min — an experience that induces similar physiological responses to entanglement in derelict gear or other large plastic items — require additional time to rest and recover at the surface to replenish on-board oxygen stores consumed while involuntarily submerged (Gregory et al. 1996, Hoopes et al. 2000, Stabenau & Vietti 2003, Harms et al. 2003, Snoddy & Southwood Williard 2009, Snoddy et al. 2009). Upon release from entanglement (and submergence), Kemp's ridley *Lepidochelys kempii* and green turtles *Chelonia mydas* spent extended periods of time recovering at the surface, potentially increasing their vulnerability to predation and anthropogenic threats, such as vessel strikes (Snoddy et al. 2009, Snoddy & Williard 2010). Despite an apparent lack of similar studies for seabirds, these animals are also likely to experience some form of physiological stress from submersion due to entanglement.

3.4. Reduced mobility

Plastic pollution may impede, obstruct, or entrap marine megafauna that rely on terrestrial environments for resting or reproduction (e.g. seabirds, pinnipeds, and sea turtles). Plastic material has been known to affect adult and nestling seabirds, entangling their legs, feet, bill, and wings (Tasker et al. 2000, Votier et al. 2011, Bond et al. 2012). Synthetic materials present on sea turtle nesting rookeries can block nesting attempts or impede hatchlings. Extensive derelict fishing gear and other beach-cast plastic is believed to prevent nesting by sea turtles, while plastic objects have been observed impeding hatchling sea turtles from reaching the sea, potentially making them more susceptible to predation and decreased energy reserves required for the frenzy swim upon entering the water (Triessnig et al. 2012).

3.5. Ingestion

It is believed that marine megafauna ingest plastic for a number of reasons, including (1) mistaking the visual characteristics of the item for food (Gregory 2009, Schuyler et al. 2012, 2014b, Hoarau et al. 2014, Duncan et al. 2019b); (2) mistaking the odor of biofouled plastic as food (Pfaller et al. 2020); (3) accidentally, through non-selective feeding strategies such as filter feeding (Besseling et al. 2015) or if otherwise mixed with natural food items (Di Beneditto & Awabdi 2014); (4) if the item is attached to or covered with natural prey (Frick et al. 2009); or (5) via trophic transfer from contaminated prey (Nelms et al. 2018).

3.6. Gastrointestinal tract damage

Ingested plastic objects may damage the gastrointestinal tract (GIT) of marine megafauna, causing ulcerations, perforations, lesions, or obstructions (Derraik 2002, Jacobsen et al. 2010, Brandão et al. 2011, Awabdi et al. 2013, Di Bello et al. 2013, Di Beneditto & Awabdi 2014, Nelms et al. 2015). Gastrointestinal ulcerations or perforations and laceration of the larynx from ingesting plastic have been documented in seabirds, marine mammals, and sea turtles, and can result in chronic infection, peritonitis, gastrointestinal motility issues, septicemia, and mortality (Day et al. 1985, McCauley & Bjorndal 1999, Levy et al. 2009, Guebert-Bartholo et al. 2011). Impaction or blockage of the GIT caused by plastic ingestion can inhibit digestion and cause pain, bloating, necrosis, hardened fecal matter, mechanical abrasion or blockage of absorptive surfaces in the digestive tract, and blockage of the cloaca which can prevent egg laying (Mader 2006, Guebert-Bartholo et al. 2011, Awabdi et al. 2013, Di Beneditto & Awabdi 2014). Seabirds that ingest high levels of plastic may exhibit slower growth rates and earlier mortality (Pierce et al. 2004), while gut compactions and minor ulcerations caused by plastic ingestion in seabirds may result in reduced disease resistance and post-fledging survival (Fry et al. 1987).

3.7. Dietary dilution

Dietary dilution can occur when ingestion of plastic limits nutrient or water absorption. The presence of inorganic and space-occupying, non-food material within the GIT can cause a false sense of satiation, leading to a reduced desire to feed (McCauley & Bjorndal 1999). Nutrient dilution is known to affect both juvenile and adult animals (Day et al. 1985, Sievert & Sileo 1993, Bjorndal et al. 1994, McCauley & Bjorndal 1999). Although sub-lethal, dietary dilution may lead to malnutrition, reduced energy, and eventual mortality. Loggerhead turtle hatchlings fed a 50% diluted diet with inert matter displayed significantly lower energy and nitrogen intake than hatchlings fed a 10% diluted diet, indicating that dietary dilution may decrease energy assimilation and allocation to somatic growth, which could reduce energy reserves and survivorship (McCauley & Bjorndal 1999). Similarly, dietary dilution may dehydrate seabird chicks with already reduced fat reserves (Auman et al. 1997). Growth rates for Laysan albatross *Phoebastria immutabilis* that had ingested high volumes of plastic were significantly lower than for chicks that had ingested low volumes of plastic (Sievert & Sileo 1993). Decreased body condition (reduced fledging weight), which can result from dietary dilution, has been found to decrease survival of juvenile seabirds (Braasch et al. 2009, Morrison et al. 2009).

