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Bay Scallop, Argopecten irradians, Restoration in the Virginia Coastal Bays: The Role of Predation on Spring Vs Fall Cohort Survival

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Bay Scallop, *Argopecten irradians*, Restoration in the Virginia Coastal Bays: The Role of Predation on Spring vs. Fall Cohort Survival

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Master of Science

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

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ABSTRACT

While the importance of predation in controlling many natural bivalve populations is well established, it is often overlooked in the restoration strategies for depleted populations. Adult bay scallops (*Argopecten irradians concentricus*) along the U.S. mid-Atlantic coast spawn multiple times per year, typically once in the early summer and again in the early fall. Larvae generally settle on seagrass leaves to avoid benthic predators, but shift to the sediment surface around 20 mm in size when they become less vulnerable to predation. The objectives of this study were to 1.) Determine proportional survival of two distinct size classes of *A. irradians* in different seasons related to the two naturally occurring cohorts found in this region, 2.) Determine the identity of key predators of *A. irradians* in the Virginia coastal bays. The goal is to incorporate this information into a restoration strategy for a Virginia seaside lagoon system where *A. irradians* have been absent since the disappearance of eelgrass in the 1930s.

Tethering experiments, conducted in re-established eelgrass during summer and fall of 2013 and 2014, of small (~10 mm SH) and large (~32 mm SH) juvenile *A. irradians* showed significant differences between the two years, likely due to the differences in the predator community. They also showed much higher predation rates in July than in August or October for both 2013 and 2014. Blue crabs are significant predators of *A. irradians* and were present only in 2014, affecting survival, especially of the large size class. Fish predators, such as pinfish, pigfish, striped burrfish, and sheepshead appear to have controlled the survival of small juvenile *A. irradians*.

Our results generally show greater survival in the fall, thus perhaps focusing on deploying small *A. irradians* in the fall would increase survival. However, the large differences in survival between 2013 and 2014 point to the importance of employing an adaptive restoration approach which incorporates real-time abundances of predators into restoration activities, allowing for the release of *A. irradians* at smaller sizes dependent on the composition of the predator assemblage.

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INTRODUCTION

Predator-prey interactions in coastal systems are increasingly being altered by both human and natural perturbations. Habitat loss, disease, and removal of top predators due to overfishing are some of the primary anthropogenic mechanisms (Lotze et al. 2006; Myers et al. 2007) that can alter marine food webs, while pulsed, natural events such as hurricanes can rapidly alter the landscape (Paerl et al. 2001). Often, marine ecological restoration focuses on restoring structured habitats, such as coral reefs, mangroves, seagrass beds, and oyster reefs, with the assumption that fauna previously documented to occur in these natural habitats will then return naturally; a hypothesis which has not been well tested (Palmer et al. 1997). While restoring these habitats is extremely important because of the numerous ecosystem services they provide (Costanza et al 1997), certain species may be recruitment limited and not return on their own, thus requiring restoration of these important animals (Hilderbrand et al. 2005; Elliott et al. 2007).

A well-documented change in marine habitats was the pandemic decline of eelgrass, *Zostera marina*, in the 1930s altering this habitat on the eastern and western Atlantic coasts (Orth et al. 2006). While *Z. marina* began to return in many areas, some locations never recovered, such as the seaside lagoons of lower Delmarva Peninsula in the mid-Atlantic region of the United States. Associated with this loss of *Z. marina* habitat was the complete elimination of the bay scallop, *Argopecten irradians* (Orth & McGlathery 2012). For almost seven decades, *Z. marina* and *A. irradians* were absent from the Virginia coastal bays (Orth et al. 2006; MacKenzie 2008; Fonseca & Uhrin 2009; Orth et al. 2012).

Beginning in 1997, a large-scale, seed-based effort to reintroduce *Z. marina* has been successful and has resulted in 1900 ha of bottom now supporting *Z. marina* (Orth et al. 2012). Benthic sampling and direct observations of this grass bed during its expansion revealed no *A. irradians* recruiting to this restored habitat suggesting that developing a viable *A. irradians* population will require a similar restoration effort by artificially introducing *A. irradians* from other source populations. In 2009, an experimental program to reintroduce *A. irradians* was initiated using individuals obtained from a southern population in North Carolina. These individuals served as spawning stock for the production of hundreds of thousands of juvenile scallops for introduction into the restored *Z. marina* bed (M. Luckenbach & R. Orth, Virginia Institute of Marine Science, unpublished data). This restoration effort has resulted in early indications of success (i.e. subsequent reproduction and new recruitment to the grass bed). However, as observed for other *A. irradians* restoration efforts conducted elsewhere (Florida's Atlantic and Gulf of Mexico coasts: Arnold 2001; 2008; Arnold et al. 2005; Long Island, New York: Tettlebach & Smith 2009) determining the most effective approach for restoring *A. irradians* involves an understanding of the life history characteristics in a particular region and elucidation of the suite of potential predators of different size classes of *A. irradians* in order to release *A. irradians* at a size that minimizes losses to predation.

Predation is an important ecological process for structuring plant and animal populations (Addicott 1974; Ferretti et al. 2010) both directly through mortality and indirectly by modifying interactions within prey populations, such as reducing competition or preventing one species from monopolizing a particular resource (Paine 1966; Addicott 1974; Micheli 1997, van Gils et al. 2012). Many plants and animals have evolved techniques to avoid or minimize predation with a variety of physical and chemical defenses, e.g. evasion tactics, camouflage, and chemical defenses (Rubinstein 1992; Wong et al. 2005; Orpwood et al. 2008). In addition, habitat type, such as seagrass beds or marshes, have been shown to alter predator-prey interactions by modifying predator foraging and increasing survival rates of prey populations (Prescott 1990; Pohle et al. 1991; Irlandi et al. 1995; Micheli 1996; Seitz et al. 2001). *A. irradians* has developed an interesting strategy to survive in a predator rich environment. Initially *A. irradians* recruit and attach to seagrass blades to minimize predation, prevent burial by sediments, and have greater access to food (Ambrose & Irlandi 1992; Garcia-Esquivel & Bricelj 1993; Bishop & Wear 2005; Carroll et al. 2010). At 15-25 mm in shell height, *A. irradians* goes through an ontogenetic shift to the sediment surface (Garcia-Esquivel & Bricelj 1993), where as adults, *A. irradians* have the capability to swim by clapping their valves together with a quick burst of speed (Bishop & Wear 2005). Determining how the predator assemblages developing in this restored system will influence *A. irradians* survival at these different life history stages will be critical for developing effective restoration strategies.

