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Author(s): Jusufovski, Dunja; Saavedra, Camilo; Kuparinen, Anna

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1 **Marine mammal–fisheries competition in contemporary harvested marine ecosystems**

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4 Dunja Jusufovski^{1*}, Camilo Saavedra² and Anna Kuparinen³

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6 ¹Organismal and Evolutionary Biology Research Programme, University of Helsinki, PO Box 65,
7 00014 Helsinki, Finland

8 ²Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, Subida a Radio Faro 50, 36390
9 Vigo, Pontevedra, Spain

10 ³Department of Biological and Environmental Sciences, University of Jyväskylä, PO Box 35, 40014
11 Jyväskylä, Finland

12 *Corresponding author: dunja.jusufovski@helsinki.fi

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20 **Running head:** Marine mammal–fisheries biological competition

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1 **ABSTRACT**

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3 Competitive interactions between marine mammals and fisheries represents one of the most complex
4 challenges in marine resource management worldwide. The development of commercial fisheries and
5 recovering marine mammal populations have contributed to decreasing of fish availability. Whilst
6 ecosystem-based fisheries management (EBFM) can counteract this decrease, achieving the EBFM
7 objectives faces certain major obstacles including insufficient or unreliable data, inapplicable
8 assessment models as well as inadequate management decisions that do not account for fisheries-
9 induced morphological alterations (FIMA) and marine mammal management. Despite a body of
10 evidence addressing various aspects of marine mammal–fisheries competition, little is known about
11 the effects of marine mammal–fisheries biological interactions affecting the fish viability and food
12 web stability. Here, we review the research done on marine mammal–fisheries *competitive biological*
13 *interactions* (hereafter as ‘*biological competition*’) by focussing on: (1) the prerequisites for marine
14 mammal–fisheries biological competition and the relevant methodologies to explore them and (2)
15 recent studies revealing the implications of FIMA and trophic interactions for the biological
16 competition. We also discuss on the implications of FIMA, eco-evolutionary feedback and prey–
17 predator dynamics for EBFM implementation in contemporary harvested ecosystems. Our main
18 findings reveal a lack of data about marine mammals’ prey choice and selectivity, the need for better
19 representation of marine mammals in modelling approaches and lastly, the necessity for additional
20 research linking FIMA, trophic interactions and the EBFM objectives. To conclude, interdisciplinary
21 approaches may serve to link all of the efforts needed to effectively and holistically support the
22 implementation of EBFM.

23

24 Keywords: Resource competition, Fisheries, Cetacean, Pinniped, Prey–predator dynamics,
25 Ecosystem-based management, Fisheries-induced

1. INTRODUCTION

2

3 Many contemporary harvested marine ecosystems are often characterised by competitive interactions
4 between humans and marine predators (Pauly et al. 1998, Trites et al. 2006). From that aspect,
5 realising sustainable long-term yields in fisheries requires an in-depth understanding of the impact,
6 these interactions have, for fish survival and the ecosystem. In this article, we attempt to review this
7 information in the published and available material and address this issue considering the
8 morphological alterations observed in fish under intensive fishing as well as their overall implications
9 for the ecosystem-based management. As an introduction to the topic, we first briefly present an
10 historical overview of marine mammal–human non-competitive and competitive interactions, then
11 describe the main impacts on and roles of marine mammals and fisheries on the ecosystem and their
12 management. We conclude by defining marine mammal–fisheries competition as well as the aim and
13 structure of this literature review.

14

1.1. Brief historical overview of competitive interactions between humans and marine mammals

17 The human exploration of marine ecosystems in search of food stands as a key moment preceding
18 the competition between fisheries and marine mammals for fish (Lavigne 2003). The oldest
19 archaeological findings of fishing tools, dating to 8800 BC, provide evidence for the beginning of the
20 development of fishing activity. While some of the oldest evidence for marine fishery-dependent
21 communities were found in Crete (6000 BC), in Egypt, around 2000 BC when fishing activity was
22 highly associated with social status (Lackey 2005). Accompanying global technical and technological
23 development, the diversification and development of fishing gear, vessels and fish preservation
24 techniques facilitated the expansion of fishing areas towards open waters (Jackson et al. 2001, Lackey
25 2005). Over time, interactions between humans and marine mammals diverged into two

1 interchangeable and often mutually non-exclusive types. First type of interaction consisted of humans
2 depending upon marine mammals as a natural resource, while the second type consisted of the
3 perception of marine mammals as a direct threat to humans' livelihoods and tradition. The first type
4 of interaction did not necessarily consist of competition, although it might have developed due to an
5 initial competitive interaction. Whether non-competitive or competitive, marine mammal–fisheries
6 interactions significantly impacted the historic abundance of marine mammals.

7 Countries in the Northern hemisphere, such as Norway, Iceland, Denmark, Russia Canada and the
8 USA, have traditionally hunted whales for oil, baleen and meat whilst also hunting seals for their fur
9 and meat (Tønnessen & Johnsen 1982, Ellis 1991, Harding & Härkönen 1999, Reeves & Smith 2006).
10 In addition, sea otters (*Enhydra lutra*) were hunted for their fur along the North Pacific coastal waters
11 of Russia, Canada and the USA (e.g. California and Alaska; Kenyon, 1969, Bodkin 2015). Until the
12 enactment of federal protection laws in the 1970s, sea otters were nearly brought to extinction through
13 hunting programmes in California and Alaska (Carswell et al. 2015). Today, much effort is put into
14 the management of this small, yet economically and ecologically important marine mammal species
15 (Carswell et al. 2015, Estes 2015).

16 In case of commercial whaling, a moratorium proposed by the International Whaling Commission
17 (IWC, 1946) has limited the removal of baleen whales since 1986, albeit Norway and Iceland were
18 exempted and continued to hunt minke (*Balaenoptera acutorostrata*) and fin (*Balaenoptera physalus*)
19 whales (see Howell & Bogstad 2010), establishing their own quotas. Based on 2017 whale catches
20 (www.iwc.int), the approximate proportion of commercial whaling, aboriginal subsistence and
21 special permit stood at 33%, 24% and 43%, respectively. Furthermore, whaling practices still remain
22 a tradition in some countries, such as Iceland, Norway (IWC 2016) and the Faroe Islands (Singleton
23 & Fielding 2017), whereas aboriginal subsistence whaling is allowed for several indigenous
24 communities in Alaska (USA), Chukotka (Russia), the West Indies (St. Vincent and the Grenadines)
25 and Greenland (Denmark; Gambell 1993, Reeves 2002). Thus far, 'scientific whaling' has been

1 conducted by the Japanese fleet in the Antarctic waters (Kalland & Moeran 2011, IWC 2016).
2 However, recent (Dec 2018) announcements by the Japanese government disclosed their intention to
3 leave the IWC and begin whaling in Japanese jurisdictional waters, whilst ceasing to hunt in Antarctic
4 waters. Additionally, 'bycatch' minke whales are being commercialised in South Korea (MacMillan
5 & Han 2011, Tatar & Jung 2018).

6 Competitive interactions for fish have reportedly led to occasional retaliation from fishermen
7 against marine mammals, ultimately contributing to the introduction of the intentional removal
8 (namely, culling) of many marine mammal species (DeMasters et al. 2001, Kaschner & Pauly 2005).
9 In the Mediterranean Sea, for example, cullings were recorded as early as the sixteenth century
10 (Bearzi et al. 2004, 2008). This marked the beginning of a long period of dolphin removals persisting
11 until the end of the twentieth century, leading to significant declines of Mediterranean and Black Sea
12 bottlenose (*Tursiops truncatus*) and short-beaked common (*Delphinus delphis*) dolphins (Mitchell
13 1975, Holcer 1994, Birkun 2002, Bearzi et al. 2004, 2008). Similar culling events occurred along the
14 Atlantic coastlines of Spain and Norway (Øien 1988, Valdés 2004). Specifically, cullings of Iberian
15 populations of small cetaceans in the northeast Atlantic lasted for centuries (Valdés 2004, 2009),
16 whilst, in Norway, culling killer whales (*Orcinus orca*) followed the herring (*Clupea harengus*)
17 population collapse, whilst resulted primarily from overfishing (Øien 1988). Culling small cetaceans
18 in Europe did not represent unique culling events, particularly given events in Japan (Kasuya 1985).

19 Pinniped species such as the grey (*Halichoerus grypus*) and ringed (*Histiophoca fasciata*) seals
20 were heavily hunted by several Baltic countries for their fur, but, more importantly, given their
21 competition with cod (*Gadus morhua*), herring and sprat (*Sprattus sprattus*) fisheries (Harding &
22 Härkönen 1999, Hansson et al. 2007). In the northeast Atlantic, grey and ringed seals were also culled
23 in UK, Norwegian and Icelandic waters (Bowen & Lidgard 2013), whilst Scotland and Iceland
24 undertook harbour seal (*Phoca vitulina*) cullings. Beyond European waters, primarily in the USA and
25 Canada, pinniped species, such as California sea lions (*Zalophus californianus*), northern sea lions

1 (*Callorhinus ursinus*), harbour seals, and Steller sea lions (*Eumetopias jubatus*), were culled (Bowen
2 & Lidgard 2013). Sea otters were perceived as a direct competitor for Alaskan and Californian
3 shellfish fisheries (including various bivalves, sea cucumbers, and crab species) that, in addition to
4 the fur trade, supported sea otter cullings (see Erlandson et al. 2005, Carswell et al. 2015).

5 Owing to various international laws and regulations (e.g. IWC regulations), retaliation or
6 unregulated kills of marine mammals are now illegal, although a large proportion of marine mammal
7 mortality (especially for small cetaceans) stems from unintentional removals or bycatch (Northridge
8 & Hofman 1999, Read et al. 2017). Yet, in comparison to the historic commercial whaling typical of
9 the twentieth century and seal hunting by indigenous nations, marine mammal populations appear to
10 be steadily recovering (IWC 2016). This observation does not hold for all marine mammal species,
11 but primarily applies to baleen whales and some seal species (Read & Wade 1999). Other marine
12 mammal species, however, have not significantly recovered, perhaps hampered by other emerging
13 threats (e.g. bycatch, pollution, diseases, etc.; Roman et al. 2013, IWC 2016).