3.8. Exposure to contaminants associated with plastic pollution

Plastic can adsorb and concentrate chemical contaminants, such as persistent organic pollutants (POPs), from the marine environment (Teuten et al. 2009). These toxic compounds can be harmful because they are inherently stable, persist for a long time, and can accumulate in adipose tissues following ingestion (D'Ilio et al. 2011). Many common polymers, such as polyethylene, have high sorptive capacities for toxicants due to their polymeric chain structure and enhanced surface area (Rochman et al. 2013). This capacity increases with degradation and a corresponding increase in surface area, which leads to the plastic becoming more hazardous the longer it remains in the marine environment (Andrady 2011). In addition to the adsorption of existing marine contaminants to their surfaces, plastic often contains toxic additives, monomers, and chemical byproducts as well as plasticizers, such as phthalates and bisphenol A (BPA), added during manufacturing (Teuten et al. 2009, Lithner et al. 2011).

POPs in marine megafauna tissues have been linked to plastic ingestion. Colabuono et al. (2010) found polychlorinated biphenyls (PCBs) and organochlorine pesticides in plastic pellets and fragments ingested by Procellariiforme seabirds in Southern Brazil, while Tanaka et al. (2013) reported that short-tailed shearwaters *Puffinus tenuirostris* found with plastic in their stomachs in the North Pacific had polybrominated diphenyl ethers in their abdominal adipose, which was also found in the same pieces of plastic. Likewise, lower chlorinated compounds were found to have transferred to short-tailed shearwaters as a result of ingesting contaminated plastic (Yamashita et al. 2011). At Midway Atoll, PCBs, polychlorinated dibenzo-p-dioxins, naphthalenes, and furans have been found in adult Laysan albatrosses (Jones et al. 1996), while PCBs were found to have transferred from contaminated plastic to streaked shearwater *Calonectris leucomelas* chicks in a feeding experiment (Teuten et al. 2009).

In addition to potential toxicity contamination via ingestion, prior research has found that transfer of chemicals that commonly occur in plastic (e.g. BPA) can occur through the skin (Geens et al. 2011, Zalko et al. 2011). Seabirds that nest on top of plastic material may absorb contaminants through their skin (Verlis et al. 2014), which could affect sexual development and potentially disrupt the endocrine system, resulting in reproductive difficulties and cancers (vom Saal et al. 2007, Talsness et al. 2009).

3.9. Reduced mobility

Plastic ingestion may affect the mobility of seabirds. Several seabird species rely on reducing wing-loading for flying and diving (Provencher et al. 2017). Thus, adding mass via ingestion may be detrimental to plastic-loaded birds (Provencher et al. 2017).

4. REVIEW OF STUDIES THAT CONSIDERED POPULATION-LEVEL EFFECTS OF PLASTIC POLLUTION ON MARINE MEGAFAUNA

4.1. Current state of knowledge on demographic impacts

Population-level assessments of plastic pollution in marine megafauna have been reported infrequently over the past 50 yr (47 studies between 1969 and 2020; entanglement, n = 26; ingestion, n = 19; or both, n = 2; Fig. 2, Dataset S1), although reports are increasing (Fig. 3). Of these studies, 7 inferred population-level effects (entanglement, n = 6; ingestion, n = 1), whereas 19 studies lacked evidence for effects (entanglement, n = 12; ingestion, n = 6; both, n = 1; Fig. 2, Table 1, Dataset S1). The remaining studies reported insufficient evidence of population-level effects (Fig. 2, Dataset S1). We found no studies directly linking plastic hazard exposure to population (abundance) trends (Dataset S1).

4.2. Summary of deleterious individual-level effects, global distribution, and species

Of all published studies that considered population-level effects in marine megafauna, 6 reported lethal (entanglement, n = 3; ingestion, n = 3) and 29 reported sub-lethal (entanglement, n = 17; ingestion, n = 11; both, n = 1) effects (Dataset S1). Lethal and sub-lethal effects included external lesions (n = 15), reduced mobility at sea or on land (n = 9), GIT damage (n = 6), starvation (n = 4), malnutrition (n = 4), nutrient dilution (n = 3), constriction (n = 3), physiological stress (n = 3), and drowning (n = 2). Most research was conducted in the Atlantic (45%) and Pacific (38%) Ocean regions (Fig. 3, Dataset S1). Studies that assessed entanglement in marine mammals comprised 51% of all published studies (Fig. 3, Dataset S1). The species with the highest number of publications from entanglement and/or ingestion included harbour seals *Phoca vitulina* (n = 6) and California sea lions (n = 5), with 8 species represented in 3 or more studies (Fig. 4, Dataset S1)

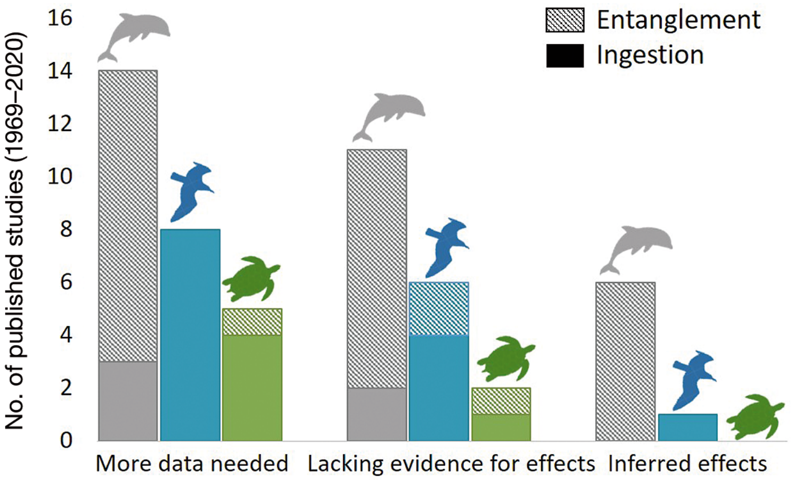

Fig. 2. Overview of findings from published, peer-reviewed studies that considered population-level effects of plastic pollution on air-breathing marine megafauna (i.e. marine mammals, seabirds, and sea turtles) worldwide between 1969 and 2020. See Dataset S1 for a complete list of species and studies as well as Table 1 for a summary of studies that inferred effects or were lacking evidence for effects

5. DISCUSSION

5.1. Assessments of population-level effects of plastic pollution on marine megafauna

Understanding plastic pollution in a population-level context is crucial for prioritization of limited conservation resources to address competing threats (Avery-Gomm et al. 2018a). Our review underscores a dearth of empirical information to inform demographic assessments of impacts. We conclude that the extent and magnitude of population-level impacts on marine megafauna remain largely unassessed and thus unknown. We do not know if this is a reflection of the low detection power of current study designs or of the magnitude of effects. It is possible that plastic pollution does not present a major conservation threat to some marine megafauna populations at current levels. Conversely, as marine habitats and prey items become more polluted in the face of increasing environmental plastic worldwide (Barnes et al. 2009), its potential to cause population-level impacts may increase or become easier to detect with greater exposure and potency of effects, the latter of which assumes researchers would be conducting assessments of these impacts. Uncertainty over demographic effects from plastic pollution is in contrast to the well-documented effects on individuals, including slow and painful deaths, which raises serious concerns for animal welfare (Votier et al. 2011, Duncan et al. 2017).

