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Ecosystem Services of Restored Oyster Reefs in a Chesapeake Bay Tributary: Abundance and Foraging of Estuarine Fishes

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Ecosystem Services of Restored Oyster Reefs in a Chesapeake Bay Tributary: Abundance and Foraging of Estuarine Fishes

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ABSTRACT

Oyster reef restoration may enhance the production of ecologically or economically important fish species, an ecosystem service, by providing refuge and foraging habitat. Predicting the effects of oyster habitat restoration on fisheries production in Chesapeake Bay requires a better understanding of fish habitat use, trophic dynamics, and the processes leading to production on a habitat-scale. The objective of this thesis was to evaluate the influence of restored subtidal oyster reefs on the abundance and foraging patterns of mobile estuarine fishes. Specifically, I compared the 1) abundance, 2) stomach fullness, 3) diet composition, and 4) daily consumption rate of fishes collected from restored oyster reef habitat and from unstructured (control) habitat in the Lynnhaven River System (LRS), Virginia, a tributary of Chesapeake Bay. I sampled fishes from April – October 2016 to assess seasonal abundance and diet trends using multi-panel gill nets, and conducted 24-hour sampling events in July and September 2016 to assess daily foraging patterns and estimate habitat-specific consumption rates. The most abundant non-filter feeding fishes collected all came from the Sciaenid (drum) family: spot (*Leiostomus xanthurus*), silver perch (*Bairdiella chrysoura)*, and Atlantic croaker (*Micropogonias undulatus*). Overall catch in oyster reef habitat was reduced relative to unstructured bottom, but species-level responses to habitat type varied. Stomach fullness trends varied by species but were associated with habitat type. Benthic prey dominated the diet of all three species, and evidence of habitat-related shifts in diet composition were apparent. Reef-affiliated prey contributed most prominently to silver perch, comprising nearly 30 – 50 % by weight. The daily consumption rate and total daily caloric intake of silver perch foraging in oyster reef habitat were nearly double the estimates from control habitat. The results suggest restored oyster reefs influence habitat use and foraging behavior in species-specific manners, likely a result of differences in functional morphology and prey preference. Restored oyster reefs in the LRS likely act as valuable forage habitat for silver perch, an important trophic link in coastal and estuarine systems. Developing realistic estimates of fisheries production on a habitat-scale requires studying species-specific trophic dynamics. Empirical estimates of the processes contributing to production are necessary to better understand the functional role of restored oyster reefs in shallow estuarine and coastal systems, and the ecosystem services these reefs may provide.

Ecosystem Services of Restored Oyster Reefs in a Chesapeake Bay Tributary: Abundance and Foraging of Mobile Estuarine Fishes

INTRODUCTION

Structurally complex reefs created by the ecosystem engineer *Crassostrea virginica* (eastern oyster) once dominated the Chesapeake Bay (Newell 1988, Hargis & Haven 1999). Beginning in the late 19th century, heavy fishing pressure, poor water quality, and disease drastically reduced both the oyster population and the extent of oyster reefs (Rothschild et al. 1994, Wilberg et al. 2011). Commercial landings of *C. virginica* in the Chesapeake Bay today are less than 1% of late 19th century levels, and the areal footprint of oyster reefs at the tributary-scale has shrunk between 50 and 100 % (zu Ermgassen et al. 2012, NOAA 2017). Recognition of this dramatic decline spurred considerable interest in oyster restoration over the past three decades (Kennedy et al. 2011). Current restoration efforts in Chesapeake Bay center on the creation of large subtidal reefs protected from fishing (no-harvest sanctuaries) that mimic the high-relief structure and complex architecture of historic reefs (U.S. Army Corps 2012). The creation of such reefs is expensive, however, with costs ranging up to $260,000 per hectare (Grabowski et al. 2012). Likewise, the closure of formerly public oyster grounds has provoked controversy amongst the fishing community and general public (Wheeler 2016).

The goals of oyster reef restoration have also expanded beyond increasing oyster abundance. Ecosystem services (benefits provided by nature to humans) such as nutrient cycling, shoreline protection, and fish production are now explicitly included in the objectives of oyster restoration projects, but these services are difficult to quantify. (Baggett et al. 2015, Coen et al. 2007, Barbier et al. 2011). Given the costs and the controversy surrounding oyster restoration, an improved understanding of the links between habitat restoration, ecological function, and ecosystem services is needed (Peterson & Lipcius 2003, Hobbs 2007). The relationship between oyster reefs, fish foraging, and fisheries production is one such linkage in need of further study.

Oyster reefs are hypothesized to support fisheries productivity via the provision of structured habitat, much like salt marshes or seagrass beds, in estuaries otherwise dominated by unstructured soft-sediments (Beck et al. 2001, zu Ermgassen et al. 2016). Structured habitat alters predator-prey interactions and modifies demographic processes, contributing to enhanced survival of new recruits to a system (Grabowski 2004, Caddy 2008). The survival of many coastal and estuarine fish species is positively associated with increased structural complexity and presence of predator refuge (Levin 1991, Tupper & Boutilier 1997, Stunz et al. 2001). The combination of hard substrate and interstitial space provided by oyster reefs also serves to promote the settlement, growth, and survival of benthic invertebrates and resident fishes at high densities (Wells 1961, Bahr & Lanier 1981, Rodney & Paynter 2006, Karp 2016). Improved foraging success stemming from the increased prey availability may enhance the growth of fishes already present within a system, resulting in a gain of nekton biomass (Powers et al. 2003, Nemerson & Able 2004).

Many mobile or transient fishes are known to frequent oyster reefs, yet the degree to which restored oyster reefs promote productivity through enhanced growth or survival is unclear (Arve 1960, Zimmerman 1989, Breitburg 1999). Few studies have directly measured survival or growth in relation to oyster reef habitat, and those that have typically focus on newly settled fishes (Stunz et al. 2002, Shervette & Gelwick 2007). Instead, comparing the relative abundance or density of fishes between habitat types represents a more common method of evaluating the role of restored oyster reefs in estuarine systems (e.g., Plunket & La Peyre 2005, Stunz et al. 2010). The net effects of improved survival or increased growth are assumed to result in a greater number of individuals occurring in 'preferred' or 'higher-value' habitats (Rozas & Minello 1997, Able 1999). In Chesapeake Bay, the Gulf of Mexico, and the Southeast Atlantic, restored oyster reefs are linked to increased catch rates and enhanced abundance of mobile fishes, particularly in comparison to unstructured bottoms (Lenihan et al. 2001, Scyphers et al. 2011, Humphries & La Peyre 2015). Both juvenile and adult demersal fishes as well adult bluefish (*Pomatomus saltatrix*) and striped bass (*Morone saxatilis)* have been found in high abundance on restored reefs (Harding & Mann 2001a, 2003, Plunket & La Peyre 2005).

Habitat use of restored oyster reefs by mobile fishes is both dynamic and context-dependent, depending not only on the presence of oyster reef habitat, but also environmental and site-level variables such as reef location, proximity to other habitats, and degree of fragmentation (Grabowksi et al. 2005, Geraldi et al. 2009, Harwell et al. 2011). These variables lead to considerable variation in the abundance of fishes associated with oyster reefs (Gregalis et al. 2009, Pierson & Eggleston 2014, Nevins et al. 2014). Additionally, previous studies in Chesapeake Bay specifically have focused on a few, relatively small, restored oyster reefs, and it is unclear whether the reported patterns in abundance apply to the large, sanctuary restored reefs constructed over the past decade (O'Beirn et al. 1999, Harding & Mann 2001b, Luckenbach et al. 2005).

Habitat-based comparisons of abundance also do not shed light on the mechanistic role restored reefs may play within a system. Instead, the study of trophic dynamics may be a better approach to understanding fish production on a habitat scale. Trophic linkages represent pathways of energy flow within a system, and trophic dynamics are regarded as primary drivers of fisheries production (Peterson & Lipcius 2003, Wong et al. 2011, Gaichas et al. 2012). If oyster reefs serve to enhance fish growth or productivity, consumption of reef-associated benthic macrofauna and resident fishes ought to represent a strong trophic pathway connecting oyster reefs to higher trophic levels (Peterson et al. 2000). The absence of such link would imply that restored reefs alter survival rather than growth, are relatively limited in their ecological impacts, or affect fish in ways yet to be fully understood. A trophic-oriented approach is particularly relevant in light of ecosystem-based fisheries management (EBFM), which necessitates an improved understanding of trophic linkages and the forage base of key fishery species (Idhe et al. 2015).

The diet and trophic ecology of fishes associated with oyster reefs is less well studied than fish abundance and density. For instance, in Chesapeake Bay, the most recent oyster reef trophic studies were conducted over a decade ago. This is, in part, due to logistical challenges of connecting mobile predators with discrete habitat types. Nektonic predators range widely and use a variety of habitats; generalist predators also dominate the Chesapeake Bay fish assemblage (Murdy et al. 1997, Buchheister & Latour 2015). The typical home range size of many species is not known, complicating efforts to link diet to prey and habitat (Beck et al. 2001, Moulton et al. 2017). Additionally, many prey types are as ubiquitous, if not more so, than their potential predators (Gillett & Schaffner 2009). Despite these difficulties, functional links between oyster reefs and mobile fishes have been established. In Florida, over half of juvenile grey snapper

(*Lutjanus griseus*) diet by weight was comprised of reef-affiliated organisms, including benthic mud crabs and resident fishes (Yeager & Layman 2011). Striped bass and bluefish consumed more teleost prey around a restored oyster reef than an unstructured bottom in the Piankatank River, Virginia, suggesting that intertidal oyster reef habitat use facilitated improved foraging opportunities on energetically rich fish prey (Harding & Mann 2001a, 2003). Combining stomach-content analysis with a detailed understanding of the available prey field in the environment is a particularly useful approach for linking prey from discrete habitats with mobile fishes (Crowder & Cooper 1982, Quan et al. 2010, Abeels et al. 2012).

The magnitude of trophic transfer from oyster reef macrofauna to higher trophic levels is also not well understood at either the individual, community, or population scale. Connecting the diet of fishes using restored reefs as habitat together with estimates of reef-associated consumption rates represents the next step in understanding the relationship between oyster reef habitat and mobile fishes, and would pave the way for process-based model estimates of oyster-reef fish production. Bioenergetics models incorporating these parameters are beginning to be developed (McCoy et al. 2017), yet they still require empirical data collected in the field. Once refined, these models could aid oyster restoration cost-benefit analyses and guide decisions regarding the placement and construction of oyster reefs within the estuarine landscape.

In sum, specific evidence regarding the ecological benefits of no-harvest subtidal sanctuary reefs for estuarine fishes in Chesapeake Bay is needed to justify continued large-scale oyster reef restoration, maintenance, and protection from harvest. Fish use of restored oyster reefs as habitat or foraging grounds has not been examined recently in

Chesapeake Bay, nor have sanctuary reefs closed to harvest been the focus of recent study. Specific linkages between oyster reef macrofauna and mobile fishes remain unclear, and the magnitude of reef-based consumption amongst is unknown. The overall objective of this thesis was to evaluate the influence of restored subtidal sanctuary oyster reefs in a sub-estuary of the Chesapeake Bay on the abundance and foraging patterns of mobile estuarine fishes, particularly those of ecological or economic importance. Specifically, I compared the 1) abundance, 2) stomach fullness, 3) diet composition, and 4) daily consumption rate of mobile estuarine fishes collected from restored oyster reef habitat and from unstructured bottom habitat in the Lynnhaven River System, Virginia. Broadly, I hypothesized that fish abundance in oyster reef habitat would either equal or exceed that of reference habitat. I also anticipated observing equal or higher levels of stomach fullness in reef-associated fishes, as well as the frequent occurrence of reef-associated macrofauna in oyster reef-caught fishes as compared to fishes caught on unstructured, soft-bottom habitat.

METHODS

Study Location

The Lynnhaven River System (LRS) is the southernmost sub-estuary of Chesapeake Bay and lies within a highly developed watershed near Virginia Beach, Virginia (Sisson et al. 2010, Lawless & Seitz 2014), with a mean river depth of 2.5 m. Despite the developed nature of the watershed, over 75% of the LRS shoreline is natural marsh (*Spartina* spp.; Lawless & Seitz 2014). In 2007 and 2008, the U.S. Army Corps of Engineers (ACoE) constructed 12 oyster reefs totaling 20.57 hectares in Broad Bay and Linkhorn Bay, segments of the Eastern Branch of the LRS. As of 2011, oyster densities on these reefs surpassed the threshold metric (15 oysters m^{-2}) and most surpassed the target metric (50 oysters m^{-2}) established by the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team to evaluate constructed reef performance (Oyster Metrics Workgroup 2011; Lipcius et al. 2015).

Site Selection

This study compared two distinct habitat types: restored oyster reef and unstructured, soft-bottom habitat (hereafter, control). Three replicate oyster reefs and three replicate control sites within the LRS were selected for study (n = 6 sites total; Figure 1). All restored reefs are permanently subtidal, closed to oyster harvest, and range in depth 1.2 – 3.5 m (Table A1). Using benthic habitat data provided by the National Oceanographic and Atmospheric Administration's (NOAA) Chesapeake Bay Office, I selected control sites located at least 750 m distant from restored reef sites with ESRI ArcGIS 10.5. Site suitability was verified in the field to ensure that control sites encompassed a similar depth range to oyster reef sites, and to eliminate sites with obstructions (pilings, buoys, etc.).

Monthly Fish Survey

Fish were sampled for abundance and diet composition 2 – 3 times per month from April to October 2016 using experimental monofilament gill nets. The gill nets were sinking-rigged and designed to fish the lower 50 – 100% of the water column. Each net measured 45.7 m long x 1.8 m deep, partitioned into three panels of mesh size 3.175 cm, 7.62 cm, and 12.7 cm (stretch) to capture a range of fish size classes (Hamley 1975). Nets were fished perpendicular to tidal flow during daytime hours (9 am – 5 pm) on both flood and ebb tides. Tidal stage (slack, flood, ebb) was noted in the field at the start of each net set. Temperature (°C), dissolved oxygen (mg L^{-1}), and salinity (psu) were recorded at the start of each net set using a handheld water quality probe (YSI Professional Plus Multiparameter Water Quality Instrument). To decrease the likelihood of stomach content evacuation by captured fish, gill net sets were limited to approximately 1.5 hours (Sutton et al. 2004). All six sites were fished on each sampling date, each with one gill net. The order in which gill nets were deployed was randomized each sampling date.

Upon net retrieval, all collected organisms were removed from the gill nets. Up to 25 individuals from a given species and size class were euthanized in an ice slurry and kept on ice for laboratory processing. Size-class determinations were based on mesh size of capture. Additional fish were identified and counted before being released. Fish sampling in this study was conducted in accordance with the College of William & Mary's Institutional Animal Care and Use Committee (Protocol #: IACUC-2014-09-17-9772-rdseit).

Additional fish sampling was conducted via otter trawl in April, May, and June 2016 to target demersal fishes, small juvenile fishes, and blue crabs (trawl dimensions: 4.8 m length, 3.81 cm body mesh, 0.96 cm cod-end mesh, mouth opening of 3 m). Tows were deployed from a small vessel for ~two minutes at a speed of ~3 km per hour directly adjacent to reef and reference sites. Tow start and tow end position were marked and recorded using a handheld GPS unit (Garmin GPSmap 78sc). Rapid depth changes, a multitude of obstructions (crab pots, buoys, other boaters), and oyster bottom itself (restored reef boundaries on maps did not exactly match boundaries in the field) limited the effectiveness of these tows. Species identifications and counts are included in the Appendix (Table A2).

Sample Processing & Diet Analysis

In the lab, all collected individuals were identified, counted, measured (fork length and total length [mm]) and weighed (nearest 0.1 g, wet weight). For each net set, the stomachs of up to 5 individuals per species and size-class were removed and placed in isotonic fixative (Normalin^{TM}) for preservation and eventual diet analysis. At a later date, these stomachs were then removed from isotonic fixative, rinsed, and individually weighed (nearest 0.001 g). Stomachs were emptied, all contents rinsed with ethanol (70%) into a clear plastic petri dish, and the empty stomachs weighed again. Prey items were sorted, identified to lowest taxonomic level, and weighed together by taxa (nearest 0.001 g).

24-Hour Fish Survey

Two 24-hour sampling events were conducted (July 19 – July 20 & September 27 – September 28 2016) to estimate total daily ration and characterize diel feeding patterns. These sampling events were broken into two 12-hour periods ('day' and 'night') on consecutive days. To reduce risks associated with nighttime vessel operation, one oyster reef site and one control site within Broad Bay were selected for sampling. The same two sites were visited in both July & September. During each sampling event, 2 – 3 gill nets were set at each site (reef and control) for approximately 2.5 hours at a time. Set times were lengthened relative to the monthly survey in an attempt to increase catch size. Upon net retrieval, all collected organisms were removed from the gill nets, and the nets were reset and fished again. Up to 10 individuals from a given species and size class were euthanized in an ice slurry and kept on ice for laboratory processing (described above). Tidal stage and water quality conditions were recorded at the start of each net set. Net sets were partitioned into six four-hour time blocks for subsequent analysis (9 am – 1 pm, 1 pm – 5 pm, 5 pm – 9 pm, 9 pm – 1 am, 1 am – 5 am, 5 am – 9 am).

Statistical Analysis of Fish Abundance

Fish abundance during the monthly survey was modeled using generalized linear (GLMs) and generalized linear mixed models (GLMMs; Venables & Dichmont 2004, Bolker et al. 2008). Two responses were examined: 1) Total fish catch; 2) Species-specific catch for the most abundant non-filter feeding fishes. For each response, number of fish captured per net was chosen as the dependent variable. The negative binomial distribution was assumed for all models, and employed together with the log-link function. Fishing effort (gill net soak time) was incorporated via an offset term included in all models (Maunder & Punt 2004). April-May sampling events (2 days, 12 net sets) were excluded from the statistical analysis due to very low catch rates (4 individuals collected). The 24-hour survey was designed to collect fishes for diet and consumption analysis. Trends in abundance were not analyzed, but species identifications and counts are included in the Appendix (Table A3).

Ten candidate models were constructed to evaluate the influence of habitat on fish catch (Table 1). In addition to Habitat Type (discrete variable; Reef or Control), models incorporated varying combinations of design and environmental variables that were hypothesized to influence fish catch. They included Month (discrete variable; June – October), Water Temperature (continuous variable), Salinity (continuous variable), and Tidal Stage (discrete variable; Flood, Slack, Ebb). Two GLMMs included sampling site as a random error term, to account for possible site effects on catch. Correlations between variables were examined prior to modeling to rule out the possibility of collinearity.

All 10 models (as well as an intercept-only null model) were run and compared using Akaike's Information Criterion (AIC), which provides evidence regarding the likelihood of a certain model, given the input data, and rewards model parsimony by penalizing over-parameterized models (Burnham & Anderson 2002, Hobbs & Hilborn 2006). Under an AIC-based model-selection framework, the model with the lowest AIC value is the 'most likely' model. Model fit to the data and adherence of data to model assumptions was evaluated using diagnostic plots (residual values vs. fitted values; quantile-quantile plots) and diagnostic statistics (including dispersion, influence, and leverage). Selection of a single 'top model' for evaluation was informed by AIC value and model fit to data, with a preference for parsimony. Model parameter estimates were deemed statistically significant at the $\alpha = 0.1$ level. All statistical analyses were conducted with the statistical program R and the packages lme4 and MASS (Venables & Ripley 2002, Bates 2010, RStudio Team 2015, R Core Team 2016).

Fish Stomach Fullness

For each individual fish, total prey weight was determined as the sum of all individual prey items (including unidentified material). Stomach fullness (Buckel et al. 1999, Laegdsgaard & Johnson 2001, Facendola & Scharf 2008) was calculated for individual fish captured during the monthly survey as

$$\frac{Total\ Prey\ Weight\ (g)}{Fish\ Wet\ Weight\ (g) - Total\ Prey\ Weight\ (g)}$$

GLMs were used to evaluate the effects of the discrete variables Habitat Type (Reef or Control) and Month (June – October) on stomach fullness for fish collected during monthly sampling (Table 2a). Because individuals collected in the same gear set are likely more similar to one another than to individuals collected elsewhere, stomach fullness values of individual fish were averaged together by gill net set. Stomach fullness values were log-transformed prior to modeling, and model results were compared using AIC. Stomach fullness was also calculated for fishes collected during the 24-hour survey and modeled using GLMs incorporating the fixed effects of Habitat Type, Time of Day (Set Time), and Month (July or September; Table 2b).

Indices of Diet Composition

For each species, two diet indices were determined for each prey taxa identified from fish collected during the monthly survey: percent frequency occurrence (% F) and percent composition by weight (% W) (Buckel et al. 1999, Pope et al. 2001). All diet indices were determined using a cluster sampling estimator that treats each gill net set ("cluster") as an independent replicate (Cochran 1977, Buckel et al. 1999). Due to limited sample size, fish were pooled by species across size classes and month of sampling, and % F and % W calculated by habitat type. If a species showed indication of diel feeding activity during the 24-hour survey (*i.e.*, statistically significant difference in stomach fullness by Set Time), % F and % W were also estimated by habitat type from stomach content data taken during hours of increased feeding activity. Prey categories used to calculate diet indices are described in Table 3. For a given species, the % F of prey type *k* (percent of stomachs containing prey type *k*) was estimated as:

$$\% F_k = \frac{\sum_{i=1}^{n} M_i \, p_{ik}}{\sum M_i} * 100$$

Where

$$p_{ik} = \frac{m_{ik}}{m_i}$$

And where

- n = Number of clusters that contain species *x*
- M_i = Number of individuals of species *x* collected in cluster *i*
- m_i= Number of individuals in a subsample of species *x* analyzed for diet from cluster *i*
- m_{ik}= Number of individuals in the subsample with food type *k* in cluster *i.*

The %W of prey type *k* was estimated for a given species as

$$\% W_k = \frac{\sum_{i=1}^{n} M_i \, q_{ik}}{\sum M_i} * 100$$

Where

$$q_{ik} = \frac{w_{ik}}{w_i}$$

And where

- w_i= Total weight of all identifiable prey in a subsample of the fish from cluster *I* analyzed for diet
- w_{ik} = Weight of prey type *k* in the subsample from cluster *i*

I used Permutational Multivariate Analysis of Variance (PERMANVOVA) to test for differences in overall diet composition between the two habitat types. PERMANOVA is a non-parametric multivariate technique that allows for the significance testing of differences between groups using distance matrices (Anderson 2001, McArdle & Anderson 2001). Sources of variation in a distance matrix are partitioned into pre-specified factor levels, and permutation tests used to generate a pseudo-F statistic and subsequent p-value. For each species, one-way PERMANOVA tests were conducted using Bray-Curtis dissimilarity matrices generated from % F and % W observations (calculated at the cluster level). Statistical significance was set at the α = 0.1 level. If significant differences between habitat were indicated by PERMANOVA, similarity percentage (SIMPER) was used to identify the prey types contributing most prominently to between-group dissimilarity (Clarke 1993, Clark & Warwick 2001). PERMANOVA and SIMPER calculations were conducted using R package *vegan* (Oksanen et al. 2017).

Habitat Contributions to Overall Diet

The potential contribution of reef-associated prey to overall fish diet was assessed by assigning each prey type a habitat category (Reef-enhanced, Control-enhanced, Unknown, Both), based on prey abundance in the environment (Table 3). Estimations of % W (monthly survey) for were then summed by habitat category and qualitatively compared between species and habitat of collection (Reef or Control). Habitat contributions were also calculated for any species showing signs of diel feeding activity.

Data regarding prey available in oyster reef habitat were available from a field survey in the LRS, conducted with settlement trays (0.122 m2 x 15 cm deep, 1.0 mm mesh liner) embedded in the reef matrix by divers and retrieved after six weeks (Karp 2016; Table 4). Trays were deployed during the summers of 2014 and 2015 (June – July) at four restored oyster reefs sites, including all three restored reefs sampled for fishes in this thesis. Mean total biomass did not differ significantly between years (Analysis of Similarity; R = 0.096, P = 0.053). Mean total abundance of prey types did differ significantly between years, and some change in species composition was observed (Analysis of Similarity; R = 0.391, P = 0.001).

Potential prey in control habitats were sampled in August 2014 with a suction sampling apparatus at two sites within the Lynnhaven River, located between 300 – 1000 m distant from control sites sampled for fishes (1-mm-mesh; suctions taken to 15 – 20cm in depth in the sediment; Seitz & Karp *unpublished data*; Table 4). These samples were collected from shallower depths (~1.5 m) than the control sites where fish were collected. Only biomass data were available, and so I also used data available from previous studies of Lynnhaven River benthic fauna in unstructured habitats to inform habitat category designations (Lawless & Seitz 2014). For example, mean polychaete biomass recorded in restored oyster reef habitat was greater compared to mean polychaete in control habitat, but polychaetes are known to occur, occasionally in high densities, in unstructured soft sediments. Thus, they were listed as available in both habitats (Lawless & Seitz 2014).

Because these mean biomass and abundance values were averages across sites (for both habitats) and years (for oyster reef habitat), they did not capture site-level or annual differences in prey field composition. Benthic prey can be patchily distributed and (as seen in the oyster reef prey data) can vary significantly year-to-year (Karp 2016); this heterogeneity was not captured this analysis. Ideally, the prey field in both habitat types would be sampled using similar methods; unfortunately, such data were not available.

Prey Selectivity by Fishes in Oyster Reef Habitat

Feeding selectivity was quantified by comparing the relative proportion of prey in stomach contents to the relative proportion of benthic prey in the environment (Lechowicz 1982). I examined selectivity for oyster reef-caught fishes only because I considered the oyster reef benthic prey data more rigorous (greater sample size, alignment with fish sampling sites, two years of sampling) and more reflective of the prey field in that habitat compared to the unstructured bottom benthic prey data. For each species, I evaluated selectivity for the 2 - 4 highest contributing prey types (by % W) for which environmental prey data were available. Two electivity indices were calculated to assess selectivity for the selected prey types. Ivlev's electivity (*E*) for a particular prey type *i* was determined as $E_i = (r_i - p_i)/(r_i + p_i)$, where the relative abundance of prey type *i* in fish stomachs is given by r_i, and the relative abundance of prey type *i* in the environment p_i. Values for E range from -1.0 to 1.0, with positive values indicating preference for a given prey type and negative values avoidance (zero indicates random feeding). Ivlev's foraging ratio (*FR*) for prey type *i* is determined as $FR_i = (r_i/p_i)$. FR values from 0 to 1 indicate negative selection, and values greater than 1 preference for a given prey type. For both metrics, % W estimated from the monthly survey stomach content data was used as r_i. Both relative biomass and relative abundance of prey in the environment were used as p_i, and were calculated using mean biomass and mean density reported in Karp 2016. Relative biomass (and relative abundance) of prey type *i* was calculated as $\frac{Biomass_i}{Total\ Biomass} * 100$. Prey types found in the environment were considered as potential prey if they occurred at least once in the stomachs of sampled fishes.

Daily Consumption Rate Estimates

Individual daily consumption (g prey consumed g predator^{-1} day^{-1}) can be estimated over a specified period using a gastric evacuation model of the form

$$C_d = 24 * E_i * \bar{S}_i^y$$

where $\bar{S}_i^y$ is mean total stomach content weight of species *i,* and 24 the number of hours in a day. y is a constant and typically set equal to 1 (Link et al. 2002). The gut evacuation rate E (hour^{-1}) is given by

$$E_i = \alpha * e^{\beta * T_p}$$

where α and β are constants and T_p is average daily temperature. This model assumes that fish feed continuously at a constant rate, but stomach samples collected over sufficiently short time periods can yield reasonably unbiased consumption estimates in the event this assumption is not met (Durbin et al. 1983).

Stomach fullness and environmental data collected during the 24-hour survey were used to estimate individual daily consumption by habitat for one of the sampled species, silver perch (*Bairdiella chrysoura*). Separate estimates were generated for July and September. $\bar{S}_i^y$ was set equal to mean daily stomach fullness (g prey g predator^{-1} day^{-1}). Stomach fullness values from individual fish were first averaged by 4-hr sampling period, resulting in 6 separate estimates of stomach fullness per habitat-month combination. I then averaged all 6 estimates to obtain a daily average value of stomach fullness. I set T_p to the mean water temperature recorded in situ during sampling (July T_p = 29.88 °C; September T_p = 24.57 °C). Standard values of α and β in the literature are 0.004 and 0.115, respectively (Link et al. 2002). Because the applicability of α and β to silver perch is not known, consumption estimates were generated by adding random variability to these constants. New values for α and β were drawn randomly at the start of each iteration from uniform distributions with a range of ½ to 1.5x the standard literature value. I input these values into the consumption equation (along with the other parameters described above) to generate a single estimate of daily consumption for both oyster reef and control habitats.

This process was then repeated 1000 times to generate a distribution of consumption estimates for each habitat. Each iteration, I sampled the original set of 6 stomach fullness estimates with replacement, calculated a new overall mean stomach fullness value, then input that value into the consumption equation with new randomly selected values for α and β. The result of these repeated calculations was a set of 1000 mean consumption estimates for both oyster reef and control habitat in July and September. Standard error was determined as the standard deviation of the set of means.

Mean daily consumption estimates from each habitat and month were then converted into consumption per individual (g prey $fish^{-1}$ day^{-1}) by multiplying the consumption estimate by the mean weight (wet weight, 0.01 g) of fish collected in each habitat type. Consumption per individual (total weight of prey consumed day^{-1}) was then partitioned into specific prey groups using both the monthly and 24-hour survey % W estimations. To examine daily consumption on an energetic basis (i.e., as a measure of prey quality), the weight of prey item *i* consumed per day was multiplied by an estimate of the caloric density of prey item *i,* taken from the literature, to yield calories consumed per prey type per day (Table 5; Pope et al. 2001). Prey item caloric estimates were summed to yield an estimate of total calories consumed per day by habitat type. Finally, to assess if the energetic value of silver perch prey varied by habitat type (regardless of total amount prey consumed), I assumed oyster reef and control consumption rates were equal and repeated the above process. Specifically, I set total daily consumption to the level estimated for an oyster-reef-caught fish in July, then partitioned that total into specific prey categories the monthly and 24-hour survey % W estimates. Literature values of caloric density were used to determine calories consumed per prey type per day, then summed to yield an estimate of total calories consumed per day by habitat type. These results were qualitatively compared between habitats and with initial consumption estimates.

RESULTS

Environmental Conditions

Water temperatures increased steadily from April to August before declining in September and October (Figure 2a; Mean: 25.6 °C; Range: 17 – 31.7 °C). Polyhaline salinity conditions persisted throughout the majority of the study (Figure 2b; Mean: 22.77 psu; Range: 15.5 - 26.23 psu), though reduced salinity was observed in October following heavy rainfall (Monthly Mean: 17.99 psu; Range: 15.5 – 21.2 psu). Dissolved oxygen remained normoxic throughout the study period (Figure 2c; Mean: 6.92 mg L^{-1}; Range: 4.08 to 9 mg L^{-1}), suggesting any observed patterns in fish abundance and diet would not be the result of physiologically stressful low-oxygen conditions.

Monthly Survey Fish Abundance

In total, 1672 individuals from 16 different species were collected over the six-month survey (Table 6). *Leiostomus xanthurus* (Spot), *Brevoortia tyrannus* (Atlantic menhaden), *Bairdiella chrysoura* (Silver perch), and *Micropogonias undulatus (*Atlantic croaker) were the four most abundant species captured and comprised over 90 % of the total catch. Relative abundance, or catch per unit effort (CPUE), increased from April to mid-summer in both habitat treatments, reaching a July peak in oyster reef habitat and an August peak in control habitat (Figure 3a). CPUE in both habitats declined in September and again in October. Water temperature was positively associated with overall catch in the most likely GLM, but overall catch was significantly lower in oyster reef habitat compared to control habitat (Table 7a; Table A4).

Monthly Survey Species-Specific Abundance

I evaluated species-specific catch rates for the top three most-abundant non-filter-feeding fishes: spot, silver perch, and Atlantic croaker, all members of the Sciaenid (drum) family. Spot CPUE followed a pattern similar to overall CPUE, increasing from April to August before declining in both September and October (Figure 3b). The most likely statistical model (with the lowest AIC value and highest weight) also indicated significant effects of both water temperature and habitat (Table 7b; Table A4). Water temperature exhibited a significant positive relationship with spot catch, while the relationship of oyster reef habitat with spot catch was negative (Table 7b).

Silver perch were collected at low levels of abundance (mean CPUE < 2 fish hour^{-1}) over the study period (Figure 3c). I did not capture silver perch at control sites in September, and mean oyster reef CPUE exceeded control CPUE in July. This July-Reef interaction was statistically significant and positive in the most likely GLM, supporting the observed increase in CPUE (Table 7c). Examination of raw data from July indicated a gill net set with a value significantly different from the other values (CPUE: 13.82 fish hour^{-1}; Grubbs Test; $P < 0.01$). When this outlier was removed and the data modeled again, no model performed better than the intercept-only model, suggesting no discernable between habitat type and silver perch abundance (Table A4).

Overall CPUE for Atlantic croaker was lowest among the three sciaenids examined, and did not exceed 1 fish hour^{-1} for either habitat type (Figure 3d). Because abundance of Atlantic croaker was low throughout the sampling period, I instead chose to model the presence or absence of croaker from two size classes: < 190 mm (hereafter, ‘small’) and >190 mm (hereafter, ‘large’; Figure 4). I assumed a binomial distribution with the logit link, employed the same suite of predictor variables as before, and selected top models using AIC-based model selection (Table A5). The most likely GLM for large croaker indicated a significant influence of habitat on the probability of fish presence; specifically, large croaker were more significantly likely to occur in oyster reef habitat in July, August, and October (Table 8a). I selected a GLM including habitat type to describe small croaker presence, and results indicated small croaker were significantly more likely to occur in control habitat compared to oyster reef habitat in June, July, and August (Table 8b). Though this model had a higher AIC value compared to other candidate models (Table A5), the chosen model maximized parsimony (number of parameters = 2), allowed for a straightforward comparison with model selected for large croaker, and still represented a plausible hypothesis, given the data (models within 4 – 7 ΔAIC can be regarded as plausible; Burnham et al. 2011).

Diet Analysis

Stomach content analysis was conducted on 629 individuals from 14 species. The three most abundant non-filter feeders (silver perch, spot, and croaker) were selected for detailed analysis of mean stomach fullness and diet composition by species and habitat type. Croaker were the largest individuals collected in this study on average (by length), followed by silver perch, then spot (Table 9). Individual daily consumption rates were estimated for silver perch. Diet indices (% F & % W) were estimated for the remaining species, but no detailed analysis performed (Table A6-A7).

Monthly Survey Stomach Fullness

The effect of habitat type on mean stomach fullness varied by species. Silver perch exhibited higher levels of mean stomach fullness in oyster reef habitat compared to control habitat across the study period (Figure 5a; Table 10a). Spot mean stomach fullness was greatest in June before declining in subsequent months (Figure 5b; Table 10b). Mean stomach fullness of reef-caught spot tended to be less than control-caught spot, but this effect was not significant in the most likely GLM (Table 10b). For Atlantic croaker, mean reef stomach fullness appeared less than mean control stomach fullness (Figure 5c). The intercept-only model performed better than the model including habitat type, suggesting a significant difference between habitats was unlikely (Table A8).

24-Hour Survey Stomach Fullness

Analysis of mean stomach fullness during the 24-hour survey revealed the influence of both time of day and habitat on fish foraging patterns. Habitat type was a significant predictor of mean stomach fullness in silver perch, and oyster reef individuals exhibited significantly higher levels of gut fullness than control individuals (Table 11a). Mean gut fullness of fish from both habitat types significantly increased in the nighttime (1:00 AM – 5:00 AM gill net set) and early morning (5:00 AM – 9:00 AM gill net set; Figure 6a; Table 11a).

Spot mean stomach fullness patterns differed from those observed in silver perch. Oyster reef individuals displayed significantly lower values of mean stomach fullness relative to control fish (Table 11b). Fish collected during the second 24-hour sampling event in September also tended to have lower mean stomach fullness values than fish collected in July (Table 11b). Time of day was not included as a parameter in the most likely GLM, and graphical examination of the data suggested relatively similar levels of mean stomach fullness across the 24-hour cycle (Figure 6b).

Croaker were not collected from the control site or during the September sampling event in sufficient numbers to statistically compare stomach fullness between habitats or months. Mean stomach fullness appeared to peak around dusk (5:00 PM – 9:00 PM gill net set; Figure 6c), but a model fit to the data including the variable Set Time did not perform better than an intercept-only model (Table A9).

Monthly Diet Composition

Silver perch fed most frequently on polychaete worms and snapping shrimp (*Alpheus heteorchaelis*) in oyster reef habitat (> 10 % F; Figure 7 – upper panel). Other prey, including mysid shrimps (primarily the opossum shrimp, *Neomysis americana*), fishes (including the naked goby, *Gobiosoma bosc*), and crabs were encountered infrequently (< 10 % F). Polychaete worms and snapping shrimp dominated the bulk of oyster reef diet by weight, together comprising nearly two-thirds % W (Figure 7 – lower panel). Mysid shrimps constituted the most frequent prey item encountered in control fish, along with amphipods, isopods, and other unidentified crustaceans. Polychaetes were encountered fairly often in control fish (> 10 % F), but snapping shrimp were not found. Control fish % W was spread amongst three major prey groups: mysids, polychaetes, and amphipods-isopods. Some unidentified material was recovered during stomach content analysis of silver perch and the other sciaenids. This category included prey items too degraded or decomposed to adequately assign a lower level of classification. Overall silver perch diet composition as measured by % F differed significantly by habitat type (One-Way PERMANOVA; F = 1.96; P = 0.047). SIMPER results indicated unidentified crustaceans, mysids and snapping shrimp, polychaete worms, and amphipods/isopods contributed most prominently to observed dissimilarity between the two habitat groups (Table 12a). None of the species, however, exhibited the high dissimilarity – standard deviation ratios (> 1.5) expected of a reliable discriminating species. Habitat type also explained a significant portion of the overall variance in the % W dissimilarity matrix (One-Way PERMANOVA; F = 1.94; P = 0.036), and SIMPER analysis suggested the same suite of prey contributed most to the observed dissimilarity (Table 12b).

For spot, polychaete worms were the primary prey type consumed from both habitat types (Figure 8 – upper panel). Copepods (primarily benthic copepods of the order Harpacticoida) were also frequently encountered, though to a lesser degree in control habitat (% F = 22) than reef habitat (% F = 44). Small crustaceans (amphipods, isopods, mysid shrimps) were encountered infrequently, as well as a variety of non-polychaete worms (including nematodes, oligochaetes, and nemerteans). Tunicates were recovered from approximately 10 % of spot stomachs from oyster reefs, but not from any control fish stomachs. Polychaetes contributed principally to overall prey weight in both habitat types (over 75 % W; Figure 8 - lower panel). One-way PERMANOVA results for both % F and % W indicated significant overall differences between habitat (% F: F = 2.0725; P = 0.098; % W; F = 2.28; P = 0.072). SIMPER analysis suggested that these dissimilarities were primarily attributable to polychaetes, copepods, and unidentifiable material, but dissimilarity – standard deviation ratios did not indicate any of these groups to be a reliable discriminating species (Tables 12c & 12d).

Croaker collected from both reef and control habitats foraged most frequently on polychaete worms and bivalve clams (Figure 9 - top panel). These two prey types also contributed the most to overall prey weight, with polychaetes comprising over 60 % W in both habitat types (Figure 9 - lower panel). Reef fish diet included mussels, shrimps, and fishes, as well as unidentified material. Control fish diet appeared less varied, including only mysid shrimps and fishes beyond the principal contributors. Overall diet composition did not vary significantly between habitat types for either % F (One-way PERMANOVA; F = 0.4613; P = 0.764) or % W (One-Way PERMANOVA; F = 0.202; P = 0.972).

Silver Perch Diet Composition, Peak Feeding Hours

When silver perch diet composition was examined in the hours of enhanced feeding (1 am – 9 am), overall diet composition as measured by either % F or % W did not differ significantly between habitats (One-Way PERMANOVA % F; F = 0.936; P = 0.533; % W; F = 0.715; P = 0.676). Silver perch in both habitats primarily consumed small crustaceans (shrimps, amphipods, isopods, mysids), as well as fish and polychaetes (Figure 10). Grass shrimp were solely identified from the stomachs of reef fish. Amphipods, isopods, and sand shrimps (*Crangon* sp.) were more frequently encountered in control fish than oyster reef fish. Polychaetes occurred more frequently in oyster reef fish than in control fish, but contributed more to % W of control fish. Polychaete % W in reef-caught fish was much lower in the 24-hour survey compared to the monthly survey. Though snapping shrimp were absent from control stomachs during the monthly survey, they occurred relatively frequently in control stomachs (nearly 15 % W) during the peak feeding hours, and constituted a similar % W for both control and reef fish. Naked gobies constituted a greater proportion of diet by weight in reef fish compared to control fish, but unidentified fishes (possibly including gobies) were a more important contributor to control fish diet by weight.

Habitat Contributions to Overall Diet

The overall contribution of reef-enhanced prey to diet observed during the monthly survey varied by species. While reefs contributed conservatively ~30 % of silver perch diet by weight, reef-prey comprised < 5 % of croaker and spot diet (Figure 11). Prey found in both habitat types constituted the bulk of diet by weight for all three species, and control-enhanced prey types contributed substantially only to the diet of Atlantic croaker. For silver perch collected during peak feeding hours, both reef-prey and prey found in both habitat types contributed to diet by weight, and over half of reef-caught silver perch diet was comprised of reef-enhanced prey types (Figure 12).

Prey Selectivity by Fishes in Oyster Reef Habitat

The % W of polychaetes and snapping shrimp in the stomachs of reef-caught silver perch exceeded both the relative abundance and relative biomass of those prey in the environment (Figure 13). Ivlev's FR and Ivlev's E indicated positive selection for both of these prey types (Table 13). Crab % W exceeded crab relative abundance on the reef, but was much less than crab relative biomass on the reef (Figure 13). Positive selection for crabs was thus indicated only when relative abundance, not biomass, was used as p_i to calculate FR and E (Table 13). The % W of naked gobies in the stomachs of silver perch was less than both relative abundance and relative biomass of naked gobies in the field, and selectivity metrics did not indicate positive selection (Figure 13; Table 13). Reef-caught spot strongly selected for polychaetes. Polychaete % W greatly exceeded both the relative abundance and relative biomass of polychaetes in the environment, and all four selectivity calculations indicated positive selection (Figure 14; Table 13). Croaker demonstrated positive selection for both polychaetes and clams

(Figure 15; Table 13). When relative abundance, not biomass, was used as p_i to calculate FR and E, both metrics provided evidence of positive selection for mussels; when relative biomass used as p_i, both indices were close to values suggesting ‘random feeding’ (Table 13). Reef-caught croaker did not show any evidence for selection of naked gobies (Table 13).

Silver Perch Daily Consumption Estimates

The estimate of daily consumption for silver perch in July (0.020 g prey g predator^{-1} day^{-1}) in oyster reef habitat exceeded and was nearly double the estimates for silver perch in control habitat (0.011 g prey g predator^{-1} day^{-1}; One-Sided Two-Sample t-test; $t = 28.45$; $p < 0.001$). Similarly, the September estimate of mean daily consumption in oyster reef habitat (0.017 g prey g predator^{-1} day^{-1}) also exceeded and was four times the control habitat estimate (0.003 g prey g predator^{-1} day^{-1} ; One-Sided Two-Sample t-test; $t = 87.45$; $p < 0.001$). Similarly, the total daily caloric intake of an individual silver perch in oyster reef habitat greatly exceeded that of a silver perch in control habitat using % W estimated from either the monthly or 24-hour survey data (Table 14a). When the consumption rate was assumed to be equivalent between habitats (set at the July oyster reef estimate, 0.0201 grams prey gram predator^{-1} day^{-1}), total daily caloric estimates varied by habitat and % W estimation (monthly survey vs. 24-hour survey; Table 14b). Using monthly % W estimations, total daily caloric intake by a reef fish still exceeded that of a control fish, but the difference was less than previously estimated. Using the 24-hour % W estimations, control fish daily intake caloric intake exceeded that of reef fish by approximately 30 calories day^{-1}.

DISCUSSION

Restored sanctuary oyster reefs influenced the foraging of mobile estuarine fishes in the Lynnhaven River System (LRS), Virginia, but did not enhance the relative abundance of fishes. Restored reefs appear to serve as valuable forage habitat for silver perch, but further research is necessary to determine if they function similarly for spot or Atlantic croaker. Differences in functional morphology, foraging behavior, and prey preference likely drive observed patterns. The study provides useful insight into the mechanistic role of large restored reefs in Chesapeake Bay tributaries, and it highlights the importance of incorporating species-specific responses and trophic dynamics into the study of oyster reef ecosystem services.

Silver Perch Consumption

This study suggests that the daily consumption rate of a mobile estuarine fish, silver perch, varies between restored oyster reef habitat and unstructured bottom in the LRS. A hypothetical silver perch foraging exclusively in oyster reef habitat is predicted to consume both a greater amount of prey and more total calories daily compared to a similar fish foraging in unstructured bottom. The diet composition of reef-captured silver perch, however, was not necessarily more energetically favorable than the diet composition of control-caught silver perch; when an identical consumption rate was applied, the total number of calories consumed was relatively similar between habitats. Instead, increased stomach fullness drove the between habitat difference in total daily caloric intake. This suggests that preferred prey types are more available in oyster reef habitat, compared to unstructured bottom, as they are perhaps concentrated into denser patches (Brandt et al. 1992, Rodney & Paynter 2006).

By aggregating preferred prey in high densities, restored reefs appear to enhance foraging success of silver perch, which in turn may positively affect the growth of these individuals. Increased prey availability and the amount of prey consumed can enhance growth rates of a number of species (Boisclair & Leggett 1989a, Sommer et al. 2001, Kennedy et al. 2008). Growth rates vary significantly both within and among populations, however, and are influenced by a range of factors besides consumption rate, including temperature, reproductive state, activity rate, prey energy density, and body size (Boisclair & Leggett 1989b, Hewett & Kraft 1993). Further research is needed to investigate whether increased consumption in oyster reef habitat translates into increased growth rates of individual silver perch.

Field-based estimates of daily consumption by other sciaenid fishes have reported values similar to this study. Daily consumption of age 0 - 1 red drum (*Sciaenops ocellatus*) in North Carolina marsh creeks was estimated between 1 – 4 % total body weight, and whitemouth croaker (*Micropogonias furnieri*) consumed between 0.9 – 5.3 % body weight in a Brazilian estuary (de Figueiredo & Vieira 2005, Facendola & Scharf 2008). Field-based consumption estimates tend to be biased low; in this study, small numbers of fish collected (particularly during the day) and a limited number of diel sampling events may have influenced my estimates. Given maintenance and growth needs, it is likely that silver perch individuals of the size range examined consume a greater amount of food daily than estimated in this study. These biases apply to both habitat types, and the significance difference in consumption rates between restored reef and unstructured bottom still warrants further investigation.

The estimates of silver perch daily consumption by habitat type (0.3 - 2 % body weight) from this study are low relative to laboratory- and model-based estimates. For instance, a calibrated bioenergetics model estimated consumption rates ranging from 6 to 38% (Mean: 14.5 %) for young-of-year silver perch inhabiting Chesapeake Bay seagrass beds (Sobocinski & Latour 2015). Consumption rates tend to decline as fish grow larger (Facendola & Scharf 2008), and published silver perch length-at-age data suggest fish collected in this thesis likely represent large young of year or age 1+ fish (Tuckey & Fabrizio 2016). This may account for some of the difference observed between studies.

Diet Composition & Habitat

Benthic prey dominated the diet of silver perch, spot, and croaker, regardless of habitat, highlighting the importance of benthic productivity to the trophic ecology of these fishes in Chesapeake Bay. Studies of fish food habits in the Bay mainstem also attribute the majority of fish consumption to non-pelagic prey types (Idhe et al. 2015, Bucheister & Latour 2016). Researchers in other shallow-water Bay habitats (seagrasses, salt marshes, etc.) have identified the importance of benthic prey as well (Hines et al. 1990, Cicchetti & Diaz 2007, Sobocinski 2014).

The presence of reef-related prey in fish stomach contents provides direct evidence that restored sanctuary reefs in the LRS are linked to mobile fishes via predation of reef-derived prey. This study indicates epibenthic crustaceans, polychaetes, resident reef fishes, and tunicates serve as linkages between restored oyster reef habitat and the three sciaenids studied, though the relative importance (as indicated by selectivity metrics) of these prey types to overall diet varied significantly by species.

Species-level differences in diet composition and the amount of reef-prey consumed are likely attributable to differences in mean body size and functional morphology. Fish length (body size) is a strong determinant of diet, and changes in body and gape size influence the kinds of prey consumed (Buchheister & Latour 2016). Observationally, croaker and silver perch tended to contain larger prey items (length or carapace width) compared to spot. Differences in functional morphology (form and function of feeding apparatus and digestive systems) amongst the scieanids manifest early in development and allow these sympatric species to partition the estuarine environment (Chao & Musick 1977, Horodysky et al. 2008, Deary & Hilton 2015, Deary et al. 2016). For instance, silver perch display terminal mouths and an oblong body, enabling anterior feeding on prey in the water column (Chao & Musick 1977, Deary & Hilton 2015). Croaker and spot have inferior mouths, along with shorter and deeper body forms, better adapted to benthic-oriented feeding habitats. Spot and croaker differ in their feeding apparatus (e.g., number and kind of pharyngeal teeth and gill rakers) and associated behavior (spot tend to forage deeper into the sediments; Chao & Musick 1977). Generally, these differences are reflected in diet results of this study, where silver perch consumed a broad diet including epibenthic and pelagic crustaceans and fish, croaker consumed a mix including polychaetes, bivalves, shrimps and fishes, and spot consumed primarily infaunal polychaetes and meiofauna.

Some diet items of silver perch were exclusively reef-derived and serve to transfer production from the reef to higher trophic levels. Of particular importance to silver perch diet were big-clawed snapping shrimp (*Alpheus heterochaelis*), identified from both monthly survey and 24-hour survey. Silver perch also appeared to consumed snapping shrimp preferentially, as evidence by positive selectivity metrics, perhaps due to snapping shrimp's high energy density. Reported food sources for *A. heterochaelis* include small invertebrate fauna (worms, amphipods), detritus, benthic microalgae, and particulate organic matter (Abeels et al. 2014). Snapping shrimp likely serve as a conduit of reef-associated primary production, basal secondary production, and detritus to silver perch in the LRS. Significant consumption of epibenthic crustaceans has also been observed in other oyster reef-trophic studies. For instance, snapping shrimp comprised between 9 – 40 % of the diet of sheepshead (*Ariopsis felis*), common snook (*Centropomus undecimalis*), ladyfish (*Elops saurus*), grey snapper, and red rum in Florida (Wasno 2014), and mud crabs nearly 50 % of the diet of juvenile grey snapper in Loxahachee Bay, Florida (Yeager & Layman 2011).

The occurrence of snapping shrimp in the stomachs of control-caught silver perch during peak evening feeding hours suggests connectivity (movement) between reef and unstructured habitats by actively foraging individuals. While snapping shrimp occur at high densities in restored oyster reefs within the LRS, they are absent from benthic samples taken in unstructured bottom. This implies prior consumption of snapping shrimp elsewhere besides the control habitat in which the silver perch were caught. Many estuarine fishes display short-term movement related to feeding on the scale of 10s – 1000s of meters (Dance & Rooker 2015, Fodrie et al. 2015, Moulton et al. 2017), and habitat connectivity is hypothesized to promote both biodiversity and productivity in aquatic systems (Sheaves 2009, Bostrom et al. 2011, Nagelkerken et al. 2015). Silver perch are likely integrating their prey resources over various habitats to compensate for differential prey availability, predation risk, or other factors (Dalghren & Eggleston 2000, Able et al. 2007). Future studies combining diet analyses with estimates of home range and site fidelity (e.g., via tagging or acoustic telemetry) would help better understand the links between fish diet, consumption, and discrete habitat types.

Several benthic prey associated with oyster reefs and found to be important in previous reef-trophic studies contributed less than expected to the diets of fish examined here. Crabs, and in particular, mud crabs (Xanthidae), comprise a substantial portion of macrofauna biomass on oyster reefs in the LRS, but evidence for selection by reef-caught fishes in this study was mixed and crabs contributed little to either % F or % W. Several studies have indicated substantial consumption of mud crabs by transient fish (Lenihan et al. 2001, Yeager & Layman 2011, Wasno 2014). For instance, mud crabs composed nearly 40 % of the diet of Atlantic croaker collected from a constructed oyster reef in Barataria Bay, Louisiana (Simonsen & Cowan 2013). Amphipods are present in high numbers on reefs in the LRS (Karp 2016), and silver perch and croaker in particular are known to forage on amphipods (Kleypas & Dean 1984, Nye et al. 2011). This underrepresentation of mud crabs and amphipods in reef caught fish diets may be driven by size of fish studied here, or by more complex predator-prey-habitat interactions, where prey selection is determined by both predator foraging behavior, structural complexity, availability of refuge, and prey behavior (Scharf et al. 2000, Scharf et al. 2006). Regardless, these results suggest restored reef macrofauna are not equally available to all predators. Rather, both prey identity and predator identity should be taken into account when considering trophic links between resident benthic prey and mobile fishes.

Polychaete worms were particularly important in the diets of all three sciaenids in both habitat types, as suggested by the high frequency occurrence, significant percent weight contributions, and positive selectivity metrics. Polychaetes were also the dominant prey type within the habitat category of prey available both on reef and in unstructured habitat. In soft-sediments, polychaetes constitute the majority of infaunal abundance, and they are routinely identified as a dominant prey group for demersal fishes (Gillett & Schaffner 2009, Nye et al. 2011, French et al. 2013, Buchheister & Latour 2015). