

**This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.**

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

**Title:** Competition between marine mammals and fisheries in contemporary harvested marine ecosystems

**Year:** 2019

**Version:** Accepted version (Final draft)

**Copyright:** © 2019 Inter-Research.

**Rights:** In Copyright

**Rights url:** <http://rightsstatements.org/page/InC/1.0/?language=en>

**Please cite the original version:**

Jusufovski, D., Saavedra, C., & Kuparinen, A. (2019). Competition between marine mammals and fisheries in contemporary harvested marine ecosystems. *Marine Ecology Progress Series*, 627, 207-232. <https://doi.org/10.3354/meps13068>

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

2

3

4 Dunja Jusufovski<sup>1\*</sup>, Camilo Saavedra<sup>2</sup> and Anna Kuparinen<sup>3</sup>

5

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

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

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

12 \*Corresponding author: [dunja.jusufovski@helsinki.fi](mailto:dunja.jusufovski@helsinki.fi)

13

14

15

16

17

18

19

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

21

22

23

24

1 **ABSTRACT**

2

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 ‘ecosystem’ 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

## 12 **Acknowledgements**

13 This review was financially supported by the University of Helsinki, Finland (DJ), the Spanish  
14 Institute of Oceanography (BOE-A-2011-2541; CS), the Academy of Finland (AK), the Natural  
15 Sciences and Engineering Research Council of Canada (AK) and European Research Council  
16 (COMPLEX-FISH 400820; AK). The authors wish to thank their colleagues at University of Helsinki  
17 for their comments and advice given regarding the review structure. We also appreciate the  
18 contributions of and comments from two anonymous reviewers, and thank them for their constructive  
19 and insightful feedback.

20

21

22

23

24

1 **Literature Cited**

2

3 Ainsworth CH, Morzaria-Luna HN, Kaplan IC, Levin PS, Fulton EA (2012) Full compliance with  
4 harvest regulations yields ecological benefits: Northern Gulf of California case study. *J Appl Ecol*  
5 49:63–72

6 Alves LCPdS, Zappes CA, Andriolo A (2012) Conflicts between river dolphins (Cetacea: Odontoceti)  
7 and fisheries in the Central Amazon: a path toward tragedy? *Zoologia (Curitiba)* 29:420–429

8 Andersen KH, Brander K (2009) Expected rate of fisheries-induced evolution is slow. *Proc Natl Acad*  
9 *Sci USA* 106:11657–11660

10 Anderson CNK, Hsieh C-H, Sandin SA, Hewitt R and others (2008) Why fishing magnifies  
11 fluctuations in fish abundance. *Nature* 452:835

12 Augé AA, Moore AB, Chilvers BL (2012) Predicting interactions between recolonising marine  
13 mammals and fisheries: defining precautionary management. *Fisheries Manag Ecol* 19:426–433

14 Bailey H, Hammond PS, Thompson PM (2014) Modelling harbour seal habitat by combining data  
15 from multiple tracking systems. *J Exp Mar Biol Ecol* 450:30–39

16 Barros NB, Jefferson TA, Parsons ECM (2004) Feeding Habits of Indo-Pacific Humpback Dolphins  
17 (*Sousa chinensis*) Stranded in Hong Kong. *Aquatic Mammals* 30:179–188

18 Bauer RK, Fromentin JM, Demarcq H, Brisset B, Bonhommeau S (2015) Co-Occurrence and Habitat  
19 Use of Fin Whales, Striped Dolphins and Atlantic Bluefin Tuna in the Northwestern Mediterranean  
20 Sea. *PLoS One* 10:e0139218

21 Bearzi G (2002) Interactions between Cetaceans and Fisheries in the Mediterranean Sea. In:  
22 Notarbartolo di Sciara, G. (ed) *Cetaceans of the Mediterranean and Black Seas: state of knowledge*  
23 *and conservation strategies. A report to the ACCOBAMS Secretariat, Monaco, February 2002.*  
24 Section 9, p 1–20

25 Bearzi G (2007) Marine conservation on paper. *Conserv Biol* 21:1–3

- 1 Bearzi G, Agazzi S, Gonzalvo J, Bonizzoni S, Costa M, Petroselli A (2010) Biomass removal by  
2 dolphins and fisheries in a Mediterranean Sea coastal area: do dolphins have an ecological impact  
3 on fisheries? *Aquatic Conserv: Mar Freshw Ecosyst* 20:549–559
- 4 Bearzi G, Fortuna C, Reeves R (2008) Ecology and conservation of bottlenose dolphins *Tursiops*  
5 *truncatus* in the Mediterranean Sea *Mammal Rev* 39:92–123
- 6 Bearzi G, Holcer D, Notarbartolo di Sciara G (2004) The role of historical dolphin takes and habitat  
7 degradation in shaping the present status of northern Adriatic cetaceans. *Aquatic Conserv: Mar*  
8 *Freshw Ecosyst* 14:363–379
- 9 Bearzi G, Politi E, Agazzi S, Azzellino A (2006) Prey depletion caused by overfishing and the decline  
10 of marine megafauna in eastern Ionian Sea coastal waters (central Mediterranean). *Biol Conserv*  
11 127:373–382
- 12 Beck CA, Iverson SJ, Bowen WD, Blanchard W (2007) Sex differences in grey seal diet reflect  
13 seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative  
14 fatty acid signature analysis. *J Anim Ecol* 76:490–502
- 15 Bejarano AC, Wells RS, Costa DP (2017) Development of a bioenergetic model for estimating energy  
16 requirements and prey biomass consumption of the bottlenose dolphin *Tursiops truncatus*. *Ecol*  
17 *Modell* 356:162–172
- 18 Belgrano A, Fowler CW (2013) Evolution. How fisheries affect evolution. *Science* 342:1176–1177
- 19 Beltran RS, Testa JW, Burns JM (2017) An agent-based bioenergetics model for predicting impacts  
20 of environmental change on a top marine predator, the Weddell seal. *Ecol Modell* 351:36–50
- 21 Birkun AJ (2002) Interactions between cetaceans and fisheries in the Black Sea. In: Notarbartolo di  
22 Sciara G (ed) *Cetaceans of the Mediterranean and Black Seas: State of Knowledge and Conservation*  
23 *Strategies*. Report to the ACCOBAMS Secretariat, Monaco, February 2002. Section 10, p 1–11

- 1 Bjørge A, Bekkby T, Bakkestuen V, Framstad E (2002) Interactions between harbour seals, *Phoca*  
2 *vitulina*, and fisheries in complex coastal waters explored by combined Geographic Information  
3 System (GIS) and energetics modelling. ICES J Mar Sci 59:29–42
- 4 Blanchard JL, Pinnegar JK, Mackinson S (2002) Exploring Marine Mammal-Fishery Interactions  
5 Using ‘Ecopath With Ecosim’: Modelling The Barents Sea Ecosystem. Sci Ser Tech Rep, CEFAS  
6 Lowestoft, 117:52p
- 7 Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals.  
8 Ecol Appl 18:77–96
- 9 Bodkin JL (2015) Historic and Contemporary Status of Sea Otters in the North Pacific. In: In: Larson  
10 SE, Bodkin JL, VanBlaricom GR (eds) Sea Otter Conservation. Elsevier Inc, p 43-61
- 11 Bodkin JL, Ballachey BE, Dean TA, Fukuyama AK, Jewett SC and others (2002) Sea otter population  
12 status and the process of recovery from the 1989 ‘Exxon Valdez’ oil spill. Mar Ecol Prog Ser  
13 241:237–253
- 14 Bograd SJ, Block BA, Costa DP, Godley BJ (2010) Biologging technologies: new tools for  
15 conservation. Introduction. Endang Species Res 10:1–7
- 16 Bogstad B, Gjørseter H, Haug T, Lindstrøm U (2015) A review of the battle for food in the Barents  
17 Sea: cod vs. marine mammals. Front Ecol Evol 3:29
- 18 Bogstad B, Hauge KH, Ulltang Ø (1997) MULTISPEC – A Multi-species Model for Fish and Marine  
19 Mammals in the Barents Sea. J North Atl Fish Sci 22:317–341
- 20 Bolnick DI, Amarasekare P, Araujo MS, Burger R and others (2011) Why intraspecific trait variation  
21 matters in community ecology. Trends Ecol Evol 26:183–192
- 22 Boonstra WJ, Ottosen KM, Ferreira ASA, Richter A and others (2015) What are the major global  
23 threats and impacts in marine environments? Investigating the contours of a shared perception  
24 among marine scientists from the bottom-up. Mar Policy 60:197–201