This study focuses on predation of *A. irradians* relative to peaks in spawning activity in the Virginia coastal bays. In this region of the Atlantic coast *A. irradians* spawns both in the late spring (May-June) and early fall (Sept-Oct) resulting in the presence of juveniles during periods when predator abundances can also vary by season, and thus have differential influence on prey survival throughout the year (Bishop et al. 2005). Elucidation of patterns of predator activity in relation to spawning activity will be a requisite piece of information in developing the most appropriate restoration strategy. The results of this study will facilitate the restoration of *A. irradians* project in the Virginia coastal bays with an understanding of survival under different potential predation scenarios. The objectives of this study were to: 1.) Determine proportional survival of two distinct size classes of *A. irradians* in different seasons related to the two naturally occurring cohorts found in this region, 2.) Determine the identity of key predators of *A. irradians* in the restored seagrass beds in the Virginia coastal bays and their inter- and inter-annual patterns of abundances.

MATERIALS AND METHODS

Study Site

Predation experiments were conducted in a dense, continuous *Zostera marina* bed in South Bay (37° 16' 3" N, 75° 48' 43" W), one of the Virginia Eastern Shore's coastal bays, in 2013 and 2014. South Bay is part of the Virginia Coast Reserve Long-Term Ecological Research Site and the site of a successful *Z. marina* restoration program. South Bay is the current location of an *Argopecten irradians* restoration project initiated in 2009.

Bay Scallop Predation Experiments

Two size classes of *A. irradians* were used in manipulative experiments during each of three specific time periods in both 2013 and 2014: early and late summer, and fall (Table 1). The two size classes represented the distinct ontogenetic pattern exhibited by *A. irradians*, where small individuals less than 15 mm attach to seagrass blades, and individuals larger than 20 mm move to the sediment where they remain and grow. *A. irradians* of each required size class were obtained from individuals reared at the Castagna Shellfish Research Hatchery at the VIMS Eastern Shore Lab. Specific sizes required for the different time periods were dependent on the spawning times of individuals at the hatchery and subsequent environmental conditions for growth of that cohort, e.g. ambient water temperatures. As these aspects were difficult to control, they accounted for some of the differences noted in the sizes of *A. irradians* used in each experiment (Table 1).

Field predation experiments utilized tethering, which has been successfully used in *A. irradians*, as well as other bivalve species and crustaceans, both for juveniles and adults incorporating artificial seagrass units, as well as monofilament line (Irlandi et al. 1995; Bologna & Heck 1999; Bishop et al. 2005; Wong et al. 2005; Carroll et al. 2010; Hernandez Cordero & Seitz 2014). Though caution must be taken to distinguish between treatment effects and interactions between tethering artifacts and the treatments (Peterson & Black 1994), tethering is a successful method in determining predation potential (Barbeau & Scheibling 1994; Aronson & Heck 1995) and can determine relative predation rates for different sizes of *A. irradians* during different times of year.

Small *A. irradians* (6-15 mm) were tethered onto artificial seagrass units (ASUs). ASUs were made from green polypropylene ribbon (generic curling ribbon with a width of 4.75 mm), tied onto a metal staple approximately 10 cm in length made from a wire coat hanger, forming two grass blades 40 cm in length. One *A. irradians* was tethered to each unit using Krazy Glue gel to attach the shell to the grass blade 10 cm off the sediment surface with the umbo region facing up. The ribbon was sanded at the 10 cm mark before gluing to remove the sheen and allow the glue to better adhere. Each *A. irradians* was dried off with a towel and shell height was measured using dial calipers before gluing, keeping the *A. irradians* out of the water for no more than 1-2 minutes. For each trial, 50 small *A. irradians* were glued to tethers and placed in the field. In addition, 10 small controls, dead *A. irradians* shells glued in the same method to ASUs, were used in each trial to determine that missing *A. irradians* were due to predation and not coming unglued from their tethers.

Large *A. irradians* (21-48 mm) were glued to a monofilament line allowing them to remain on the bottom but not swim away. Tethers were made using the same metal staples from wire coat hangers with 20 cm of 15 lb test fishing line tied to the top. Each *A. irradians* was dried with a towel to remove epiphytic growth and shell height measured using dial calipers before gluing the end of the fishing line to the left valve using Krazy Glue gel, keeping the *A. irradians* out of the water for no more than 5 minutes. For each trial, 50 large *A. irradians* and 10 large controls, dead *A. irradians* shells, were glued to tethers.

Once *A. irradians* were attached to their tethers, they were kept in flow-through seawater tables until deployment, usually overnight. Prior to transport to the field site *A. irradians* were carefully examined to insure they were still alive and firmly attached to their tethers. They were then packed in a large cooler in layers separated by burlap soaked in seawater for transport to the field site, approximately 1.5-2.5 hours.

In South Bay, five transect lines were established approximately three meters apart at the study location. These lines were made of 15 lb test fishing line tied to metal washers spaced 50 cm apart, with 24 washers per line. At the end of the lines, loops of bungee were tied that slipped around tall PVC stakes anchoring the line to the bottom. The metal staples on the tethers were pushed through the washers along the line, so that the tethers were easily recoverable by following along the line. Each transect line had 10 small and 10 large *A. irradians*, alternating in size along each line, with 2 controls of each size randomly assigned a position on each line.

A single predation trial was 24 hours. After 24 hours, *A. irradians* along each transect line were examined for presence, absence, or if damaged, type of shell damage (crushed, whole shell, etc.). All *A. irradians* along each line were removed regardless of condition and replaced with a new set of tethered *A. irradians*. These 24 hour trials were repeated 4 times during a weeklong period in July, August, and October 2013 and 2014 (except August 2013, when only 3 trials were completed).

In the 2014 trials, another control was added to the experiment. Ten *A. irradians* of each size were glued to tethers and transported in the cooler, but not placed in the field. Instead they were brought back to the lab to assess survival during transportation.