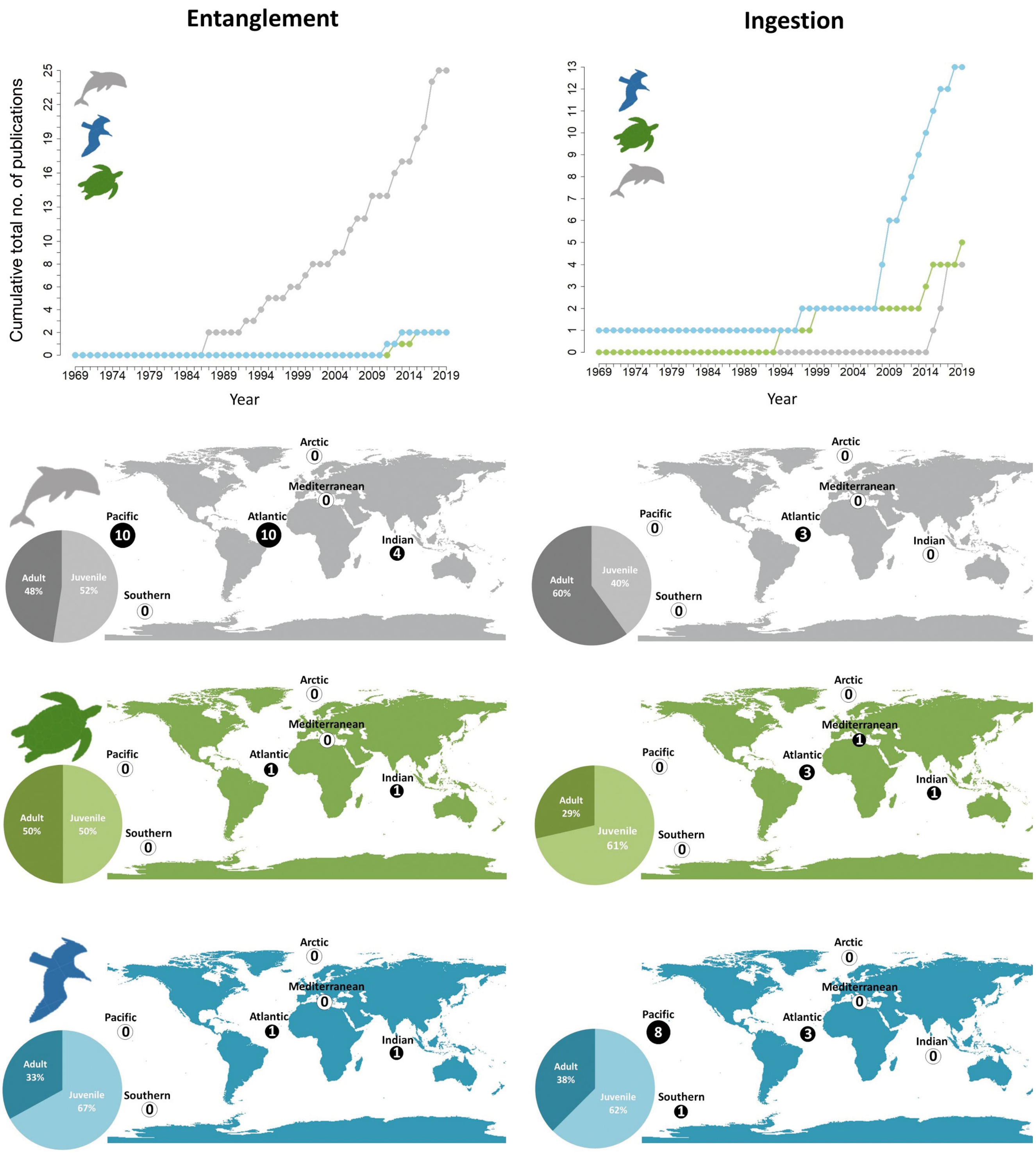

Fig. 3. Number of published, peer-reviewed studies that considered population-level effects of plastic pollution (entanglement and ingestion) on marine mammals (grey), sea turtles (green), and seabirds (blue) published between 1969 and 2020 (scatterplots), per age-class (pie charts) and ocean basin (maps). See Dataset S1 for a complete list of species and studies

Establishing population baselines and identifying trends for many marine megafauna populations is challenging due to their extensive migrations and large ranges. A crucial step will be to estimate the proportion of individuals in a population that are killed by plastic exposure in relation to their population size as well as the mortality they incur from other anthropogenic impacts (Browne et al. 2015). Popula-

Table 1. Published, peer-reviewed studies that inferred population-level effects or were lacking evidence for effects of plastic pollution on air-breathing marine megafauna (i.e. seabirds, marine mammals, and sea turtles) worldwide between 1969 and 2020. See Dataset S1 for further information and a complete list of studies, including those that needed more data to draw inferences. See Section 2 for definitions of population-level effect categories. Full references for studies cited in the table, and not in the main article, can be found in Dataset S1

Taxa	Species	Threat; no. entangled/ ingested; study period	Lethal or sub-lethal individual-level effect	Age class	Population-level effect	Key findings	Reference
Seabird	Flesh-footed shearwater (*Puffinus carneipes*)	Ingestion; 34; 2011	Reduced body size and nutrient intake	Fledgling	Inferred effects	Study reports that 89% of fledglings in this study are expected to experience morbidity or mortality due to plastic ingestion, and that these data may help explain population decline	Lavers et al. (2014)
Seabird	Northern gannet (*Morus bassanus*)	Entanglement; 525; 2005–2010	195 of 525 entangled animals died; 190 of which were attributed to entanglement	Juvenile; Adult	Lacking evidence for effects	Study reports that the presence of plastic in the population is concerning, but currently not impacting the population.	Votier et al. (2011)
Seabird	Short-tailed shearwater (*Puffinus tenuirostris*)	Ingestion; 164; 2012	171 birds necropsied, but plastic did not affect body condition of 164 that exhibited ingestion	Chick	Lacking evidence for effects	Study reports that despite high prevalence of plastic ingestion, their findings show no physical detriment to the chicks, meaning ingestion would have no effect on the population as a whole	Cousin et al. (2015)
Seabird	Waved albatross (*Phoebastriairrorata*)	Ingestion; 6; 1999–2007	43 dead animals, 6 of which ingested plastic; mortality not attributed to ingestion	Chick; Adult	Lacking evidence for effects	Study reports that plastic ingestion is rare in this species and therefore is likely to have little to no effect on the population	Anderson et al. (2008)
Seabird	Brown booby (*Sula leucogaster*)	Entanglement; 122; 2013	Unspecified	Juvenile; Adult	Lacking evidence for effects	Study reports that entanglement is likely only a minor source of injury and mortality at the population level	Lavers et al. (2013)
Seabird	Laysan albatross (*Phoebastria immutabilis*)	Ingestion; 245; 1994–1995	Ingestion causes satiation and reduced resistance to lead poisoning and avian pox virus	Chick	Lacking evidence for effects	Study reports that plastic ingestion causes stress to individuals, but has little to no effect on population	Auman et al. (1997)
Seabird	Wedge-tailed shearwater (*Puffinus pacificus*)	Ingestion; 13; 2005	Unspecified	Adult; Fledgling; Chick	Lacking evidence for effects	Study reports that plastic ingestion is not common in wedge-tailed shearwaters and does not appear to affect the population	Hutton et al. (2008)