- 1 Botsford LW, Castilla JC, Peterson CH (1997) The Management of Fisheries and Marine Ecosystems.  
2 Science 277:509–515
- 3 Bowen WD (1997) Role of marine mammals in aquatic ecosystems. Mar Ecol Prog Ser 158:267–274
- 4 Bowen WD, Lidgard D (2013) Marine mammal culling programs: review of effects on predator and  
5 prey populations. Mammal Rev 43:207–220
- 6 Bowen WD, Tully D, Boness DJ, Bulheier BM, Marshall GJ (2002) Prey-dependent foraging tactics  
7 and prey profitability in a marine mammal. Mar Ecol Prog Ser 244:235–245
- 8 Burgess MG, Diekert FK, Jacobsen NS, Andersen KH, Gaines SD (2016) Remaining questions in the  
9 case for balanced harvesting. Fish Fish 17:1216–1226
- 10 Carswell LP, Speckman SG, Gill VA (2015) Shellfish Fishery Conflicts and Perceptions of Sea Otters  
11 in California and Alaska. In: Larson SE, Bodkin JL, VanBlaricom GR (eds) Sea Otter Conservation.  
12 Elsevier Inc, p 333–367
- 13 Castellini M (2000) History of polar whaling: insight into the physiology of the great whales. Comp  
14 Biochem Physiol A 126:153–159
- 15 Cerviño S, Cardador F, Howell D, Jardim E and others (2009) An age-length cannibal model for  
16 South hake with GADGET. ICES WGHMM REPORT 2009 [[link](#)]
- 17 Chadés I, Curtis JMR, Martin TG (2012) Setting Realistic Recovery Targets for Two Interacting  
18 Endangered Species, Sea Otter and Northern Abalone. Conserv Biol 26:1016–1025
- 19 Christie KS, Gilbert SL, Brown CL, Hatfield M, Hanson L (2016) Unmanned aircraft systems in  
20 wildlife research: current and future applications of a transformative technology. Front Ecol Environ  
21 14:241–251
- 22 Clapham PJ, Berggren P, Childerhouse S, Friday NA, Kasuya T, Kell L and others (2003) Whaling  
23 as science. BioSci 53:210–212

- 1 Coll M, Santojanni A, Palomera I, Tudela S, Arneri E (2007) An ecological model of the Northern  
2 and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts. *J Mar Syst* 67:119–  
3 154
- 4 Coll M, Palomera I, Tudela S, Sardà F (2006) Trophic flows, ecosystem structure and fishing impacts  
5 in the South Catalan Sea, Northwestern Mediterranean. *J Mar Syst* 59:63–96
- 6 Constable AJ (2011) The ecosystem approach to managing fisheries: achieving conservation  
7 objectives for predators of fished species. *CCAMLR Science* 8:37–64
- 8 Cornejo-Donoso J, Antezana T (2008) Preliminary trophic model of the Antarctic Peninsula  
9 Ecosystem (Sub-area CCAMLR 48.1). *Ecol Modell* 218:1–17
- 10 Cornick LA, Neill W, Grant WE (2006) Assessing competition between Steller sea lions and the  
11 commercial groundfishery in Alaska: A bioenergetics modelling approach. *Ecol Modell* 199:107–  
12 114
- 13 Costa ME, Le Pendu Y, Neto EM (2012) Behaviour of *Sotalia guianensis* (van Beneden, 1864)  
14 (Cetacea, Delphinidae) and ethnoecological knowledge of artisanal fishermen from Canavieiras,  
15 Bahia, Brazil. *J Ethnobiol Ethnomed* 8:1–18
- 16 Cronin MA, Gerritsen HD, Reid DG (2012) Evidence of low spatial overlap between grey seals and  
17 a specific whitefish fishery off the west coast of Ireland. *Biol Conserv* 150:136–142
- 18 Das K, Lepoint G, Loizeau V, Debacker V, Dauby P, Bouquegneau JM (2000) Tuna and Dolphin  
19 Associations in the North-east Atlantic: Evidence of Different Ecological Niches from Stable  
20 Isotope and Heavy Metal Measurements. *Mar Pollut Bull* 40:102–109
- 21 Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007) Trophic cascades triggered by  
22 overfishing reveal possible mechanisms of ecosystem regime shifts. *P Natl Acad Sci USA*  
23 104:10518–10523

- 1 Daura-Jorge FG, Cantor M, Ingram SN, Lusseau D, Simoes-Lopes PC (2012) The structure of a  
2 bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen.  
3 Biol Lett 8:702–705
- 4 de Oliveira Santos MC, Rosso S, Aguiar dos Santos R, Bulizani Lugato SH, Bassoi M (2002) Insights  
5 of small cetacean feeding habits in southeastern Brazil. Aquat Mamm 28:38–45
- 6 Deagle BE, Kirkwood R, Jarman SN (2009) Analysis of Australian fur seal diet by pyrosequencing  
7 prey DNA in faeces. Mol Ecol 18:2022–2038
- 8 Deagle BE, Thomas AC, Shaffer AK, Trites AW, Jarman SN (2013) Quantifying sequence  
9 proportions in a DNA-based diet study using Ion Torrent amplicon sequencing: which counts count?  
10 Mol Ecol Resour 13:620–633
- 11 Dede A, Salman A, Tonay AM (2015) Stomach contents of by-caught striped dolphins (*Stenella*  
12 *coeruleoalba*) in the eastern Mediterranean Sea. J Mar Biol Assoc UK 96:869–875
- 13 Dellinger T, Trillmich F (1988) Estimating diet composition from scat analysis in otariid seals  
14 (Otariidae): is it reliable? Can J Zool 66:1865–1870
- 15 DeMasters DP, Fowler C, Perry S, Richlen M (2001) Predation and Competition: The impact of  
16 fisheries on marine-mammal populations over the next one hundred years. J Mammal 82:641–651
- 17 Diaz Pauli B, Heino M (2013) Ecological and evolutionary effects of harvesting: lessons from the  
18 candy-fish experiment. ICES J Mar Sci 70:1281–1286
- 19 Doniol-Valcroze T, Lesage V, Giard J, Michaud R (2012) Challenges in marine mammal habitat  
20 modelling: evidence of multiple foraging habitats from the identification of feeding events in blue  
21 whales. Endang Species Res 17:255–268
- 22 Dunlop ES, Baskett ML, Heino M, Dieckmann U (2009) Propensity of marine reserves to reduce the  
23 evolutionary effects of fishing in a migratory species. Evol Appl 2:371–393
- 24 Dunshea G (2009) DNA-Based Diet Analysis for Any Predator. PLoS ONE 4(4): e5252
- 25 Ellis R (1991) Men and whales. Alfred A, Vol. Knopf, New York

1 Elliott Smith EA, Newsome SD, Estes JA, Tinker MT (2015) The cost of reproduction: differential  
2 resource specialization in female and male California sea otters. *Oecologia* 178:17–29

3 Elvarsson BP (2013) An implementation of the statistical framework Gadget for common minke  
4 whales in Icelandic waters. Status update on multispecies modeling effort. International Whaling  
5 Commission (IWC). SC/F13/SP7.

6 Elvarsson BP (2015) Evaluating stock structure hypotheses using genetically determined close  
7 relatives: a simulation study on North Atlantic fin whales. *ICES J Mar Sci* 72:661–669

8 Elvarsson B, Víkingsson G, Stefánsson G (2013) An implementation of the statistical framework  
9 Gadget for common minke whales in Icelandic waters. International Whaling Commission (IWC).  
10 SC/65a/EM01.

11 Enberg K, Jorgensen C, Dunlop ES, Heino M, Dieckmann U (2009) Implications of fisheries-induced  
12 evolution for stock rebuilding and recovery. *Evol Appl* 2:394–414

13 Erlandson JM, Rick TC, Estes JA, Graham MH, Braje TJ, Vellanoweth RL (2005) Sea otters,  
14 shellfish, and humans: 10,000 years of ecological interaction on San Miguel Island, California.  
15 Proceedings of the sixth California Islands symposium. Institute for Wildlife Studies Arcata,  
16 California. p 58–69 [\[link\]](#)

17 Esteban R, Verborgh P, Gauffier P, Giménez J, Guinet C, de Stephanis R (2016) Dynamics of killer  
18 whale, bluefin tuna and human fisheries in the Strait of Gibraltar. *Biol Conserv* 194:31–38

19 Estes JA (2015) Natural History, Ecology, and the Conservation and Management of Sea Otters. In:  
20 Larson SE, Bodkin JL, GR V (eds) *Sea Otter Conservation*. Elsevier Inc p 19–41

21 Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B (2016) Megafaunal Impacts on Structure  
22 and Function of Ocean Ecosystems. *Annu Rev Env Resour* 41:83–116

23 Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey  
24 selection by sea otters: patterns, causes and implications. *J Anim Ecol* 72:144–155

