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A Review of Predator-Prey Interactions within Marine Ecosystems with a Focus on Top Predator Influences on Ecosystem Stability and Fisheries Management Implications

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Introduction

Within an ecosystem there are multiple interactions between organisms. In a balanced system, these interactions form a sustainable food web with top and bottom predators living in stability with producers. These interactions between predators and prey can also influence, directly or indirectly, other organisms and therefore other parts of the ecosystem.

The basis for studying predator-prey interactions is to first understand the food webs that result from the relationships labeled as predator-prey. Food webs consist of groupings of food chains. On the bottom of the food chain are the producers that utilize energy from the sun and chemically transform it into storable energy. These producers will be consumed by the primary consumer, which will be consumed by the secondary consumer, and finally the tertiary consumer will devour the secondary consumer. The food chain does not have to stop at the tertiary consumer level and can continue up until a final top predator is reached or until energy is exhausted and can no longer be passed on (Power, 1992). There is no limit on the number of organisms that can be involved in this scenario and it can become very complicated. However, for every food chain and food web, there are top predators. The top predator, in the first example given, is the tertiary consumer. The tertiary consumer has a great influence on the dynamics of the ecosystem and the organisms living within it.

The primary influence that the top predator has on lower trophic levels is through the act of consumption. The act of that consumption causes the lower trophic consumers to change their behavior in multiple ways to avoid being consumed by the top predator. These behavioral changes include seeking refuge, changing their habitat, or changing their diet to avoid predator encounter risk. These direct influences then cause indirect influences by affecting primary consumers. Since the secondary consumer is focusing more energy on avoiding the tertiary and less on consuming the primary, the primary's predation risk is reduced (Fig 1). The primary can now change its behavior to focus more on reproduction and eating and less on fleeing from the secondary. This is defined as an indirect influence because, while the top predator is not preying directly on the primary consumer, the primary consumer's behavior and interactions with the secondary consumers have changed based on the top predator's behavior (Dill, 2003).

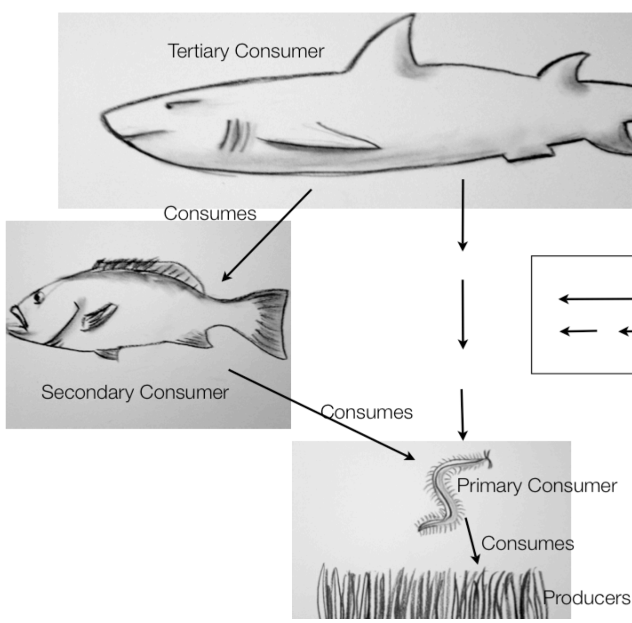


Figure 1: Diagram demonstrating indirect and direct effects within a food web with four trophic levels. The tertiary's consumption changes the secondary's behavior, making the Tertiary indirectly affect the primary.

The top predator helps to maintain all of these trophic interactions by controlling ecosystems from the top down. If the top predator is removed, a trophic cascade and regime shift can occur, which means that a different consumer on the same or a lower trophic level replaces the top predator. This has been happening in many ecosystems on a global scale and has been a focus of many studies. In 2007, Daskalov looked at the influence of the loss of top predators on the populations of lower trophic levels in the Black Sea during the 1950's and 1960's. He found that as the pelagic predatory fish catch decreased, A) the small planktivorous fish population increased, B) the gelatinous plankton biomass increased, C) the zooplankton biomass decreased, D) the phytoplankton biomass decreased, and E) the oxygen concentration of the water decreased. His analysis showed the significant impact top predator loss could have on ecosystems via trophic cascades, where populations of all trophic levels changed due to top predator loss. Trophic cascades and regime shifts change the ecosystem food web and create a new "stable" organization of predator-prey interactions. However, an ecosystem's ability to establish a stable state takes time and can lead to positive and negative effects on humans and the organisms within the ecosystem (Heithaus, 2008). For example, if an ecosystem is dominated by an economically important species, then the ecosystem can be utilized by humans for consumption and utilized by other organisms as a habitat. However, if the removal of species causes a cascade shift that creates a new ecosystem unwanted by humans and unlivable by the current species, neither the current inhabitants or humans can or will utilize it. This is the inherent risk that is taken when the removal of a top predator occurs and a trophic cascade shift is initiated.

Humans have been impacting food webs increasingly because of a greater removal of organisms (Pauley, 1998). Fisheries all over the world have experienced a decrease in the average trophic level of their catches. When a top predator dies out, a trophic cascade shift occurs, in which a fish at a formerly lower trophic level becomes the top predator. Pauley showed this in 1998 when he studied the decreasing mean trophic level reported by the Food and Agricultural Organization from 1950 to 1994. The reported global trophic level of fish inland and off the coasts, according to Food and Agricultural Organization's global fisheries statistics, has decreased steadily over the forty-four year period. He interpreted this to be due to continued overfishing of the top predators. If this continues, it could lead to a complete change in the ecosystem in an effort to maintain stability.

The influence of marine predator-prey interactions can influence habitats far from where the original interactions take place. The stability of a tropical ecosystem leads to a stable influx of nutrients to temperate ones through the movement of water transported by currents, allowing the temperate ones to thrive on the nutrients. Stable food webs can also have an impact on terrestrial ecosystems, by providing a stable food supply to the terrestrial consumers. The top predators are responsible for maintaining the interactions that provide stability to marine ecosystems and allow these far reaching interactions to be maintained.

The influences of top predators on ecosystem stability and an understanding of these interactions will help us understand how ecosystems function and allow us to model the influence of human impact on these ecosystems due to overfishing and top predator loss. Through these new models an understanding of how to maintain ecosystem stability could be reached. This understanding can help us develop systems to better maintain marine ecosystems for fishing, recreational or atheistic reasons for years to come.

Objectives

The objective of this paper is to review the effects top predators have on and within marine ecosystems, although the full impact that they have isn't well understood. This paper will define and explain different types of direct and indirect interactions of predators on prey, the types of models or observing techniques currently used to study these interactions, the reasons for top predator loss and the impact top predator loss could have on marine ecosystems.