Table 1. Continued from previous page

Taxa	Species	Threat; no. entangled/ ingested; study period	Lethal or sub-lethal individual-level effect	Age class	Population-level effect	Key findings	Reference
Marine mammal (cetacean)	North Atlantic right whale (*Eubalaena glacialis*)	Entanglement; 21; 1979–2009	Entanglement responsible for increased energy cost and drag, impeded foraging efficiency	Juvenile; Adult	Inferred effects	Study reports that chronic entanglement causes greater energy costs, impeding reproductive investment and blubber thickness	Van der Hoop et al. (2017)
Marine mammal (cetacean)	North Atlantic right whale (*Eubalaena glacialis*)	Entanglement; 55; 1980–2011	Reduced foraging ability and disrupted swimming performance due to drag	Juvenile; Adult	Inferred effects	Study reports that the added drag from entanglement combined with other sources of energetic stress such as lactation or migration may affect the population over time	Pettis et al. (2017)
Marine mammal (pinniped)	Hawaiian monk seal (*Neomonachus schauinslandi*)	Entanglement; 173; 1982–1998	Unspecified	All age classes	Inferred effects	Study reports that high entanglement occurrence likely leads to mortality, which could be a significant threat to this small island subpopulation	Henderson (2001)
Marine mammal (pinniped)	California sea lion (*Zalophus californianus*)	Entanglement; 19; 1992	Unspecified	Juvenile; Adult	Inferred effects	Study reports that this level of entanglement at such a small colony may negatively impact the population	Harcourt (1994)
Marine mammal (pinniped)	Northern fur seals (*Callorhinus ursinus*)	Entanglement; Unspecified; 1960–1985	0.4% entanglement rate in 1985, at least two orders of magnitude greater than in the 1940s	Juvenile; Adult	Inferred effects	Study reports that changes in pup numbers and unexpected mortality in juveniles provide correlative evidence for population decline	Fowler (1987)
Marine mammal (pinniped)	Guadalupe fur seal (*Arctocephalus townsendi*)	Entanglement; 10; 2003–2015	Unspecified	Unspecified	Inferred effects	Study reports that data from this study and the current population status of this species forms correlative evidence of a negative population-level effect of plastic pollution	Barcenas-de la Cruz et al. (2018)
Marine Mammal (pinniped and cetacean)	Mysticetes; Odontocetes; Elephant seal (*Mirounga angustirostris*); Northern fur seal (*Callorhinus ursinus*); Harbor seal (*Phoca vitulina*); California sea lion (*Zalophus californianus*)	Entanglement; 3 Mysticetes, 9 Odontocetes, 35 elephant seals, 5 fur seals, 4 harbour seals, 276 sea lions; 2003–2015	Unspecified	Unspecified	Lacking evidence for effects	Study reports that the entanglement rates reported in this study are unlikely to impact populations	Barcenas-de la Cruz et al. (2018)

Table 1. Continued from previous page

Taxa	Species	Threat; no. entangled/ ingested; study period	Lethal or sub-lethal individual-level effect	Age class	Population-level effect	Key findings	Reference
Marine mammal (pinniped)	Antarctic fur seal (*Arctocephalus gazella*)	Entanglement; 1,033; 1989–2013	One death reported due to entanglement	All age classes	Lacking evidence for effects	Study reports that rates of entanglement are low (0.016%) and involve mostly juvenile males; thus, entanglement is unlikely to affect the population	Waluda & Staniland (2013)
Marine mammal (pinniped)	Australian fur seal (*Arctocephalus pusillus*)	Entanglement; 106; 1996–2002	Entanglement rates range from 0.024% to 0.059% per season; 1 death attributed to entanglement	All age classes	Lacking evidence for effects	Study reports that entanglement rates are negligible and unlikely to impact population	Hofmeyr et al. (2006)
Marine mammal (pinniped)	New Zealand fur seal (*Arctocephalus forsteri*); Australian sea lion (*Neophoca cinerea*)	Entanglement; 91 fur seals, 35 sea lions; 1989–2002	High rates of entanglement (45% in fur seals and 74% in sea lions), only 5 of which were killed (fur seals)	All age classes	Lacking evidence for effects	Study reports that despite high occurrence of entanglement, fur seal populations increased by 16%. Authors also report stable sea lion populations, although entanglement-related mortality may slow their recovery	Page et al. (2004)
Marine mammal (pinniped)	California sea lion (*Zalophus californianus*) Pacific harbour seal (*Phoca vitulina*)	Entanglement; 157 sea lions, 11 seals; 2001–2005	Unspecified	Unspecified	Lacking evidence for effects	Study reports that the low level of entanglement reported in this study is not likely to impact the population	Moore et al. (2009)
Marine mammal (pinniped)	New Zealand fur seal (*Arctocephalus forsteri*)	Entanglement; 185; 1995–2005	185 seals reported entangled over the past ten years, with an average of 19 ± 2; 4 deaths attributed to entanglement	All age classes	Lacking evidence for effects	Study reports low mortality rates due to entanglement and a population that appears to be increasing, indicating that entanglement is unlikely to impact the population	Boren et al. (2006)
Marine mammal (pinniped)	Antarctic fur seal (*Arctocephalus gazella*)	Entanglement; 208; 1988–1989	None documented	All age classes	Lacking evidence for effects	Study reports that current rate of entanglement (0.4%), most of which are juvenile males, are unlikely to impact population	Arnould & Croxall (1995)
Marine mammal (pinniped)	Australian fur seal (*Arctocephalus pusillus*)	Entanglement; 89; 1997–2012	None documented	All age classes	Lacking evidence for effects	Study reports that the population is currently increasing; thus, entanglement is unlikely to affect the population	Lawson et al. (2015)

