When large marine predators feed on fisheries catches: Global patterns of the depredation conflict and directions for coexistence

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Abstract
The sustainable mitigation of human–wildlife conflicts has become a major societal and environmental challenge globally. Among these conflicts, large marine predators feeding on fisheries catches, a behaviour termed "depredation," has emerged concomitantly with the expansion of the world's fisheries. Depredation poses threats to both the socio-economic viability of fisheries and species conservation, stressing the need for mitigation. This review synthesizes the extent and socio-ecological impacts of depredation by sharks and marine mammals across the world, and the various approaches used to minimize it. Depredation was reported in 214 fisheries between 1979 and 2019 (70% post-2000) and affected fleets from 44 countries, in all sectors (commercial, artisanal and recreational), and in all major fishing techniques (nets, traps and hook-and-lines). A total of 68 predator species were involved in depredation (20 odontocetes, 21 pinnipeds and 27 sharks), and most (73%) were subject to either by-catch and/or retaliatory killing from fishers when interacting with gear. Impacts on fishers were primarily associated with catch losses and gear damage but often lacked assessments. Deterrence was a major mitigation approach but also the least effective. Gear modifications or behavioural adaptation by fishers were more promising. This review highlights the need for improved monitoring, and interdisciplinary and integrated research to quantify the determinants and impacts of depredation in the socio-ecological dimension. More importantly, as the conflict is likely to escalate, efforts directed towards changing perceptions and integrating knowledge through adaptive co-management are raised as key directions towards coexistence between fisheries and large marine predators.

KEYWORDS
fisheries interactions, human–wildlife conflicts, marine mammals, mitigation, sharks, socio-ecosystem sustainability

1 | INTRODUCTION

The expansion of human populations has inevitably generated interactions and conflicts with wildlife, primarily through increased competition for habitats and resources (Woodroffe, Thirgood, & Rabinowitz, 2005). Human–wildlife conflicts (hereafter “HWC”) have been defined as occurring when the actions of humans or wildlife have an adverse effect on the other, or represent threats (actual
or perceived) by wildlife to human property, economy, security, recreation and safety (Nyhus, 2016). While HWC have long existed and been historically addressed by deleterious means for species, sometimes contributing to their extinction, wildlife conservation has only recently become a key consideration in their management (Conover, 2001; Redpath et al., 2013). As such, the mitigation of HWC, defined as efforts to maintain wildlife species while minimizing their negative effects on humans, has emerged as a major challenge for communities worldwide and a primary field of research (Madden, 2004; Nyhus, 2016).

Conflicts where wildlife feeds on resources grown, raised or captured by humans generate a broad range of socio-economic, ecological and conservation impacts, and are among the most widespread HWC (Woodroffe et al., 2005). For instance, large terrestrial carnivores feeding on livestock, a behaviour termed “depredation” developed by many species of felids and canids, illustrates the complexity of mitigating HWC (Insikp & Zimmermann, 2009; Treves, Wallace, Naughton-Treves, & Morales, 2006). For humans, livestock depredation incurs substantial socio-economic costs and poses threats to public safety (Thirgood, Woodroffe, & Rabinowitz, 2005). For predators, it increases the risk of death or injuries associated with equipment and/or lethal responses from humans and modifies the natural ecology, potentially altering their role in ecosystems (McManus, Dickman, Gaynor, Smuts, & Macdonald, 2015; Newsome et al., 2015). While culling was the primary way of dealing with this conflict for decades, the critical conservation status of most large carnivores has required managers to find alternative non-lethal responses to mitigate depredation (Treves & Karanth, 2003). However, maintaining both these species and the economic viability of activities while satisfying public opinion has often remained deeply intractable (Dickman, 2010; Redpath, Bhatia, & Young, 2015; Redpath et al., 2013).

While livestock depredation is a long established HWC, large marine predators feeding on fisheries catches has emerged as another form of depredation, concomitantly with the global expansion of fisheries (Hamer, Childerhouse, & Gales, 2012; Mitchell, McLean, Collin, & Langlois, 2018; Northridge, 1984, 1991; Read, 2008; Wickens, 1995). By reducing catches for fishers, causing damage to fishing gear, increasing risks of by-catch or lethal retaliation and provisioning predators with easy-to-capture and sometimes new prey resources, the depredation conflict affects marine socio-ecological systems at all levels (Bearzi, Piwetz, & Reeves, 2019; Gilman, Laporta, Martinez Portela, Santos, & Pierce, 2008; Werner, Northridge, Press, & Young, 2015). Specifically, the conflict poses threats to food security and the socio-economic viability of particular fisheries which human communities may rely on, and threats to the conservation of ecosystems and marine megafauna species, most of which are severely depleted or still recovering from past exploitation. In a marine context made increasingly tense by historical overfishing, increasing demand for seafood and high conservation values of marine predators, the resolution of the depredation conflict in fisheries has become a major priority for many fishers, communities, managers, conservationists and scientists (Guerra, 2019).

Despite the pressing need, the best mitigation approaches for depredation by large marine predators that accounts for socio-economic, ecological and conservation stakes, remain unclear. This review aims to assess the current state (and trends) of depredation across the world’s fisheries, to examine the socio-economic and ecological impacts of depredation, and to assess the mitigation solutions that have been implemented. We use this analysis to identify knowledge gaps and highlight key directions for achieving effective and long-term mitigation of the conflict.

2 DATA COLLECTION AND SYNTHESIS

2.1 Literature review

A review of literature published between 1979 and 2019 was conducted using Google Scholar. Primary search terms included “depredation” and “fisheries”, and were extended to “catch damage” or “catch removal”. Searches were of information in abstracts, full texts and titles. The review focused on sharks, odontocetes (toothed whales) and pinnipeds, although other taxa such as cephalopods and teleosts may also be involved in depredation (e.g.
Briceño, Linnane, Quiroz, Gardner, & Pecl, 2015; Raphael, Joseph, & Edwin, 2017). Case studies and reviews were considered, and returns were included if explicitly addressing depredation, that is: reporting occurrences of sharks and/or marine mammals feeding on catches on or in fishing gear, and/or assessing the extent of such occurrences, their socio-economic or ecological impacts, and/or investigating ways to mitigate the issue. Searches were primarily directed towards studies published as peer-reviewed articles in scientific journals but also considered other types of document (books, technical reports, academic dissertations and proceedings of workshops and conferences) if relevant. Reference lists of all documents were also cross-checked, and any relevant additional studies were included.

Studies included in the review were grouped by fishery. These were defined as a unique combination of a fishing sector, target species, fishing technique, the country flag of the fishing fleet and the geographic fishing area. Three fishing sectors were considered: recreational, artisanal and a commercial sector including industrial, semi-industrial and any small-scale fishery not described as artisanal (hereafter “commercial”). Fishing techniques were grouped into 6 categories: (a) longlines—a main line with series of baited hooks—included demersal, pelagic and vertical longlines; (b) hook-and-line—a main line with a single baited hook—included handlines, droplines, trolls, rods-and-lines, pole-and-lines, jigging lines and drumlines; (c) static nets, included gillnets, trammel nets, tangle nets and weirs; (d) seines, included purse seines, round-haul nets and lampara nets; (e) trawls, included both bottom and midwater trawls; and (f) traps, included pots, trap-nets, fyke nets, hoop nets, double-bag nets and creels. For fishing fleets operating within Exclusive Economic Zones (EEZ), the country having jurisdiction within EEZs was used as the reference for the fishing area. When countries operated different fishing fleets of the same fishing sector, targeting the same species and using the same gear over multiple, spatially segregated EEZs (e.g. soak time, haul speed) or the use of decoys (dummy gear to fool the predators). Evidence of effectiveness of these measures at both reducing the frequency or the intensity of depredation and indirect or opportunity costs (associated with additional non-fishing time caused by depredation—Peterson, Mueter, Criddle, & Haynie, 2014) had been assessed in fisheries.