Review

Predator's Direct Effects on Prey

Direct effects are those between two organisms interacting with each other. Predators directly affect their prey when they consume, chase, intimidate and otherwise influence them. The most direct way a predator can interact with its prey is by consuming it and, therefore, removing it from the current population. If a large portion of the prey's population is consumed, it can affect the remaining prey's ability to survive and lead to the removal of that species from the ecosystem. If the top predator stops consumption due to lack of prey number, migration or better availability of another prey, then that should lead to an increase in the number of the original prey that were being consumed. For example, if a predator is migratory, then for a span of time it will consume the prey. When the predator moves on to another area the prey can be released from predation and resupply their numbers through reproduction. This leads to a balancing act between the prey's population number and the predator's food consumption levels. Consumption is a highly influential direct interaction and the most easily observed. If any prey are removed through consumption, then its genes cannot be passed on, which shapes the prey's genetic population structure (Menge 1981). This means that consumption can direct the prey's population to change morphologically or behaviorally depending on characteristics of the prey being selected for (such as size, reproductive status, age, mobility, etc.). However, consumption is not the only direct effect that exists.

The predator does not have to be consuming prey to affect the behavior of the prey. The very presence of a predator can cause a prey to react due to intimidation (Wirsing 2008). The prey has to take into account the risk of moving, hunting and otherwise exposing itself to the predator. These are called risk effects. Risk effects can be shown in prey habitat use, density, energy state and reproductive outputs (Heithaus, 2008). For example, bottlenose dolphins decrease their use of shallow habitats when the tiger shark population in their ecosystem increases. They are also less likely to go to the interior of sea grass habitats when shark abundance is high. This behavior is considered a risk effect. The dolphins avoid the areas where the tiger sharks are most likely foraging. Therefore, they eat in the less productive areas and accept a decrease in energy intake to decrease their chances of being attacked (Heithaus, 2006). Small sun-fish do the same thing when largemouth bass are present. The smaller sunfish, which are at high risk for predation, will forage in the less productive grass habi-tats to avoid being eaten when the bass are present in the pelagic areas. We know that this is behavior based on a risk effect because the larger sunfish, which are not at risk for predation by bass, do not choose to forage in the grass areas and instead fish in the open area where the more productive food is. The smaller fish are at higher risk than the larger and therefore have a higher risk ef-fect. The predator in this case not only influences the prey's behavior, but also influences the entire population's size distribution by separating the small from the large (Werner, 1983).

The condition of the prey can also influence their response to a predator. Green turtles, for instance, will use certain habitats to hide from tiger sharks. When the tiger shark population increases, the healthy turtles that do not need as much energy will use the safer habitats that yield less energy. If a turtle is sick or injured it will take a higher risk and use the area where sea grass is the most abundant, which is also where tiger sharks are most likely to attack. Therefore, the sick turtles choose to forage in a more dangerous area because of the better energy payoff. These turtles have to take the predation risk, because they need the energy to heal and, therefore, are more likely to be eaten than the healthy turtles that can deal with a lower energy intake (Heithaus 2007).

If an animal is in a group, it is less likely to react to a predator's presence. Bottlenose dolphins form groups when predators are present. This is known to reduce their risk of predation so they are less likely to move to a different habitat to avoid the predator. They have taken precautions by forming a group and, as a result, their risk effect is decreased (Heithaus 2001). Furthermore, when bottlenose dolphins form groups they are more likely to be aggressive against sharks when competing for food since the risk effect is decreased (Acevedo-Gutiérrez 2002).

The environment also influences how much of a risk effect there is on the prey. White sharks at Seal Island in South Africa prey on the local cape fur seals. However, the predation of white sharks on cape seals decreases as the ambient light increases. This is because the light makes it easier for the seals to spot the predator and take evasive action (Hammerschlag 2006). The prey takes this into account and either does not hunt at night or hunts in groups. On Taboguilla Island, the prey's use of habitats is correlated with the ease of escape of the prey within that habitat. If the habitat has many three-dimensional crevices that allow for easy escape, then the prey is more likely to spend time foraging. The prey knows that it can escape easily so the predator's influence is lessened and therefore the risk effect is decreased (Menge 1981). This influence would correlate with the type of prey and the escape capabilities of the prey within each ecosystem. On Taboguilla Island, the three-dimensional habitat is conducive to highly maneuverable fish with a high turning angle. However, maneuverability decreases with body length. If the prey is small and has high maneuverability then the three-dimensional hiding places are ideal for decreasing the risk effects of predators. If the prey is large and doesn't have good maneuverability then small nooks and crannies would be useless (Domenici, 2001).

Finally, the type of predator or level of risk the predator has on a prey influences the way the prey reacts to the predator. For example, bottlenose dolphins react differently depending on what types of sharks are present. Some sharks are active hunters of dolphins while others pose a low threat or no threat. Dolphins have been observed to change their behavior based on these differences. For example, white sharks are known to be avid predators of dolphins. When a white shark is present, the dolphins are more agitated and are known to use evasive maneuvers to avoid the shark. However, dusky sharks only occasionally eat dolphins and therefore pose a medium threat. The dolphins use a more passive approach to the presence of a dusky shark and have been seen maintaining a distance from the shark but not rapidly swimming away from it (Heithaus 2001). Finally, since nurse sharks do not predate on dolphins at all the dolphins do not change their behavior when a nurse shark is present and are even observed foraging in the same area (Herzing 1996).

These interactions transform and influence the two populations. Genetically and behaviorally, the prey and predators change themselves to try and come out on top. The predator-prey arms race can be modeled to measure how the species influence each other. The strength of the interaction needs to be taken into account first. Top predators don't just feed on one particular prey. Many are migratory and have a limited temporal influence on the prey's behavior. Therefore, the strength of the interaction is determined by the proportion of prey consumed per unit of predator biomass per day. This can be shown by the equation (Bascompte 2005):

$$\frac{(Q/B)_J \text{ X } DC_{IJ}}{B_I} = \text{the strength of the interaction of the predator on the prey}$$

Where Q is the consumption of food within a population (per unit time), B is the biomass of the entire predator population under equilibrium conditions (Pauley 1986), (J) is the name of the predator, (i) is the name of the prey, $(Q/B)_J$ is the number of times a unit of biomass or the predator, consumes its own weight per day, B_i is the biomass in grams of the prey (Bascompte 2005) and DC_{ij} is the percentage of the prey in the diet of the predator (Opitz 1996). The stronger the interaction the greater the influence the prey and predator have on each other (Bascompte 2005).

