Charles University in Prague, Faculty of Science

Department of Ecology

Marine Mammals as Apex Predators

Bachelor Thesis

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I hereby declare that I am the sole author of this bachelor thesis and that I have not used any sources other than those listed in the bibliography and identified as references. I further declare that I have not submitted this thesis at any other institution in order to obtain a degree.

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Summary

Amongst marine mammals there are many predators, however only four species can be considered truly apex predators. Polar bears, killer whales, leopard seals and sperm whales all dominate their environments, moreover, killer whales and sperm whales hold their position at the top of trophic relationships globally. Apart from being generally abundant and being large in relation to their closely related species, these four predators share very little. They differ in social structure, foraging ecology, life histories and levels of intraspecific cooperation. Very few studies focus on what characteristics makes each one of them such a dominant predator. Considering how abundant these species and their prey are, there is not enough research exploring predatory and non-predatory interactions with other large mammalian predators of our oceans. Our understanding of trophic relationships, large predators' influence on species hierarchy and ecosystem balance is poor. Considering the influence human population has on the oceans and large marine predators, more future research should be focused on exploring the complex interspecific relationships.

Key words

apex predators, marine mammals, killer whale, *Orcinus orca*, polar bear, *Ursus maritimus*, leopard seal, *Hydrurga leptonyx*, sperm whale, *Physeter macrocephalus*

Abstrakt

Mezi mořskými savci najdeme mnoho predátorů, nicméně pouze čtyři druhy z nich můžeme považovat za pravé vrcholové predátory. Medvědi lední, kosatky dravé, tuleni leopardí a vorvani obrovští jasně vládnou ve svých prostředích, kosatky a vorvani jsou navíc na vrcholu globálně. Kromě toho, že jsou tyto druhy obecně hojné v počtech jedinců a že jsou relativně velcí v porovnání s blízce příbuznými druhy, nesdílí tito čtyři predátoři mnoho. Liší se v tvorbě sociálních skupin, ekologii lovu, life-history znacích a úrovních vnitrodruhové spolupráce. Jen velmi málo studií se zaměřuje na zkoumání konkrétních charakteristik, které by jednotlivé predátory dělaly tak dominantními. Když zvážíme, jak hojné tyto druhy i jejich kořist jsou, je vidno, že studií, které by zkoumaly predační nebo nepredační interakce s dalšími velkými savci – predátory, bylo provedeno nedostatečné množství. Naše porozumění trofickým vztahům, vlivu velkých predátorů na hierarchii druhů a rovnováhu ekosystému je chabé. Zvážíme-li, jak velký vliv má lidská populace na naše oceány a velké mořské predátory, je zjevné, že je třeba se v budoucím výzkumu zaměřit na zkoumání komplexních mezidruhových vztahů.

Klíčová slova

vrcholoví predátoři, mořští savci, kosatka dravá, *Orcinus orca*, medvěd lední, *Ursus maritimus*, leopard seal, *Hydrurga leptonyx*, vorvaň obrovský, *Physeter macrocephalus*

Table of Contents

Introduction

Large marine mammals influence ecosystem through trophic cascades and thus have impact on populations of many other marine species. For many large mammals the most dangerous and for some the only threat is humans. The human population has destructive effect on a lot of marine ecosystems caused by pollution, fishing (including bycatch) and whaling. Population declines caused by human activity have been documented in many marine species. However, we know virtually nothing about complex changes and imbalance of the ecosystems we as humans can trigger by removing (or partially removing) apex predators, locally or globally. Therefore, it is very important to study apex predators of our oceans in depth, so we are able to better understand what their domination means to the ecosystems they inhabit and species they interact with directly, indirectly, in both predatory and non-predatory ways.

It is not always easy to determine whether a large carnivorous mammal is an apex predator or not. We lack a unified definition of the term and we do not know if mesopredators can take on the role of an apex predator with everything it consists of because we are unsure of what this 'everything' is. In comparison to land predators, the marine top predators and the trophic relationships they help to form are in vast majority of cases poorly studied.

The predators discussed in this thesis are indisputably rulers of their environments. But why are there merely a few apex predators in all marine waters of the world and how is it possible that polar bears, killer whales, sperm whales and leopard seals do not face any natural threats or even comparable competition? Answering these questions is harder than it may seem and the answers may, due to the lack of research, often take form of speculations and call for being explored further.

In the following chapters I am trying to present a summary of relevant information about the apex predators among marine mammals. I discuss what makes them top predators in their environments as well as point out the missing evidence and uncertainties. I compare their prey species and foraging ecology in hope to find similarities in comparably dominant predators of limited (polar bears and leopard seals) and global (killer whales and sperm whales) distribution. I try to suggest reasons why these four mammals established their position at the top of the ecosystems and whether the globally dispersed ones are truly dominant across all of their distribution areas. I believe this thesis offers a good summary of the admittedly little we know about top predators' influence on marine ecosystems' structure and highlights possible areas of future study in order to better understand oceanic relationships and the brittle balance of our sea environments so we can responsibly regulate our human impact on oceanic organisms and ecosystem as a whole and improve the way we protect, or at the very least coexist with, different environments.

1 Defining apex predators in marine mammals

Firstly, it is important to define what mammals are and are not apex predators. If we define an apex predator as an organism that has no natural predators, we are left with merely a few examples in the ocean. Some only consider the killer whales (*Orcinus orca*) and polar bears (*Ursus maritimus*) to be truly apex carnivores ([1]Kiszka et al., 2015), others include members of Phocidae, Odobenidae, Ziphiidae, sperm whales, dolphins and sea otters in the list.

Another definition suggests that apex predators are characterized by top-down interactions, inhibition of smaller animals and promotion of biodiversity ([2]Wallach et al., 2015) and that they are vulnerable to extinction ([3]Ripple et al., 2014). Removing or overharvesting apex consumers then shifts the established balance of the ecosystem, whether it is through purposeful manipulations or natural population declines, reintroductions, or extinctions, the evidence points to the fact that the top-down interactions are essential in structuring ecosystems. This theory supports the claim that even sea otters belong to apex carnivores. ([4]Estes et al., 2011, [5]Estes & Duggins, 1995). However, they are commonly preyed on by killer whales ([6]Jefferson et al., 1991) and thus will be excluded from this thesis.

1.1 The line between apex predators and mesopredators

Predators are also divided into groups by size, although this has been disputed to be imprecise and unrelated to the ecological aspects of the problem, so other factors and typical behavioral traits are used as well to define the predator either as a large apex predator or a mesopredator. But is there a clear line between the two groups? To answer the question let's have a look at a phenomenon called mesopredator release. It is an ecological phenomenon occurring when the top-down control is removed. In some cases, mesopredators can take on a role of an eradicated top predator and their behavior shifts to adapt and resemble the one of the apex predator. However, mesopredators have fundamentally different relationships with humans and ecosystems, and should be able to exploit prey resources more thoroughly than top predators ([7]Prugh et al., 2009). This is a key difference that speaks against the possible mesopredators' ability to replace apex predators in ecosystems, suggesting that they remain mesopredators and show mesopredators traits and behavior even in a system without an apex predator ([2]Wallach et al., 2015).

Apex predators are usually, although not without exceptions, larger, and their size among other traits makes them relatively safe from predation. That is why, when trying to define apex predators, we can also characterize them by manners in which they limit their population growth, such as bottom-up regulation (population size declines with declining abundance of prey), and self-regulating mechanisms that the mesopredators lack. Studies on bears, large cats and others offer evidence that social interactions, rather than resource availability, enable self-regulation in top predator populations ([2]Wallach et al., 2015).

1.2 Established definition

What organisms will be considered apex predators for the sake of this thesis? First important point is that an apex predator has a few to no natural predators ([2]Wallach et al., 2015). Carnivorous mammals with no predators at all, mammals with no or very few

documented cases of predation on adults, and mammals that are rarely hunted by another predator and if so, mainly not as a food source, are chosen for the purposes of this thesis.

Second criterion, an apex predator creates structured hierarchy of species through cascading effects in the food chain and is a key part in maintaining biodiversity and balance of an ecosystem ([4]Estes et al., 2011).

And last but not least, an apex predator should have at least some population self-regulating mechanisms. It is suggested that self-regulating mechanisms may be tied to social interactions that influence life history traits responsible for decelerating the population growth ([2]Wallach et al., 2015). The social interactions in question were studied mainly on terrestrial predators and because this theory is quite new there is usually not enough evidence of self-regulating mechanisms of our chosen species.

The definition of predation used in my characterization of apex predators is according to Weller limited to situations in which an animal expends time and energy to locate living prey, and exerts additional effort to kill and consume it. It excludes parasitism, filter feeding, scavenging, or browsing ([8]Weller, 2009).

1.3 Excluded species

1.3.1 Sea otters (Enhydra lutris)

I have already mentioned a few reasons why sea otters could be considered apex predators. They are responsible for the biodiversity of an ecosystem, their presence causes abundance of plants, namely Alaskan kelp forests, as they are on top of the three-trophic-level cascade ([5]Estes & Duggins, 1995). This and their vulnerability to extinction, so common in apex predators, would speak for including them, however, sea otters are a common, even though not always preferred, prey of sharks, killer whales, Russian brown bears, and bald eagles ([8]Weller, 2009).

1.3.2 Beaked whales (Ziphiidae)

Beaked whales definitely have the potential to be on the top, they are deep-diving predators with remarkable characteristics that allow them to dive as deep as 1,000m ([9]Tyack et al., 2006, as cited in Southall et al., 2019). Their ecology is very similar to the one of sperm whales. Both are deep diving. Both frequently inhabit shelf-edge and the Gulf Stream waters, although there are slight differences, sperm whales generally prefer warmer off shelf water and beaked whales tend to stay in the colder shelf edge parts ([10]Waring et al., 2001). Their diets and feeding behavior are also similar, both feed on cephalopods, mainly squid ([10]Waring et al., 2001, [11]MacLeod et al., 2003). However, unlike sperm whales, beaked whales are a common prey of white sharks, despite their size ([12]Long & Jones, 1996, as cited in Heithaus, 2001).

1.3.3 Pinnipedia

Pinnipeds present the possibly most hunted group of marine mammals. Large Arctic pinnipeds like walruses (Odobenidae) and bearded seals (*Erignathus barbatus*) despite their size, and in case of walruses even despite their ability to defend themselves and wound the

attacker significantly, are not safe from predation from polar bears ([8]Weller, 2009, [13]Ovsyanikov, 1995).

More globally widespread elephant seals (*Mirounga spp.*) face predation by sharks and killer whales. Elephant seals, fur seals (*Arctocephalus spp.*) and other pinnipeds inhabiting the Antarctic are often preyed on by leopard seals (*Hydruga leptonyx*).

Steller sea lions and California sea lions are commonly hunted by killer whales ([8]Weller, 2009, [14]Maniscalco et al., 2007), fur seals, Steller, California, New Zealand and Australian sea lions often become prey for sharks ([8]Reidman, 1990, as cited in Weller, 2009, [15]Anderson et al., 2008, [16]Loughlin & York, 2000).