Table 1. Continued from previous page

Taxa	Species	Threat; no. entangled/ ingested; study period	Lethal or sub-lethal individual-level effect	Age class	Population-level effect	Key findings	Reference
Marine mammal (cetacean and pinniped)	Harbour porpoise (*Phocoena phocoena*); harbour seals (*Phoca vitulina*); grey seal (*Halichoerus grypus*)	Ingestion and entanglement; 5 porpoises, 6 harbour seals, and 6 grey seals; 1990–2014	6,587 carcasses found, of which 1622 allowed for necropsy; 14 cases of entanglement and 17 of ingestion reported	Juvenile; Adult	Lacking evidence for effects	Study reports that despite high standings, few animals interacted with plastic; thus, current rates are unlikely to cause population-level effects	Unger et al. (2017)
Marine mammal (pinniped)	South American fur seal (*Arctocephalus australis*)	Ingestion; 9; 2015	Unspecified	Juvenile; Yearling	Lacking evidence for effects	Study reports that there is no clear evidence that plastic ingestion causes a population-level effect in South American fur seal populations	Denuncio et al. (2017)
Marine mammal (cetacean)	North Atlantic right whale (*Eubalaena glacialis*)	Entanglement; 519; 1980–2009	No mortality was attributed to entanglement, but reduced reproductive success and increased susceptibility to disease are inferred	All age classes	Lacking evidence for effects	Study reports that while there is a high occurrence of entanglement, no mortality is reported due to entanglement	Knowlton et al. (2012)
Turtle	Loggerhead turtle (*Caretta caretta*)	Ingestion; 121; 1995–2016	Little evidence that plastic items caused impactions, obstructions, or perforations in the gut, as well as dietary dilution	Juvenile; Adult	Lacking evidence for effects	Study reports that the amounts of ingestion by juvenile loggerheads are low and do not appear to pose a significant threat to the population	Doménech et al. (2019)
Turtle	Olive ridley turtle (*Lepidochelys olivacea*)	Entanglement; 18; 1996–2011	18 entangled turtles, 2 of which were reported dead	Juvenile	Lacking evidence for effects	Study reports that 18 entanglement events across 15 years are unlikely to affect the population	Santos et al. (2012)

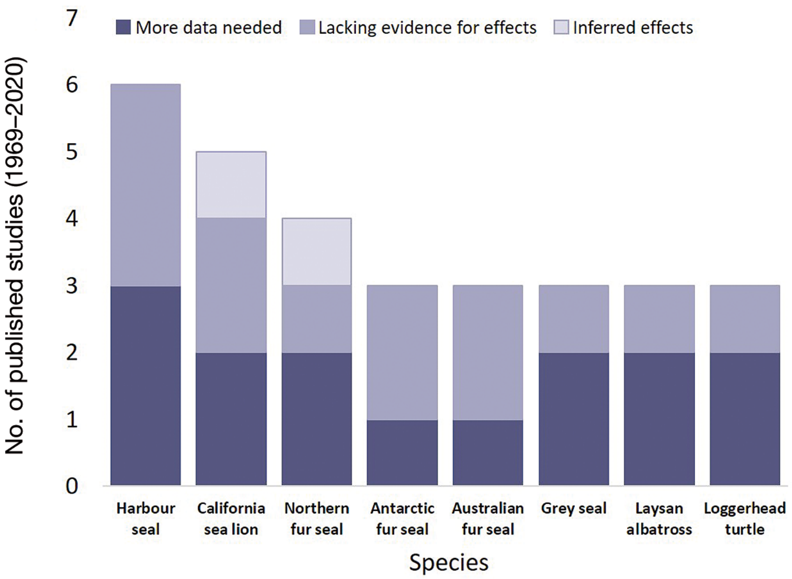

Fig. 4. Number of published, peer-reviewed studies that considered population-level effects of plastic pollution in species of air-breathing marine megafauna (i.e. seabirds, marine mammals, and sea turtles) that were reported in 3 or more studies worldwide between 1969 and 2020. See Dataset S1 for a complete list of species and studies

tion models can help elucidate potential impacts by incorporating a suite of metrics including relative contribution of a given lifestage (e.g. mature females), the size and growth rate of a population, mortality rates of different lifestages, and reproductive parameters (Bolten et al. 2011, Browne et al. 2015). Such approaches will permit side-by-side analyses of relative effects of multiple threats, including plastic, on marine megafauna population dynamics, rather than evaluating each threat in isolation. Outputs of these multi-threat assessments of population-level effects can provide managers and researchers with appropriate context in which to set conservation priorities.

5.2. Patterns in plastic pollution effects on marine megafauna

Although the list of species and catalog of effects on individual animals known to suffer detrimental effects from plastic pollution is incomplete, it is growing (Vegter et al. 2014, Gall & Thompson 2015, Kühn & van Franeker 2020). A more representative dataset of these effects, with spatial and temporal variation represented, will be necessary to better discern patterns and trends that could lead to population-level assessments. Where differential effects on species have been examined (Di Beneditto & Awabdi 2014, Kühn & van Franeker 2020), patterns are apparent, but effects from habitats that differ by species generally remain unknown. One exception may be large-scale monitoring of northern fulmars *Fulmarus glacialis* as a means to understand the role of different habitats on plastic ingestion (e.g. Provencher et al. 2009, van Franeker et al. 2011, Avery-Gomm et al. 2012, 2018b, Kühn & van Franeker 2012, Trevail et al. 2015, Terepocki et al. 2017). Some marine habitats bear an especially high plastic pollution load, such as remote islands within oceanic current fields (e.g. Midway Atoll). Spatial hotspots in plastic hazards have shown to be associated with dynamic oceanographic and geographic features such as frontal zones (Witherington 2002, Witherington et al. 2012, González Carman et al. 2014) as well as proximity to human population centers (Browne et al. 2010, González Carman et al. 2014). While understanding the impacts of marine plastic does not require a complete dataset on the spatio-temporal intersection of plastic and marine megafauna by species and population, it will require sufficient representative data to model these effects.