Predator Identity Determination

Several field techniques were used to determine potential predators of *A. irradians* during these experiments. First, six two-minute otter trawl samples were taken in South Bay, near the study site, during May, July, August, September, and October of 2013 and 2014 to determine the diversity and abundance of mobile fish species and large (>20 mm) mobile predators such as *Callinectes sapidus* (blue crabs). Second, epibenthic samples were collected using a suction sampler and 0.8 m^2 enclosed ring (Edgar et al. 2001) for smaller predators (e.g., mud crabs, shrimp, and small blue crabs) in 2013 and 2014. In 2013, 18 samples were collected from the entire bed surrounding the experimental area in April, July, Sept. and Nov, while in 2014, 8 samples were collected from the adjacent area in July and October. Third, 4 GoPro cameras (Hero3+ black editions) were placed in the grassbed during daytime hours approximately 20-30 cm from several tethered *A. irradians* and allowed to film for the duration of the battery life, approximately 2 hours.

Based on data from the otter trawls and benthic samples as well as information from published accounts, laboratory experiments were conducted in 2014 with several species of fish and crabs that were the most likely candidates to prey on *A. irradians*. *Lagodon rhomboides* (pinfish), *Orthopristis chrysoptera* (pigfish), *Chilomycterus schoepfi* (striped burrfish), *Callinectes sapidus* (blue crabs), and *Panopeidae* (mud crabs) were collected from South Bay and acclimated in the laboratory in either 5-gallon buckets for 2 days prior to feeding trials (July 2014) or in 20-gallon tanks for 2 weeks prior to feeding trials (August and October 2014). Prior to these trials, test animals were starved for 48 hours. Because of gape limitation issues, all fish and mud crabs were offered only small *A. irradians* while *C. sapidus* were offered both large and small *A. irradians*. All predators were separated by species, but there was often more than one animal per tank. In each trial, several tethered and un-tethered *A. irradians* were placed with the predators and observed for 48 hours. After 48 hours, all animals were released back into the field.

Statistical Analyses

Continuous size data of *A. irradians* were placed into bins as size class where *A. irradians* < 15 mm were small and *A. irradians* > 20 mm were large, corresponding to the different life history strategies. Since presence-absence data are in binary format, the data were fit to a generalized linear mixed-effects model with a binomial error distribution and a logit link function to determine the magnitude of the size, month, and year effect on the survival of *A. irradians*. Different models were constructed treating size as either continuous or binned into size classes, and then compared using Akaike Information Criteria (AIC). The best model used size class and month as fixed effects and date nested in month as a varying intercept random effect. Analysis of deviance was performed on the generalized linear mixed effects model to assess the significance of my treatments. Generalized linear models fit to a binomial distribution were conducted on survival by size using continuous size data for each size class individually. Odds ratios were found to determine if predators had a preference for size within each size class.

Generalized linear models fit to a poisson distribution were conducted on fish abundance by year from the otter trawls for total predator abundance as well as abundance for specific species *L. rhomboides*, *O. chrysoptera*, *C. schoepfi* and *C. sapidus* and *Panopeidae* from the suction samples. Analysis of deviance were performed on the generalized linear models to assess significance between the years.

All analyses were run using R v3.0.2 (R Core Team 2013). Models were performed using the package 'lmerTest' (v2.0) (Kuznetsova et al. 2013), and figures were created with the package 'ggplot2' (v0.9) (Wickham 2009).

RESULTS

Argopecten irradians survival was significantly different between 2013 and 2014 ($F_{1,2293} = 66.23$, $p<0.001$). In July 2013, the small size class had a much higher mortality (68%) than the large one (12%) (Figure 1), but in July 2014, the large size class had a much higher mortality (80%) than the small one (39%). The difference in mortality between the size classes was not as drastic for August 2013, where the large size class (4%) had a lower mortality than the small (22%), and October 2013 where the small size class (8%) had a slightly lower mortality than the large (15%). Mortality in August 2014 was very similar between large (33%) and small (29%) sizes, but there was a slightly higher mortality in the small size class (33%) compared to the large (12%) in October 2014 (Figure 1). Tethered control *A. irradians* (dead scallops glued on tethers) had very high levels of recovery, averaging 96% for the small size and 98% for the large size across all months, indicating that tethering was an effective method of determining relative survival. Thus, *A. irradians* missing from tethers were presumed to have been eaten by predators; in some cases tethers had shell remnants on them, indicative of predation. Across all months, there was an average of 30% of missing small *A. irradians* with shell remnants present and 39% of large *A. irradians* with shell remnants present (Figure 1).

Generalized linear mixed models were run using continuous size data and binned into size class, but based on AIC values, it was determined that size class (AIC = 2261.6) was a better fit than continuous size data (AIC = 2269.9). Analysis of deviance performed on the best model showed a strong interaction between size class and month ($\chi^2 = 218.214$, $p < 0.001$). However, it also showed that *A. irradians* survival was affected by both size class ($\chi^2 = 5.358$, $p = 0.021$) and month ($\chi^2 = 80.664$, $p < 0.001$). Specific estimates can be seen in Table 2. A generalized linear model conducted on the small size class, showed that as size of the tethered *A. irradians* increased by one millimeter, the odds of their survival decreased by 0.88 times. For the large size class, as the size of the tethered *A. irradians* increased by one millimeter, the odds of their survival increased 1.13 times.

Potential predators collected in trawls varied in species composition between 2013 and 2014 (Figure 2, Appendix I). There was a significant difference in total fish abundance per year ($F_{1,677} = 6.208$, $p = 0.013$) and in abundance per year for individual species *Lagodon rhomboides* ($F_{1,58} = 5.882$, $p = 0.018$), *Orthopristis chrysoptera* ($F_{1,58} = 12.54$, $p < 0.001$), and *Chilomycterus schoepfi* ($F_{1,58} = 8.826$, $p = 0.004$). *Callinectes sapidus* were not present in 2013, but were significantly more abundant in trawls in 2014 ($F_{1,58} = 8.015$, $p = 0.006$) (Figure 2). In suction samples, there were revealed significantly more *Panopeidae* in 2014 than 2013 ($F_{1,50} = 29.45$, $p < 0.001$) (Figure 3). Micropredators, such as shrimp, amphipods, and isopods, were also observed in suction sampling (Table 3). Observational data of predators eating *A. irradians* in tanks (Table 4) revealed only two species that consumed bay scallops: *C. sapidus* and *C. schoepfi*. *A. irradians* were not consumed by *L. rhomboides*, *O. chrysoptera*, or *Panopeidae*. GoPro cameras deployed in the field revealed only *C. sapidus* and possibly *Archosargus probatocephalus* (sheepshead) eating *A. irradians* from tethers, and personal observation included *Busycon* spp. (whelks) eating *A. irradians* from tethers.

