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Acknowledgments

Abstract

Anthropogenic change is impacting the distribution and survival of marine megafauna and their prey. Humans are changing every aspect of the marine environment, with effects reaching as large as changing the composition of marine environments to directly overexploiting species through the fishing industry. The role that marine megafauna play in balancing ecosystems, including as top apex predators, leads to detrimental results in the absences and population declines of these species. Migrations and declines due to threats on marine apex predator species will alter their environments by causing mesopredator release and changes in community structure, which is often associated with reduced productivity. If such human activities persist unchecked, the collapse of many marine megafauna and their prey, which contribute to biodiversity and ecosystem services, will be inevitable. This review assesses the impacts of anthropogenic effects on marine megafauna by examining (1) how changing abiotic conditions in the ocean alters the distributions of the prey species used by marine megafauna, (2) how climate warming and unsustainable fishing practices have caused dramatic population declines in these prey species, and (3) how direct human interactions with marine megafauna cause top-down effects. These alterations to marine trophic interactions will be interpreted with respect to how they ultimately affect marine biodiversity and ecosystem function.

Introduction

        Marine vertebrates consist of diverse groups of organisms that inhabit coastal and open oceans (Pimiento et al., 2020). They consist of large charismatic species that provide numerous human ecosystem services (Sequeira et al., 2018). These ecosystem services include tourism and recreation that are significant contributors to economies (Hammerschlag et al., 2019). Marine vertebrates as top apex predators in their ecosystem also allow them to regulate other provisioning services, such as important commercial fish species, that are then available for human consumption and provides food security (Hammerschlag et al., 2019). Because of their importance to humans economically and as charismatic and beloved natural icons, marine vertebrates are heavily threatened due to human exploitation and other anthropogenic changes (Sequeira et al., 2018). Since many marine vertebrates are top predators and have large body masses, they exert considerable control in their ecosystems through their foraging and activity (Pimiento et al., 2020). They exhibit control in the environment through nutrient cycling, controlling food webs, and reducing disease transmission, making them important ecosystem regulators (Hammerschlag et al., 2019). All of these factors make marine vertebrates upper-level consumers in their communities. Changes in their environment, such as a loss of prey due to overexploitation and shifting ranges, can cause detrimental impacts to marine vertebrates and threaten the persistence of their habitat. Loss of prey often leads to marine vertebrates seeking food in an unfamiliar habitat and leaving their previous environment unbalanced, observed most strongly in complex coastal habitats (Sequeira et al., 2018). The concept of marine vertebrates and their prey shifting their ranges to seek other food resources and responding to anthropogenic changes will be referred to as redistribution. The inability of these predators to respond to direct and indirect anthropogenic stressors can lead to declines in their abundance that can have

devastating consequences for ecosystem structure, functioning, and resilience (Baum & Worm, 2009).

   Anthropogenic change directly and indirectly affect the balance of ecosystems. These pressures include human-induced environmental changes and proximate interactions through fisheries and other direct activities (Tam et al., 2017). Marine ecosystems are especially vulnerable to changes in their stability and structure because they are sensitive to abiotic factors that regulate their environment. While terrestrial ecosystems warm faster than marine ecosystems, slight differences in ocean temperature have profound effects on species ranges and habitat integrity (Burrows et al., 2011). The ocean stores and uptakes carbon dioxide but increases in carbon dioxide and temperature have caused chemical processes, such as ocean acidification and deoxygenation, that change the composition of the ocean (Henson et al., 2017). Rapid changes in ocean composition can be detrimental to species if they cannot respond to these changes.

   In addition to changing abiotic conditions, direct pressures from human interactions place massive threats on marine trophic cascades by greatly reducing the presence of important ecosystem regulators, such as marine vertebrates. Grubbs et al. (2016) define marine trophic cascades as a tri-trophic interaction where predation release results in inverse trends in predator and prey abundance. Prey populations become higher than normal and result in increased predation or reductions in their prey species (Grubbs et al., 2016). Marine vertebrate upper-level consumers in marine environments can have substantial declines due to direct overharvesting or reductions in their food sources because of human exploitation. Significant impacts on trophic cascades involving these species result as their community's stability and structure are disrupted (Heithaus et al., 2008). Community structure (defined as the abiotic factors and all of its

inhabitants in a marine vertebrate's environment) in marine ecosystems is highly influenced by physical and physiological disturbance, competition, predation, and recruitment (Pinnegar et al., 2000). Due to many anthropogenic threats, recruitment can change trophic cascades as marine vertebrates move into new populations searching for new food sources.

Cetaceans (whales, dolphins, and sirenians) and elasmobranchs (sharks, rays, and skates) are two marine vertebrate groups that are highly mobile ecosystem regulators (Sequeira et al., 2018). Cetaceans are a versatile group of marine mammals that consume an array of organisms, ranging from zooplankton to large whales. Some of them are top predators that help regulate the abundance and distribution of their prey species, and their absence creates disruptions in their trophic cascades. Cetaceans have important influences on energy flux but do not provide drastic nutrient contributions in the environment, meaning they provide some significance to productivity but have a more significant impact on shaping the biodiversity in their habitat (Katona & Whitehead, 1988 & Roman et al., 2014). Their direct consumption of prey causes unpredicted events on food webs in their absence. Since they are upper trophic level consumers that consume more prey than the entire world fishery stock, their prey would be left unregulated and increase in abundance (Katona & Whitehead, 1988). The behavior of the prey of cetaceans would also change as the dynamics within the trophic cascade change in the absence of their predators.

Elasmobranchs have highly variable diets that can change depending on their environment (Bucking, 2015). Even though they have versatile prey consumption, their diet correlates with their habitat and migration patterns, complicating their role in trophic cascades (Valls et al., 2017). Species within this group occupy many different positions in trophic cascades, with sharks mainly being upper-level consumers. At the same time, rays and skates are variable in

their roles as both predator and prey (Navia et al., 2017). Like cetaceans, elasmobranchs exert control over their prey directly through consumption and indirectly through their ability to influence prey behavior because of their presence (Navia et al., 2010). The population declines of elasmobranchs are especially worrisome because their long gestation periods and low fecundity impacts their ability for population recovery (Hoenig & Gruber, 1990).

Sea turtles and other marine mammals besides cetaceans (pinnipeds, sirenians, and sea otters) are other groups categorized as marine vertebrates with variable diets and distribution patterns, influencing their community structure. Marine megafauna include many other groups, such as seabirds and marine reptiles, but the groups mentioned above are the most common prey among the largest marine megafauna. The effect of these groups will be focused on in their context as prey to marine megafauna. Sea turtles, pinnipeds, sirenians, and sea otters are unique groups in food webs due to their roles as predator and prey (Estes et al., 2016). In their absence due to common anthropogenic threats, such as entanglement in fishing gear and exploitation, productivity and biodiversity are diminished as it alters their community structure. Their predators are forced to seek other food resources or face death, which results in a new predator emerging in the area that rearranges the existent trophic cascade. Their prey demonstrates an inverse relationship in their absence with increases in their numbers that can deplete lower trophic level organisms. Their importance as trophic mediators set off many cascading events in their absence.