That is to mention only the largest predators of pinnipeds, moreover, we can enumerate other terrestrial threats that prey mostly on pups of Otariids like wolves, eagles and brown bears, brown hyenas or arctic foxes, just to name a few ([8]Weller, 2009).

But we can also find important predators amongst the pinnipeds. In the Southern Hemisphere it is leopard seals (*Hydrurga leptonyx*) and walruses in the Northern Hemisphere. Even though walruses are known to be benthic feeders, they are habitual consumers of various species of seals (Phocidae; [17]Lowry & Fay, 1984). They have the potential to be apex predators of the Arctic but in this imaginary competition they are surpassed by polar bears. Although both of the two large predators usually share the space and resources amicably, they can and do easily wound one another. Polar bears prey on walruses rather scarcely but from time to time walruses become their primary food source ([13]Ovsyanikov, 1995) and that is why for the purpose of this thesis I will not consider them apex predators.

Leopard seals are the only truly apex predators found in pinnipeds, the reasons for which are explained further in the thesis.

1.3.4 Delphinidae

We have already established that killer whales, members of delphinids, are the ocean's most ferocious predators. It would be only logical to assume that we might find more similarly successful predators in this group. However, evidence of predation on dolphins can be found, moreover, predation pressure is an important factor in shaping of dolphin schools ([18]Norris & Dohl, 1980, as cited in Maldini, 2003). And most dolphins are often hunted by various species of sharks ([12]Heithaus, 2001, [8]Weller, 2009, [19]Sprogis et al., 2018). Predation by killer whales on some of the dolphin species was also documented. Although predation on tropical and open-ocean delphinids is low to none, these species are commonly hunted by sharks ([6]Jefferson et al., 1991, [20]Crovetto et al., 1992, [21]Constantine et al., 1998).

The one species suspiciously missing from the enumeration of killer whales and sharks prey is Risso's dolphin (*Grampus griseus*). The most plausible explanation for this is the lack of research done on Risso's dolphin, sharks and killer whales are likely predators of this species ([22]Bearzi et al., 2011).

2 Polar bear (*Ursus maritimus*)

2.1 Apex predator traits

We have already established that polar bears are one of the true apex predators in marine mammals ([1]Kiszka et al., 2015). They primarily hunt ringed seals (*Phoca hispida*) and to a lesser degree bearded seals which are more important to bears in the western arctic, however, there is some evidence of polar bears occasionally preying on harp seals, walruses beluga and bowhead whales ([23]Stirling, 2009, [24]Stirling & Archibald, 1977, [25]Freeman, 1973, [26]Galicia et al., 2016). It is clear that ringed and bearded seals are the main prey of polar bears because they display flight response upon noticing polar bear's presence more instantly than for example harp seals ([27]Smith & Stirling, 2019).

The trophic relationships of the Arctic have been extensively studied and confirm polar bear's position at the very top ([28]Hobson & Welch, 1992). Polar bears are along with the arctic foxes (that solely prey on pups) the main predators of ringed seals, thus it safe to suggest that they have a significant effect on the Arctic fauna hierarchy ([29]Smith & Lydersen, 1991). It can be assumed that polar bears have indirect effects on the ecosystem's hierarchy, too, because they often consume only the blubber of ringed seals and leave the carcasses behind for smaller bears, arctic foxes or bird to scavenge ([30]Stirling & McEwan, 1975, [24]Stirling & Archibald, 1977).

2.2 Distribution and habitat

Polar bears inhabit the circumpolar Arctic (see *Fig. 1*) and they are sea ice dependent. In 2018 the estimated global population was about 23,000 bears. The global population is divided into 19 subpopulations based on variables such as site fidelity and genetics. Ringed seals present the major prey for each one of the subpopulations and thus it is logical that polar bear habitat directly corresponds with distribution of ringed seals ([31]Stirling & Øritsland, 1995, [32]Hamilton & Derocher, 2019).

Polar bears are distributed in Arctic areas of annual ice cover over the continental shelf, in some areas they might move to multiyear ice cover seasonally, remaining sea ice bound year-round. Annual sea ice in lower latitudes, such as Hudson Bay and Foxe Basin, melts thoroughly every year, thus forcing bears to move on land to fast for several months ([33]Laidre et al., 2008, [34]Derocher, 2004). Fasting occurs in all subpopulations and is usually tightly connected to break-up and freeze-up dates of annual ice that affect the abundance and accessibility of prey. During this time polar bears use stored adipose tissue and are able to survive and successfully reproduce ([34]Watts & Hansen, 1987, as cited in Derocher, 2004, [35]Stirling & Derocher, 1993, [36]Sciullo et al., 2017).

Bears depend on sea ice for several reasons, all of which are very well documented. They need ice covered areas to hunt, to breed, and to access terrestrial denning areas, sometimes even to den on ice cover as we can see in northerly areas such as Beaufort Sea. ([33]Laidre et al., 2008, [35]Stirling & Derocher, 1993).

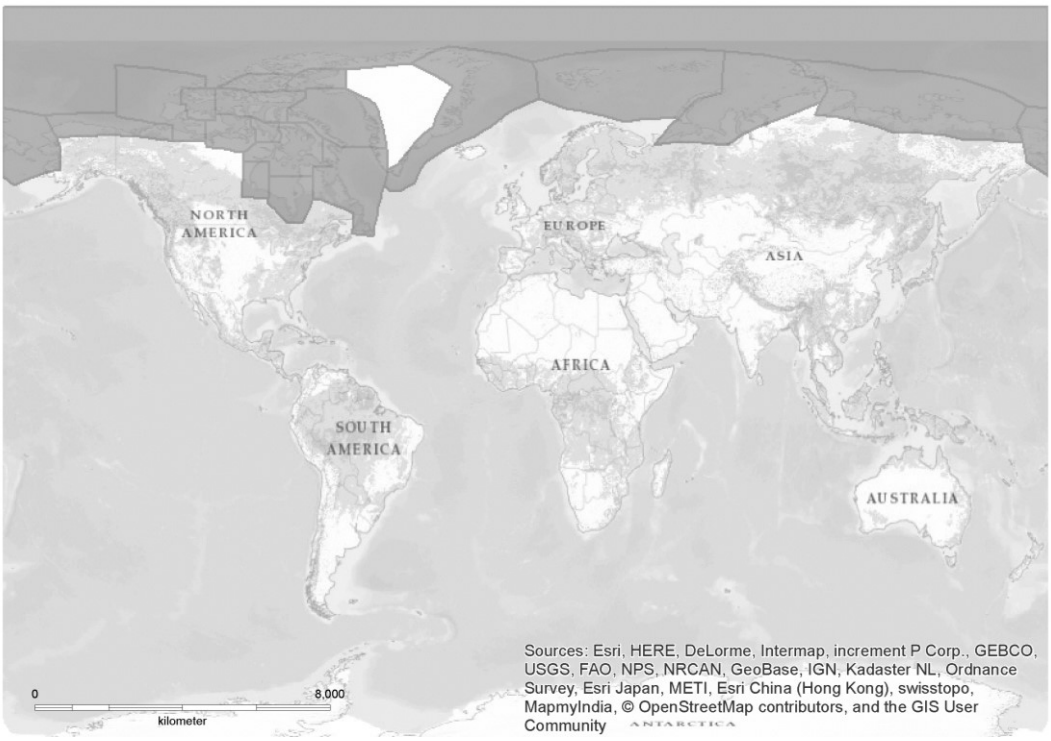

Figure 1 *Map of polar bear distribution, compiled by IUCN ([37]Wiig et al., 2015)*

2.3 Foraging ecology

As mentioned previously, polar bears depend on sea ice for foraging on species of seals, most importantly ringed seals which are present in the diet of all 19 polar bear subpopulations ([32]Hamilton & Derocher, 2019). Studies agree that bears prefer taking ringed seal pups and adults to juveniles, estimating that pups constitute from 38-50% of all ringed seal prey, the older studies stating the higher limit ([38]Pilfold, 2012, [24]Stirling & Archibald, 1977). The differing data may be explained by different study areas or polar bear foraging ecology changing during the years between the studies. However, the tendency for preying upon ringed seal pups, mainly in spring, is clear.

The additional prey species differ from area to area. Typically, polar bears include bearded seals in their diet, locally available species like beluga whales and harp seals are important prey to bears in some areas. Researchers also described cases of polar bears feeding on bowhead whales in Alaskan waters ([39]Bentzen et al., 2007). In nutrient-rich waters, for example in Baffin Bay, the prey species diversity is the highest ([40]Galicia et al., 2015, [41]Thiemann et al., 2008).

Polar bear foraging activity is tied to behavior and life history of their main prey species, ringed seals. The sustenance intake increases in spring before the break-up of sea ice that forces polar bears on the land thus reducing their preying possibilities to minimum. The most common hunting habitats are on land-fast ice, because those areas present the perfect environment for ringed seal subnivean birth lairs and breathing holes. Polar bears hunt by waiting by the breathing holes for a resurfacing seal, digging seals out from their lairs or less often stalking hauled-out individuals on ice ([23]Stirling, 2009, [24]Stirling & Archibald, 1977). One of the reasons polar bears choose still-hunting may be because walking and swimming uses strikingly more energy than lying down and waiting. Studies show that even a successful

moving-hunt does not cover the energetic costs of the movements for polar bears ([42]Stirling & Derocher, 1990).

During the open-water period most seals become pelagic and polar bears lose the opportunity to prey on them as catching prey in the water is rather difficult for them and not worth the energy spent ([38] Pilfold et al., 2012). Due to the reduced possibilities of foraging, bears fast during the period from break-up to freeze-up of the ice. This fasting period takes about four months but it is getting progressively longer as the dates of break-up and freeze-up become earlier due to the warming climate, fasting takes up to 8 months for pregnant females ([36]Stirling et al., 1977, as cited in Sciullo et al., 2017, [43]Johnson et al., 2019, [34]Derocher, 2004). Polar bears might occasionally take advantage of the onshore food resources ([42]Stirling & Derocher, 1990). The long fasting periods are only possible upon consumption of high-energy prey in spring and the ability to store the energy in adipose tissue, making it accessible for long periods of time ([36]Sciullo et al., 2017, [34]Watts & Hansen, 1987, as cited in Derocher, 2004, [24]Stirling & Archibald, 1977).

3 Killer whale (*Orcinus orca*)

3.1 Apex predator traits

Killer whales are carnivorous apex predators and without a doubt one of the most successful predators in the world. Humans are the only major threat to killer whales, they have no natural predators. ([44]Ford, 2009, [1]Kiszka et al., 2015)

They are responsible for many pinniped population declines and inhibition of population recovery and their top-down influence is also well documented in case of the killer whale-otter-kelp cascade in Alaska ([1]Kiszka et al., 2015, [45]Estes et al., 1998). Killer whales ecological influence lies in establishing trophic relationships by direct predator pressure and by behaviorally mediated indirect interactions ([1]Kiszka et al., 2015).

Killer whales are not likely to show drastic changes in their population size when changes in prey abundance occur ([46]Barrett-Lennard et al., 1995). This may point to the fact that not only bottom-up factors but also self-regulating mechanisms take part in their population control.

