UNIVERSITY OF CALIFORNIA, SAN DIEGO

Sub-lethal Predator Effects on Juvenile Growth in the Genus *Sebastes*

A Thesis submitted in partial satisfaction of the requirements for the degree Master of Science

in

Biology

by

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2014

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University of California, San Diego

2014

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ABSTRACT OF THE THESIS

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The study of predator effects is typically focused on the finalistic aspect of such interactions. Although direct predation is undoubtedly important, there is a far less studied realm that is equally, if not, more important than the direct effects of predation. Here we examine the indirect growth effects of predator and prey interactions by using predator stimuli experimentation. Juvenile rockfishes of the genus *Sebastes* were introduced to predation stimuli and within generation effects on

growth were measured. Multiple experiments were run while manipulating visual chemical stimuli. It was discovered that the existence of predation stimuli resulted in a consistent negative growth effect on both body length and height in juvenile rockfish. Although sub-lethal predator effects significantly stunted growth in both mean body length and height, weight was not affected. It has been seen that juvenile survivorship can differentiate based on size relationships, and therefore stunted growth of juvenile fish by predation presence may lead to changes in survivorship. This study also reinforces the theory that energy allocation and metabolism may play a key role in the way that fish are affected by predation.

INTRODUCTION

Fish of different trophic levels are constantly interacting. One of the most significant interactions is the one between a predator and its prey. Fish in particular are unceasingly presented with predatory threat. This is especially true in pristine marine ecosystems and for juvenile fish in general. Pristine marine ecosystems have been shown to be exceptionally predator rich (Friedlander & DeMartini 2002, Sandin et al. 2008, DeMartini et al. 2008, Williams et al. 2011) and juvenile fish must deal with the fact that essentially every other fish is their predator. Predation is highly dependent on gape size limitation, leaving smaller fish with myriad predators (Persson et al. 1996, Pettersson & Hedenström 2000, Dorner & Wagner 2003, Eklöv & Jonsson 2007). When compared to other biomes, the marine habitat possesses a higher predatory threat. Small fish have to deal with a longer food chain and hence more secondary predators than other biomes (Hairston Jr & Hairston Sr 1993). When people think about predator and prey interactions, they typically focus on lethal effects. This way of thinking is expressed in the scientific world, with the majority of predatory research investigating mortality and its implications. The emphasis is concentrated on these lethal effects and focus on trophic level density shifts that are associated with direct predation (Pinnegar et al. 2000, Friedlander & DeMartini 2002, Shurin et al. 2002, Sandin et al. 2008, DeMartini et al. 2008, Sandin 2010, Ruttenberg et al. 2011, Walsh et al. 2012). Although these shifts that are influenced by direct predation are undoubtedly important, there is a far less studied realm that is equally, if not, more important than direct predation (Preisser & Bolnick 2005, Werner & Peacor 2006

Creel & Christianson 2008). Previously little studied, sub-lethal effects have garnered attention due to their importance and potential for far reaching consequences. These effects can materialize into many adaptations, including behavioral shifts, morphological changes, and changes in growth rate.

When fish are stressed by predators they can respond behaviorally. Fish are known to make changes in their feeding behavior when there is a predator present. There is often a direct trade-off between predation risk and foraging (Godin & Smith 1988, Krause & Godin 1996). Predator presence can lead to changes in the prey's feeding behavior, ultimately leading to a decrease in their effective feeding area and rate of food intake (Prejs 1987, Fraser & Gilliam 1992, Steele 1998). A fish cannot reach its growth potential when it is feeding at a rate lower than its optimal level and will physiologically respond to the tradeoff between predation risk and the optimal amount of food (Brown & Kotler 2004). These fish will also react to differing food quality based on predation risk (Schmitt & Holbrook 1985). Threat of predation often plays a key role in the selection of habitat by fish. If a habitat proves to be predator intense, prey fish may allocate to safer habitats (Holbrook and Schmitt 1988a, 1988b, Werner and Hall 1988, Gotceitas 1990, Halpin 2000). The trade-off is generally between predatory threat level and food availability or quality (Cerri & Fraser 1983, Schmitt & Holbrook 1985). As a consequence of these trade-offs, multiple species of fish have been known to experience ontogenetic shifts. Ontogenetic shifts are suspected to be present within a population of conspecifics when there is distinct variation in food and habitat use based on body size. Predation risk and resource acquisition ability are

commonly related to body size and this relationship is believed to lead to such shifts (Werner & Gilliam 1984, Werner & Hall 1988). Ontogenetic shifts can result in a dynamic web of ecological interactions involving competition and predation.

In addition to behavioral effects, physiological changes can occur without changes in behavior. When a fish encounters a predator it is afflicted with some amount of hormonal stress. Even if a fish only sees a predator, it can become stressed, and its heightened levels of cortisol can be measured (Woodley & Peterson 2003, Breves & Specker 2005, Barcellos et al. 2007). It has been shown that even though these stresses may be short, they can lead to long lived metabolic disturbances (Mazeaud et al. 1977, Bonga 1997). Prey efficiency in converting ingested food to body mass can be lowered when stress from predatory risk is present (Hawlena & Schmitz 2010). This leads to the idea that growth can be affected independently from food availability. Growth in prey fish can be indirectly affected through behavioral changes induced by predators, but it is also possible that the stress alone can result in a growth effect. Growth in fishes is labile and this quality is intensified in juveniles (Allen & Horn 2006); juvenile fish have the ability to grow exceptionally fast and hence have the potential for big differences in growth under different levels of predatory threat.

Somatic growth in fish can be altered in many ways. The most commonly investigated parameter is length. It has been commonly seen that the presence of a predator will reduce the short term growth in length of the prey fish (Fraser & Gilliam 1992, Connell 1998, Steele 1998, Steele & Forrester 2002, Stallings 2008). Although

there have been two studies showing increased growth (Persson et al. 1996, Johnson & Belk 1999), these two studies calculated growth from otoliths and on a much longer time scale of looking at growth that occurred over multiple years compared the previously mentioned studies that had durations of no more than a few months. This emphasizes the importance of time scale when looking at growth interactions. The few sub-lethal predator effect studies that have looked at changes in short term growth in terms of mass, have also shown a significant reduction when predator stimuli is present (Fraser & Gilliam 1992, Woodley & Peterson 2003). It has been shown that these parameters can also be changed simultaneously to develop a difference in allometry. The relationship between height and length has received much attention due to the concept of gape size limitation. In all studies, the environment with predators led to a fish with increased body depth (Bronmark & Pettersson 1994, Pettersson & Brönmark 1999, Byström et al. 2003, Andersson 2006, Eklöv & Jonsson 2007, Chivers et al. 2007, Robinson et al. 2007, Domenici 2008). This strategy appears to be advantageous for a prey fish that is trying to outgrow the gape of its predator. The one study that compared length and weight relationships between populations with or without predators found negative allometric growth when predators were present (Patimar et al. 2009). Negative allometric growth was defined as an allometry coefficient (b) below 3 in the classic length weight relationship of $W = aL^b$ .This means that the fish under predatory stress were growing by an over-proportional increase in length relative to weight. It was proposed that this may lead to an advantage in swimming speed. In more extreme cases, instead of a change in growth

rates, the fish will change its morphology more drastically with the addition, subtraction, or displacement of features. The family of fish that has received the most attention for its phenotypic plasticity is *Gasterosteidae*. When predation risk or predator type changes, Sticklebacks have been shown alter dorsal spines, pelvic spines, and lateral bony plates (Hoogland & Morris 1956, Reimchen 1992, 1994, Bell et al. 2004, Shapiro et al. 2004). Predators can affect the growth of their prey in many ways. Knowledge of within generation inducible morphological changes is essential to understanding the ability of fish to react to stressors. Altered growth can have cascading effects on other aspects of a fish's life history and hence it is very important to understand the magnitude and mechanism for such changes.

A majority of the studies discussed thus far have focused on presence versus absence of predators. However, means of detection and subsequent response to predators is also meaningful. Two of the main systems used are the visual system and olfactory system. Fish can intake a visual stimulus and make decisions based on what they see (Siebeck et al. 2009). Chemical cues can also play a large role in how fish react and behave when a predation threat is present (Sweatman 1988, Smith 1992, Kats & Dill 1998, Holmes & McCormick 2010, Lönnstedt et al. 2012, Manassa & McCormick 2012, 2013, Mitchell & McCormick 2013). The importance of chemical cues to growth has been shown strongly for freshwater snails (Crowl 1990), but has yet to be fully explored in fish. Growth differences have been found independently for visual (Woodley & Peterson 2003) and chemical (Andersson 2006) stimuli. In one study, a multiple stimulus approach was taken. The treatments presented were

chemical alone and a combination of visual and chemical simultaneously. It was presented that chemical was the acting stimulus due to the result of the visual and chemical treatment increasing the effect only slightly and not being significantly different than the chemical alone treatment (Bronmark & Pettersson 1994). The effect of predator stimuli on the growth of strictly marine species of fish has yet to be investigated. With scarce previous research, it is important to experiment with multiple proxies for predator presence to explore generality of the affect that predators have on their prey in the marine environment.