The population declines or extinction of marine megafauna and their prey due to various anthropogenic changes could affect the stability of marine ecosystems. Even though possible conclusions have been suggested based on the reductions of marine megafauna and their prey, significant gaps still exist in the role that anthropogenic change plays on this trend. Acquiring

information on marine ecosystems is limited due to the difficulty of observing marine organisms (especially large ones) in their environment for extended periods (Bowen, 1997). Their high mobility complicates the ability to study specific individuals and their effect in an ecosystem, especially since they can move across highly variable ocean habitats (Hammerschlag et al., 2015). Along with this complication, marine research is expensive, and manipulative experiments are nearly impossible (Bowen, 1997). The difficulties listed above have resulted in a limited understanding of how anthropogenic change affects populations of large marine vertebrate species and their interactions in the environment. This paper will address this knowledge gap and analyze the effects of anthropogenic change on marine megafauna and their prey and demonstrate their importance in their environments. This will be done by outlining the (1) impact of changing abiotic conditions in the ocean on the distribution of important prey of marine megafauna, (2) dramatic population declines due to climate warming and unsustainable fishing practices on these prey, and (3) effects of direct human interactions with marine megafauna populations.

Human Effects on Abiotic Ocean Conditions

Changing conditions in marine ecosystems affect the survival and distribution of important prey species of many marine megafauna. Humans impact climate warming through the combustion of fossil fuels (Hertzberg & Schreuder, 2016). This activity changes the marine environment that ecosystem regulators rely upon to maintain ocean productivity. The burning of fossil fuels influences climate warming and other abiotic conditions by increasing atmospheric carbon dioxide levels. Photosynthetic organisms, such as algae and phytoplankton, play essential roles in fixing CO_2, with oceanic phytoplankton accounting for over half of the world's net global primary productivity (Beardall & Raven, 2004). Climate warming and carbon dioxide

typically create increased productivity in marine photosynthetic organisms, which explains why the oceans serve as a major carbon sink, absorbing about 30% of CO_2 emissions since the Industrial Revolution (Beardall & Raven, 2004). Nonetheless, a rapid increase of atmospheric CO_2 by 1.8 ppm year^{-1} has still occurred over the past four decades (Beardall & Raven, 2004 & Umair et al., 2020). Increases in CO_2 threatens the processes of photosynthetic organisms with carbon increases at this rate. Phytoplankton are extremely sensitive to environmental change and respond with changes in their biomass and community composition (Litchman et al., 2012). Under increased carbon dioxide, light, and temperature, phytoplankton cell sizes increase to account for increased activity under these conditions (Finkel et al., 2010 & Litchman et al., 2012). Increases in the amount of exported carbon additionally alter the resource use availability of phytoplankton, which decreases their productivity due to less exportation of limiting nutrients such as nitrogen and iron (Finkel et al., 2010). Although phytoplankton are highly plastic in their response to the environment, the rapidity of carbon accumulation in the ocean does not allow enough time for the maintenance of productive cell size and composition that allow for resource use efficiency, which threatens their quality as prey items for higher trophic level consumers (Finkel et al., 2010 & Litchman et al., 2012).

As photosynthetic organisms increase their activity with higher carbon levels and contribute to exportation through organic nutrient use, the nutrients dissipate downwards to lower depths (Moore et al., 2018). Increased productivity causes more nutrient abundance at lower depths, creating a phenomenon called nutrient trapping (Moore et al., 2018). Nutrient trapping due to increased productivity because of climate warming and increased carbon dioxide levels from increased human contribution to CO_2 emissions could relocate biological materials to deeper depths and increase ocean stratification (Moore et al., 2018 & Nagelkerken & Connell, 2015).

The combustion of fossil fuels that leads to increased CO_2 affects ocean net primary production (NPP) and export production (sinking particulate flux, EP) (Fu et al., 2016). Ocean stratification creates layers in the ocean due to large differences in the materials and nutrients in them, causing a vertical distribution of phytoplankton that affects primary productivity and energy transfer to higher trophic levels (Mellard et al., 2011). As opposed to a poorly mixed water column where these organisms are only contained within a thin layer, phytoplankton in stratified columns can exist throughout the water column across a mixed layer and a deep chlorophyll maximum (DCM) and not solely at the evolutionarily stable strategy depth where there is an equal limitation of light and nutrients (Mellard et al., 2011). Because the depths of the mixed layer and the DCM are not stable due to fluctuations in elemental composition and temperature, phytoplankton often change their location within the water column and force their consumers to redistribute (Mellard et al., 2011). Higher temperatures heighten the effects of stratification, which has an inverse relationship with NPP and EP. As stratification increases, NPP and EP in these areas decrease, leading to overall declines in productivity (Fu et al., 2016). The CO_2 contribution from human activities ultimately results in reduced ocean productivity. Vertical nutrient transport is also limited in high stratification areas, inhibiting the flow of nutrients back to phytoplankton at the surface and keeps the nutrients trapped in the depths (Hutchins & Fu, 2017).

If nutrient trapping and the redistribution of phytoplankton to lower depths occur globally, it could become a major issue for the persistence of phytoplankton communities. Even though they possess the plasticity to respond in low nutrient conditions, the combination of warming temperatures and increased CO_2 place further constraints on phytoplankton populations' ability to grow (Van de Waal & Litchman, 2020). Because of less vertical transport of nutrients to

phytoplankton at the surface in areas of high stratification, marine productivity is depleted at the ocean surface and causes consumers of phytoplankton to have to sink to deeper ocean levels where there is a higher abundance of phytoplankton. The effects of abiotic ocean conditions on phytoplankton exhibits a bottom-up impact on all consumer trophic levels in marine systems. Consumers of phytoplankton include zooplankton and krill, which are also popular prey items for filter-feeding marine megafauna. As a result of zooplankton and krill becoming more abundant at deeper depths, filter-feeding marine megafauna would also have to redistribute to lower levels, demonstrated in Figure 1, processes [1] and [2].

The bottom-up effects from smaller prey items could have extensive consequences on the trophic cascades of baleen whales. If zooplankton and krill sinking to lower levels interfere with these whales' life-history strategies, great whales could experience detrimental effects on specific areas, such as reproduction and survival (Springer et al., 2003). Intensified stratification causing a depletion in oxygen is more prominent at lower depths (Hutchins & Fu, 2017). As a result, zooplankton and krill survival could be significantly reduced and further limit their availability to whales. Whales could search for other food sources that are more accessible in the area or move to a habitat where zooplankton or krill are more readily available. The increased use of nutrients at lower depths by phytoplanktonic consumers would limit the vertical transport of nutrients to phytoplankton at the surface in addition to intensified stratification. Phytoplankton cell size at the surface could greatly reduce as a result and provide fewer nutrients to redistributed zooplankton and krill. If zooplankton and krill remain at lower depths, their biomass could also decrease. Whales would receive insufficient nutrients and would have to consume larger amounts of zooplankton and krill. The numbers and survival of baleen whale prey would reduce, and the whales would be forced to redistribute themselves to survive.