3.2 Distribution and ecological differences

Killer whales are along with humans the most widely distributed mammals in the world (see *Fig. 2*). They inhabit all oceans and most seas showing preference for coastal, temperate, highly productive waters ([44]Ford, 2009). The global abundance estimate is 50,000 individuals of all ecotypes, however the number is likely higher ([47]Reeves et al., 2017).

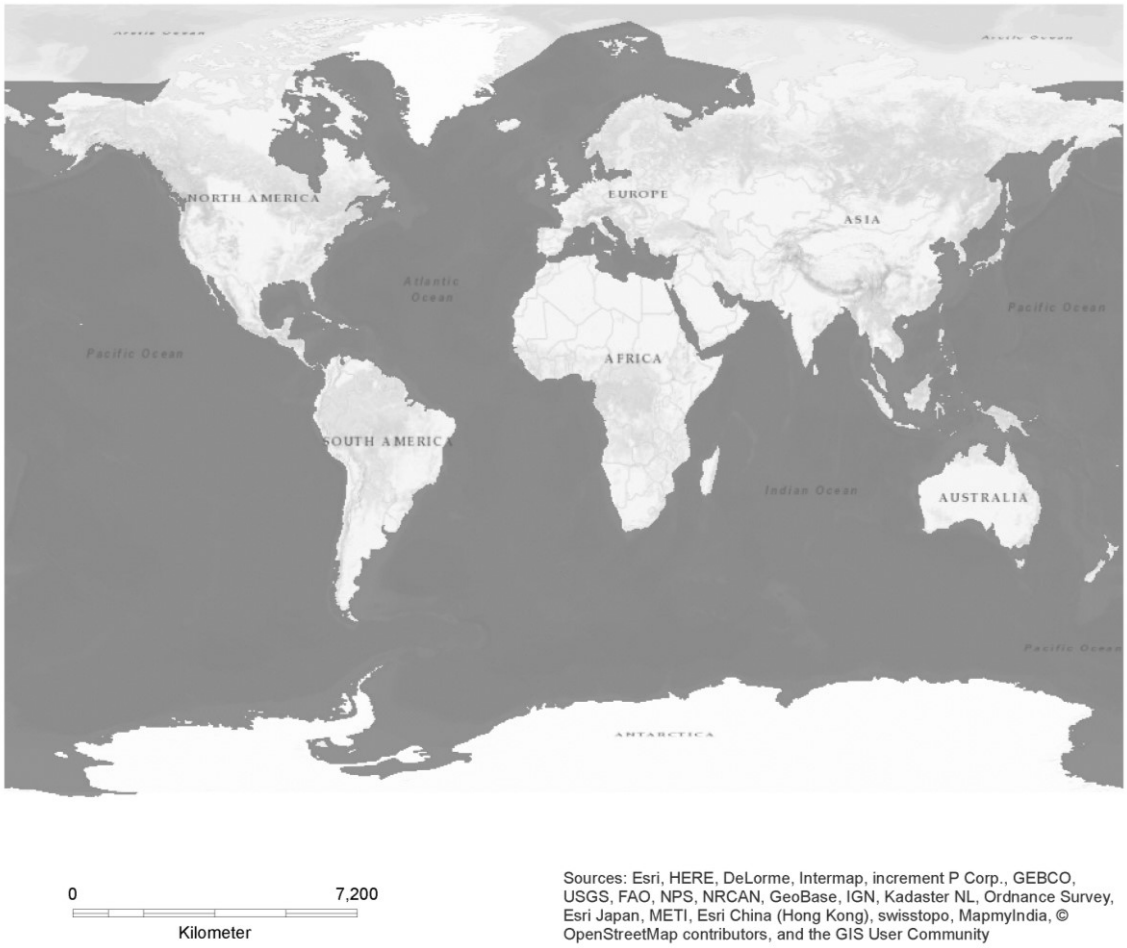

Figure 2 Map of killer whale distribution, compiled by IUCN ([47]Reeves et al., 2017)

Among killer whales we can find various ecotypes that differ in morphology, genetics, ecology, behavior and taken prey, the ecotypes do not interbreed with each other. It has been suggested many times since the 1980s that the different forms can be distinct species. Despite the evidence presented by many independent studies, the ecotypes are still officially seen to belong to one species *Orcinus orca*. The differences are most notable in Arctic, Antarctic and adjacent areas. In North Pacific we can find three types: the transient mammal eating type whale, the resident type whale feeding on large fish and the offshore whale which presumably feeds on sharks ([44]Ford, 2009, [48]Filatova et al., 2019, [49]Ford et al., 2014, [50]Pitman & Ensor, 2003).

In the Antarctic there are type A mammal eating (primarily hunting whales) open-water whales with circumpolar distribution, type B whales hunting pinnipeds on pack ice and inhabiting inshore waters, and type C whales feeding on fishes. Even though the Arctic and Antarctic types conspicuously resemble each other, there are divergences between Arctic and Antarctic killer whales in general and each of the three types in each region differs from the other two in habitat preferences, morphology and reproduction isolation. Furthermore, divergence among the Antarctic ecotypes seems to be more pronounced than that of North Pacific ones ([50]Pitman & Ensor, 2003). However, especially in recent literature, types A, B and C are often used to describe the non-Antarctic killer whales as well ([51]Pitman et al., 2020).

Differences amongst North Atlantic killer whales have also been described. Ecotype 1 mainly preys on herring, Atlantic mackerels or bluefin tunas and other fish, sometimes taking seals as prey too. This varies among the ecotype's groups. Ecotype 2 is highly specialized and feeds on baleen whales. Hitherto, there is very few data on which the assumptions about ecology and distribution of this killer whale type are based ([52]Jourdain et al., 2019).

Ecotype D was described for the first time 50 years ago and little research has been done on this subantarctic killer whale type in recent years. It is morphologically easily distinguishable from the other ecotypes and inhabits subantarctic waters around New Zealand and the southern tip of South America ([51]Pitman et al., 2020).

Caribbean killer whales are not as obviously varied as the Arctic, Antarctic or Atlantic ones, although they are showing some similarities to Atlantic type 2 and to whales of tropical West African waters ([53]Weir et al., 2010). They feed on various sea turtle species and marine mammals ([54]Bolaños-Jiménez et al., 2014). The available data suggests that killer whales inhabit tropical waters during all seasons, however it is unclear whether the same groups stay in the areas all year round or whether groups seasonally come and go.

3.3 Foraging ecology

Killer whales are generalists in their diets as a species, however ecotypes and even regional groups in those ecotypes specialize on various kinds of prey. So when discussing foraging strategies and ecology of killer whales, it is important to distinguish whales based on their varying types of prey, for they use different strategies to hunt them. However, those strategies are often similar across the globe, whether the whale is from North Pacific or the Antarctic waters. Thus the focus will not be so much on geographical distribution differences but rather on prey type, we establish four groups based on the foraging ecology: seal-eating (whales feeding on porpoises and delphinids included), whale-eating, fish-eating, and offshore killer whales.

3.3.1 Seal and dolphin-eating killer whales

Seal-eating killer whales are the Arctic transient killer whales or the Antarctic type B whales. Although we can find killer whales that feed on pinnipeds in other parts of the world too, they are not so clearly specialized and or little research has been done on them to assign one of the types with certainty. Generally, they inhabit wide shallower waters than resident type whales, often with winter ice cover ([48]Filatova et al., 2019).

Attack strategies vary depending on the prey species, however, there is one important thing that killer whales that feed on seals, porpoises and dolphins have in common and it is operating rather on the water surface and rarely diving deep to handle their prey. It is argued that the reason behind this strategy lies in characteristic constraints of their chosen prey. Due to their size, killer whales might exceed the diving capacities of significantly smaller seals or porpoises, they can also take advantage of their prey returning to the surface to breathe and wait close to the surface rather than spend energy on deep dives. Furthermore, mammal-eating killer whales rarely use echolocation while hunting because their prey is able to recognize killer whale sounds frequency ([55]Miller et al., 2010, [46]Barrett-Lennard et al., 1995).

There is little known about killer whales' foraging activity during the night but it is suggested that feeding at night is less common than during the day, especially considering that due to the lacking use of vocalization to locate prey, transient killer whales likely depend on visual cues which would make foraging at night more challenging ([56]Dahlheim & White, 2010, [55]Miller et al., 2010).

Transient killer whales travel and forage in groups no bigger than 10 animals ([46]Barrett-Lennard et al., 1995). They form matrilineal social groups, the young may leave in early adulthood or stay longer as there is a tendency to create lifelong bonds with mothers. The adult males may become lone individuals, sometimes loosely associating with other groups but forming no strong bonds. The groups are of mixed ages and sexes ([44]Ford, 2009, [56]Dahlheim & White, 2010, [57]Baird & Whitehead, 2000). Transient killer whales tend to inhabit the same areas all year round and specialize on feeding on regional mammals, never taking fish, possibly due to high abundancies of their preferred prey. Foraging strategies are highly cooperative and coordinated, sharing caught prey is a common practice ([58]Cosentino, 2015, [59]Kryukova et al., 2012, [46]Barrett-Lennard et al., 1995).

Killer whales access pinnipeds either near their haul-out places in shallow nearshore waters or trying to reach them by leaping onto shore and dragging their prey into water. In Antarctica, the most common strategy is spyhopping around ice floes with Antarctic seal species on them (often fur or crabeater seals), then swimming in high speed towards the floes and abruptly turning in front of them or proceeding under the floe, thus creating a big wave resulting in tipping the floe over and or washing the animal off into water ([50]Pitman & Ensor, 2003, [60]Visser et al., 2008). Killer whales reducing the floe size by breaking it up or whales pushing the floe away from pack ice to open water areas to reduce the haul-out chances of the washed off animal were also documented ([60]Visser et al., 2008). It seems that this type of hunting is extremely agitating for the seals and after the final coordinated wash-off there is not much fight and consumption occurs very soon after, especially in comparison with foraging strategies of Arctic whales.

In the northern hemisphere, hunting pinnipeds straight in the water is a prevalent strategy. The moves were documented on many prey species, seals and walruses. The most common tactic is hitting the prey with a fluke or hitting with a fluke near the prey, this may be preferred because it is the least risky and still very efficient strategy. It is closely followed in frequency by submerging the prey using the whole body weight. Less frequent but still important strategies are hitting the prey with head and attacking it under water ([59]Kryukova et al., 2012). Some tactics used only to scare and confuse the prey, like false attacks, were also described. However, it is clear that hunting strategies of killer whales are very sophisticated and complex.

Hunting harbor porpoises, Dall's porpoises and dolphins consists of different and seemingly not as complex tactics. In most documented cases of killer whale attacks on porpoises, the prey was shortly chased in high speed and repeatedly rammed from below being forced above water ([58]Cosentino, 2015, [56]Dahlheim & White, 2010). Attacks on dolphins are very similar, only the high speed chase takes significantly longer. Hunting both dolphins and porpoises is usually done in larger groups, the numbers often exceeding 15 individual killer whales ([56]Dahlheim & White, 2010).