Once the strength of the interaction is determined, the predator and prey densities, as well as the influences of the habitat, types of predators and prey, the behavioral responses and escape capabilities of these animals can be taken into account. These will allow the relative risk effects on the prey to be determined and help to predict the influence that the predator will have on that prey. Food webs, however, include more than just one predator and one prey species. In order to determine the predator's influence on the ecosystem as a whole, one needs to look at the interactions, other than direct effects, that top predators can have on ecosystems.

Predator's Indirect effects on Prey

Indirect effects are the effects top predators have on the flora and fauna that their prey influence. For example, when an oyster toadfish consumes a mud crab, it is removing the mud crab, the main predator of juvenile oysters, from the ecosystem. When the toadfish eats the mud crabs, the oyster population can increase. While a decrease in predation on lower trophic levels due to the removal of predators is the most obvious indirect interaction, indirect interactions have a multitude of variations that involve many different species (Grabwoski 2004). Every indirect interaction must involve at least two direct interactions. The direct interactions form a chain of interactions that lead to one indirect interaction and influence an ecosystem. The first step in studying these indirect interactions is to organize them. There are a few ways to organize indirect interactions, and the type of organization depends on how the indirect interactions are categorized.

One way of categorizing indirect interactions is to separate them into *indirect interactions* and *indirect modifications*. Using this organizational scheme, an *indirect interaction* is defined as a series of direct interactions that influence the abundance of another species and an *indirect modification* is a series of direct interactions that lead to a change in the relationship between two species (Wootton 1993). Both of these types of interactions are seen in Shark Bay, Australia. Tiger sharks consume green turtles and dugongs, causing a decreased competition for the other users of the sea grass beds that green turtles and dugongs occupy. The tiger sharks directly affect the abundance of dugongs and green turtles causing an indirect interaction with the other users of sea grass beds. Tiger sharks also affect the behavior of bottlenose dolphins and their use of the coastal habitats by causing the dolphins to limit their use of foraging habitats where tiger sharks are present. The tiger sharks cause the dolphins to move to other foraging habitats, leading to a behavioral change in the dolphins, creating an indirect modification (Heithaus 2002). However, this way of categorizing indirect interactions is not the only form of organization that is used in scientific studies. Sometimes, when studying indirect relationships, the indirect interactions and indirect modifications are not separated and are both referred to as indirect interactions. In this organizational scheme, all the indirect interactions are placed into different categories based on the number of animals, types of interactions and complexity of the interaction.

For this type of categorization, Menge (1995) described nine generalized types of indirect interaction. These nine indirect interactions are not the only indirect interactions that exist, but most other indirect interactions that are observed are more detailed derivations of these nine.

The most common indirect interaction described by Menge is keystone predation. This is defined as the influence a predator has on a species through the decrease of the species' main predator and is the one most frequently and easily observed. For example, in Shark Bay, Australia, tiger sharks are known to migrate to warmer waters. This means that their abundance changes seasonally along the coast of the bay (Heithaus, 2000). When the shark numbers increase, cormorant uses of the edges of the sea grass ecosystems decrease due to the increased risk of shark predation. When the cormorants move away, the teleost community can increase in abundance due to a decrease in predation risk from the seabirds (Heithaus 2009).

The second indirect effect is tri-trophic interactions. It involves an increase in vegetation due to the decrease in the main herbivore population. For example, green turtles will choose different foraging grounds when tiger sharks are present. This is a direct reaction to the tiger shark's population increasing, as discussed previously, but the green turtles choice to graze in safer areas allows the sea grass to grow in the areas they avoid. This then allows other animals to have an abundance of food because of the decreased herbivory by green sea turtles. The tiger sharks are effectively increasing the vegetation for lower trophic levels (Heithaus 2007).

The third interaction is called Exploitation Competition (Fig. 2). This is when a predator's population is reduced because another predator is consuming or reducing access to the first predator's prey. For example, when the clam species *Mya arenaria* sense the presence of the red rock crab, *Cancer productus*, they bury themselves into the sand to avoid predation. This decreases the food available for shore birds that can only harvest clams that are not buried deeply (Dill 2003). Therefore, the red rock crabs decrease shorebird food availability.

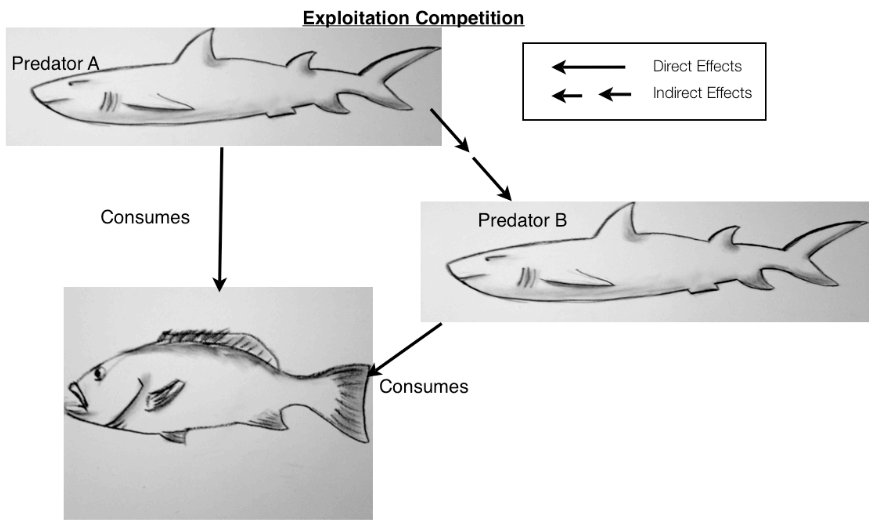
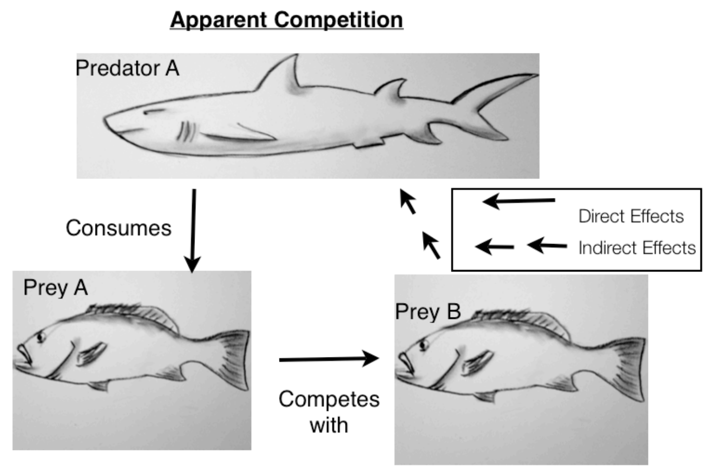


Figure 2: A diagrammatic representation of exploitation competition. Predator A consumes predator B's food source. This limits the food availability for predator B and decreases B's population numbers.