METHODS

Study species

The Splitnose Rockfish (*Sebastes diploproa)*, Treefish (*Sebastes serriceps)*, and Flag Rockfish (*Sebastes rubrivinctus)* are of the family *Sebastidae*. These three fish compromise the vast majority of young rockfish found around La Jolla, California, commonly found in drifting kelp mats as recent recruits and young juveniles (Mitchell & Hunter 1970, Boehlert 1977, Hobday 2000). Rockfish were chosen for a multitude of reasons. One important reason is that recently settled juveniles can be found on kelp paddies. Recently recruited juveniles allow for the largest growth potential and least potential for latent environmental effects. Rockfish are known to dominate many fish communities along the west coast continental United States and are very speciose, with at least 72 species along the northeast Pacific. They also appear in essentially all habitats known in their range (Love et al. 2002). All juvenile rockfish species were found in heterospecific aggregations within the drifting kelp mats, ensuring consistent living conditions and pre-experiment habitat. It is assumed that all species have comparable pre-catch predation threat because all three species were found together on any single kelp paddy. All live predator experiments were begun with approximately uniform starting size (39.50 cm – 42.67 cm average tank SL). Each experiment was monospecific, with only one species for all tanks. All three species of rockfish are closely phylogenetically related (Hyde & Vetter 2007). Due to these reasons and the highly similar early life histories

between these three species, the use of a meta-analytical approach to lump the experiments is a reasonable method to analyze the overall affect of predator presence.

Collection & Husbandry

All fish were collected from offshore drifting kelp mats. After accumulating drift kelp into a small area in order to aggregate all fish in one location next to the boat, the juvenile fish were obtained using large hand nets. Fish were then transferred to buckets and water was aerated with mobile respirators. The seawater in the buckets was replenished multiple times during transit to prevent the water temperature from rising too high. Fish were then delivered to the aquarium room at Scripps Institution of Oceanography to be separated in to different aquaria.

Collection of juvenile rockfish recruits occurred year around. Collection effort took place from June 2010 through June 2012. There are many aspects of the offshore drifting kelp system that result in high variability in juvenile *Sebastes* collection success. The first source on variability lies in the abundance of drifting kelp mats. Storm activity and large wave events are one large aspect that leads to the creation of the mats. Also, El Niño events are a particularly strong forcing on mat creation in Southern California. The abnormally warmer water temperatures and nutrient poor water lead to degradation and healthy kelp, and ultimately leads to increased kelp mat abundance. It has been seen that high kelp mat abundance is not the ideal condition, but instead a solitary mat that is distant from alternative protective structure and does not allow for dissolution of recruits among multiple drifting kelp mats. It was found that the ideal characteristics for finding large amounts of juvenile fish is a kelp mat

that is fairly degraded, dense, isolated in distance from other kelp mats, and of manageable size (<2m^2). The second main source of variability is the fish themselves. Even if the most ideal kelp mat is found, there is a high probability of finding few to no fish. Although collection effort occurred throughout the entire two years, some months did not yield enough individuals to be experimentally feasible from individual day trips. These months included March through May, December, and January.

All experiments were performed within a wet lab at Scripps Institution of Oceanography (SIO). The wet lab has been outfitted with a flow through system of ambient seawater. Fresh seawater is pumped up from the end of the pier at SIO. A flow through system was chosen to eliminate the confounding variable of differences in water composition of the individual tanks. For all tanks the inflow of water was set to 44 ml/sec. The temperature of the incoming water was ambient, coinciding with the temperature of surface waters at the end of the Scripps pier. Although there was a correlation between growth parameters and temperature fluctuation, experimental and control tanks for any given experiment trended together. There was no significant effect of temperature on the experiment response (Figure 1).

For all experiments the fish were fed once a day. In most cases, fish were fed flake food (Aquatic Eco-systems Inc.). Feeding occurred until satiation. Each tank was given pinches of food in sequence until the fish lost interest and the food began collecting on the bottom of the tank. Feeding continued in all tanks until the last tank ceased from eating. For only the first experiment, mini mysis shrimp (H2O Life Mini Marine Mysis Shrimp) were used, but a change in feed was initiated due to

unreliability of inventory. The tanks were siphoned for fecal matter and excess food on every third day. All tanks were siphoned for the same amount of time to control for the amount of stress induced by the siphoning procedure. The tank with the most detritus was siphoned first and every other tank was subsequently siphoned for the same amount of time.

Experiment Details

All experiments were conducted on *Sebastes* with between 4-14 fish per tank (Table 1). The variance in the number of individuals used per tank is a consequence of the highly variable collection success. For each experiment, the number of fish per tank was dependent on the total number of juveniles collected, which were randomly divided among control and experiment tanks. Effects of different numbers of fish per tank between experiments are controlled for by having the same amount of fish per tank for control and experimental tanks in each experiment. Any density effects will be experienced evenly among all tanks and hence controlled for. Mortality was very low across all experiments, especially considering that recently recruited juveniles were being studied. The mean survival proportion for all fish was 0.96. Of the six experiments analyzed, only two had tanks that incurred mortality. All experiments were run for a duration of one month.

Experimental Design

Live Predator

The live predator studies were conducted in eight small (10 gallon/37.9 liter) aquarium tanks. For these experiments a mature Grass Rockfish (*Sebastes rastrelliger*,

~25cm TL) was used as the predator. The experimental setup was comprised of one large (50 gallon/189.3 liter) predator tank, with four experimental tanks surrounding it. One of three possible iterations was performed for any given experiment (Figure 2, a, c, d). For example, if the experiment was a “chemical only” experiment, then all four tanks surrounding the predator tank would exhibit what can be seen in Figure 1a. For all experiments, there were also four control tanks (Figure 2, b). Removable PVC slates were fabricated to fit between the predator tank and the experimental tanks, allowing the experimenter to control visual contact among tanks. All outside panels of the experimental and control tanks were covered in waterproof paper to limit visual stimulus reaching the experimental tanks.

For experiments including the visual stimulus, the PVC slates were removed for three hours each day to allow for view of the predator for each experimental tank. The predatory fish was fed one live conspecific (to the juvenile study species) daily. If the experiment included the visual stimulus, the conspecific fish was supplied to the predator tank while the PVC inhibitor slates were not present. The predator tank was drilled and tapped to allow for seawater from the predator tank to flow into the experimental tanks. Valves were attached using bulkheads to allow for regulation of the amount of water flowing into each tank. For experiments including the chemical stimulus, water was constantly fed to each experimental tank from the predator tank at the standard flow of 44 ml/sec. If the experiment did not include the chemical stimulus, then the valves were closed and each tank was supplied with ambient pier

seawater. Experiments were run with all possible combinations of visual and chemical stimuli.

Artificial Predators

The artificial predator studies were conducted in ten small (10 gallon/37.85 liter) aquarium tanks. Each aquarium was outfitted with panels of foam to block out view of the researcher and fish in surrounding aquaria. For each experiment there were five treatment tanks and five control tanks. The five experimental tanks were each outfitted with an apparatus that exhibited the visual predator presence stimulus. An artificial Predator Emulation Device (PED) was built to mimic the visual cue of an attacking predator (Figure 3). The use of an artificial predator allowed for complete control on the amount of visual predator presence stimuli that experimental fish were exposed to. The "predators" enter the tanks intermittently and randomly. The intervals between attacks were produced using a random number generator and a truncated Poisson distribution set to a mean waiting time of six minutes and a maximum waiting time of twelve minutes. The mean waiting time was chosen based on derivation from the predation visitation rates observed previously on a reef in Curacao (Sandin & Pacala 2005). The maximum waiting time was chosen to eliminate the possibility of receiving a time interval that is excessively long.

The system was run via a program written using LabVIEW software. The predator apparatus was made out of all nylon and PVC parts to inhibit corrosion. The PEDs were attached to each experimental tank using a custom made PVC stand that was fastened to each tank via set screws. The LabVIEW program sends information to

the Data Acquisition Module (National Instruments, USB 6501) which in turn sends an electrical signal to the solid state relays (Clare, CPC1218Y). This will switch the DC load allowing for the DC motors(Battery space MT-300) to operate. The DC motors then power the attached nylon spur gears (McMaster-Carr, 57655K53) that run along the nylon gear racks (McMaster-Carr, 57655K63). The mimic predators are attached to the ends of the gear racks. The movement of the gear rack “shoots” mimic predators in and out of the tanks rapidly, emulating a predator attack on the fish within the aquaria.