- 1 Etnier MA, Fowler CW (2010) Size Selectivity in Marine Mammal Diets as a Guide to Evolutionarily  
2 Enlightened Fisheries Management. *N Am J Fish Manage* 30:588–603
- 3 Evans K, Hindell MA, Thiele D (2003) Body fat and condition in sperm whales, *Physeter*  
4 *macrocephalus*, from southern Australian waters. *Comp Biochem Physiol A Mol Integr Physiol*  
5 134:847–862
- 6 FAO (2016) The State of World Fisheries and Aquaculture 2016. Contributing to food security and  
7 nutrition for all. Rome pp 200 [[link](#)]
- 8 Fanshawe S, Vanblaricom GR, Shelly AA (2003) Restored Top Carnivores as Detriments to the  
9 Performance of Marine Protected Areas Intended for Fishery Sustainability: a Case Study with Red  
10 Abalones and Sea Otters. *Conserv Biol* 17:273–283
- 11 Fernández R, Santos MB, Carrillo M, Tejedor M, Pierce GJ (2009) Stomach contents of cetaceans  
12 stranded in the Canary Islands 1996–2006. *J Mar Biol Assoc UK* 89:873–883
- 13 Fernández R, García-Tiscar S, Begoña Santos M, López A, Martínez-Cedeira JA, Newton J, Pierce  
14 GJ (2011) Stable isotope analysis in two sympatric populations of bottlenose dolphins *Tursiops*  
15 *truncatus*: evidence of resource partitioning? *Mar Biol* 158:1043–1055
- 16 Finerty SE, Wolt RC, Davis RW (2009) Summer activity pattern and Field Metabolic Rate of adult  
17 male sea otters (*Enhydra lutris*) in a soft sediment habitat in Alaska. *J Exp Mar Biol Ecol* 377:36–  
18 42
- 19 Folkow LP, Haug T, Nilssen KT, Nordoy ES (2000) Estimated food consumption of minke whales  
20 *Balaenoptera acutorostrata* in Northeast Atlantic waters in 1992-1995. *NAMMCO Sci Publ* 2:65–  
21 80
- 22 Forcada J, Malone D, Royle JA, Staniland IJ (2009) Modelling predation by transient leopard seals  
23 for an ecosystem-based management of Southern Ocean fisheries. *Ecol Modell* 220:1513–1521
- 24 Forrest RE, Savina M, Fulton EA, Pitcher TJ (2015) Do marine ecosystem models give consistent  
25 policy evaluations? A comparison of Atlantis and Ecosim. *Fish Res* 167:293–312

- 1 Fortune SME, Trites AW, Mayo CA, Rosen DAS, Hamilton PK (2013) Energetic requirements of  
2 North Atlantic right whales and the implications for species recovery. *Mar Ecol Prog Ser* 478:253–  
3 272
- 4 Fowler CW, Belgrano A, Casini M (2013) Holistic Fisheries Management: Combining  
5 Macroecology, Ecology, and Evolutionary Biology. *Mar Fish Rev* 75:1–36
- 6 Franco-Trecu V, Drago M, Costa P, Dimitriadis C, Passadore C (2017) Trophic relationships in apex  
7 predators in an estuary system: A multiple-method approximation. *J Exp Mar Biol Ecol* 486:230–  
8 236
- 9 Gambell R (1993) International management of whales and whaling: an historical review of the  
10 regulation of commercial and aboriginal subsistence whaling. *Arctic* 46:97–107
- 11 Garcia SM, Kolding J, Rice J, Rochet MJ and others (2012) Conservation. Reconsidering the  
12 consequences of selective fisheries. *Science* 335:1045–1047
- 13 Garcia SM, Zerbi A, Aliaume C, Do Chi T, Lasserre G (2003) The ecosystem approach to fisheries.  
14 Issues, terminology, principles, institutional foundations, implementation and outlook. FAO, Rome  
15 [\[link\]](#)
- 16 Gerber LR, Morissette L, Kaschner K, Pauly D (2009) Ecology. Should whales be culled to increase  
17 fishery yield? *Science* 323:880–881
- 18 Gladilina EV, Gol'din PE (2014) New Prey Fishes in Diet of Black Sea Bottlenose Dolphins, *Tursiops*  
19 *truncatus* (Mammalia, Cetacea). *Vestn Zool* 48:83–92
- 20 Gleason M, McCreary S, Miller-Henson M, Ugoretz J and others (2010) Science-based and  
21 stakeholder-driven marine protected area network planning: A successful case study from north  
22 central California. *Ocean Coast Manag* 53:52–68
- 23 Godwin EM, Noad MJ, Kniest E, Dunlop RA (2016) Comparing multiple sampling platforms for  
24 measuring the behavior of humpback whales (*Megaptera novaeangliae*). *Mar Mam Sci* 32:268–286

1 Goedegebuure M, Melbourne-Thomas J, Corney SP, Hindell MA, Constable AJ (2017) Beyond big  
2 fish: The case for more detailed representations of top predators in marine ecosystem models. *Ecol*  
3 *Modell* 359:182–192

4 Goetz S, Read FL, Santos MB, Pita C, Pierce GJ (2014) Cetacean–fishery interactions in Galicia (NW  
5 Spain): results and management implications of a face-to-face interview survey of local fishers.  
6 *ICES J Mar Sci* 71:604–617

7 Goldsworthy SD, Bulman C, He X, Larcome J, Littnan C (2003) Trophic interactions between marine  
8 mammals and Australian fisheries: an ecosystem approach. In: Gales N, Hindell M, Kirkwood R  
9 (eds) *Marine Mammals: Fisheries, Tourism and Management Issues*. CSIRO Publishing,  
10 Collingwood, Australia, p 62–99

11 Goldsworthy SD, Page B, Rogers PJ, Bulman C and others (2013) Trophodynamics of the eastern  
12 Great Australian Bight ecosystem: Ecological change associated with the growth of Australia's  
13 largest fishery. *Ecol Modell* 255:38–57

14 Gonzalvo J, Giovos I, Moutopoulos DK (2014) Fishermen's perception on the sustainability of small-  
15 scale fisheries and dolphin-fisheries interactions in two increasingly fragile coastal ecosystems in  
16 western Greece. *Aquatic Conserv Mar Freshw Ecosyst* 25:91–106

17 Gormley AM, Slooten E, Dawson S, Barker RJ, Rayment W, du Fresne S, Bräger S (2012) First  
18 evidence that marine protected areas can work for marine mammals. *J Appl Ecol* 49:474–480

19 Guénette S, Heymans SJJ, Christensen V, Trites AW (2006) Ecosystem models show combined  
20 effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias*  
21 *jubatus*) in Alaska. *Can J Fish Aquat Sci* 63:2495–2517

22 Hammond PS, Lacey C, Gilles A, Viquerat S and others (2017) Estimates of cetacean abundance in  
23 European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys,  
24 Scotland, UK pp 40

- 1 Hammond PS, Macleod K, Berggren P, Borchers DL and others (2013) Cetacean abundance and  
2 distribution in European Atlantic shelf waters to inform conservation and management. *Biol*  
3 *Conserv* 164:107–122
- 4 Hansson S, Hjerne O, Harvey C, Kitchell JF, Cox SP, Essington TE (2007) Managing Baltic Sea  
5 fisheries under contrasting production and predation regimes: ecosystem model analyses. *Ambio*  
6 36:265–271
- 7 Harding KC, Härkönen TJ (1999) Development in the Baltic grey seal (*Halichoerus grypus*) and  
8 ringed seal (*Phoca hispida*) populations during the 20th century. *Ambio* 28:619–627
- 9 Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, Grimes DJ and others (1999) Emerging  
10 Marine Diseases – Climate Links and Anthropogenic factors. *Science* 285:1505–1510
- 11 Harvey C, Cox SP, Essington TE, Hansson S, Kitchell JF (2003) An ecosystem model of food web  
12 and fisheries interactions in the Baltic Sea. *ICES J Mar Sci* 60:939–950
- 13 Harwood J (2001) Marine Mammals and Their Environment in the Twenty-First Century. *J Mammal*  
14 82:630–640
- 15 Harwood J, McLaren I (2004) Modelling interactions between marine mammals and fisheries: model  
16 structures, assumptions and data requirements CIESM Workshop Monographs n°25, Venice, p 37–  
17 42
- 18 Haug T, Lindstrøm U, Nilssen KT (2010) Variations in Minke Whale (*Balaenoptera acutorostrata*)  
19 Diet and Body Condition in Response to Ecosystem Changes in the Barents Sea. *Sarsia* 87:409–422
- 20 Heino M, Baulier L, Boukal DS, Ernande B, Johnston FD and others (2013) Can fisheries-induced  
21 evolution shift reference points for fisheries management? *ICES J Mar Sci* 70:707–721
- 22 Heino M, Dieckmann U (2008) Detecting fisheries-induced life-history evolution: an overview of the  
23 reaction-norm approach. *Bull Mar Sci* 83:69–93
- 24 Heino M, Díaz Pauli B, Dieckmann U (2015) Fisheries-Induced Evolution. *Annu Rev Ecol Evol S*  
25 46:461–480