The fourth interaction is called apparent competition (Fig. 3), which is the reduction of one species' population because another has increased its population. Apparent competition helps a third species have access to the increased population as a food source. An example of this is found on Tatoosh, an island near the tip of Washington State. In this site, barnacles and limpets compete for space amongst the rocky areas. The barnacles are known to be the better competitors for space, and they limit the limpet population (Wootton 1993). The Glaucaus winged gulls consume both the barnacles and the limpets (Irons 1986). When the barnacles decrease the limpet's population and increase their own population the gulls benefit because, while they may have lost the limpets as a food source, they have an increased barnacle food source that other birds don't like to eat. They benefit from the decrease in limpets through the increase in barnacle populations.

Figure 3: A diagrammatic representation of apparent competition. Prey A competes with prey B causing a decrease in prey B's population. This causes the food availability to increase for the predator.



The fifth interaction is indirect mutualism (Fig. 4). It is the benefit two species provide for each other through the consumption of two prey species that are in competition with each other. This interaction is more likely to occur if the competition is strong (Vandermeer 1980). An example of this can be found between tiger sharks and bottlenose dolphins. Tiger sharks eat green sea turtles and bottlenose dolphins eat teleosts (Heithaus 2000, Barros 1998). These facts appear to be unrelated; however, teleosts and green sea turtles share the same habitat, and therefore compete for space. When the tiger sharks consume turtles, they are limiting the number of turtles that the teleosts have to compete against for space. When the dolphins eat the teleosts, the dolphins are limiting the number of teleosts that are competing against turtles for space. The two predators benefit from this interaction because, neither prey's population can expand enough to outcompete the other because the predators are limiting the population size and the prey's ability to compete. Therefore, both sharks and dolphins continue to have a supply of food. So, the dolphins benefit from the sharks consumption of the turtles, and the sharks benefit from the dolphins consumption of the teleosts. The predators benefit each other by limiting the competition between the two prey species.

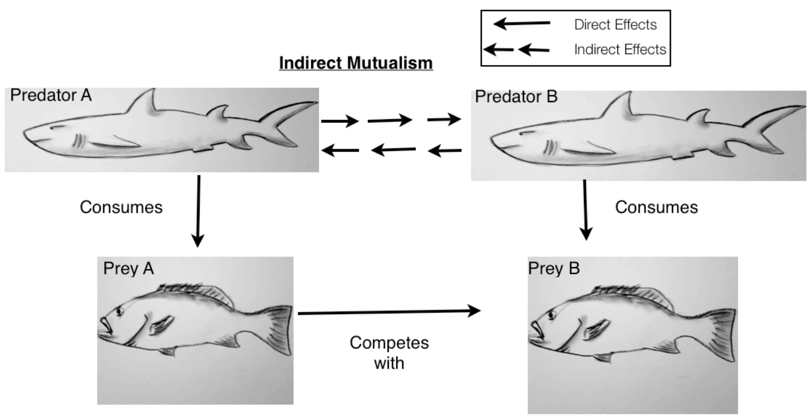
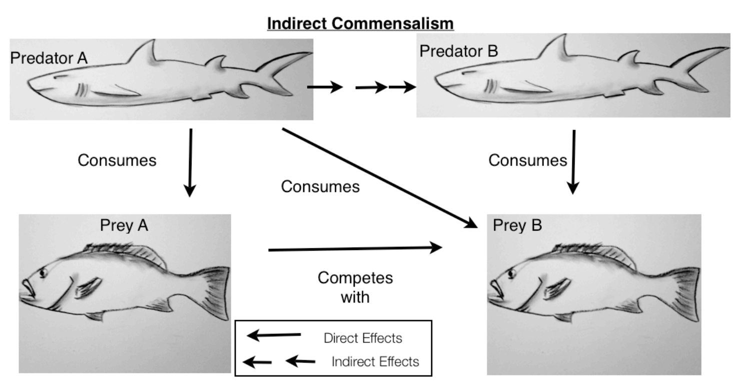


Figure four: A diagrammatic representation of indirect Mutualism. Predator's A and B consume each other's main prey's competitors. This limits the populations of the two prey and decreases competition between the two species. This allows the two species to continually coexist and feed both predators.

This dynamic changes slightly with in the sixth interaction called, indirect commensalism. Indirect commensalism is the interaction of two species that are almost indirect mutualists except that one has a more generalized diet and consumes both types of prey. To explain this type of indirect interaction, the example from indirect mutualism can be expanded by making the tiger shark not only consume the green sea turtles but the teleosts as well. With indirect mutualism, both predators benefit from each other's consumption because they feed on different prey species. In indirect commensalism one predator could use both prey species as a food source, but doesn't need both species to survive. One predator benefits because its main food source or prey is limited in competition by another predator and will not be outcompeted by the other prey, while the other does not benefit because it could consume either prey and does not need a certain species to survive. The teleosts will survive to feed the dolphins, because the sharks eat the green turtles and limit the competition that could occur. This only works if the shared prey is not the main food source for both predators, which would lead to overconsumption. The difference between indirect mutualism and indirect commensalism is that the tiger shark could potentially eat both food sources so-

Figure five: A diagrammatic representation of indirect commensalism. Predators A and B consume each other's main prey's competitors. This decreases the competition between the two species allowing both predators to have a continued food source. However, Predator A consumes Prey A as well as prey B, so predator A doesn't benefit from the decreased competition, only Predator B does.



the survival of one over the other is not important for survival. However, the dolphin needs one food source to survive, so the dolphin benefits from the sharks eating of the green turtles that could potentially outcompete the teleosts.

Habitat facilitation is the seventh indirect effect. It occurs when one species alters its habitat, which results in an impact on a population of another species. When tuna consume small schooling fish, they cause the small schooling fish to move upward in the water column, toward seabirds. When this happens, the small schooling fish enter the seabirds' habitat. This changes the food availability within the seabird habitat. The seabirds take advantage of this by consuming the small schooling fish. By consuming the small schooling fish, the tuna changed the small fishes' habitat and increased the seabirds' food consumption (Dill 2003). Another example of this interaction is demonstrated by the burrowing of the tilefish. Tilefish make burrows along cliff walls, and these burrows become homes for many other species when abandoned by the tilefish. The removal of tilefish by its main predator decreases the number of burrows. This then increases the competition amongst the invertebrates that cohabitate the burrows because there are fewer burrows to choose from (Coleman 2002).