Some marine megafauna species or populations may be more tolerant of plastic interactions. Photographic studies of humpback whales *Megaptera novaeangliae* entangled in ghost (or active) gear in Alaska and the Gulf of Maine, USA, revealed that the majority of animals (52–78%) had, in the past, been non-lethally entangled, suggesting that animals were eventually able to free themselves and survive the interaction (Neilson et al. 2009). In the Gulf of Maine, 48–65% of humpbacks were entangled between 1997 and 2002, of which 8–25% were estimated to entangle annually (Robbins & Mattila 2004). There are similar patterns of apparent tolerance with ingestion. Approximately 37% of 371 leatherback turtles *Dermochelys coriacea* autopsied from 1968–2007 had plastic in their GIT, yet of those, only 12 (8.7%) appeared to die from it (Mrosovsky et al. 2009). Research also suggests that 75% of ingested plastic in petrels was no longer present within a month if no new plastic was consumed (van Franeker & Law 2015). By contrast, documented entanglement rates for grey seals *Halichoerus grypus* from photo ID techniques in southwest England from 2004–2008 revealed that 64% of entanglement events resulted in serious injuries, with significantly lower recapture rates of entangled seals, suggesting an elevated post-release mortality rate (Allen et al. 2012). Likewise, a surprisingly small amount of plastic (i.e. 0.5 g or one-tenth of a typical plastic bag) has been shown to block the digestive tract in juvenile green turtles (Santos et al. 2015), yet as much as 75 g (149 plastic items) can accumulate and remain in the gut of sea turtles without causing apparent damage (Hoarau et al. 2014). Lutz (1990) reported on plastic remaining in the gut of an apparently healthy captive loggerhead turtle for 4 mo. In the aforementioned cases, the volume, surface area, and rigidity of the plastic material was likely more important than its mass. More research is needed to understand plastic-interaction effects on demographic vital rates between species and populations.

In many marine megafauna species, effects of plastic pollution are likely to occur in marine habitats where detection of events is difficult or impossible (Gregory 2009). Thus, mortality caused by plastic pollution is likely to be under-reported. The comparatively large number of studies that assessed population-level effects in pinnipeds suggests that they may be easier to document given their close association with terrestrial habitats for reproduction, which would also apply to seabirds. Although sea turtles are also associated with terrestrial environments (i.e. nesting females), most species and populations tend to have large ranges and are not closely linked to these areas for the majority of their lives. Turtles and cetaceans that suffer serious injuries and subsequent mortality from plastic pollution may be more likely to die in open water, especially in the case of small juvenile sea turtles.

5.3. Recommendations for improving assessments of plastic pollution effects on marine megafauna

Plastic pollution can lead to lethal and sub-lethal effects, yet the latter are more difficult to identify and may be more prevalent and possibly even have broader population-level implications than lethal effects (Hoarau et al. 2014, Gall & Thompson 2015). A handful of exemplar studies have focused on increased hydrodynamic drag, physiological stress, and nutrient dilution (e.g. McCauley & Bjorndal 1999, Snoddy et al. 2009, Snoddy & Williard 2010, van der Hoop et al. 2017; see Table 1). Linking sub-lethal effects with measurable fitness consequences (such as reduced energy acquisition and assimilation, increased energetic demands, and potentially harmful behavioral changes) from laboratory or field-based research will allow researchers to develop models that can assess long-term impacts in individuals and ultimately, populations. Field studies should combine tagging or telemetry techniques with physiological analyses to measure or infer post-plastic-interaction survival rates, growth rates, reproductive output, and health status for individual animals. For example, post-release mortality in juvenile sea turtles entangled in gillnets off the North Carolina coast was documented using both satellite telemetry and analysis of blood biochemistry (Snoddy & Williard 2010). With advances in tagging technology, it will become logistically easier to assess the extent to which sub-lethal effects may become lethal or result in reproductive impairment. Moreover, information from tracking studies can be used to estimate potential transport of plastic mass entangling or ingested by seabirds and other marine megafauna (Provencher et al. 2017).

Acute, coarse-scale effects from plastic pollutants (e.g. entanglement, gut impaction) are more easily demonstrated than are chronic effects on a finer scale. Where investigated, microplastics appear to be ubiquitous in marine megafauna (Lusher et al. 2018, Duncan et al. 2019a, Nelms et al. 2019). However, gaps remain in our understanding of plastic ingestion, particularly microplastics and their potential to transfer and persist through marine food webs to marine megafauna or to be ingested directly by them (Nelms et al. 2018). Future research should assess the levels and effects of both microplastics and contaminants in animals of lower trophic levels, including the role that ingestion may play in biomagnifying adsorbed toxic chemicals common in plastic pollution up the food chain to marine megafauna.