14

15 **1.2. Roles of marine mammals and fisheries in contemporary marine food web and their** 16 **relation to ecosystem-based fisheries management**

17 Marine mammals have a wide range of trophic niches. As key species in various marine
18 ecosystems, they play a crucial role in underlying ecological processes that preserve ecosystem
19 functioning (see Bowen 1997, Pauly et al. 1998). Marine mammals contribute to both top-down and
20 bottom-up control through trophic interactions. With respect to top-down control, the consequences
21 of removing the top predators normally precedes an increase in mesoconsumers in the trophic web as
22 well as a decrease in the lower trophic level such as that found in foraging fish, detritivores and
23 grazers (Heithaus et al. 2008, Roman et al. 2014). Marine mammals may also exert a bottom-up
24 control in a trophic web contributing to an ecosystem`s productivity through the defecation of iron-
25 and nitrogen-rich excreted. This reportedly holds true for coastal ecosystems, where cetaceans and

1 pinnipeds forage and feed, notably stimulating primary production through defecation as well as
2 distributing and dispersing nutrients due to their rapid ascent and descent (Roman & McCarthy 2010,
3 Lavery et al. 2014, Roman et al. 2014). In oceanic ecosystems, the mixing of nutrients correlates more
4 strongly with baleen and large toothed whales (see Roman & McCarthy 2010), owing to their size
5 and diving abilities. While marine mammals directly affect the abundance of target species, their
6 indirect effect crucially boosts the ecosystem productivity. Thus, some studies suggest that, in the
7 role as top predators and ecosystem engineers marine mammals facilitate rather than harm fisheries,
8 strengthening their concomitant economies in the long term (see Yodzis 2001, Gerber et al. 2009,
9 Morissette et al. 2012, Lavery et al. 2014, Roman et al. 2014).

10 In agreement with the theory of trophic interactions, fisheries can operate at the same trophic level
11 as top predators, albeit causing severe adverse effects observed at all structural levels (Trites et al.
12 2006, Daskalov et al. 2007). In contrast to marine mammals that co-evolve with their prey, developing
13 a specialisation in prey choice or becoming rather indiscriminate in terms of prey preferences (Trites
14 et al. 2006), fishing tools are primarily size selective, targeting mostly large and economically
15 valuable fish (Heino & Dieckmann 2008). Considering the amount of fisheries uptake, such selective
16 removal can cause negative changes in the life-history traits of the target species in the long-term,
17 including declines in body size and the age of maturation, potentially, in turn, negatively affecting
18 fecundity and the viability of the fish population (Sharpe & Hendry 2009, Wright & Trippel 2009,
19 Kuparinen et al. 2014). Some studies have indicated that through persistent intensive fishing, such
20 fisheries-induced morphological alterations (FIMA) can lead to increased fluctuations in recruitment
21 (Anderson et al. 2008), for instance, negatively affecting fisheries catches as well as fish stock
22 recovery (Enberg et al. 2009). By contrast, while marine mammal species can also exhibit a specific
23 prey size preference (e.g. as observed in seal and cetacean species), their prey choice does not strictly
24 depend upon prey size, instead extending to intra- and interspecific competition and the ecosystem's

1 carrying capacity (see Lindeberg & Pyenson 2006). These differences between fisheries and marine
2 mammals will be expanded upon and further discussed in the relevant sections below.

3 The overexploitation of fish stocks spurred by the industrialisation of fisheries, has exhausted a
4 number of diverse marine ecosystems (Jackson et al. 2001) and contributed to, *inter alia*, the global
5 stagnation of fisheries landings in the 1980s (Pauly et al. 2003, Trites et al. 2006, FAO 2016). As a
6 response to depleted yields, the primary measures employed in fisheries management have focussed
7 on technological improvements to fishing tools rather than the better acquisition of field data, analysis
8 of the situation and identifying the causes of fish decline as proposed by the scientific community.
9 Moreover, in certain fisheries-dependent communities, this situation yet again ignited older criticisms
10 of marine mammals. This hampered the comprehensive and thorough analysis of the situation that
11 took into account for anthropogenic factors potentially contributing to the declines in fish catches,
12 such as an unsustainable fishing intensity, illegal fishing activities and the disregard of various fishing
13 regulations (Kaschner & Pauly 2005, Gerber et al. 2009). For fish and marine mammals, a prolonged
14 state of overexploited fishing stocks, can postpone or entirely impeded fish stocks recovery
15 (Hutchings 2000) as well as diminish the chances of marine mammal survival through longer periods
16 of starvation (see Esteban et al. 2016).

17 In response to contemporary threats to the fishing sustainability and the functioning of marine
18 ecosystems, a holistic approach to marine resources management is needed (Botsford et al. 1997).
19 Ecosystem-based fisheries management (EBFM) represents a managerial approach that consolidates
20 human and environmental well-being (Link 2002, Pikitch et al. 2004). The effective implementation
21 of EBFM requires an understanding of ecosystem processes, the direct and indirect impact of fisheries
22 on the ecosystem, the preservation of trophic interactions considering the top predators competing for
23 the same fish as fisheries as well as the application of effective approaches accounting for
24 uncertainties about the prey–predator dynamics (see Constable 2011). Whilst various case studies and
25 attempts at implementing EBFM exist, it is clear that the application of knowledge and particularly,

1 recent insights into the dynamics of marine mammal–fisheries competition play important roles in
2 reaching EBFM-related goals. Therefore, a detailed discussion of fish–marine mammal dynamics
3 within harvested ecosystems and its significance for the EBFM implementation will be further
4 addressed in the relevant sections below.

5

6 **1.3. Defining marine mammal–fisheries biological competition**

7 Understanding competition between marine mammals and fisheries is not as straightforward and
8 intuitive as one might assume (DeMasters et al. 2001, Kaschner & Pauly 2005). In total, 11 species
9 of baleen whales, 63 species of toothed whales, 31 pinniped species, and one otter species reportedly
10 interact with fisheries in various ways (King 1964, Jefferson et al. 1993). Previous studies elaborated
11 upon definitions and implications of marine mammal–fisheries competition (Trites et al. 1997, 2006,
12 Matthiopoulos et al. 2008), whereby each addressed different aspects of the competition, highlighting
13 certain shared prerequisites necessary for the marine mammal–fisheries competition to occur. In
14 particular, this entails the exploitation of the same resource with notable temporal and spatial overlap,
15 whilst the competitive nature of the interaction suggests that one competitor’s gain in resource results
16 in another’s loss (also known as the ‘surplus-yield’ concept). Furthermore, competition between
17 marine mammals and fisheries encompasses two types of interactions: operational and biological
18 (Fig. 1., Northridge & Hofman 1999, Goldsworthy et al. 2003). Operational interactions are the most
19 obvious type of marine mammal–fisheries interaction, referring specifically to marine mammal
20 interference with fishing activities, primarily fishing gear (e.g. depredation; Goetz et al. 2014).
21 Biological (or ecological) interactions (hereafter as ‘*biological competition*’) can be direct, whereby
22 fisheries and marine mammals evidently target the same resource (Goldsworthy et al. 2003). Apart
23 from direct interactions, indirect biological interactions (i.e. ‘the food-web competition’) occur at the
24 level of primary production, cascading throughout the entire food web and reflecting the organic
25 production necessary to sustain both competitors (Trites et al. 1997, 2006).

1 Biological and operational competitive interactions between marine mammals and fisheries are
2 rarely observed separately. In this context, insights gained from research on biological interactions
3 complement our understanding of operational interactions, whereas the opposite does not always
4 apply. The challenges lie in identifying and measuring direct and indirect biological competition
5 which requires special attention, since the effects of marine mammal–fisheries biological competition
6 are latent and can potentially accumulate across trophic levels and over time. For instance, if one
7 observes this from an individual level, where different prey experience different predation pressures
8 due to their individual variability (e.g. sex, age, developmental stage or health status), any change or
9 lack of synchronicity in prey–predator dynamics resulting from that individual variability in
10 responses will inevitably affect the strength and impact of biological competition. Inadequately
11 managed or unaccounted for shifts and disruptions in the dynamic ecological processes governing an
12 ecosystem could lead to its dysfunctionality. Thus far, previous studies addressing marine mammal–
13 fisheries competition have examined the impact and significance from the perspective of principles
14 and assumptions of trophic interactions’ theory (e.g. DeMasters et al. 2001), the development of
15 methodological approaches (Kaschner & Pauly 2005, Matthiopoulos et al. 2008), the importance of
16 biological interactions and ecological complexity (Harwood & McLaren 2004, Pierce et al. 2004,
17 Kaschner & Pauly 2005, Matthiopoulos et al. 2008) and the need for more effective and
18 interdisciplinary conservation measures (Bearzi 2007, Leslie & McLeod 2007).

19 Therefore, this article aims to review and synthesise existing knowledge gained from studies
20 exploring biological competition between marine mammals and fisheries targeting the same fish
21 species. Since marine mammals comprise species originating from different taxonomic groups
22 (cetaceans [order *Cetacea*], pinnipeds [superfamily *Pinnipedia*], the otter family [*Mustelidae*],
23 sirenians [order *Sirenia*] and polar bears [family *Ursidae*]), we specifically address the interaction
24 between fisheries and cetaceans, pinnipeds as well as sea otters given that these appear to interact
25 most often with fisheries. Furthermore, in this review we, first, synthesise the existing knowledge of

1 the prerequisites of marine mammal–fisheries biological competition presenting a cross-section of
2 relevant information and methods used in research on marine mammal–fisheries biological
3 competition. Next, we provide insights into recent studies highlighting the implications of FIMA for
4 marine mammal–fisheries biological competition at the individual and population levels and discuss
5 how FIMA, eco-evolutionary processes, and prey–predator dynamics reflect on the implementation
6 of the EBFM objectives. By disentangling the issue of marine mammal–fisheries biological
7 competition, we strive to better describe the potential consequences of the biological competition, not
8 simply to achieve sustainable fisheries. That is, we also aim to better link marine resource exploitation
9 and conservation through the implementation of evidence-based recommendation on ecosystem
10 functioning for contemporary harvested ecosystems.

11

12 **2. METHODOLOGY**

13

14 We conducted a literature search focusing on two specific areas:

- 15 1) existing knowledge and methodology relevant for understanding marine mammal–fisheries
16 biological competition;
- 17 2) recent insights into implications of prey–predator dynamics experiencing FIMA and their
18 relevance for marine mammal management as well as the EBFM objectives.