The eighth interaction is apparent predation. This is the indirect decrease of a non-prey item by a predator or the indirect increase of a predator by a non-prey, through the reduction of a prey species that the other depends on to survive. Spiny lobsters are well known for consuming sea urchins. When this happens, algal cover increases causing coral cover to decrease. The predation of lobster on urchins decreases coral cover indirectly (Shears 2002). Another example occurs when crabs consume isopods, which are algal grazers. This decrease in isopod abundance increases algal cover. This leads to an increase in the number of other herbivores in a system because of the increase food availability. The crab increases a predator's population, the herbivore, through the consumption of isopods. (Bruno 2005)

Finally, indirect defense is the indirect reduction or increase of a predator by a non-prey through reducing/increasing competition or by reducing/increasing a predator's recruitment rate. The Hawaiian Islands are known to house many top predators including four different species of sharks. These sharks overlap in diet, vertical distribution, and, sometimes, geographical distribution. Sand bar and grey reef sharks in particular have very similar diets. Tiger sharks also inhabit this area and are known to consume sand bar sharks. When they consume the sand bar sharks, they decrease the competition for grey reef sharks and, therefore, increase grey reef shark number (Papastamatiou 2006).

Since an indirect interaction is two or more direct interactions, these examples are just the main nine ways that direct interactions influence the ecosystem. However, the examples do not show the strength of the interactions or allow scientists to analyze the influences that indirect interactions have. Normally this would mean using a model or a mathematical representation of indirect interactions to determine the strengths of the interactions, but there has not been a model developed that is able to explain the extent to which indirect effects affect ecosystems. This is because as you look at one indirect effect you are looking at multiple direct effects, and if you try to look at an ecosystem you have to look at multiple indirect and direct interactions to determine the extent one indirect interaction could have. Each of the nine interactions described above takes into account a different number of species and a different number of positive versus negative interactions. The number of variations of interactions and the extent of their influence makes it difficult to measure or specifically analyze the entire effect on ecosystems.

Typically, studies of indirect effects look at small interactions and observe the results of manipulating those interactions. This direct observation allows for an understanding of one interaction in depth. Menge and Lubchenco (1990) observed an interaction between whelks and the ecosystems they were invading. This allowed the scientists to observe the effects, both direct and indirect, that the whelks had on the ecosystem. To see if the interactions were significant Menge looked at each interaction and measured the results. He then utilized the large statistically significant interactions in his model, but did not use smaller interactions that lacked statistical significance. The issue with this form of study was that the study did not have any consistent variables that could be applied to all ecosystems. Each study had to be unique to the ecosystem it was conducted in. It also allowed for a lot of interpretation by the observing scientists. Finally, it looked at the interactions but not the relative strength of the influence each interaction had on the ecosystem. Therefore, Menge developed a model to look at all the statistically significant interactions within an ecosystem that also take into account the strength of the influence of each direct and indirect interaction on the ecosystem (Menge 1995).

Modeling Indirect and Direct interactions Within an Ecosystem

To be able to fully understand the impact indirect effects have, an interaction web is useful. An interaction web is similar to a food web, with one big exception. Food webs only focus on predator-prey interactions. An interaction web takes into account interactions that are outside of consumption. An interaction web should include competition, mutualism, predation and a host of other interactions that show the basic community structure of an ecosystem. An interaction web should also take into account the life histories of the predators and the relationships the predators maintain (Heithaus 2007). Once this web is illustrated, the strength of those relationships should be added into the web. The strength or degree of association each indirect interaction could have can be determined through the use of Pearson product-moment correlations. Each effect that is determined to be ecologically significant needs to be analyzed using univariate and multivariate regression techniques to make certain that a full understanding of each interaction is calculated. Once the strength or statistical value is attained, it is added to the “interaction web.” In this way, all relationships are examined to determine how they interact with each other (Menge 1995). A full study into the interactions and reactions each animal and plant has within an ecosystem should be taken into account. This will allow a study to be conducted that can fully illustrate the full impact that indirect and direct effects of top predators can have of ecosystems.

In 1995, Menge used interaction webs to study indirect effects. He analyzed twenty-three past interaction webs that had been created and evaluated for marine rocky intertidal interactions using manipulations within the ecosystem to map each interaction. Using these webs and the studies produced with them, he determined the strength and types of indirect interactions present in this type of habitat. While analyzing the studies, he identified the nine main indirect interactions (see above) that occur within marine ecosystems. He also looked at the effect indirect interactions could have on the ecosystems. The manipulations performed in each experiment increased the number of direct and indirect interactions, did not influence the strength of the indirect interactions on ecosystems, did not change with web size after the manipulations, and 40-50% of the changes resulting from the manipulations were from indirect interactions. Menge determined that an increase in species number could cause an increase in the number of strong interactions that flora and fauna can have. Species number also has a strong effect on the number of direct interactions, indirect interactions and pathways that create indirect interactions. Menge also determined that nearly half of all indirect effects identified within the twenty-three experiments were from the influence of predators. He found that keystone predation is the most common of the observed indirect effects and exploitation competition was the least common of the observed effects. Finally, Menge predicted that in future studies it would be observed that as the number of omnivores increased, the number of indirect interactions would increase. This was all from the analysis of "interaction webs" that looked at all relationships in an ecosystem. If more of these webs were produced then each ecosystem could be understood more fully and managed properly.

Top Predator Loss

Throughout the world there has been a decline in marine top predator populations. It has been estimated that 90% of the large predatory fish population are gone (Myers 2003). Marine mammals and other top predators are also showing a decline in numbers. This is a large problem because of the impact top predators have on ecosystems. The intricacy of the interactions top predators have within and upon ecosystems makes it difficult to predict what happens once marine predators are removed. The most obvious effect that the loss of top predators can have is called a trophic cascade. This was described above as the loss of a top predator leading to a lower trophic level becoming a top predator. This is commonly looked at with direct interaction studies, but when you take into account the indirect effects, top predators have a much greater impact on ecosystems than previously thought and their loss can have dire consequences for the ecosystem's stability and health.

It has been predicted that as large shark populations decrease in number due to an increase in overfishing and mortality due to shark finning, the smaller elasmobranch counterparts will increase in population. A shark survey, conducted off the coast of North Carolina since 1972, shows a range of declines of population size from an 87% decrease for sandbar sharks to a 99% decrease for bull, smooth hammerhead and dusky populations. Concurrently other studies have shown an increase in the sharks' main prey, mesopredatory elasmobranchs. As the sharks decrease the smaller elasmobranchs increase in population and will take over as top predator (Myers 2007). This is called a mesopredator release hypothesis and is defined by Ritchie in 2009 as the eruption of the mesopredator, a middle trophic level predator, after the decline of an apex, or top predator, population.