DISCUSSION

Results reveal that the size of juvenile *Argopecten irradians* and the time of year that they are deployed affect their survival and will be an important consideration in their restoration success to the Virginia seaside lagoons. Overall, the lowest survival of *A. irradians* was in July compared to both August and October in 2013 and 2014. However, survival patterns by size class were different between the two years (Figure 1), presumably driven by inter-annual and seasonal differences in the predator assemblage (Figure 2).

There are several tethering artifacts that must be addressed with this study. First, the tethers behave differently in different seasons based on the density in the grass in the beds. The biomass of the grass bed in July is much higher than in October, a natural progression of *Z. marina*. Thus with a lower biomass of grass in the fall, it would be easier for predators to access *A. irradians*, however there was much lower predation in the fall due to the smaller numbers of predators. In the summer, the artificial seagrass units the *A. irradians* are glued to fold over in the currents along with the natural grass. This could potentially bring the small *A. irradians* closer to the bottom than 10 cm, making them more accessible to predators, but it is unlikely this contributed to higher predation as the grass biomass was higher, making it more difficult for predators to get to the small *A. irradians*. Secondly, the tethers would affect the two sizes of *A. irradians* differently. Small *A. irradians* naturally tether themselves to seagrass blades (Garcia-Esquivel & Bricelj 1993), so being glued to artificial seagrass units is not changing their predator avoidance mechanism. However, the predator avoidance mechanism of the large *A. irradians* is to swim away from predators (Garcia-Esquivel & Bricelj 1993), which is greatly altered by attaching them to tethers. It is likely that the predation on the large *A. irradians* was artificially increased by tethering more than predation on the small *A. irradians*.

Seagrass beds support a rich array of vertebrate and invertebrate fauna, many of which serve as both prey and predator (Orth et al. 1984). Our assessment of the faunal community from trawling and suction gear during these predation experiments noted a variety of benthic and epibenthic species, a number of which are potential predators of *A. irradians*. Most notable and generally considered both prey and predator in marine systems is *Callinectes sapidus* (blue crab),which prey on *A. irradians*, feeding throughout the summer and fall (Carroll et al. 2014; Hernandez Codero & Seitz 2014). Adult *C. sapidus* are capable of crushing the shells of *A. irradians* up to 40 mm in size (Ambrose & Irlandi 1992; Bishop et al. 2005; personal observation) and are presumed to have had an impact on the mortality of the large size class of *A. irradians* in this study. When *C. sapidus* abundance was low in 2013 the large size class of *A. irradians* had low mortality, but when *C. sapidus* abundance was greater in summer 2014 the mortality of the larger *A. irradians* was very high (Figure 1, Figure 2). *C. sapidus* is also capable of consuming the small size class of *A. irradians* used in this experiment (Hernandez Codero & Seitz 2014), which had a high mortality in July 2013, when *C. sapidus* were not abundant, suggesting that there were likely other predators during 2013 that had an impact on the smaller *A. irradians*. Interannual variation of the *C. sapidus* population is likely affected by recruitment differences, food availability, or physiochemical conditions (Lipcius & Van Engel 1990; Ralph et al. 2013). Micheli (1997) found that in North Carolina, *C. sapidus* abundance was 2.4 times greater in July than in October, meaning that seasonal abundances of *C. sapidus* would also impact the community.

We collected *C. sapidus* data from both otter trawls and suction sampling. Suction sampling is more efficient in sampling the smaller-sized crabs than otter trawls (Orth & Van Montfrans 1987). We collected a large number of *C. sapidus* in trawl samples in May and July of 2014, and many small *C. sapidus* in the suction sampling during October, when new recruits are abundant, contributing to the population for the following year (Figure 2, Figure 3). *C. sapidus* is a voracious predator of *A. irradians*, as well as numerous other bivalves (Micheli 1997; Seitz et al. 2001), and thus understanding its predatory behavior as a key predator will greatly increase the success of a restoration project. *Panopeidae* crabs were present in significantly higher numbers in 2014 than 2013 (Figure 3), and could prey on smaller *A. irradians*, as they are able to climb grass blades to access juvenile *A. irradians* attached to the blades (Pohle et al. 1991; Bishop et al. 2005). However, the high numbers of *Panopeidae* were in 2014, not 2013 when there was high mortality in the small *A. irradians*, meaning perhaps they are not having as strong an impact on *A. irradians* survival as previous thought.

Catch efficiencies of otter trawls, especially through submerged vegetation, are low (Rozas & Minello 1997), meaning our abundances are likely low estimates. Despite low efficiencies, otter trawl nets are useful in making relative comparisons of abundances of fish and crustaceans (Orth & Heck 1980). Suction sampling had relatively high efficiencies of collecting small crab species (Orth & van Montfrans 1987), meaning that the abundances from our suction samples were likely more accurate than the otter trawls. Orth and van Montfrans (1987) found that otter trawls underestimated crab densities by 1 to 2 orders of magnitude compared to suction sampling; thus, our large *C. sapidus* densities are likely underestimates.

Fish assemblages in the grass bed varied seasonally and inter-annually (Figure 2), potentially affecting *A. irradians* survival. Many fish species are already seeing shifts in their species distributions due to climate impacts, but *Lagodon rhomboides* (pinfish) have especially been noted in the Chesapeake Bay in larger numbers after mild winters (Sobocinski et al. 2013). Potential predators of small *A. irradians*, *L. rhomboides* and *Orthopristis chrysoptera* (pigfish) were more abundant during 2013 than 2014, though I lack direct evidence that they consumed juvenile *A. irradians* in our experiments. *A. irradians* shells are occasionally observed in the gut of *L. rhomboides* (Adams 1976; Czapla 1991), and several have reported *L. rhomboides* as a potential predator on bivalve molluscs (Carr and Adams 1973; Livingston 1982; Tanikawa-Oglesby 1996). Bishop and colleagues (2005) and Carr and Adams (1973) suggested that *O. chrysoptera* also occasionally consume bivalve molluscs, such as *A. irradians*. Both *L. rhomboides* and *O. chrysoptera* appear to be opportunistic feeders (Carr & Adams 1973), and although *A. irradians* is a novel prey species, not having existed in this area for over 70 years, there is a good chance they could eat them at small sizes, especially if their distributions are shifting north (Shaffler et al .2013, Sobocinski et al. 2013). The *L. rhomboides* we observed in laboratory tanks nipped at but did not consume the *A. irradians*; this does not preclude the possibility that they fed on them in the field. *O. chrysoptera* also never consumed *A. irradians* in the tank experiments, but they didn't adapt well to the tanks and may have needed a longer acclimation time, but could still eat *A. irradians* in the field. Size likely plays a big role in fish consumption of *A. irradians*, and the small size class of scallops used in tanks may have been too large for these fish to consume. Temperature (Barber & Blake 1983), food availability, and water flow speed (Eckman et al. 1989) affect the growth of juvenile scallops, accounting for the difference in sizes between the two years. Future feeding studies should utilize a wider range of small scallops, perhaps over several weeks in the summer when the scallops have the quickest growth rate, to determine what size *L. rhomoides* and *O. chrysoptera* are able to consume.