Attempts to mitigate depredation were grouped into lethal and non-lethal measures. Lethal measures included authorized and regulated practices aimed at killing specific marine predator individuals directly involved in depredation events, or any individuals from populations known to be involved in depredation. Three categories of non-lethal measures were considered: (a) gear modification included all technological systems used to either protect the catch or to reduce the attractiveness of the gear, as well as complete changes in fishing techniques (from one of the six techniques used in the study to another of these techniques); (b) deterrence included Acoustic Deterrent Devices (ADDs, regrouping all devices termed ADDs, Pingers and Acoustic Harassment Devices), non-lethal explosives (e.g. seal bombs, crackers, fireworks) and gunshots (non-targeted shots), physical harassment, chemical, electrical, electromagnetic and light repellents, echolocation disruptors, playsbacks of sounds from predators; and (c) behavioural avoidance included the identification of peak times/areas of depredation, move-on responses (fishers leaving areas when faced with depredation), the adjustment of operations (e.g. soak time, haul speed) or the use of decoys (dummy gear to fool the predators). Evidence of effectiveness of these measures at both reducing the frequency or the intensity of depredation events and maintaining acceptable catch rates was searched in the review studies, whether emanating from interviews with fishers or from experimental trials.

2.2 | Summarizing the data

The number of fisheries for which depredation was reported was the primary metric used to assess the patterns of the interactions. The metric was summarized temporally (by year), spatially (by country and major fishing area of the Food and Agriculture Organization—“FAO”), per fishing sector, fishing technique and per depredating taxa (sharks, odontocetes, pinnipeds) and species when available. For sharks, which depredating species are often difficult to identify, the review was extended to studies reporting information on depredation from experimental research fishing surveys.

The effects of depredation on marine predators were assessed qualitatively through four categories: (a) by-catch (death of individuals captured on or in the fishing gear); (b) injuries (evidence of wounds from contact with fishing gear on free ranging individuals or on individuals released alive from incidental captures); (c) retaliatory killing (deliberate killing of individuals by fishers associated with depredation); and (d) modification of the role of depredating species in ecosystems (change in diet and foraging areas, effects of food subsidies on life history parameters).

The socio-economic effects of depredation were grouped into three categories: catch loss, damage to fishing gear and additional direct/indirect costs. Where possible, catch loss was assessed quantitatively across fisheries using the proportion of the total catch (landed + depredated) lost because of depredation as a standardized metric. Gear damage, which included nets torn off in static nets, seines, trawls and traps, and lines cut off, bent and broken hooks in longlines and hook-and-line fisheries, was examined qualitatively, as whether reported or not in fisheries. The third category was also qualitatively reviewed as whether additional direct costs (increased fuel consumption in anticipation or in response to depredation) and indirect or opportunity costs (associated with additional non-fishing time caused by depredation—Peterson, Mueter, Criddle, & Haynie, 2014) had been assessed in fisheries.

3 | GLOBAL EXTENT OF THE CONFLICT

A total of 324 studies, of which 247 were published in peer-reviewed journals, were used to describe depredation by sharks and marine mammals in fisheries. Of these studies, 272 (84%) were published after 2000 and 172 (53%) after 2010 (Figure 1).
The review identified 214 distinct fisheries subject to depredation between 1979 and 2019, including 148 (69%) in the commercial sector, 50 (23%) in the artisanal sector and 16 (8%) in the recreational sector (Table 1 and ESM 1 Table 1). Depredation was reported in fisheries operated by 44 countries and in all FAO areas except areas 18 and 88 (Figure 2). The areas with the most depredation were areas 27 (Northeast Atlantic, \( n = 38 \)) followed by areas 77 (East Pacific, \( n = 22 \)), 37 (Mediterranean Sea, \( n = 21 \)) and 57 (East Indian Ocean, \( n = 20 \)) (Figure 2). Information about the depredating taxa was available for all fisheries (ESM 1 Table 1). Pinnipeds and odontocetes were the taxa most involved in depredation with a total of 112 and 98 fisheries, respectively (Table 1). The largest numbers of fisheries depredated by odontocetes were in the Mediterranean Sea (\( n = 17 \)), the Northeast Atlantic (\( n = 15 \)) and the West Indian Ocean (\( n = 14 \)) (Figure 2). Pinniped depredation was prevalent in the North Atlantic (\( n = 23 \) and 12 fisheries in FAO areas 27 and 21, respectively) and in the East Pacific (\( n = 15 \)) (Figure 2). Shark depredation was reported in 39 fisheries, primarily in low latitudes with the greatest incidence in the Indian Ocean (Table 1 and Figure 2).

**TABLE 1** Summary of the number of fisheries for which depredation by large marine predators was reported between 1979 and 2019, per fishing sector (bold), per fishing technique and per taxa (odontocetes, pinnipeds and/or sharks) involved

<table>
<thead>
<tr>
<th></th>
<th>Total</th>
<th>Odontocetes only</th>
<th>Pinnipeds only</th>
<th>Sharks only</th>
<th>Odontocetes &amp; Sharks</th>
<th>Odontocetes &amp; Pinnipeds</th>
<th>Pinnipeds &amp; Sharks</th>
<th>All 3 taxa</th>
</tr>
</thead>
<tbody>
<tr>
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<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Commercial</td>
<td>148</td>
<td>45 (30)</td>
<td>70 (47)</td>
<td>7 (5)</td>
<td>10 (7)</td>
<td>8 (5)</td>
<td>2 (1)</td>
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<tr>
<td>Static nets</td>
<td>37</td>
<td>6 (16)</td>
<td>28 (76)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Longlines</td>
<td>52</td>
<td>22 (42)</td>
<td>3 (6)</td>
<td>6 (12)</td>
<td>10 (19)</td>
<td>4 (8)</td>
<td>2 (4)</td>
<td></td>
</tr>
<tr>
<td>Hooks and Lines</td>
<td>17</td>
<td>5 (29)</td>
<td>10 (59)</td>
<td>1 (6)</td>
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<tr>
<td>Seines</td>
<td>9</td>
<td>4 (44)</td>
<td>4 (44)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1 (11)</td>
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<td>Trawls</td>
<td>13</td>
<td>5 (39)</td>
<td>8 (62)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Traps</td>
<td>20</td>
<td>3 (15)</td>
<td>17 (85)</td>
<td></td>
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<tr>
<td>Artisanal</td>
<td>50</td>
<td>26 (52)</td>
<td>18 (36)</td>
<td>2 (4)</td>
<td>1 (2)</td>
<td>2 (4)</td>
<td>1 (2)</td>
<td></td>
</tr>
<tr>
<td>Static nets</td>
<td>20</td>
<td>11 (55)</td>
<td>8 (40)</td>
<td></td>
<td></td>
<td>1 (5)</td>
<td></td>
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<tr>
<td>Longlines</td>
<td>17</td>
<td>8 (47)</td>
<td>5 (29)</td>
<td>2 (12)</td>
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<tr>
<td>Hooks and Lines</td>
<td>9</td>
<td>5 (56)</td>
<td>3 (33)</td>
<td></td>
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<td></td>
<td></td>
<td>1 (11)</td>
</tr>
<tr>
<td>Seines</td>
<td>3</td>
<td>2 (67)</td>
<td>1 (33)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Traps</td>
<td>1</td>
<td></td>
<td>1 (100)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Recreational</td>
<td>16</td>
<td>5 (31)</td>
<td>3 (19)</td>
<td>6 (38)</td>
<td>1 (6)</td>
<td></td>
<td></td>
<td>1 (6)</td>
</tr>
</tbody>
</table>