One such mesopredator has already increased in population and made an impact. In the northwest Atlantic Ocean, large shark populations have declined and, as a result, cow nose ray populations have increased. In 1996, sampling during the cow nose ray migration showed that after the cow nose rays had moved through an area the scallop populations were almost completely removed (Myers 2007). A ray population increase has lead to an elimination of the bay scallop population, which is considered an important resource species within that ecosystem (Heithaus 2007). If the bay scallops are eliminated, then competition for space decreases and a new species will move in. Any animals that need to feed off the scallops, including the cow nose ray, will either; die, find a new resource, or move away. In 2004, North Carolina's scallop fishery was closed, and remained closed as of 2007, because of the decreased scallop population due to increased cow nose ray consumption of the scallops. Rays are also feeding on clams and oysters. This is causing a general depletion of fishery catch of clams and oysters by bivalve fisheries (Myers 2007). When top predators decline in number, entire ecosystems are affected.

Another example took place in the Northern Pacific. Human activities were removing or displacing sea otters from their natural habitat. When this happened, the urchins that were normally eaten by the sea otters increased in population. This lead to the kelp beds decreasing in number due to increased consumption by the urchins. Any animal that lived in the kelp forests was negatively affected by the removal of the sea otters (Paine 1980, Shears 2002). The loss of one top predator almost changed an entire ecosystem. These examples demonstrated what could happen when top predators are removed from an ecosystem. While the top predator population has been decreasing globally, very few studies have been conducted to understand the effects of that decrease on the ecosystem.

Human behavior also impacts the predator decrease indirectly. In the Northwest Atlantic Ocean, bluefish are being overfished. From the 1980's to 2005 fishing of bluefish increased fourfold, and total stock biomass decreased 72% from 1982 to 1997. These fish, however, are not the top predator in the ecosystem. Short fin makos are the main consumer of bluefish. Since the bluefish population has been decreasing, the short fin mako population has decreased, as well, due to lack of food. These two decreases in population have led to an increase in Atlantic mackerel and Atlantic herring populations. While the fishermen are not directly reducing the top predator population, they are indirectly causing the makos numbers to decrease and the mackerel and herring to increase in number (Wood 2008).

Modeling Impacts of Top Predator Loss

To study these fisheries, Mass Balance Models have been developed. These models look at the movement of biomass through an ecosystem and focus on the diets of different groups within that ecosystem (Heithaus 2008). In one study, these models were used to explain the effect of removing piscivorous demersal fish from the Gulf of St. Lawrence due to overfishing. The fishing was stopped, but after ten years the fish population had not increased. A study was conducted to see how the ecosystem had changed functionally since marine mammals replaced the main top predator, piscivorous demersal fish. Biomass, fish catch rates and diets of caught fish were taken into account to see what effect the predator change had on northern shrimp, mainly the species *Pandalus borealis*, which were the main prey of the fish. The study found that halibut and marine mammals were now the top predators in the ecosystem, and the decrease in piscivorous fish lead to a massive increase in the northern shrimp population. The removal of the top predator lead to more predators moving in and lower trophic levels becoming the top predator and increasing in population (Sakenoff 2006).

These models helped to show how the ecosystem reacted to the top predator population decrease. However, these models oversimplify interactions by only looking at biomass movement and diet, not changes in behavior, population sizes or type/number of species. Furthermore, these models require a large amount of data (Sakenoff 2006). The models also use the assumptions that diets do not change and that energy is cycled within a system, which are not valid assumptions. These types of models are being adapted to include risk effects of top predators interacting with the ecosystem (Heithaus 2008). Currently, the Mass Balance models are being upgraded to take into account indirect and direct interactions, in order to more accurately predict the full impact of the loss of a top predator in ecosystems where the diets and interactions of the animals are well known.

Research and Future Research:

However, to fully understand the effect that top predator population declines could have on the ocean, a full understanding of how ecosystems function with and without top predators has to take place. Fisheries must be managed with predator indirect and direct effects on prey in mind, while still maintaining the fisheries stability. While fisheries only contribute to roughly 1% of the global economy, for some coastal communities and islands, fisheries can contribute 60% of their economy. Northern Chile is 40% fishermen. If an economy like that loses its fisheries due to a limited vision from the fisheries manager, it could lose 40% of its jobs leading to an economic collapse (Weber 1994).

Historically, managers have used a single species management perspective because multi-species approaches take more time and effort. This short-sightedness has led to the collapse of many fisheries (Ellen 2012). For example, the sardine stocks off the coast of Japan and California saw a complete collapse in the 1940's due to poor management policies that lead to overfishing (Botsford 1997). The managers focused on the sardine's ability to reproduce and managed the fishery using that information. What wasn't taken into account was that the recruitment and survival rates for top predators, such as sea lions, would drop. This decrease in top predator numbers led to the decreased control from the upper trophic levels and eventually led to the collapse of the ecosystem (Crowder 2008) because fishing quotas were based solely on sardine recruitment.

The fishery managers in New England and Newfoundland made the same mistake by using the "maximum sustainable yield" method. The take rates allowed under this method were determined by the reproductive cycle of the target species and nothing else. This led to the shutdown of both the Georges Bank Fishery and the Grand Bank Fishery due to fishery collapse by way of overfishing (Roughgarden 1996).

These are just three examples of fisheries that have been unsuccessfully managed due to a single-species managing approach. Currently many fisheries still regulate the fishing and removal of organisms using the "Maximum Sustainable Yield" (MSY) method. MSY uses a species' reproductive rates, growth rates and survival rates to try and increase the population growth of one species. Underneath this kind of single species managing style, 44% of the fisheries in use by humans are considered to be over or fully exploited (Botsford 1997). Many of the fish that are being overfished are top predators. Fishing regulations must look at the impact of removing a top predator on the lowest trophic level.

Instead of looking at the decrease in top predators as a problem, some fisheries managers have been looking at removing top predators as a solution to the decrease in commercial fishing stock. Off the Canadian east coast fishers have requested the removal of seals to increase fishing catch. In 2001, Yodiz studied the suggestion of removing top predators to increase fishing catch. In his paper, he called for multi-species modeling to understand the effects of fisheries on the ecosystem to see what the effects of removing top predators could be and urged caution before anything was done that could not be reversed.

Astles (2006) described one such method called a risk assessment model. His model used the relationships between harvest levels and fish stocks to determine what level of fishing should occur. However, it requires a lot of data to be able to form a good quantitative analysis to determine a sustainable catch, which requires a lot of time and energy to attain. Furthermore, a good ecosystem analysis, like a risk assessment model, would take into account any anthropogenic effects on the ecosystem and the endangered statuses of flora and fauna. It should also take into account global change and migration of other fish into the area (Botsford 1997).