- 1 Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top  
2 predator declines. *Trends Ecol Evol* 23:202–210
- 3 Hernandez-Milian G, Berrow S, Santos MB, Reid D, Rogan E (2015) Insights into the Trophic  
4 Ecology of Bottlenose Dolphins (*Tursiops truncatus*) in Irish Waters. *Aquat Mamm* 41:226–239
- 5 Hidalgo M, Olsen EM, Ohlberger J, Saborido-Rey F and others (2014) Contrasting evolutionary  
6 demography induced by fishing: the role of adaptive phenotypic plasticity. *Ecol Appl* 24:1101–1114
- 7 Holcer D (1994) Prospective of cetology in Croatia. *European Research on Cetaceans* 8:120–121
- 8 Houle JE, Andersen KH, Farnsworth KD, Reid DG (2013) Emerging asymmetric interactions  
9 between forage and predator fisheries impose management trade-offs. *J Fish Biol* 83:890–904
- 10 Houle JE, de Castro F, Cronin MA, Farnsworth KD and others (2016) Effects of seal predation on a  
11 modelled marine fish community and consequences for a commercial fishery. *J Appl Ecol* 53:54–  
12 63
- 13 Howell D, Bogstad B (2010) A combined Gadget/FLR model for management strategy evaluations  
14 of the Barents Sea fisheries. *ICES J Mar Sci* 67:1998–2004
- 15 Huber HR, Jeffries SJ, Brown RF, DeLong RL, VanBlaricom GR (2001) Correcting aerial survey  
16 counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Mar Mam Sci* 17:276–  
17 293
- 18 Hui TCY, Morita Y, Kobayashi Y, Mitani Y, Miyashita K (2017) Dietary analysis of harbour seals  
19 (*Phoca vitulina*) from faecal samples and overlap with fisheries in Erimo, Japan. *Mar Ecol* 38:1–12
- 20 Huisamen J, Kirkman SP, van der Lingen CD, Watson LH and others (2012) Diet of the Cape fur  
21 seal *Arctocephalus pusillus pusillus* at the Robberg Peninsula, Plettenberg Bay, and implications for  
22 local fisheries. *Afr J Mar Sci* 34:431–441
- 23 Huss M, de Ross AM, Van Leeuwen A, Gårdmark A (2014) Facilitation of fisheries by natural  
24 predators depends on life history of shared prey. *Oikos* 00:1–10
- 25 Hutchings JA (2000) Collapse and recovery of marine fishes. *Nature* 406:882–885

1 Hutchings JA (2009) Avoidance of fisheries-induced evolution: management implications for catch  
2 selectivity and limit reference points. *Evol Appl* 2:324-334

3 Hutchings JA (2015) Thresholds for impaired species recovery. *Proc R Soc B* 282:20150654

4 ICES (2015) Report of the Working Group on Marine Mammal Ecology (WGMME), 9–12 February  
5 2015, London, UK. ICES CM 2015/ACOM:25. pp 114 [\[link\]](#)

6 ICES (2016) Sec. 10 Hake in Divisions 8.c and 9.a (Southern stock) 10.1. In Report of the Working  
7 Group for the Bay of Biscay and the Iberian waters Ecoregion (WGBIE), Copenhagen, Denmark.  
8 ICES CM 2016/ACOM:12 pp 34 [\[link\]](#)

9 ICES (2017) Interim Report of the Working Group on Multispecies Assessment Methods (WGSAM),  
10 San Sebastian, Spain. ICES CM 2017/SSGEPI:20, pp 395 [\[link\]](#)

11 International Whaling Commission (IWC), [www.iwc.int](http://www.iwc.int) (accessed 28 Feb 2019)

12 Iverson SJ, Field C, Don Bowen W, Blanchard W (2004) Quantitative Fatty Acid Signature Analysis:  
13 A New Method of Estimating Predator Diets. *Ecol Monogr* 74:211–235

14 IWC (1946) International Convention for the Regulation of Whaling, 1946. Schedule. As amended  
15 by the Commission at the 66th Meeting Portorož, Slovenia, October 2016 [\[link\]](#)

16 IWC (2016) Report of the 65th Meeting of the International Whaling Commission and Associated  
17 Meetings and Workshops, Cambridge. pp 382 [\[link\]](#)

18 Jackson JB, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the  
19 recent collapse of coastal ecosystems. *Science* 293:629–637

20 Jacobsen NS, Gislason H, Andersen KH (2014) The consequences of balanced harvesting of fish  
21 communities. *Proceedings of the Royal Society B: Biological Sciences* 281:2013–2701

22 Jarman SN, Gales NJ, Tierney M, Gill PC, Elliott NG (2002) A DNA-based method for identification  
23 of krill species and its application to analysing the diet of marine vertebrate predators. *Mol Ecol*  
24 11:2679–2690

25 Jefferson T (1993) FAO species identification guide. Marine mammals of the world. FAO, Rome

- 1 Johansson J, Kristensen NP, Nilsson J-Å, Jonzén N (2015) The eco-evolutionary consequences of  
2 interspecific phenological asynchrony - a theoretical perspective. *Oikos* 124:102–112
- 3 Johnson CM, Beckley LE, Kobryn H, Johnson GE, Kerr I, Payne R (2016) Crowdsourcing Modern  
4 and Historical Data Identifies Sperm Whale (*Physeter macrocephalus*) Habitat Offshore of South-  
5 Western Australia. *Front Mar Sci* 3:167
- 6 Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS and others (2007) Managing Evolving  
7 Fish Stocks. *Ecology* 318:1247–1248
- 8 Jørgensen C, Taylor E, Fiksen Ø (2010) Modelling fishing-induced adaptations and consequences for  
9 natural mortality. *Can J Fish Aquat Sci* 67:1086–1097
- 10 Kalland A, Moeran B (2010) Japanese Whaling?: End of an Era, Vol. Routledge
- 11 Kaschner K (2004) Modelling and Mapping Resource Overlap between Marine Mammals and  
12 Fisheries on a Global Scale. University of British Columbia, Berkeley and Los Angeles, USA
- 13 Kaschner K, Pauly P (2005) Competition between Marine Mammals and Fisheries: Food for Thought.  
14 In: Salem D, Rowan A (eds) *The state of the animals III*. Humane Society Press, Washington, DC
- 15 Kaschner K, Stergiou K, Weingartner G, Kumagai S (2004) Trophic levels of marine mammals and  
16 overlap in resource utilization between marine mammals and fisheries in the Mediterranean Sea.  
17 CIESM Workshop Monographs n°25, Venice, p 51–58
- 18 Kaschner K, Watson R, Christensen V, Trites AW, Pauly D (2001) Modeling and Mapping Trophic  
19 Overlap between Marine Mammals and Commercial Fisheries in the North Atlantic, Vancouver,  
20 B.C., Canada p 35-45
- 21 Kastelein RA, Vaughan N, Walton S, Wiepkema PR (2002) Food intake and body measurements of  
22 Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. *Mar Environ Res* 53:199–218
- 23 Kasuya T (1985) Fishery-dolphin conflict in the Iki Island area of Japan. *Marine mammals and*  
24 *fisheries* p 253–272
- 25 Kenyon, KW (1969) The Sea Otter in the Eastern Pacific Ocean. *North American Fauna* 68:1–352

- 1 King JE (1964) *Seals of the World*. British Museum (Natural History), London.
- 2 King RA, Read DS, Traugott M, Symondson WO (2008) Molecular analysis of predation: a review  
3 of best practice for DNA-based approaches. *Mol Ecol* 17:947–963
- 4 Koen-Alonso MM, Yodzis P (2004) Modelling food webs: a bioenergetic-allometric approach  
5 CIESM Workshop Monographs n°25, Venice, p 43–49
- 6 Koen-Alonso MM, Yodzis P (2005) Multispecies modelling of some components of the marine  
7 community of northern and central Patagonia, Argentina. *Can J Fish Aquat Sci* 62:1490–1512
- 8 Konishi K, Hakamada T, Kiwada H, Kitakado T, Walløe L (2014) Decrease in stomach contents in  
9 the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. *Polar Biol* 37:205–  
10 215
- 11 Kornev SI, Korneva SM (2006) Some Criteria for Assessing the State and Dynamics of Sea Otter  
12 (*Enhydra lutris*) Populations in the Russian Part of the Species Range. *Russ J Ecol* 37:172–179
- 13 Kovacs KM, Lydersen C, Overland JE, Moore SE (2011) Impacts of changing sea-ice conditions on  
14 Arctic marine mammals. *Mar Biodiv* 41:181–194
- 15 Kuparinen A, Boit A, Valdovinos FS, Lassaux H, Martinez ND (2016) Fishing-induced life-history  
16 changes degrade and destabilize harvested ecosystems. *Sci Rep* 6:22245
- 17 Kuparinen A, Hutchings JA (2014) Increased natural mortality at low abundance can generate an  
18 Allee effect in a marine fish. *R Soc Open Sci* 1:140075
- 19 Kuparinen A, Stenseth NC, Hutchings JA (2014) Fundamental population-productivity relationships  
20 can be modified through density-dependent feedbacks of life-history evolution. *Evol Appl* 7:1218–  
21 1225
- 22 Laake JL, Browne P, DeLong RL, Huber HR (2002) Pinniped diet composition: a comparison of  
23 estimation models. *Fish Bull* 100:434–447
- 24 Lackey RT (2005) Fisheries: History, Science and Management. In: Lehr JH, Keeley J (eds) *Water*  
25 *Encyclopedia: Surface and Agricultural Water*. John Wiley and Sons, Inc., New York, p 121–129