Details on whether only one or a combination of multiple taxa was reported depredating per fishery are provided. Percentages were calculated out of the total number of fisheries per sector and per fishing technique. Bold indicates per fishing sector.
For all fishing sectors, the majority of fisheries for which depredation was first reported occurred in the last two decades, with 62% of the depredated commercial fisheries after 2000, 63% of the depredated artisanal fisheries after 2008 and 81% of the depredated recreational fisheries after 2005 (Figure 3a). All fishing techniques experienced depredation in commercial fisheries but longlines were the technique most involved, with 52 fisheries (35% of commercial fisheries) followed by static nets (25%) (Table 1). These two...
techniques were also the most affected by depredation in the artisanal sector, with 17 (33%) and 20 (39%) of longline and static net fisheries, respectively (Table 1). Hook-and-line was the only fishing technique of recreational fisheries subject to depredation. Odontocetes and pinnipeds depredated catches in all fishing techniques. However, odontocetes were primarily involved in depredation in longline fisheries \( (n = 48, \text{i.e.} \ 70\% \text{ of depredated longline fisheries and} \ 49\% \text{ of fisheries depredated by odontocetes}) \) (Table 1). This technique was also subject to extensive depredation by sharks \( (n = 26 \text{ fisheries, i.e.} \ 32\% \text{ of depredated longline fisheries and} \ 67\% \text{ of fisheries depredated by sharks}) \). Together, sharks and odontocetes were involved in 50% of the depredated hook-and-line fisheries \( (n = 21) \). For both techniques, predators either partially consumed or fully removed the fish caught directly from the hooks (Hamer et al., 2012; Mitchell, McLean, Collin, & Langlois, 2018). Pinnipeds were primarily involved in depredation in static net fisheries \( (n = 39, \text{i.e.} \ 68\% \text{ of depredated static net fisheries and} \ 35\% \text{ of fisheries depredated by pinnipeds}) \) and trap fisheries \( (n = 18, \text{i.e.} \ 86\% \text{ of depredated trap fisheries and} \ 16\% \text{ of fisheries depredated by pinnipeds}) \) (Table 1). For static nets, fish caught was partially or fully depredated by predators often tearing the nets in the process (Reeves et al., 2001; Wickens, 1995). In trap fisheries, pinnipeds were reported either entering the gear (e.g. Königson, Fjälling, Berglind, & Lunneryd, 2013 for trap-nets, Campbell, Holley, Christianopoulos, Caputi, & Gales, 2008 for lobster pots) or damaging the gear (damaged bait doors or torn net parts of the trap) to access the fish inside (e.g. Westerberg, Lunneryd, Fjälling, & Wahlberg, 2008; Wickens et al., 1992). Odontocete depredation was reported in 3 trap fisheries, with, in one instance, evidence of dolphins opening and damaging bait doors to access crab pots (Noke & Odell, 2002). Depredation by odontocetes and pinnipeds was reported in 12 seine fisheries and 13 trawl fisheries (Table 1). For both fishing techniques, predators were documented actively entering the net during operations (sometimes by sliding over surface float lines of seines for pinnipeds) and/or removing fish trapped between meshes from outside the net (e.g. Broadhurst, 1998; Lyle, Willcox, & Hartmann, 2016; Santana-Garcon et al., 2018; Shaughnessy, Semmelink, Cooper, & Frost, 1981; Wise, Silva, Ferreira, Silva, & Sequeira, 2007).

A total of 68 species were reported depredating in fisheries, including 20 odontocete, 21 pinniped and 27 shark species (Table 2 and Figure 3b). This represents 28% and 63% of the world species of odontocetes and pinnipeds, respectively. In odontocetes, 50% of depredating species were from the Delphinidae family. Two odontocete species, the Amazon river dolphin (Inia geoffrensis, Iniidae) and the Tucuxi (Sotalia fluviatilis, Delphinidae), are freshwater species (Table 2). Six shark species were identified depredating from research experimental fishing (ESM 1 Table 2). Of the 27 depredating sharks, 14 (52%) were from the Carcharhinidae family. While 81% of odontocete and pinniped species were first reported depredating before 2010, 63% of the depredating shark species were first documented between 2010 and 2019 (Figure 3b). The species most reported depredating were common bottlenose dolphins (Tursiops truncatus, Delphinidae) and killer whales (Orcinus orca, Delphinidae) among odontocetes (37 fisheries each), grey seals (Halichoerus grypus, Phocidae) and harbour seals (Phoca vitulina, Phocidae) among pinnipeds (27 and 26 fisheries, respectively), and cookiecutter sharks (Isistius brasiliensis, Dalatiidae) (6 fisheries) among sharks (Table 2). Common bottlenose dolphins and Australian/Cape fur seals (Arctocephalus pusillus spp., Otariidae) were the only two species documented depredating in fisheries using all fishing techniques.

![Figure 3](https://example.com/figure3.png)