The attacks usually do not take longer than several minutes, however, there is evidence of killer whales playing with their prey before killing it or of extremely long kill attempts which can last close to two hours. Those are usually training attacks for killer whales calves and they appear to be of great importance, given the complexity of killer whale foraging tactics. The data suggests that training attacks occur in all world populations of transient killer whales. The attack is often lead by the adults of the group with the calves imitating mostly, but not exclusively, the less risky acts (hitting with flukes and submerging of prey). In Antarctic populations killer whales sometimes let their prey escape or haul-out on ice floes seemingly on purpose, in order to give their calves a chance to learn. Often the training sessions for calves do not result in a kill at all ([59]Kryukova et al., 2012, [60]Visser et al., 2008, [50]Pitman & Ensor, 2003). This can also be seen as evidence for coordination and cooperation in killer whale group foraging.

3.3.2 Whale-eating killer whales

Whale-eating killer whales belong to the transient, mammal-eating, type A or type 2 ecotypes. Evidence of predation and attacks on some whale species are available for the Caribbean killer whales, too ([54]Bolaños-Jiménez et al., 2014). Amongst their prey there are pygmy sperm whales (*Kogia breviceps*), Antarctic minke whales (*Balaenoptera boraenensis*) and common minke whales (*B. acutorostrata*) and many other baleen whales, including blue whales (*B. musculus*) and bowhead whales (*Balaena mysticetus*). Predation on large baleen whales is not limited to vulnerable, sick individuals or calves only. Although successful kills of healthy adult large baleen whales are scarcer, there is evidence they are not uncommon ([6]Jefferson et al., 1991). Interestingly, even though species of large whales, for example humpback whales (*Megaptera novaeangliae*), are abundant in both southern and northern Pacific, migrating north with their calves seasonally, most attacks on humpback whales by killer whales occur in southern areas ([56]Dahlheim & White, 2010, [61]Testino et al., 2019).

Attacks on whales usually occur in groups of 5-20 killer whales. The size of the group does not always correspond with the size of the possible prey, however large whales are often attack by larger hunting groups ([44]Ford, 2009). Social structure of the groups, lack of vocalization and no deep diving while hunting are characteristics no different from the seal- and dolphin-eating killer whales.

Hunting whales is typically a coordinated, cooperative act, as is usual for killer whales in general. It is suggested that cooperative hunting increases the energy intake and decreases risk of injury. Killer whales bite the flukes and flippers of their prey to slow them down or stop altogether, they leap onto backs of larger individuals to slow them down or possibly drown them. When attacking a larger group of whales (for example sperm whales, although very little successful attacks on healthy adult individuals were observed), the killer whales charge into the pod in order to isolate one animal from the group and focus attacks only on it ([62]Gemmell et al., 2015). The predators oftentimes only consume tongues, lips and throats of their mysticete prey, records show that killer whales attack the head region of their large prey with a certain preference. This strategy can also provide some safety from being injured by the prey's flukes in anti-predatory attempt ([6]Jefferson et al., 1991). The predators usually do not consume the whole animal, one of the reasons why might be that whales sink upon death so feeding on larger portions of the carcass would only be possible in shallow waters ([44]Ford, 2009). During the hunt on minke whales, no chasing in higher speeds takes place and the

attack is usually of a long duration, up to a few hours ([56]Dahlheim & White, 2010, [63]Pitman et al., 2001).

Mammal-eating (seal, dolphin and whale eating) killer whales share many similarities and the groups often overlap. In some areas (for example North Pacific) there have been observed interspecific shifts in preferred prey, possibly as a reaction to seasonally or regionally abundant prey ([56]Dahlheim & White, 2010). Those shifts never occur between North Pacific resident and transient whales but consumption of marine mammals in fish-eating North Atlantic ecotype 1 has been observed ([64]Samarra et al., 2018, [44]Ford, 2009).

3.3.3 Fish-eating killer whales

Fish-eating killer whales are represented in North Atlantic ecotype 1, resident whales of North Pacific and Antarctic type C. North Atlantic fish-eating whales are generalists mainly choosing herring stock as prey, however within the ecotype three subpopulations can be found with higher specialization on either herring, mackerel or bluefin tuna ([52]Jourdain et al., 2019). Other killer whale populations feed mainly on salmonids and their diet can include lumpfish and Pacific halibuts as well. The predators are responsible for recent decrease of halibut population near Iceland ([44]Ford, 2009, [65]Ford et al., 1998, [64]Samarra et al., 2018). At least in some areas of the world, following of the fish prey seasonal migration has been observed in killer whales groups ([52]Jourdain et al., 2019, [44]Ford, 2009). Deeper waters (both near and offshore) are typical for fish-eating whales ([48]Filatova et al., 2019).

Social organization of resident killer whales is different from mammal-eating ones and it has been studied extensively. The groups are usually larger, bonds stronger and individuals are rarely seen leaving the group for more than a couple of hours. Killer whales create pods of mixed ages and sexes, binding together the basic unit of killer whale group organization – matrilines. Individual matrilines often leave the pod to travel apart or join another pod, even though there is a strong preference to travel with the original pod more than with others. Pods comprise of 2-49 animals, 18 on average ([44]Ford, 2009).

Foraging behavior varies depending on the type of prey. Killer whales feeding on salmonids usually hunt individually or in small groups (mother and offspring). Herring-eating killer whales of North Atlantic hunt cooperatively herding their prey in a ball and then striking the sides of the ball with their flukes and feed on weakened animals, this is usually achieved in larger groups ([44]Ford, 2009). For North Pacific killer whales, hunting usually starts with a short high speed chase near rocky shorelines, continued by series of 3 minute dives which were followed by longer deep dives lasting up to 7 minutes, usually resulting in killer whale surfacing with prey. Prey sharing occurs in vast majority of cases. This type of hunting is usually done by small groups of 2 or 3 whales, mainly mother and the offspring, or lone adult males which can also choose to join a hunting female ([66]Ford & Ellis, 2006). Fish-eating whales use echolocation copiously to locate their prey ([46]Barrett-Lennard et al., 1995).

3.3.4 Offshore killer whales

Here I will discuss both the offshore killer whales ecotype and whales with (yet) undistinguished ecotype that also prey on elasmobranchs such are populations in tropical and South Atlantic, New Zealand waters and possibly others ([67]Best et al., 2014, [53]Weir et al.,

2010, [68]Visser, 2007). They inhabit more open-ocean waters and continental shelf, so far there is lack of evidence for any significant preference of either. However, they are more rarely found in nearshore waters which is presumably connected to their type of prey – fish and elasmobranchs ([69]Dahlheim et al., 2008).

Social structure of offshore killer whale groups have not been studied in such detail as for the other two basic ecotypes. The groups are usually large, comprised of 75-100 individuals of mixed sexes and ages ([69]Dahlheim et al., 2008).

Rays, sharks, fin-fish and cetaceans have all been documented as prey of these killer whales. New Zealand killer whales feed on large sharks such as basking (*Cetorhinus maximus*) or mako (*Isurus oxyrinchus*) sharks ([68]Visser, 2007, [49]Ford et al., 2014). North Pacific offshores significantly prefer sharks over other types of prey, mainly feeding on blue sharks (*Prionace* glauca; also found in stomachs of South African whales; [67]Best et al., 2014) or Pacific sleeper sharks (*Somniosus pacificus*). They do not react at all to presence of marine mammals. Similarly to fish-eating killer whales, offshores are very vocal when hunting and locating their prey ([49]Ford et al., 2014).

There is not enough information about foraging strategies of offshore or shark-feeding killer whales. It is clear that some populations are highly specialized and some, for example the New Zealand whales, are more opportunistic feeders ([68]Visser, 2007). Whether a shark-eating killer whale is more of a generalist (and also feeds on fish) or a specialist differs from area to area and it has not been thoroughly studied.

4 Leopard seal (*Hydrurga leptonyx*)

4.1 Apex predator traits

Leopard seals seem to be the biggest threat to Antarctic pinnipeds, cephalopods, and Adélie penguins. Predation pressure from leopard seals on different species varies regionally. The relationship of leopard seals and Adélie penguins is not solely predatory, they are also competitors for krill. We can however safely assume that their impact on many seal species is significant and they oftentimes inhibit their population recoveries, supporting evidence of this effect is documented for crabeater and fur seal populations ([70]Siniff & Stone, 1985, [71]Baum & Worm, 2009). Along with the killer whales they are on top of the trophic cascades, and with basically no predation from the aforementioned whales (very few records document leopard seals being killed by killer whales, other research suggests that killer whales deliberately avoid leopard seals), they are therefore apex predators according to our definition ([72]Pitman & Durban, 2012, [60]Visser et al., 2008, [8]Weller, 2009).

4.2 Distribution and habitat

Leopard seals have circumpolar distribution in Southern Ocean (see *Fig. 3*), seasonally migrating to subantarctic areas, too, the most northern place being Cook Islands. The animals in subantarctic regions are usually juveniles that are forced to migrate due to increased competition for food resources during winter months ([73]Hückstädt, 2015, [70]Siniff & Stone, 1985, [74]Paulian, 1957 as cited in Borsa, 1990). The estimated global population size is between 222,000-440,000 animals. The densities vary from 0,003-0,151 individuals/km^2,

leopard seals are generally solitary and their density is dependent on the amount of pack-ice available for haul-out. Spatial separation is related to age, as aggressive behavior occurs more often in older seals ([75]Rogers, 2009).

Figure 3 *Map of leopard seal distribution, compiled by Luis Hückstädt ([73]Hückstädt, 2015)*

4.3 Foraging ecology

Leopard seals are generalists in their diet. They prey on krill, fish, cephalopods, marine mammals and penguins. Their feeding behavior changes in relation to time of the year and seasonal abundance of prey (see *Fig. 4*). During austral winter, leopard seals feed primarily on krill (*Euphausia superba*) for which they compete with other krill-eating species of penguins and seals. In November, austral spring, fur seal pups (*Arctocephalus gazella*) become the preferred prey, in late summer leopard seals feed heavily on penguins. Despite seal prey making up the smallest portion of species taken by leopard seals in general, they are still responsible for crabeater seals (*Lobodon carcinophaga*) population declines in some Antarctic areas ([70]Siniff & Stone, 1985, [76]Lowry et al., 1988). Many other seal species are taken as prey, including Ross (*Ommatophoca rossii*), Wedell (*Leptonychotes weddellii*) or elephant seals (*Mirounda leonina*; [75]Rogers, 2009). Even though seal pups are preferred as prey during spring, sub-adults and adults are fed upon too, presumably in different times of the year and or different regions ([77]Hiruki et al., 1999).