- 1 Laidre KL, Jameson RJ (2006) Foraging Patterns And Prey Selection In An Increasing And  
2 Expanding Sea Otter Population. *J Mammal* 87:799–807
- 3 Laidre KL, Jameson RJ, DeMaster DP (2001) An estimation of carrying capacity for sea otters along  
4 the California coast. *Mar Mam Sci* 17:294–309
- 5 Lankau RA, Strauss SY (2011) Newly rare or newly common: evolutionary feedbacks through  
6 changes in population density and relative species abundance, and their management implications.  
7 *Evol Appl* 4:338–353
- 8 Larson SD, Hoyt ZN, Eckert GL, Gill VA (2013) Impacts of sea otter (*Enhydra lutris*) predation on  
9 commercially important sea cucumbers (*Parastichopus californicus*) in southeast Alaska. *Can J Fish*  
10 *Aquat Sci* 70:1498–1507
- 11 Lassalle G, Gascuel D, Le Loc'h F, Lobry J, Pierce GJ and others (2012) An ecosystem approach for  
12 the assessment of fisheries impacts on marine top predators: the Bay of Biscay case study. *ICES J*  
13 *Mar Sci* 69:925–938
- 14 Lassen H, Kelly C, Sissenwine M (2014) ICES advisory framework 1977–2012: from Fmax to  
15 precautionary approach and beyond. *ICES J Mar Sci* 71:166–172
- 16 Laugen AT, Engelhard GH, Whitlock R, Arlinghaus R and others (2014) Evolutionary impact  
17 assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to  
18 fisheries management. *Fish Fish* 15:65–96
- 19 Lavery TJ, Roudnew B, Seymour J, Mitchell JG and others (2014) Whales sustain fisheries: Blue  
20 whales stimulate primary production in the Southern Ocean. *Mar Mamm Sci* 30:888–904
- 21 Lavigne D (2003) Marine mammals and fisheries: The role of science in the culling debate. In: Gales  
22 N, Hindell M, Kirkwood R (eds) *Marine Mammals: Fisheries, Tourism and Management Issues*.  
23 CSIRO Publishing, Collingwood, Australia, p 31–47
- 24 Law R, Plank MJ, Kolding J (2012) On balanced exploitation of marine ecosystems: results from  
25 dynamic size spectra. *ICES J Mar Sci* 69:602–614

- 1 Lee OA, Olivier P, Wolt R, Davis RW, Weltz F (2009) Aggregations of Sea Otters (*Enhydra lutris*  
2 *kenyonii*) Feeding on Fish Eggs and Kelp in Prince William Sound, Alaska. *Am Midl Nat* 161:401–  
3 405
- 4 Leslie HM, McLeod KL (2007) Confronting the challenges of implementing marine ecosystem-based  
5 management. *Front Ecol Environ* 5:540–548
- 6 Levermann N, Galatius A, Ehlme G, Rysgaard S, Born EW (2003) Feeding behaviour of free-ranging  
7 walrus with notes on apparent dextrality of flipper use. *BMC Ecol* 3:1–13
- 8 Lewy P, Vinther M (2004) A stochastic age-length-structured multispecies model applied to North  
9 Sea stocks. *ICES CM* 2004/ FF:20, 33 pp [[link](#)]
- 10 Linchant J, Lisein J, Semeki J, Lejeune P, Vermeulen C (2015) Are unmanned aircraft systems  
11 (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. *Mammal*  
12 *Rev* 45:239–252
- 13 Lindeberg DR, Pyenson ND (2006) Evolutionary Patterns in Cetacea: Fishing Up Prey Size through  
14 Deep Time. In: Estes JA, DeMaster DP, Doak DF, Williams TM, Brownell Jr RL (eds) *Whales,*  
15 *whaling, and ocean ecosystems.* University of California Press, Berkeley and Los Angeles,  
16 California p 67–81
- 17 Lindstrøm U, Smout S, Howell D, Bogstad B (2009) Modelling multi-species interactions in the  
18 Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod,  
19 herring and capelin. *Deep-Sea Res PT II* 56:2068–2079
- 20 Link JS (2002) What Does Ecosystem-Based Fisheries Management Mean? *Fisheries* 27:18–21
- 21 Link JS, Bundy A, Overholtz WJ, Shackell N and others (2011) Ecosystem-based fisheries  
22 management in the Northwest Atlantic. *Fish Fish* 12:152–170
- 23 Lockyer C (2007) All creatures great and smaller: a study in cetacean life history energetics. *J Mar*  
24 *Biol Ass UK* 87:1035–1045

- 1 Lonergan M, Duck CD, Thompson D, Mackey BL, Cunningham L, Boyd IL (2007) Using sparse  
2 survey data to investigate the declining abundance of British harbour seals. *J Zool* 271:261-269
- 3 Lundström K, Hjerne O, Alexandersson K, Karlsson O (2007) Estimation of grey seal (*Halichoerus*  
4 *grypus*) diet composition in the Baltic Sea. *NAMMCO Sci Publ* 6:177–196
- 5 Lundström K, Hjerne O, Lunneryd S-G, Karlsson O (2010) Understanding the diet composition of  
6 marine mammals: grey seals (*Halichoerus grypus*) in the Baltic Sea. *ICES J Mar Sci* 67:1230–1239
- 7 Mackinson S, Blanchard JL, Pinnegar JK, Scott R (2003) Consequences of alternative functional  
8 response formulations interactions in models exploring whale-fishery. *Mar Mam Sci* 19:661–681
- 9 MacMillan DC, Han J (2011) Cetacean by-catch in the Korean Peninsula—by chance or by design?  
10 *Hum Ecol* 39:757–768
- 11 Marshall KN, Stier AC, Samhouri JF, Kelly RP, Ward EJ (2016) Conservation Challenges of Predator  
12 Recovery. *Conserv Lett* 9:70–78
- 13 Matthiopoulos J, Smout S, Winship AJ, Thompson D, Boyd IL, Harwood J (2008) Getting beneath  
14 the surface of marine mammal–fisheries competition. *Mammal Rev* 38:167–188
- 15 Méheust E, Alfonsi E, Le Ménec P, Hassani S, Jung J-L (2014) DNA barcoding for the identification  
16 of soft remains of prey in the stomach contents of grey seals (*Halichoerus grypus*) and harbour  
17 porpoises (*Phocoena phocoena*). *Mar Biol Res* 11:385–395
- 18 Mèndez-Fernandez P, Bustamante P, Bode A, Chouvelon T and others (2012) Foraging ecology of  
19 five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen  
20 isotope ratios. *J Exp Mar Biol Ecol* 413:150–158
- 21 Meynier L, Morel PCH, Chilvers BL, Mackenzie DDS, Duignan PJ, MacLatchey D (2014) Foraging  
22 diversity in lactating New Zealand sea lions: insights from qualitative and quantitative fatty acid  
23 analysis. *Can J Fish Aquat Sci* 71:984–991
- 24 Mizroch SA, Rice DW (2006) Have North Pacific killer whales switched prey species in response to  
25 depletion of the great whale populations? *Mar Ecol Prog Ser* 310:235–224

- 1 Moore MJ (2014) How we all kill whales. *ICES J Mar Sci* 71:760–763
- 2 Mori M, Butterworth DS (2006) A first step towards modelling the krill–predator dynamics of the  
3 Antarctic ecosystem. *CCAMLR Science* 13:217–277
- 4 Morissette L, Brodie PF (2014) Assessing the trophic impacts of marine mammals: From metabolism  
5 to food web indices. *Mar Mam Sci* 30:939–960
- 6 Morissette L, Christensen V, Pauly D (2012) Marine Mammal Impacts in Exploited Ecosystems:  
7 Would Large Scale Culling Benefit Fisheries? *PLoS ONE* 7(9):e43966.
- 8 Morissette L, Hammill MO, Savenkoff C (2006) The Trophic Role of Marine Mammals in the  
9 Northern Gulf of St. Lawrence. *Mar Mam Sci* 22:74–103
- 10 Morissette L, Kaschner K, Gerber LR (2010a) Ecosystem models clarify the trophic role of whales  
11 off Northwest Africa. *Mar Ecol Prog Ser* 404:289–302
- 12 Morissette L, Kaschner K, Gerber LR (2010b) ‘Whales eat fish’? Demystifying the myth in the  
13 Caribbean marine ecosystem. *Fish Fish* 11:388–404
- 14 Morzaria-Luna HN, Ainsworth CH, Kaplan IC, Levin PS, Fulton EA (2012) Exploring trade-offs  
15 between fisheries and conservation of the vaquita porpoise (*Phocoena sinus*) using an Atlantis  
16 ecosystem model. *PLoS One* 7:e42917
- 17 Newsome SD, Bentall GB, Tinker MT, Oftedal OT, Ralls K, Estes JA, Fogel ML (2010) Variation  
18 in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  diet–vibrissae trophic discrimination factors in a wild population of California  
19 sea otters. *Ecol Appl* 20:1744–1752
- 20 Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA  
21 (2009) Using stable isotopes to investigate individual diet specialization in California sea otters  
22 (*Enhydra lutris nereis*). *Ecology* 90:961–974
- 23 Newsome SD, Yeakel JD, Wheatley PV, Tinker MT (2012) Tools for quantifying isotopic niche space  
24 and dietary variation at the individual and population level. *J Mammal* 93:329–341

