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A predator-based methodology for studying predator-prey relationships in fishes

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Capstone of Ashley Vettese

Submitted in Partial Fulfillment of the Requirements for the Degree of

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NOVA SOUTHEASTERN UNIVERSITY
HALMOS COLLEGE OF ARTS AND SCIENCES

A predator-based methodology for studying predator-prey relationships in fishes.

By

Ashley Vettese

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

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Abstract

Changes in the ocean including acidification, increasing temperatures, loss of habitat, and increased hypoxic events has the potential to change predator-prey relationships. These changes in single interactions can then have effects on population sizes, community structures, and changes in trophic cascades. Understanding how changing abiotic factors impact predator-prey relationships will be crucial for understanding what populations and communities will look like under future ocean conditions. In this review, the goals are to (1) summarize the current knowledge on how changing ocean conditions affect predator-prey relationships; (2) describe an example predator-based approach to examine how changing these changing factors impact predator-prey relationships; and (3) test the effectiveness of this method on a simple predator-prey relationship between the marine mesopredator fish lane snapper (*Lutjanus synagris*) and ghost shrimp prey (*Palaemonetes paludosus*). The results of this study summarize over 60 studies relating to factors affecting predator-prey relationships and outlines a methodology appropriate for studying predator-prey interactions. The results of the predation trials revealed that predation efficiency of the lane snapper was significantly impacted by temperature, while habitat complexity was found not to be statistically significant.

Keywords: *Lutjanus synagris*, predator-prey relationship, habitat complexity, acidification, warming, oxygen

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Introduction

Oceans are drastically changing at a rate that research and mitigation efforts are unable to keep up with. The loss of seagrasses, mangroves, and coral reefs combined with steadily increasing temperature and CO₂ levels are a variety of factors that could potentially impact predator-prey interactions. Species interactions are among the most important forces structuring ecological communities (Gilman et al. 2010). The relationships between predator and prey impact population sizes as well as community structure, and some interactions with keystone species can even influence an entire ecosystem (Estes et al. 2011). Understanding how these factors affect predation can help in efforts to mitigate the negative effects of the changing ocean and sustainability endeavors. Predators are usually more affected by the environmental changes occurring in the ocean than smaller prey items. Because of this predation efficiency is a good metric for measuring how these variables affect predator prey interactions. Each of the changes affects species in different ways.

The factors that will be discussed here are habitat complexity, temperature, acidification, and oxygen. Complex habitats are crucially important for use as prey refuges for producers, primary consumers, and juveniles of top-tier predators. Over the years, there has been a large loss of complex habitats – coral reefs and mangroves – mainly due to anthropogenic sources. Generally, a decrease in complexity or structure results in an increase in predation (Gotceitas and Colgan 1989). Oceans have been steadily warming over the years, and an increase in temperature often results in an increase in metabolic needs, which in turn often leads to an increase in predation activities.

There is a major difference in reactions to temperatures between mobile and sessile species. Mobile species have the advantage of being able to move to more hospitable environments, while sessile species must adapt to the change in temperature. These species-specific differences will affect the outcomes of predator-prey interactions. In combination with increasing temperatures, the oceans are also becoming more acidic (Chivers et al. 2013). An increase in CO₂ has been observed to cause a decrease in predation (Ferrari et al. 2015), as well as impacting developmental, physiological, behavioral, and reproductive processes in marine life (Chivers et al. 2013). The changes caused by increased levels of CO₂ are vast and each species is impacted differently. Due to the increases in temperature and CO₂, oxygen levels in the oceans

are decreasing (Edjung et al. 2008). There are also more frequent and longer-lasting hypoxic episodes, which increases the stress that marine communities experience during these events. Overall, a decrease in oxygen levels causes a decrease in predation. These factors cause a variety of changes in predator-prey interactions and could work in combination to make changes more drastic or cancel each other out. In either scenario, the changes have the potential to greatly impact the structure and function of marine communities worldwide.

There are three main goals of this review: (1) Summarize the current knowledge on how changing oceans change the result or intensity of predator-prey interactions. (2) Outline a simple but effective methodology for testing how a factor affects a predator-prey relationship, with a focus on measuring the predation efficiency of the predator. (3) Test the effectiveness of this method on a simple predator-prey interaction, the lane snapper (*Lutjanus synagris*) and an invertebrate prey. A minor goal for this review is to provide a detailed base of knowledge for future researchers.

Methods

Literature Review

For this project, a search was done across the databases *Web of Science* and *ScienceDirect*. Search terms used were “predation”, “predation efficiency”, “habitat complexity”, “ocean acidification”, “climate change”, “temperature”, “warming”, “oxygen”, “hypoxic events”, “trophic cascades”, “predator-prey interactions”. The literature search at first was confined to those later than the year 2000, but after following references in recent studies, the literature review was expanded to include studies dating back to year 1980. The studies found included those that utilized both field and laboratory studies, as well as studies covering many different species and predator-prey relationships.

Predation Trials

The lane snapper (*Lutjanus synagris*) was used as the predator and ghost shrimp (*Palaemonetes paludosus*) was used as prey. Individuals of *Lutjanus synagris* were collected via hook-and-line and handheld nets either by researchers or a third-party collector from the waters

of Broward, Miami-Dade, and Monroe Counties. The shrimp used in the predation trials were collected via dip nets from shallow water areas of Broward County. All persons and methods of fish collection were covered under Florida Fish and Wildlife Conservation Commission (FWC) Special Activity License No. SAL-17-1980A-SR issued to D. Kerstetter as Principal Investigator. Individuals of *L. synagris* measured 10.2-15.5 cm, and individuals of *P. paludosus* measured an averaged 2.2 cm. Fish were housed in a 175-gallon aquaria, divided into 12 sub-aquaria, with one individual per tank so there was no potential interference from tagging each fish individually. The fish were acclimated for at least two weeks prior to being used in trials. Fish were maintained and cared for under Nova Southeastern University (NSU) Institutional Animal Care and Use Committee (IACUC) protocol 2018.03.DK5 issued to D. Kerstetter as Principal Investigator and renewed annually.

Trials were conducted at four different temperature levels (15°C, 20°C, 25°C, and 30°C) and kept at a constant salinity of 20 ppm. Habitat complexity was replicated using wooden dowel rods (1/4-inch diameter) as non-flexible complexity and 4-5 blades of plastic eelgrass attached to a small piece of dowel rod as flexible complexity. Both complexity types had three different levels of habitat complexity: Level 1 had 4 clusters of complexity per aquaria (Figure 1a), level 2 had 9 clusters per aquaria (Figure 1b), and level 3 had 16 clusters per aquaria (Figure 1c). Trials were conducted in aquaria measuring 60 cm x 60 cm x 25 cm, with a piece of PVC to serve as shelter for the predator.

Predators were starved for 24 hours before trials, and then placed in the experimental arena for a twenty-four-hour acclimation period. To begin the trial, 10 prey items were introduced into the experimental arena with the predator. The interaction was recorded at 1080-pixel resolution and saved as a MP4 file with a GoPro model Hero 2 camera (GoPro, Inc. for a one-hour trial period. After the one-hour trial period, the predator was removed from the tank and the number of prey items consumed was recorded. Fish were allowed at least a 24-hour rest period before beginning starvation for the next trial.

Statistical Analysis

Statistics were completed in R (R Core Team, 2020) and consisted of nested factorial ANOVA. A factorial ANOVA was done to determine whether temperature, habitat complexity type, and level of complexity independently or interactively affect predation efficiency. A non-

parametric Kruskal-Wallis test was done to determine the significance of temperature and complexity on predation efficiency. Figures were made using the package ggplot2 (Wickham, 2016).

A post-hoc analysis was done to determine which treatments were significantly similar to each other. Dunn tests were performed to compare each specific treatment to each of the others and determine which specific treatment comparisons yielded significant differences. These metrics were then used to confirm the results of the post-hoc analysis.

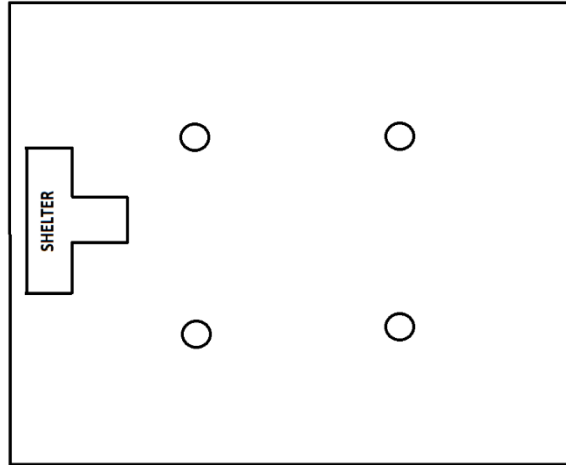


Figure 1a. Schematic of trial tank setup, showing level 1 complexity and the provided shelter.

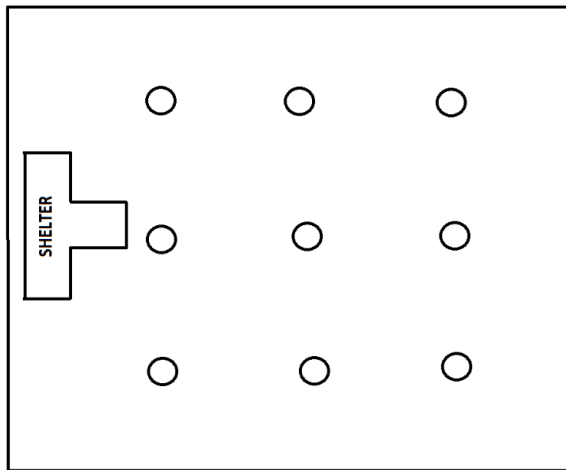


Figure 1b. Schematic of trial tank setup, showing level 2 complexity and the provided shelter.

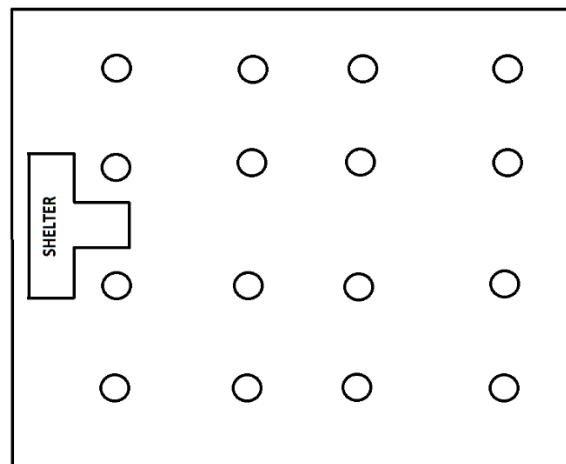


Figure 1c. Schematic of trial tank setup, showing level 3 complexity and the provided shelter.

Results

Literature Review

The results of the literature review yielded over 60 studies focusing on predator-prey interactions. Most of the studies were on vertebrate species (68%), and 32% of studies were on invertebrates, illustrated in Figure 2a. The breakdown of factors being studied is outlined in Figure 2b. Most studies were on habitat complexity (30%) and acidification (34%).

Measuring Predation Efficiency

There are many ways that predation efficiency has been measured within all marine taxa. Most studies measure the number or percentage of prey items eaten within the experimental time (Allan et al. 2013; Anderson 1984; Coen et al. 1983; Ferrari et al. 2015; Grabowski 2004; Howard 2009; Miller et al. 2014; Munday et al. 2010; Nowicki et al. 2012; Pincebourde et al. 2012; Sagasti et al. 2001; Stoner 1982; Taylor and Eggleston 2000), while another portion of studies instead measure the number or percentage of prey surviving after the experimental time (Beukers and Jones 1998; Chivers et al. 2014; Coull and Wells 1983; Edjung et al. 2008; Ferrari et al. 2011b; Mattila 1992; Peterson 1982; Sandberg 1994; Tallqvist et al. 1999). Some studies measured how certain factors influenced the time to complete a predation event. For example, Cripps et al. (2011) measured the time it took dottybacks (*Pseudochromis fuscus*) exposed to different levels of CO₂ to recognize and respond to prey items entering the experimental area, the number of strikes on the prey item, and whether those strikes were successful. Landes and Zimmer (2012) studied the effect of acidification, warming, and acidification and warming combined on the prey handling time of green crabs *Carcinus maenas*. Miller (2013) also tested the effect of warming water temperatures on the handling times of the dogwhelk *Nucella lapillus*. Shin et al. (2005) investigated the effect of short-term hypoxia on the time of consumption and biomass consumed of the swimming crab *Thalamita danae* on the mussel *Brachidontes variabilis*. Some studies have taken the study of predation efficiency a step further to also investigate the accuracy of predators (Gotceitas and Colgan 1989; Gotceitas 1990; Savino and Stein 1982). These studies all tested the predation efficiency and accuracy in varying degrees

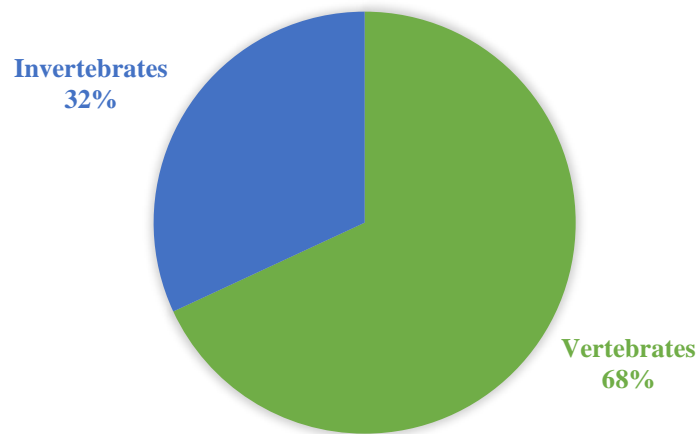


Figure 2a. A chart representing the percentage of studies on vertebrates versus invertebrates in the literature review.

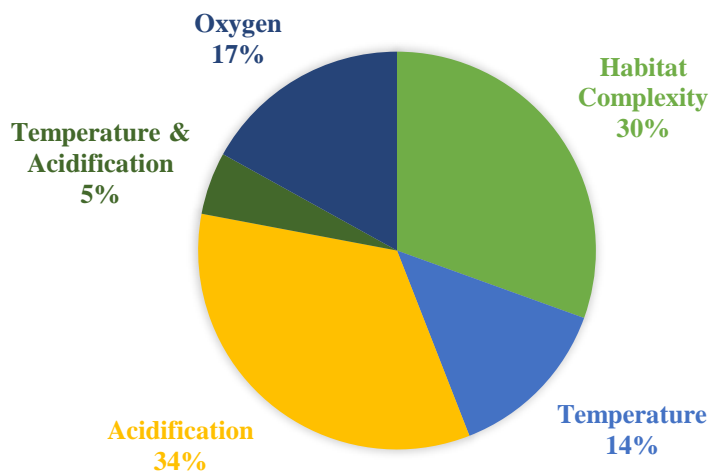


Figure 2b. A chart representing the breakdown of factors studied in the studies of the literature review.

of habitat complexity, and not only measured how many prey items were eaten by the predators, but how many attempted strikes were successful during the experiment.

Lab experiments

The methods used to measure predation efficiency vary depending on the factor that is being tested. Habitat complexity in the lab can be either natural or artificial. Beukers and Jones (1998) used live coral heads of three different complexities (*Pocillopora damicornis*, *Acropora nasuta*, and *Acropora nobilis*) to determine how coral complexity influenced the predation of juvenile damselfish. Grabowski (2004) simulated a temperate reef environment using unaggregated oyster shells and oyster clusters to provide varying levels of complexity. Nelson (1979) and Stoner (1982) both used natural seagrass blades that were detached from the plant and clumped in various densities to gradually increase habitat complexity. Coull and Wells (1983) tested a variety of simulated habitats using both natural structures (dried algae, fresh algae, stones, gravel) as well as artificial structures (plastic bottle brushes). Studies that use artificial vegetation are split between using plastic seagrasses (Anderson 1984; Coen et al. 1981; Heck and Thoman 1981) and using sections of polypropylene rope (Gotceitas and Colgan 1989; Gotceitas 1990; Savino and Stein 1982; Savino and Stein 1989). Matilla (1992) used plastic straws to simulate decaying reeds and wooden dowels for growing reeds, and Minello and Zimmerman (1983) used plastic straws mounted in mesh to simulate *Spartina* cordgrass structure. Studies that focused on increased CO₂ on predator-prey interactions were done so by putting a pH controller into the tanks, and a solenoid injected CO₂ into the tanks whenever the pH levels strayed from the set point. Temperature studies were completed by using both heaters and chillers to maintain the experimental arena at the desired temperature, and studies on oxygen's effect on predation events were done by bubbling N₂ gas into aquaria, with an oxygen probe continually measuring the oxygen content of the water and turning on and off the N₂ bubbling as needed to maintain the desired level.

Field experiments

While most experiments measuring predator-prey interactions are conducted in a laboratory setting, where most environmental factors can be controlled, some researchers have completed field studies determining the impact of either habitat complexity or elevated CO₂ on the outcome of these predation events. Field studies concerning predator efficiency is difficult

due to the transient nature of most predators as well as attempting to control many variables out in the wild, however, there are some methods that have been successful in this endeavor. The two most common methods are predator exclusion and an open experimental arena with either sedentary prey items or prey with high site fidelity.

The predator exclusion method of field studies involves the physical restriction of predators from the experimental arena, allowing for the survival of the prey species without risk of predation, afterwards comparing the survival to areas where predators were allowed. A study done by Vince et al. (1976) consisted of an exclusionary field study in which exclosures were built on circular plots of a saltmarsh ecosystem, one plot covered with grass of a low complexity (*Spartina alterniflora*) and the other with a grass of higher complexity (*Spartina patens*). The exclusionary fences prevented movement of the saltmarsh killifish (*Fundulus heteroclitus*) onto the marsh. It was found that the exclosures led to an increase of the youngest age-class of the pulmonate snail *Melampus bidentatus*, a common prey item for *F. heteroclitus*, on both the higher and lower complex marsh environments. In a natural marsh environment, the less complex marshes are normally scarce of smaller *M. bidentatus* due to killifish being able to enter the marsh and consume the snails. The exclusion of killifish from the experimental marsh area allowed for the size distribution of *M. bidentatus* to resemble that of the high marsh area, where killifish normally cannot enter to forage for snails.

Peterson (1982) conducted a field study that consisted of excluding predators from a shallow shoal-grass (*Halodule wrightii*) bed. Experimental areas were enclosed in plastic mesh, small enough to exclude large predators, but large enough to let smaller predators into the enclosure, in either unvegetated, partially vegetated, or densely vegetated areas of the shoal grass bed. Two species of clam, the hard clam *Mercenaria mercenaria* and the dog clam *Chione cancellata*, were placed in these enclosures at varying densities and left in the enclosures for a period of seven months after which the clams' status was determined (alive, missing, dead with undamaged shells, dead with rasped shells, or dead with crushed shells). This process was repeated once for a total of two trials. Peterson found that the densities of *M. mercenaria* declined 54% in the first experiment and 84% in the second experiment in comparison to the control enclosures. Densities of *C. cancellata* showed a similar pattern, with a significant decline of 45% and 67% in the two experiments. Peterson's study shows that for these two burrowing

clams, seagrasses serve as a crucial refuge from predation pressure. This is especially true for *Chione cancellata*, which burrows to a shallower depth than *Mercenaria mercenaria*, and therefore is more likely to be found and eaten by predators

Conducting a field study using an open experimental arena is challenging, since the researchers must account for the possibility of migration of both predators and prey from the area. For this reason, most of the studies utilizing this method have chosen a prey species that is either sedentary or exhibits high site fidelity, so that the possibility of random movement away from the experimental arena is unlikely. These studies also conduct a control experiment involving a group of prey with no predation risk, to ensure that the majority of the prey stay within the experimental arena. Beukers and Jones (1998) studied the interaction between lemon damselfish (*Pomacentrus moluccensis*) recruits and two of its natural predators: a pseudochromid, the brown dottyback (*Pseudochromis fuscus*), and a serranid, the chocolate hind (*Cephalopholis boenak*). The field experiment consisted of constructing 20 patch reefs with two coral species of differing complexity, the more complex *Pocillopora damicornis* and the less complex *Acropora nobilis*. Each patch reef was stocked with twenty juvenile damselfish, which have a high site fidelity, and aside from a few outliers stay within the reef that they recruit to. After two months, a census was taken of all the patch reefs to determine the number of juvenile damselfish that were preyed upon. Beukers and Jones (1998) found that the density of surviving juvenile damselfish was significantly higher on reefs with the more complex coral (*P. damicornis*). There was also a significant interaction between coral complexity and predator density. Reefs of the less complex *A. nobilis* that also had predators had a lower abundance of surviving damselfish than all other combinations on the reefs. These results confirmed both hypotheses of the study: that predators affect the survivorship of new recruits onto the reef and that the predator's efficiency is affected by the availability and complexity of habitat refuge. This study showed that for some predator-prey interactions, changes in habitat can have significant effects on predation rates.

Munday et al. (2010) studied the predator-prey relationship between newly settled Ward's damselfish (*Pomacentrus wardi*) and its common predators, the moon wrasse (*Thalassoma lunare*), the brown dottyback, and the inshore lizardfish (*Synodus variegatus*). Juvenile damselfish were exposed to three levels of CO₂ (the control level 550 ppm, and the

experimental levels 700 ppm and 850 ppm) for four days, and then were placed on the reef from which they were collected and monitored twice daily for two days. Behavioral observations over the course of the experiment showed that juvenile damselfish that were exposed to 850 ppm CO₂ exhibited riskier behaviors than those from other treatments, being more active and straying farther from the safety of the reef. This reflected in the predation results, where juvenile damselfish exposed to elevated CO₂ levels saw a 9-fold and 5-fold higher mortality rates for 850 and 700 ppm CO₂, respectively, in comparison to control levels of CO₂. This study showed that elevated levels of CO₂ altered the behavior of fish, which then translates to higher mortality rates not only in controlled laboratory settings, but also out in the wild.

Ferrari et al. (2011b) conducted a study similar to Munday et al. (2010) using a different damselfish species, the whitetail damsel (*Pomacentrus chrysurus*). Juvenile *P. chrysurus* were exposed to 390, 700, and 850 ppm CO₂, placed on the reef, and monitored for two days. Ferrari's behavioral observations were the same as Munday's, with damselfish exposed to elevated CO₂ being more active and moving further away from the reef, making them more vulnerable to predation. Ferrari's predation results were also the same, damselfish exposed to elevated levels of CO₂ had significantly lower survival rates within the two days of monitoring. This result further confirms that CO₂ can significantly alter the outcome of predator-prey interactions, and thus has the potential to impact community composition on reefs and other ecosystems.

Chivers et al. (2013) took a step further in examining how CO₂ affects the outcome of predator-prey interactions, by studying how elevated CO₂ levels impairs GABA-A receptors in the brain of juvenile ambon damselfish (*Pomacentrus amboinensis*) and how to restore GABA-A function to change survival rates of juvenile *P. amboinensis* on the reef. The GABA-A receptor is a major inhibitory neurotransmitter receptor in the brains of vertebrates (Nilsson et al. 2012). The Chivers et al. (2013) study involved exposing juvenile damselfish to elevated levels of CO₂ as well as a predator learning exercise. Some damselfish were then treated with gabazine, an antagonist of the GABA-A receptor, which would restore the receptor's function. Damselfish were then placed on a group of patch reefs similar to the methods employed by Munday et al. (2010) and Ferrari et al. (2011). The damselfish were monitored for four days, and the surviving number of damselfish were recorded at the end of the four days. Chivers et al. (2013) found that the number of surviving damselfish did not significantly differ between fish that were kept at

control levels of CO₂ with predator learning and fish that were exposed to the highest level of CO₂, treated with gabazine, and exposed to the predator learning exercise. In comparison, fish that were exposed to elevated CO₂ but not treated with gabazine prior to predator learning were unable to identify potential predators and had the lowest survival rate of the four treatments. These results show that although exposure to elevated CO₂ significantly decreases the survival rate of juvenile damselfish, gabazine was successful in mitigating the effect of CO₂ to allow for the fish to learn the crucial predator avoidance skill to avoid predation. Chivers et al. (2013) is the first study to show how CO₂ impairment at the neuronal level causes changes in learning which leads to a measurable and significant change in survival in the wild.

Nelson (1979) conducted a field study in which stakes were used to mark three sites of an eelgrass bed: the sparsely covered edges, the heavily vegetated middle, and an intermediate area. These sites were sampled quarterly for the abundance of amphipods, of which *Melita appendiculata* was the most common. The study found that the site that was sparsely vegetated had significantly lower abundances than the intermediate and heavily vegetated areas, which were not significantly different from each other. The only quarter that differed from the general results was in May, during which there was no significant difference among amphipod abundance. Nelson suggests that this is due to predatory fish, predominantly the pinfish *Lagodon rhomboides*, was entering the estuary across the seagrass bed before moving out to sea.

Coull and Wells (1983) conducted a small field experiment that tested the predation efficiency of blennies (*Helcogramma medium*) on meiofauna extracted from *Corallina officinalis*, an intertidal alga. The study involved draining four naturally occurring intertidal rock pools, removing all attached algae and snails, and placing dried and dead *Corallina* into two of the pools. Meiofauna collected from *Corallina* were placed in equal amounts in all four pools, followed by four blennies that were starved for 24 hours. The blennies were allowed to forage in the rock pool for four hours, the time of low tide, and after all fauna was collected from the pool and counted. The abundance of meiofauna difference significantly between the no structure pools and pools with *Corallina*, with 84% of meiofauna remaining in *Corallina* pools and only 31% meiofauna surviving in the rock pools with no structure, showing that the complex structure of *C. officinalis* significantly reduces predation by blennies, which would explain why copepod

and other meiofauna densities are higher within assemblages of *C. officinalis* in comparison to assemblages of other species of algae.

Heck and Thoman (1981) conducted a study on a natural turtlegrass (*Thalassia testudinum*) bed in the northern Gulf of Mexico. The study consisted of tethering a variety of invertebrate prey (*Neopanope texana*, *Neopanope packardii*, *Panopeus herbsti*, *Libinia dubia*, *Pagurus bonariensis*, *Callinectes sapidus*) to a length of monofilament fishing line. These tethered prey items were then placed in stands of turtlegrass or in drift algae accumulations in the morning and were collected again after 24 hours. Prey was also placed on patches of bare sand to serve as a control. The study found that significantly less prey items were eaten in the two vegetated habitats in comparison to the bare sand habitat, and there was no significant difference between the two vegetation types, showing that the presence of habitat complexity for prey to use as a refuge can impact the outcome of predator-prey interactions. Wilson et al. (1987) also conducted a tethering experiment, using juvenile blue crabs (*Callinectes sapidus*) as the prey tethered in eelgrass (*Zostera marina*) in four densities: no, low, medium, and high density. Results of Wilson's study indicate that lowest predation rate occurred in areas of medium seagrass density, with statistically similar predation rates in areas of low or high densities, and the greatest predation rate in the no seagrass area. The similar results found in the low- and high-density areas may be due to the predators also needing a certain amount of habitat complexity in order to be safe enough to forage for food. These field studies, although small in number, only provide additional confirmation to the numerous laboratory studies that have shown how both increased CO₂ levels and increased habitat complexity decreases the feeding efficiency of predators.

Table 1. Summary of literature review from 1980 to present listing advantages and disadvantages of conducting laboratory and field experiments in relation to predation efficiency.

Laboratory Experiments		Field Experiments	
Advantages	Disadvantages	Advantages	Disadvantages
Near total control of experiment parameters	Natural behaviors may be altered due to lab setting	Able to study fish in their naturally occurring state	Most predators are mobile and difficult to study in the field unless caged in or have high site fidelity
Ability to focus experiment on one variable	Results may be skewed due to unknown relationship between variables		Due to the need for enclosures, the effects of factors such as competition or foraging patterns may be lost
			Any variables that cannot be controlled in the field can affect results

Habitat Complexity

Predator efficiency is a function of the detection, pursuit, and capture of prey organisms; all of which may be inhibited by increasing habitat biomass (Stoner 1982). In general, predation efficiency decreases as habitats become more complex, as an increased complexity gives prey species more places to hide and inhibits movement for larger predators and thus decreasing the encounter rate between predator and prey. There is a tradeoff, however, between habitat complexity and prey abundance. Areas of greater complexity often have a higher abundance of prey, and open areas with little to no complexity typically have a lower prey abundance. Savino and Stein (1989) conducted a study comparing the predation efficiency of two predators, largemouth bass (*M. salmoides*) and northern pike (*Esox lucius*), in which both predators suffered a significant reduction in predation success as structural complexity was increased. Savino and Stein concluded that an intermediate level of complexity optimizes predation efficiency, as the prey abundance remains relatively high while also maintaining a steady encounter rate.

Threshold hypothesis

When studying predation efficiency in response to habitat complexity, the threshold hypothesis must be considered. The threshold hypothesis most simply states that predation rates will remain elevated among low to moderate levels of habitat complexity until a certain level is reached, after which point predation rates will even out and remain unchanged (Heck and Thoman 1981). The precursor to the threshold hypothesis was first suggested in a study done by Nelson (1979), who tested the predation of pinfish on the grass shrimp (*Palaemonetes vulgaris*) utilizing different densities of eelgrass blades (0, 15, 35, and 75 blades/tank). Nelson's results show that while higher blade densities did decrease the number of shrimps consumed, the tests were not significantly different over moderate densities of eelgrass blades. Nelson concluded that predation rate was not a linear function of habitat density, but more of a step function that evens out after a certain density is reached. Later studies confirmed that the relationship between habitat complexity and predator efficiency was non-linear (Heck and Thoman 1981; Savino and Stein 1982; Coull and Wells 1983).

A study by Gotceitas and Colgan (1989) set out to prove the effects of the threshold hypothesis. The study used juvenile bluegill sunfish (*Lepomis macrochirus*) as the prey and

largemouth bass as the predator in experiments that tested both the prey's choice of refuge and the predator's foraging success within multiple combinations of habitat complexity. The experimental arena was comprised of two separate refuge areas with one containing a plot of 100 stems of green polypropylene rope to serve as the control, and the other with a plot of 50, 250, 300, 350, 400, 450, 500, and 1,000 stems/m². Ten juvenile bluegills were used per one bass for a 30-minute foraging period. During the 30 minutes observations were made to determine where prey chose to go when attacked by the predator, the total number of attacks the predator made, and the number of prey captured during the trial. Predator foraging success was calculated by dividing the number of attacks by the number of prey consumed. The study found that predator foraging success was significantly lower in stems densities greater than 350 stems/m², and that prey significantly chose refuge in densities greater than 450 stems/m². Regression analysis showed that the relationship between foraging success and blade density was significantly different from a linear relationship, and logistical analysis showed that the relationship significantly fit into a logistic model, and from the logistic model the threshold level to significantly reduce predator foraging success was estimated to be 276 stems/m². Gotceitas and Colgan (1989) were quick to mention that the threshold level of complexity necessary to reduce foraging success can be affected by the features of available cover as well as the predator and/or prey species being tested. It is also important to mention that these results may only apply to this specific combination of predator, prey, and complexity.

Different density of same complexity type

Padial et al. (2009) utilized the same complexity type (*Eichhornia azurea*, a floating macrophyte) at different densities: none, low, and high. Under these conditions, the predation rate of *Moenkhausia sanctaefilomenae* was examined on two macroinvertebrates (*Cypricercus* sp. ostracods and larvae of *Chironomus* sp. midges). Trials consisted of 50 individuals of *Cypricercus* and 20 individuals of *Chironomus* in an experimental arena, in which three *M. sanctaefilomenae* were released and allowed to feed for four hours. The predation rate of *M. sanctaefilomenae* was significantly decreased in the high complexity treatment for both prey species. However, there was no significant difference between the predation rates observed in the low and no complexity treatments. These results show how limited predator foraging is in highly

complex environments, and how even a small loss of complexity can significantly impact predation success.

Utilizing different complexity types

Some studies have also sought to determine the effects of complexity on predation utilizing different types of habitat in increasing complexity, rather than varying the density of the same habitat type. Coull and Wells (1983) studied the predation efficiency of a blenny (*Helcogramma medium*) upon meiofauna within five different kinds of habitat complexity: the algae *Corallina officinalis* (dried), stones, beach gravel, plastic bottle brushes, and fresh algae with meiofauna removed. The blennies were tested over a 24-hour period, and the meiofauna remaining was counted after the 24-hour trial had completed. The study found that predation was highest in trials with little to no structure (stones and gravel) than trials using both dried and fresh algae, although the dried *C. officinalis* was the most effective deterrent of predation by *H. medium* (76% prey surviving). The study also completed a smaller field experiment using four intertidal rock pools, with dried *C. officinalis* in two pools and two pools left bare. An equal amount of meiofauna and four blennies was added to each pool for a 4-hour trial period. The results of the field experiment found that 84.1% of the meiofauna remained in the algae pools, while only 31.6% of meiofauna remained in the bare pools. These results are similar to the lab experiments, proving that without the complex *C. officinalis* as a habitat refuge, predation was much higher.

A study by Mattila (1992) examined the effects of habitat complexity on the predation efficiency of two fishes: the European perch (*Perca fluviatilis*) and the ruffe (*Gymnocephalus cernua*). The amphipod *Corophium volutator* was used as prey in experiments with the perch and the limnic isopod *Asellus aquaticus* was used in experiments with *Gymnocephalus cernua*. Plastic straws, wooden dowel rods, and rubber corks were used to increase the complexity of the experimental arena. Mattila found that while predation efficiency did decrease as habitat complexity increased, the difference in efficiency was drastically reduced if the prey species were able to successfully utilize the type of complexity to hide from the predator. This experiment utilized three different complexity types: sand, gravel, and plant cover. Mattila (1992) found that the prey species were more likely to avoid the predator in the plant cover in

comparison to sand and gravel cover, which caused the drastic reduction in predation efficiency of both species in plant complexity trials.

Beukers and Jones (1998) conducted an experiment to look at success rates of three predator species (*Pseudochromis fuscus*, *Cephalopholis boenak*, and *Thalassoma lunare*) capturing juvenile lemon damselfish (*Pomacentrus moluccensis*) within the shelter of three different coral species varying in complexity. The results of the study found that the different coral substratum had a significant effect on the amount of *P. moluccensis* surviving the experiment. In general, juvenile damselfish survival was lowest in habitats comprised of *Acropora nasuta* and *A. nobilis*, the least complex corals, and higher in the more complex *Pocillopora damicornis*. There was also a significant interaction between predator species and coral complexity on *P. moluccensis* survivorship. Both *P. fuscus* and *C. boenak* were most successful in the least structurally complex coral *A. nobilis*. However, there were differences among the predators. *P. fuscus* had a higher percentage of success in *P. damicornis* than in *A. nasuta*, while *C. boenak* exhibited the opposite pattern. Beukers and Jones (1998) suggested that these opposing results are due to species-specific differences in predator behavior.

Stoner (1982) investigated the effect of increasing biomass of macrophyte structure (*Halodule wrightii*, *Thalassia testudinum*, and *Syringodium filiforme*) on the predation success of pinfish. Stoner found that regardless of macrophyte type, the predation success of pinfish significantly decreased with increasing seagrass biomass. Among the different biomasses, *H. wrightii* always resulted in the lowest foraging efficiency of pinfish, significantly lower than the other seagrass species, showing that *H. wrightii* was unable to be utilized by the prey species as a refuge. Stoner mentions that the hypothesis that predator efficiency will decrease with increasing macrophyte surface area does not hold across all seagrass species. Rather, predator efficiency depends upon the morphology of the seagrass and the ability of individual prey organisms to conceal themselves from predators.

Habitat complexity and aspects of predation

There are also studies that investigated specific aspects of a predation event, such as search and handling times of prey. Anderson (1984) studied the effect of low (220 stems/m²) and high (670 stems/m²) complexity of *Elodea* plants on the search and handling time of largemouth bass (*Micropterus salmoides*) on guppies (*Lebistes reticulatus*). Anderson found that the

increased structural complexity significantly lengthened the time required by the predator to search for and handle prey. The study also found that the high complexity environment had a strong dependence of search time on capture order, causing the third and fourth prey items captured required much longer search time than the first two.

Gotceitas (1990) found that juvenile bluegill sunfish spent significantly more time foraging for prey in a habitat complexity of 500 stems/m² than in complexities of 100 or 250 stems/m². Foraging success of bluegills was also significantly different among the three complexities, with the most success in 100 stems/m². Savino and Stein (1982) studied the predatory behavior of largemouth bass, making observations of the predator's searching, pursuing, attacking, and capturing of prey. Results concluded that nearly all predatory behaviors declined significantly as stem density was increased from 0 to 250 stems/m² and 50 to 1,000 stems/m². Savino and Stein suggest that the threshold where these behaviors change, and predation success peaks between densities of 50 and 250 stems/m².

Table 2. Summary of studies examining the effect of habitat complexity on predation efficiency. Experiments are detailed as “lab” for laboratory experiments and “field” as appropriate.

Author	Predator/Prey	Complexity Type (A= artificial)	Complexity Density	Predation Efficiency
Vince et al. 1976 (lab)	<i>Fundulus heteroclitus</i> / <i>Orchestia grillus</i>	<i>Spartina alterniflora</i>	Low: 2593 stems/m ² High: 18457 stems/m ²	Low > high
Nelson 1979 (lab)	<i>Lagodon rhomboides</i> (small), <i>Lagodon rhomboides</i> (large), <i>Palaemonetes vulgaris</i> / <i>Melita appendiculata</i>	<i>Zostera marina</i>	0, 15, 35, 70 blades/tank	<i>L. rhomboides</i> (small): 0 > *15 = 70 >* 35 <i>L. rhomboides</i> (large): 0 = 15 = 35 >* 70 <i>P. vulgaris</i>: 0 >* 15 = 35 = 70
Coen et al. 1981 (lab)	<i>Lagodon rhomboides</i> / <i>Palaemon floridanus</i> ¹ , <i>Palaemonetes vulgaris</i> ²	Bare sand ^a , <i>Vallisneria</i> grass ^b (A), <i>Digenia</i> <i>simplex</i> ^c	<i>Vallisneria</i> : 25 plants <i>D. simplex</i> : 20% bottom cover ^c , 100% bottom cover ^d	Single prey: a > b > c > d Both prey: 2-b > 1-b > 2-c > 1-c > 2-d > 1-d
Heck and Thoman 1981 (lab)	<i>Fundulus heteroclitus</i> / <i>Palaemonetes pugio</i>	Bare sand ¹ , eelgrass ² (A)	Low: 274 shoots/m ² Medium: 464 shoots/m ² High: 674 shoots/m ²	1 >* 2-low >* 2-med >* 2-high
Heck and Thoman 1981 (field)	Natural predators / Xanthid, majid, hermit, and portunid crabs	Bare sand ¹ , red algae ² , <i>Thalassia testudinum</i> ³	Low: bare sand Medium: red algae High: <i>T. testudinum</i>	Spring: 1 >* 3 = 2 Summer: 1 >* 3 = 2
Peterson 1982 (field)	Whelks (<i>Busycon sp.</i>) / <i>Mercenaria mercenaria</i> ¹ , <i>Chione cancellata</i> ²	<i>Halodule wrightii</i>	Low: unvegetated Med: thinly vegetated High: thickly vegetated	Winter (1): low > high > med Summer (1): low > high > med Winter (2): low > med > high Summer (2): low > med > high
Stoner 1982 (lab)	<i>Lagodon rhomboides</i> (25- 33 mm SL) and (48-67 mm SL) / Amphipods (<i>Cymadusa</i> <i>compta</i> and <i>Melita</i> <i>elongata</i>)	<i>Halodule wrightii</i> ^H , <i>Thalassia testudinum</i> ^T , <i>Syringodium filiforme</i> ^S , Bare sand ^B	(H): 5, 20 g/tank (T): 5, 20, 40 g/tank (S): 5, 20, 40 g/tank (B): 0	Predator 1- prey density (60/tank): H5 >* B > S5 = T5 >* H20 >* S20 = T20 >* T40 = S40 Predator 1- prey density (100/tank): H5 > B > T5 > S5 > H20 > T20 > S20 > T40 > S40 Predator 2- prey density (60/tank): B >* H5 > S5 = T5 >* H20 >* S20 = T20 >* T40 > S40

Table 2 (continued)

Author	Predator/Prey	Complexity Type	Complexity Density	Predation Efficiency
Stoner 1982 (lab)	<i>Lagodon rhomboides</i> (25-33 mm SL) and (48-67 mm SL) / Amphipods (<i>Cymadusa compta</i> and <i>Melita elongata</i>)	<i>Halodule wrightii</i> ^H , <i>Thalassia testudinum</i> ^T , <i>Syringodium filiforme</i> ^S , Bare sand ^B	(H): 5, 20 g/tank (T): 5, 20, 40 g/tank (S): 5, 20, 40 g/tank (B): 0	Predator 1- prey density (60/tank): H5 >* B > S5 = T5 >* H20 >* S20 = T20 >* T40 = S40 Predator 1- prey density (100/tank): H5 > B > T5 > S5 > H20 > T20 > S20 > T40 > S40 Predator 2- prey density (60/tank): B >* H5 > S5 = T5 >* H20 >* S20 = T20 >* T40 > S40
Savino and Stein 1989 (lab)	<i>Micropterus salmoides</i> / <i>Lepomis macrochirus</i>	Polypropylene rope (A)	0, 50, 250, 1000 stems/m ²	0 = 250 >* 50 >* 1000
Coull and Wells 1983 (lab)	<i>Helcogramma medium</i> / Meiofauna	<i>Corallina officinalis</i> (dried), stones (25-30cm), gravel (~2.9mm), plastic bottle brushes, fresh algae (<i>Cystophora retroflexa</i> , <i>Zonaria turneriana</i> , <i>Caulerpa brownii</i> , <i>Champia novaezealandiae</i>)	Lowest: no structure Stones Gravel <i>Champia</i> <i>Cystophora</i> <i>Caulerpa</i> Bottle brush <i>Zonaria</i> Highest: <i>Corallina</i>	Gravel > no structure > stones >* bottle brush >* <i>Champia</i> > <i>Zonaria</i> > <i>Caulerpa</i> > <i>Cystophora</i> >* <i>Corallina</i>
Coull and Wells 1983 (field)	<i>Helcogramma medium</i> / Meiofauna	Dried <i>C. officinalis</i>	Algae present or not	No <i>Corallina</i> >* <i>Corallina</i>
Minello and Zimmerman 1983 (lab)	<i>Lagodon rhomboides</i> ¹ , <i>Micropogonias undulatus</i> ² , <i>Sciaenops ocellatus</i> ³ , <i>Cynoscion nebulosus</i> ⁴ / <i>Penaeus aztecus</i>	<i>Spartina</i> straws (A)	Lowest: 0 stems/m ² 220 stems/m ² 440 stems/m ² Highest: 880 stems/m ²	(1): 0 >* 220 = 440 (2): 0 >* 440 >* 880 (3): 0 > 880 (4): 0 = 880
Anderson 1984 (lab)	<i>Micropterus salmoides</i> / <i>Lebistes reiculatus</i>	<i>Elodea</i> plants (A)	Low: 200 stems/m ² High: 670 stems/m ²	Low >* High

Table 2. (continued)

Author	Predator/ Prey	Complexity Type	Complexity Density	Predation Efficiency
Wilson et al. 1987 (field)	Natural predators/ Juv. <i>Callinectes sapidus</i>	<i>Zostera marina</i>	None: Bare sand Low: 12.19 g (dry weight) Medium: 43.24 g High: 79.04 g	Med >* Low = High > None
Mattila 1992 (lab)				
Beukers and Jones 1998 (lab)	<i>Pseudochromis fuscus</i> ¹ , <i>Cephalopholis boenak</i> ² , <i>Thalassoma lunare</i> ³ / Juvenile <i>Pomacentrus</i> <i>moluccensis</i>	<i>Acropora nobilis</i> ^a , <i>Pocillopora</i> <i>damicornis</i> ^b , <i>Acropora nasuta</i> ^c	Low: <i>A. nobilis</i> Medium: <i>P. damicornis</i> High: <i>A. nasuta</i>	1 > 2 >* 3 >* No predator <i>A. nobilis</i> >* <i>A. nasuta</i> > <i>P.</i> <i>damicornis</i> 3-b = 3-c = 3-a = 2-b >* 1-c >* 2-c >* 1-b = 2-a = 1-a
Beukers and Jones 1998 (field)	<i>Pseudochromis fuscus</i> , <i>Cephalopholis boenak</i> / <i>Pomacentrus moluccensis</i>	<i>Pocillopora damicornis</i> , <i>Acropora nobilis</i>	Low: <i>A. nobilis</i> High: <i>P. damicornis</i>	<i>A. nobilis</i> > <i>P. damicornis</i>
Grabowski 2004 (lab)	<i>Opsanus tau</i> ¹ / <i>Panopeus herbstii</i> ² / <i>Crassostrea virginica</i>	Unaggregated oyster shell, oyster clusters	Low: unaggregated oyster shells High: unaggregated shells and oyster clusters	1-low >* 1-high 2-low >* 2-high >* 1&2-low >* 1&2- high
Padial et al. 2009 (lab)	<i>Moenkhausia</i> <i>sanctaeofilomenae</i> / <i>Cypricerces sp.</i> ¹ , <i>Chironomus</i> <i>sp.</i> ²	<i>Eichhornia azurea</i>	(NH): No structural heterogeneity (LH): Low heterogeneity (HH): High heterogeneity	1: HH >* LH > NH 2: HH >* LH > NH

(1) Numeric superscripts following predator or prey name corresponds to the numbers in the “Predation Efficiency” column

(2) Letter superscripts following complexity types corresponds to the letters in the “Predation Efficiency” column

*- Corresponds to a significant ($P < 0.05$) effect of habitat complexity on predation efficiency

Temperature

The effect of temperature on predator-prey interactions can be difficult to evaluate because temperature is a factor commonly evaluated both on its own as well as in combination with ocean acidification and changing oxygen levels. Global average sea surface temperature is projected to increase 1.1-6.4 °C by 2100 (Munday et al. 2008). Increased ocean temperatures can drive geographic range shifts, reduced pelagic duration, life history modification, shift in breeding season, reproductive decline, reduced productivity, and reduced performance. Each fish has its own optimal temperature range within which a fish shows its highest performance of foraging, swimming, and other aerobically supported activities. Within the upper limits of this optimal thermal range fish exhibit increases in metabolic rates and activity levels, however, feeding rates decline once the optimal temperature is exceeded (Nowicki et al. 2012). Elevated temperatures have also been shown to cause increases in predator consumption rates (Carr and Bruno 2013). These elevated temperatures could seriously impact the outcome or strength of predator-prey interactions and cause an increase in the strength of top-down controls in marine communities.

Temperature and predation efficiency

Leonard (2000) sought to understand the effect temperature had on a specific rocky intertidal interaction between a barnacle (*Semibalanus balanoides*) and its predator, the dog whelk (*Nucella lapillus*). Leonard conducted a field study in two areas of a natural rocky intertidal environment with the commonly occurring *Ascophyllum nodosum*, a canopy-forming alga. By manipulating the *A. nodosum* canopies to have zero, intermediate, or total cover Leonard was able to study the positive and negative interactions between the algae, barnacles, and whelks. Leonard found that the number of barnacles and whelks differed among the three sites, with the highest number of barnacles existing in completely cleared areas or high temperature areas and lowest in areas of total cover and therefore lowest temperatures, with the whelks inhabiting the opposite pattern. Throughout the duration of the study Leonard found that there were never any whelks in the completely cleared areas of the canopy, which explains the high numbers of barnacles in these areas. Leonard explains that with the areas of high temperature being unsuitable for the whelks, they are unable to consume the abundant barnacles in these areas.

Allan et al. (2015) conducted lab experiments testing the effect of temperature changes on the predator-prey interaction between the brown dottyback and the Ward's damselfish (*Pomacentrus wardi*). Both predator and prey species were exposed to either present-day temperatures (~26.7 °C) or elevated temperatures (~29.6 °C) for a week before experiments began. Trials were conducted by placing one predator and one prey into an experimental arena and filming the interaction for 10 minutes or until the prey was consumed. The predation success and predation rate (capture success divided by number of attacks made) were recorded for each trial. Results showed that capture success was significantly higher in the elevated temperature treatment (47% success) than in control temperature treatment (5.8% success). Predation rate was also significantly affected by elevated temperature, being higher in the elevated temperature treatment than in the control treatment. Researchers attributed these results to two potential factors. The first being an observed decrease in prey reactivity and performance at elevated temperature, the second an observed increase in predation rate and movement about the experimental arena, described as an "increase in predator motivation to capture prey" (Allan et al. 2015). This study especially highlights the importance of studying both sides of a predator-prey relationship, as predator and prey were oppositely affected by increased temperatures. Such differences in response to stressors will skew the overall outcomes of predator-prey interactions, potentially having effects that extend into the population and community effects.

Aspects/Stages of predation

Miller (2013) studied the effect that temperature had on not only predation success but drilling and ingestion times of the dog whelk *N. lapillus* consuming the blue mussel (*Mytilus edulis*). Utilizing hydrophones and time lapse video Miller was able to record and time the period that a whelk was drilling into a mussel and eating it. The results of the study showed that increasing water temperatures significantly reduced the drilling and ingestion rate of whelks, specifically, a 1 °C increase in temperature reduced the average ingestion time by 3.6 hours. Temperature was also significant to the combined drilling and ingestion time, where a 1 °C temperature increase caused a reduction in the length of overall attack by 4.1 hours. With the average sea surface temperature projected to rise 2.8 °C by the end of the century, this increase in foraging efficiency could translate to a much higher predation rate upon blue mussels by whelks, and therefore potentially causing a major shift in blue mussel populations in the area.

Pincebourde (2012) studied how the feeding rate of a sea star (*Pisaster ochraceus*) on California mussels (*Mytilus californianus*) was affected by increased temperatures. The potential effects of increasing sea temperatures on *P. ochraceus* is of great importance due to its role as a keystone species in its habitat. Due to sea stars being exposed to air temps during low tide, Pincebourde tested elevated temperatures both when exposed at low tide (BT_e) and when immersed at high tide (BT_i). Pincebourde found that the feeding rate of *P. ochraceus* was strongly and interactively influenced by BT_e and BT_i, with the lowest predation rate occurring where bouts of elevated BT_e and BT_i followed each other with no overlapping, in comparison to when bouts of elevated temperatures occurred simultaneously. Predation rates were also significantly lowered when periods of elevated BT_e and BT_i fluctuated rather than occurring constantly, likely due to the sea star being able to acclimate to the higher temperature during the constant treatments. Pincebourde's study provides evidence of complex interactive effects between sea and air temperatures on the predation rate of this vital keystone species.

Table 3. Summary of studies examining the effect of increased temperature on predation efficiency. Experiments are detailed as “lab” for laboratory experiments and “field” as appropriate

Author	Predator/ Prey	Temperature Treatments	Predation Efficiency
Leonard 2000 (field)	<i>Nucella lapillus</i> / <i>Semibalanus balanoides</i>	Low: natural <i>Ascophyllum nodosum</i> canopy Med: cleared <i>A. nodosum</i> canopy High: above <i>A. nodosum</i> canopy	Med > Low > High
Carr and Bruno 2007 (lab)	<i>Lytechinus semituberculatus</i> / <i>Ulva spp.</i>	Low: 14 °C High: 28 °C	High >* Low
Landes and Zimmer 2012 (lab)	<i>Carcinus maenas</i> / <i>Littorina littorea</i> (small and large)	Control (C): 8-18 °C, pH- 8.0 pH: 8-18 °C, pH- 7.7 Temp (T): 13-23 °C, pH- 8.0 pH + T: 13-23 °C, pH- 7.7	Control <i>C. maenas</i>- Small <i>L. littorea</i> : T > pH+T > C >* pH Large <i>L. littorea</i> : pH > T > pH+T >* C Treated <i>C. maenas</i>- Small <i>L. littorea</i> : T > pH > pH+T >* C Large <i>L. littorea</i> : T >* pH > C > pH+T
Nowicki et al. 2012 (lab)	<i>Amphiprion melanopus</i> / <i>Artemia nauplii</i>	Low: 28.5 °C Med: 30 °C High: 31.5 °C	420µatm CO₂: Med > Low > High 520µatm CO₂: Med >* Low > High 969µatm CO₂: High > Med >* Low
Pincebourde 2012 (lab)	<i>Pisaster ochraceus</i> / <i>Mytilus californianus</i>	Body Temp (BT)_{immersed}: 13.2 °C BT_i Down: 10.3 °C BT_i Up: 16.1 °C BT_{emersed}: 17.5 °C BT_e Chronic: 26.3 °C BT_e Acute: 23.6 °C (Experiment 1): BT _i x BT _e (Experiment 2): one variable changing a- BT _i Up x BT _e b- BT _i Down x BT _e c- BT _i x BT _e Chronic d- BT _i x BT _e Acute (Experiment 3): two variables changing a- BT _i Down x BT _e Chronic b- BT _i Down x BT _e Acute c- BT _i Up x BT _e Acute d- BT _i Up x BT _e Chronic	1 >* 2c > 2d > 2b = 3a > 2a >* 3b >* 3c >* 3d

Table 3. (continued)

Author	Predator/ Prey	Temperature/ Treatments	Predation Efficiency
Miller 2013 (lab)	<i>Nucella lapillus</i> / <i>Mytilus edulis</i>	10 °C, 12 °C, 14 °C, 16 °C, 18 °C	18 °C > 16 °C > 14 °C > 12 °C > 10 °C
Miller et al. 2014 (lab)	<i>Nucella lapillus</i> / <i>Mytilus edulis</i>	Low: 24.4 °C High: 27.4 °C +Risk: predation risk from <i>Carcinus maenas</i> -Risk: no predation risk <i>C. maenas</i>	-Risk/Low >* -Risk/High >** +Risk/Low >* +Risk/High
Allan et al 2015 (lab)	<i>Pseudochromis fuscus</i> / <i>Pomacentrus wardi</i>	Low: 26.7 °C High: 29.6 °C	High >* Low
Ferrari et al. 2015 (lab)	<i>Pseudochromis fuscus</i> / <i>P.ambionensis</i> , <i>P. nagasakiensis</i>	(1): Low CO ₂ (440 µatm)/ Low temp (28 °C) (2): High CO ₂ (995 µatm)/ High temp (31 °C) (3): High CO ₂ / Low temp (4): Low CO ₂ / High temp	Predation rate: 2 >* 3 = 1 > 4
Allan et al 2017 (lab)	<i>Pseudochromis fuscus</i> / <i>Pomacentrus wardi</i>	(1): Low temp (26.7 °C) /Low CO ₂ (405 µatm) (2): High temp (29.6 °C) /High CO ₂ (930 µatm) (3): Low temp/ High CO ₂ (4): High temp/ Low CO ₂	4 >* 2 >* 3 >* 1

* Corresponds to a significant (p < 0.05) effect of temperature on predation efficiency

Acidification

The relationship between ocean acidification and predator-prey interactions involving fishes is one that has not yet been widely studied; most research focuses instead on calcifying organisms (e.g., corals and oysters). However, some recent studies found that increased levels of dissolved carbon dioxide in the water can affect a fish's metabolic, developmental, and behavioral processes. These changes can be detrimental to coral reef associated fish and increase the destruction of coral reef ecosystems on top of the effects from increasing CO₂. Larger fish predators on coral reefs are important to help balance community structure and abundance of smaller fish species. Some reef fishes, grazing herbivorous fishes especially, have a key functional role in the health of coral reef communities (Munday et al. 2008).

Effect of acidification on prey behavior

Cripps et al. (2011) utilized a two-channel choice chamber to determine how elevated CO₂ levels affected a coral reef meso-predator's ability to smell and respond to prey odor. Researchers exposed the brown dottyback to three levels of CO₂: control or present day (450 μatm), medium (600 μatm), or high (950 μatm). After exposure, fish were placed into a two-channel choice chamber for eight minutes, with one channel injected with prey skin extracts while the other channel was seawater. A second experiment was conducted where the fish were placed into an experimental tank, and the fish's activity and behavior was recorded for 20 minutes after which food was introduced into the tank, and the fish's feeding behavior was recorded for another five minutes. For the first experiment, researchers found that fish exposed to present day levels of CO₂ spent significantly more time (~ 60%) in the channel injected with prey odor, while fish exposed to medium and high levels of CO₂ spent approximately 20% less time in the chamber containing prey odor compared to control fish. For the second experiment, fish exposed to high levels of CO₂ displayed a significant increase in activity level, sometimes double the activity levels of fish exposed to control or medium levels of CO₂. The feeding behavior of *P. fuscus* was significantly altered by exposure to elevated CO₂, with medium levels of CO₂ increasing the time it took to respond to food being introduced to the tank as well as decreasing the number of strikes fish made for the food. Fish in the high CO₂ treatment also followed the same pattern as those in the medium CO₂ treatment, but not as severe. The researchers here found that detecting available prey becomes increasingly difficult to predators

when exposed to elevated CO₂ levels, even though both the predator and prey are more active under elevated CO₂ conditions.

Dixson et al. (2010) conducted a very similar experiment but focused on how a prey fish's ability to detect a predator was affected by elevated CO₂. The orange clownfish (*Amphiprion percula*) was reared in either control seawater or seawater with a CO₂ level of 1000 ppm. Experiments were conducted when *A. percula* was at the end of their larval phase to determine if elevated CO₂ impacted their ability to respond to olfactory cues of predatory species and for their ability to distinguish between the olfactory cues of predatory and non-predatory species. The predatory species used was the rock cod (*Cephalopholis cyanostigma*) and the dottedback (*P. fuscus*), and the non-predatory species used was the surgeonfish (*Acanthurus pyroferus*) and the rabbitfish (*Siganus corallinus*). Researchers used these species to conduct seven different flume choice experiments: (1) untreated water v. untreated water (blank control); (2) *C. cyanostigma* v. untreated water; (3) *P. fuscus* v. untreated water; (4) *A. pyroferus* v. untreated water; (5) *S. corallinus* v. untreated water; (6) *C. cyanostigma* v. *A. pyroferus*; and (7) *P. fuscus* v. *S. corallinus*. The results showed that settlement stage clownfish larvae reared in high CO₂ water exhibited significantly different preferences than larvae reared in control seawater for all comparisons. Larvae from the high CO₂ treatment chose the channel containing an olfactory cue over untreated water 100% of the time. These larvae were unable to distinguish between the chemical cues of predators and non-predators, spending about an equal amount of time in each channel. The study proved that clownfish larvae completely lose their ability to detect predators and distinguish them from non-predators, and such a dramatic shift in predator avoidance can greatly increase encounter and therefore mortality rates among settling larvae, which can then lead to population decline.

Climate change and temperature

Landes and Zimmer (2012) conducted a study on how increased pH levels and elevated temperature affected green crabs, periwinkles (*Littorina littorea*), and their predator-prey relationship; finding that while acidification negatively affected each species individually, it did not alter the interaction between them. Crabs and three size classes of periwinkles were treated for five months in one of four treatments: control temperature and pH (8-18 °C and 8.0), acidification (8-18 °C and 7.7), warming (13-23 °C and 8.0), or acidification and warming (13-

23 °C and 7.7). After exposure researchers measured the handling times of the crabs and the shell thickness of the periwinkles, finding that the shells of the smaller snails were thicker after the warming-and-acidification treatment than any other treatment. Researchers concluded that both warming and acidification had negative impacts on individuals of *C. maenas* and *L. littorea*, however, did not seem to impact their interactions. Crabs took the same time to handle the snail, and handling time was only dependent on snail size. This study emphasizes the importance of studying multiple predator-prey interactions under elevated CO₂ conditions, as some predation processes will see no net change while others will change drastically.

Nowicki et al. (2012) also conducted a study that sought to determine the effects of both elevated CO₂ levels and temperature on predation events. Researchers tested the effects and potential interaction of elevated CO₂ and temperature on the foraging behavior and success of the black anemonefish (*Amphiprion melanopus*). Juvenile anemonefish were reared for three weeks in temperature and CO₂ levels corresponding to current-day (28.5 °C and 420 µatm CO₂), mid-century (30.0 °C and 530 µatm CO₂), and late-century (31.5 °C and 960 µatm CO₂) atmospheric projections in a fully crossed design. After the exposure time the fish's routine activity and feeding activity, as well as their feeding rate, was tested and recorded. Results showed that CO₂ and temperature had a significant interactive effect on feeding rate when CO₂ and temperature were at their highest. Temperature was also found to have an independent effect on consumption rate, with a 22% increase at 30 °C than at 28.5 °C or 31.5 °C, and there was no independent CO₂ effect on consumption rate or activity level. The previous two studies highlight the importance of understanding the effects of multiple environmental stressors on predator-prey relationships.

A study conducted by Allan et al. (2017) on the effects of elevated temperature and CO₂ on the relationship between the brown dottyback (*Pseudochromis fuscus*) and the Ward's damselfish (*Pomacentrus wardi*) yielded interesting results. Researchers exposed both *P. fuscus* and *P. wardi* to two temperatures (27 and 30 °C) with two CO₂ levels (405 and 930 µatm) in a fully crossed design for one week prior to experiments. After exposure, one predator and one prey from the same treatment were placed into an experimental arena and their interaction was filmed for 10 minutes or until the prey had been consumed. From the recording the capture success, attack rate, and predation rate (number of captures divided by number of attacks) were measured. Reactivity and escape speed of the prey was also measured. The researchers found

that elevated temperatures had a more significant effect on predation success than elevated CO₂ levels. Capture success was greatest in the high temperature-control CO₂ treatment and lowest in the control temperature-control CO₂ treatment. Results for attack rate and predation rate followed the same pattern as capture success. CO₂ levels alone and the interaction between temperature and CO₂ levels were not found to have any significant effect on attack rate and predation rate however, whereas CO₂ and the temperature/CO₂ interaction did significantly impact capture success. This study firmly confirms the results of Allan et al. (2015), where predator and prey had opposite responses to elevated temperatures and CO₂, causing a predator-prey interaction with a strengthened predator and debilitated prey, which will increase the strength of the outcome of this predator-prey interaction.

Pomacentrus experiments

From 2010 to 2015, multiple studies were conducted out of the same institution on one genus of fish, the *Pomacentrus* damselfishes. Together, these studies offer an extensive and wide-reaching overview on the effects of increasing CO₂ levels on the relationship between predator and prey. Munday et al. (2010) conducted a study exposing juvenile damselfish (*Pomacentrus wardi*) and juvenile clownfish (*Amphiprion percula*) to increasing levels of CO₂ (390-current day, 550, 700, and 800 ppm CO₂). Then tested their olfactory ability and if olfactory impairment led to increased mortality. The tests of olfactory impairment were conducted in two channel flumes, with one channel flushed with seawater and the other with predator cues. Mortality assessments were conducted in the field after exposure to elevated CO₂ and olfactory impairment tests. Results for the clownfish showed that almost all fish in the 390 and 550 ppm CO₂ treatments showed a complete avoidance of the predator cue within eight days post hatch. Clownfish reared in 700 ppm CO₂ initially avoided the predator cue, however, fish began spending 30-45% of their time in the predator cue four days after hatching. Clownfish in the 850 ppm CO₂ treatment only avoided the predator for one day post hatch. After the first day fish exposed to the highest CO₂ level showed a strong attraction to the predator cue, growing to spending over 94% of the time in the predator cue eight days post hatch. Juvenile damselfish exhibited a pattern similar to clownfish, with fish in the control or 550 ppm CO₂ treatment maintaining a strong avoidance of the predator cue. Fish exposed to 700 and 850 ppm CO₂ showed an initial avoidance of the predator cue, but quickly changed to a complete attraction to

the cue. During the field experiments, fish exposed to elevated levels of CO₂ showed riskier behaviors than fish exposed to present day levels of CO₂. Damselfish exposed to elevated CO₂ had a 9-fold (850 ppm) and 5-fold (700 ppm) higher mortality rates compared to the control within the first 30 hours on the reef. Researchers suggested that 700 ppm CO₂ is near the threshold level of CO₂ that will begin to cause behavioral and physiological changes to fish.

Ferrari et al. (2011a) sought to see how different species within *Pomacentrus* are impacted by elevated CO₂ in order to determine if one species may be better at adapting to increasing CO₂. To do this, researchers exposed four species of damselfish (*Pomacentrus chrysurus*, *Pomacentrus amboinensis*, *Pomacentrus moluccensis*, and *Pomacentrus nagasakiensis*) to three CO₂ concentrations (390, 700, and 850 ppm CO₂) for four days. After CO₂ exposure, fish were put through behavioral tests consisting of introducing food to the fish, a four-minute behavioral observation period, followed by a predator cue injection and another four-minute observational period. During the behavioral observation period researchers noted how many feeding strikes were made and the number of lines marked along the tank the fish crossed. A field study was also conducted after the behavioral experiments in which *P. chrysurus* were introduced onto a small patch reef where their behavior was observed for three minutes and their survival monitored for 48 hours after introduction onto the reef. Results of the laboratory experiments showed that all four species showed a similar antipredator response to the predator cue at the lowest CO₂ level, and that increased levels of CO₂ reduced the antipredator response to a certain degree depending on the species of damselfish. *P. nagasakiensis* proved to be the least affected by the increase in CO₂, while the other three species showed significant losses in their antipredator response at both 700 and 850 ppm CO₂, although *P. amboinensis* was always the most affected species. The 700 ppm CO₂ treatment provided the greatest variability in intensity of the fish's response, seeming to confirm that 700 ppm CO₂ is near the threshold limit as talked about previously in Munday et al. (2010). The results of the field experiments found that *P. chrysurus* exhibited much riskier behavior when exposed to elevated levels of CO₂ than control levels, moving further and higher away from the reef. Elevated CO₂ *P. chrysurus* also suffered a significantly higher mortality rate within the first 30 hours on the reef, with a 5-fold (700 ppm) to 7-fold (850 ppm) increase in mortality on the reef. The results of this study show that interspecific variation in response to increasing CO₂ levels have the potential to change

community structures, with some species able to outcompete others due to their advantage within these stressful conditions.

Ferrari et al. (2011b) added on to the previous study, in which both prey (*P. chrysurus*, *P. amboinensis*, *P. moluccensis*, and *P. nagasakiensis*) and predator (the dottyback *Pseudochromis fuscus*) were exposed to present day (440 μatm) or elevated (700 μatm) CO₂ levels for four days. After exposure, one predator and eight damselfish (two individuals from each species—one small and one large) were placed together in a tank and their interaction was recorded for 24 hours, after which the remaining number and species of damselfish remaining was recorded. The predation rate was affected by the size class of prey items and there was an interactive effect between size class and CO₂ treatment. However CO₂ treatment alone did not have a significant impact. CO₂ treatment only had a significant effect on mortality rate among the small size class of damselfish, with no species-specific preference. For the large size class of damselfish there was no effect of CO₂ treatment on mortality however for present day CO₂ levels, predator preference favored *P. nagasakiensis* and *P. chrysurus* and this preference was reversed in the elevated CO₂ treatment. This study suggests that although the outcome of predator-prey interactions may not always be shown through predation or mortality rates, major changes could occur if a predator were to completely change its prey preference under high CO₂ conditions.

And finally, in 2015, Ferrari et al. (2015) built off the previous study by looking at the effects of elevated CO₂ on predation rate as well as predator selectivity. The study used two damselfish species (*P. amboinensis* and *P. nagasakiensis*) and the dottyback (*P. fuscus*) exposed to present day (440 μatm) or elevated (995 μatm) CO₂ levels crossed with ambient (27.8 °C) or elevated (31.0 °C) temperature. Both predator and prey were treated to a six day temperature acclimation period followed by a four day CO₂ acclimation period, after which six damselfish (three of each species) and one predator were placed into a tank, and the predator-prey interaction was recorded for 22 hours. After the trial, the number and species of damselfish consumed was recorded. Researchers found a significant interaction between CO₂ and temperature on predation rate, increasing from about 30% to 70% when both CO₂ and temperature were elevated. CO₂ and temperature alone did not significantly impact predation rate. Elevated CO₂ and elevated temperature alone caused a reversal in predator selectivity, where the dottyback normally preferred *P. amboinensis* over *P. nagasakiensis* but switched to

select *P. nagasakiensis* over *P. amboinensis*. However, the interaction between CO₂ and temperature had a significant and antagonistic effect on predator selectivity, exhibited by the predator losing any preference and selecting both species equally. This study highlights the importance of testing multiple stressors on predator-prey interactions because while there was no increase in predation rate, there was a complete reversal or abandonment of prey preference, which can drastically shift population numbers and community structures. This study also demonstrates that some studies that only focus on one stressor (CO₂, temperature, oxygen) may not give the most accurate representation of what is happening during predation events, and the importance of looking at co-occurring stressors on the behaviors and outcomes of predator-prey relationships.

Climate change and physiology

While the previous studies are important in understanding how elevated CO₂ levels can alter predators, prey, and their interaction, there are also studies that focus deeper than predation processes and behavior. For example, Allan et al. (2012) conducted a study using *Pseudochromis fuscus* as the predator and juvenile *Pomacentrus amboinensis* as prey to determine how elevated CO₂ effects the prey reaction distance and capture success in this predator-prey interaction. The study consisted of recording a 10-minute interaction between the predator and the newly introduced prey and was a fully crossed design between control (~880 pCO₂) and treated (~440 pCO₂) predator and prey. Results of the study showed that when both predator and prey were subjected to the same treatment (present day or elevated CO₂) then the capture success was about the same. However, the capture success significantly decreases, from 14-33%, when either the predator or prey was treated to elevated CO₂ while the other was acclimated to present day CO₂. Elevated CO₂ was also found to increase the prey reaction time, with the shortest prey reaction time occurring in prey exposed to present day CO₂ levels. Because of the similarity in results when both predator and prey were exposed to the same treatment the authors suggest that while elevated CO₂ can have negative impacts on both predator and prey, the effects may mitigate each other to end up with the same conclusion and are likely to be dependent on the sensitivity of each species to elevated CO₂.

A study conducted by Domenici et al. (2010) tested the effect of elevated CO₂ levels on the behavioral lateralization of settlement stage larvae of the damselfish (*Neopomacentrus*

azysron). Behavioral lateralization is the tendency to favor the right or left side during behavioral activities, and in fishes lateralized individuals perform better in cognitive tasks, schooling behavior, spatial orientation, and escape reaction times (Domenici et al. 2010). Behavioral lateralization is a good indicator of higher brain function. To test this, researchers exposed *N. azysron* to present-day (440 μatm) or elevated (880 μatm) CO_2 levels for four days. After exposure, the behavioral lateralization of the fish was tested using a two-channel chamber. Results showed that fish exposed to elevated levels of CO_2 showed no preference for right or left turns, whereas fish exposed to present-day CO_2 levels showed lateralization. These results prove that increasing CO_2 will cause serious harm to the brain function of fishes, as well as have severe negative impacts on not just a fish's behavior but its physiology.

Chivers et al. (2014) took this research a step forward, studying how elevated CO_2 levels impacted the function of the GABA-A receptor. This study is one of the first to truly focus on how elevated CO_2 physiologically effects fish, while most studies only look at the behavioral effects. The methodology involved exposing juvenile damselfish (*Pomacentrus amboiensis*) to normal (440 μatm) or elevated (987 μatm) CO_2 , then treating some fish exposed to elevated CO_2 with gabazine to determine if gabazine was able to reverse the effects of elevated CO_2 levels. A second experiment was conducted in the field to determine how fish exposed to elevated CO_2 and treated with gabazine would survive. All fish were then conditioned to detect predator odors and tested for their response to predator odors either one or five days postconditioning. Results of the experiment showed that fish exposed to control levels of CO_2 displayed an anti-predator response one day after conditioning, whereas fish treated with CO_2 and gabazine did not show any different response to the predator odor showing that gabazine did not have an effect on the learning deficiency caused by elevated CO_2 levels. Five days after conditioning, the same results were found in control fish, while fish in the elevated CO_2 group exhibited a gabazine x cue interaction. The fish that were treated with gabazine after CO_2 exposure exhibited an anti-predator response, showing that gabazine treatment allowed fish to learn predator cues. The fish not treated with gabazine did not show any signs of recognizing the predator odors. The results of the second experiment showed significantly different survival rates in the wild. Fish that were exposed to elevated CO_2 but not treated with gabazine prior to predator learning had a much lower survival rate than those fish treated with gabazine, with 50% of fish dying within 24 hours.

Researchers were able to prove that gabazine treatment was able to counteract the effects of elevated CO₂ on a fish's learning ability.

Table 4. Summary of studies examining the effect of increased CO₂ levels on predation efficiency. Experiments are detailed as “lab” for laboratory experiments and “field” as appropriate

Author	Predator/ Prey	CO ₂ Treatment	Results
Dixson et al. 2010 (lab)	<i>Cephalopholis cyanostigma</i> & <i>Siganus corallinus</i> (predator), <i>Acanthurus pyroferus</i> & <i>Siganus corallinus</i> (non-predator) / <i>Amphiprion percula</i> larvae	Low CO₂: pH 8.15 High CO₂: pH 7.8 Two-choice flume experiment: (Expt 1): control seawater vs. control seawater (Expt 2): predator odor vs. control seawater (Expt 3): non-predator odor vs. control seawater (Expt 4): predator odor vs. non-predator odor	Prey preference: Low CO₂- Newly hatched: control > non-predator >* predator Settlement stage: control = non-predator >* predator High CO₂- Newly hatched: control > non-predator >* predator Settlement stage: predator > non-predator >* control
Munday et al. 2010 (field)	Natural predators / <i>Pomacentrus wardi</i>	Low: 390 ppm CO ₂ Med: 700 ppm CO ₂ High: 850 ppm CO ₂	Prey mortality rate: High >* Med >* Low
Cripps et al. 2011 (lab)	<i>Pseudochromis fuscus</i> / <i>Pomacentrus moluccensis</i>	Low: 444 μatm CO ₂ Med: 607 μatm CO ₂ High: 925 μatm CO ₂	Predation rate: High > Low >* Med
Ferrari et al. 2011a (field)	Natural predators / <i>Pomacentrus chrysurus</i>	Low: 390 ppm CO ₂ Med: 700 ppm CO ₂ High: 850 ppm CO ₂	Prey survival rate: Low >* Med >* High
Ferrari et al. 2011b (lab)	<i>Pseudochromis fuscus</i> / <i>Pomacentrus moluccensis</i> ^a , <i>Pomacentrus ambionensis</i> ^b , <i>Pomacentrus nagasakiensis</i> ^c , <i>Pomacentrus chrysurus</i> ^d	Low: 440 μatm CO ₂ High: 700 μatm CO ₂	Prey mortality rate: Small recruits (≤14.5 mm): (a): High >* Low (b): High >* Low (c): High >* Low (d): High >* Low Large recruits (>14.5 mm): (a): High > Low (b): Low > High (c): Low > High (d): Low > High

Table 4. (continued)

Author	Predator/ Prey	CO₂ Treatment	Results
Allan et al. 2012 (lab)	<i>Pseudochromis fuscus</i> / <i>Pomacentrus ambionensis</i>	(Treatment 1): High CO ₂ predator (880 µatm)/ High CO ₂ prey (Treatment 2): Low CO ₂ predator (440 µatm)/ Low CO ₂ prey (Treatment 3): Low CO ₂ predator/ High CO ₂ prey (Treatment 4): High CO ₂ predator/ Low CO ₂ prey	Predation rate: 1 > 2 >* 3 >* 4
Landes and Zimmer 2012 (lab)	<i>Carcinus maenas</i> / <i>Littorina littorea</i> (small and large)	Control (c): 8-18 °C, pH- 8.0 pH: 8-18 °C, pH- 7.7 Temperature (T): 13-23 °C, pH- 8.0 pH + T: 13-23 °C, pH- 7.7	Control <i>C. maenas</i>- Small <i>L. littorea</i> : T > pH+T > C >* pH Large <i>L. littorea</i> : pH > T > pH+T >* C Treated <i>C. maenas</i>- Small <i>L. littorea</i> : T > pH > pH+T >* C Large <i>L. littorea</i> : T >* pH > C > pH+T
Nowicki et al. 2012 (lab)	<i>Amphiprion melanopus</i> / <i>Artemia nauplii</i>	Low: 420 µatm CO ₂ Med: 530 µatm CO ₂ High: 960 µatm CO ₂	Predation rate: 28.5 °C: Low > Med > High 30 °C: Med > High > Low 31.5 °C: High >* Low > Med
Chivers et al. 2013 (field)	Natural predators / <i>Pomacentrus amboinensis</i>	(Treatment 1): Low CO ₂ (440 µatm)/ No predator learning (Treatment 2): High CO ₂ (987 µatm)/ No Gabazine/ Predator learning (Treatment 3): High CO ₂ / Gabazine/ Predator learning (Treatment 4): Low CO ₂ / Predator learning	Predation rate: 1 > 2 >* 4 > 3
Ferrari et al. 2015 (lab)	<i>Pseudochromis fuscus</i> / <i>P.ambionensis</i> , <i>P. nagasakiensis</i>	(Treatment 1): Low CO ₂ (440 µatm)/ Low temp (28 °C) (Treatment 2): High CO ₂ (995 µatm)/ High temp (31 °C) (Treatment 3): High CO ₂ / Low temp (Treatment 4): Low CO ₂ / High temp	Predation rate: 2 >* 3 = 1 > 4
Allan et al 2017 (lab)	<i>Pseudochromis fuscus</i> / <i>Pomacentrus wardi</i>	(Treatment 1): Low temp (26.7 °C) /Low CO ₂ (405 µatm) (Treatment 2): High temp (29.6 °C) /High CO ₂ (930 µatm) (Treatment 3): Low temp/ High CO ₂ (Treatment 4): High temp/ Low CO ₂	Predation rate: 4 >* 2 >* 3 >* 1

* Corresponds to a significant (p < 0.05) effect of elevated CO₂ on predation efficiency

Oxygen

Oxygen as a factor in predator-prey relationships is akin to temperature because it can be evaluated on its own or in conjunction with temperature and ocean acidification in the bigger picture of climate change. Severe oxygen conditions reduce populations or even eliminate taxa, as animals die or flee from affected areas. Further, reproductive success, somatic growth and predator-prey interactions are also affected by oxygen conditions (Edjung et al. 2008). It has become increasingly more important to determine how oxygen levels can affect predator-prey interactions because under normoxic conditions predation is a major process that regulates many populations densities and community structure (Johansson 1999).

Oxygen and predation efficiency

Edjung et al. (2008) conducted a study to determine the effect of moderate ($\geq 2-6$ mg O₂) and severe (≤ 2 mg O₂) hypoxia on the foraging of a few species of benthic macrofauna (*Macoma balthica*, *Halicryptus spinulosus*, *Monoporeia affinis*, and *Pontoporeia femorata*). Results of the moderate hypoxia experiments showed that all predators showed no significant change in foraging among different oxygen levels, except for *M. affinis*. *M. affinis* showed a significant increase in foraging at the lowest oxygen concentration tested. Results of the severe hypoxia treatments were much different than the moderate hypoxia treatments. For both *M. balthica* and *H. spinulosus* there was no significant change in foraging uptake within the severe hypoxia treatments. *M. affinis* and *P. femorata* however showed a significant increase in foraging under severe hypoxia conditions, as well as a significantly lowered survival rate throughout the course of the experiment. Edjung suggests that the lack of change in feeding of *M. affinis* and *H. spinulosus* caused by sublethal oxygen concentrations could explain the reduction of abundance and biomass of benthic deposit feeders observed in the area where the study took place.

Tallqvist et al. (1999) researched the predation efficiency of the European flounder (*Platichthys flesus*) on *Bathyporeia pilosa* under four oxygen treatments (20%, 30%, 40%, and 100% O₂) during a 24-hour trial period. Results showed that there was a significant decrease in predation rate between 100% v 30%, 100% v 20%, 40% v 30%, and 40% v 20%. There was also some mortalities of *P. flesus* in the 20% O₂ trials. Researchers suggest that enhanced energy demand due to the stress of hypoxia increases the rate of predation.

Sandberg (1994) showed that predation rates of the isopod *Saduria entomon* decreased with decreasing oxygen levels. The study involved testing the predator's predation rates on two amphipod prey species (*Corophium volutator* and *Bathyporeia pilosa*) under varying concentrations of oxygen (17%, 30%, 50%, and 95% O₂). For this study, there was a significant decrease in predation rate below 30% O₂, with 88% of *C. volutator* surviving. For trials using *B. pilosa* as the prey species, there was once again a significant decrease in predation rate below 30% O₂, with 73% *B. pilosa* survival.

Johansson (1999) also studied the influence of low oxygen levels on the predation rate of *S. entomon*. Johansson conducted a series of experiments to test the consumption of *M. affinis* by *S. entomon* at 5%, 8%, 16%, 33%, 47%, 63%, and 93% oxygen concentration to determine what concentration of oxygen causes predation rate to fall significantly and at what oxygen concentration feeding stops altogether. Results shows that the predation rate of *S. entomon* was significantly lower between different oxygen concentrations. Specifically, the predation rates were significantly higher at 63% and 93% than at 8%, 16%, and 33%, and the predation rate at 47% was significantly higher than at 8% and 16%. Johansson found that the predation rate began significantly reducing at 33%, matching the results found by Sandberg a few years prior. There was no oxygen concentration tested which caused a complete cessation in feeding by *S. entomon*.

Consumer and prey stress models

Howard (2009) explained two models that can be used to predict predation scenarios during and following a hypoxia event. The first is called the *consumer stress model*, in which prey species experience a prey refuge during hypoxic episodes due to decreased predation rates of their predators. In this scenario, the prey species is usually more tolerant of hypoxic conditions than their predators and therefore experience less mortality. The other scenario is called the *prey stress model*, in which prey species are typically more vulnerable to hypoxic conditions than their predators and predation rates are increased. Howard tested the effect that hypoxic conditions had on blue crabs (*Callinectes sapidus*) feeding on rangia clams (*Rangia cuneate*). A choice experiment was conducted with crabs being introduced to two clams, one under normoxic conditions and the other under hypoxic conditions (< 0.75 mg O₂/L). Howard found that the crabs chose the hypoxia-stressed clams in 73% of trials completed, significantly higher than crabs that chose normoxic clams. Howard's results show that blue crabs fed

significantly more on hypoxia-stressed clams than non-stressed clams, and that the rangia clams' response to hypoxia can make them more vulnerable to their predators.

Sagasti et al. (2001) examined the effects of periodic hypoxia on the feeding and predation within an estuary's epifaunal community, as well as the effects of hypoxia on feeding by a highly tolerant sessile species and on predation by the most abundant, small mobile predators within the community. Researchers in this study conducted four experiments: (1) the mud crab *Neopanope sayi* feeding on the polychaete *Nereis succinea*. (2) blue crabs (*C. sapidus*) and flatworms (*Stylochus ellipticus*) feedings on barnacles (*Balanus improvisus*). (3) a nudibranch (*Doridella obscura*) preying on bryozoans (*Membranipora tenuis*). And (4) the relatively intolerant mud crab (*N. sayi*) as predator with the relatively tolerant barnacles (*B. improvisus*) as the prey to determine if prey species can utilize hypoxic conditions as a predation refuge. Results of the first experiment found that *N. sayi* experienced a significant decrease in predation towards the end of the 2-day hypoxic event but showed no change at the beginning of the hypoxic event. Results of the second and third experiment were similar, where the predation rate of *Sty. ellipticus* and *D. obscura* significantly decreased in the low oxygen conditions (0.5-1 mg O₂/l). In contrast to the other experiments, blue crabs did not experience a significant decrease in feeding rate during the hypoxic event, however blue crabs did experience a high mortality rate, indicating that blue crabs are very intolerant to hypoxia. Throughout all the experiments prey species were more tolerant to hypoxia than their predators. This can cause prey using hypoxic events as temporary predation refuges due the episodic nature of hypoxic events. However, with hypoxic events becoming more frequent and increasing in duration, these prey species could become less tolerant.

Aspects/Stages of predation

A study conducted by Legeay and Massabuau (2000) on *Carcinus maenas*, a species of shore crab considered a "pest" in the study region, found that its ability to continue normal feeding during hypoxic events was dependent upon the crab's moulting pattern. By testing arterial and venous blood of *C. maenas*, the study found that in the summer when shore crabs had recently moulted they were able to feed in water with oxygen as low as 1-1.5 mg/l with only a minor switch to anaerobic metabolism. In contrast, in winter, intermoult shore crabs are the least resistant to hypoxia. Intermoult shore crabs relied more heavily on anaerobic metabolism

and exhibited more mortality than recently moulted crabs. Shin et al. (2005) tested the effects of intermittent exposure to reduced oxygen levels on the predation rate and prey handling behavior of the swimming crab (*Thalamita danae*). Researchers subjected crabs and their mussel prey (*Brachidontes variabilis*) to three oxygen levels (1.5, 4.0, and 8.0 mg O₂/l), and the breaking time (Bt), eating time (Et), and handling time (Ht) were recorded as well as the number of mussels eaten by the crabs. Results of the study found that consumption of mussels varied significantly among oxygen levels, with higher consumption at 8.0 mg O₂ than at 4.0 and 1.5 mg O₂, and there was no significant difference between the consumption rate at 4.0 and 1.5 mg O₂. Both eating and handling time increased significantly under reduced oxygen levels, while breaking time varied insignificantly. The results of this study show that reduced oxygen levels can greatly alter the predation rate, both in number of prey eaten and time taken to consume prey items.

Taylor and Eggleston (2000) described the effects of episodic hypoxia on the predator-prey relationship between blue crabs (*C. sapidus*) and an infaunal clam (*Mya arenaria*), including how hypoxia effects mutual interference of two predators. The study involved exposing both species to three oxygen treatments: normoxia (≥ 6 mg O₂), moderate hypoxia (3-4 mg O₂) post acclimation to normoxia, and moderate hypoxia post acclimation to severe hypoxia (≤ 1.5 mg O₂), and then allowing crabs to feed for a 48-hour trial period. Taylor and Eggleston found that for the single predator trials the predation rate was significantly higher under normoxic conditions and moderate hypoxia post severe hypoxia, in comparison to moderate hypoxia post normoxia. The two-predator trials also saw significantly different predation rates under differing oxygen levels, and Taylor and Eggleston found that mutual interference between the two crabs altered the functional response of crabs across all oxygen treatments.

Table 5. Summary of studies examining the effect of decreased oxygen levels on predation efficiency

Author	Predator/ Prey	Oxygen Concentration	Predation Efficiency
Sandberg 1994 (lab)	<i>Saduria entomom</i> / <i>Corophium volutator</i> ^a <i>Bathyporeia pilosa</i> ^b	(Experiment 1): 17%, 30%, 50%, 95% (Experiment 2): 35%, 50%, 95%	(1): 95% > 50% > 30% >* 17% (2): 95% > 50% >* 35%
Johansson 1999 (lab)	<i>Saduria entomom</i> / <i>Monoporeia affinis</i>	5%, 8%, 16%, 33%, 47%, 63%, 93%	93% > 63% >* 47% >* >16% > 33% >* 8% > 5%
Tallqvist et al. 1999 (lab)	Juvenile <i>Platichthys flesus</i> / <i>Bathyporeia pilosa</i>	20%, 30%, 40%, 100%	100% >* 40% >* 30% > 20%
Taylor & Eggleston 2000 (lab)	<i>Callinectes sapidus</i> / <i>Mya arenaria</i> (6 clams/tank) ^a & (24 clams/tank) ^b	(Treatment 1): Normoxia (≥ 6.0 mg DO/l) (Treatment 2): Moderate hypoxia (~ 3.0 mg DO/l) post high oxygen acclimation (≥ 6.0 mg DO/l) (Treatment 3): Moderate hypoxia post low oxygen acclimation (≤ 1.5 mg DO/l)	One <i>C. sapidus</i> present- 1b >* 3a > 3b > 1a >* 2b >* 2a Two <i>C. sapidus</i> present- 3b >* 2a > 2b > 1b >* 3a >* 1a
Sagasti et al. 2001 (lab)	Experiment 1: <i>Neopanope sayi</i> / <i>Nereis succinea</i> & <i>Balanus improvisus</i> Experiment 2: <i>Stylochus ellipticus</i> / <i>B. improvisus</i> Experiment 3: <i>Doridella obscura</i> / <i>Membranipora tenuis</i> Experiment 4: <i>Callinectes sapidus</i> / <i>B. improvisus</i> Experiment 5: <i>N. sayi</i> / <i>B. improvisus</i>	All experiments: low oxygen- (0.5-1.0 mg O ₂ /l) high oxygen (4.5 mg O ₂ /l)	(1): <i>N. succinea</i>: Days 0-1 post exposure: High = Low Days 2-4: High >* Low <i>B. improvisus</i>: Days 0-1: High >* Low Days 2-4: High >* Low (2): High O ₂ >* Low O ₂ (3): High O ₂ >* Low O ₂ (4): Day 5/High > Day 4/Low > Day 4/High > Day 5/Low > Day 3/High > Day 3/Low > Day 2/High > Day 2/Low > Day 1/High = Day 1/Low (5): During hypoxia- High O ₂ >* Low O ₂ Post hypoxia- Low >High

Table 5. (continued)

Author	Predator/ Prey	Oxygen Concentration	Predation Efficiency
Shin et al. 2005 (lab)	<i>Thalassidroma danae</i> / <i>Perna viridis</i>	Low O₂ : 1.5 mg O ₂ /l Med O₂ : 4.0 mg O ₂ /l High O₂ : 8.0 mg O ₂ /l	High >* Low > Med
Edjung et al. 2008 (lab)	<i>Monoporeia affinis</i> , <i>Malcoma balthica</i> , <i>Halicryptus spinulosus</i> / <i>Skeletonema costatum</i>	Expt 1: High- 10 mg O ₂ /l Med- 6 mg O ₂ /l Low- 3 mg O ₂ /l Expt 2: High- 10.6 mg O ₂ /l Low: 0.8 mg O ₂ /l Expt 3: High- 8.9 mg O ₂ /l Low-1.6 mg O ₂ /l	(1): <i>M. affinis</i> : Low >* High > Med <i>M. balthica</i> : High > Low > Med <i>H. spinulosus</i> : High > Med > Low (2): <i>M.affinis</i> : High >* Low <i>M. balthica</i> : High > Low <i>H. spinulosus</i> : High > Low (3): <i>M.affinis</i> : High >* Low <i>M. balthica</i> : Low > High <i>H. spinulosus</i> : High > Low
Howard 2009 (lab)	<i>Callinectes sapidus</i> / <i>Rangia cuneata</i>	High: 90-100% DO Low: < 0.7 5mg O ₂ /l	High >* Low
*- Corresponds to a significant (p < 0.05) effect of decreased oxygen on predation efficiency			

Trophic Cascades

As previously stated, there are many factors that can influence the outcome of predator-prey interactions. In recent years many of these factors have been drastically changing, mainly due to habitat loss and climate change. And while there are many studies that investigate how these changing factors influence the outcome of a single predator-prey relationship, research must also be taken a step further to see how these changes will impact populations and communities, especially in communities dominated by top-down effects. The strength of top-down controls varies within and between marine communities, often due to abiotic factors, as they are major mediators of predator-prey interactions (Kishi et al. 2005). In a review by Harley et al. (2006) it was mentioned that because species respond independently to changes in abiotic factors that all species interactions, including predator-prey interactions, could be altered through these changes in abiotic factors.

Carr and Bruno showed that future predicted temperatures significantly increased the strength of a marine community's top-down effect. In general, higher trophic levels are more sensitive to elevated temperatures (Gilman et al. 2010), and Kratina et al. (2012) showed that these sensitivities have the possibility to cause impacts downward through the food chain, also known as trophic cascades, as well as stronger eutrophication effects due to increased nutrient levels. This study also showed that overall communities will be susceptible to trophic cascades due to the predicted elevated temperatures of the future. Freitas et al. (2007) sought to understand the effect increasing temperatures had on the interaction between the bivalve *Macoma balthica* and one of its crustacean predators, the shrimp *Crangon crangon*. This specific predator-prey interaction was especially intriguing to study due to *M. balthica* currently living within the upper limits of its temperature range today, and that any continued increase in temperature will have a negative impact on *M. balthica* populations. This study suggests that with increasing temperatures the growth potential of *C. crangon* will increase more than that of *M. balthica*, due to the implied increase in predation pressure by *C. crangon*. This increase in growth potential could then cause a shift in food web structure and function, potentially by edging out another predator of *M. balthica*.

Conversely, there are some studies that contradict the results found by Carr and Bruno (2013) and Freitas et al. (2007). There have been some studies that have found that while both

the predator and prey were significantly impacted by a change in abiotic factors, there was no net change to the outcome and strength of the trophic interactions at work. For example, the study done by Grabowski (2004) on how increasing habitat complexity influence a three-tiered trophic interaction with the oyster toadfish (*Opsanus tau*) as the highest trophic level, the mud crab (*Panopeus herbstii*) as the middle level, and juvenile oysters (*Crassostrea virginica*) at the lowest trophic level. Grabowski's results indicated that toadfish only significantly affected crab mortality at a lower complexity, however, oyster mortality rate was still significantly lowered under these conditions. So while the predator-prey interaction between toadfish and mud crab, and mud crab and oyster, were significantly altered due to a change in habitat complexity, the overall outcome of the entire trophic interaction remained unchanged. Similar results were found by Landes and Zimmer (2012) on the interaction between green crabs (*Carcinus maenas*) and periwinkles (*Littorina littorea*).

These divergent results show the importance of closely examining multiple different trophic interactions, especially those of commercial importance, those involving keystone species, and those that are highly regulated by top-down controls. The effects of factors such as increased habitat complexity, warming, and increased CO₂ are so species-specific that researchers will be unable to make generalizations as to how food web and community structures will be impacted in a decreasingly complex, but increasingly warming and acidified world.

Predation efficiency experiments

A total of 15 lane snapper individuals were used for the predation efficiency trials. In total, 140 trials were completed, with 35 at each of the four temperatures tested (five replicates per complexity treatment tested). The holding tank system had some disease issues in the form of a species of freshwater fungus ("Ich", *Ichthyophthirius multifiliis*). The disease was vigorously monitored, with any fish showing symptoms being moved to an isolation tank and treated accordingly. Fish were not used in trials if they were showing symptoms of the disease.

Behavioral observations

Several behavioral observations were made of both predator and prey upon reviewing the filmed trials. One of the most obvious distinctions when observing prey behavior was their

ability to cling to and therefore hide themselves within the flexible complexity, something the prey did not do with the non-flexible complexity of the wooden dowel rods. In trials using non-flexible complexity, most shrimp remained on the bottom of the experimental arena.

Observations of predator behavior during trials shows that the predator spent less time moving about the trial arena searching for prey when the temperature was lower (15 °C), this most likely is because at lower temperature fish tend to reduce movement and feeding to conserve energy. Predators also spent less time moving throughout the arena at lower levels of habitat complexity. At these lower complexities (0,1), fish spent most of their time either in a corner or in the provided shelter. This behavior opposes the behavior observed at higher temperatures. Since the size of fish used in this experiment are mostly young adults, it would make sense that these fish had to balance between searching for food while also limiting time away from shelters to protect themselves from their own predators. This observed behavior could be due to the fish needing a certain level of habitat complexity in order to feel safe to move about the arena in search of food. At higher temperatures, fish have a higher metabolic need, and will then take more risks in order to look for prey.

Predation efficiency trials

The predation efficiency of *L. synagris* was significantly affected by increased temperature and complexity overall ($p < 0.05$). However, post-hoc analyses confirmed that complexity type ($p > 0.05$) and complexity level ($p > 0.05$) had no significant effect on predation rate, while there was a significant difference in predation rate between each temperature sampled (Fig 1). Predation efficiency was highest in the 30 °C trials (83% of prey consumed), followed by 25 °C trials (42%), 20 °C trials (16%), and the lowest predation efficiency was at 15 °C (11%).