19 We collected the relevant published literature (including journal articles, reviews, PhD theses,
20 technical reports and conference papers) through extensive literature searches performed in 2018
21 focussed on these two specific areas. We used the Google Scholar, Scopus, ScienceDirect and Ovid
22 search engines for our literature search. In these literature searches, manuscripts published from 2000
23 through 2017 were considered in an attempt to capture the most recent research on the above topics.
24 The searches were not limited by geographical area or language, although English was applied in all
25 search engines. References were consulted in all of the papers selected, and we included papers based

1 on the significance of their findings for the focus areas and the selection criteria rather than year of
2 publication.

3 We performed three independent literature searches to address the knowledge and case studies on
4 the marine mammal–fisheries interactions as well as the two specific areas. The selection of literature
5 collected from all searches relied on the manuscript title and abstract screening. For the first literature
6 search, we used random combinations of the following keywords: ‘marine mammals’, ‘fisheries’,
7 ‘competition’, ‘pinniped’, ‘cetaceans’, ‘sea otter’, ‘conflicts’, ‘marine predator’ and ‘food web’. This
8 initial wide literature search allowed us to define specific systematic categories (see Supplemented
9 Table S1).

10 Second literature research was done to complement the first literature search and specifically to
11 address the first specific area. Here, we used random combinations of these keywords: ‘cetaceans’,
12 ‘pinnipeds’, ‘sea otter’, ‘fisheries’, ‘competition’, ‘observations’, ‘diet’, ‘feeding ecology’,
13 ‘modelling’, ‘consumption’ and ‘ecosystem dynamics’. The third literature search was conducted to
14 address the second specific area using random combinations of the following keywords: ‘marine
15 mammals’, ‘fisheries’, ‘competition’, ‘pinniped’, ‘cetaceans’, ‘sea otter’, ‘ecosystem-based’,
16 ‘community’, ‘conservation’, ‘fisheries-induced’ and ‘interdisciplinary’.

17 We selected the collected literature from all searches according to specific selection criteria with
18 respect to two focus areas. Selection criteria supporting the first focus area included studies and their
19 respective methodology that: (1) contributed to an understanding of spatial, temporal and resource
20 overlap between marine mammals and fisheries; (2) marine mammal dietary studies; and (3) model-
21 based approaches that incorporated marine mammal–fisheries biological competition. The selection
22 criteria supporting the second focus area encompassed studies addressing: (1) the effects of FIMA on
23 the individual fish traits and their consequences for prey–predator dynamics; (2) how FIMA reflected
24 the fish availability; and (3) appropriate marine mammal management with respect to FIMA and the
25 EBFM objectives.

1 The material collected through the literature searches resulted in total of 220 selected papers. We
2 systematically categorised the literature collected as papers that are relevant for field observation
3 methodology (including habitat modelling, n = 33), dietary studies (n = 71), modelling approaches (n
4 = 63), FIMA implications for fish availability and prey-predator dynamics (n = 25) and marine
5 mammal management associated with FIMA and EBFM (n = 28). A full list of the selected papers is
6 available in Supplemented Table S1.

7

8 **3. THE COMPLEXITY OF MARINE MAMMAL–FISHERIES BIOLOGICAL** 9 **COMPETITION**

10

11 **3.1. Spatial, temporal and resource overlap as indicators of marine mammal–fisheries** 12 **biological competition**

13 To determine marine mammal–fisheries spatial and temporal overlap, firstly, information on
14 marine mammal distribution and abundance is primarily acquired through systematic land- or boat-
15 based observations (see Godwin et al. 2016, Vincent et al. 2017), large scale and aerial surveys of
16 vast marine areas frequented by cetaceans as well as seal and sea otter haul out sites (e.g. Huber et al.
17 2001, Laidre et al. 2001, Bodkin et al. 2002, Lonergan et al. 2007, Bauer et al. 2015, Hammond et al.
18 2013, 2017). Furthermore, tagging animals with radio, GPS or satellite loggers (e.g. Tinker et al.
19 2007a, b, Cronin et al. 2012, Oksanen et al. 2014, Godwin et al. 2016) or attaching cameras
20 (colloquially, ‘critter-cameras’; see Bowen et al. 2002, Parrish et al. 2008) allow researchers to track
21 and monitor marine mammals’ foraging ranges, feeding behaviours, and success in the wild. In some
22 cases, tracking tagged commercial fish species can reveal their potential predators (see Wahlberg et
23 al. 2014). Unmanned aircraft systems (UAS) or drones represent a highly effective tracking and
24 monitoring tool due to their cost-effectiveness, practicality and low-noise interference (Linchant et
25 al. 2015, Christie et al. 2016). Ultimately, information gathered through various methods of distance

1 sampling allows researchers to further estimate marine mammal distribution and range of feeding
2 area ranges using various model designs (e.g. SCANS 2006a, b, Thomas et al. 2010, Bailey et al.
3 2012). Apart from population-level data, information on individual variation in the distribution,
4 feeding behaviour and foraging strategy can be acquired through photo-identification using a
5 photographic record of an individual's unique morphological characteristics, such as marks, notches,
6 skin or nose scars as well as the specific pigmentation typically found on the ventral part of the body
7 or fluke (Lee et al. 2009, Urian et al. 2015). Alternatively, data collected through interviews with
8 fishermen can provide an indication of marine mammal occurrence, feeding behaviours as well as
9 feeding on fish aggregates commercially important to fisheries (see Weise & Harvey 2005, Alves et
10 al. 2012, Gonzalvo et al. 2014).

11 Mapping of the spatial, temporal, and resource overlaps has revealed how most of fisheries and
12 marine mammal encounters concentrate along coastal areas in the Northern hemisphere, particularly
13 in those areas characterised by strong upwelling events (Kaschner et al. 2001). This is reportedly
14 significant for small marine mammal species such as dolphins, porpoises and seals, whilst less or no
15 spatial and temporal overlap is noted for baleen whales that forage in deeper oceanic waters (Kaschner
16 et al. 2001, Kaschner 2004). Here, the validation of resource overlap between fisheries and marine
17 mammals relies on field observation, but also dietary studies. Traditional qualitative and quantitative
18 approaches for studying diet in marine mammals include analyses of stomach contents, fatty acids
19 contents in the blubber, and stable isotopes in muscle tissue (Pierce & Boyle 1991, Pierce et al. 2004)
20 and faecal analysis (Pierce & Boyle 1991). Since marine mammal species exhibit a diverse range of
21 foraging strategies and prey selectivity, ranging from a general and opportunistic to a more specific
22 prey preference, dietary studies are crucial to determining trophic levels. A species' trophic level
23 describes its position with respect to other organisms as well as indicating the qualitative and
24 quantitative nature of their relationship (reviewed in Young et al. 2015). A lingering problem,
25 however, in marine mammal dietary studies is small sample sizes whereby accurate estimates in diet

1 studies become possible only for species or regions where the sample sizes are adequate (Pierce et al.
2 2004). Samples of stomach contents, muscle and fat tissue are primarily acquired from bycatch or
3 stranded animals (Pierce & Boyle 1991), but also from hunted animals during commercial whaling
4 (e.g. Olsen & Holt 2001, Johnson et al. 2016), aboriginal subsistence (e.g. Castellini 2000) or
5 ‘scientific’ (e.g. Folkow et al. 2000, Haug et al. 2010, Konishi et al. 2014, Johnson et al. 2016)
6 whaling. It is important to note that dietary contents can significantly differ depending upon the origin
7 of the sample (see Evans et al. 2003, Hernandez-Milian et al. 2015). Moreover, the non-random
8 sampling as well as the health status of animals used for stomach content analyses might affect the
9 interpretation of results (see Pierce et al. 2004 for more biases).

10 To overcome such uncertainties in trophic-level determinations, dietary methods are often
11 combined with one another or various methods of marine mammal observation (see summary in Table
12 1), whereby stomach content analyses are combined with the stable $^{14/15}\text{N}$ analysis, or in the case of
13 determining habitat fidelity, $^{12/13}\text{C}$ analysis (Pierce et al. 2004). The stable isotope analysis is applied
14 to muscle or blubber tissue in cetaceans and vibrissae in seals and sea otters. Since stable isotope
15 analysis lacks detailed dietary information, it cannot provide information on the prey species recently
16 consumed (Pierce et al. 2004, Newsome et al. 2012, Scheinin et al. 2014). Dietary studies occasionally
17 reveal new prey species in a marine mammal diet (see Gladilina & Gol’din 2014) and allows us to
18 determine marine mammal prey selectivity or detect a shift in prey. More importantly, in marine
19 mammal dietary studies it often remains challenging to discern whether a change in diet occurred due
20 to prey availability, seasonality, habitat, population density-dependent or ontogenetic/individual
21 behavioural differences (see Tinker et al. 2007a using sea otters as an example). For instance, female
22 Californian sea otters show a significantly diverse range in prey specialisation compared to males,
23 which increases with a reduction in the habitable coastline (Estes et al. 2003, Elliott Smith et al. 2015).
24 Interestingly, studies exploring killer whales populations that specialise in preying upon other great
25 whales identified a switch to a sea otter and Steller sea lion diet (Mizroch & Rice 2006) as well as

1 grey seals that switched from preying upon fish to harbour seals and porpoises (see van Bleijswijk et
2 al. 2014, van Neer et al. 2015), might be explained by depletion of the original primary prey or
3 individual prey preferences.

4 Prey variation related to distribution and abundance can play a crucial role in the prey choice of
5 pinnipeds (Laake et al. 2002, Lundström et al. 2010) as well as sea otters (Laidre & Jameson 2006).
6 Standard faecal analysis represents the most common method used in determining the diet
7 composition amongst pinnipeds, which relies on hard parts in faecal samples, such as otoliths, used
8 to identify prey as well as for Quantitative Fatty Acid Signature Analysis or QFASA (see Table 1 for
9 examples). For instance, historic faecal samples and reconstructing the biomass eaten through a model
10 showing the frequency of size-specific portions allows us to determine the occurrence of salmon in
11 the harbour seal diet (see Laake et al. 2002). However, the disadvantage of using standard faecal
12 analysis lies in potentially under- or overestimating the representation of fish otoliths found in faeces
13 due to a highly digested stage of prey (see Dellinger & Trillmich 1988 for details). By contrast,
14 QFASA detects and measures the unique signatures of fatty acids in prey samples and carries a
15 demonstrated high accuracy in prey species identification (see Iverson et al. 2004).