- 1 Northridge SP, Hofman RJ (1999) Marine mammal interactions with fisheries. In: Twiss JR, Reeves  
2 RR (eds) Conservation and management of marine mammals. Smithsonian Institution Press,  
3 Washington, USA, p 99–119
- 4 Nye JA, Gamble RJ, Link JS (2013) The relative impact of warming and removing top predators on  
5 the Northeast US large marine biotic community. *Ecol Modell* 264:157–168
- 6 Oksanen SM, Ahola MP, Lehtonen E, Kunnasranta M (2014) Using movement data of Baltic grey  
7 seals to examine foraging-site fidelity: implications for seal-fishery conflict mitigation. *Mar Ecol*  
8 *Prog Ser* 507:297–308
- 9 Olsen E, Holt JC (2001) A note on common minke whale (*Balaenoptera acutorostrata*) diets in the  
10 Norwegian Sea and the North Sea. *J Cetacean Res Manage* 3:179–183
- 11 Øien N (1988) The distribution of killer whales (*Orcinus orca*) in the North Atlantic based on  
12 Norwegian catches, 1938–1981, and incidental sightings, 1967–1987. *Rit Fiskideildar*
- 13 Österblom H, Hansson S, Larsson U, Hjerne O, Wulff F, Elmgren R, Folke C (2007) Human-induced  
14 Trophic Cascades and Ecological Regime Shifts in the Baltic Sea. *Ecosystems* 10:877–889
- 15 Papastavrou V, Leaper R, Lavigne D (2017) Why management decisions involving marine mammals  
16 should include animal welfare. *Mar Policy* 79:19–24
- 17 Parrish FA, Marshal GJ, Buhleier B and Antonelis GA (2008) Foraging interactions between monk  
18 seals and large predatory fish in the Northwestern Hawaiian Islands. *Endang Species Res* 4:299–  
19 308
- 20 Parsons KM, Piertney SB, Middlemas SJ, Hammond PS, Armstrong JD (2005) DNA-based  
21 identification of salmonid prey species in seal faeces. *J Zool Lond* 266:275–281
- 22 Pauly D, Christensen V, Guénette S, Pitcher TJ and others (2002) Towards sustainability in world  
23 fisheries. *Nature* 418:689–695
- 24 Pauly D, Christensen V, Waters C (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating  
25 ecosystem impact of fisheries. *ICES J Mar Sci* 57: 697–706

- 1 Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine  
2 mammals. *ICES J Mar Sci* 55:467–481
- 3 Pierce GJ, Santos MB, Learmonth JA, Mente E, Stowasser G (2004) Methods for dietary studies on  
4 marine mammals. In: *Investigating the roles of cetaceans in marine ecosystems*. CIESM Workshop  
5 Monographs n° 25, Venice, p 29–36
- 6 Pierce GJ, Boyle PR (1991) A review of methods for diet analysis in piscivorous marine mammals.  
7 *Oceanogr Mar Biol Annu Rev* 29:409–486
- 8 Plagányi EE (2007) Models for an ecosystem approach to fisheries. *FAO Fisheries Technical Paper*.  
9 No. 477. Rome, FAO.
- 10 Plagányi EE, Punt AE, Hillary R, Morello EB and others (2014) Multispecies fisheries management  
11 and conservation: tactical applications using models of intermediate complexity. *Fish Fish* 15:1–22
- 12 Pikitch EK, Santora C, Babcock EA, Bakun A and others (2004) Ecology. Ecosystem-based fishery  
13 management. *Science* 305:346–347
- 14 Piroddi C, Coll M, Steenbeek J, Macias Moy D, Christensen V (2015) Modelling the Mediterranean  
15 marine ecosystem as a whole: addressing the challenge of complexity. *Mar Ecol Prog Ser* 533:47–  
16 65
- 17 Piroddi C, Bearzi G, Gonzalvo J, Christensen V (2011) From common to rare: The case of the  
18 Mediterranean common dolphin. *Biol Conserv* 144:2490–2498
- 19 Pompa S, Ehrlich PR, Ceballos G (2011) Global distribution and conservation of marine mammals.  
20 *P Natl Acad Sci USA* 108:13600–13605
- 21 Prato G, Gascuel D, Valls A, Francour P (2014) Balancing complexity and feasibility in  
22 Mediterranean coastal food-web models: uncertainty and constraints. *Mar Ecol Prog Ser* 512:71–88
- 23 Punt AE, MacCall AD, Essington TE, Francis TB and others (2016) Exploring the implications of  
24 the harvest control rule for Pacific sardine, accounting for predator dynamics: A MICE model. *Ecol*  
25 *Modell* 337:79–95

1 Read AJ, Brownstein CR (2003) Considering other consumers: Fisheries, predators, and Atlantic  
2 herring in the Gulf of Maine. *Conserv Ecol* 7:2

3 Read AJ, Wade PR (1999) Status of Marine Mammals in the United States. *Conserv Biol* 14:929–  
4 940

5 Read FL, Evans PGH, Dolman SJ (2017) Cetacean Bycatch Monitoring and Mitigation under EC  
6 Regulation 812/2004 in the Northeast Atlantic, North Sea and Baltic Sea from 2006 to 2014. A  
7 WDC Report. pp 68 [[link](#)]

8 Rechsteiner EU, Rosen DA, Trites AW (2013) Seasonal Resting Metabolic Rate and Food Intake of  
9 Captive Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*). *Aquat Mamm* 39:241–252

10 Reeves RR (2002) The origins and character of ‘aboriginal subsistence’ whaling: a global review.  
11 *Mammal Rev* 32:71–106

12 Reeves RR, Smith TD (2006) Taxonomy of World Whaling, Operations and Eras. In: Estes JA,  
13 DeMaster DP, Doak DF, Williams TM, Brownell Jr RL (eds) Whales, whaling, and ocean  
14 ecosystems. University of California Press, Berkeley and Los Angeles, California, p 82–98

15 Roman J, Altman I, Dunphy-Daly MM, Campbell C, Jasny M, Read AJ (2013) The Marine Mammal  
16 Protection Act at 40: status, recovery, and future of U.S. marine mammals. *Ann N Y Acad Sci*  
17 1286:29–49

18 Roman J, Estes JA, Morissette L, Smith C and others (2014) Whales as marine ecosystem engineers.  
19 *Front Ecol Environ* 12:377–385

20 Roman J, McCarthy JJ (2010) The whale pump: marine mammals enhance primary productivity in a  
21 coastal basin. *PLoS One* 5:e13255

22 Ruckelshaus M, Klinger T, Knowlton N, Demaster DP (2008) Marine Ecosystem-based Management  
23 in Practice: Scientific and Governance Challenges. *Bioscience* 58:53–63

24 Ruzicka JJ, Steele JH, Ballerini T, Gaichas SK, Ainley DG (2013) Dividing up the pie: Whales, fish,  
25 and humans as competitors. *Prog Oceanogr* 116:207–219

- 1 Saavedra C, Cabrero A, Cedeira J, Cerviño S and others (2014) Including cetaceans in multi-species  
2 assessment models using strandings data: why, how and what can we do about it? In: *Frontiers in*  
3 *Marine Science*. Conference Abstract: IMMR | International Meeting on Marine Research 2014,  
4 Peniche, Portugal. pp 1
- 5 Saavedra C (2017) Multispecies population modelling of the common dolphin (*Delphinus delphis*),  
6 the bottlenose dolphin (*Tursiops truncatus*) and the southern stock of European hake (*Merluccius*  
7 *merluccius*), in Atlantic waters of the Iberian Peninsula. PhD dissertation, University of Vigo, Vigo,  
8 Spain
- 9 Sagarese SR, Laretta MV, Walter JF (2017) Progress towards a next-generation fisheries ecosystem  
10 model for the northern Gulf of Mexico. *Ecol Modell* 345:75–98
- 11 Santos MB, German I, Correia D, Read FL and others (2013) Long-term variation in common dolphin  
12 diet in relation to prey abundance. *Mar Ecol Prog Ser* 481:249–268
- 13 Santos MB, Pierce GJ, Hartmann MG, Smeenk C and others (2002) Additional notes on stomach  
14 contents of sperm whales *Physeter macrocephalus* stranded in the north-east Atlantic. *J Mar Biol*  
15 *Ass UK* 82:501–507
- 16 Santos MB, Saavedra C, Pierce GJ (2014) Quantifying the predation on sardine and hake by cetaceans  
17 in the Atlantic waters of the Iberian peninsula. *Deep-Sea Res Pt II* 106:232–244
- 18 Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC, Punt A (2014) REVIEW: On  
19 the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *J*  
20 *Appl Ecol* 51:1575–1583
- 21 SCANS (2006a) Design-based abundance estimates from SCANS-II. In Burt, M. L., D. L. Borchers,  
22 & F. Samarra (eds), *Small Cetaceans in the European Atlantic and North Sea*. Final Report to the  
23 European Commission under project LIFE04NAT/GB/000245. St. Andrews: 31