**Figure 3** Cumulative annual values of (a) the total number of fisheries reported as subject to depredation per sector (commercial, artisanal and recreational) and (b) the total number of species of large marine predators (odontocetes, pinnipeds and sharks) reported depredating on fisheries catches between 1979 and 2019.
<table>
<thead>
<tr>
<th>Species</th>
<th>Total</th>
<th>Longline</th>
<th>Hook &amp; Line</th>
<th>Static net</th>
<th>Seine</th>
<th>Trawl</th>
<th>Trap</th>
</tr>
</thead>
<tbody>
<tr>
<td>Odontocetes</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Common bottlenose dolphin (T. truncatus, Delphinidae)</td>
<td>37</td>
<td>5</td>
<td>11</td>
<td>15</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Killer whale (O. orca, Delphinidae)</td>
<td>37</td>
<td>29</td>
<td>6</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>False killer whale (P. crassidens, Delphinidae)</td>
<td>18</td>
<td>15</td>
<td>3</td>
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<td></td>
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<tr>
<td>Sperm whale (P. macrocephalus, Physeteridae)</td>
<td>14</td>
<td>14</td>
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<tr>
<td>Short-finned pilot whale (G. macrocephalus, Delphinidae)</td>
<td>8</td>
<td>7</td>
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<td>1</td>
<td></td>
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<tr>
<td>Rough-toothed dolphin (S. bredanensis, Delphinidae)</td>
<td>6</td>
<td>1</td>
<td>5</td>
<td></td>
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<tr>
<td>Risso's dolphin (G. griseus, Delphinidae)</td>
<td>5</td>
<td>2</td>
<td>3</td>
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<tr>
<td>Indo-Pacific bottlenose dolphin (T. aduncus, Delphinidae)</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
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<tr>
<td>Short-beaked common dolphin (D. delphis, Delphinidae)</td>
<td>3</td>
<td>2</td>
<td>1</td>
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<tr>
<td>Indian Ocean humpback dolphin (S. plumbea, Delphinidae)</td>
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<td>1</td>
<td>2</td>
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<td>Striped dolphin (S. coeruleoalba, Delphinidae)</td>
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<td>1</td>
<td>2</td>
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<td>Long-finned pilot whale (G. melas, Delphinidae)</td>
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<td>1</td>
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<tr>
<td>Spinner dolphin (S. longirostris, Delphinidae)</td>
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<tr>
<td>Atlantic spotted dolphin (S. frontalis, Delphinidae)</td>
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<tr>
<td>Indo-Pacific finless porpoise (N. phocoenoides, Phocoenidae)</td>
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<tr>
<td>Melon-headed whale (P. electra, Delphinidae)</td>
<td>1</td>
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<td>Steller sea lion (E. jubatus, Otariidae)</td>
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<th>Species</th>
<th>Total</th>
<th>Longline</th>
<th>Hook &amp; Line</th>
<th>Static net</th>
<th>Seine</th>
<th>Trawl</th>
<th>Trap</th>
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<td>Sharks</td>
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<tr>
<td>Cookiecutter shark (<em>I. brasiliensis</em>, Dalatiidae)</td>
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<td>Blue shark (<em>P. glauca</em>, Carcharhinidae)</td>
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<td>Blacktip shark (<em>C. limbatus</em>, Carcharhinidae)</td>
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<tr>
<td>Oceanic whitetip shark (<em>C. longimanus</em>, Carcharhinidae)</td>
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<tr>
<td>Pigeye shark (<em>C. amboinensis</em>, Carcharhinidae)</td>
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<tr>
<td>Porbeagle shark (<em>L. nasus</em>, Lamnidae)</td>
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<tr>
<td>Spiny dogfish shark (<em>S. acanthias</em>, Squalidae)</td>
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<tr>
<td>Australian blacktip shark (<em>C. tiliosti</em>, Carcharhinidae)</td>
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<tr>
<td>Bluntnose sixgill shark (<em>H. griseus</em>, Hexanchidae)</td>
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<tr>
<td>Dusky shark (<em>C. obscurus</em>, Carcharhinidae)</td>
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<tr>
<td>Galapagos shark (<em>C. galapagensis</em>, Carcharhinidae)</td>
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<tr>
<td>Great white shark (<em>C. carcharias</em>, Lamnidae)</td>
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<tr>
<td>Grey reef shark (<em>C. amblyrhynchus</em>, Carcharhinidae)</td>
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(Continues)
Information about the exact depredating species was missing for 32 fisheries, and this uncertainty primarily involved shark species (ESM 1 Table 1).

4 | ECOLOGICAL EFFECTS

While depredation can benefit marine predators through reducing foraging effort, reports of negative effects associated with direct interactions with gear and/or fishers were by far the most common. By-catch (46% of fisheries) and retaliatory killing (25%) were the most prevalent. Together, these affected 45 predator species (73% of the 62 depredating species, excluding species identified from research fishing), including 8 “vulnerable,” 8 “endangered” and 1 “critically endangered” species on the IUCN Red List.

Instances of by-catch and injuries were reported in 46% and 19% of all fisheries. Sharks had the largest proportion of by-catch (in 61% of fisheries—Figure 4a), primarily occurring in longlines (77% of the longline fisheries depredated by sharks) (Figure 4b). For odontocetes, 19 of the 20 depredating species have been subject to by-catch, with a prevalence in static nets (80% of the static net fisheries depredated by odontocetes) and seines (71%) (Figure 4b). All pinniped species were caught in depredated fisheries, primarily in trawls (88% of the trawl fisheries depredated by pinnipeds), followed by seines (67%) and static nets (55%) (Figure 4b). These results suggest that depredation can be a primary cause of marine predator by-catch in fisheries, in line with studies that concurrently examined the two processes (Read, 2008; Werner et al., 2015). The attraction of accessing easy-to-catch prey on fishing gear appears to outweigh the high risks of becoming hooked, trapped or entangled. This is highlighted in trawl and seine fisheries where individuals purposely enter the nets and where by-catch rates are subsequently the highest (Fertl & Leatherwood, 1997; Jaiteh, Allen, Meeuwig, & Loneragan, 2013; Lyle et al., 2016).

Retaliatory killing was reported in 23% of the fisheries and was directed towards sharks, pinnipeds and odontocetes (Figure 4a). This practice occurred in the form of fishers using harpoons, fire guns or explosives to kill marine predators either during depredation events, or when randomly encountering individuals from a species known or believed to depredate on their catches. Retaliatory killing is generally illegal and while commonly reported in studies published in the 1980s and 1990s, it still occurred in recent years. For example, intentional shooting of common bottlenose dolphins in the Mediterranean Sea and southern sea lions off Brazil and Chile was reported between 2015 and 2019 (Machado et al., 2016; Pardalou & Tsikliras, 2018; Pont et al., 2016; Sepúlveda et al., 2018). Similar practices were heavily detrimental for killer whale populations in Alaska and the Southern Ocean (Busson et al., 2019; Matkin, 2019).
In the Amazon Basin, retaliatory killing, paired with by-catch, was described as the main driver of rapid declines of Amazon river dolphins and Tucuxis populations (Alves, Zappes, & Andriolo, 2012; Loch, Marmontel, & Simoes-Lopes, 2009).

Changes in natural foraging behaviour and distribution were reported for common bottlenose dolphins involved in depredation on static nets in the Mediterranean Sea (Blasi, Giuliani, & Boitani, 2015). For another two fisheries, both depredated by killer whales, positive effects of food provisioning on the life history of local populations were demonstrated (Esteban, Verborgh, Gauffier, Giménez, Guinet, & Billard, 1984; Tixier, Authier, Gasco, & Guinet, 2015).

The potential effects of depredation on the ecological role of predators in ecosystems were assessed in only three fisheries. Changes in natural foraging behaviour and distribution were reported for common bottlenose dolphins involved in depredation on static nets in the Mediterranean Sea (Blasi, Giuliani, & Boitani, 2015). For another two fisheries, both depredated by killer whales, positive effects of food provisioning on the life history of local populations were demonstrated (Esteban, Verborgh, Gauffier, Giménez, Guinet, & Billard, 1984; Tixier, Authier, Gasco, & Guinet, 2015).

### 5 | SOCIO-ECONOMIC IMPACTS

The socio-economic impacts of depredation were mainly assessed in studies through the amount of catch removed by predators from fishing gears. Of the fisheries for which such assessments were available (n = 82), commercial trap fisheries were subject to the largest proportion of losses (27% ± 18 SE of catch per fishery) but estimates were available for only 3 fisheries (Figure 5a). Assessments were primarily available in commercial longline fisheries (n = 31) and indicated mean proportions of catches lost to depredation of 11% ± 2 SE (Figure 5a). This greater availability of assessments is likely due to marine predators partially consuming catches when depredating in tuna/swordfish pelagic longline fisheries, leaving quantifiable evidence. In these fisheries, catch losses were, for instance, reported as being equivalent to USD 500,000 per year off the Seychelles (Rabearisoa, Sabarros, Romanov, Lucas, & Bach, 2018) and between USD 390,000-690,000 per year per vessel off Hawaii (Gilman, 2007).