16 Molecular or DNA barcoding of prey species enjoys increasing use in prey identification and,
17 when combined with stomach content analysis, can assist in identifying potential resource overlap
18 with fisheries (see Méheust et al. 2014). This rather non-invasive method has been used to identify
19 prey species for whales, dolphins and pinnipeds (Jarman et al. 2002, Parsons et al. 2005, Méheust et
20 al. 2014). DNA barcoding has proven particularly useful in the identification of the soft parts of highly
21 decomposed prey (see Deagle et al. 2009) or damaged fish otoliths found in the samples of faeces,
22 vomited food (e.g. from seals) or the stomach contents of dead animals (King et al. 2008, Dunshea
23 2009). However, DNA barcoding alone is insufficient in quantitative analyses of diet composition
24 since variation in prey proportions amongst different DNA sequencing can occur due to factors such
25 as the sequencing direction and quality amongst different species (see Deagle et al. 2013). Yet, DNA

1 barcoding is particularly useful in dietary studies of baleen whales that consume small-sized or fast
2 digestible prey such as krill (e.g. Jarman et al. 2002). Furthermore, in the absence of hard or uniquely
3 discernible parts of the ingested prey, the detection and quantification of krill, particularly
4 crustaceans, must rely on the prior knowledge on the marine mammal diet as well as optimised DNA
5 sequencing through improved primers and minimising biases originating from variation in DNA
6 amongst conspecifics and different species (King et al. 2008, Dunshea 2009).

7 Using the data available on marine mammal abundance, distribution, diet composition and
8 foraging strategies, spatial models can be applied to project the range of a foraging habitat and, thus,
9 estimate the potential of spatial, temporal and resource overlap (see Doniol-Valcroze et al. 2012).
10 Yet, changing environmental conditions and human activities (i.e. prey depletion) can reduce the
11 reliability of such models and yield unrealistic estimates whilst insufficiently accounting for marine
12 mammal–fisheries biological competition on fish availability (Santos et al. 2013). Under conditions
13 of prey depletion, marine mammals might rely on other food sources such as fish farms (see
14 Sepúlveda et al. 2017, Piroddi et al. 2011) or migrate in search of better feeding grounds (Santos et
15 al. 2002, Bearzi et al. 2006, Scheinen et al. 2014). Moreover, the prey quality, an important factor in
16 prey selection (Bowen et al. 2002), can greatly affect the range of distribution and site fidelity of, for
17 instance, cetaceans due to the significant relationship between diet quality and cost of living (see
18 Spitz et al. 2012). Specifically, cetaceans with high metabolic costs, such as the common dolphin and
19 harbour porpoise (*Phocoena phocoena*) will develop adequate foraging strategies and, if necessary,
20 forage more to satisfy their need for energy-rich prey. By contrast, sea otters adopt diverse
21 behavioural responses and foraging strategies under high intraspecific competition as well as
22 depending upon prey population density (see Tinker et al. 2007a, b).

23 Understanding the metabolic needs of marine mammals highlights the importance of obtaining
24 data on the energetic requirements which, in most cases, stems from studies of marine mammals in
25 captivity. Obtaining information on the energetic requirements from marine mammals in the wild can

1 be difficult due to unpredictable environmental and working conditions as well as due to their shy
2 and elusive nature (Kastelein et al. 2002, Lockyer 2007). Sea otters are, however, an exception from
3 this rule since most of their activities can be observed on the surface or haul out sites (see Finerty et
4 al. [2009] for Field Metabolic Rate estimations in wild sea otters). Yet, studying marine mammals
5 that can be held in enclosed facilities, provides a controlled environment where we can observe
6 changes in food intake due to season, sex or age (e.g. Kastelein et al. 2002), energetic requirements
7 (e.g. Rechsteiner et al. 2013) and feeding behaviours (e.g. Levermann et al. 2003). Estimates for daily
8 or annual energy intake, metabolic rates, and the length–weight relationship, for instance, obtained
9 from animals in captivity allow us to preliminary estimate predation (see Santos et al. 2014).
10 Moreover, research on animals in captivity has also been used to test the reliability of certain dietary
11 methods or to improve such methods (e.g. Iverson et al. 2004, Parsons et al. 2005, Dunshea 2009,
12 Deagle et al. 2013, Tyrrell et al. 2013). Energetic requirements measured in captivity, however, can
13 underestimate the energetic requirements of wild and highly migratory marine mammals (Lockyer
14 2007), making further estimates such as those on quantifying predation rather difficult. Yet, through
15 the development of more sophisticated biologging technology, making direct measurements of
16 different energetic parameters on wild-ranging and large marine mammals is becoming increasingly
17 reliable (see Bograd et al. 2010). Information on the energetic requirements together with population
18 size, structure, and diet can be used to quantify predation, enabling a better estimate of the natural
19 mortality of the fish species and can be used to minimise uncertainties in fish stock assessments.

20

21 **3.2. Modelling approaches: connecting fish, marine mammal and fisheries dynamics**

22 Diverse model-based approaches have emerged as a response to the questions regarding marine
23 resource availability and management, as well as the biological and ecological characteristics of target
24 species, populations, and entire ecosystems that can change under a variety of pressures of an
25 anthropogenic or environmental origin. To that end, model-based approaches can be applied to

1 disentangle factors and processes driving fisheries and marine mammals towards biological
2 competition (Pierce et al. 2004, Plagányi 2007) as well as to explore potential functional and structural
3 changes of the ecosystem under marine mammal–fisheries biological competition (e.g. Morissette et
4 al. 2006). The development of models addressing marine mammal–fisheries interactions can be
5 elegantly presented: starting from a simple question of ‘who eats what?’ to ‘who eats how much of
6 what’ and finally, ‘who eats how much of what where’ (see Kaschner & Pauly 2005). While models
7 integrating marine mammal–fisheries interactions have been exhaustively addressed elsewhere (see
8 Harwood & McLaren 2004, Plagányi 2007, ICES WGMME 2015), here we focus our attention on
9 the widely used model-based approaches that contribute to an understanding of prey–predator
10 dynamics and marine mammal–fisheries biological competition. The models presented here account
11 for one- or two-way interactions, whilst encompassing the relevant trophic levels. We present these
12 models as follows: (1) extended single-species assessment models (ESAM); (2) multispecies,
13 minimum realistic models (MRM), such as Multi-species model for the Barents Sea (MULTSPEC)
14 and Globally applicable Area Disaggregated General Ecosystem Toolbox (GADGET); (3) Models of
15 Intermediate Complexity for Ecosystems assessments (MICE); (4) bioenergetics models, (5)
16 individual- or agent-based models (IBM or ABM) such as OSMOSE and INVITRO, and (6) dynamic
17 ecosystem or end-to-end models (e.g. Atlantis, Ecopath with Ecosim or EwE). Table 2 summarises
18 the main characteristics and suitability of these models with respect to marine mammal–fisheries
19 biological competition.

20 In general, the initial steps addressing marine mammal–fisheries interactions rely on ESAMs that
21 integrate predation simply as a component of natural mortality or describe it as an analogue to
22 pressure from fishing (see Plagányi 2007). In the initial applications of ESAM in European waters, a
23 simple combination of single- and multispecies models explored the potential interaction between
24 commercially important fishing stocks (i.e. cod, capelin [*Mallotus villosus*] and shrimp stocks) and
25 three species of baleen whales in Icelandic waters (Stefánsson et al. 1997). Similarly, the MULTSPEC

1 model used in studies of the Barents Sea, allowed for observation of the direct and indirect effects of
2 fisheries and marine mammals—that is, minke whale and harp seal (*Phoca groenlandica*), on three
3 commercial fish species: cod, capelin, and herring (Bogstad et al. 1997). Whilst the model’s
4 assumptions did not allow for the reliable quantification of the fish removal by the baleen whales, it
5 demonstrated that the marine mammals studied notably contribute to the natural mortality of fish and,
6 if ignored, the future fish catches might be underestimated.

7 Yet, such models should be used with caution, since merely including marine mammals in initial
8 fish stock assessment models does not adequately take into account differences in life history and
9 ecology of fish and marine mammals (Morissette et al. 2014). For instance, combining multi-species
10 functional response (MSFR) and the Bayesian approach can be used to quantify fish removal by
11 marine mammals, providing a better description of the predator’s choice of prey whilst accounting
12 for prey availability (see Smout et al. 2013).

13 MRM models, such as Scenario Barents Sea (SCENARIO), BOREal Migration and CONsumption
14 model (BORMICON), GADGET and Stochastic Multi-Species model’ (SMS) represent practical
15 tools for addressing trophic interactions between fish stocks and marine mammals due to their
16 minimal data requirements (Plagányi 2007, ICES WGMME 2015). In addition to the ESAM models,
17 MULTSPEC, SCENARIO, BORMICON, and SMS (see Schweder et al. 2000, Lewy & Vinther 2004,
18 Lindstrøm et al. 2009, ICES WGSAM 2017), GADGET was applied to explore fish–marine mammal
19 dynamics in the Norwegian and Barents seas (e.g. Howell & Bogstad 2010). Aside from the single-
20 species assessments of several European fish stocks (e.g. Cerviño et al. 2009, ICES WGBIE 2016),
21 GADGET was also used in multispecies contexts, such as the modelling of Icelandic minke
22 (Elvarsson 2013, Elvarsson et al. 2013) and fin whale (Elvarsson 2015) populations as well as to
23 address northeast Atlantic toothed whale populations, that, for the first time, consisted of common
24 and bottlenose dolphins (Saavedra et al. 2014, Saavedra 2017). Other study cases relying on MRM
25 models worth noting focussed on the Barents Sea, Antarctic waters and Celtic Sea (see Tjelmeland

1 & Lindstrøm 2005, Mori & Butterworth 2006, Houle et al. 2016). These studies provided better
2 insights into predation pressures experienced by juvenile and adult-stage fish, and the indirect effects
3 of their respective fisheries on predators as well as the concomitant community.