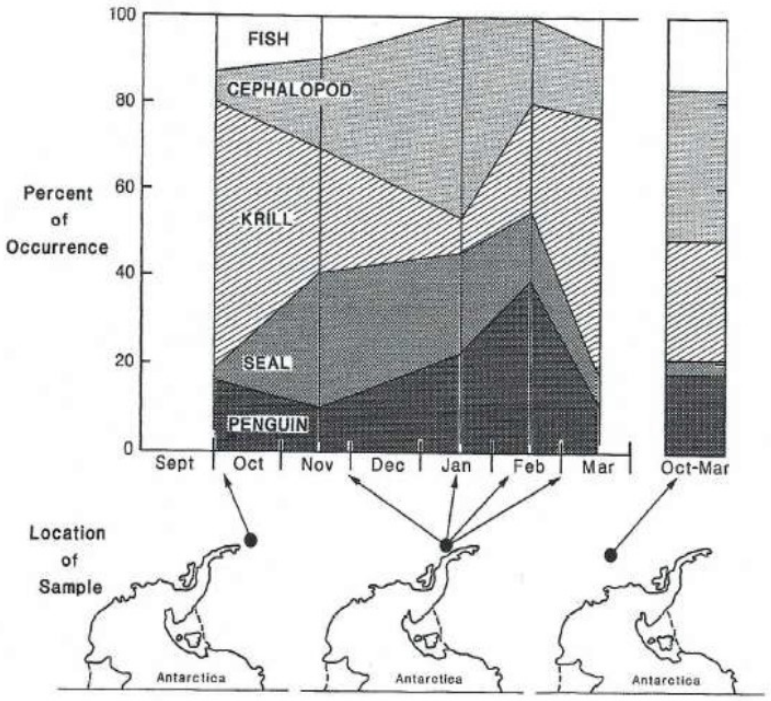

Figure 4 *Frequency of occurrence (%) of food items in the stomachs of leopard seals in relation to time of the year ([70]Siniff & Stone, 1985)*

The type of prey taken and hunting techniques chosen vary among individuals and depend on local prey abundance, individual hunting skills and size of predator in relation to prey ([78]Rogers & Bryden, 1995). Juveniles ordinarily feed on krill and penguins, as the smaller prey does not require many special hunting skills or size advantage ([77]Hofman et al., 1977 as cited in Hiruki et al., 1999).

Both seal and penguin hunting strategies have been studied extensively, although there is more information regarding the predation on penguins, mainly Adélie penguins (*Pygoscelis adeliae*), but other species including macaroni penguins (*Eudyptes chrysolophus*) are part of leopard seal diet as well ([78]Rogers & Bryden, 1995, [74]Borsa, 1990, [70]Siniff & Stone, 1985). Techniques and strategies used to hunt seals and penguins often resemble each other or overlap, one individual could use all of them or just prefer some. Leopard seals are territorial and cooperative hunting is very rare, the success rate of an individually hunting seal is probably high enough for them not to explore cooperative strategies ([77]Hiruki et al., 1999, [79]Ainley et al., 2005).

When hunting Adélie penguins, the predators deliberately choose to hunt near large penguin colonies, paying little to no attention to smaller ones ([76]Lowry et al., 1988, [79]Ainley et al., 2005). It is connected to the fact that predation on penguins occurs in late summer when penguins breed and care for their younglings. The penguin traffic in large breeding colonies is significantly higher, as more penguins must pass the leopard seal line more often in order to provide enough sustenance ([79]Ainley et al., 2005). Commonly, leopard seals create a line near the fast-ice, where the penguins stay, and submerged, with only nostrils above water, wait for them to depart. This is called patrolling. Four other penguin-hunting strategies were described. Similar to patrolling is ambushing when seals wait hidden between ice floes near penguin landing beach and attack passing penguins. Before mid-November, leopard seals can

take advantage of newly forming thin ice and wait underneath it, breaking it with their heads upon spotting a penguin and catching it from below. Seals also stalk penguins on ice floes, trying to grab them or force them into water. The predators can hunt and catch the swimming penguins in open water, too ([78]Rogers & Bryden, 1995). Caught penguins are then held in leopard seal's teeth and slung in an arc resulting in a neck snap, then crashed onto the water surface to be ripped open ([73]Hückstädt, 2015).

Three seal-hunting strategies are recognized, two of which are very similar to the ones already described in regards to obtaining penguin prey. It is stalking when leopard seals will swim into the cove fully submerged with only their nostrils above water to breathe and then lunge at approaching seals. Open-water hunting does not require any amount of hiding, the predator simply lunges at passing seals. And finally an approach unique to seal-hunting, the rapid approach on a wave when the predator rides on a swell swimming in high speed and then lunges at seals on the beach The caught prey is then consumed in the water outside of the cove, being killed in a similar manner as penguins, being thrashed against the water surface or drowned. Leopard seals sometimes play with their prey, let it escape and then recapture it, this usually occurs only after a couple of seal pups were consumed ([77]Hiruki et al., 1999).

Hunting for fish (and presumably also krill and cephalopods) constitutes of leopard seals diving under fast-ice for 5-10 minutes, coming back to breathe and repeating this for several hours ([79]Ainley et al., 2005).

An interesting phenomenon worth mentioning is food caching by leopard seals, which against all odds appears in marine environments too. Food caching is defined as a satiated predator that proceeds with killing prey to store it or defend it for later consumption and generally it is a response to increased variety of prey, habitat and competition. Since leopard seals are territorial, both intra- and inter-specific competition for food resources occur. Food caching is one of the strategies that prevent scavenging on caught prey by other animals. Not reducing that risk might result in kleptoparasitism or theft prey by others. Three food caching behaviors exist in carnivores: hiding, defending and combination of both. Leopard seals engage in all of them. In regions with lower intraspecific competition, leopard seals prefer hoarding and hiding of prey in kelp, under coastal ice or in shallow water secured by rocks. ([80]Krause & Rogers, 2019).

5 Sperm whales (*Physeter macrocephalus*)

It is very hard to ascertain whether sperm whales should be considered truly apex predators or not for several reasons but mainly for the lack of evidence for either. Let me just briefly discuss the inconclusive reasons for and against.

Sperm whales are globally distributed deep diving predators feeding on large cephalopods. Due to their size they are relatively safe from predation despite lacking highly sophisticated anti-predatory strategies. They are often subjected to harassment by killer whales and rare attempts of predatory attacks predominantly on their calves ([81]Whitehead, 2009, [63]Pitman et al., 2001, [6]Jefferson et al., 1991).

Accounts of killer whale attacks on sperm whales almost always describe formations of a rosette or a marguerite with their flukes sticking out as the main anti-predatory strategy. Their tails are definitely strong enough to possibly harm the attacker, however observations of

intentional tail-slapping aimed at the attacker are rare. So is diving (which would seem like a good strategy as sperm whales can easily beat killer whales in time and depths of their dives) or trying to swim away, rendering the sperm whales quite helpless ([63]Pitman et al., 2001, [81]Whitehead, 2009). It is interesting to note that even solitary males, unburdened by calves, do not dive when exposed to killer whales. They rather choose to come closer to the surface to create a (for males uncharacteristic) social formation and they express this behavior even during their foraging or resting dives ([82]Curé et al., 2013).

It is also hard to establish the impact sperm whales have on species hierarchy since the trophic relationships of deep-sea organisms are poorly understood. We know basically nothing about numbers of squid in deep ocean but it is assumed that sperm whales dominate the trophic level in the amount of biomass consumed ([81]Whitehead, 2009).

5.1 Distribution and habitat

As said before, sperm whales are globally distributed and occupy all of the world's oceans similarly to killer whales (see *Fig. 5*). In contrast to killer whales, females prefer warmer waters (above 15°C), so they are more likely to be found in tropical and subtropical waters, further from shore, with depths greater than 1000m. Male sperm whales can be found near pack ice in both hemispheres but they migrate to reproduce in warm waters and young males accompany females in lower latitudes for several years of their lives. Seasonal north-south migration occurs but it is not understood thoroughly. The population is estimated to be of 360,000 animals ([81]Whitehead, 2009).

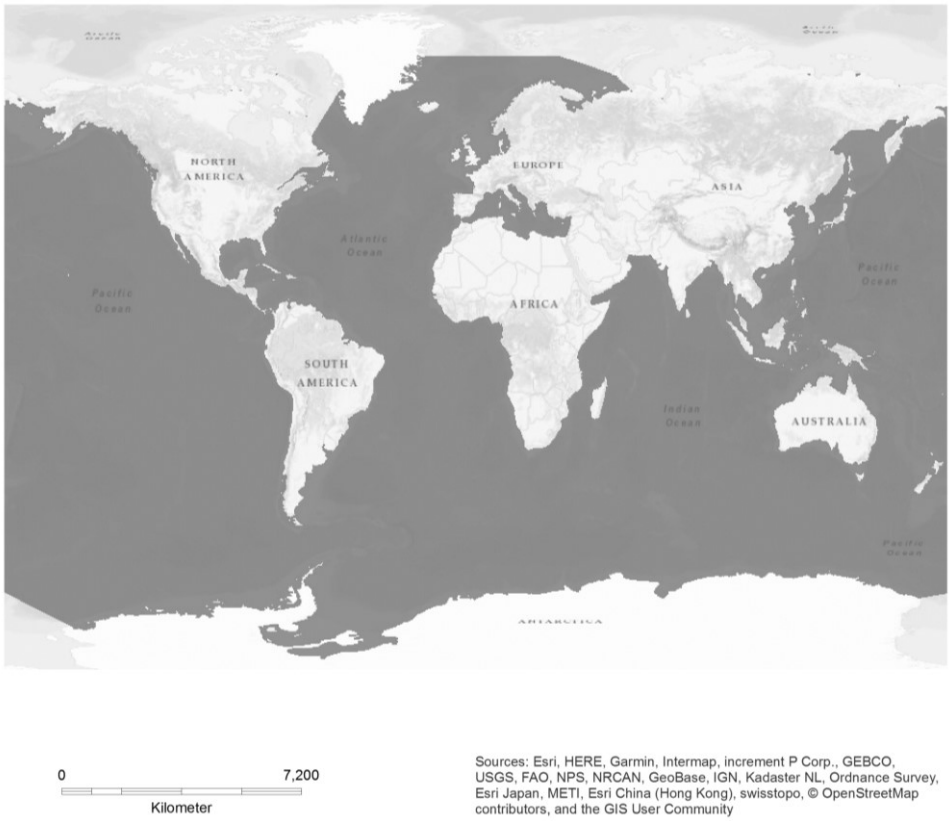

Figure 5 *Map of sperm whale distribution, compiled by IUCN ([83]Taylor et al., 2008)*

5.2 Foraging ecology

Sperm whales primarily feed on large squid but can sometimes take various species of demersal fish. Males often prey on larger squid than females and are also more likely to consume sharks, rays and other fish, especially in higher latitudes ([81]Whitehead, 2009). They are generalists but may locally specialize in most abundant species ([84]Davis et al., 2007). At least 16 cephalopod families have been described as sperm whales' prey, including the largest cephalopod species giant (*Architeuthis dux*) and colossal squid (*Mesonychoteuthis hamiltoni*; [85]Clarke et al., 1993, [81]Whitehead, 2009).

Foraging dives usually take from 30 to 55 minutes and sperm whales can dive to depths exceeding 1000 m, however most foraging dives are to depths of 500 m if not limited by the ocean depth. During foraging they make several deep dives in between which they rest near the surface for about 9 minutes. Males characteristically forage individually, females that spend their lives in close societies forage together but they spread over 1 km or more. Sperm whales spend the majority of their lives foraging. The frequency of dives does not change during day or night times. ([84]Davis et al., 2007, [81]Whitehead, 2009).