- 1 SCANS (2006b) Model-based abundance estimates from SCANS-II. In Burt, M., D. Borchers, & C.  
2 Paxton (eds), Small Cetaceans in the European Atlantic and North Sea. Final Report to the European  
3 Commission under project LIFE04NAT/GB/000245. St. Andrews: 20
- 4 Scheinin AP, Kerem D, Lojen S, Liberzon J, Spanier E (2014) Resource partitioning between  
5 common bottlenose dolphin (*Tursiops truncatus*) and the Israeli bottom trawl fishery? Assessment  
6 by stomach contents and tissue stable isotopes analysis. J Mar Biol Assoc UK 94:1203–1220
- 7 Schumacher JD, Kruse GH (2005) Toward sustainable ecosystem services from the Aleutian  
8 Archipelago. Fish Oceanogr 14:277–291
- 9 Schweder T (2001) Protecting whales by distorting uncertainty: non-precautionary mismanagement?  
10 Fish Res 52:217–225
- 11 Schweder T, Hagen GS, Hatlebakk E (2000) Direct and indirect effects of minke whale abundance  
12 on cod and herring fisheries: A scenario experiment for the Greater Barents Sea. NAMMCO Sci  
13 Publ 2:120–133
- 14 Sepúlveda M, Pavez G, Santos-Carvallo M, Balbontín C, Pequeño G, Newsome SD (2017) Spatial,  
15 temporal, age, and sex related variation in the diet of South American sea lions in southern Chile.  
16 Mar Mam Sci 33:480–495
- 17 Sharpe DMT, Hendry AP (2009) Life history change in commercially exploited fish stocks: an  
18 analysis of trends across studies. Evol Appl 2:260–275
- 19 Sinclair EH, Vlietstra LS, Johnson DS, Zeppelin TK and others (2008) Patterns in prey use among  
20 fur seals and seabirds in the Pribilof Islands. Deep-Sea Res Pt II 55:1897–1918
- 21 Sinclair EH, Zeppelin TK (2002) Seasonal and Spatial Differences in Diet in the Western Stock of  
22 Steller Sea Lions (*Eumetopias jubatus*). J Mammalogy 83:973–990
- 23 Singleton BE, Fielding R (2017) Inclusive hunting: examining Faroese whaling using the theory of  
24 socio-cultural viability. Maritime Studies 16:6

1 Smith MD, Fulton EA, Day RW (2015) Using an Atlantis model of the southern Benguela to explore  
2 the response of ecosystem indicators for fisheries management. *Environ Model Softw* 69:23–41

3 Smout S, Rindorf A, Hammond PS, Harwood J, Matthiopoulos J (2013) Modelling prey consumption  
4 and switching by UK grey seals. *ICES J Mar Sci* 71:81–89

5 Stefánsson G, Sigurjónsson J, Víkingsson G (1997) On Dynamic Interactions Between Some Fish  
6 Resources and Cetaceans off Iceland Based on a Simulation Model. . *J North Atl Fish Sci* 22:357–  
7 370

8 Spitz J, Trites AW, Becquet V, Brind'Amour A, Cherel Y, Galois R, Ridoux V (2012) Cost of living  
9 dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator  
10 foraging strategies. *PloS one* 7:e50096

11 Spitz J, Ridoux V, Trites AW, Laran S, Authier M (2017) Prey consumption by cetaceans reveals the  
12 importance of energy-rich food webs in the Bay of Biscay. *Prog Oceanogr* 166:148–158

13 Spitz J, Rousseau Y, Ridoux V (2006) Diet overlap between harbour porpoise and bottlenose dolphin:  
14 An argument in favour of interference competition for food? *Estuar Coast Shelf Sci* 70:259–270

15 Swain DP, Benoît HP (2015) Extreme increases in natural mortality prevent recovery of collapsed  
16 fish populations in a Northwest Atlantic ecosystem. *Mar Ecol Prog Ser* 519:165–182

17 Tatar B, Jung C (2018) Getting to know the consumer: Toward mitigation of illegal whale meat  
18 consumption in South Korea. *Mar Policy* 89:116–123

19 Tegner MJ, Dayton PK (2000) Ecosystem effects of fishing in kelp forest communities. *ICES J Mar*  
20 *Sci* 57:579–589

21 Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S and others (2010) Distance software:  
22 design and analysis of distance sampling surveys for estimating population size. *J Appl Ecol* 47:5–  
23 14

24 Tinker MT, Bentall G, Estes JA (2007a) Food limitation leads to behavioral diversification and  
25 dietary specialization in sea otter. *PNAS* 105:560–565

- 1 Tinker MT, Costa DP, Estes JA, Wieringa N (2007b) Individual dietary specialization and dive  
2 behaviour in the California sea otter: Using archival time–depth data to detect alternative foraging  
3 strategies. *Deep Sea Res II* 54:330–342
- 4 Tjelmeland S, Lindstrøm U (2005) An ecosystem element added to the assessment of Norwegian  
5 spring-spawning herring: implementing predation by minke whales. *ICES J Mar Sci* 62:285–294
- 6 Torres MÁ, Coll M, Heymans JJ, Christensen V, Sobrino I (2013) Food-web structure of and fishing  
7 impacts on the Gulf of Cadiz ecosystem (South-western Spain). *Ecol Modell* 265:26–44
- 8 Tønnessen JN, Johnsen AO (1982) The history of modern whaling, Vol. University of California  
9 Press, Berkeley and Los Angeles
- 10 Travers M, Watermeyer K, Shannon LJ, Shin YJ (2010) Changes in food web structure under  
11 scenarios of overfishing in the southern Benguela: Comparison of the Ecosim and OSMOSE  
12 modelling approaches. *J Mar Syst* 79:101–111
- 13 Trites AW, Christensen V, Pauly D (1997) Competition Between Fisheries and Marine Mammals for  
14 Prey and Primary Production in the Pacific Ocean. *J Northw Atl Fish Sci* 22:173–187
- 15 Trites AW, Christensen V, Pauly D (2006) Effects of fisheries on ecosystems: just another top  
16 predator? In: Boyd IL, Wanless S, Camphuysen CJ (eds) *Top predators in marine ecosystems*.  
17 Cambridge University Press, Cambridge, p 11–27
- 18 Tromeur E, Loeuille N (2017) Balancing yield with resilience and conservation objectives in  
19 harvested predator-prey communities. *Oikos* 126:1780–1789
- 20 Twardek WM, Elvidge CK, Wilson ADM, Algera DA and others (2017) Do protected areas mitigate  
21 the effects of fisheries-induced evolution on parental care behaviour of a teleost fish? *Aquatic*  
22 *Conserv: Mar Freshw Ecosyst* 27:789–796
- 23 Tyrrell LP, Newsome SD, Fogel ML, Viens M, Bowden R, Murray MJ (2013) Vibrissae growth rates  
24 and trophic discrimination factors in captive southern sea otters (*Enhydra lutris nereis*). *J Mammal*  
25 94:331–338

- 1 Urian K, Gorgone A, Read A, Balmer B and others (2015) Recommendations for photo-identification  
2 methods used in capture-recapture models with cetaceans. *Mar Mam Sci* 31:298–321
- 3 Uusi-Heikkilä S, Whiteley AR, Kuparinen A, Matsumura S, Venturelli PA and others (2015) The  
4 evolutionary legacy of size-selective harvesting extends from genes to populations. *Evol Appl*  
5 8:597–620
- 6 Uusi-Heikkilä S, Wolter C, Klefoth T, Arlinghaus R (2008) A behavioral perspective on fishing-  
7 induced evolution. *Trends Ecol Evol* 23:419–421
- 8 van Bleijswijk JDL, Begeman L, Witte HJ, Ijsseldijk LL, Brasseur S, Gröne A, Leopold MF (2014)  
9 Detection of grey seal *Halichoerus grypus* DNA in attack wounds on stranded harbour porpoises  
10 *Phocoena phocoena*. *Mar Ecol Prog Ser* 513:277–281
- 11 van Neer A, Jensen LF, Siebert U (2015) Grey seal (*Halichoerus grypus*) predation on harbour seals  
12 (*Phoca vitulina*) on the island of Helgoland, Germany. *J Sea Res* 97:1–4
- 13 Valdés HF (2004) El problema pesquero con los delfines y su persecución en Galicia (Siglos XIII al  
14 XX). *Cuadernos de Estudios Gallegos*, Tomo LI (Fascículo 117), 313
- 15 Valdés HF (2009) Pescadores y delfines en el norte de España. Historia de su interacción desde la  
16 Edad Media hasta el siglo XX. *Itsas Memoria. Revista de Estudios Marítimos Del País Vasco*,  
17 6:629–641.
- 18 Villasante S, Arreguín-Sánchez F, Heymans JJ, Libralato S and others (2016) Modelling marine  
19 ecosystems using the Ecopath with Ecosim food web approach: New insights to address complex  
20 dynamics after 30 years of developments. *Ecol Modell* 331:1–4
- 21 Vincent C, Huon M, Caurant F, Dabin W, Deniau A and others (2017) Grey and harbour seals in  
22 France: Distribution at sea, connectivity and trends in abundance at haulout sites. *Deep Sea Res II*  
23 141:294–305
- 24 Wade PR, Reeves RR, Mesnick SL (2012) Social and Behavioural Factors in Cetacean Responses to  
25 Overexploitation: Are Odontocetes Less “Resilient” Than Mysticetes? *J Mar Biol* 2012:1–15