However, if great whales can obtain enough nutrients at deeper depths or find another food source, they could promote phytoplankton blooms at the surface due to their contribution of vertical transport through fecal material (Roman et al., 2014). With zooplankton and krill occupying deeper depths due to nutrients sinking, whales would move resources from lower to upper water depths, which could be especially important to provide nutrients for phytoplankton at the surface, promoting their growth (Roman et al., 2014). This effect from deep-diving great whales could allow enough nutrient recombination and vertical transport that would enable enough phytoplankton growth to occur at the surface, creating a bottom-up effect that would support more zooplankton near the surface. Because of their highly migratory behavior, it seems more likely that great whales would move to areas with more food resources instead of diving deeper for prey and expending more energy for zooplankton and krill that have decreased biomass and energy contribution. The ability of phytoplankton to potentially receive nutrients at the surface and maintain prey availability closer to the surface due to the behavior of whales is promising if the whales are not able to redistribute to other areas to find other prey.

In addition to the effects on baleen whales, filter-feeding sharks could be largely affected since they are large zooplankton consumers. Whale sharks and basking sharks are mostly near-surface feeders, so greater biomass of zooplankton at deeper depths could reduce these organisms' ability to find prey (Cárdenas-Palomo et al., 2018 Sims & Quayle, 1998). Due to their highly migratory nature, whale sharks should be able to move to areas with more near-surface zooplankton as long as those areas are within their climate niche (Macena & Hazin, 2016). If intensified stratification of phytoplankton and the redistribution of zooplankton occurs globally, zooplankton may be severely limited in whale sharks' diet or completely eliminated, which would decrease some of the nutrients that they gain exclusively from this prey item (Cárdenas-

Palomo et al., 2018). Basking sharks locate zooplankton prey based on areas of plankton-rich water and spend significant amounts of time feeding in these areas (Sims & Quayle, 1998). Their ability to detect zooplankton hotspots of high quality and quantity could pinpoint areas of high productivity (Sims & Quayle, 1998). If they can only perform this behavior at the surface where they have been observed feeding, their ability to find prey could be severely hindered due to phytoplankton reductions and sinking.

Many filter-feeders depend on zooplankton and krill to obtain essential nutrients in their diet. Bodies of water connected to glaciers, icebergs, and sea ice receive a rapid influx of biological materials trapped in these sources due to climate warming when these sources melt (Schmidt et al., 2016). Greenhouse gas emissions from humans are the main contributor to melting ice, causing this release of iron (Mitchell et al., 2006). Phytoplankton absorbs the iron deposited from melting ice to conduct biochemical processes, but their uptake is limited depending on the bioavailability of the iron (Schmidt et al., 2016). The phytoplankton process the little available iron and then transfers it to zooplankton and krill consumers who excrete this waste and contribute to the nutrient trapping and stratification at deep depths (Schmidt et al., 2016). The Southern Ocean is a place where this process is demonstrated with major declines in surface nutrients, and the influx of biological materials from melting ice contributes to further nutrient trapping because of cold water sinks (Moore et al., 2018). Due to the increased pace of sinking and trapped nutrients at deep depths due to climate warming, the nutrients cannot recombine in a water column because the rate of nutrient trapping is faster than the speed of flushing (Moore et al., 2018). As a result, the capture of these materials contributes to climate warming in this area with low surface level productivity (Moore et al., 2018). Warming ocean temperatures in arctic climates lead to further melting ice and more export of biological materials that may also become

trapped due to the decrease in surface productivity and phytoplankton and phytoplanktonic consumers. In addition to lower surface level productivity, the productivity at deeper depths may be further exacerbated by zooplankton and krill consumption of poor-quality phytoplankton low in iron (Finkel et al., 2010).

Reduced availability of iron could be a problem for higher trophic level consumers. If phytoplankton do not process as much iron and limit the amount available for phytoplanktonic consumers, artic and sub-arctic filter feeders may not obtain a sufficient amount of iron in their diet. Ingesting low levels of biological materials causes a decrease in these materials available for phytoplankton because there is less cycling of essential nutrients in filter-feeding organisms' fecal material. The marine ecosystem becomes less productive, and phytoplankton biomass could decrease (Ratnarajah et al., 2017). Zooplankton, krill, and their consumers would not receive sufficient iron, affecting their biomass and health. If marine megafauna filter-feeding populations and their prey decline rapidly because of depleted iron availability, they are forced to redistribute themselves to areas containing sufficient iron. These areas could surpass some organisms' thermal tolerance, forcing them to adapt to the different climate conditions rapidly or not survive.

If human activities and contributions to climate warming continue, marine megafauna that consume organisms that occupy increasingly stratified water columns will be forced to move. Climate warming creates intensified stratification that results in less overall productivity in phytoplankton and causes the materials that they export to become trapped at lower depths. Consumers of phytoplankton feed off of them towards the surface where phytoplankton are typically located. As a result of less nutrient recombination at deep depths, phytoplankton could sink and cause a redistribution of zooplankton and krill to deep depths to feed, which also changes the distribution of marine megafauna to deep depths. Due to thermal constraints, some

marine megafauna may not be able to exhibit this behavior and could face population declines. Climate warming due mainly to human greenhouse gas emissions results in melting ice with trapped iron that is a primary limiting nutrient in oceanic systems. If the iron is not in a bioavailable state, it could result in diminished prey quality for marine megafauna. The effects of climate warming due to human activities are widespread and have various effects on trophic cascades that also extend to larger marine megafauna prey.

Climate Warming and Human Exploitation on Fish Abundance

Phytoplankton, krill, and zooplankton are shared prey species of fish and marine megafauna filter-feeders, and declines and redistributions of these planktonic prey have direct effects on fishes that humans regularly exploit for food. Phytoplankton and zooplankton susceptibility to decreased iron levels resulting in reduced productivity reduce the quality of prey available to fish. Frederiksen et al. (2006) describe that some fish species are relatively insensitive to some aspects of prey availability but are more responsive to prey quality changes. If important fish prey of marine megafauna is sensitive to the declining quality of phytoplankton and zooplankton prey, they could move to areas containing higher quality prey. Even though certain types of fish species are insensitive to some prey availability changes, they could become sensitive if redistribution rates and decreases in the survival of prey become substantial.