6 Top predators of limited distribution

Polar bears are the most recently diverged species of the *Ursus* taxon. Their speciation from brown bears (*Ursus arctos*; [86]Shields et al., 2000) was rather rapid, bringing fast morphological changes and enabling brisk adaptation to a very specific niche, previously unoccupied by any other big predators ([34]Derocher, 2004). Modern polar bear ancestors likely were not challenged with many competitive interactions and together with rapid morphological diversification it presented an important ecological opportunity, thus polar bears quickly and efficiently adapted to the new ecological niche with a great success, rendering them to this day the only land predators that mainly prey on marine mammals. It is also noted that such rapid adaptation can be explained by less complex biotic interactions of recently inhabited low temperature environments ([87]Luna-Aranguré et al., 2020).

The only possibly competing predators might be killer whales that visit the Arctic pack ice areas in summer upon break-up of sea-ice ([44]Ford, 2009). Due to progressively earlier break up of sea-ice, killer whales' range expands closer to polar bears and rather than being competitors for seals, killer whales might be presenting a feeding opportunity for polar bears which can scavenge bowhead whale carcasses that were killed by killer whales and washed up on shore. This trend, however, may only be temporary as declining sea-ice might eventually significantly limit polar bears' feeding opportunities altogether ([26]Galicia et al., 2016).

There are, however, downsides to being perfectly equipped only for the life in a very specific environment and I propose several reasons why the range of such a powerful top predator is not wider. It can be suggested that due to the fast adaptation and lack of competition, polar bears had a chance to specialize on a few prey species, all of which are closely tied to the marine environment. So even though polar bears are quite opportunistic feeders, they are limited to only a handful of feeding tactics due to their specialization and high energetic costs of hunting strategies other than still-hunting. They lack the skills to hunt wider range of animals and even when those skills are observed, they are usually assigned to individuals and have little to no influence on the long-term hunting success of the whole

subpopulation or group. All of the reasons above combined suggest that polar bears are not able to diversify in regards of their prey species range. This lack of more opportunistic feeding behavior or behavior plasticity poses a possible disadvantage in long-term fate of polar bear populations in this rapidly changing Arctic climate.

In comparison with polar bears, leopard seals probably did not succeed and secure their role as apex predators due to occupying previously empty niche, other seals-predators both smaller and comparable in size are often found in Antarctica. The size of leopard seals likely contributed to them becoming top predators as it enables them to defeat larger prey but it probably is not the major factor considering their main prey is significantly smaller (krill and penguins) and only a few seal species are regularly taken as prey ([70]Siniff & Stone, 1985).

Leopard seals' biggest advantage might lie in their generalist diet and opportunistic feeding behavior. They are capable of changing their dietary preferences seasonally and regionally as the abundance of their prey changes too. Prey availability influences their reproductive strategies, their generalist diet allows a bit more flexibility in breeding timing which is a highly synchronized process in other seal species. Moreover, their reproductive cycle is displaced by a month from the one of Crabeater seals which is likely an evolutionary response to sustenance availability for females and pups ([70]Siniff & Stone, 1985). The ability to change dietary preferences might also be a contributing factor to leopard seals' distribution northwards, not rendering them limited to solely Antarctic waters and offering more ecological flexibility.

7 The world-wide apex predators

Sperm whales and killer whales are both globally distributed, although each of them shows preference for different areas, depths and temperatures. Their foraging ecology and prey choice also vary significantly so they do not compete as predators despite overlapping in geographical distribution. Sperm whales compete for prey with beaked whales (Ziphiidae) and elephant seals (*Mirounga spp.*; [81]Whitehead, 2009) but it remains unclear how big of an impact the competing animals have on the prey species populations and to estimate the predators' roles in deep-sea ecosystems, the trophic relationships and quantitative ecology of deep ocean must be studied more thoroughly. However, it seems possible that sperm whales due to their size, energetic requirements and global distribution generally impact the cephalopod deep-sea populations the greatest.

Killer whales are the most successful predators of marine ecosystems in terms of number and variety of prey species, the impact on life history and behavior of such species and the general effect on trophic relationships. Even though they prefer temperate waters they occupy warmer and even tropical areas, too. So let's compare the predator in two vastly different environments.

7.1 Killer whales in temperate and cold waters

As it was said before, in colder climates various ecotypes can be very clearly distinguished. Here we can also find killer whales more abundantly and their impact on the ecosystems has been studied more thoroughly than the one of warm open-sea, likely due to

their abundance and higher preference for near-shore areas that make direct observations (even opportunistic ones) easier and more frequent.

In both Arctic and Antarctic waters, killer whales are common with average density of 0.2-0.4 whales/100km^2 ([88]Forney & Wade, 2007). Being generalist species but having specialist ecotypes is a factor which is probably greatly contributing to killer whales securing their position at the top. This way, resources are not being overly depleted and one area can support large populations of large predators. The skills for hunting certain prey type are intransferable between ecotypes, the skills are learned and the strategies are usually sophisticated and complex, involving complex in-group communication, pointing to the fact that social structures and social behavior is very important for the species survival and success. Size, cleverness and all the factors mentioned above seem to be contributing factors that enable killer whales to stay on the top of the tropic cascades with no formidable opponents. If compared to for example polar bears (with which they overlap in chosen prey and distribution), killer whales have year-round unlimited access to their prey species and do not face hard challenges regarding the timing of their life histories.

Killer whales seem to be dominating all cold and temperate areas with the exception of the Arctic pack-ice areas where we typically find polar bears. However, killer whales frequent those areas in summer when the polar bears are fasting on land and the risk of getting stranded in ice is possibly reduced.

7.2 Killer whales in tropical and subtropical waters

Killer whales in warmer oceans are less abundant and population densities are usually significantly lower, less than 0.1 whales/100km^2 ([88]Forney & Wade, 2007) with the exception of Indonesia, where the population densities are quite comparable to polar killer whales. Ecotypes are usually not clearly recognized, most could be likened to offshore killer whales and they probably mostly feed on different types of pelagic fish. Very little is known about social organization and foraging ecology of these open-water killer whales and therefore it is very hard to speculate why they are holding the top position in their ecosystems. In warmer waters they also face competition in the form of sharks which are top predators not only in the tropics and subtropics and they prey on dolphins and fish, just like killer whales.

Fish (including some elasmobranchs) seem to be the main food source for these killer whales. Predation on dolphins has been documented in many parts of the world so it is only logical to assume, these fast-swimming mammals would make up a great portion of tropical killer whale diets. Having said that, they are suspiciously not very prevalent in killer whales diet, however there is generally very little information about killer whale or dolphin interactions, behavior and their abundancies in majority of the regions.

Although, killer whales are known to take dolphins regularly, there is a noticeable discrepancy between the numbers of dolphins and the numbers of other mammals taken as prey. In Arctic and Antarctic regions this could be explained by sufficient abundance of other mammal prey. Hunting dolphins could also be too disadvantageous in terms of energetic requirements (as hunting a dolphin requires a longer high-speed chase than for example hunting a Dall's porpoise, also a fast-swimming animal) but to my knowledge there are no studies comparing those energetic requirements.

It may be possible that most tropical killer whales are at least in behavior closely similar to fish-eating or offshore killer whales which would suggest they mainly take fish and avoid mammal prey or just take dolphins as prey rarely (for example predation on tropical franciscana dolphin, *Pontoporia blainvillei*, has been documented; [89]Santos, 2005). Anti-predatory strategies, shifts in dolphin behavior upon being exposed to killer whale sounds and or attacks by killer whales have been observed but mostly for temperate and cold water dolphins ([90]Gowans et al., 2007, [91]Dahlheim & Towell, 1994). Many warm water species are documented prey of various sharks, for example common bottlenose dolphins (*Tursiops truncates*), Indo-pacific bottlenose dolphin (*Tursiops aduncus*) or Indo-pacific humpback dolphin (*Sousa chinensis*; [92]Morteo et al., 2017, [93]Wcisel et al., 2010, [94]Heithaus & Dill, 2006, [19]Sprogis et al., 2018, [95]Bouveroux et al., 2018). Most of the predator-prey interactions with large predators occur offshore, be it sharks or potentially killer whales. Thus, these interactions are not studied enough to offer valuable insight into tropical killer whale diet, possible attacks on dolphins, or competitive interactions between killer whales and sharks.

So although it seems logical for predator-prey relationships of killer whales and dolphins to occur in tropical and subtropical waters, there is simply insufficient data to support the existence or non-existence of this relationship.

7.3 Dominating different depths and areas

It seems clear from the facts discussed above that even though geographic distribution of killer whales and sperm whales overlaps, they both hunt in diametrically different environments. Sperm whales dominate the ocean depths focusing on large deep-water cephalopod prey and assuming from their estimated biomass consumption of these species they have the biggest impact on their populations out of all deep diving predators such as beaked whales. Their competition with other deep diving predators is also alleviated by partial niche-partitioning ([96]Praca & Gannier, 2008). Considering how little we know about trophic relationships of more easily accessible and observable species, we know virtually nothing about the ecosystem structure of the deep ocean and thus it is hard to establish what impact exactly sperm whales or beaked whales have.

Sperm whales' size may seem like one of the main reason why they are top predators able to hunt very large cephalopods and avoid predation. Even though it may be true for the former (in combination of morphological adaptations), it is not clear in regards to the latter. Killer whales hunt large baleen whales (including the largest blue whale, *Balaenoptera musculus*) regularly and still attacks on adult sperm whales are rare. Maybe their size in combination with dangerous jaws and some level of top predator ferocious behavior makes them not worth the hassle as prey. Those are, however, only speculations since existing studies do not show extremely sophisticated anti-predatory strategies nor do we have enough studies commenting on sperm whale-killer whale niche partitioning or quantifying their predatory and non-predatory interactions.

Killer whales generally keep close to the water surface and do not deep dive to hunt. They dominate cold and temperate surface waters without a doubt. It is possible that in some areas of the tropics they are outcompeted by sharks which often prey on the same species and that might explain why their densities in warmer waters are significantly lower. But, again, there is not enough research exploring niche partitioning of sharks and killer whales or even

reliable estimates of population sizes and densities of killer whales in the tropics and mainly open-ocean areas.

Conclusion

Large marine mammals definitely show a lot of apex predator traits and we can say that polar bears, killer whales and leopard seals are without a doubt top predators. Regarding sperm whales, what we know points to the fact they fall into this group as well, however, more research exploring their interactions with killer whales and their impact on deep-ocean ecosystems should be done. There is generally not enough studies that explore oceanic trophic relationships in depth. We lack these studies for almost all oceanic environments but mostly for open-ocean waters where any interactions are significantly harder to observe. We only have evidence of marine apex predators structuring the hierarchy of species and directly influencing balance of the ecosystems in case of killer whales – sea otters – sea urchins – kelp cascade and some effects are suggested in the case of polar bears that present the primary predators of polar seals and create scavenging opportunities for other Arctic animals. Marine environment and the size of the mammal top predators poses challenges to study of the ecosystem's behavior without the top predator's presence, purposeful manipulation simply is not possible and thus we are dependent on opportunistic observational research. So far we only have evidence of the sea otter – kelp cascade clearly being controlled by killer whales. Before killer whale predation on sea otters increased in the end of the last century, sea otters preyed heavily on urchins and prevented deforestation of kelp forests that has now, with elevated sea urchin density, increased significantly ([45]Estes, 1998). To my knowledge, there are no more studies presenting evidence of marine ecosystems without top predators.