Chilomycterus schoepfi (striped burrfish) was the only fish observed to consume *A. irradians* in my tank experiments. This is consistent with Adams (1976) who reported that *A. irradians* made up 95% of the diet of *C. schoepfi*. *C. schoepfi* were not seen in any of our 2013 trawls, but were present in small numbers during 2014 (Figure 2). They tend to be solitary and though they may be eating some *A. irradians*, it is unlikely that their abundance in the seagrass bed was sufficient to account for the observed mortality in *A. irradians*. *C. schoepfi* are similar to *Sphoeroides maculatus* (northern puffer) in that they have a beak which is used to crush molluscs, allowing them to eat some *A. irradians* of larger sizes (Adams 1976). *S. maculatus* are also *A. irradians* predators (Tanikawa-Oglesby 1996), but were only seen in very low numbers in South Bay. Other bay scallop predators noted in the literature include *Opsanus tau* (oyster toadfish) and *Archosargus probatocephalus* (sheepshead) (Ambrose & Irlandi 1992), both of which were observed in South Bay during 2013 and 2014 (Figure 2). Future tank experiments using these species would help to verify their predation on *A. irradians*.

Predation is an important process in shaping communities, and when reintroducing a prey species to a system, predation plays an important role in the success of the project. Predators may differ slightly along latitudinal gradients, but the most common predators all along *A. irradians* range seem to be decapod crustaceans and large gastropods, with some predation by fish and birds (Adams 1976; Prescott 1990; Bologna & Heck 1999; Carroll et al. 2010). Many of these predators are generalist predators, which are often present in high abundances, such as *C. sapidus* in Virginia, and can have strong impacts on reintroduced prey populations (Ward et al. 2008). *A. irradians* have a life history strategy in which shifting the use of its habitat balances maximizing growth from settlement to adult and minimizing predation risk throughout its two year life span. Binning the scallops by size class allowed assessment based on these different life history stages. However, when looking at each size class individually, predators prefer the larger *A. irradians* from the small size class, but the smaller *A. irradians* from the large size class. Juanes (1992) shows that crustacean predators often choose smaller sized molluscs as prey, because they are able to break their shells with exerting less energy and a reduced risk of claw damage, which would explain why predators, especially *C. sapidus* chose the smaller *A. irradians* from the large size class. Micheli (1995) states that crustacean predators of clams target intermediate sizes with the constraints being ease of handling and risk of inflicting claw damage. For the small size class, the larger *A. irradians* may be easier to handle and provide more energy to the predator, causing their preference. Different predators may preferentially choose different sizes, such as fish being limited by gape size, but with the main predators being decapod crustaceans, an intermediate size seems to be preferred.

Current restoration practices to reintroduce *A. irradians* to the Virginia coastal bays involve large-scale spawning, settlement, and maintaining recently settled individuals in a hatchery. Individuals attaining a shell height of >5 mm are subsequently transferred to the field-and maintained in cages to minimize predation through spawning, a technique similar to that used on the Florida Gulf coast by Arnold and colleagues (2005). This process requires routine maintenance of cages to remove fouling organisms and to separate bay scallops into additional cages to minimize competition for space and food as they grow. These latter steps are both time consuming and expensive. Ward and colleagues (2008) suggest that to have the greatest success of a reintroduced prey species, they must be released in high densities and reduce vulnerability to predators. Scaling up field-based effort to deploy sufficiently large numbers of *A. irradians* spawning stock is costly and potentially limiting to a successful restoration effort. The *A.irradians* mortality data and the results from a previous project documenting mortality of recently settled *A. irradians* by micro-predators (Lefcheck et al. 2014), when coupled to an understanding of life history dynamics of the bay scallop, have important implications for the restoration of the bay scallop in Virginia's seaside bays (Orth & McGlathery 2012), determining that an optimum solution would be to release caged *A. irradians* at a size that minimizes the risk to predation.

My data suggests that a key element in this restoration equation is an understanding of major potential predators and their seasonal and annual patterns of abundance (Tanikawa-Oglesby 1996; Carroll et al. 2014). A. irradians have different spawning periods based on latitude, with peaks in spawning mid-summer in New England (Tettelbach et al. 1999) and peaks during the winter in Florida with the ability to spawn year-round (Bologna 1998). They have successful populations in all these systems, likely due to a combination of their life history strategies and predators present in each system. Multiple spawning events allow A. irradians to survive, even if predators differ year to year. This can make restoration difficult and makes an adaptive restoration strategy the best solution. Abundance of one major predator in our system, C. sapidus, had a significant influence on A. irradians in 2014 and the release of smaller A. irradians in early summer from cages would have had negative consequences on their survival. Data from two years of predation experiments, and estimation of potential predators from trawls and suction samples, suggests release of small and large bay scallops later in the summer and fall would lead to optimal survival of both size classes, but add to the costs for maintaining them in cages. Using an adaptive restoration strategy that takes real-time predator abundances into account would allow for the most successful restoration of A. irradians in the Virginia Coastal Bays, especially in the event of climate-induced shifts in abundance of specific A. irradians predators (Schaffler et al. 2013; Sobocinski et al. 2013). Understanding a system and the trophic interactions within the system are important for successful restoration, and an adaptive approach takes into account how systems are constantly changing and shifting, which could alter the best restoration strategy from year to year.