Critical aspects of prey availability determine their effect on fish. Different fish species respond to changes in their prey items differently, depending on the severity of the changes. If a fish contains a relatively low range of temperature tolerance, they will not be able to redistribute themselves if phytoplankton and zooplankton occupy a new area with a different temperature range, resulting in a decline in the survival of fish. Even though other fish species will respond to changes differently, they are likely to suffer if prey quantity becomes extremely low (Frederiksen

et al., 2006). An exceptional loss in quality and abundance of prey reduces their biomass. Fish predators that consume this prey experience decreased biomass, and their biomasses fluctuate with prey abundance and quality (Frederiksen et al., 2006). With the loss of long spine sea urchins on Caribbean reefs and consequent fluctuations in benthic community structure, parrotfish have become an important species in these areas (Shantz et al., 2020). Researchers have used parrotfish biomass as an assessment of the health of reefs, and their biomass can control the shift of a reef from coral-based to algae-based (Shantz et al., 2020). Parrotfish are some of the largest herbivores present on reefs, but with the decrease of other grazers, such as long spine sea urchins, smaller sizes in these individuals has become highly selected for, and algal cover on reefs has increased (Shantz et al., 2020). As a result, parrotfish quality and size have greatly diminished and affected the structure of their environment. In addition to the change in quality and abundance of algal prey for parrotfish, changes in their community structure can also affect their biomass, and as a result, affect their consumers with a loss of larger prey items. If these species continue to experience reductions in size, they could continue to produce smaller offspring that are less fit than previous generations and are of less quality and abundance for predators.

In addition to the effects that anthropogenic change can have on the prey of fish that can lead to their relocation, these threats dictate many of their habitats' survival and persistence. Warming ocean temperatures alter the structural integrity of a fish's ecosystem and cause their habitat to be transformed, resulting in the loss of prey and shelter (Smale, 2020). As a result of habitat reconfiguration, fish are being pushed closer to the poles and face extinction in areas where redistribution is impossible (Perry et al., 2005). Two of these habitats that are being most dramatically affected include kelp forests and coral reefs. Kelp forests face range contractions

and habitat transformations after decades of ocean warming (Smale, 2020 & Wernberg et al., 2016). Temperate species that typically occupy the area are being replaced by subtropical and tropical species that are more suited for the warming temperatures in the area (Wernberg et al., 2016). For fish species to obtain optimal thermal temperature and shelter conditions, they have shifted their ranges to accommodate these needs (Smale, 2020). Increases in temperature and CO_2 have transformed coral reef habitats with major coral bleaching events due to ocean acidification that limit their calcification ability (Hoegh-Guldberg, 2011). Their rapid declines and slow growth cause them to be outcompeted by benthic species, such as seaweeds and soft corals, that alter their previous environment (Hoegh-Guldberg, 2011). Changes in the community composition and loss of essential food sources and habitat lead to major fish losses in coral reefs, either due to relocation or death (Hoegh-Guldberg, 2011). These altered environments and other transfigured environments of many fish ultimately lead to losses in biomass as fish with rapid growth, reproduction cycles, and high fecundity can redistribute and adapt to rapid changes in their environments better than their larger predators (Perry et al., 2005).

Marine megafauna generally display long lifespans and late maturity, making them less able to adapt and evolve with environmental changes (Scales et al., 2018). Decreasing biomass and loss of habitat in fish and their prey has adverse effects on marine megafauna. Losing apex predators in an area, such as toothed cetaceans and sharks, due to redistributions to follow better diet options or decreases in survival due to other anthropogenic factors would allow for the introduction of a new top predator, often resulting in mesopredator release. Mesopredators reduce the existing area's biodiversity by creating an imbalance in the system through disruption in community structure and trophic cascades (Ritchie & Johnson, 2009). Ruppert et al. (2013) observed this behavior when mid-size mesopredator fish (15 cm - 40 cm) increased in abundance

in two coral reef ecosystems around Australia with the decline of top shark predators in the areas. Figure 2A demonstrates the trophic cascade when it is balanced with the presence of shark predators. The decline in sharks also leads to a decrease in herbivorous fishes as they are more heavily predated upon by increased fish mesopredators (Ruppert et al., 2013). Due to the declines of coral reef structural integrity from anthropogenic threats such as warming temperature and increased CO_2, these habitats further stress the trophic cascade (Hoegh-Guldberg, 2011 & Ruppert et al., 2013). Further declines in herbivorous fishes occur with declining conditions of coral reefs, which leave less food available for mesopredators and unregulated growth of algae on live corals (Ruppert et al., 2013). In the presence of top shark predators, herbivorous fishes are more abundant, suggesting a link between the abundances of sharks and herbivorous fishes (Ruppert et al., 2013). Because of this connection, sharks can control the recovery rate for coral reef ecosystems, and with their lessened presence due to redistributions and declines in survival, coral reef trophic cascades may never be allowed to fully recover (Figure 2B & Ruppert et al., 2013).

Overfishing heightens the effect of all the threats facing fish described above. Overfishing has increased in recent years and has led to misconceptions about the amount of fish available in the ocean (Bearzi, 2002). Some of the most widely caught marine fish species have declined in number, exploiting populations by 50-70% with some losses exceeding 90% (Baum & Worm, 2009 & Bearzi, 2002). In addition to the declines in catches, fisheries target the largest fish and compete with marine megafauna for the largest prey items, demonstrated in Figure 1 with the removal of larger fish and its changes on cetacean predation. The declining catches among fisheries indicate a loss in biomass of important commercial fish species. Removing larger fish reduces population recovery potential due to smaller fish having less fecundity and lower larval

survival rates (Birkeland & Dayton, 2005). Significant declines in larger fish and top predators

changes the ecosystem community and even causes selective evolution towards smaller-bodied,

low/mid-trophic level fish, further solidifying the prevention of recovery (Birkeland & Dayton,

2005 & Engelhard et al., 2011).

Fisheries respond by "fishing down marine food webs" and exploiting the next largest fish in

biomass, preventing the recovery of larger fish and substantially reducing sustenance from

marine megafauna diets (Bearzi, 2002). Marine megafauna also target the next largest fish and

create a reciprocal relationship with marine fisheries. The reduction of the largest fish by

fisheries and marine megafauna is demonstrated in Figure 1 with the red "X's" eliminating the

larger fish over the smaller ones. The increased pressures from marine fisheries and marine

megafauna on larger fish reduce productivity in the area and impact trophic cascades because

fish are a mid-trophic level species that help regulate interactions. Due to an increase in

overfishing, larger and smaller fish begin occupying new habitats outside their usual scope.

Marine megafauna populations decline if they cannot find another food resource or if they cannot

meet their dietary needs. Common and bottlenose dolphins have experienced range shifts and

reductions in response to their sardine prey being overfished (Giannoulaki et al., 2017).

Previously abundant, these predators have sharply declined in their habitats of the Greek Seas

that have been directly linked to sardine reductions and intensive fishing pressure on smaller

pelagic fish (Giannoulaki et al., 2017). With these species preferring cooler waters, it may be

challenging for them to redistribute based on warming ocean temperatures and negatively affect

their possibility of recovery (Giannoulaki et al., 2017). Scarce availability of prey and increased

fishing pressure could increase competition in another habitat if these dolphins can relocate and

result in detrimental effects on their populations even more if they cannot compete and occupy a niche in a new area (Bearzi, 2008).