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) uses a multi-species ecosystem approach to manage fisheries. The managers of the krill fishery realized the effect the fishery was having on the local ecosystem and started monitoring predators and prey separately from the krill. The CCAMLR wanted to make certain that any fishing activities did not largely influence or change the way the ecosystems around the fisheries functioned and that the local biodiversity was maintained. To do this the CCAMLR modeled entire food webs of the fishery ecosystems. They then determined interactions that affect the krill fishery by looking at the strong interactions. If a predator feeds substantially on the krill then it is monitored. If krill is not a large part of a predator's diet then it is not considered a strong interaction and is not monitored. This helped the managers develop operational objectives based on the impact the fishery would have on the predators and prey and the conservation status of the flora or fauna involved. The fishery managers then maintained a median amount of predator productivity within the fishery. This way the predators are maintained, and the krill or other fished species can continue to be fished. They also monitored direct and indirect effects of fishing on the ecosystem with the goal of maintaining a fishery while still maintaining an ecosystem's stability and productivity (Constable 2004). This type of monitoring is a good step towards a productive and efficient way of studying and maintaining top predator populations.

Scientists must strive to map the current global ecosystem interactions and predict what could happen if fish catch does not decrease. This will be difficult since there is not one model or equation that can predict top predator influences. Scientists need to focus on what can realistically be accomplished and try to emphasize conservation and caution while still fishing and researching within marine systems

Summary and Conclusion

The top predator declines seen globally are having and will continue to have far reaching effects upon marine systems. Hutchings (2000) found that the longer populations are depleted, the longer they take to recover. Fisheries that had been declining for fifteen years showed a forty percent failure to recover even after another fifteen years of no use (Hutchings 2000). The decline of top predators is causing trophic cascades, fishing stock loss and fishery collapses. If conservation of top predators is not a key focus, the population decline will continue and the chance of reversing the population decrease will take longer or potentially become impossible.

The first step in understanding top predators and the significant role that they play in maintaining the relationships and subsequent sustainability of marine ecosystems. In order to properly manage fisheries and ecosystems, scientists and fisheries managers must take into account both indirect and direct effects of top predators. Direct effects include not just the obvious effects of consumption, but also factors like risk effects caused by fear or intimidation, and, as shown above, indirect effects, such as within Shark Bay, Australia, involve multiple species and can have equally large impacts on ecosystem stability (Hiethaus 2001). The preys' and the predators' habitat choices, health, population numbers, size, age and hunting choices must be taken into account to fully understand an ecosystem and what the removal of a top predator could have on that ecosystem. With this type of studying method managers can better manage and scientists can better understand fisheries and the effect overfishing of top predators could have on populations. Changing the way fisheries are managed globally is not going to be simple. It will require time and effort. Scientists and managers need to work together to start trying to change the way that fisheries are managed or top predators will continue to be overfished, "managed" fisheries will continue to collapse, and humans could lose the ocean as a sustainable resource.

References

Acevedo-Gutiérrez A., (2002) "Interactions between Marine Predators: Dolphin Food Intake Is Related to Number of Sharks." *Marine Ecology Progress Series.* 240: 267-71.

Acevedo-Gutierrez A., and Parker N., (2000) "Surface Behavior Of Bottlenose Dolphins Is Related To Spatial Arrangement Of Prey." *Marine Mammal Science.* 16(2): 287-98.

Astles K.L., Holloway M.G., Steffe A., Green M., Ganassin C., and Gibbs P.J., (2006) "An ecological method for qualitative risk assessment and its use in the management of fisheries in New South Wales, Australia." *Fisheries Research,* 82: 290–303.

Barros N. B., and Wells. R. S., (1998) "Mammalogists Prey and Feeding Patterns of Resident Bottlenose Dolphins (*Tursiops Truncatus*) in Sarasota Bay, Florida." *Journal of Mammalogy.* 79(3): 1045-059.

Bascompte J., Melian C. J., and Sala E., (2005) "Interaction Strength Combinations and the Overfishing of a Marine Food Web." *Proceedings of the National Academy of Sciences.* 102(15): 5443-447.

Botsford L. W., Castilla J.C., Peterson C.H., (1997) "The Management of Fisheries and Marine Ecosystems." *Science.* 277 (509): 509-515.

Coleman F. C., and Williams S.L., (2002) "Overexploiting Marine Ecosystem Engineers: potential Consequences for Biodiversity." Trends in Ecology & Evolution. 17(1): 40-44.

Constable A.J., (2004) "Managing Fisheries Effects on marine Food Webs in Antarctica: Tradeoffs Among Harvest Strategies, Monitoring, and assessment in Achieving Conservation Objectives." *Bulletin of Marine Science.* 74(3): 583-605.

Crowder L.B., Hazen E.L., Avissar N., Bjorkland R.,Latanich C., and Ogburn M.B., (2008) " The Impacts of Fisheries on Marine Ecosystems and the Transition to Ecosystem-Based Management." *Annual Review of Ecology, Evolution, and Systematics.* 39: 259–78.

Daskalov G. M., Grishin A.N., Rodionov S., and Mihneva V., (2007) "Trophic Cascades Triggered by Overfishing Reveal Possible Mechanisms of Ecosystem Regime Shifts." *Proceedings of the National Academy of Sciences.* 104(25): 10518-0523.

Dill L. M., Heithaus M.R., and Walters C.J., (2003) "Behaviorally Mediated Indirect Interactions In Marine Communities And Their Conservation Implications." *Ecology.* 84(5): 1151-157.

Domenici P., (2001) "The Scaling of Locomotor Performance in Predator-prey Encounters: From Fish to Killer Whales." *Comparative Biochemistry and Physiology.* 131: 169-182.

Ellen H., (2012) “The Persistence of a Concept: Maximum Sustainable Yield.” *The International Journal of Marine and Coastal Law*. 27(4): 763-771.

Grabowski J. H., (2004) "Habitat Complexity Disrupts Predator–Prey Interactions But Not The Trophic Cascade On Oyster Reefs." *Ecology.* 85(4): 995-1004.

Hammerschlag N., Martin R.A., and Fallows C., (2006) "Effects of Environmental Conditions on Predator–prey Interactions between White Sharks (*Carcharodon Carcharias*) and Cape Fur Seals (*Arctocephalus Pusillus Pusillus*) at Seal Island, South Africa." *Environmental Biology of Fishes.* 76(2-4): 341-350.