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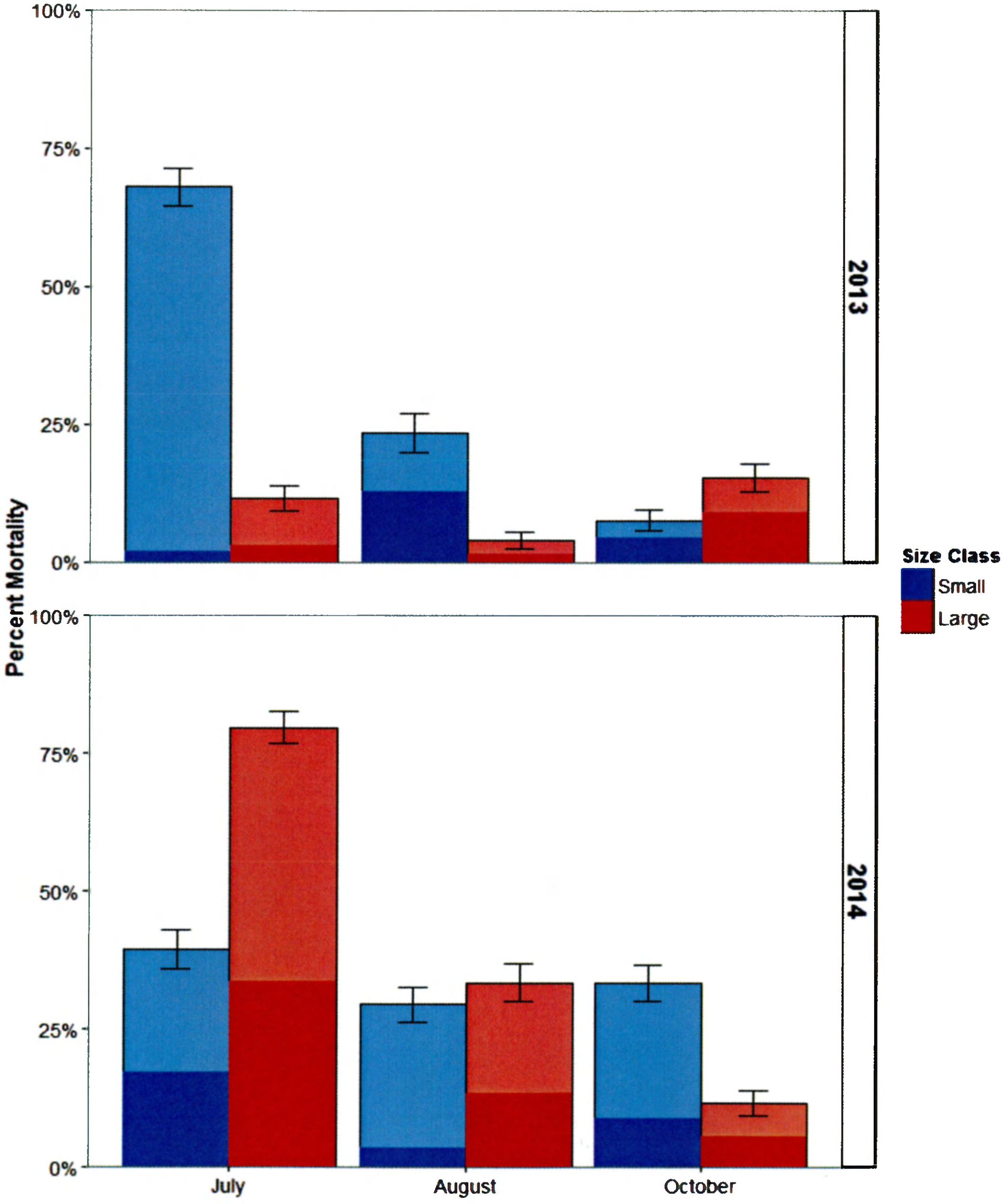

Figure 1. Mean percent mortality of *Argopecten irradians* from small and large size classes in 2013-14. Dark shading represents shell remnants left on tethers. Lighter shading represents scallops completely missing from tethers. Error bars represent standard error of the mean.