Some marine megafauna may not have the option of redistributing themselves. Some cetaceans inhabit a body of water that confines them, such as the Mediterranean or the Black Sea, and face increased pressure and stress from the loss of prey items. The ability of populations to recover from damaged ecosystems reduces because there is no migration allowed in or out of the area. Semi-enclosed or completely enclosed bodies of water experience less diversity, so threats to their ecosystems can have exaggerated effects that are not observed in the open ocean. Top predators play an important role in these ecosystems because only a few species regulate the dynamics in these enclosed areas (Möllmann et al., 2008). Overfishing in confined bodies of water impacts prey reductions stronger than in open ocean systems, posing dangerous threats to population declines of key species in the area. Bearzi et al. (2008) directly linked a decline of common dolphins in the central Mediterranean Sea to unsustainable fishing practices, causing unprecedented prey depletion. Possible explanations for their decline were investigated, such as redistribution to other areas of the Mediterranean Sea, but they were not found outside of their native region. The limited range existent among common dolphins could have detrimental impacts on their population and trophic cascades in which they are the top predator. As larger prey depletes from the area, fisheries' and common dolphins' resource overlap becomes increasingly similar, experiencing more contact with each other. As a result, fisheries are directly reducing common dolphin populations, with the dolphins becoming entangled in fishing lines (Bearzi et al., 2008). If this contact continues, common dolphins could disappear from the area and create a significant loss of biodiversity in the Mediterranean Sea. Exploitative fishing

activities in other enclosed bodies of water could have similar effects in their ecosystems, causing a global problem of biodiversity and productivity declines.

Marine megafauna in ideal non-enclosed and protected areas can still be affected by the threats of overexploitation. Protected areas provide areas for spawning activities of large fish that help contribute to many sharks' diets. In addition to the seasonal migrations from larger spawning fish that contribute as a food source, the fish prey in the area helps sharks achieve enough energy to sustain them without having to leave the area and expend energy searching for prey (Mourier et al., 2016). When a shark's traveling time increases to find prey, their searching time must also increase, resulting in more energy expended searching for food than they would spend in the initial habitat (Charnov, 1976). This concept is demonstrated in Figure 3, using the idea of optimal foraging time for sharks. Searching outside of these areas also often exhibits low predation success rates (Mourier et al., 2016). Because of the migration of spawning fish in protected areas and the availability of sufficient prey items, sharks have higher biomass and abundance than in non-remote and heavily overfished areas and avoid foraging outside of their aggregation areas (Goetze et al., 2018). These conditions create inverted biomass pyramids in pristine areas, where predators contain higher biomass than their prey, which could be detrimental to shark populations if migrations from spawning fish were severely limited or disappeared (Mourier et al., 2016). Due to the overfishing of spawning fish outside of protected areas, these fish are facing declines that could be detrimental to the health of sharks (Mourier et al., 2016). If the amount of spawning fish becomes severely limited to where sharks may not consume enough fish biomass, they may be forced to undertake the energetically costly task of locating food outside of their protected areas. Shark abundance in pristine and protected areas could severely decline as they may have to leave the site with significant prey declines and may

not survive. Outside of protected waters, sharks also become more susceptible to anthropogenic changes that can further affect their survival (Heithaus et al., 2007).

Alterations in fish habitats due to climate warming can shift their ranges and force their predators to seek alternative food sources. Due to thermal constraints, many predators may not exhibit redistribution and may have to seek different diet options altogether or face threats to their survival. Human exploitation of fish increases these adverse effects as it actively competes with marine megafauna for the largest prey items. Marine megafauna in enclosed bodies of water are especially susceptible to losses in their prey quantity due to overfishing. Once large prey items are depleted from diets, predators seek other food options, which could induce recruitment into a trophic cascade that they previously did not exist in.

<u>Direct Human Activities on Marine Megafauna</u>

Direct threats with fisheries can result in overfishing or entanglement of marine megafauna that deplete susceptible predator populations. These human activities can also result in behavioral changes of marine megafauna that causes them to shift their diets towards species that they previously never interacted with. Some of these prey species are other marine megafauna, such as sea turtles, pinnipeds, and sirenians. In addition to changes in their predator's behavior, human activities work directly on these other marine megafauna groups that threaten their populations and further deplete food sources from their predators. Sea turtles aggregate and return to where they were born during nesting season to lay their eggs. The abundance of sea turtles available at a given area at a specific time attracts predators (mainly tiger sharks) who come to the area specifically to consume these turtles (Fitzpatrick et al., 2012). Sea turtles are among some of the marine megafauna most affected by marine debris entanglement and ingestion, with a high occurrence of incidents and amount of plastic ingested (Claro et al., 2019).

With this threat commonly being linked to their cause of death, marine debris leads to declines in individuals and in populations of sea turtles (Thiel et al., 2018). Decreases in these critical prey species can cause sharks to redistribute in search of new prey. Since they are attracted to areas where sea turtles are nesting, they would have to venture outside areas that they are unfamiliar with at this time of year, leading to changes in trophic cascades due to interacting with different predators and prey. Fur seals and sea lions are other marine megafauna prey especially susceptible to marine litter. In addition to facing entanglement and ingestion, their populations are further depleted due to hunting pressures from humans (MacDiarmid et al., 2016). Because of their energy-rich quality, losses in these prey items result in a loss of important prey from marine megafauna, such as white sharks and killer whales (MacDiarmid et al., 2016). These predators are forced to find new habitats with other energy-rich food sources.

Dugongs are a type of sirenian that feed on seagrass in shallow, coastal waters. They constitute a significant source of energy for some sharks in shallow seagrass habitats. However, they face entanglement and overexploitation, which is further exacerbated by their slow reproductive cycles, making their population unable to grow more than 5% per year (Pusineri et al., 2013). The slow growth rates and disappearance of dugongs in many seagrass habitats off Australia's coast could be incredibly detrimental to tiger sharks that prey on them in the area. Tiger sharks predate on dugongs when they exhibit high prey densities and return to these areas seasonally to feed on these herbivores (Heithaus et al., 2007). With tiger shark presence, dugongs adapt their foraging behavior to mitigate the effects of predation risk. They have often observed feeding in shallow seagrass habitats, but when their foraging coincides with seasonal tiger shark presence in the area, dugongs feed in deeper waters with less presence of tiger sharks even though it may have less seagrass biomass (Wirsing et al., 2007). This "landscape of fear"

changes dugongs' spatial ecology, which can be detrimental to their population if they continue to be removed from their environment due to anthropogenic changes (Gallagher et al., 2017 & Wirsing et al., 2007). Due to their residential nature, the combination of risk from predation from tiger sharks and threats, such as overexploitation and entanglement, could cause unprecedented declines in their populations. Tiger sharks that only feed in the area seasonally would have a delayed response due to not being present in dugong hotspot areas at all times of the year and may not respond immediately to dugong declines. As a result, they may not quickly find other food sources that bring the same energy gain as dugongs do seasonally. If dugongs are not present in deeper waters because of being eliminated due to anthropogenic threats, tiger sharks may have to redistribute farther to areas that they are unfamiliar with at the time of the year, resulting in high energy expenditure without any return. In addition to not meeting their energy demands, they could contact other apex predators that they do not normally encounter, causing high competition and prey depletion of their new food source.