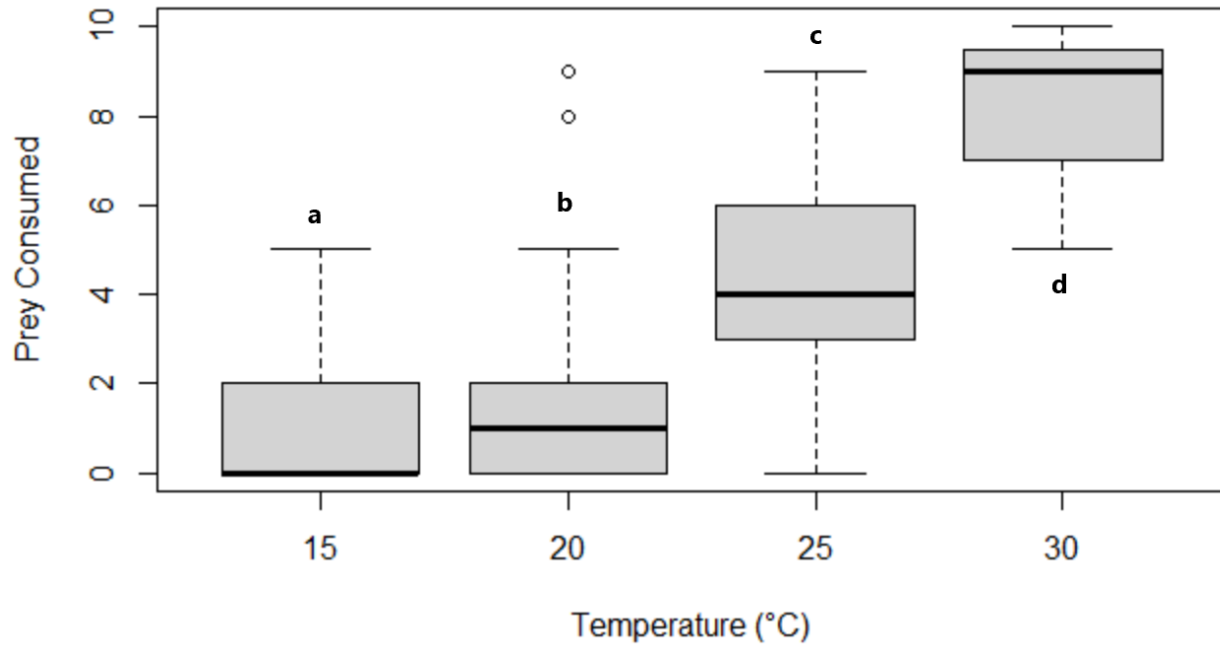


Figure 3. Predation efficiency of *L. synagris* at different temperature treatments. Black bars represent median values. Letters represent significant differences in predation efficiency between treatments.

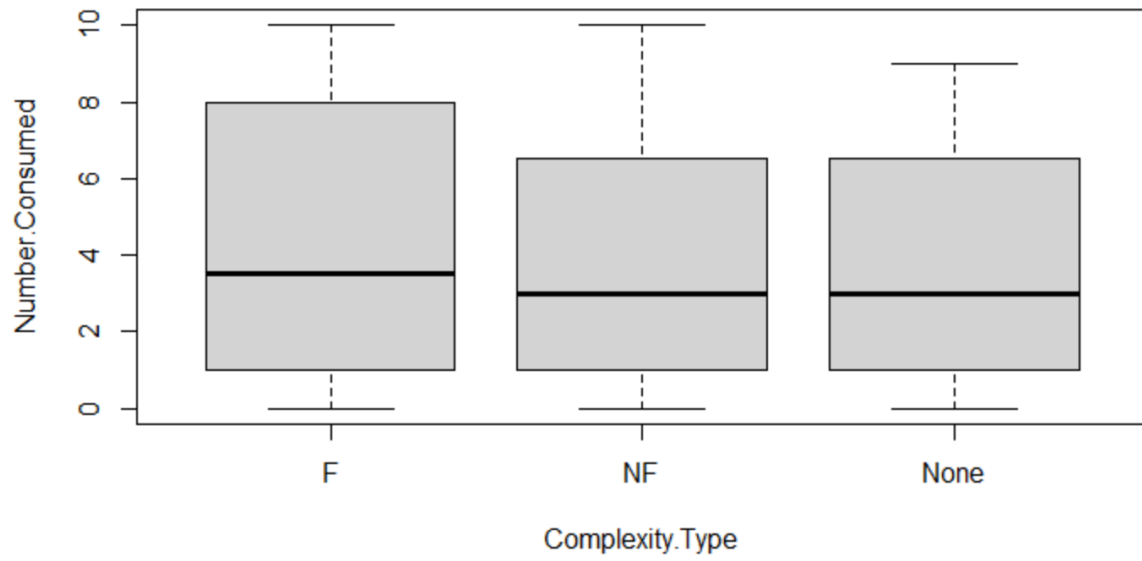


Figure 4. Predation efficiency of *L. synagris* at flexible (F), non-flexible (NF), and no complexity. Black bars represent median values.

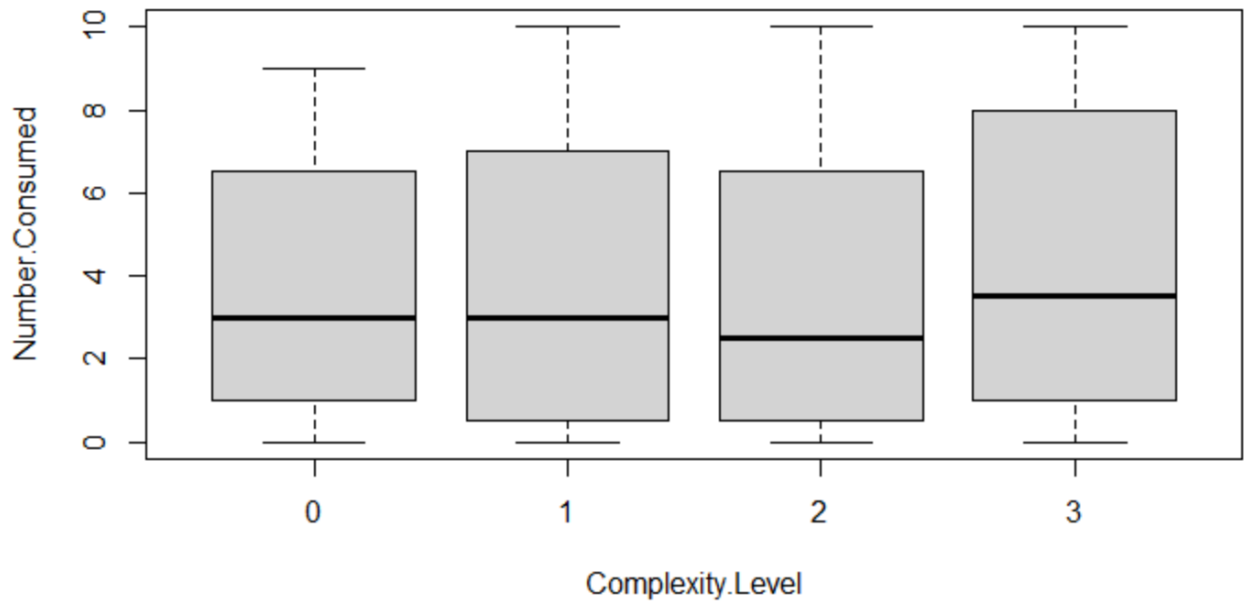


Figure 5. Predation efficiency of *L. synagris* at different complexity levels. Black bars represent median values.

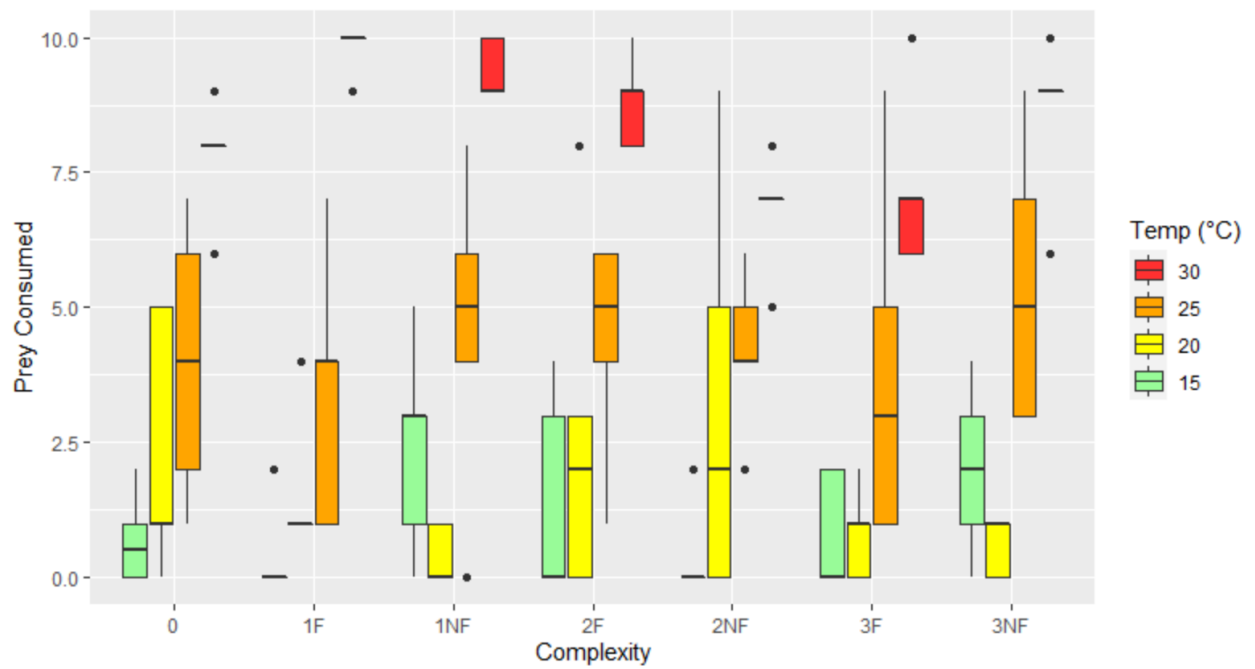


Figure 6. Predation efficiency of *L. synagris* at different levels of flexible (F) and non-flexible (NF) complexity at 15 °C (green), 20 °C (yellow), 25 °C (orange), and 30 °C (red). Black bars represent median values, and filled dots represent outliers.

Discussion

The results of this study show that increasing temperatures significantly impacts the predation efficiency of *Lutjanus synagris*. There was a much higher predation efficiency at higher temperatures than at lower temperatures, which is similar to results found in studies previously discussed (Leonard 2000, Miller 2013, Pincebourde et al. 2012). These results are not surprising, as an increase in temperature would require predators to increase their energy consumption to make up for their increased metabolic rate. Unfortunately, we were unable to see a significant effect of complexity on predation efficiency. This is probably due to not using a complex enough density for the predator species chosen. *L. synagris* are chase predators, so they are quickly able to change direction and move about a complex area in order to obtain prey. Other studies involving similar species involved complexity densities higher than what was explored in this study.

Predation efficiency is a function of the detection, pursuit, and capture of prey (Stoner 1982). Predation efficiency as well as individual aspects of a predation event can all be altered, inhibited, or magnified by the factors discussed here. It has been proven that for most predators, across a variety of habitats, an intermediate amount of habitat complexity optimizes their predation efficiency, and that a loss or increase in habitat could significantly impact their predation rate. This intermediate habitat density is different for each predator and even each specific predator-prey interaction, depending on the prey's ability to successfully utilize the habitat complexity available.

It has been shown both in this study and previous studies that temperature has a very large effect on predation efficiency. Due to an increase in metabolic rates, a majority of studies confirm that it is expected to see a significant increase in predation rate with increasing temperatures. In contrast decreased oxygen levels, which are known to occur more often in areas of high temperature, can significantly decrease predation rate. There have been no studies to date that have investigated how higher temperature combined with lower oxygen levels would affect a predator- prey interaction. These two competing factors could have a deleterious effect on predation efficiency, in which there is no net change in the outcome or strength of predator-prey interactions. Also, one of these factors may be a stronger influence on predation efficiency, and the interaction would have the expected results.

The effect of climate change on predator-prey interactions is interesting to study because of the many ways that increased CO₂ levels affect both predator and prey. Changes in predator and prey can be developmental and behavioral, and there are multiple different ways that they can be changed. This results in a very wide and not well understood amount of changes in a predator-prey interaction. There has been evidence of increased movement and activity for both predator and prey, an increase in predation rate, and in a few cases a fatal attraction to predator odor cues. Increased CO₂ levels also have been shown to cause many developmental issues in the brains of prey species, causing major mobility issues that make it near impossible for prey to successfully avoid predation. Any number of these changes can cause significant impacts on the outcome of predator-prey interactions, and if any effects can be combined the effect could be magnified and have detrimental effects on population numbers and therefore community structure.

Oceans are drastically changing at a rate that research is unable to keep up with. The loss of seagrasses, mangroves, and coral reefs combined with steadily increasing temperature and CO₂ levels adds up to a variety of combining factors that could potentially impact predator-prey interactions. With all this potential for change in individual interactions, it is overwhelming to imagine how individual interactions will combine to cause changes that can happen at the community level. These changing factors have the ability to influence not just population sizes and ratios, but also fundamental community structure and functioning across a variety of marine habitats. One of the most important areas of future research would be to study not just a single species' response to changing factors, but how both predator and prey respond. And if these changing factors impact the result or strength of these predator-prey interactions. Studying these interactions will be especially important for communities with a keystone species, where a potential impact on the keystone species would have a consequential impact on the entire community. This area of research will also be important for those species that are of great commercial value, as changes to those interactions can have major economic repercussions.

Conclusions

Changing factors in the ocean have the potential to change the outcome or strength of a predator-prey relationship. Through these changing predator-prey interactions, population sizes

and community structure and functioning can be altered and cause a variety of repercussions throughout the marine ecosystem. Through the extensive literature review and experiment described here, it is shown that research on predator-prey relationships should be predator-based, as predators are more likely to experience stress from these changes and have stronger responses in comparison to prey. However, a prey's response to stressors cannot be discounted, and should not be ignored in future research.

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