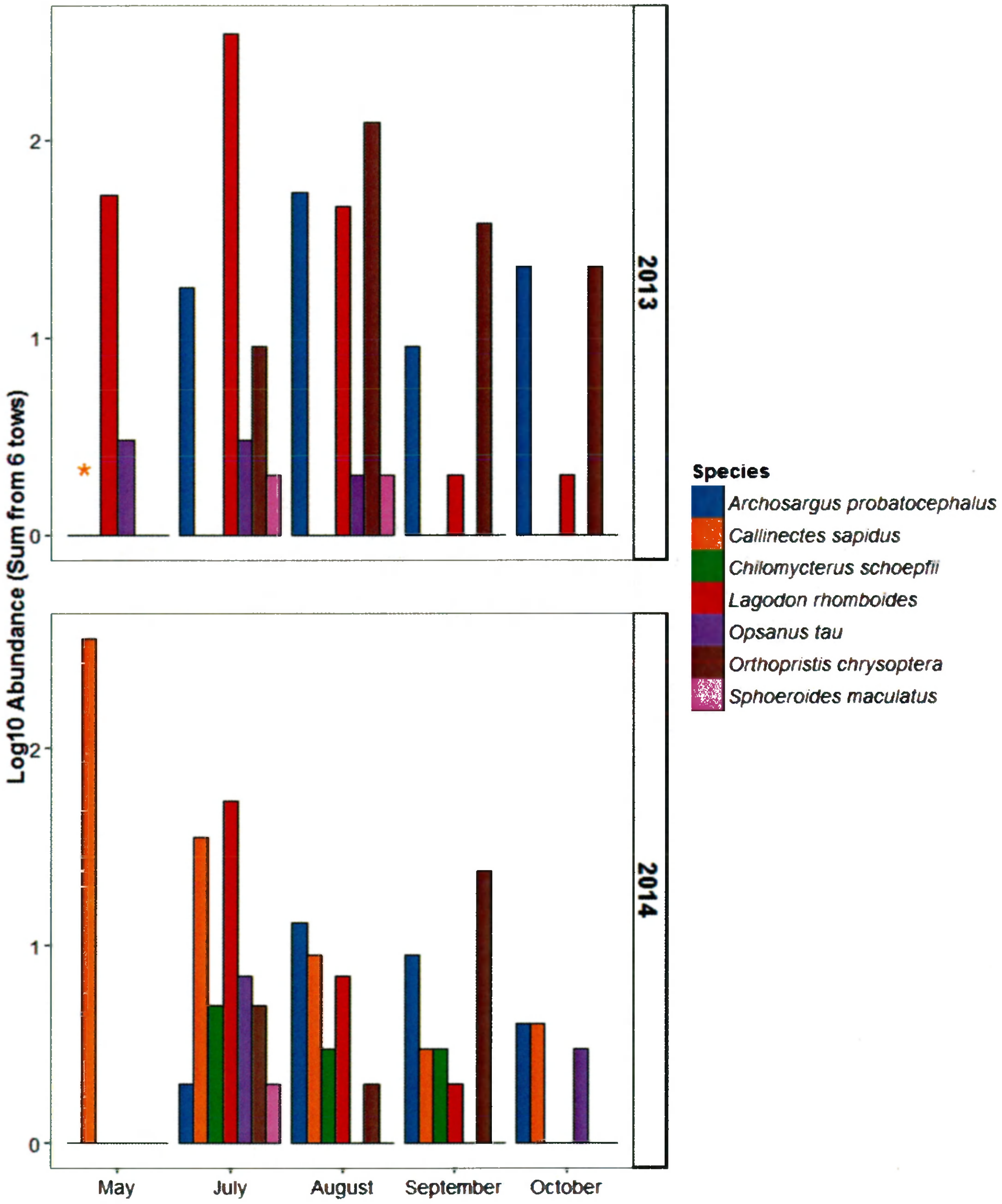

Figure 2. Sum of abundances of potential *Argopecten irradians* predators collected from six otter trawls each month from May 2013 to October 2014 in a restored *Zostera marina* bed in South Bay, VA. * represents few blue crabs found but the exact number is unknown.

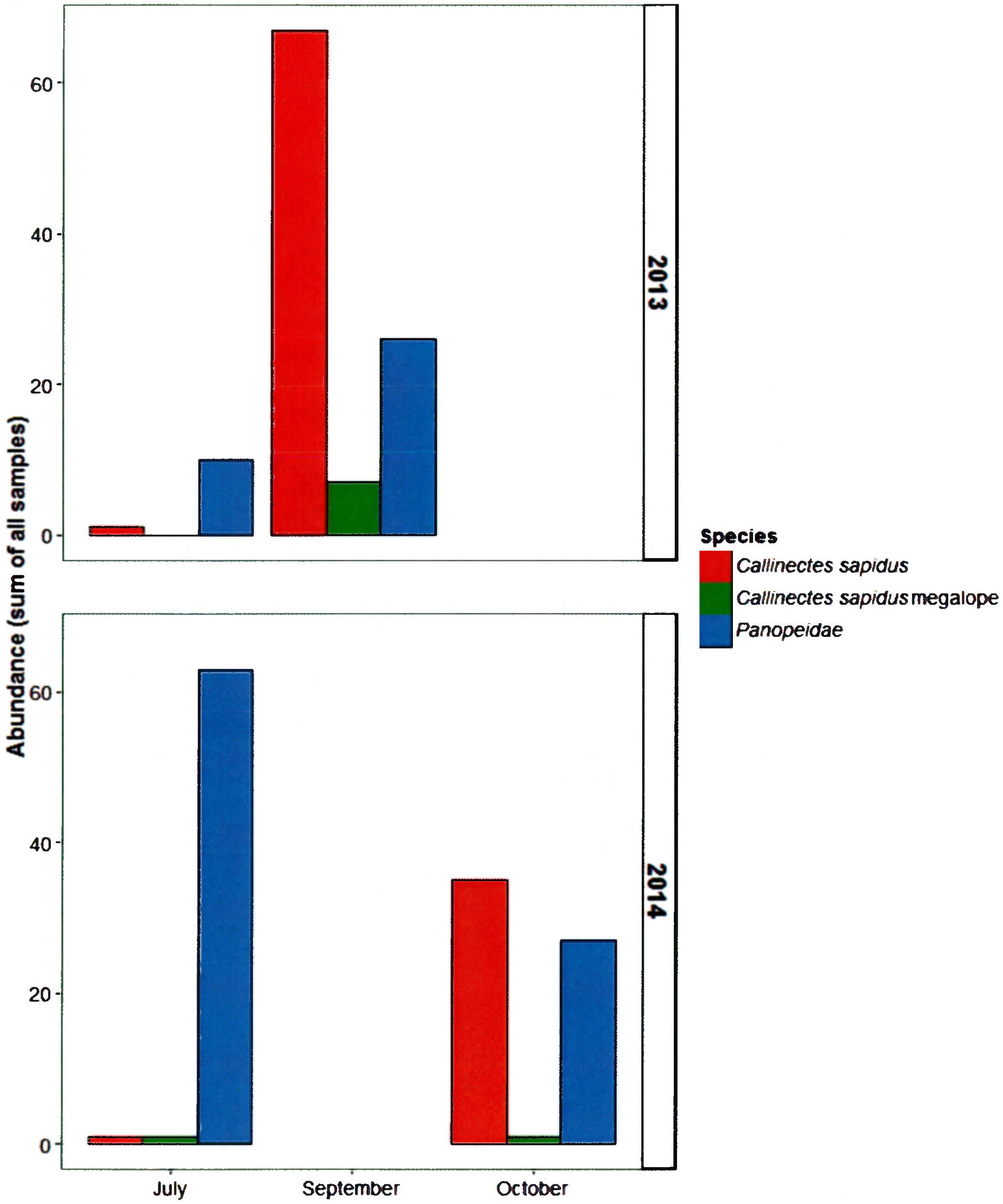

Figure 3. Sum of abundances of crab species collected in suction samples in South Bay, VA. Eighteen two-minute samples were collected in July and September of 2013 and eight two-minute samples were collected in July and October of 2014.

Table 1. Sizes of tethered *Argopecten irradians* for each month

Month	**Small size class mean (mm)**	**Small size standard deviation**	**Large size class mean (mm)**	**Large size standard deviation**
July 2013	10.83	1.84	35.46	3.22
August 2013	12.62	1.84	43.04	3.17
October 2013	8.07	0.85	28.27	3.51
July 2014	8.04	1.02	27.68	2.71
August 2014	9.23	1.06	33.42	3.46
October 2014	12.10	1.40	26.88	1.95
Total	10.15	2.26	32.46	6.14

Table 2. Fixed effects output from generalized linear mixed-effects model. Bold indicates significance.