Heithaus M. R., (2001) "Predator-prey and Competitive Interactions between Sharks (order Selachii) and Dolphins (suborder Odontoceti): A Review." *Journal of Zoology, London.* 253: 53-68.

Heithaus M. R., (2001) "Shark Attacks On Bottlenose Dolphins (*Tursiops aduncus*) In Shark Bay, Western Australia: Attack Rate, Bite Scar Frequencies, and Attack Seasonality." *Marine Mammal Science.* 17(3): 526-39.

Heithaus, M. R., (2000) "The Biology of Tiger Sharks, *Galeocerdo Cuvier*, in Shark Bay, Western Australia: Sex Ratio, Size Distribution, Diet, and Seasonal Changes in Catch Rates." *Environmental Biology of Fishes.* 61: 25-36.

Heithaus, M. R., and Dill L.M., (2006) "Does Tiger Shark Predation Risk Influence Foraging Habitat Use by Bottlenose Dolphins at Multiple Spatial Scales?" *Oikos.* 114(2): 257-264.

Heithaus M. R., Frid A., Wirsing A.J., and Worm B., (2008) "Predicting Ecological Consequences of Marine Top Predator Declines” 23: 202–210.

Heithaus M. R., Wirsing A.J., Burkholder D., Thomson J., and Dill L.M., (2009) "Towards a Predictive Framework for Predator Risk Effects: The Interaction of Landscape Features and Prey Escape Tactics." *Journal of Animal Ecology.* 78(3): 556-562.

Heithaus M. R., Wirsing A.J., Dill L.M., Fourqurean J.W., Frid A., Burkholder D., Thomson J., and Bejder L.., (2007) "State-dependent Risk-taking by Green Sea Turtles Mediates Top-down Effects of Tiger Shark Intimidation in a Marine Ecosystem." *Journal of Animal Ecology.* 76: 837-844.

Heithaus M. R., Wirsing A.J., Thomson J., and Burkholder D., (2008) "A Review of Lethal and Non-lethal Effects of Predators on Adult Marine Turtles." *Journal of Experimental Marine Biology and Ecology.* 356(1-2): 43-51.

Heithaus M. R., Dill L.M., Marshall G., and Buhleier B., (2002) "Habitat Use and Foraging Behavior of Tiger Sharks (*Galeocerdo cuvier*) in a Seagrass Ecosystem." *Marine Biology* 140(2): 237-248.

Herzing D. L., (1996) “Vocalizations and associated underwater behavior of Free ranging Atlantic Spotted Dolphins, *Stenella frontalis* and Bottlenose Dolphins *Tursiops truncatus.” Aquatic Mammals.* 22(2): 61-79.

Hutchings J.A., (2000) “Collapse and recovery of marine fishes.” *Nature.* 406: 882-885.

Irons D.B., Anthony R.G., Estes J.A., (1986) “Foraging Strategies of Glaucous-Winged Gulls in a Rocky Intertidal Community.”*Ecology .* 67(6): 1460-1474.

Levine S., (1980) “Indirect Mutualism: Variations on a theme.” The American Naturalist, 116 (3): 441-448

Menge B. A., and Lubchenco J., (1981) "Community Organization in Temperate and Tropical Rocky Intertidal Habitats: Prey Refuges in Relation to Consumer Pressure Gradients." *Ecological Society of America*. 51(4): 429-450.

Menge B. A., (1995) "Indirect Effects in Marine Rocky Intertidal Interaction Webs: Patterns and Importance." *Ecological Monographs* 65(1): 21-74.

Myers R.A., Worm B., (2003) “Rapid worldwide depletion of predatory fish communit- ies.” *Nature.* 423(6937): 280-283.

Myers R. A., Baum J.K., Shepherd T.D., Powers S.P., and Peterson C.H., (2007) "Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean." *Science.* 315(5820): 1846-850.

Opitz S., 1996. Trophic interactions in Caribbean coral reefs. *International Center for Living Aquatic Resource Management*. pp 1-356.

Pauley D., (1986) “Simple Method for Estimating the Food Consumption of Fish Populations from Growth Data and Food Conversion Experiments.” *Fishery Bulletin.* 84(4): 827-840.

Pauley D., Christensen V., Dalsgaard J., Froese R., and Torres Jr. F., (1998) "Fishing Down Marine Food Webs." *Science.* 279(860): 860-63.

Paine R. T., "Food Webs: Linkage, Interaction Strength and Community Structure." *Journal of Animal Ecology.* 49 (1980): 667-85.

Papastamatiou Y.P., Wetherbee B.M., Lowe C.G., Crow G.L., (2006) “Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion.” *Marine Ecology Progress Series*. 320: 239–251.

Power M. E., (1992) "Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy." *Ecology.* 73(3): 733-46.

Ritchie E.G., Johnson C.N., (2009) “Predator interactions, mesopredator release and Biodiversity Conservations.” *Ecology Letters*. 12:982-998

Roughgarden J. and Smith F., (1996) “Why Fisheries collapse and what to do about it.” *Ecology.* 93:5078-5083.

Savenkoff C., Savard L., Morin B., and Chabot D., (2006) "Main Predators and Prey of the Northern Shrimp (*Pandalus Borealis*) in the Northern Gulf of St. Lawrence during the Mid-1980s, Mid-1990s, and Early 2000s." *Canadian Technical Report of Fisheries and Aquatic Sciences.* 2639(8): 1-32.

Weber P., (1994) “Net Loss: Fish, jobs and the marine environment.” *World watch Paper.* pp 1-76.

Werner E. E., Gilliam J.F., Hall D.J., and Mittelbach G.G., (1983) "An Experimental Test of the Effects of Predation Risk on Habitat Use in Fish." *Ecological Society of America*. 64(6): 1540-1548.

Wirsing A. J., Heithaus M.R., Frid A., and Dill L.M., (2008) "Seascapes of Fear: Evaluating Sublethal Predator Effects Experienced and Generated by Marine Mammals." *Marine Mammal Science.* 24(1): 1-15.

Wooton J.T., (1993) “Indirect Effects and Habitat Use in an Intertidal Community: Interaction Chains and Interaction Modifications” *The American Naturalist*, 141(1):71-89.

Yodzis P., (1994) "Predator-Prey Theory and Management of Multispecies Fisheries." *Ecological Applications.* 4(1): 51-58.

Wood A.D., Wetherbee B.M., Juane F., Kohler N.E., Wilga C., (2009) “Recalculated diet and daily ration of the shortfin mako (*Isurus oxyrinchus*), with a focus on quantifying predation on bluefish (*Pomatomus saltatrix*) in the northwest Atlantic Ocean.” *Fishery Bulletin*. 107(1):76-88.