According to prey redistribution and availability, when marine megafauna relocate, their absence or presence has various effects on the trophic cascades that exist. Whaling was a process that began in Japan in the late 1940s that seeks to kill and capture the most massive whales for industrial purposes (Springer et al., 2003). Severely diminished great whale stocks result from whaling, completely depleting some areas of larger whales (Springer et al., 2003). Removing large whales from their food webs has adverse effects on the balance and structure of their ecosystem (Engelbrecht et al., 2019). These whales exert top-down and bottom-up effects on other species that interact with them, which becomes evident when the whales are removed or depleted from the environment. Fewer whales to regulate their prey (zooplankton, krill, and fish) cause a decline in biodiversity as the trophic cascade becomes unbalanced, and a new top

predator emerges. The previous prey item of the whales loses the predator that controlled their population, causing them to demonstrate mesopredator release and grow in number and deplete their prey source.

In addition to the top-down effects that cetaceans exert, they can also have bottom-up impacts on other species. Killer whales are a cetacean that relies heavily on larger whales as a food source depleted by the industrial whaling industry. As marine fisheries fish "down marine food webs," killer whales exhibit the same behavior (Bearzi, 2002). The presence of great whales helped balance the killer whale trophic cascade, and their removal has caused a disturbance in the predatory behavior of killer whales. Because the large whales decline, killer whales change their behavior by consuming the next largest prey alternative. Figure 1 demonstrates this idea with the trophic interactions between killer whales and larger cetaceans, forcing killer whales to consume smaller whales or other prey. Following the decline of whale populations, seals experienced reductions in their numbers because of increased predation from killer whales (Springer et al., 2003). A sequential decline from larger to smaller prey occurs and prevents the recovery of the initial trophic cascade and damages other trophic cascades. Changing predatory patterns may be complicated for some killer whales because they specialize in ecotypes, otherwise known as specific prey groupings (Springer et al., 2003). They prefer certain prey items, so if that prey item reduces, they are forced to focus on a new ecotype, which may be difficult if they cannot adapt quickly enough.

Once an area is devoid of prey items for killer whales, they redistribute themselves to new places and introduce themselves as the new top predator. Since apex predators are the top predators, their populations are not controlled because they have no natural predators (Springer et al., 2003). A consequence of this behavior has affected organisms that killer whales do not

naturally feed on because they have had to introduce themselves to new environments where food resources were available. An example of this is the introduction of killer whales into the sea otter trophic cascade in kelp forests. When sea otters are the top predators, they consume sea urchins, which indirectly promotes kelp growth. Killer whale predation upon sea otters causes a change in the trophic cascade, and sea urchins proliferate and decimate the kelp population, leading to a loss in biodiversity (Estes et al., 1998). Kelp forests are left devastated with killer whales feeding on sea otters, demonstrating an unintended consequence of the reduction of larger prey items due to anthropogenic change changing the feeding behavior of killer whales.

Sea otters already experienced threats to their population before the introduction of killer whales in their trophic cascade. Due to the maritime fur trade, their populations reduced until otters became protected and were allowed to recover. Even though otters are now protected, their recovery has been slower than other marine mammals (Moxley et al., 2019). Some populations almost recovered fully, but their colonization was sporadic because they have limited dispersal ability (Estes et al., 1998). The decimation of sea otter populations linked to direct declines on their populations from humans and killer whale predation consequently resulted in the loss of prey items once again for killer whales. The loss of prey for killer whales is further exacerbated by new incidental attacks observed from great white shark attacks on sea otters (Moxley et al., 2019). Due to the decline of kelp forests off the coast of California, sharks are venturing closer to the coast where there is less kelp cover and coming into contact with more sea otters that have lost much of their habitat (Moxley et al., 2019). Even though the attacks are not predatory and the sharks are not consuming the sea otters, the attacks are usually fatal and are further decimating sea otter populations (Moxley et al., 2019). The redistribution of sharks in new areas where they were previously not present due to expanded ranges has many unintended

consequences that stretch beyond the direct consumption of prey. They are altering trophic cascades that they have previously never been involved in just like killer whales, resulting in the disappearance of sea otters and the alteration of their trophic cascades.

Killer whale sightings have been observed in areas used by elasmobranchs. Killer whales previously coexisted with various elasmobranchs without preying on them, only interacting due to their similar diets. However, killer whale predation events on higher-order elasmobranchs have recently been observed. According to Engelbrecht et al. (2019), locals of False Bay, South Africa, discovered a pair of killer whales in the area. Floating shark carcasses washed up on beaches, and white shark and sevengill shark numbers declined almost overnight. These events were traced back to predation by killer whales, as indicated by measurements of teeth indentations on the carcasses. Most notable from these events was the consumption of only the livers from these sharks, indicating that a killer whale ecotype specializing in higher-order elasmobranchs may be evolving (Engelbrecht et al., 2019).

In addition to the direct consumption of sharks, killer whales may also indirectly affect higher elasmobranch order behavior. White sharks seasonally time their foraging behavior with juvenile elephant seal migrations (Jorgensen et al., 2019). Killer whales existing with white sharks that generally consume these elephant seals cause precipitous declines in white shark numbers in the area (Jorgensen et al., 2019). Evidence exists for white shark relocation to areas where juvenile elephant seals are still abundant but without the presence of killer whales, indicating that white sharks are changing their behavior based on the presence of killer whales (Jorgensen et al., 2019). Direct and indirect pressures from killer whales on white shark abundance and distribution could disrupt the trophic cascades present in the areas. Both species have extensive

niche overlaps, so if the white sharks cannot respond to new killer whale presences in their habitat, significant declines in their population could result.

In addition to facing added pressures from other marine megafauna redistributions, elasmobranchs are facing unprecedented declines through the fishing industry. Fisheries bycatch serves as a significant driver of reductions in elasmobranch biomass and deaths, affecting 102 of 118 globally threatened species (Polovina et al., 2009 & Žydelis et al., 2009). Most of these species are also untargeted by the fishing industry, resulting in avoidable deaths (Žydelis et al., 2009). In coastal areas that are home to high species richness and increased productivity, artisanal fishers target these areas more that include many different apex shark predators, which severely declines the biodiversity and productivity present (Žydelis et al., 2009). Because sharks are top apex predators, declines in their populations would threaten their ecosystem's integrity and have irreversible consequences. Some elasmobranchs are detected in nets before they have died or are released after being caught, but survival is not guaranteed due to the physiological changes during stress and handling (Ellis et al., 2017). Sharks are also involved in the shark finning trade, where their fins are used as a biological resource in various food products (Jaiteh et al., 2017). Shark finning further impacts survival because many sharks die immediately due to finning, reducing the number of sharks in the population (Jaiteh et al., 2017). This consequence has detrimental effects on the population size and recovery ability for sharks (Jaiteh et al., 2017).