Although many marine megafauna species are difficult to house in captivity, controlled studies can potentially shed light on post-entanglement and post-ingestion fate in marine megafauna. These studies will need to be evaluated on a case-by-case basis in terms of animal welfare, but surrogate species could potentially be used for endangered ones. These studies can control the amounts and types of plastic ingested, including chemical-laden plastic, as well as track weathering, dosage, and components of the introduced items. Researchers can concurrently track changes in feeding, weight, growth rates, and other behaviors to gain a better understanding of how marine megafauna might be affected, which can ultimately be used to infer possible population-level impacts where interaction rates are well documented or believed to be high.

Attributing marine megafauna mortality to plastic ingestion or entanglement is complex and challenging, even for trained veterinary pathologists. In many cases, cause of death may be recorded as a symptom of entanglement or ingestion, such as infection, which may mean plastic pollution mortalities are under-recorded. Conversely, an animal that died with plastic in its stomach may be assumed to have been killed by it, when it is possible that the animal was not feeding normally due to compromised health (Casale et al. 2016, Lynch 2018, Rodríguez et al. 2018, Nelms et al. 2019). Marine megafauna can face several confounding threats such as fisheries interactions, habitat degradation, noise pollution, and climate change, which may become interactive, additive, or negating. Controlled studies (see previous paragraph) may help determine the impacts of additive effects, such as ingesting contaminated plastic. Further research is needed to better understand how other threats interact with the risk posed by plastic pollution.

Methodologies used to assess effects of plastic risk exposure need to be carefully considered. Differences in plastic collection techniques from dead (e.g. causes of death for necropsied animals) or live (e.g. esophagus lavage or feces) animals can make it difficult to draw meaningful comparisons within and amongst studies (Casale et al. 2016, Lynch 2018, Rodríguez et al. 2018, Nelms et al. 2019). To avoid overestimating ingestion frequency and amounts among individuals, researchers are now beginning to call for studies to publish both positive and negative results to better understand the overall impacts of plastic pollution (Nelms et al. 2015, Lynch 2018). Most sea turtle and seabird plastic ingestion studies have used frequency of occurrence to assess ingestion; however, this metric does not depict the amount of material that was actually ingested by the animal, which limits its usefulness and can bias—sometimes substantially—results in terms of actual risk (Lynch 2018). Where possible, Lynch (2018) recommends that researchers measure plastic ingestion by debris mass per turtle mass (g kg^{-1}) in order to better identify at-risk populations.

We recommend a strong emphasis on thorough veterinary examinations of live animals and necropsies of dead animals. The development of a global database of effects of plastic pollution from health assessments and necropsies would help provide information on the extent and frequency of plastic interactions with marine megafauna (Nelms et al. 2015).

5.4. Next phases for plastic pollution research and mitigation

Potential solutions to hazardous plastic in the environment are as complex as for any other pollutant, involving sociopolitical considerations for changing human behavior as well as engineering solutions to mitigate escape of plastic during transport, to improve efficiency of waste collection and disposal, and to develop alternative and more degradable materials (Gold et al. 2013, Provencher et al. 2020). Although these solutions are outside the scope of our review, we point to avenues of investigation that would inform solutions benefitting marine megafauna specifically.

A fundamental piece of the puzzle is understanding the origins of plastic pollution that pose a hazard to marine animals. Forensic investigations into errant plastics have revealed general source points and original usage categories (Woodall et al. 2015), but this work is at a scale dwarfed by the global scope of plastic pollution. Conversely, data on plastic waste mismanagement by country (Jambeck et al. 2015) provides information on a broad scale, but does not identify hazard origins relative to marine habitats. Modeling ocean surface currents has the potential to describe geographic origin of plastic pollution in drift patches (van Sebille et al. 2012), which can identify human population centers for outreach and technology transfer. Plastic pollution sources might also come from identifying original usage. Original use identification could be as direct as matching shapes, colors, and lettering of plastic in marine habitats to cataloged items, and as inferential as assuming use applications based on resin identification from spectroscopy (Zettler et al. 2013, Rocha-Santos & Duarte 2015).

Comprehensive efforts to better understand and mitigate the effects of plastic pollution on marine species and ecosystems worldwide are urgently needed. Mitigation can be achieved in part by reducing the use of disposable and short-lived plastic items and more effective recycling programs (Hopewell et al. 2009). Reducing the exposure of marine megafauna to plastic will require lowering the plastic loading rate. Based on studies of the origin of plastic pollution cast on marine beaches (Pruter 1987, Derraik 2002) and at sea (Ryan et al. 2009), there are many sources. Identifying major origins of plastic pollution would guide public outreach efforts, enforcement, and export of trash management technology and methods. Re-designed or modified fishing gear, coupled with policy initiatives that include economic incentives or deterrents, should be developed as a means to reduce gear loss and discarding at sea (Wilcox et al. 2016).

Finally, we highlight and encourage the multidisciplinary nature of potential solutions to threats from marine plastic pollution. Ocean research is not likely to result in information helpful for reducing this threat without work coordinated between resource experts, oceanographers, sociologists, materials scientists, and specialists in achieving human behavior change.

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