4 MICE models, similar to MRM models, were developed to adequately encompass the minimally
5 required complexity of ecological, environmental and anthropogenic components in order to provide
6 support to decision-making processes in fisheries and conservation management (reviewed in
7 Plagányi et al. 2014). Alongside ESAMs, MRM models as well as ecosystem and specific IBM (i.e.
8 INVITRO) models, the primary characteristics of MICE models render them suitable for management
9 strategy evaluation (MSE) approaches that include scientific recommendations and can verify the
10 success of proposed management actions (see Plagányi et al. 2014). Yet, in comparison to MRM,
11 MICE models enable more realistic and applicable recommendations for management given the
12 inclusion of lower trophic levels as well as non-target species (Plagányi et al. 2014, Punt et al. 2016).
13 One such example stems from the study addressing the Californian Current Ecosystem (CCE) where
14 the direct impact of fisheries was estimated for two target foraging fish species, one non-target species
15 and ‘other’ prey species. As such, an exploration of the indirect fisheries effect on the California sea
16 lion and brown pelican (*Pelecanus occidentalis*) demonstrated in the context of CCE a lack of
17 information on the prey-predator dynamics with regards to predator-specific demographic trends and
18 prey sensitivity to environmental factors (see Punt et al. 2016).

19 Researchers often use bioenergetic models to compensate for the lack of data on the energetic
20 requirements of wild marine mammals and enable estimates of species-specific energetic
21 requirements for both single- and multispecies interactions (Koen-Alonso & Yodzis 2004, 2005,
22 Plagányi 2007). For instance, energetic requirements and annual prey biomass were estimated for the
23 Atlantic bottlenose population (Bejarano et al. 2017) to determine the impact of marine mammals on
24 fisheries’ success (e.g. Read and Brownstein 2003), which also proved useful for conservation
25 purposes (e.g. Fortune et al. 2013). In the Gulf of Alaska, the magnitude of biological competition

1 between Steller sea lions and fisheries was assessed by comparing predators' annual energetic
2 requirements and fish availability under various fishing regimes (Cornick et al. 2006). Bioenergetics
3 models assist in quantifying predation pressure and are, in some cases, form an integral part of a
4 tailored approach aiming to project energetic requirements based on fish and marine mammal species
5 as well as the concomitant fisheries (e.g. Bjørge et al. 2002, Forcada et al. 2009). Inferring daily
6 energetic requirements, the caloric value of prey and the abundance of killer whales that prey upon
7 sea otters and Steller sea lions indicates that these predators do not have a sufficiently strong prey
8 removal to induce significant declines in the abundance of sea otters' and sea lions' (see Williams et
9 al. 2004).

10 The multispecies model INVITRO allows for the evaluation of management strategies and their
11 effects on ecosystem dynamics (Plagányi 2007). INVITRO and other IBMs rely on true individuals,
12 whilst ABMs apply 'individuals' representing conceptual units, that is, fishing fleets, schools or
13 various subsets of a population (Plagányi 2007, ICES WGMME 2015). By contrast, OSMOSE
14 ('Object-oriented Simulator of Marine ecOSystem Exploitation') is an ABM and MSE model (ICES
15 WGMME 2015). Whilst OSMOSE is a biomass model and shares similarities with specific ecosystem
16 models (e.g. Ecopath), in contrast to INVITRO, it limits the inclusion of the top trophic levels (see
17 Plagányi 2007). Furthermore, whilst suitable for MSE, OSMOSE and INVITRO remain more
18 sensitive and responsive to the level of specific functional groups exposed to fishing or other pressures
19 than on the ecosystem level. This is specifically corroborated when compared to, for instance Atlantis
20 or EwE (see Travers et al. 2010, Forrest et al. 2015). Other examples of recent studies using IBM
21 include models developed to address specific case studies, such as the ecophysiological IBM
22 simulating energy intake and expenditure amongst individual female Weddell seals (*Leptonychotes*
23 *weddellii*; see Beltran et al. 2017). Combining bioenergetics model with species-specific prey
24 selectivity and behavioural traits as well as female seal life histories, this IBM allows for a more in-

1 depth understanding of the individual contribution to the energetic budget and population
2 requirements.

3 From end-to-end models, researchers agree that Atlantis and EwE currently represent the best
4 approaches to addressing complete trophic webs of exploited ecosystems and marine mammal–
5 fisheries biological competition (Plagányi 2007, ICES WGMME 2015, Villasante et al. 2016). As
6 encompassing as they are, ecosystem models in general represent computationally intensive and data-
7 demanding models in comparison to ESAM and MRM, although attempts to minimise these trade-
8 offs exists (see Prato et al. 2014 for EwE). Furthermore, complex ecosystem models can potentially
9 underestimate key functional groups (e.g. top trophic levels) due to limited or unreliable data,
10 rendering their application for management purposes quite difficult (Morissette et al. 2014,
11 Goedegebuure et al. 2017). Atlantis, for instance, is a spatially explicit model encompassing a wide
12 range of components in a marine ecosystem, from biophysical and operational, fisheries-related
13 components to socio-economic characteristics (Plagányi 2007, ICES WGMME 2015). Atlantis has
14 been used extensively in the northwest Atlantic to test for the effects of pinniped predation and
15 fisheries on demersal fish stocks (Link et al. 2011). Similarly, Atlantis was applied in other regions
16 of the world to explore topics such as the benefits of compliance to different fishing regulations in
17 the Northern Gulf of California ecosystem and fisheries (Ainsworth et al. 2012), to identify key
18 indicators for ecosystem-based management of the southern Benguela ecosystem (Smith et al. 2015)
19 as well as to verify potential fishery losses under specific conservation measures needed for the
20 survival of the critically endangered vaquita (*Phocoena sinus*; Morzaria-Luna et al. 2012).

21 EwE, a dynamic ecosystem model, shares structural similarities with Atlantis and typically
22 contains two components—the Ecosim and Ecopath—or, occasionally, three components when
23 Ecospace, its spatial component, is included (Plagányi 2007). Furthermore, Ecopath and Ecosim
24 (Ecopath’s mass-dynamic simulation routine) have been used independently or jointly for a wide
25 range of interactions concerning marine mammals, fish, and fisheries within a specific ecological,

1 managerial, and socio political contexts (Pauly et al. 2000, ICES WGMME 2015). In the last 30 years,
2 EwE have been applied to more than 500 ecosystems (Villasante et al. 2016) and used to address a
3 variety of topics such as: resource overlap and interaction between marine mammals and fisheries
4 (e.g. Blanchard et al. 2002, Mackinson et al. 2003, Morissette et al. 2010a, b, 2012), understanding
5 structural and functional properties of food webs in large ecosystems for better ecosystem-based
6 management (e.g. Cornejo-Donoso & Antezana 2008, Torres et al. 2013, Piroddi et al. 2015, Sagarese
7 et al. 2017) as well as for specific cases to determine the fisheries' effect on top predators whilst
8 testing an ecosystem's ability to sustain various fisheries simultaneously (e.g. Goldsworthy et al.
9 2013). Alternatively, EwE (or its individual component) has been used for various 'custom-made
10 models' for the purpose of, for instance, identifying key functional groups in highly harvested
11 ecosystems (e.g. Coll et al. 2006, 2007); developing a regional end-to-end model exploring the impact
12 of issues such as predation on the Steller sea lions by killer whales, fish availability, and fisheries on
13 the Alaskan ecosystem functioning (see Guénette et al. 2006, Ruzicka et al. 2013); or quantifying
14 marine mammal–fisheries biological competition (including operational interactions) for a more
15 realistic estimation of fisheries' impact on the ecosystem, in particular, on top predators (see Lassalle
16 et al. 2012). The EwE specifically assists in revealing the importance of the combined impact of
17 fisheries, predation by grey seals and eutrophication on shifting regimes observed in the Baltic Sea
18 (see Hansson et al. 2007, Österblom et al. 2007). More precisely, the model revealed a strong top-
19 down control of grey seals on cod as well as cod on sprat (Harvey et al. 2003), whilst the release of
20 predation on cod led to an increase in the abundance of cod as well as a subsequent decrease in cod
21 numbers due to severe fishing intensity and climate change (Österblom et al. 2007).

22

23 **4. MARINE MAMMAL–FISHERIES BIOLOGICAL COMPETITION IN HARVESTED** 24 **ECOSYSTEMS**

25

1 **4.1. Why we need to consider FIMA and trophic interactions in EBFM?**

2 Traditional approaches to fisheries management, such as the precautionary approach or maximum
3 sustainable yield (MSY), promote the minimisation of natural and fishing mortality through the
4 regulation of fishing quotas, effort, and gear (Pauly et al. 2002). However, these actions appear
5 inadequate, as they propose short-term management actions whilst underestimating the role of
6 ecosystem processes and their integrity in the provision of resources (Lassen et al. 2014). By contrast,
7 EBFM advocates for the importance of balanced exploitation as a means to maintain biodiversity at
8 all levels as well as preserving the balance throughout the food web and ensuring high fishery yields
9 in the future (Leslie & McLeod 2007, Zhou et al. 2010, Garcia et al. 2012). Existing cases of EBFM
10 implementation serve to strengthen its primary principles in preserving marine food web interactions,
11 accounting for the incidental impact of fisheries on the ecosystem (particularly those related to non-
12 target species) as well as considering the socio-economic context of the human demand for fish (see
13 Ruckelshaus et al. 2008). Recognising the observed FIMA in individual fish and the potential adverse
14 effects it could have on prey–predator interactions, EBFM should account for eco-evolutionary
15 processes and their persistent negative consequences (see Jørgensen et al. 2007, Laugen et al. 2014)
16 in order to accomplish a truly holistic approach to natural resource management. By definition, the
17 holistic fisheries management should acknowledge all structural levels and processes in an
18 ‘ecosystem’ and an ‘evosystem’ with respect to their independent and coupled effects (see Fowler et
19 al. 2013).