There does not seem to be one or a few shared traits that make the four animals as successful in taking a place at the top as they all are. Polar bears just seem to be lucky to inhabit a previously unoccupied niche and adapting to the extreme conditions successfully. Being generalists seem to bring many advantages to leopard seals that are able to shift between prey species opportunistically and killer whales that seem to be forced to specialize within their ecotypes, possibly to avoid intraspecies competition due to their general abundance. Sperm whales appear to owe their dominant position to the morphological adaptations which allow them to dive deep and for long periods of time. It is obvious that size plays a role in all four species, killer whales are the largest delphinids, sperm whales one of the largest cetaceans, leopard seals one of the largest seals and polar bears are definitely the largest Arctic pagophilic animals. Killer whales are also one of the most intelligent mammals which shows in their hunting strategies that include complex cooperation and communication. They are capable of passing their knowledge to the younglings and the group cooperation appears to be crucial in hunting animals manifold larger than themselves. Speed allows them to prey on fast species such as Dall's porpoises, dolphins and sharks. While sperm whales live in close groups which likely gives them advantage when facing an attack, they show less cooperative hunting than killer whales and there is no evidence of them sharing prey (although it would be hard to observe due to the depths where hunting takes place). Polar bears and leopard seals show little to none cooperation when acquiring prey, however they are generally more opportunistic feeders.

Reasons why the four mammal species could be so dominant in their environments that I listed above are all merely speculations and suggestions. The truth is we do not have enough data available that focuses on any of the aspects in depth and that satisfyingly answers the question why this or that species is at the top of the ecosystem and what makes it such an efficient predator. We generally poorly understand oceanic relationships, we know virtually

nothing about deep-ocean dynamics and due to the reduced possibilities to observe animals at open-sea we know very little even about interactions between very abundant species (namely killer whales and dolphins).

Oceans cover over 70% of our planet's surface and it is a shame we are at the very beginning of understanding how its ecological communities function. So, let me finish with a couple of questions that I think are worth exploring further in the future. Are there self-regulating population mechanisms in marine apex predators that are similar to the ones found in some land top predators that distinguish them from mesopredators? What reason is there for killer whales to not hunt dolphins to a bigger extent even though both are abundant, is it because of the energetic requirements or do the tropical killer whales present another strictly fish-eating ecotype genetically and morphologically distinct from others? Is there a significant competition between killer whales and sharks? Do attacks on sperm whales occur more often than we presently assume? What trophic cascades are directly impacted by polar bears/leopard seals/killer whales/sperm whales and what would the ecosystem look like without its top predator? What do interactions between abundant and geographically overlapping large species look like at open sea? And finally, quantitative research of (not only) deep ocean's organisms, abundance and density estimates for large marine mammals in less accessible areas (such as open ocean) are needed to be able to imagine and develop new hypothesis about interactions and relationships of those organisms.

Because understanding what makes an apex predator, what exactly the top predator influences and what trophic cascades it is responsible for is crucial for protecting our oceans more efficiently.

8 References

1. Kiszka, J., Heithaus, M. & Wirsing, A. Behavioural drivers of the ecological roles and importance of marine mammals. *Mar. Ecol. Prog. Ser.* **523**, 267–281 (2015).
2. Wallach, A. D., Izhaki, I., Toms, J. D., Ripple, W. J. & Shanas, U. What is an apex predator? *Oikos* **124**, 1453–1461 (2015).
3. Ripple, W. J. *et al.* Status and Ecological Effects of the World's Largest Carnivores. *Science* **343**, 1241484–1241484 (2014).
4. Estes, J. A. *et al.* Trophic Downgrading of Planet Earth. *Science* **333**, 301–306 (2011).
5. Estes, J. A. & Duggins, D. O. Sea Otters and Kelp Forests in Alaska: Generality and Variation in a Community Ecological Paradigm. *Ecological Monographs* **65**, (1995).
6. Jefferson, T. A., Stacey, P. J. & Baird, R. W. A review of Killer Whale interactions with other marine mammals: predation to co-existence. *Mammal Rev.* **21**, 151–180 (1991).
7. Prugh, L. R. *et al.* The Rise of the Mesopredator. *BioScience* **59**, 779–791 (2009).
8. Weller, D. W. Predation On Marine Mammals. *Encyclopedia of Marine Mammals* 923–932 (2009).
9. Southall, B. L., Benoit-Bird, K. J., Moline, M. A. & Moretti, D. Quantifying deep-sea predator–prey dynamics: Implications of biological heterogeneity for beaked whale conservation. *J. Appl. Ecol.* **56**, 1040–1049 (2019).
10. Waring, G. T., Hamazaki, T., Sheehan, D., Wood, G. & Baker, S. Characterization of beaked whale (Ziphiidae) and sperm whale (*Physeter macrocephalus*) summer habitat in shelf-edge and deeper waters off the Northeast U.S. *Mar. Mammal Sci.* **17**, 703–717 (2001).
11. MacLeod, C. D., Pierce, G. J. & Santos, M. B. Review of Data on Diets of Beaked Whales: Evidence of Niche Separation and Geographic Segregation. *J. Mar. Biol. Assoc. UK* **83**, 651–665 (2003).
12. Heithaus, M. R. Predator–prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *J. Zool.* **253**, 53–68 (2001).
13. Ovsyanikov, N. G. Polar bear predation of walruses on Wrangell Island. *Bull. Mosc. Assoc. Nat. Sci. Sect. Biol.* **100**, (1995).
14. Maniscalco, J. M., Matkin, C. O., Maldini, D., Calkins, D. G. & Atkinson, S. Assessing Killer Whale Predation on Steller Sea Lions from Field Observations in Kenai Fjords, Alaska. *Mar. Mammal Sci.* **23**, 306–321 (2007).
15. Anderson, S. D., Becker, B. H. & Allen, S. G. Observations and prey of white sharks, *Carcharodon carcharias*, at Point Reyes National Seashore: 1982 - 2004. *Calif. FISH GAME* **94**, 33–43 (2008).
16. Loughlin, T. R. & York, A. E. An accounting of the sources of Steller sea lion, *Eumetopias jubatus*, mortality. *U Natl. Mar. Fish. Serv. Mar. Fish. Rev.* **62**, 40–45 (2000).
17. Lowry, L. F. & Fay, F. H. Seal eating by walruses in the Bering and Chukchi Seas. *Polar Biol.* **3**, 11–18 (1984).
18. Maldini, D. Evidence of predation by a tiger shark (*Galeocerdo cuvier*) on a spotted dolphin (*Stenella attenuata*) off O'ahu, Hawai'i. *Aquat. Mamm.* **29**, 84–87 (2003).

19. Sprogis, K. R., King, C., Bejder, L. & Loneragan, N. R. Frequency and temporal trends of shark predation attempts on bottlenose dolphins (*Tursiops aduncus*) in temperate Australian waters. *J. Exp. Mar. Biol. Ecol.* **508**, 35–43 (2018).
20. Crovetto, A., Lamilla, J. & Pequeño, G. Lissodelphis Peronii, Lacépède 1804 (delphinidae, Cetacea) Within the Stomach Contents of a Sleeping Shark, *Somniosus Cf. Pacificus*, Bigelow and Schroeder 1944, in Chilean Waters. *Mar. Mammal Sci.* **8**, 312–314 (1992).
21. Constantine, R., Visser, I., Buurman, D., Buurman, R. & Mfadden, B. Killer Whale (*Orcinus orca*) Predation on Dusky Dolphins (Lagenorhynchus obscurus) in Kaikoura, New Zealand. *Mar. Mammal Sci.* **14**, 324–330 (1998).
22. Bearzi, G., Reeves, R. R., Remonato, E., Pierantonio, N. & Airoldi, S. Risso's dolphin *Grampus griseus* in the Mediterranean Sea. *Mamm. Biol.* **76**, 385–400 (2011).
23. Stirling, I. Polar bear (*Ursus maritimus*). *Encyclopedia of Marine Mammals* 888–890 (2009).
24. Stirling, I. & Archibald, W. R. Aspects of Predation of Seals by Polar Bears. *J. Fish. Res. Board Can.* **34**, 1126–1129 (1977).
25. Freeman, M. M. R. Polar Bear Predation on Beluga in the Canadian Arctic. *ARCTIC* **26**, 162–163 (1973).
26. Galicia, M. P., Thiemann, G. W., Dyck, M. G., Ferguson, S. H. & Higdon, J. W. Dietary habits of polar bears in Foxe Basin, Canada: possible evidence of a trophic regime shift mediated by a new top predator. *Ecol. Evol.* **6**, 6005–6018 (2016).
27. Smith, T. G. & Stirling, I. Predation of Harp Seals (*Pagophilus groenlandicus*) by Polar Bears (*Ursus maritimus*) in Svalbard. *ARCTIC* **72**, 197–202 (2019).
28. Hobson, K. A. & Welch, H. E. Determination of trophic relationships within a high arctic marine food web using d13C and d15N analysis. *Mar. Ecol. Prog. Ser.* 9–18 (1992).
29. Smith, T. G. & Lydersen, C. Availability of suitable land-fast ice and predation as factors limiting ringed seal populations, *Phoca hispida*, in Svalbard. *Polar Res.* **10**, 585–594 (1991).
30. Stirling, I. & McEwan, E. H. The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. *Can. J. Zool.* **53**, 1021–1027 (1975).
31. Stirling, I. & Øritsland, N. A. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. *Can. J. Fish. Aquat. Sci.* **52**, 2594–2612 (1995).
32. Hamilton, S. G. & Derocher, A. E. Assessment of global polar bear abundance and vulnerability. *Anim. Conserv.* **22**, 83–95 (2019).
33. Laidre, K. L. *et al.* Quantifying the Sensitivity of Arctic Marine Mammals to Climate-Induced Habitat Change. *Ecol. Appl.* **18**, S97–S125 (2008).
34. Derocher, A. E. Polar Bears in a Warming Climate. *Integr. Comp. Biol.* **44**, 163–176 (2004).
35. Stirling, I. & Derocher, A. E. Possible Impacts of Climatic Warming on Polar Bears. *ARCTIC* **46**, 240–245 (1993).