However, in many fisheries, marine predators (primarily odontocetes and pinnipeds) were described removing whole fish from gear, forcing the use of alternative assessment methods. For example, methods relying only on fish remains were shown to underestimate the depredated amount of fish by grey seals by 46% in salmon trap-net fisheries of the Baltic Sea (Fjälling, 2005). Statistical models have been necessary and used to assess losses due to killer and sperm whale depredation in demersal longline fisheries targeting sablefish in Alaska (Peterson & Hanselman, 2017) and toothfish in the Southern Ocean (Gasco, Tixier, Duhamel, & Guinet, 2015; Söffker et al., 2015). For the latter, the depredated volume was estimated equivalent to USD 15M per year across the major fishing
areas (Tixier, Burch, et al., 2019). Despite efforts to improve these methods, they remain likely to underestimate catch losses, because not accounting for undetected events (e.g. depredation occurring at great depths—Richard et al., 2020; Towers et al., 2019), nor hidden processes further reducing catches indirectly such as predators taking the bait (Thode et al., 2016) and/or scaring the catch by their presence around the gear (Moore, 2003; Nichols, Eldredge, & Cadrin, 2014; Wickens et al., 1992).

The actual costs incurred to fishers, involving extra expenditure and time, generally lacked quantitative assessments, likely because most are hardly tangible and require a combination of observations and sociological surveys to be measured. Gear damage, as a visible impact which financial cost can be estimated from extra purchases of gear, received the most attention. It was reported in 91 fisheries (43% of all depredated fisheries) and was the most prevalent in the artisanal sector (54% of depredated artisanal fisheries), followed by the commercial (39%) and recreational (38%) sectors. Hook-and-line and longline techniques had damages reported over 23-47% of fisheries. Seine, static net and trap showed greater occurrences ranging from 54% to 100% of fisheries (Figure 5b). In static net fisheries, damage by grey and harbour seals were estimated to cost approximately USD 60,000 per year for eastern Canada fisheries (Farmer & Billard, 1984), and those caused by common bottlenose dolphins approximately USD 11,000 per year per vessel for Italian commercial fisheries (Monaco, Cavallé, & Peri, 2019).

While studies assessing gear damage often mentioned the time spent repairing gear as non-fishing time generating additional cost for fishers, it was only assessed in one fishery (17–31 days per fisher per year due to damage by Mediterranean monk seals in Greece—Ríos, Drakulic, Paradinas, Milliou, & Cox, 2017). The same pattern was observed for costs associated with extra distances travelled and time spent at sea because of depredation, with theoretical costs mentioned in studies for 19 fisheries, but quantified for only 5 (ESM 1 Table 1). Only two studies, one on grey seal depredation in Massachusetts (Gruber, 2014) and one on killer whale depredation in Alaska (Peterson et al., 2014), provided full socio-economic assessments of extra fuel consumption, work time and food expenditures caused by the conflict, associated with extra effort to both compensate catch losses and implement avoidance strategies.

### 6 | MITIGATION ATTEMPTS

An array of technological and behavioural approaches have been used to reduce depredation over the last 40 years. Among non-lethal mitigation approaches, deterrence approaches were attempted in 61
fisheries, followed by behavioural avoidance (46 fisheries) and gear modification (29 fisheries) (Table 3).

6.1 | Deterrence

While deterrence was the approach most often implemented (specifically ADDs and non-lethal explosives/gunshots, in 24 and 19 fisheries, respectively), they were also the least successful in minimizing depredation (effective in only 25% and 5% of these fisheries, respectively) and the most subject to uncertainty around harmful effects.

Acoustic deterrence, attempted through a large range of ADDs marketed by private companies under various names (e.g. Pingers, Acoustic Alarms, Seal Scarer, Dolphin Interactive Deterrent, Orcasaver, etc.) and characterized by high amplitude sounds (130-200 dB re 1 mPa 1 m from the source), often generated responses from odontocetes and pinnipeds in early trials but were not effective at minimizing depredation on the long-term (Buscaino et al., 2009; Cox, Read, Swanner, Urian, & Waples, 2004; Götz & Janik, 2013; Maccarrone et al., 2014; Santana-Garcon et al., 2018; Sepúlveda et al., 2007; Snape et al., 2018; Tixier, Gasco, Duhamel, & Guinet, 2015). Among the six fisheries reporting effective ADDs, one successful implementation was in Scotland where ADDs deployed in rivers prevented grey and harbour seals from reaching recreational fisheries upstream (Graham, Harris, Denny, Fowden, & Pullan, 2009).

The limited effectiveness of devices was attributed to the high attractiveness of depredation making individuals willing to undergo pain to their hearing system, with probable long-term physiological impacts from repeated exposures (Götz & Janik, 2010). This is supported by the ineffectiveness of other deterrents, such as the use of non-lethal explosive devices also found on the market (seal bombs, seal crackers, etc.), with reports from fisheries in South Africa (Shaughnessy et al., 1981), Alaska (Dahlheim, 1988; Matkin, Ellis, Von Ziegesar, & Steiner, 1986), Florida (Zollett & Read, 2006) and Chile (Sepúlveda et al., 2018).

6.2 | Behavioural avoidance

Among behavioural avoidance measures, targeting times and/or areas of low risk of depredation and move-on practices were the two most common measures (21 and 15 fisheries, respectively), with effectiveness reported in 57% and 53% of the fisheries, respectively, but unknown for the remaining 43% and 47%.

<table>
<thead>
<tr>
<th>Non-lethal mitigation approaches</th>
<th>n fisheries</th>
<th>% Effective</th>
<th>% Non-Effective</th>
<th>% unknown</th>
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<td>Catch protection</td>
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<td>6</td>
<td>35</td>
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<tr>
<td>Reduced attractiveness (mesh size, net concentration)</td>
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<td>Full change of fishing technique</td>
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</table>

Bold values referred to numbers in the legend, while other values were percentages.
of the fisheries (Table 3). This large uncertainty may be due to behavioural avoidance including easy-to-implement measures not requiring direct investments or gear purchases from fishers/companies and often developed by fishers themselves without scientific intervention. However, behavioural avoidance still attracted attention in fisheries where data on operations were available. For instance, multi-variate statistical analyses highlighted times of year or areas of high probability of depredation for pinnipeds (e.g. Cosgrove et al., 2015; González, Vega, & Yáñez, 2015; Pon et al., 2012), for odontocetes (e.g. Cruz, Menezes, Machete, & Silva, 2016; Goetz, Laporta, Martinez Portela, Santos, & Pierce, 2011; Hernandez-Milian et al., 2008; Muñoz-Lechuga, Rosa, & Coelho, 2016; Passadore, Domingo, & Secchi, 2015; Pennino, Rotta, Pierce, & Bellido, 2015; Rocklin et al., 2009; Söffker et al., 2015; Tixier, Burch, et al., 2019; Tixier, Giménez, et al., 2019) and for sharks (e.g. MacNeil, Carlson, & Beerkircher, 2009; Rabearisoa et al., 2018; Ryan, Taylor, McAuley, Jackson, & Molony, 2019). In some regions, the use of satellite tagging increased knowledge on preferred areas of predators, and therefore, on areas where fishers were the most likely to be subject to depredation (e.g. Cronin, Gerritsen, Reid, & Jessopp, 2016; Oksanen, Niemi, Ahola, & Kunnasranta, 2015; Stepanuk, Read, Baird, Webster, & Thorne, 2018; Straley et al., 2014; Thorne, Baird, Webster, Stepanuk, & Read, 2019). Move-on practices, although commonly used by fishers, were shown effective only when vessels travelled distances sufficiently large to reduce the chances of being actively followed by predators (Forney, Kobayashi, Johnston, Marchetti, & Marsik, 2011; Janc et al., 2018; Tixier et al., 2018; Tixier, Vacquie Garcia, Gasco, Duhamel, & Guinet, 2015). Adjustments in the way fishers used their gear to reduce opportunities for species to depredate, such as decreasing soaking time or increasing the hauling speed, proved also effective in both static net and longline fisheries (Cosgrove et al., 2013, 2015; Janc et al., 2018; Tixier, Vacquie Garcia, et al., 2015).

Altogether, behavioural avoidance measures have been recommended to fishers in many fisheries but they come with costs, essentially associated with increased travelling, non-fishing time and workload, that should not overcome the benefits of implementing them. Typically, avoiding peak areas of depredation, which are often highly productive areas, or implementing move-on responses, may force fishers to operate in areas of lower fishing success. While short-term trade-offs between catch rates and depredation are made by fishers towards maximizing fishing success regardless of interactions with marine predators (Richard, Guinet, Bonnel, Gasco, & Tixier, 2018), no studies were found to have assessed the overall optimal costs/benefits ratios of non-avoidance vs. avoidance practices on the medium-term (for instance over a full fishing season) or on the long-term (over multiple years).

6.3 | Gear modification

Unlike behavioural avoidance, gear modification mitigation approaches require financial and technological investments, and should maintain high catch rates, minimize interference with operations, limit environmental impacts and obey regulations. Gear modifications aimed at protecting the catch were tried in 17 fisheries. While reported potentially successful in 14 of these 17 fisheries, their long-term effectiveness at reducing depredation sometimes lacked data support (Table 3). For example, low-cost fish protection systems showed promising results in pelagic longline fisheries but conclusions were limited by experimental trials being too short to produce sufficient evidence (Hamer, Childerhouse, McKinlay, Double, & Gales, 2015; Rabearisoa, Bach, Tixier, & Guinet, 2012). Despite these limitations, some systems, like the so-called “cachalotera” or “umbrella” (Brown, Brickle, Hearne, & French, 2010; Goetz et al., 2011; Moreno, Castro, Mújica, & Reyes, 2008), have been fully implemented in several fisheries, suggesting some level effectiveness. Successful gear modifications in reducing depredation have also been reported from trials in hook-and-line (troll) fisheries in the Gulf of Mexico with a system of wires flapping around hooks (Zollett & Read, 2006) and in trap fisheries of Australia with pots fitted with exclusion devices (Campbell et al., 2008).

However, the most effective instances of gear modification came from salmon fisheries of the Baltic Sea faced with heavy grey seal depredation, and where extensive research efforts have led to multiple adjustments of trap-nets (Westerberg et al., 2008). Among these changes, the use of stronger net material, a double-net chamber equipped with a new lifting system for fishers, increased mesh size in the leading part of the net and a modified entrance were sequentially tested and implemented. Combined, these modifications led to an effective system both reducing attractiveness of the gear for seals and keeping them away mechanically (Calamniius, Lundin, Fjälling, & Königson, 2018; Hemmingsson, Fjälling, & Lunneryd, 2008; Kauppinen, Siira, & Suuronen, 2005; Lehtonen & Suuronen, 2004; Lunneryd, Fjälling, & Westerberg, 2003; Suuronen et al., 2006; Varjopuro & Salmi, 2006). In the same region, gillnet cod fisheries successfully switched to pots to reduce seal depredation (Hedgärde, Berg, Kindt-Larsen, Lunneryd, & Königson, 2016; Königson, 2011; Königson et al., 2015; Stavenow, Ljungberg, Kindt-Larsen, Lunneryd, & Königson, 2016).

Changing to alternative fishing techniques are likely the most costly measures, sometimes requiring the purchase of new boats. The success of this approach depends on the fishing region, the target species and the capacity of fishers to use different gear. For example, a switch from longlines to pots was recently allowed in the sablefish fishery the Gulf of Alaska to prevent sperm whales from depredateing catches (Hanselman, Pyper, & Peterson, 2018). However, while successful in reducing depredation, this switch may not allow fishers using small vessels to reach the catch levels they would have had with longlines due to the limited capacity of these vessels to carry sufficient pots. A similar change in toothfish fisheries of the Southern Ocean proved inconclusive, as not producing sufficiently high catch rates although suppressing depredation (Boonzaier et al., 2012; Guinet, Tixier, Gasco, & Duhamel, 2015).
6.4 | Legal lethal mitigation

Legal lethal mitigation measures were rare and primarily reported in Northern Europe in response to grey and harbour seal depredation (Butler et al., 2008; Westerberg et al., 2008). In this area, subsets of individuals within populations having specialized into depredation and/or foraging in areas overlapping those used by fishers, promoting selective killing approaches instead of generalized culling at haul-out sites (Graham, Harris, Matejusová, & Middlemas, 2011; Königson et al., 2013). However, while selective removals were effective at reducing grey seal depredation, this was unsuccessful in the Swedish eel fyke-net fishery (Königson, 2011) and more conservation sensitive for declining seal populations in the UK (Graham, Harris, & Middlemas, 2011).

7 | DEPREDATION IN FISHERIES: AN EMERGING ISSUE?

The increasing number of studies on depredation in fisheries over the last 40 years indicates that the conflict is an emerging problem across the globe. This may be explained by a combination of factors, either associated with depredation being increasingly reported in fisheries for which the issue has long existed but was not considered problematic before, or depredation being newly occurring in other fisheries.

Firstly, the conflict has become socio-economically and/or ecologically problematic in many regions or fisheries. For fisheries in which depredation was already occurring in the early years and that have undergone a decrease in catch rates due to declining fish stocks, a greater pressure of the conflict on the socio-economic margins of fishermen may have led them to increasingly report it. Concomitantly, the decline of fish resources may have contributed to depredation having grown in frequency and intensity. For instance, in the Mediterranean Sea, overfished stocks may have caused common bottlenose dolphins to engage more in depredation (Bearzi, 2002; Blasi et al., 2015; Brotons, Grau, & Rendell, 2008; Göñener & Özdemir, 2012; Reeves et al., 2001). Some studies also described depredation as locally growing attributable to the increase of marine predator populations, especially marine mammal populations that were depleted by exploitation until the 1970s and may be now recovering following strong conservation measures. For example, the emergence of depredation in the North Atlantic, Northeast Pacific, off South America and South Africa was often attributed to locally increasing pinniped populations (Beeson & Hanan, 1996; Butler, Middlemas, Graham, & Harris, 2011; Collins, Crummeiy, Neal, & Fitzgerald, 1993; De la Torriente, Quinones, Miranda-Urbina, & Echevarría, 2010; Jouanella, Suuronen, Millar, & Koljonen, 2006; Olsen, Galatius, & Härkönen, 2018; Westerberg et al., 2008; Wickens et al., 1992). In addition, depredation may also be locally growing as a result of the behaviour being socially transmitted and learnt over time by individuals within populations and across generations, as hypothesized, for instance, in highly social odontocetes (e.g. Esteban, Verborgh, Gauffier, Giménez, Guinet, et al., 2016; Powell & Wells, 2011). However, while some studies highlighted long-term, spatial spreads in depredation (e.g. Schakner, Lunsford, Straley, Eguchi, & Mesnick, 2014 in the Northeast Pacific), evidence of increasing trends in the frequency or the severity of depredation and correlations between these trends and learning mechanisms or changes in predator abundances or fish stock availability are still limited.

Secondly, increased numbers of studies and depredation cases may be associated with changes undergone by fisheries over the last 60 years globally. The collapse of many fish stocks and the environmental effect of fishing activities such as by-catch have led the adoption of more selective fishing techniques such as longlining. Unlike other techniques, longlining is characterized by a catch being fully exposed underwater to large predators and first reports of depredation occurred shortly after the technique developed in the 1950s (Sivasubramaniam, 1964). The worldwide expansion of longlining, and especially across fisheries in high latitudes in the 1980s, is concomitant with an increase of reports of depredation and has likely led to longlining being the technique most affected by depredation (69 longline fisheries in this review, representing 32% of the depredated fisheries).