20 Eco-evolutionary feedbacks in dynamic trophic interactions can pervasively effect all structural
21 levels (Kuparinen et al. 2016); thus, identifying its implications within the context of EBFM remains
22 critical for the overall structural stability and ecosystem phenology (see Lankau & Strauss 2011,
23 Johansson et al. 2015, Kuparinen et al. 2016). Moreover, from the individual to the population level,
24 the cascading effect of FIMA can ultimately render certain management measures inefficient since it
25 affects the population reference points (see Heino et al. 2013). Whilst several mechanisms of eco-

1 evolutionary processes are recognised (reviewed in Bolnick et al. 2011), the size-selective removal
2 of fish reportedly represents a prevailing pressure driving phenotypic and behavioural trait changes
3 in fish, the latter being more experimentally documented (e.g. Uusi-Heikkilä et al. 2008, Heino et al.
4 2015). In comparison to the size selectivity of fishing gear, the size selectivity of prey in marine
5 mammal diets has developed through evolutionary time; however, it is also transferrable from mother
6 to calf or pup in most marine mammal species (Etnier & Fowler 2010, Estes et al. 2003). Fishing
7 selectivity and intensity can induce different responses, such as in direction of change in individual
8 traits depending upon whether the fishing pressure is directly applied on growth or maturation, or
9 indirectly, through the selectivity of one trait whilst affecting its associated traits (see Heino et al.
10 2015). Marine mammals, by contrast, demonstrate a general consistency in prey size selectivity across
11 numerous study cases targeting fish species of less than 30 cm in body size (see Etnier & Fowler
12 2010). Despite this, biases may still affect the prey selectivity in the marine mammal diet, such as
13 through prey availability as well as intra- and interspecific competition. For instance, when compared
14 to the size selectivity of commercial fisheries within the similar spatial, temporal and resource
15 contexts, marine mammals appeared to intentionally target smaller-sized fish (Etnier & Fowler 2010).
16 Elucidating those factors driving marine mammals to target certain prey sizes over others as well as
17 detecting the window of opportunity in terms of prey size for both marine mammals and fisheries
18 poses significant challenges in distinguishing their impact upon potential individual trait changes in
19 fish.

20 Careful investigation of empirical case studies addressing marine mammal–fisheries biological
21 competition on a lower spatial scale could provide an insight into how the species' life histories of
22 predator and prey affect their responses to fishing pressure as well as the direction and magnitude of
23 eco-evolutionary feedback on an individual level. Alternatively, modelling the coupled effects of
24 fishing and predation, whilst observing life-history and behavioural traits as well as how these
25 contribute to natural mortality, can predict different trends in individual fish traits. Some recorded

1 trends are: increases in natural mortality accompanying decreases in fish body size, increased growth
2 rates (due to additional risks related to foraging and energy allocations) and increased investments in
3 reproduction (precisely, as a consequence of increased exposure to predation due in reproduction-
4 related behavioural or morphological traits; Jørgensen et al. 2010). At the population level, the effects
5 of predation and fishing may entail greater consequences for fish biomass, recruitment, stock recovery
6 and, ultimately, their management (see Jørgensen et al. 2007, Hutchings 2009). Although some
7 researchers argue that the theoretically estimated rate of evolution in fish is slow (see Andersen &
8 Brander 2009) and the strength of phenotypic plasticity in some fish species can dampen the
9 evolutionary changes in individual traits (see Hidalgo et al. 2014): others highlight the cumulative
10 effect of size-selective fishing that can impair the recovery of population size to its pre-exploited level
11 or completely prevent it (see Kuparinen & Hutchings 2014, Hutchings 2015, Swain & Benoit 2015).

12 In the increasingly harvested ecosystems the biological competition among marine mammals and
13 fisheries inevitably impacts the connectivity and structure of marine trophic interactions (see Estes et
14 al. 2016). Thus, any disturbance or weakening observed in prey–predator interactions acts as an
15 indication of structural disruptions in an ecosystem caused by fisheries (Pauly et al. 2002). In fact, a
16 body of research has explored the implications of trophic interactions on fisheries’ sustainability
17 (Worm et al. 2009). Studies applying IBM, ABM and ecosystem models have significantly
18 contributed to understanding the prey–predator dynamics, a change in the diet of marine mammals,
19 and how these reflect on the stability of the food web. The intensity of the biological competition
20 depends upon prey availability and distribution as well as the accessibility of prey to the competitors.
21 Furthermore, prey accessibility will vary in dependence to the scope of resource overlap between
22 competitors, environmental conditions and the effect of non-target species in trophic interactions
23 (Bogstad et al. 2015). Additionally, we should consider other relevant ecological processes on EBFM
24 including intra- and interspecific competition for prey among different species of marine mammals.
25 As examples, we can take the case of grey and harbour seal trophic overlap in the North Sea (ICES

1 WGMME 2015), as well as the potential of resource competition between marine mammals, fisheries,
2 and other marine megafauna, such as sharks, marine birds, as well as predatory fish (e.g. Huss et al.
3 2014). For instance, the resource competition between cod, harp seals and minke whales in the
4 Barents Sea was explored given the availability of shared prey and historic environmental conditions
5 in an attempt to reveal possible mechanisms of the competition (Bogstad et al. 2015). Here, the
6 developmental stage of fish (i.e. juvenile and adult fish) was carefully considered, identifying
7 different susceptibilities and vulnerabilities to specific pressures. More importantly, this highlights
8 the importance of accounting for the different trophic positions occupied by the same individual
9 throughout its development.

10 Ultimately, understanding the importance and implications of trophic interactions to achieving
11 sustainable fishing and ecosystem functioning not only facilitates achieving the EBFM objectives,
12 but also in recovering the current state of any prey and predator populations (e.g. Chadés et al. 2012).

13

14 **4.2. Benefits of preserving prey–predator dynamics in reaching the EBFM objectives**

15 The need to manage the negative impact of fishing on the individuals and the ecosystems, balanced
16 harvesting that assigns fishing rates proportional to species productivity represents an effective
17 approach to achieving the EBFM objectives (Law et al. 2012). With respect to prey–predator
18 dynamics, preserving ecosystem resilience and functioning becomes feasible through balanced
19 removal of prey and predator (see Tromeur & Loeuille 2017). Yet, implementing balanced harvesting
20 remains challenging due to the increased fishing pressure on juvenile fish (Burgess et al. 2016) as
21 well as the difficulty associated with measuring the population or individual productivity of the target
22 species (Jacobsen et al. 2014). For instance, higher productivity at the lower trophic levels implies
23 more sustainable fishing at these levels than removing species with a lower productivity at a higher
24 trophic level (e.g. Law et al. 2012). Predator removal through culling programmes stands as an
25 effective means of reducing predator abundance; nonetheless, such programmes offer a short-term

1 solution not always resulting in an increase in the target species population (see Morissette et al. 2012,
2 Houle et al. 2013), since its effects are difficult to project and measure (Bowen & Lidgard 2013).
3 Thus, the scientific community recommends precautionary approach to managing marine mammals
4 such as the top predators (which also includes moderate harvesting) to avoid adverse effects on the
5 fish and economic losses for fisheries due to sudden and unregulated predator population increase
6 (see Augé et al. 2012). This occurred in many pinniped populations which following historical
7 declines thrived under protection programmes, in some cases, leading to increased biological
8 competition with fisheries and commercial fish stock declines (Augé et al. 2012, Marshall et al. 2016).

9 In addition to marine mammal removal, which can potentially disrupt the finely tuned trophic
10 connectivity throughout the ecosystem, fewer unexpected outcomes might result from ensuring the
11 survival and viability of marine mammal populations (Augé et al. 2012, Garcia et al. 2012,
12 Papastavrou et al. 2017). This requires an adequate ‘package’ of mutually complimentary and
13 synchronised conservation and management measures that could ensure the preservation of the
14 trophic web and long-term, sustainable harvesting. Amongst various actions targeting different
15 species or habitats of interest, for instance establishing of marine protected areas (MPAs) and holistic
16 monitoring and managing fish stocks through the appropriate involvement of relevant stakeholders
17 represent a step towards EBFM (Leslie & McLeod 2007, Augé et al. 2012).

18 In general, MPAs focus on protection of vital breeding and feeding areas, although these are
19 species-specific and can vary depending upon spatial and temporal scales (see Pompa et al. 2011,
20 Scales et al. 2014). While new empirical evidence on the successful application of MPAs in favour
21 of marine mammal protection continues to emerge, such as findings from the Banks Peninsula Marine
22 Mammal Sanctuary in New Zealand (see Gormley et al. 2012) maintaining a balance between
23 exploitation and conservation objectives calls for the long-term monitoring and continuous re-
24 evaluation of the efficiency of applied management actions (Marshall et al. 2016). This also entails
25 inclusion of protective measures for fish stock that, not only consider natural predators (see Fanshawe

1 et al. 2003 for sea otters), but also examine potential FIMA or predation effects or both. In the specific
2 case of angling of largemouth bass (*Micropterus salmoides*), MPAs appear useful for preventing the
3 loss of phenotypic diversity through the promotion of aggressive behavioural traits and thus, ensuring
4 survival of bass through more cautious and aggressive protection of nests (see Twardek et al. 2017).
5 This, however, might not apply to ongoing evolutionary change (see Dunlop et al. 2009 for the
6 potential effects of MPAs for fisheries-induced evolution). In cetaceans, for instance, social and
7 behavioural traits demonstrate baleen whale characteristics—that is, being shy and elusive—
8 benefited their recent recovery, whilst the rather opportunistic feeding behaviour of toothed whales
9 exposes them to incidental catches by fishing gear, rendering their recovery difficult (see Wade et al.
10 2012). Because cetaceans exhibit complex social behaviour within their population, focal group or as
11 individuals, conservation measures must account for their social as well as physical well-being since
12 they directly affect the survival and viability of a species, thereby increasing the effectiveness of
13 conservation efforts (Wade et al 2012, Marshall et al. 2016).

14 Ensuring sustainable fishing regimes and preserving marine environments are crucial EBFM
15 objectives that require supporting protective acts and legislation, established through collaboration
16 between scientists and relevant stakeholders (e.g. Gleason et al. 2010). Local stakeholders, such as
17 artisanal fishermen with their small communities are tightly connected to fishing activities and
18 possess a rich ethno-ecological knowledge of local megafauna providing additional knowledge of
19 historic shifts in abundance, distribution, and behavioural patterns of the relevant megafaunal species
20 (see Costa et al. 2012, Zappes et al. 2014). Such interdisciplinary approaches help ensure more
21 effective conservation measures, but also directly involve the most affected stakeholders, such as
22 fishermen and their communities, in decision-making processes that ultimately affect their own
23 livelihood. Additionally, successful coexistence and collaboration amongst fishermen and marine
24 mammals exist to the benefit of both, as is the case of the cooperative fishery between artisanal

1 fishermen and the resident bottlenose dolphin population in southern Brazil (e.g. Daura-Jorge et al.
2 2012).