36. Sciullo, L., Thiemann, G. W., Lunn, N. J. & Ferguson, S. H. Intraspecific and temporal variability in the diet composition of female polar bears in a seasonal sea ice regime. **3**, 672-688 (2017).
37. Wiig, Ø. *et al. Ursus maritimus*. (2015) doi:10.2305/IUCN.UK.2015-4.RLTS.T22823A14871490.en.
38. Pilfold, N. W., Derocher, A. E., Stirling, I., Richardson, E. & Andriashek, D. Age and Sex Composition of Seals Killed by Polar Bears in the Eastern Beaufort Sea. *PLoS ONE* **7**, e41429 (2012).
39. Bentzen, T. W. *et al.* Variation in winter diet of southern Beaufort Sea polar bears inferred from stable isotope analysis. *Can. J. Zool.* **85**, 596–608 (2007).
40. Galicia, M. P., Thiemann, G. W., Dyck, M. G. & Ferguson, S. H. Characterization of polar bear (*Ursus maritimus*) diets in the Canadian High Arctic. *Polar Biol.* **38**, 1983–1992 (2015).
41. Thiemann, G. W., Iverson, S. J. & Stirling, I. Polar bear diets and Arctic marine food webs: insights from fatty acid analysis. *Ecol. Monogr.* **78**, 591–613 (2008).
42. Stirling, I. & Derocher, A. E. Factors Affecting the Evolution and Behavioral Ecology of the Modern Bears. *Bears Their Biol. Manag.* **8**, 189-204 (1990).
43. Johnson, A. *et al.* Temporal and intra-population patterns in polar bear foraging ecology in western Hudson Bay. *Mar. Ecol. Prog. Ser.* **619**, 187–199 (2019).
44. Ford, J. Killer whale (*Orcinus orca*). *Encyclopedia of Marine Mammals* 650–656 (2009).
45. Estes, J. A. Killer Whale Predation on Sea Otters Linking Oceanic and Nearshore Ecosystems. *Science* **282**, 473–476 (1998).
46. Barrett-Lennard, L. G., Heise, K., Saulitis, E., Ellis, G. & Matkin, C. The Impact of Predation on Steller Sea Lion Populations. *Rep North Pac Univ Mar Mammal Res Consort Univ Br Columbia Vanc BC Can* (1995).
47. Reeves, R., Pitman, R. L. & Ford, J. *Orcinus orca.* https://www.iucnredlist.org/species/15421/50368125 (2017).
48. Filatova, O. A. *et al.* Large-scale habitat segregation of fish-eating and mammal-eating killer whales (*Orcinus orca*) in the western North Pacific. *Polar Biol.* **42**, 931–941 (2019).
49. Ford, J. K. B., Stredulinsky, E. H., Ellis, G. M., Durban, J. W. & Pilkington, J. F. Offshore Killer Whales in Canadian Pacific Waters: Distribution, Seasonality, Foraging Ecology, Population Status and Potential for Recovery. *Fish. Oceans Can.* **88**, (2014).
50. Pitman, R. L. & Ensor, P. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *J. Cetacean Res. Manag.* **5**, 131–139 (2003).
51. Pitman, R. L. *et al.* Enigmatic megafauna: type D killer whale in the Southern Ocean. *Ecology* **101**, e02871 (2020).
52. Jourdain, E. *et al.* North Atlantic killer whale *Orcinus orca* populations: a review of current knowledge and threats to conservation. *Mammal Rev.* **49**, 384–400 (2019).
53. Weir, C. R., Carvalho, I. & Collins, T. Killer whales (*Orcinus orca*) in Angolan and Gulf of Guinea waters, tropical West Africa. *J. Mar. Biol. Assoc. UK* **90**, 1601–1611 (2010).

54. Bolaños-Jiménez, J. *et al.* Distribution, feeding habits and morphology of killer whales *Orcinus orca* in the Caribbean Sea: Killer whales of the Caribbean Sea. *Mammal Rev.* **44**, 177–189 (2014).
55. Miller, P. J. O., Shapiro, A. D. & Deecke, V. B. The diving behaviour of mammal-eating killer whales (*Orcinus orca* L., 1758): variations with ecological not physiological factors. *Can. J. Zool.* **88**, 1103–1112 (2010).
56. Dahlheim, M. E. & White, P. A. Ecological aspects of transient killer whales *Orcinus orca* as predators in southeastern Alaska. *Wildl. Biol.* **16**, 308–322 (2010).
57. Baird, R. W. & Whitehead, H. Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* **78**, 2096–2105 (2000).
58. Cosentino, A. M. First record of Norwegian killer whales attacking and feeding on a harbour porpoise. *Mar. Biodivers. Rec.* **8**, e108 (2015).
59. Kryukova, N. V., Kruchenkova, E. P. & Ivanov, D. I. Killer whales (*Orcinus orca*) hunting for walruses (*Odobenus rosmarus divergens*) near Retkyn Spit, Chukotka. *Biol. Bull.* **39**, 768–778 (2012).
60. Visser, I. N. *et al.* Antarctic peninsula killer whales (*Orcinus orca*) hunt seals and a penguin on floating ice. *Mar. Mammal Sci.* **24**, 225–234 (2008).
61. Testino, J. P., Petit, A., Alcorta, B. & Pacheco, A. S. Killer Whale (*Orcinus orca*) Occurrence and Interactions with Marine Mammals Off Peru. *Pac. Sci.* **73**, 261-273 (2019).
62. Gemmell, G. L., McInnes, J. & Wijeyeratne, G. de S. Short Note: Killer Whale (*Orcinus orca*) Predation on Whales in Sri Lankan Waters. *Aquat. Mamm.* **41**, 265–271 (2015).
63. Pitman, R. L., Ballance, L. T., Mesnick, S. I. & Chivers, S. J. Killer whale predation on sperm whales: observations and implications. *Mar. Mammal Sci.* **17**, 494–507 (2001).
64. Samarra, F. I. P. *et al.* Prey of killer whales (*Orcinus orca*) in Iceland. *PLOS ONE* **13**, e0207287 (2018).
65. Ford, J., Ellis, G., Barrett-Lennard, L. & Morton, A. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can. J. Zool.* **76**, 1456–1471 (1998).
66. Ford, J. & Ellis, G. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Mar. Ecol. Prog. Ser.* **316**, 185–199 (2006).
67. Best, P. *et al.* Confirmation of the occurrence of a second killer whale morphotype in South African waters. *Afr. J. Mar. Sci.* **36**, 215–224 (2014).
68. Visser, I. N. Killer whales in New Zealand waters: Status and distribution with comments on foraging. in (2007).
69. Dahlheim, M. E. *et al.* Eastern temperate North Pacific offshore killer whales (*Orcinus orca*): Occurrence, movements, and insights into feeding ecology. *Mar. Mammal Sci.* **24**, 719–729 (2008).
70. Siniff, D. B. & Stone, S. The Role of the Leopard Seal in the Tropho-Dynamics of the Antarctic Marine Ecosystem. *Antarctic Nutrient Cycles and Food Webs* (1985).
71. Baum, J. K. & Worm, B. Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.* **78**, 699–714 (2009).

72. Pitman, R. L. & Durban, J. W. Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Mar. Mammal Sci.* **28**, 16–36 (2012).
73. Hückstädt, L. *Hydrurga leptonyx*. (2015) doi:10.2305/IUCN.UK.2015-4.RLTS.T10340A45226422.en.
74. Borsa, P. Seasonal occurrence of the leopard seal, *Hydrurga leptonyx*, in the Kerguelen Islands. *Can. J. Zool.* **68**, 405–408 (1990).
75. Rogers, T. L. Leopard Seal (*Hydrurga leptonyx*). *Encyclopedia of Marine Mammals* 673–674 (2009).
76. Lowry, L. F., Testa, J. W. & Calvert, W. Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula. *Polar Biol.* **8**, 475–478 (1988).
77. Hiruki, L. M., Schwartz, M. K. & Boveng, P. L. Hunting and social behaviour of leopard seals (*Hydrurga leptonyx*) at Seal Island, South Shetland Islands, Antarctica. *J. Zool.* **249**, 97–109 (1999).
78. Rogers, T. & Bryden, M. M. Predation of Adélie penguins (*Pygoscelis adeliae*) by leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. *Can. J. Zool.* **73**, 1001–1004 (1995).
79. Ainley, D. G., Ballard, G., Karl, B. J. & Dugger, K. M. Leopard seal predation rates at penguin colonies of different size. *Antarct. Sci.* **17**, 335–340 (2005).
80. Krause, D. J. & Rogers, T. L. Food caching by a marine apex predator, the leopard seal (*Hydrurga leptonyx*). *Can. J. Zool.* **97**, 573–578 (2019).
81. Whitehead, H. Sperm Whale (*Physeter macrocephalus*). *Encyclopedia of Marine Mammals* 1091–1097 (2009).
82. Curé, C. *et al.* Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds: implications for anti-predator strategies. *Sci. Rep.* **3**, 1-7 (2013).
83. Taylor, B. L. *et al. Physeter macrocephalus*. (2008) doi:10.2305/IUCN.UK.2008.RLTS.T41755A160983555.en.
84. Davis, R. *et al.* Diving behavior of sperm whales in relation to behavior of a major prey species, the jumbo squid, in the Gulf of California, Mexico. *Mar. Ecol. Prog. Ser.* **333**, 291–302 (2007).
85. Clarke, M. R., Martins, H. R. & Pascoe, P. The Diet of Sperm Whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philos. Trans. Biol. Sci.* **339**, 67–82 (1993).
86. Shields, G. F. *et al.* Phylogeography of Mitochondrial DNA Variation in Brown Bears and Polar Bears. *Mol. Phylogenet. Evol.* **15**, 319–326 (2000).
87. Luna-Aranguré, C., Soberón, J. & Vázquez-Domínguez, E. A tale of four bears: Environmental signal on the phylogeographical patterns within the extant *Ursus* species. *J. Biogeogr.* **47**, 472–486 (2020).
88. Forney, K. A. & Wade, P. R. Worldwide Distribution and Abundance of Killer Whales. in *Whales, Whaling, and Ocean Ecosystems* (ed. Estes, J.) 145–162 (University of California Press, 2007). doi:10.1525/california/9780520248847.003.0012.
89. Santos, M. B. Killer whale (*Orcinus orca*) predation on a franciscana dolphin (*Pontoporia blainvillei*) in Brazilian waters. *Lat. Am. J. Aquat. Res.* **4**, 69–72 (2005).

90. Gowans, S., Würsig, B. & Karczmarski, L. The Social Structure and Strategies of Delphinids: Predictions Based on an Ecological Framework. in *Advances in Marine Biology* vol. 53 195–294 (Elsevier, 2007).
91. Dahlheim, M. E. & Towell, R. G. Occurrence and Distribution of Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*) in Southeastern Alaska, with Notes on an Attack by Killer Whales (*Orcinus orca*). *Mar. Mammal Sci.* **10**, 458–464 (1994).
92. Morteo, E., Rocha-Olivares, A. & Abarca-Arenas, L. G. Abundance, Residency, and Potential Hazards for Coastal Bottlenose Dolphins (*Tursiops truncatus*) Off a Productive Lagoon in the Gulf of Mexico. *Aquat. Mamm.* **43**, 308–319 (2017).
93. Wcisel, M., Chivell, W. & Gottfried, M. D. A Potential Predation Attempt by a Great White Shark on an Indo-Pacific Humpback Dolphin. *South Afr. J. Wildl. Res.* **40**, 184–187 (2010).
94. R. Heithaus, M. & M. Dill, L. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos* **114**, 257–264 (2006).
95. Bouveroux, T. N., Caputo, M., Froneman, P. W. & Plön, S. Largest reported groups for the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) found in Algoa Bay, South Africa: Trends and potential drivers. *Mar. Mammal Sci.* **34**, 645–665 (2018).
96. Praca, E. & Gannier, A. Ecological niches of three teuthophageous odontocetes in the northwestern Mediterranean Sea. *Ocean Sci.* **4**, 49–59 (2008).