Lastly, increased numbers of studies may indicate a global shift in the approaches used to address the conflict. Growing awareness of the value of biological diversity has led to a shift from competition approaches relying on eradication of problematic wildlife to a coexistence model (Nyhus, 2016). This shift, observed at the governance and scientific levels, but also in local communities, emerged in the 1990s and has led to increased management and research efforts on depredation as a conflict typically involving a strong need for reconciliation between human activities and species with high conservation priorities.

8 | FUTURE DIRECTIONS

8.1 | Improving monitoring

Determining the extent of depredation, its impacts and the species involved are key conditions for understanding and managing the conflict. Yet, this review has shown this information was often lacking or incomplete, highlighting a need for improved monitoring of the issue.

Visual observations on the occurrence of depredation events, including information on the depredating species and the number of depredating individuals, paired with data on fishing operations (date/time, coordinates, effort, etc.) and catches (number and weight of fish per species, included partially depredated fish) can be an effective monitoring approach and should be implemented in fisheries. For example, this approach has been implemented across toothfish fisheries and, combined with photo-identification data (photographs of depredating marine mammals taken from fishing vessels and allowing for individual identification), now yields extensive long-term datasets (Guinet et al., 2015; Tixier, Gasco, et al., 2015). However,
visual monitoring is not applicable in fisheries where large fleets of small boats are prevalent and/or in poorly managed fisheries. Artisanal and recreational fisheries typically involve the complexity of working with large fleets. Studies on depredation found for these sectors predominantly used sociological surveys. While surveys may generate information on depredation, assessments were sometimes biased by socio-economic factors such as financial compensations or incentives (Bearzi, Bonizzoni, & Gonzalvo, 2011). Furthermore, visual approaches may be unreliable to assess the extent of the conflict or to identify the species involved in cases where depredation occurs outside of spatiotemporal ranges of possible observations from fishing vessels. In many trap and static net fisheries, predators were found interacting with the gear at night (Fujimori, Tixier, Duhamel, & Guinet, 2018; Goetz, Wolff, Stotz, & Villegas, 2008; Güclüsoy, 2008; Nichols et al., 2014) or at times when fishers were away from their equipment (Morteo, Rocha-Olivares, Arceo-Briseno, & Abarca-Arenas, 2012; Sepúlveda et al., 2018). In longline fisheries, where the gear is often left unattended while soaking, predators often interact with the gear set near the surface (pelagic longlines) or at depth before fishers return for retrieval (Hernandez-Milian et al., 2008; Richard et al., 2020).

Alternative monitoring approaches may be used to tackle these limitations. Electronic monitoring cameras on-board vessels, which have recently emerged to replace or supplement observers in fisheries (Bicknell, Godley, Sheehan, Votier, & Witt, 2016), can potentially improve the monitoring of depredation by recording partially depredated catches, damaged gear and/or by-catch of depredating species in data poor fisheries. Acoustic recorders can be effective at detecting, and even quantifying, unseen depredation by odontocetes, as evidenced by studies on sperm whales (Mathias, Thode, Straley, & Andrews, 2013; Thode et al., 2015; Thode, Wild, Mathias, Straley, & Lunsford, 2014) and false killer whales (Hernandez-Milian et al., 2008; McPherson et al., 2004) depredating on longline catches. Underwater cameras and, more recently, accelerometer devices, have been used as ways to detect cryptic depredation events but unlike acoustics, usually cover small proportions of gear and can hardly be used to fully quantify the conflict unless extensively deployed (IOTC, 2007; Lyle et al., 2016; Mathias, Thode, Straley, & Folkert, 2009; Richard et al., 2020; Thode et al., 2016). Underwater cameras can also help identify the depredating species. For example, this approach, paired with genetic analyses conducted on depredated fish remains, has allowed for the various shark species depredating in fisheries of Western Australia to be determined (Fotedar, Lukehurst, Jackson, & Snow, 2019; Mitchell, McLean, Collin, Taylor, et al., 2018). The recent rise of these techniques has likely contributed to the observed increase in the number of shark species known to depredate on fishery catches in the last decade (Figure 3b).

8.2 Quantifying the determinants of depredation

A multitude of both anthropogenic and environmental factors can drive the occurrence and the scale of depredation. While these factors, which include socio-economic, spatiotemporal and ecological determinants, have been extensively studied in terrestrial systems (Inskip & Zimmermann, 2009), their understanding remains limited for depredation in fisheries and yet is critical to developing mitigation strategies.

Studies of spatiotemporal factors have identified peak areas of depredation associated with strong overlaps between natural foraging grounds of predators and fishing operations (González et al., 2015; Nitta & Henderson, 1993; Seminara, Barbosa-Filho, & Penu, 2019; Stepanuk et al., 2018; Wickers, 1995) and/or distances from haul-out sites for pinnipeds (Cronin, Jessopp, Houle, & Reid, 2014; Hückstädt & Antezana, 2003). Similarly, peak in depredation were associated with seasonal variation in species co-occurrence with fisheries due to their phenology (reproduction or migrations) (Bombau & Szteren, 2017; De María, Barboza, & Szteren, 2014; Janc et al., 2018). The role of natural prey availability and whether species are more likely to switch to depredation when/where their prey become scarce are still unclear. More generalist species may also be more inclined to develop depredation. This is supported by the species most often reported depredating, such as common bottlenose dolphins, grey and harbour seals, typically being generalist predators (Austin, Bowen, & McMillan, 2004; Rossman et al., 2015; Tollit et al., 1998). For some other species (e.g. killer whales) with culturally transmitted behaviours and sometimes high levels of specialization, a switch to depredation may be conditioned by whether or not the fish caught by fishers is part of their natural diet. While a cosmopolitan distribution likely contributes to the species found interacting with many fisheries worldwide, depredation appears to occur on fish naturally predated by local populations (Esteban, Verborgh, Gauffier, Giménez, Guinet, et al., 1984; Peterson et al., 2013; Similä, 2005; Tixier, Giménez, et al., 2019). Other biological determinants may occur at the individual level and include personality, social learning and/or sex/age-dependent factors. For example, only adult male grey seals have been implicated in depredation (Königson et al., 2013).

The behaviour of fishers and, specifically, the extent to which their action makes the fish an accessible, attractive and predictable resource for predators are likely key determinants of depredation. High spatial density of fishing equipment and low selectivity of gear, as well as discarding practices, were described as acting as attractants for large predators (Gilman, 2007; Nishida & Tanio, 2001; Noke & Odell, 2002; Pardalou & Tsikliras, 2018; Reyes, Hucke-Gaete, & Torres-Florez, 2013; Rocklin et al., 2009). Predictability strongly influences the likelihood of predators feeding on human subsidies (Oro, Genovart, Tavecchia, Fowler, & Martinez-Abrain, 2013). With fishers often exploiting repetitively the same areas at consistent times of the year, the predictability of caught fish is high. Socio-cultural factors, such as perceptions, can influence the level of tolerance of fishers towards depredation and, therefore, the degree to which it is reported (Dickman, 2010). Perceptions of depredation may be disproportionate to the actual scale of the conflict, with a tendency of fishers to attribute decreased fishing success to marine predators and overestimate or overreport the problem (Bearzi et al.,
2011; Machado et al., 2016; Rechimont, Lara-Domínguez, Morteo, Martínez-Serrano, & Equihua, 2018). This tendency was assumed resulting from large marine predators being a visible and conspicuous part of the environment of fishers often seen as a risk or competitors (Iriarte & Marmontel, 2013; Pardalou & Tsiklias, 2018) and can be strengthened by economic factors such as the value of the fish (Lauriano, 2004).