3

4 **5. CONCLUSIONS AND FUTURE RESEARCH**

5

6 Focussing on two specific areas, the synthesis of knowledge on marine mammal–fisheries biological
7 competition presented here is purposefully narrowed-down and biased towards its focus and
8 approach. However, while the literature gathered here is not the most exhaustive of relevant scientific
9 research, we have strived to present the most representative examples of studies and their
10 methodologies complimenting the two areas of focus.

11 Given the long history of human conflicts with marine mammals for commercially viable fish
12 species, the research synthesised here demonstrates the continuous effort to explore the direct and
13 indirect effects of biological competition. To this end, the notable proliferation of methodology,
14 particularly model-based approaches, provided insights for data-limited ecosystems and species,
15 investigating the availability of fish for fisheries and marine mammals with respect to the ecosystem
16 characteristics, management objectives and regulations as well as the aims of national or international
17 policies and strategies. Nonetheless, difficulties obtaining information about marine mammals’
18 choices and the selectivity of prey and, consequently, their adequate representation in currently used
19 assessment models, calls for further improvements to model-based approaches.

20 Overexploitation, climate change, eutrophication and mismanagement represent some of the main
21 contemporary threats to the global marine environment. Many natural scientists agree that overfishing
22 currently stands as the greatest threat to the sustainability of contemporary marine ecosystems (see
23 Boonstra et al. 2015). Yet, because climate change directly affects the distribution of species through
24 changes to favourable environmental conditions, the effects of warming need to be directly addressed
25 in the hope of counteracting any damaging effects. A rising number of studies have already

1 demonstrated the potential losses caused by the changing climate *vis-à-vis* the availability of fish for
2 fisheries, prey and predator demography and their health status as well as the overall feedback on the
3 ecosystem functioning (e.g. Harvell et al. 1999, Tegner & Dayton 2000, Schumacher et al. 2005,
4 Kovacs et al. 2011, Nye et al. 2013, Konishi et al. 2014).

5 Given these ongoing threats, advancing towards a holistic EBFM whilst reducing uncertainties
6 regarding FIMA and fisheries' incidental impacts on all structural levels, represents an ambitious but
7 necessary step in managing the biggest threat to marine ecosystems for the preservation of their
8 functioning and services. Latent risks, such as FIMA and eco-evolutionary feedbacks induced by
9 fishing or other coupled pressures, need to be thoroughly accounted for in the long-term forecasting
10 of fish availability. In addition, a specific monitoring strategy could potentially detect changes to
11 individual traits. Alternatively, the protection of key species at the top trophic levels is increasingly
12 supported by relevant stakeholders in the fishing industry. Such supporters increasingly recognise the
13 importance of these species for the long-term sustainability of fishing yields and the stability of the
14 food web that sustains it. To this end, researchers need to provide recommendations and guidelines
15 with a demonstrated feasibility, which primarily includes technical, logistical, and economic
16 feasibility. Moreover, to strengthen the role and credibility of researchers when providing advice, the
17 adoption of the precautionary approach should be warranted since pushing it too far may also lead to
18 mismanagement (see Schweder 2001).

19 Diminishing fish availability, however, is not the only threat human activities have brought upon
20 marine mammal existence (see Moore 2014). Thus, marine mammal conservation measures should
21 be 'tailored' according to the species-specific life history, site fidelity, and foraging habitats as well
22 as individual phenotypic or behavioural traits based on the selectivity of the threat in question (e.g.
23 bycatch and collisions with ships). Yet, understanding the often entangled processes of marine trophic
24 interactions, selective harvesting and especially latent evolutionary changes, in particular, under a
25 growing number of other threats, emphasises the significance of future applied research in ecosystem-

1 based management and conservation. Moreover, whilst the ecological impact of fishing on marine
2 environments can be easily recognised by the general public and relevant stakeholders, preliminary
3 social inquiries illustrate how the evolutionary impact of fishing on fish availability is much more
4 difficult to communicate (see Diaz Pauli & Heino 2013). Given the importance of a holistic approach
5 to EBFM implementation, facilitated by adopting strategic frameworks and legislation as well as
6 encouraging participatory stakeholder involvement, an obvious need exists for further
7 interdisciplinary studies. That is, future interdisciplinary studies should provide a way to effectively
8 address the lack of knowledge and adequate methods to balance human demands for fish whilst
9 simultaneously addressing the obvious necessity of protecting marine resources and their
10 environment.

11

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4 **Tables with legends**

5 **Table 1.** Examples of studies and methods used for investigating marine mammal diet as well as fisheries – marine mammal resource overlap and
 6 potential for biological competition according to marine mammal taxonomic groups (Quantitative Fatty Acid Signature Analysis or QFASA).

<i>Marine mammal group</i>	<i>Applied methods</i>							<i>Examples of study cases (study/sampling area)</i>
	<i>Field observation methodology</i>	<i>Stomach content analysis</i>	<i>^{14/15}N analysis</i>	<i>^{12/13}C analysis</i>	<i>Fatty acid analysis</i>	<i>Faecal analysis</i>	<i>Other methods</i>	
Sea otters	+	-	-	-	-	+	Tagging, aging	Watt et al. 2000 (Alaska, USA, S Bering Sea)
	+	-	-	-	-	-	Tagging, capture-recapture	Estes et al. 2003 (California, USA, NE Pacific)
	-	-	-	-	-	+	-	Kornev & Korneva, 2006 (Kamchatka, Russia, NW Pacific)
	+	-	-	-	-	-	-	Laidre & Jameson 2006 (Washington, USA, NW Atlantic)
	+	-	-	-	-	-	Biologging	Tinker et al. 2007a (California, USA, NE Pacific)
	+	-	-	-	-	-	Tagging	Tinker et al. 2007b (California, USA, NE Pacific)
	+	-	-	-	-	-	Photo ID	Lee et al. 2009 (Alaska, USA, N Pacific)
	-	-	+	+	-	-	-	Newsome et al. 2009, 2010 (California, USA, NE Pacific)
	-	-	+	+	-	-	Bayesian mixed model	Newsome et al. 2012 (California, USA, NE Pacific)
	+	-	-	-	-	-	-	Larson et al. 2013 (SE Alaska, USA, N Pacific)

<i>Marine mammal</i>	<i>Applied methods</i>							<i>Examples of study cases</i> (<i>study/sampling area</i>)
	<i>group</i>	<i>Field observation methodology</i>	<i>Stomach content analysis</i>	<i>^{14/15}N analysis</i>	<i>^{12/13}C analysis</i>	<i>Fatty acid analysis</i>	<i>Faecal analysis</i>	
Sea otters	-	-	+	+	-	-	-	Tyrell et al. 2013 (in captivity, USA)
	-	-	+	+	-	-	-	Elliot Smith et al. 2015 (California, USA, NE Pacific)
Pinnipeds	-	-	-	-	+	-	-	Laake et al. 2002 (Columbia River, NE Pacific)
	-	-	-	-	-	+	-	Sinclair & Zeppelin 2002 (Bering Sea, N Pacific)
	-	-	-	-	+	-	Attached cameras	Iverson et al. 2004 (in captivity, Canada)
	-	-	-	-	+	-	-	Beck et al. 2007 (E Canada, NW Atlantic)
	-	+	-	-	-	-	-	Lundström et al. 2007, 2010 (Sweden, N and Central Baltic Sea)
	-	+	-	-	-	+	Bayesian approach	Sinclair et al. 2008 (Central Bering Sea, N Pacific)
	-	-	-	-	-	+	DNA barcoding	Deagle et al. 2009 (SE Australia, SW Pacific)
	-	-	-	-	-	+	-	Huisamen et al. 2012 (SW Africa, SE Atlantic)
	-	-	+	+	+	-	GPS telemetry	Waite et al. 2012 (E Russia, NE Pacific)
	-	-	-	-	-	-	DNA barcoding	Deagle et al. 2013 (in captivity, USA)
+	-	-	-	+	-	-	Meynier et al. 2014 (New Zealand, NW Pacific)	
-	-	-	-	-	-	-	DNA barcoding	Hui et al. 2017 (SE Japan, NW Pacific)

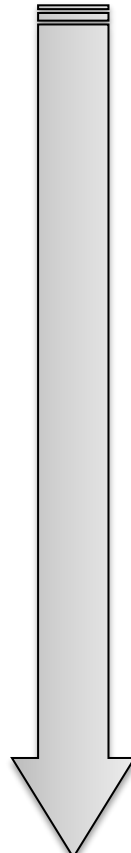
<i>Marine mammal group</i>	<i>Applied methods</i>							<i>Examples of study cases (study/sampling area)</i>
	<i>Field observation methodology</i>	<i>Stomach content analysis</i>	<i>^{14/15}N analysis</i>	<i>^{12/13}C analysis</i>	<i>Fatty acid analysis</i>	<i>Faecal analysis</i>	<i>Other methods</i>	
Pinnipeds	-	-	+	+	-	-	-	Sepúlveda et al. 2017 (S Chile, SE Pacific)
Pinnipeds	-	+	-	-	-	-	DNA barcoding	Méheust et al. 2014 (NW France, NE Atlantic)
+ toothed whales	-	+	+	+	-	-	-	Franco-Trecu et al. 2017 (Uruguay estuary, SW Atlantic)
Toothed whales	-	-	+	+	-	-	Heavy metal measurements	Das et al. 2000 (SW France, NE Atlantic)
	-	+	-	-	-	-	-	de Oliveira Santos et al. 2002 (SE Brasil, SW Atlantic)
	-	-	-	-	-	-	Analysis of morphological data, lactation; feeding observations	Kastelein et al. 2002 (in captivity, UK)
	-	+	-	-	-	-	-	Barros et al. 2004 (Hong Kong, S China Sea)
	-	+	-	-	-	-	-	Spitz et al. 2006 (NW Spain, NE Atlantic)
	-	+	-	-	-	-	-	Fernández et al. 2009 (Canary Islands, NE Atlantic)
	+	+	-	-	-	-	-	Bearzi et al. 2010 (W Greece, E Mediterranean)
	-	-	+	+	-	-	Genetic analysis	Fernández et al. 2011 (NW Spain, NE Atlantic)
	+	+	+	-	-	-	-	Meissner et al. 2012 (E France, NW Mediterranean)