- 1 Wahlberg M, Westerberg H, Aarestrup K, Feunteun E, Gargan P, Righton D (2014) Evidence of  
2 marine mammal predation of the European eel (*Anguilla anguilla* L.) on its marine migration. Deep  
3 Sea Res Part 1 Oceanogr Res Pap 86:32–38
- 4 Waite JN, Trumble SJ, Burkanov VN, Andrews RD (2012) Resource partitioning by sympatric Steller  
5 sea lions and northern fur seals as revealed by biochemical dietary analyses and satellite telemetry.  
6 J Exp Mar Biol Ecol 416-417:41–54
- 7 Watt J, Siniff DB, Estes JA (2000) Interdecadal patterns of population and dietary change in sea otters  
8 at Amchitka Island, Alaska. Oecologia 124:289–298
- 9 Weise MJ, Harvey JT (2005) Impact of the California sea lion (*Zalophus californianus*) on salmon  
10 fisheries in Monterey Bay, California. Fish Bull 103:685–696
- 11 Williams TM, Estes JA, Doak DF, Springer AM (2004) Killer appetites: Assessing the role of  
12 predators in ecological communities. Ecology 85:3373–3384
- 13 Wright PJ, Trippel EA (2009) Fishery-induced demographic changes in the timing of spawning:  
14 consequences for reproductive success. Fish Fish 10:283–304
- 15 Worm B, Hilborn R, Baum JK, Branch TA and others (2009) Rebuilding Global Fisheries. Science  
16 325:578–585
- 17 Yodzis P (2001) Must top predators be culled for the sake of fisheries? Trends Ecol Evol 16:78–84
- 18 Young JW, Hunt BPV, Cook TR, Llopiz JK and others (2015) The trophodynamics of marine top  
19 predators: Current knowledge, recent advances and challenges. Deep Sea Res II 113:170–187
- 20 Zappes CA, Gatts CEN, Lodi LF, Simões-Lopes PC and others (2014) Comparison of local  
21 knowledge about the bottlenose dolphin (*Tursiops truncatus* Montagu, 1821) in the Southwest  
22 Atlantic Ocean: New research needed to develop conservation management strategies. Ocean Coast  
23 Manag 98:120–129

- 1 Zhou S, Smith AD, Punt AE, Richardson AJ and others (2010) Ecosystem-based fisheries
- 2 management requires a change to the selective fishing philosophy. Proc Natl Acad Sci USA
- 3 107:9485–9489

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><sup>14/15</sup>N analysis</i>	<i><sup>12/13</sup>C analysis</i>	<i>Fatty acid analysis</i>	<i>Faecal analysis</i>	<i>Other methods</i>	
<b>Sea otters</b>	+	-	-	-	-	+	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><sup>14/15</sup>N analysis</i>	<i><sup>12/13</sup>C analysis</i>	<i>Fatty acid analysis</i>	<i>Faecal analysis</i>	
<b>Sea otters</b>	-	-	+	+	-	-	-	Tyrell et al. 2013 (in captivity, USA)
	-	-	+	+	-	-	-	Elliot Smith et al. 2015 (California, USA, NE Pacific)
<b>Pinnipeds</b>	-	-	-	-	+	-	-	Laake et al. 2002 (Columbia River, NE Pacific)
	-	-	-	-	-	+	-	Sinclair & Zeppelin 2002 (Bering Sea, N Pacific)
	-	-	-	-	+	-	<b>Attached cameras</b>	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)
	-	+	-	-	-	+	<b>Bayesian approach</b>	Sinclair et al. 2008 (Central Bering Sea, N Pacific)
	-	-	-	-	-	+	<b>DNA barcoding</b>	Deagle et al. 2009 (SE Australia, SW Pacific)
	-	-	-	-	-	+	-	Huisamen et al. 2012 (SW Africa, SE Atlantic)
	-	-	+	+	+	-	<b>GPS telemetry</b>	Waite et al. 2012 (E Russia, NE Pacific)
	-	-	-	-	-	-	<b>DNA barcoding</b>	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)

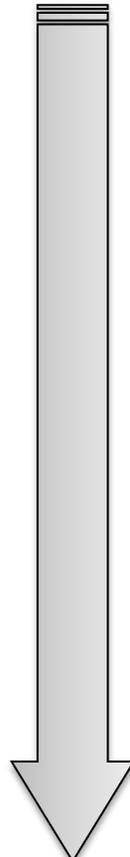
<i>Marine mammal group</i>	<i>Applied methods</i>							<i>Examples of study cases (study/sampling area)</i>
	<i>Field observation methodology</i>	<i>Stomach content analysis</i>	<i><sup>14/15</sup>N analysis</i>	<i><sup>12/13</sup>C analysis</i>	<i>Fatty acid analysis</i>	<i>Faecal analysis</i>	<i>Other methods</i>	
<b>Pinnipeds</b>	-	-	+	+	-	-	-	Sepúlveda et al. 2017 (S Chile, SE Pacific)
<b>Pinnipeds</b>	-	+	-	-	-	-	DNA barcoding	Méheust et al. 2014 (NW France, NE Atlantic)
<b>+ toothed whales</b>	-	+	+	+	-	-	-	Franco-Trecu et al. 2017 (Uruguay estuary, SW Atlantic)
<b>Toothed whales</b>	-	-	+	+	-	-	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><sup>14/15</sup>N analysis</i>	<i><sup>12/13</sup>C analysis</i>	<i>Fatty acid analysis</i>	<i>Faecal analysis</i>	<i>Other methods</i>	
<b>Toothed whales</b>	-	-	+	+	-	-	-	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)
<b>Baleen whales</b>	-	-	-	-	-	-	DNA barcoding	Jarman et al. 2002 (S Australia, SE Indian Ocean)
	-	+	-	-	-	-	-	Konishi et al. 2014 (Ross Sea, E Antarctica)

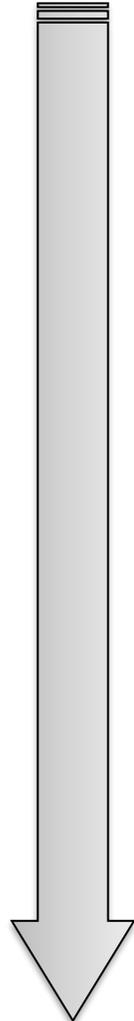
8

9

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.

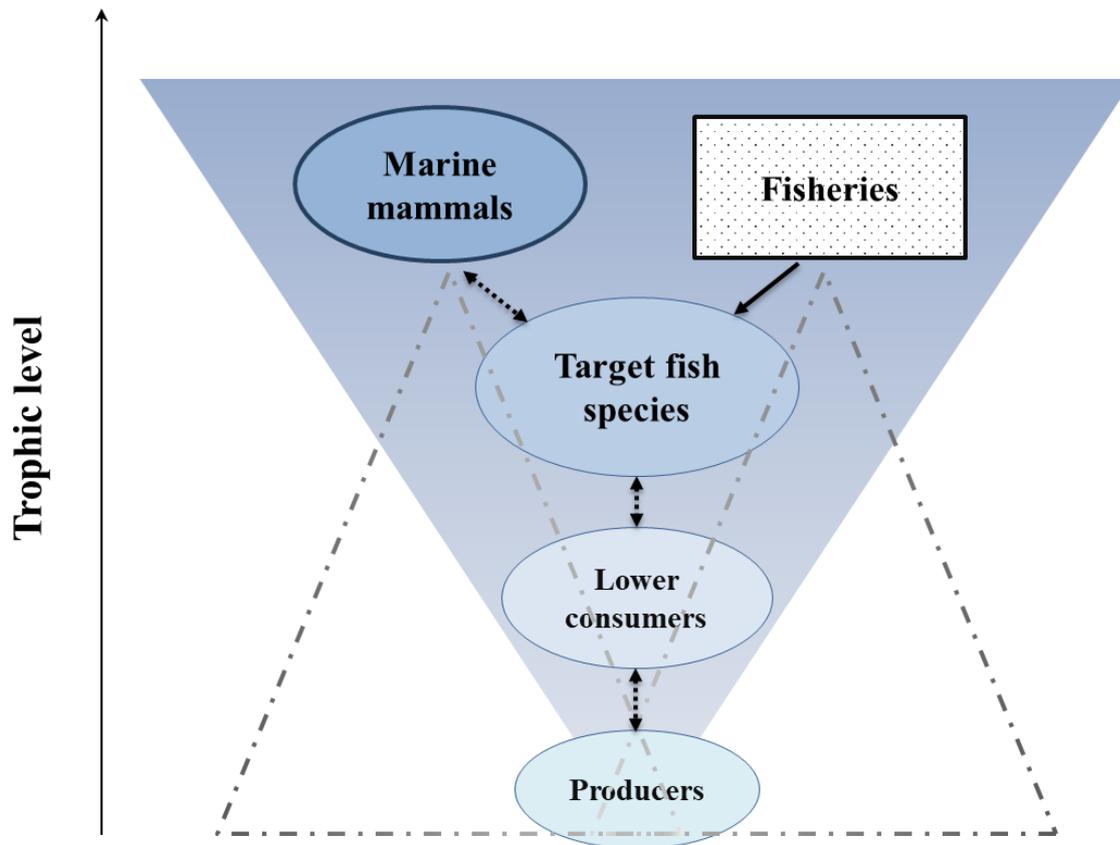


<i>Model category (abbreviation/acronym)</i>	<i>Primary model characteristics and application</i>	<i>Prey–predator interactions and predator function</i>	<i>Supporting EBFM objectives</i>
Extended Single-species Assessment Models (ESAM)	<ul style="list-style-type: none"> <li>- extended fisheries assessment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



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

17 **Figures with legends**



18

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.