Shark finning on pelagic shark species is especially detrimental to their populations. They occupy the open ocean, so relocating to new areas devoid of industrial fishing fleets is severely limited. As a result, some pelagic sharks have begun to redistribute themselves to deeper depths in the presence of heavy fishing areas. The high fishing presence may be reducing the availability of prey resources closer to the surface, in addition to the fear of being caught,

pushing blue sharks deeper vertically in search of food and safety (Queiroz et al., 2010). Relocating deeper exposes these sharks to a new diet composed of more cephalopods than mesopelagic fish, changing the previous trophic cascade in the area (Queiroz et al., 2010). Even though blue sharks are diving deeper, they are constrained by the quality of the water column and thermal tolerance, threatening their survival if they are not able to maintain a depth long enough to find food and remain safe from bycatch or shark finning (Queiroz et al., 2010). The redistribution ability of blue sharks is especially important due to being one of the most threatened elasmobranch species, especially by exploitation from the fishing industry. Because of this, the dispersal ability of these sharks out of areas with high fishing presence, not just vertical redistribution, is important. Blue sharks have displayed horizontal distribution more commonly due to resource depletion and anthropogenic threats, with juveniles exhibiting more horizontal distribution over time (Queiroz et al., 2010). The ability of juveniles to respond and learn about potential risks shows the potential promise of their redistribution abilities and future growth.

Combinations of increased direct anthropogenic threats on sharks have led to overall declines in the spatial distributions of many populations (Moro et al., 2020). With range contractions due to the increased presence of fishing and finning, critical habitats for sharks are being threatened. Birkmanis et al. (2020) developed the Exclusive Economic Zone (EEZ) that determines future habitat suitability projections for pelagic sharks. Through this model, the habitat available for requiem sharks, which occur in coastal and warmer waters, is predicted to decline, whereas habitat for mackerel sharks, which occur in cooler, open ocean environments, will experience increases in their habitat area (Birkmanis et al., 2020). Increased climate warming impacts sharks' ability to respond to range contractions, potentially threatening severe declines in their

numbers. Since their ability to relocate may be diminished unless they can respond quickly enough, their absence as top apex predators will significantly affect the structure of the communities from which they are lost, with potential effects on ecosystem function. Due to their slow life-history strategies (i.e., low birth rates and long adult maturation) and dispersal ability potentially limited by changes in marine systems, the viability of populations of many shark species is severely threatened if anthropogenic stressors are not reduced.

Due to increased direct pressures from human activity, marine megafauna populations are being severely threatened. Because fisheries act on important prey items for them, they are moving to areas where they have historically not spent any time, putting them in contact with species that they do not commonly interact with. This leads to the restructuring of trophic cascades present in the area and changes in the behavior between unfamiliar species. If fisheries are allowed to persist unregulated, they could directly and indirectly cause unpredicted species declines and redistributions that would change the biodiversity present in the area.

Conclusion

Observed marine megafauna redistributions and population declines result from direct and indirect anthropogenic changes on marine megafauna and their prey. The changes that humans have induced in the marine environment affect marine megafauna at all levels. The detrimental effects they have on their environment and prey items have indirect negative consequences on their distributions and survival. Direct overexploitation and unintended deaths resulting from bycatch cause severe declines in marine megafauna populations. To increase the population numbers of these species, the threats to these animals need to be recognized. Declines in large numbers of these various organisms would have irreversible consequences resulting in habitat collapses and major biodiversity losses. Marine ecosystems provide an extensive array of

ecosystem services, and marine megafauna's presence helps maintain their respective environments' productivity and stability (Worm et al., 2006). Their absence reduces ecosystem services because of trophic downgrading.