Variable	Category	Estimate	Standard Error	z-value	p-value
Intercept		0.6436	0.2104	3.058	**0.002**
Size class	Small	0			
	Large	2.0012	0.1921	10.418	**<0.001**
Month	July 2013	0			
	August 2013	1.5568	0.3637	4.280	**<0.001**
	October 2013	1.4860	0.3137	4.737	**<0.001**
	July 2014	-1.1252	0.2890	-3.894	**< 0.001**
	August 2014	0.1458	0.2864	0.509	0.611
	October 2014	0.7696	0.2984	2.579	**0.010**
Size class (Large) x Month (August 2013)		-0.5834	0.3787	-1.540	0.123
Size class (Large) x Month (August 2014)		-2.1331	0.2456	-8.685	**< 0.001**
Size class (Large) x Month (July 2014)		-3.3040	0.2521	-13.108	**< 0.001**
Size class (Large) x Month (October 2013)		-2.5641	0.3044	-8.424	**< 0.001**
Size class (Large) x Month (October 2014)		-1.0203	0.2718	-3.754	**< 0.001**

Table 3. Total micropredator abundance from suction samples. Eight 2-minute suction samples were conducted for each date in 2014. Eighteen 2-minute suction samples were conducted in 2013.

Date	***Ampithoe longimana***	***Gammarus mucronatus***	***Dulichiella appendiculata***	***Erichsonella attenuata***	***Hippolyte pleuracanthus***
7/3/2013	247	250	68	177	181
7/8/2014	22	6	49	347	436
10/7/2014	31	0	152	142	756

Table 4. Consumption of *Argopecten irradians* in laboratory experiments with potential predators.

Predator species	**Date**	**Predator size (cm)**	**Number of predators**	***A. irradians* offered on tethers**	**Number of *A. irradians* eaten**
Panopeidae	July 2014	~ 1	5	2 small, 2 large	0
	October 2014	8-12	8	5 small, 5 large	0
Callinectes sapidus	July 2014	~ 10	2	2 small, 2 large	2 small
	July 2014	25	1	2 small, 2 large	2 small, 2 large
	October 2014	8-12	2	5 small, 5 large	0
Lagodon rhomboides	July 2014	~ 10	4 (divided between 2 tanks)	4 small, 2 large	0
	August 2014	10.5-11	4	5 small	0
Orthopristis chrysoptera	July 2014	~ 20	2 (divided between 2 tanks)	4 small, 2 large	0
	August 2014	18	1	5 small	0
	October 2014	6-12	5 (divided between 2 tanks)	10 small	0
Chilomycterus schoepfi	July 2014	~ 5	1	2 small, 1 large	1 small
	August 2014	7-8.5	3	5 small	5 small
	October 2014	11	1	5 small	5 small

Appendix I

Table 1. Total abundances for each species from otter trawls. Six 2-minute trawls were conducted on each date except 5/17/2013 when only five trawls were conducted.

Species Name	Common Name	Total	5/17/ 2013	7/1/ 2013	8/6/ 2013	9/5/ 2013	10/3/ 2013	5/8/ 2014	7/8/ 2014	8/5/ 2014	9/11/ 2014	10/7/ 2014
Bairdiella chrysoura	American Silver Perch	2096	2	10	152	12	12	0	1402	365	120	21
Syngnathus fuscus	Northern Pipefish	541	15	12	18	6	0	21	146	99	46	16
Lagodon rhomboides	Pinfish	500	52	341	45	1	1	0	53	6	1	0
Menidia menidia	Atlantic Silverside	465	5	11	80	6	8	8	259	4	60	24
Callinectes sapidus	Blue Crab	369	0	0	0	0	0	356	0	8	2	3
Orthopristis chrysoptera	Pigfish	217	0	8	122	37	22	0	4	1	23	0
Archosargus probatocephalus	Sheepshead	124	0	17	53	8	22	0	1	12	8	3
Leiostomus xanthurus	Spot Croaker	49	4	28	0	0	0	0	16	0	1	0
Syngnathus floridae	Dusky Pipefish	42	0	0	27	7	1	0	1	5	1	0
Centropristis striata	Black Sea Bass	30	2	19	4	0	0	0	1	2	2	0
Mycteroperca microlepis	Gag Grouper	28	0	4	11	6	0	1	2	2	2	0
Opsanus tau	Oyster Toadfish	13	2	2	1	0	0	0	6	0	0	2
Chilomycterus schoepfii	Striped Burrfish	8	0	0	0	0	0	0	4	2	2	0
Paralichthys dentatus	Summer Flounder	8	0	4	0	0	0	0	2	2	0	0
Tautoga onitis	Tautog	8	0	2	0	0	0	0	0	1	1	4

Cynoscion nebulosus	Spotted Seatrout	6	0	0	0	0	0	0	3	3	0	0
Conger oceanicus	American Conger Eel	4	0	2	0	2	0	0	0	0	0	0
Sphoeroides maculatus	Northern Puffer	3	0	1	1	0	0	0	1	0	0	0
Sphyraena borealis	Northern Sennet	3	0	0	0	0	0	0	0	3	0	0
Anchoa mitchilli	Bay Anchovy	2	1	0	0	0	0	0	1	0	0	0
Chaetodon ocellatus	Spotfin Butterflyfish	2	0	0	0	0	0	0	0	0	1	1
Dasyatis americana	Southern Stingray	2	2	0	0	0	0	0	0	0	0	0
Diplodus holbrookii	Spottail Pinfish	2	0	0	1	1	0	0	0	0	0	0
Prionotus carolinus	Northern Sea Robin	2	0	0	0	0	0	2	0	0	0	0
Argopecten irradians	Bay Scallop	1	0	0	0	0	0	0	0	0	0	1
Caranx sp	Jack sp.	1	0	0	0	0	0	0	1	0	0	0
Eucinostomus gula	Silver Jennie	1	0	0	0	0	0	0	0	0	1	0
Fistularia tabacaria	Cornetfish	1	0	0	0	0	0	0	0	0	1	0
Menticirrhus saxatilis	Northern Kingfish	1	0	0	0	0	0	0	0	1	0	0
Panopeidae sp.	Mud crab	1	0	0	0	0	0	0	0	1	0	0
Sciaenops ocellatus	Red Drum	1	0	1	0	0	0	0	0	0	0	0
Stephanolepis hispida	Planehead Filefish	1	0	0	1	0	0	0	0	0	0	0
Synodus foetens	Inshore Lizardfish	1	0	0	0	0	0	0	0	0	1	0
Urophycis regia	Spotted Codling	1	0	0	0	0	0	1	0	0	0	0

VITA

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Erika was born in Winchester, Virginia, on July 26, 1990. She graduated from John Handley High School in Winchester in 2008 and went on to earn a B.S. in Biology with minors in Environmental Studies and German from St. Mary's College of Maryland in 2012. Erika entered the Master of Science program at the School of Marine Science, Virginia Institute of Marine Science, College of William and Mary in 2012.