Response Metrics

The fish were measured to record change in four parameters - standard length (SL,cm), total length (TL,cm), height (cm), and weight (g). The individuals were measured twice during the course of each experiment, at the beginning and at the end of each experiment. Lengths and heights were measured within small plastic re-sealable bags that were partially filled with seawater to reduce stress on the fish. Digital Calipers were used to measure lengths and height. After lengths and height were measured, the fish would be taken out of the bag and placed on a weighing dish. The fish were placed in a weighing dish with another weighing dish on top to reduce the risk of the fish jumping out. The dishes are then tilted to let any excess water drip out and quickly put on the balance. This aspect of the measuring process took no longer than 45 seconds to minimize stress of the fish from being out of seawater. After the initial measurement, the fish were monitored for one day to make sure they returned to normal behavior. After confirmation of normal behavior, each experiment

was started. It never took longer than the initial one day waiting period to confirm normal behavior.

Bite Rate Experiment

Over 55 hours of film data were collected and analyzed to obtain average bite rates for predator and control treatments. This experiment was run using the simultaneous chemical and visual treatment (Figure 2, c). This bite rate was calculated in order to gain an estimate of the amount of food intake for each treatment. A "bite" was defined as a wide gulp, seen through exaggerated mouth and gill movements, typically with a fast, forward movement towards food. Each day, 10 minute videos (1 treatment tank and 1 control tank) were taken while feeding occurred. From previous experiments, it had been observed that satiation occurred well before the 10 minutes of feeding and hence the 10 minute max was chosen to make sure all tanks were at satiation. For each video the number of bites for each of the fish in that tank was recorded. The tank average was then computed. The tank averages for each video were then used as the individual data points for statistical testing.

Statistical Analysis

A Student's t-test was performed for each parameter of each experiment. The tests were performed to analyze the null hypothesis that the mean growth of predator and control tanks was the same. Given that the goal was to synthesize results from across predator treatments, a meta-analytical approach was followed. In order to examine the changes in fish body growth between all predator and control treatments,

a weighted response ratio approach was administered. A response ratio is a measure of proportionate change and is often used for meta-analysis in ecology. A response ratio can capture the effect magnitude across the results of multiple independent experiments. For the analysis of this paper a log response ratio was used (Hedges et al. 1999).

$$L_i = \ln(\overline{X}_{\mathrm{Exp}}) - \ln(\overline{X}_{\mathrm{Cont}})$$

This equation represents the linear transformed ratio of mean outcome in the experimental group to that in the control group. For a given experiment and parameter, $\overline{X}_{\mathrm{Exp}}$ and $\overline{X}_{\mathrm{Cont}}$ are the mean for all experimental and control tanks. A log transformation was used to obtain a linear metric. As a result, changes in the numerator and denominator of the ratio affect the ratio equally. A log transformation also normalizes the distribution of the data points when the sample size is small. All equations and a description of how they were used can be found in the Appendices C and D, respectively.

When using a response ratio it is important to select the proper model. The random-effects model includes between-experiment variance weighting, while the fixed-effect model does not. The selection of a random-effects model for this study was based on the idea that each of the experiments in this study does not have identical effect size. Instead, a response ratio is being used to estimate the mean of a distribution of effects and hence within-experiment and between-experiment variation should be considered. The methods of Hedges and Borenstein were widely used with some alterations supported by The Handbook of Research Synthesis and Meta-

Analysis (Hedges et al. 1999, Cooper et al. 2009, Borenstein et al. 2010). A Student's t-test was also performed to test the null hypothesis that bite rates were the same between predator and control tanks.

RESULTS

The three common species of *Sebastes* found under kelp paddies showed very similar initial mean sizes and early growth. All mean initial parameters were consistently similar between experimental and control tanks (Table 2). The maximum difference between experimental and control tank means for any given experiment was 0.92mm in length, 0.52mm in height, and 0.20g in weight. When comparing initial measurements, congenerics exhibited similar allometry (Figure 4, Figure 5).

After analyzing the 55 hours of bite rate data it was determined that there was no significant difference between the average bite rates of predator and control treatments ($t = 1.82$, $df = 57$, $p = 0.088$). The mean bite rate for experimental tanks was 44.98 bites/video and 49.37 bites/video for control tanks. The standard errors were 1.39 and 1.95, respectively.

When looking at each individual experiment, the direction of difference for both standard length and height between experiment and control were all homogeneous. All experiments showed a reduction in growth for tank means in standard length and height (Figure 6, Figure 7, Figure 8). One of the experiments with both the visual and chemical stimuli (Exp. 5) exhibited a significant difference in the mean change in standard length between the predator and control treatments ($t = 2.523$, $df = 6$, $p = 0.045$). The experiment with the chemical only treatment (Exp. 4) showed the next greatest difference between treatment and control for standard length and height, but was not significant ($t = 2.190$, $df = 6$, $p = 0.071$), ($t = 1.971$, $df = 6$, $p =$

0.096). When all live predator experiments were compared using a response ratio, the mean change in standard length and height among experimental tanks were significantly less than that of the control tanks ($\bar{R}^*$= 0.855, 95% CI = [0.766, 0.944], p = 0.028), ($\bar{R}^*$= 0.886 , 95% CI = [0.797, 0.975], p = 0.004). There was no significant difference in weight ($\bar{R}^*$= 0.945, 95% CI = [0.758, 1.132], p = 0.594) (Figure 9).

DISCUSSION

This study tested for evidence of sub-lethal effects of predators on the growth rates of prey fishes from the southern California Bight. We completed 6 experiments with slightly varying conditions to explore the impact of predators and the generality of the findings. The experimental results, when considered individually, revealed limited evidence of negative effects of predators on the growth rates of prey (i.e., 1 out of 6 experiments showed reductions in growth rates due to predator stimulus; Figure 6). However, when the results of all of the individual experiments were considered together, there was common support for the model that predators have a consistent and negative effect on the growth rates of prey. This aggregating approach of data analysis appears robust, given that each experiment showed trends in the same direction, though logistical limits prevented sufficient replication in each individual experiment for case-by-case statistical significance. The response ratio result coupled with the result from the bite rate experiment makes a strong argument that the reductions in growth may be related to a stress induced metabolism change in the predator treatment fish, as opposed to a simple reduction in feeding.

A majority of predator induced growth studies in fish have taken place in the freshwater environment (Crowl 1990, Fraser & Gilliam 1992, Bronmark & Pettersson 1994, Pettersson & Brönmark 1999, Johnson & Belk 1999, Eklöv & Svanbäck 2006, Andersson 2006, Eklöv & Jonsson 2007, Chivers et al. 2007, Robinson et al. 2007, Domenici 2008, Patimar et al. 2009). A large part of the research has also taken place as observational studies(Fraser & Gilliam 1992, Connell 1998, Johnson & Belk 1999,

Forrester & Steele 2000, Steele & Forrester 2002, Stallings 2008, 2009, Patimar et al. 2009). One major issue with observational studies of sub-lethal effects of predators on prey growth in fish is the environment. In an observational study, it is impossible to mimic the visual and chemical stimuli without making significant alterations that would completely defeat the purpose of an observational study. The lack of research on predator induced growth on marine fish in experimental aquaria is evident, with one study using brackish waters (Woodley & Peterson 2003) and one truly marine study (Munch & Conover 2003). The single previous experimental marine study focuses on the Atlantic Silverside, a short-lived species that is reproductive within one year and have very high turnover. It has also been shown that a majority of mature individuals die after completion of their first spawning event (Bayliff 1950, Conover et al. 2012). Such a short lived species does not allow for nearly as much wide scale deduction. The genus *Sebastes* is a relatively long lived genus (Love et al. 2002, Hyde & Vetter 2007). It was important to choose a study genus with complex life history. A genus with such attributes allows for larger scale inferences on the growth effects being studied. It is apparent that more research must be performed to discover the sub-lethal effects of marine predatory fish on the growth of their prey and the mechanisms behind these effects.

Individual Results

This is one of the first marine studies to examine the growth effect of predatory fish on their prey through experimentation. It was hypothesized that the effect of predator stimuli on growth would result in either allometric differences or an overall

stunting of growth. Although a difference in allometry between control and treatment was not found, there was an overall stunting of somatic growth with the introduction of predator stimuli. The negative growth effect on both body length and height in juvenile rockfish was found across all experiments. The stunting of growth in length in each experiment follows a trend that had been found in previous studies (Fraser & Gilliam 1992, Connell 1998, Steele 1998, Steele & Forrester 2002, Stallings 2008). The finding of a consistent stunting of growth in height however, is a novel discovery that had not previously been found in marine fish.

The difference in growth of weight between treatments of predator presence and control did not have a distinguishable trend. There are two possible reasons for this outcome. First, the amount of measurement error for the weight parameter was much higher than that of the length parameters. The measurement error coupled with the aspect that the juvenile fish being used weighed so little, most likely lead to the inconclusive result. The other possible explanation is that there is a trend that is not being seen or a trend that may require more examination to be seen.