### 8.3 Interdisciplinary research and integrated approaches

Depredation is typically a HWC affecting both human livelihoods and natural systems, through a broad range of social, economic and ecological pathways. However, while interdisciplinary research encompassing the socio-ecological dimension of the conflict is required (Nyhus, 2016), our review found this to be a major knowledge gap. A large proportion of studies had a narrow focus on either socio-economic, or the ecology and the conservation components of depredation (ESM 1 Table 1). Some publications did reflect the emergence of interdisciplinary approaches, at both the individual (researcher) and collective (collaborations across researchers of diverse expertise/background) levels. Biologists are starting to incorporate aspects of the behaviour of fishers driving depredation through methods derived from Animal Ecology and Human Sciences (Dalla Rosa & Secchi, 2007; Hückstädt & Krautz, 2004; Mitchell, McLean, Collin, Taylor, et al., 2018; Passadore et al., 2015; Powell & Wells, 2011; Richard et al., 2018; Pon et al., 2012). Instances of collective interdisciplinary research were highlighted in scientific programs on depredation involving biologists and fishery scientists, but also cross-sectoral (transdisciplinary) collaborations with industry representatives (fishers, companies, gear suppliers, etc.). These programs, found for example in South Africa (Wickens et al., 1992), Alaska (Straley et al., 2015), the UK (Butler et al., 2008), the Baltic Sea (Bruckmeier & Larsen, 2008; Westerberg et al., 2008) and in the Southern Ocean (Guinet et al., 2015), have led to major advances on both the understanding and the mitigation of the conflict and, therefore, should be further developed across other depredation situations.

The capacity of interdisciplinary research to mitigate depredation can be further enhanced by the use of integrated tools. Among these, practical implementations of ecosystem-based models to holistically examine the ecological effects of the conflict are still lacking. For instance, provisioning effects on life history parameters of depredating populations, paired with a displacement of predation pressures caused by opportunities to depredate, are likely to change the role and the impact of predators in ecosystems (Newsome et al., 2015). In addition, depredation may indirectly affect fish stocks by engaging fishers to increase their fishing effort to recoup catch losses (Peterson et al., 2014). While ecosystem models may help to assess effects on trophic interactions associated with fishery and depredation pressures, other tools may allow for more integrated incorporations of both socio-economic and ecological perturbations of the conflict. Among these tools, multi-agent-based models (e.g. Marley et al., 2017) or bio-economic models (Béné, Doyen, & Gabay, 2001; Gourguet et al., 2013; Trijoulet, Dobby, Holmes, & Cook, 2018) are frameworks that could be developed to identify and understand the trade-offs occurring in socio-ecosystems subject to depredation. These approaches can help assess the sustainability of such socio-ecosystems and provide relevant information for decision makers.

### 8.4 Resolving human–human conflicts in governance

The large range of socio-economic and ecological impacts of depredation makes it a conflict theoretically bringing all actors (fishers, fishing companies, scientists, managers, conservationists) together around a common objective of minimization despite different interests. Yet, the means to achieve this objective can greatly diverge across actors and lead to strong human–human conflicts hampering mitigation efforts. While governance plays a critical role in promoting coexistence, the resolution of these human–human conflicts is an essential prerequisite to the success and the sustainability of solutions implemented (Guerra, 2019). Typically, the use of culling or lethal control of depredating species, as often advocated by fishing communities but refuted by environmentalists, has crystallized debates around the management of many depredation cases (Butler et al., 2008; Cook, James, & Bearzi, 2015; Moore, 2003; Wickens et al., 1992). These practices have often proved ineffective at reducing depredation and pose conservation and ethics concerns. However, they still appear strongly embedded as a priority mitigation solution in perceptions of fishers, sometimes leading institutions to comply as a way to release tensions among stakeholders.

Changing perceptions is, in fact, a critical process on the road to coexistence with depredating predators (Cummings, Lea, & Lyle, 2019; Frank, 2016; Guerra, 2019). This is challenging given the complexity of factors influencing perceptions, as including cultural environments, history, personal experiences and sometimes beliefs and myths (Dickman, 2010). For example, cultural beliefs may negatively portray large marine predators, generating fear and hatred among communities reinforcing retaliation in the case of depredation (Alves et al., 2012). History may also play a crucial role since marine predators have been viewed as resources commercially exploited until recent times (30-40 years ago) and their eradication has been encouraged by governments until the 1970s. This factor is typically illustrated by differences in perceptions between old and new generations of fishers (Gonzalvo, Giovos, & Moutopoulo, 2015; Jog, Sule, Bopardikar, Patankar, & Sutaria, 2018). Increased knowledge sharing between stakeholders was proposed as a key prerequisite for success in changing perceptions (Bruckmeier & Larsen, 2008). This should be directed towards allowing fishers and managers to understand the ecology and the conservation concerns around species, but also the scientists and environmentalists to understand the socio-economic stakes around fishing (Lescroël et al., 2016; Redpath et al., 2013).
Knowledge sharing can be facilitated by adaptive co-management, an emerging mode of governance particularly suited to the resolution of HWC (Lundmark, Matti, & Sandström, 2014; Treves et al., 2006; Treves, Wallace, & White, 2009). This mode relies on participatory management through integration of multiple systems of knowledge with learning and retroactive loops across stakeholders in response to new information and/or changes (Armitage et al., 2009; Folke, Hahn, Olsson, & Norberg, 2005). Adaptive co-management was successfully implemented in Scotland for seal depredation (Butler et al., 2015), but the program involved lethal mitigation, making it hardly applicable globally. As advocated by Varjpuro (2011), increasing understanding of all socio-ecological components of depredation through a wide diversity of actors and knowledge systems, with a capacity to respond to the dynamic nature of the conflict (changes in species behaviour and populations, in fish markets, regulations, etc.), are key determinants of sustainable mitigation. This is underway in some depredation cases, with the industry, scientists and managers already cooperating through simultaneous lines of efforts (behavioural adaptations and technological systems), sharing knowledge, running tests and evaluating results in a feedback/adaptive fashion (e.g. Guinet et al., 2015; Straley et al., 2015), and should be implemented in far more situations.

9 | CONCLUSION

This review has demonstrated the considerable extent of the depredation conflict in the world’s fisheries, with instances reported from all oceans, at nearly all latitudes, in all major fishing sectors (industrial, artisanal and recreational) and for nearly all fishing techniques. Yet, the global magnitude of the issue reported here should be considered as underestimated since a number of depredation cases likely remain unreported in the scientific literature. The conflict is likely to escalate in coming decades as human pressures on marine resources increases in response to increasing demand. In some regions, this escalation may be accelerated by the recovery of historically exploited local predator populations. The high levels of depredation paired with conservation concerns of some of the species involved stresses the need for lasting mitigation solutions. As in terrestrial systems, a shift towards cooperative, adaptive, cross-sectoral and integrated initiatives is needed to reach coexistence between fisheries and large marine predators in regard to depredation. Expanding research to the socio-ecological dimension of the conflict, mobilizing stakeholders and resources under a common mitigation objective, integrating knowledge and changing perceptions, are, combined, a framework suitable for sustainable mitigation that should grow in significance.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The literature selected for the review, information on studies included in the synthesis and data used to produce the results are available in Electronic Supplementary Material 1.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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