Due to the difficulties in studying marine vertebrates and limited knowledge of their genetics and life histories, we are only beginning to understand how anthropogenic change affects their populations and their invertebrate prey (DiBattista et al., 2009). Many marine megafauna deaths are also underreported and result from illegal activities, likely resulting in population declines that vastly surpass the current projected population numbers. It is crucial now more than ever to understand the consequences of human-induced change and take immediate action before the damage becomes irreversible. Because of historical views that marine megafauna do not play especially important ecological roles in their environments, little data exists for the impact that their disappearance and redistribution would have on their various trophic cascades and the entire ocean as a whole (Estes et al., 2016). Understanding how the environment and marine megafauna prey items influence their distribution and migration patterns would help assess how anthropogenic change changes these life-history traits. Even if some species are highly plastic in their habitat use, the thermal tolerance of many species could be exceeded, causing prey redistributions and declines. In addition to conducting more research and gaining a more clear understanding of anthropogenic change on marine megafauna and their prey, implementing CO_2 mitigation policies and reducing overfishing are essential for ensuring the future survival of many marine populations. Humans and marine megafauna can coexist, but for this to happen, humans must work to reduce the current damage that they have caused.
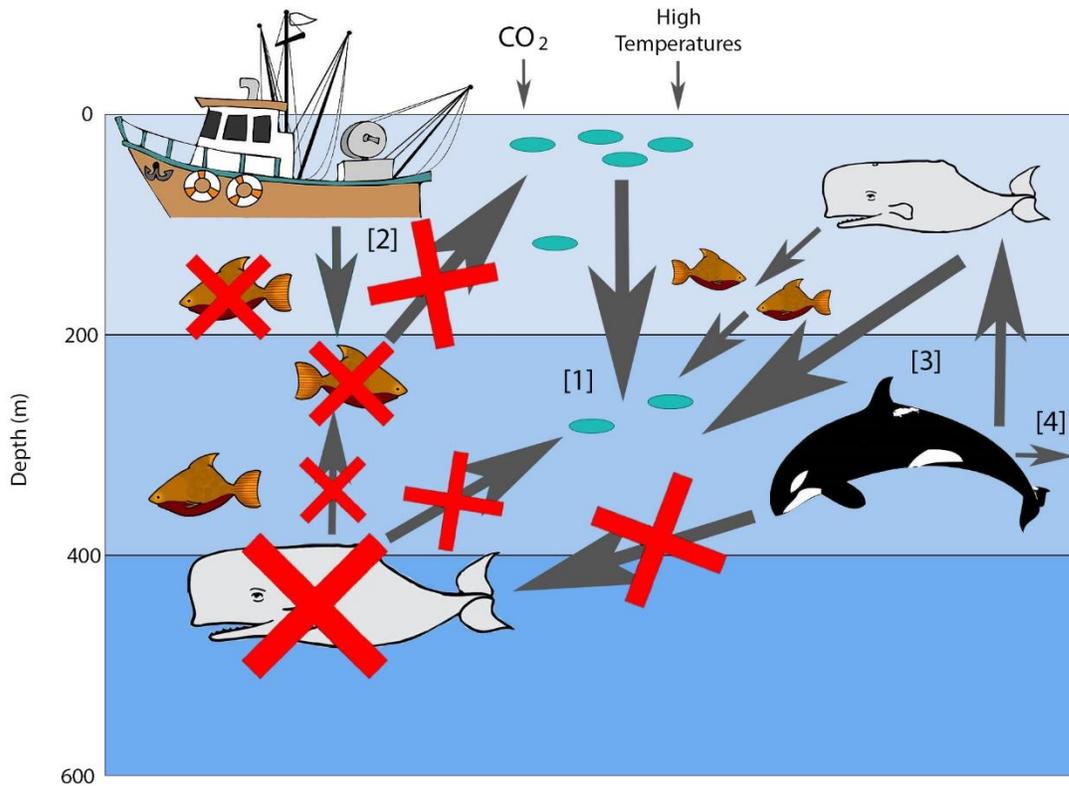
Figure 1: The model above demonstrates altered trophic interactions due to anthropogenic change. The red "X's" show the elimination of these organisms in trophic cascades where they existed before alterations due to anthropogenic change. [1] Indirect effects of human change result in phytoplankton moving to deeper depths, causing zooplankton and krill to respond by sinking deeper to track their food source. As a result, fish and cetacean predators of zooplankton and krill must sink to lower depths to obtain food, causing organisms that feed on zooplankton and krill predators also to change their feeding habits and redistribute themselves. [2] Overfishing and whaling activities have led to a loss of organisms in the environment, especially large fish and whales. [3] Cetacean predators of these organisms have had to adjust their feeding behavior due to these human activities and often have to make dietary switches to smaller prey items. [4] Some cetaceans, such as killer whales, have had to seek new environments with entirely different prey types to meet their dietary needs.
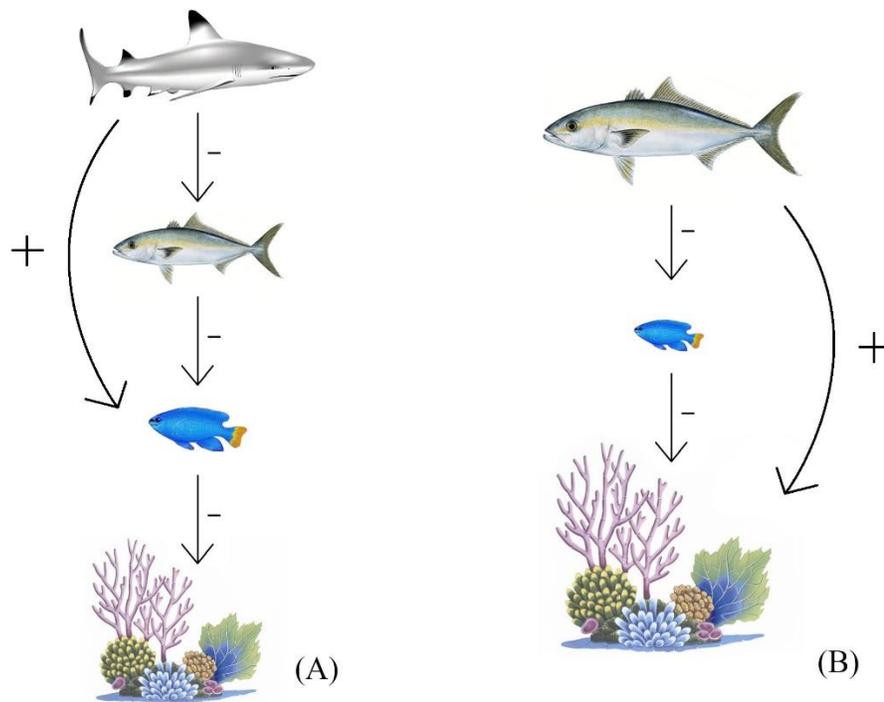
Figure 2: (A) When shark predators are present, they control the abundance of mesoconsumers that feed off herbivorous fish. Because sharks help control mesoconsumer populations, they have a positive indirect effect on the abundance of herbivorous fish. Higher numbers of herbivorous fish, in turn, consume algae growing on live corals that help maintain the health of the corals and, ultimately, the community. (B) Removing sharks from their environment increases the abundance of mesoconsumers, which decreases herbivorous fish through direct consumption. Mesoconsumers have a positive indirect interaction with algae growing on corals that remains unregulated due to less herbivorous fish grazing. Uncontrolled algal growth alters the number of primary consumers and changes the integrity of the ecosystem. Without the presence of sharks, the ecosystem is imbalanced and is slow to recover. The size of the image representing each trophic level reflects population abundance under that ecological scenario.

LOAD

10
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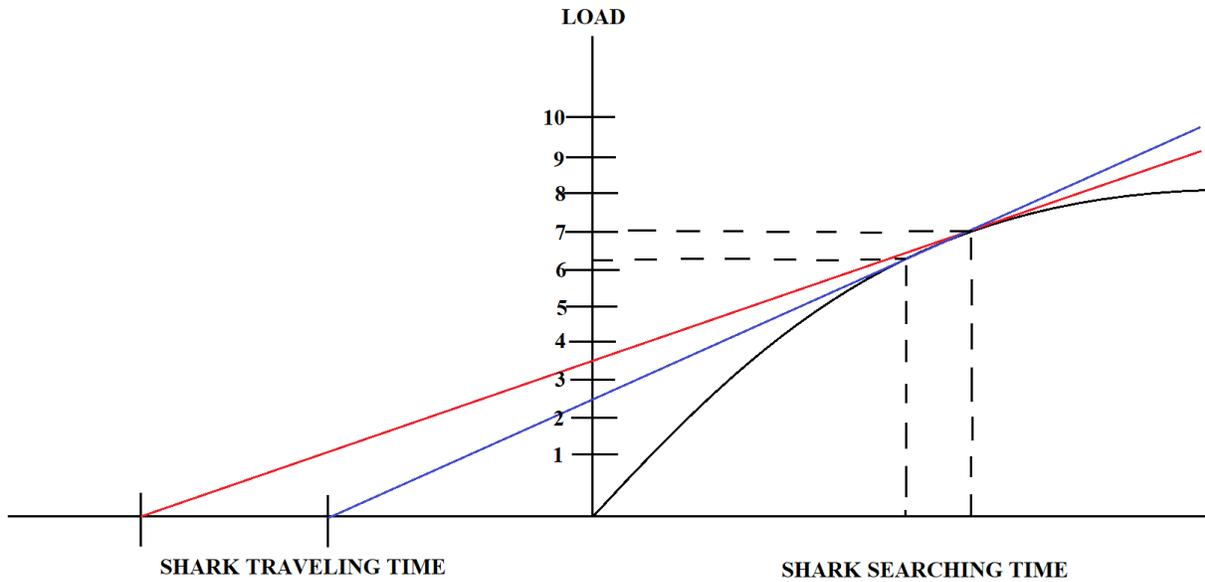3
2
1

SHARK TRAVELING TIME

SHARK SEARCHING TIME

Figure 3: This figure demonstrates the increase in searching time for a shark predator as its traveling time increases. A shark often travels to an area to find food, and once it reaches this area, it begins to search for food. The model assumes that there is no prey available from the traveling time to the searching time. "Load" represents the cumulative resource intake of a given shark. The black line demonstrates that cumulative resource intake should increase as a shark's searching time increases. The red line corresponds with a larger traveling and searching time while the blue line correlates with a shorter traveling time and searching time. When a shark ventures outside of their usual habitat, it experiences a higher energy expenditure searching for food, which may not compensate for the amount of energy spent to find food. Reducing the amount of time finding prey helps decrease the amount of time a shark has to spend searching for food (Charnov, 1976).

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