Response Ratio

After analyzing each of the experiments individually, it was apparent that there was an overall trend for both decreased length and height. Individual experiments had marginal significance when analyzed independently and this is likely due to the constraints of this experiment. We found it important to explore the generality of the effect that predators were having on their prey. To accomplish this we needed a way to

investigate the independent magnitude of effect size across a series of replicate experiments. All experiments were comprised of a set of controls that were compared to a type of predator threat. The exact form of predator presence was varied but there was always some form of predator stimulus. In order to accomplish our goal, we administered a meta-analytical approach to lump the entire series of experiments into one response in order to explore over a range of conditions (Appendix C + D). Across all forms of predator presence, growth in both length and height was consistently stunted relative to the controls.

Since this study was fairly novel, it was important to be as exploratory as possible when investigating the effect predator presence on prey growth. This was attained by conducting numerous short term experiments, while varying predator treatments and the use of multiple prey species. This approach allowed for the ability to explore much more in a short time period. A response ratio meta-analytical approach was the best method to capture the overall effect of multiple predator presence experiments on prey growth.

Single Generation Importance

This study was constructed to look extensively at single generation growth effects and capabilities. Investigating changes on the single generation level allows for the understanding of an effect at a basal level. In order to examine large scale changes, it is necessary to first understand the fundamentals. It is important to look at growth effects at such a primary level because of the concept of phenotypic plasticity. The

concept of phenotypic plasticity was first introduced by biologists Richard Woltereck and Herman Nilsson-Ehle. It was Nilsson-Ehle who first used the term to describe the effects of environment on the phenotype of an organism in 1914 (Agrawal 2001, Hastings & Gross 2012). In general, fish are known to have exceedingly labile growth that continues throughout an individual's entire life cycle (Allen & Horn 2006). This experiment sought to explore this ability in the presence of predator stimuli. The structure of the experiment allowed for isolation of the potential plasticity that the juvenile rockfish inherently possessed.

Size-selective Mortality

A majority of size selective mortality research in juvenile fish has shown that mortality rates are lower with increasing body size (Parker 1971, Peterson & Wroblewski 1984, Hargreaves & LeBrasseur 1986, Miller & Crowder 1988, Post & Evans 1989, Pepin 1991, Paszkowski & Tonn 1994, Carr & Hixon 1995, Sogard 1997, Scharf & Buckel 1998, Scharf et al. 2000, Juanes et al. 2002, Connell 2002). This relationship is often referred to as the "Bigger is Better" hypothesis. Although there is some evidence for non-selective mortality, there is an overall consensus that it is better to be larger for survival purposes (Carr & Hixon 1995). The main three advantageous attributes that have been postulated include decreased vulnerability to predators through starvation resistance, "gape size limitation," and tolerance to environmental extremes (Sogard 1997). The advantageous attribute that is linked to predation is decreased vulnerability to predators. Fish can escape the mortality threat from predators through gape size limitation. If a given individual can grow large enough to

outsize the gape of its predator, then it has successfully excluded that predator from its mortality gamut.

When initially looking at the results of this experiment it may seem as if it is going against the main hypothesis and findings in the field of predator affected growth patterns. This experiment found that growth was stunted in both length and height, which is the direct opposite of the "Bigger is Better" hypothesis. It is important to keep in mind that in the natural world, there is much going on in terms of time scales and factors. These experiments specifically excluded physical interaction between the predator and prey and hence there was not preferential predation or mortality based on gape-size or predator preference. This experiment shows that with competition, resource availability, and predation induced mortality all controlled for, the growth of the prey fish is still altered by predator stimuli. The fact that this finding seemingly goes against the "Bigger is Better" hypothesis does not mean that either is wrong, it only leads to the idea that in nature, there are different time scales and factors to account for. This experiment showed an overall stunting in growth, while the "Bigger is Better" hypothesis leads to the idea that natural selection is a factor also at work with predators preferentially feeding on the smaller individuals. These individuals are being chosen because they are weaker or because the individuals that grew faster had escaped the predator gauntlet through means of gape size limitation.

Compensatory Growth

There are examples and situations where being smaller is better, but the overarching consensus is that in terms of survivorship and fitness, becoming larger at a more rapid pace is the optimal strategy. The theory that direct-predation is what is not allowing for the stunting effect to be seen in the long term has been presented, but an alternate theory may be that we are seeing compensatory growth at work. The idea of compensatory growth was first mentioned in 1915, when it was observed that rats with stunted growth for a period of time could then achieve a much accelerated rate of growth when conditions became favorable (Osborne & Mendel 1915). Although compensatory growth is quite ubiquitous among different organisms, fish have been shown to have a particularly robust response (Bohman 1955, Dobson & Holmes 1984, Jobling & Baardvik 1994, Ali et al. 2003). In one rare case, the individuals that were compensating for lack of previous growth overcompensated and even outgrow individuals of the same age that were growing at normal rates (Hayward et al. 1997). In general, compensatory growth brings the stunted individuals back to the optimal growth trajectory of individuals that have not been subjected to any stage of growth impairment. In another study, fish that exhibited rapid compensatory growth at the end the larval phase and settled at the same size had a much lower mortality rate than the fish that grew at a normal trajectory (Hamilton et al. 2008) . The lower mortality rate was attributed to a being in better condition with higher energy reserves and it was postulated that this was due to the higher selective intensity in the previous selective environment. The stunted growth that has been displayed in this study could possibly be the first stage of an exhibition of compensatory growth. It would be interesting for

future studies to see if the stunted growth in these experiments could be compensated for after complete removal of predator stimuli and to take it a step further and see how well each group survives when allowing direct predation back into the equation.

Bite Rate

When presented with a result of suppressed growth, the first inclination for many is to associate this with the intake of energy resources. In general this has been attributed to changes in the amount of foraging time and the quality of food consumed when predators are present (Schmitt & Holbrook 1985, Prejs 1987, Fraser & Gilliam 1992, Steele 1998, Brown & Kotler 2004). Interestingly, while the fish appeared to behave differently in the presence of predator cues (e.g., aggregating in distant corners of the tank) there were no obvious differences in the perceived foraging behavior of these individuals. Videographic analysis of foraging behavior supported these observations, as the bite rate experiment resulted in a non- significant result. It is important to note that the predator cue was stopped prior to feeding, so any effect of the predator on foraging would have to be linked to memory. Instead, the foraging results suggest that the effect of predators on growth rate is mediated hormonally and physiologically rather than directly through altered foraging patterns.

Cortisol

A fish being exposed to predators will be affected hormonally through heightened levels of cortisol (Woodley & Peterson 2003, Breves & Specker 2005). It is well known that in fish, cortisol is the primary stress hormone (Bonga 1997,

Mommsen et al. 1999). Heightened levels of cortisol have been shown to be correlated with decreased growth rates in past studies (Barton et al. 1987, Woodley & Peterson 2003, Peterson & Small 2005). The biochemistry behind this relationship has been studied thoroughly. For many species, experiments agree that heightened levels of cortisol in fish is also directly related to decreases in Insulin-like Growth Factor I (Kajimura et al. 2003, Dyer et al. 2004, Peterson & Small 2005, Leung et al. 2008, Won & Borski 2013). The decrease in IGF- I is attributed to more than one interaction, but cortisol induced resistance of IGF – I to Growth Hormone is playing a key role in this interaction (Duan et al. 1995, Kajimura et al. 2003, Pierce et al. 2011, Won & Borski 2013). Cortisol was unable to be measured in this study due to the minimum amount of blood needed for assays and the small size of the juvenile fish. Due to this constraint, a bite rate experiment was run to test the hypothesis that there was a difference in feeding between treatments. The incapability to garner cortisol data from the experiments resulted in the inability to quantitatively link cortisol to growth rates. Despite this shortfall, the insignificant result for a difference in bite rate between treatment and control and previous research lead to the conclusion that stress and ultimately the biochemical interactions that are triggered by stress, are the link from predator stimuli to the decreased growth rates in this study.

Population Dynamics

Although this study was focused on a single generation, the long term implications for population dynamics must be considered. Population dynamics consists of three main functions. The functions consist of growth rates, recruitment

rates, and mortality rates. The results of this study can be related to each one of these functions. The experiments directly monitored growth rates in juvenile fish. Juvenile fish are going to have little direct effect on a population's total biomass, but in a population where predator presence is high, it can be seen that alteration in growth rates can consequently have a large overall affect through modified recruitment rates and mortality rates. If a fish is constantly presented with predator stimuli, it may cause this fish to continually not reach its growth potential and hence take longer to become as large and ultimately as fecund. Fecundity can be severely affected by depressed growth. This is due to the general within-species relationship between fecundity and length (Bagenal 1978, Wootton 1979, Parrish et al. 1986, Elgar 1990, DeMartini 1991). Fecundity and size are positively related with fecundity as the cube of length (Miller & Kendall 2009). The idea of delayed sexual maturity is a compacting problem. Developmental plasticity is known to be highest in fish among all vertebrates. This characteristic is represented through extreme sexual lability (Atz 1964, Warner 1978, 1984). In fish, maturity is known to coincide with size much more so than age. Not only is delayed sexual maturity a temporal problem with a later onset in ability to create gametes, but it also limits the amount of eggs created by a stunted female. Stunted growth can also have serious consequences to reproductive output with disruption of sex ratios in hermaphroditic species (Sadovy 1996). The reduced growth rates from this experiment may also indirectly lead to lower recruitment rates through higher mortality. As stated earlier, when a fish's growth rate is stunted it leaves that individual with more possible predators for a longer duration and

consequently a higher probability of mortality. Small changes in early life growth rates and mortality rates have been estimated to result in tenfold variation in fish recruitment (Houde & Hoyt 1987). Although there are many steps between the results of this study and population growth, it is an important base point of knowledge that allows for speculative extrapolation.