<i>Marine mammal group</i>	<i>Applied methods</i>							<i>Examples of study cases (study/sampling area)</i>
	<i>Field observation methodology</i>	<i>Stomach content analysis</i>	<i>^{14/15}N analysis</i>	<i>^{12/13}C analysis</i>	<i>Fatty acid analysis</i>	<i>Faecal analysis</i>	<i>Other methods</i>	
Toothed whales	-	-	+	+	-	-	-	Mèndez-Fernandez et al. 2012 (NW Spain, NE Atlantic)
	-	+	-	-	-	-	-	Gladilina and Gol'din 2014 (S Ukraine, Black Sea)
	-	+	-	-	-	-	-	Dede et al. 2015 (W Turkey, E Mediterranean)
	-	+	-	-	-	-	-	Hernandez-Milian et al. 2015 (Ireland, NE Atlantic)
	+	+	-	-	-	-	Monte Carlo resampling	Spitz et al. 2017 (W France, NE Atlantic)
Baleen whales	-	-	-	-	-	-	DNA barcoding	Jarman et al. 2002 (S Australia, SE Indian Ocean)
	-	+	-	-	-	-	-	Konishi et al. 2014 (Ross Sea, E Antarctica)

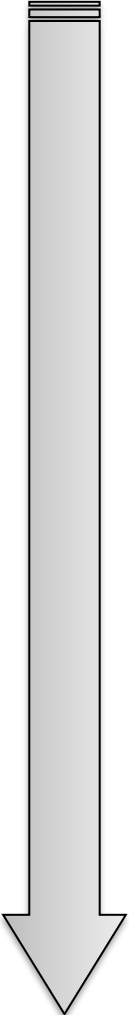
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10 Table 2. Summary of the main models addressing direct and indirect marine mammal–fisheries biological competition in harvested ecosystems,
 11 in the order of increasing complexity and number of trophic interactions (direction depicted by the grey arrow). Models differ based on the
 12 primary characteristics, type of prey-predator interactions, ‘efficient’ vs ‘hungry’ predator (according to Plagányi 2007) and support to decision-
 13 makers to achieve the EBFM objectives. An ‘efficient’ predator forages and feeds until satiated while a ‘hungry’ predator continually feeds.

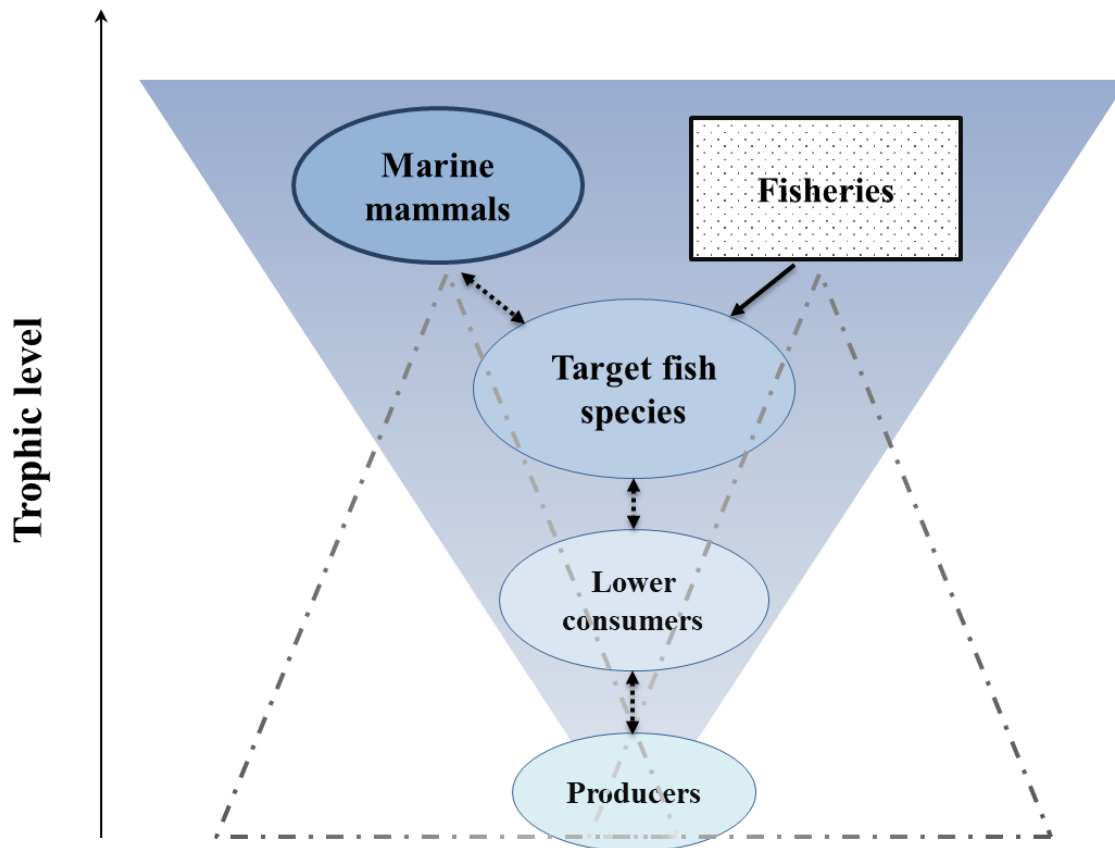


<i>Model category (abbreviation/acronym)</i>	<i>Primary model characteristics and application</i>	<i>Prey–predator interactions and predator function</i>	<i>Supporting EBFM objectives</i>
Extended Single-species Assessment Models (ESAM)	<ul style="list-style-type: none"> - extended fisheries assessment models - minimal biological processes included 	<ul style="list-style-type: none"> - one-way interaction where predators affect fish - ‘efficient’ predator - predation included as an outside driver similar to a ‘fishing fleet’ 	<ul style="list-style-type: none"> - predation quantification depends on model assumptions - yields preliminary understanding of fisheries–marine mammals dynamics
Multispecies Minimum Realistic Models (MRM)	<ul style="list-style-type: none"> - mainly an extension of MSVPA age-length structured, addressing multiple fleets and fishing areas context and system oriented - minimal inclusion of population dynamics as well as operating on minimum data input 	<ul style="list-style-type: none"> - one – or two-way interaction - apply various functional responses based on available information on predator abundance, diet composition and consumption estimates - primarily an ‘efficient’ predator, although GADGET has both - prey and predators densities can be limited by their carrying capacities 	<ul style="list-style-type: none"> - addresses direct and indirect effects of fisheries on fish and predators - used more for theory testing and less for fisheries management (except for GADGET)
Models of Intermediate Complexity for Ecosystems assessments (MICE)	<ul style="list-style-type: none"> - from single-species to ecosystem models - similar to MRM, ecosystem and context specific - can include a minimum of ecological, environmental, management, and socio-economic components 	<ul style="list-style-type: none"> - two-way interaction - ‘efficient’ predator - predator linked, for instance, on prey survival or reproductive success - various functional responses used depending upon available data on predator diet composition and prey preference - prey and predators densities can be limited by their carrying capacities 	<ul style="list-style-type: none"> - aids testing scenarios of different biological, environmental, managerial, and socio-economic parameters - provides a tool to form strategic and tactical managerial actions - first-level modelling that considers stakeholders’ opinion



<i>Model category (abbreviation/acronym)</i>	<i>Primary model characteristics and application</i>	<i>Prey–predator interactions and predator function</i>	<i>Supporting EBFM objectives</i>
Bioenergetic models	<ul style="list-style-type: none"> - includes from 1–7 species - based on the species-specific energetic or allometric trophodynamics of the individual species - at a minimum, basic biological and diet consumption data are needed while other energetic parameters can be estimated 	<ul style="list-style-type: none"> - accounts for individual variability in prey-predator dynamics - convenient when only biomass data on prey/predator are available - ‘efficient’ and ‘hungry’ predator 	<ul style="list-style-type: none"> - provides estimates for the energetic requirements as well as quantifying predation with regards to the prey and predator energy uptakes - considers the ecosystem’s energy budgets and flow - generate projections of the fish availability to fisheries and predators
Agent-Based Models or Individual-Based Models (ABM or IBM)	<ul style="list-style-type: none"> - from a multispecies to ecosystem model - following the individual’s growth, reproduction and survival - an individual has a critical effect on the system dynamics - some are more suitable for fish predators (e.g. OSMOSE) from single-species to whole ecosystem models 	<ul style="list-style-type: none"> - accounts for individual variability in prey-predator dynamics - in OSMOSE, predation is typically a function of prey size and the spatial co-occurrence of predator and prey - ‘hungry’ predator 	<ul style="list-style-type: none"> - as ecosystem models, provides insight into the direct and indirect effects of the biological competition - allows for considering a combination of anthropogenic pressures to facilitate decision-making
Ecosystem or end-to-end models	<ul style="list-style-type: none"> - dynamic, aggregate state and/or spatial models - accounting for the entire marine trophic web and geochemical processes - includes size and/or age structures - computationally and data demanding models 	<ul style="list-style-type: none"> - apply various functional responses describing the predators’ response to prey population trends (e.g. ‘foraging arena’ in Ecosim), but also prey vulnerability to predator and refuge - primarily ‘efficient’ predator 	<ul style="list-style-type: none"> - most successful in accounting for non-target species - as ABM, provides insight into the impact of the biological competition on the ecosystem level within a socio-economic context - considers a variety of anthropogenic pressures

17 **Figures with legends**



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19

20 **Figure 1.** Trophic levels in marine ecosystems increasing from producers to top predators and
 21 fisheries, adapted from Trites et al. 1997, 2006. The transient blue triangle encompasses the extent of
 22 direct competition between fisheries and marine mammals. The dotted-line grey triangles describe
 23 the indirect or ‘food-web competition’ with a clear lack of resource overlap between the two top
 24 competitors. The two-way dotted arrows denote the direction of trophic interactions between the main
 25 trophic groups, while the one-way arrow describes the direction of fisheries’ impact on the target fish
 26 species.