Caveats

The main constraint of this experiment was the number of fish available. There were a multitude of reasons for the inability to constantly capture fish in large enough numbers to be experimentally feasible. The largest hindrance was the high variability in juvenile *Sebastes* collection success. Given that experiments needed to be commenced at the same time, catching fish at the same time and same size was critical. Another barrier was the amount of boat availability to go searching for drifting kelp mats. If a boat could have been used much more regularly, this issue could have been alleviated. Weather and sea conditions often restricted the ability to go out to sea by small boat, which makes schedule flexibility an important mitigating factor. The amount of aquarium space was also a constraint for this experiment. With more aquarium space, a much larger experiment could be run that would allow for more permutations, resulting in more exploratory power. One factor that could alleviate many of the constraints mentioned above is funding. Additional funding would allow for more boat days, higher schedule flexibility, and more aquaria.

Future studies

The ability to implement a major factorial design for future studies would be ideal for further experimentation. This would allow the comparison of all possible treatments at once and investigate the interworking of the two stimuli. The way they react in concert may be different then how they stimulate the fish when they are alone. These predator stimuli need to be further dissected to discover their role on emerging growth patterns. It would be interesting to use a tropical genus of fish and to also compare multiple species from different habitat guilds to see if the there is a consistent pattern and to compare across guild types and region. Similarly, the use of different and multiple predator types may also lead to compelling results. The exploration of different feeding food for the juvenile fish is a possible enhancement for further experimentation. It is possible that there is a type of fish feed that allows for larger growth potential.

Conclusion

This study highlights the importance of understanding the sub-lethal effects that predators can have on the somatic growth of their prey. It was shown that the presence of predator stimuli results in stunted growth in both length and height of juvenile rockfish. The presence of visual, chemical, and the combination of both stimuli, each can lead to reductions in growth rates in these juvenile fish. This finding gives support to the idea that fish take a multi stimuli approach to recognize the potential threat of a predator. The idea that the stunting of growth is occurring predominately due to stress and the metabolic consequences associated with this stress is a novel finding and will require further investigation. This exploration of predator

induced sub-lethal growth effects adds another piece to the puzzle of the relationship between predators and their prey. With fish having one of the most complicated and flexible life histories, this basal interaction can be used to help answer many of the more perplexing ecological questions that have yet to be fully answered.

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Appendix A: Figures

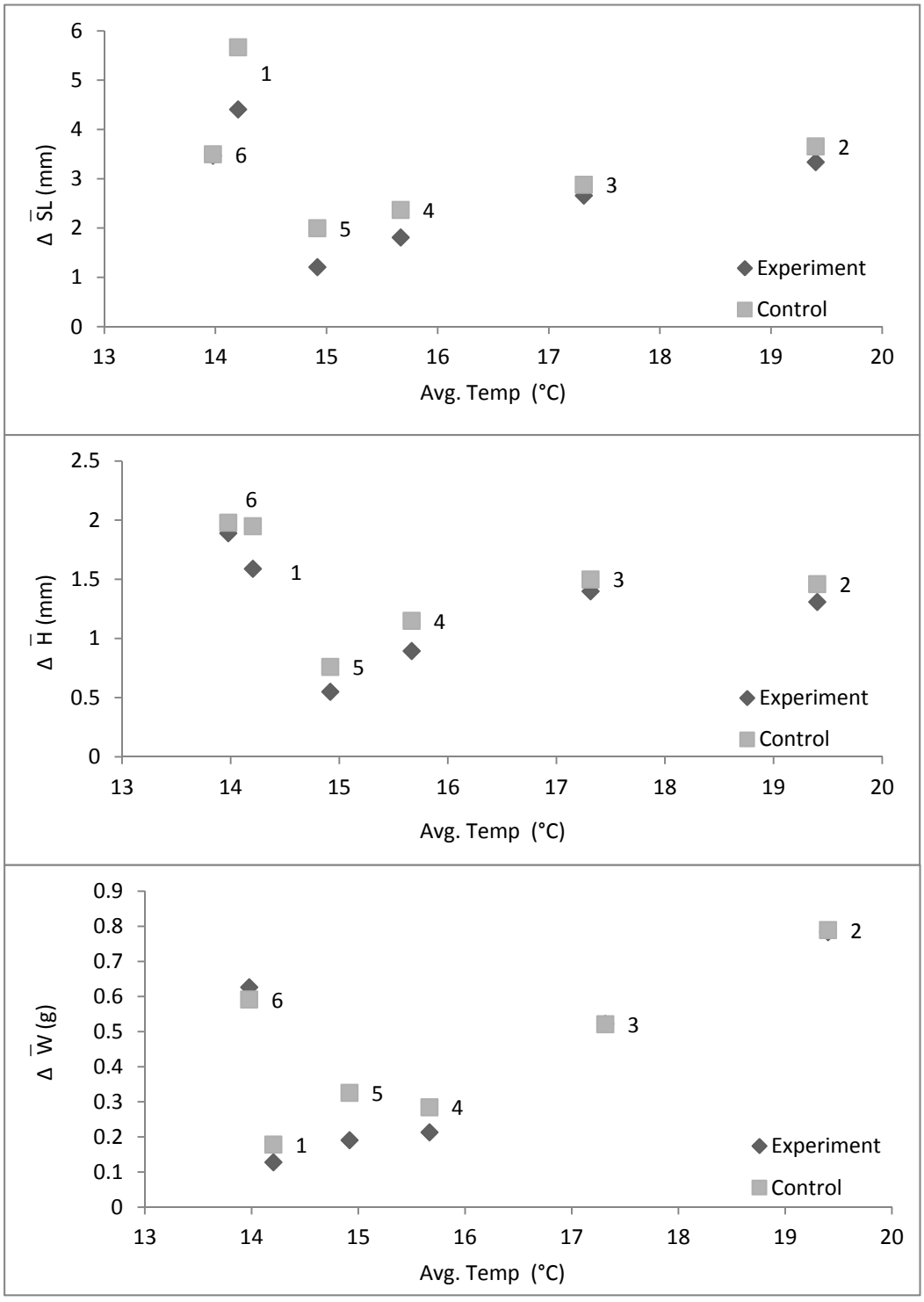

Figure 1 – Mean change in SL (mm), height (mm), and weight (g) compared with the mean temperature for each experiment. There was no significant effect of temperature on the experiment response.

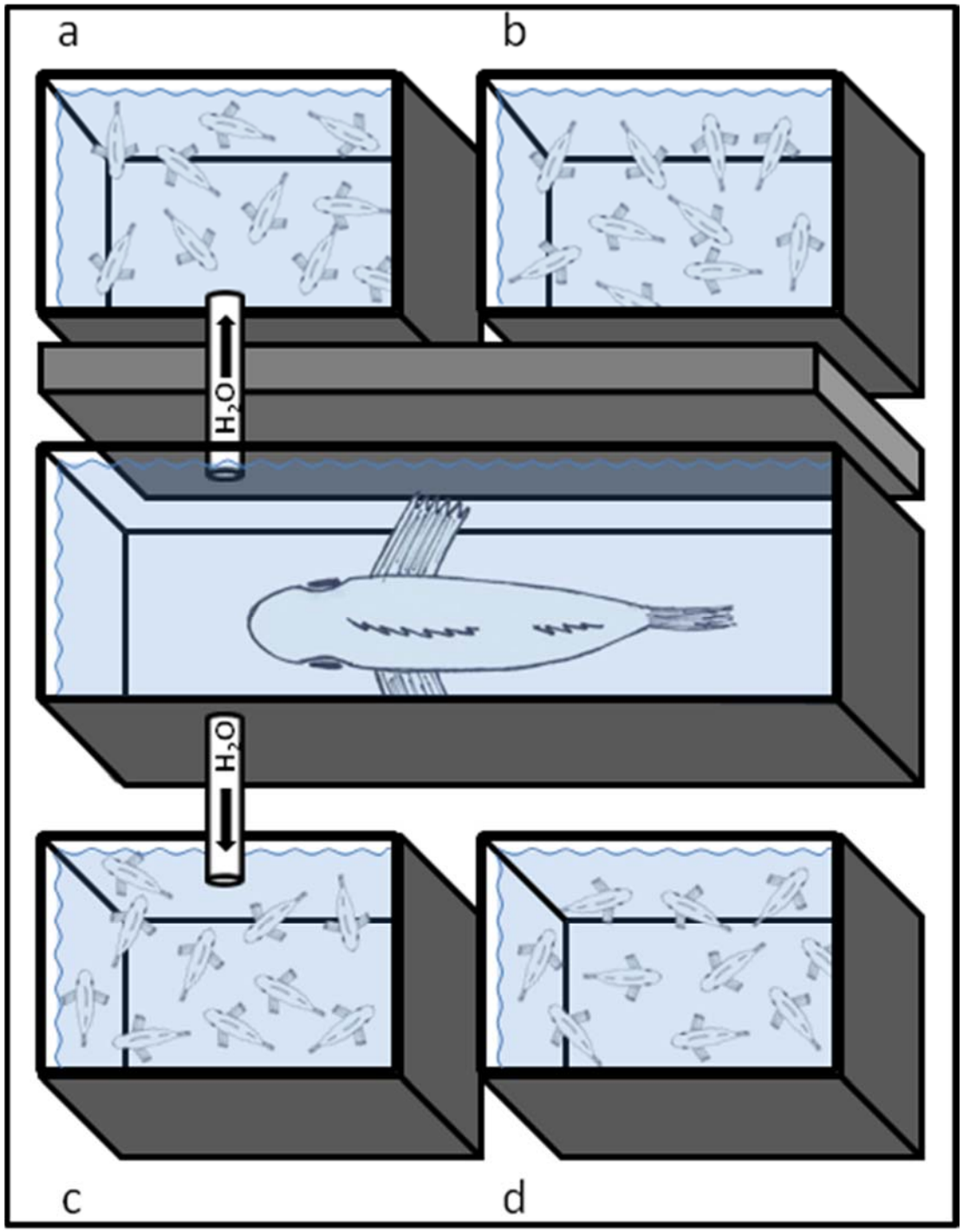

Figure 2 – All possible live predator treatments. (a) Chemical only (b) Control (c) Chemical & Visual (d) Visual only. This is a virtual representation to show all possible experiment types and the control in one figure. Each live predator experiment included four tanks that were all the same treatment (a, c, or d) and four control (b) tanks.

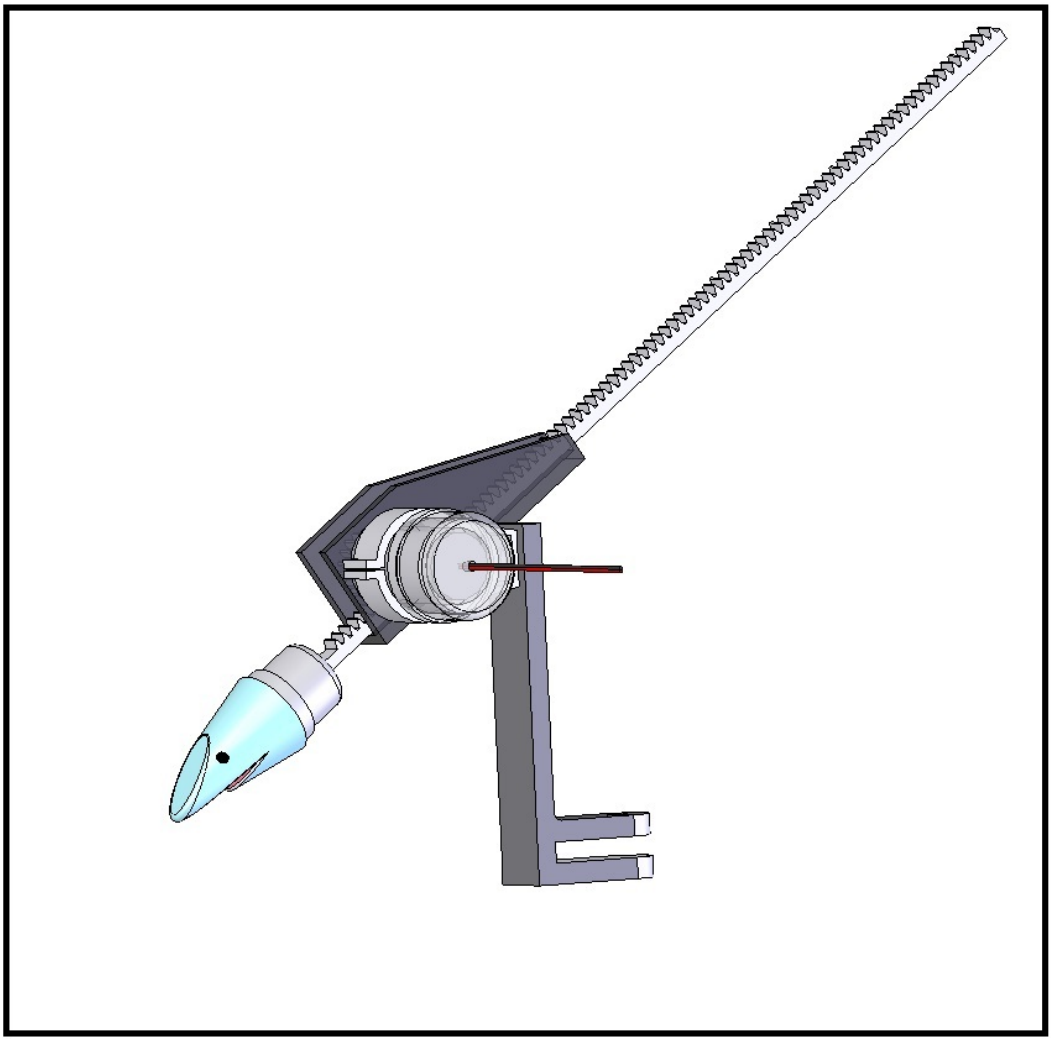

Figure 3 – Predator Emulation Device (PED). An apparatus built to provide visual predator presence stimuli. PEDs were used to mimic the visual cue of an attacking predator.

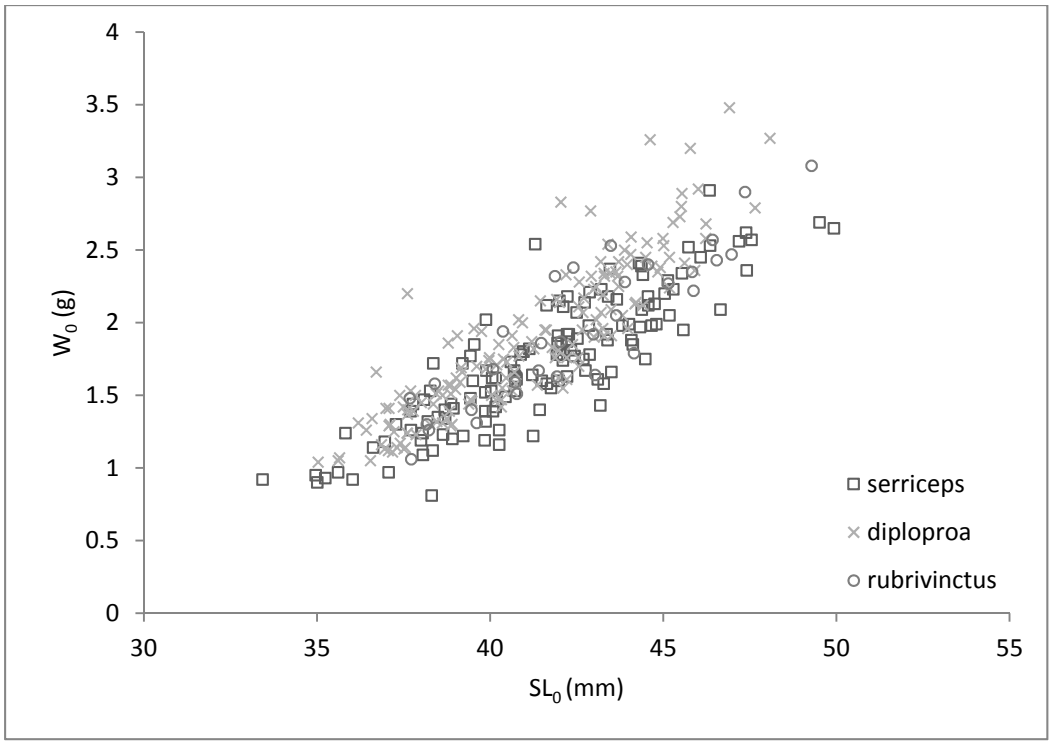

Figure 4 – Initial SL (mm) and initial weight (g) for all fish of each species (*S. serriceps*, *S. diploproa*, *S. rubrivinctus*). The relationship for each species is presented. Congenerics had similar allometry.

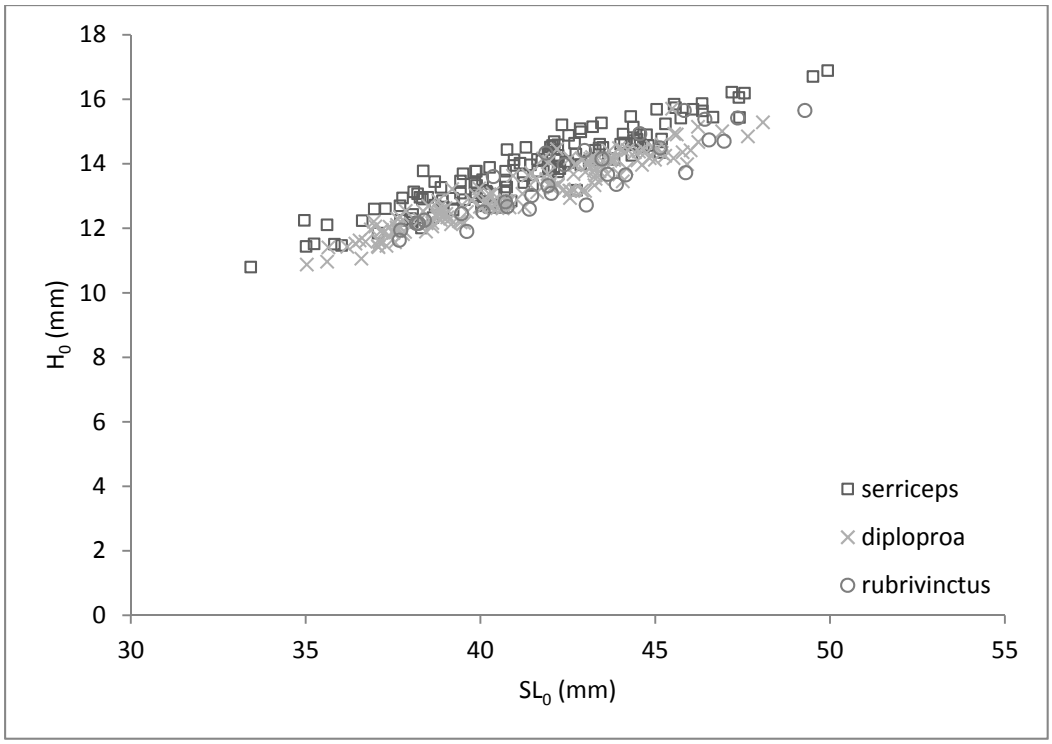

Figure 5 – Initial SL (mm) and initial height (mm) for all fish of each species (*S. serriceps*, *S. diploproa*, *S. rubrivinctus*). The relationship for each species is presented. Congenerics had similar allometry.

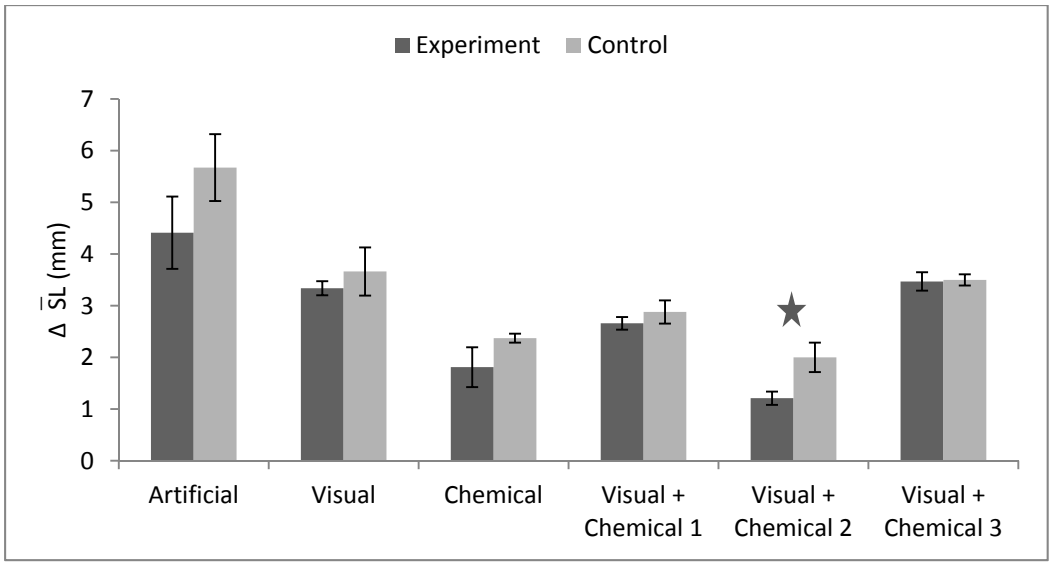

Figure 6 – Mean change in SL (mm) for all tanks of each treatment (experiment, control). The bars represent the actual change and the error bars are representative of standard error. A star signifies a significant difference.

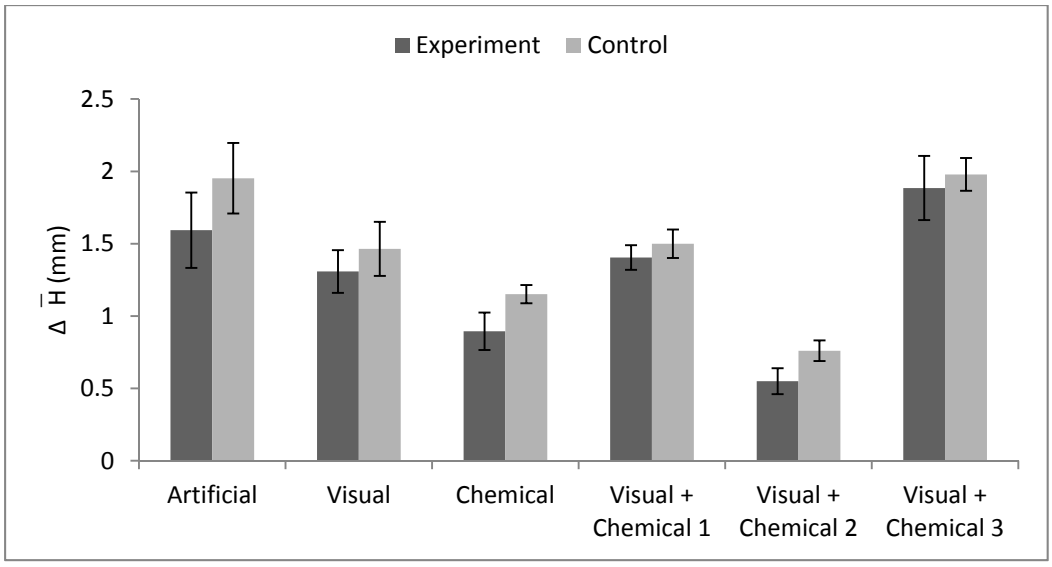

Figure 7 – Mean change in height (mm) for all tanks of each treatment (experiment, control). The bars represent the actual change and the error bars are representative of standard error.

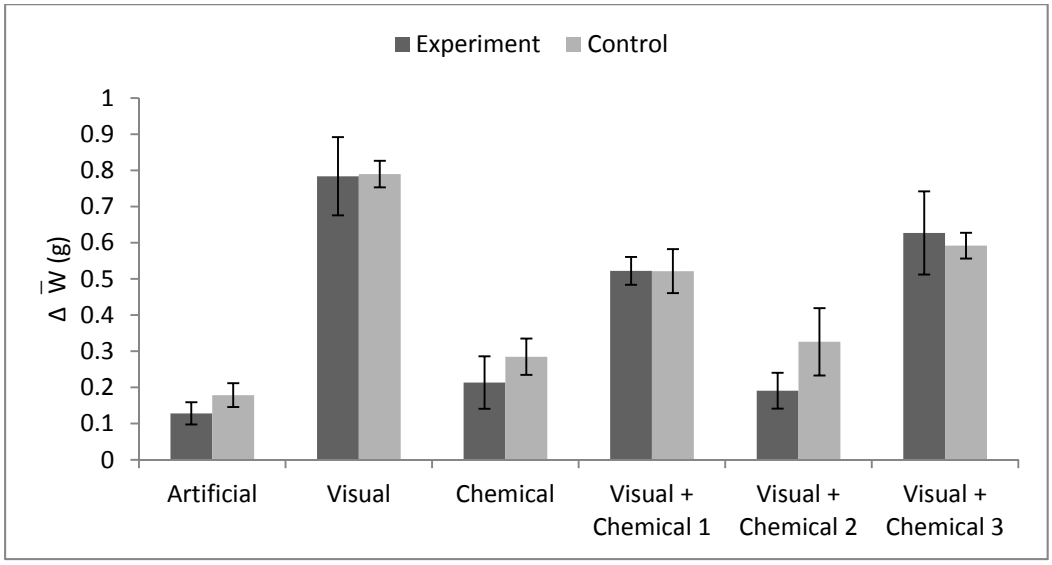

Figure 8 – Mean change in weight (g) for all tanks of each treatment (experiment, control). The bars represent the actual change and the error bars are representative of standard error.

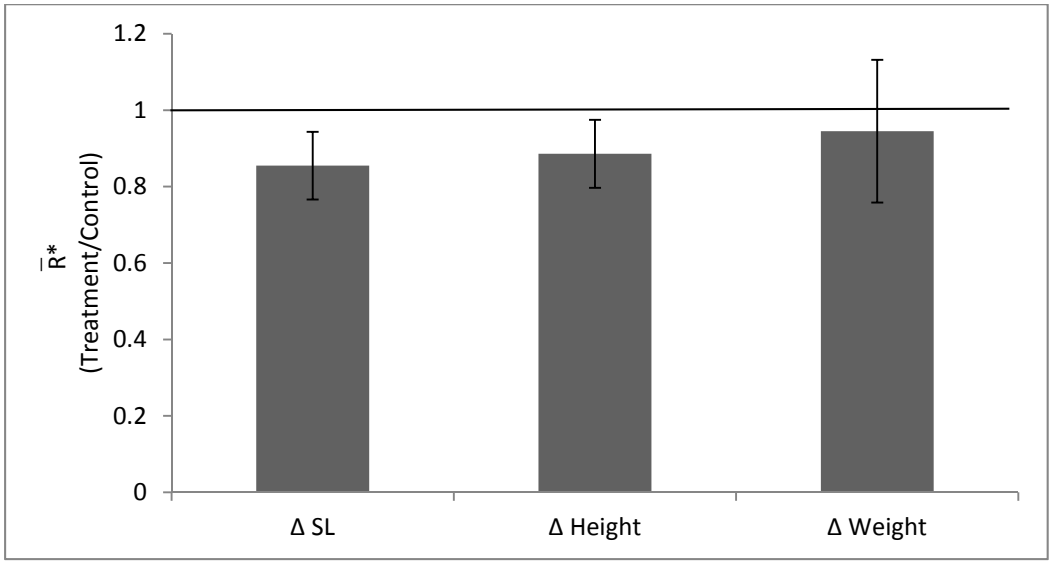

Figure 9 – Weighted Mean Response Ratio values ($\bar{R}^*$) for each growth parameter. Error bars represent 95% confidence interval limits based on a Gaussian distribution A ($\bar{R}^*$) and its corresponding CI < 1 signifies the treatment response to be significantly less than the control response.

Appendix B: Tables

Table 1- Experiment details

Experiment	Treatment	Species	#/tank
1	PED (Visual)	diploproa	10
2	Visual	serriceps	10
3	Both	serriceps	6
4	Chem	diploproa	10
5	Both	diploproa	7
6	Both	rubrivinctus	4

Table 2 - Initial means and standard errors of tank means for all parameters and experiments

Experiment	$\bar{SL}_{0(exp)}$	$\bar{SL}_{0(cont)}$	$\bar{H}_{0(exp)}$	$\bar{H}_{0(cont)}$	$\bar{W}_{0(exp)}$	$\bar{W}_{0(cont)}$
1	20.31 (0.13)	19.71 (0.36)	7.66 (0.09)	7.82 (0.07)	0.22 (0.01)	0.38 (0.01)
2	41.08 (0.61)	41.99 (0.94)	13.59 (0.31)	13.91 (0.34)	1.59 (0.15)	1.76 (0.10)
3	41.95 (0.23)	41.11 (0.31)	14.24 (0.14)	13.89 (0.14)	1.94 (0.10)	1.74 (0.05)
4	43.07 (0.36)	42.26 (0.31)	13.62 (0.11)	13.47 (0.07)	2.21 (0.09)	2.11 (0.04)
5	39.56 (0.46)	39.44 (0.47)	12.67 (0.12)	12.67 (0.26)	1.61 (0.04)	1.58 (0.08)
6	42.90 (0.39)	42.19 (0.90)	13.79 (0.18)	13.27 (0.33)	1.99 (0.13)	1.93 (0.15)

Appendix C: Stats Appendix A

1. $L_i = \ln(\overline{\mathrm{X}}_{\mathrm{Exp}}) - \ln(\overline{\mathrm{X}}_{\mathrm{Cont}})$

2. $v_i = \frac{\frac{\sum_{i=1}^{n}(x_{i_E} - \bar{x}_E)^2}{n-1}}{(n_E \bar{x}_E^2)} + \frac{\frac{\sum_{i=1}^{n}(x_{i_C} - \bar{x}_C)^2}{n-1}}{(n_C \bar{x}_C^2)}$

3. $w_i = \frac{1}{v_i}$

4. $Q = \sum_{i=1}^{k} w_i\,(L_i)^2 - \frac{\left(\sum_{i=1}^{k}[(w_i)(L_i)]\right)^2}{\sum_{i=1}^{k} w_i}$

5. $\hat{\sigma}_\lambda^2 = \frac{Q-(k-1)}{(\sum_{i=1}^{k} w_i) - \left(\frac{\sum_{i=1}^{k} w_i^2}{\sum_{i=1}^{k} w_i}\right)}$

6. $w_i^* = \frac{1}{v_i + \hat{\sigma}_\lambda^2}$

7. $\bar{L}^* = \frac{\sum_{i=1}^{k}[(w_i^*)(L_i)]}{\sum_{i=1}^{k}[w_i]}$

8. $\overline{\mathrm{V}}^* = \frac{1}{\sum_{i=1}^{k} w_i^*}$

9. $SE_{\bar{L}^*} = \sqrt{\overline{\mathrm{V}}^*}$

10. $Z = \frac{|\bar{L}^*|}{\sqrt{\overline{\mathrm{V}}^*}}$

11. $\bar{R}^* = exp(\bar{L}^*)$

12. $CI^* = \bar{R}^* \pm (SE_{\bar{L}^*} \times 1.96)$

Appendix D: Stats Appendix B

For each parameter examined, the first step was to calculate the log response ratios (L_i), within study error variances (v_i), and weighted within study error variances (w_i). For a given experiment and parameter, $\bar{X}_E$ and $\bar{X}_C$ are the mean for all experimental and control tanks. Let *n* denote the sample size.

$$\textbf{1.}\quad L_i = ln\left(\bar{X}_{Exp}\right) - ln(\bar{X}_{Cont})$$

$$\textbf{2.}\quad v_i = \frac{\frac{\sum_{i=1}^{n_E}\left(X_{i_E}-\bar{X}_E\right)^2}{n_E-1}}{\left(n_E\bar{X}_E^2\right)} + \frac{\frac{\sum_{i=1}^{n_C}\left(X_{i_C}-\bar{X}_C\right)^2}{n_C-1}}{\left(n_C\bar{X}_C^2\right)}$$

$$\textbf{3.}\quad w_i = \frac{1}{v_i}$$

A Q-statistic was computed for each parameter analyzed. The Q-statistic is needed to calculate the between experiment variation. Let *k* denote the number of studies.

$$\textbf{4.}\quad Q = \sum_{i=1}^{k} w_i\,(L_i)^2 - \frac{\left(\sum_{i=1}^{k}[(w_i)(L_i)]\right)^2}{\sum_{i=1}^{k} w_i}$$

The next step when using a random-effects model was to calculate the between experiment variance ($\hat{\sigma}_\lambda^2$) and the random-effects weight (w_i^*).

$$\textbf{5.}\quad \hat{\sigma}_\lambda^2 = \frac{Q-(k-1)}{\left(\sum_{i=1}^{k} w_i\right)-\left(\frac{\sum_{i=1}^{k} w_i^2}{\sum_{i=1}^{k} w_i}\right)}$$

$$\textbf{6.}\quad w_i^* = \frac{1}{v_i+\hat{\sigma}_\lambda^2}$$

Next, the summed weighted error variance ($\overline{V}^*$), weighted mean of the log response ratio ($\bar{L}^*$), and standard error ($SE_{\bar{L}^*}$) were calculated.

$$\textbf{7.}\quad \bar{L}^* = \frac{\sum_{i=1}^{k}\left[\left(w_i^*\right)(L_i)\right]}{\sum_{i=1}^{k}[w_i]}$$

$$\textbf{8.}\quad \overline{V}^* = \frac{1}{\sum_{i=1}^{k} w_i^*}$$

$$\textbf{9.}\quad SE_{\bar{L}^*} = \sqrt{\bar{V}^*}$$

In order to test the null hypothesis that the mean true effect size is zero, a Z-score was produced.

$$\textbf{10.}\ Z = \frac{|\bar{L}^*|}{\sqrt{\bar{V}^*}}$$

For intuitive purposes, the weighted mean of the log response ratio was back transformed.

$$\textbf{11.}\ \bar{R}^* = exp(\bar{L}^*)$$

The weighted mean of the response ratio can now be compared to a value of 1 to see if the experimental values ($\dot{R} < 1$) or control values ($\dot{R} > 1$) were relatively higher.

Finally, the 95% confidence interval values were calculated.

$$\textbf{12.}\ CI^* = \bar{R}^* \pm (SE_{\bar{L}^*} \times 1.96)$$

If these confidence intervals do not include the value of one, then the difference between control and experiment values can be considered statistically significant at a significance level of P = 0.05.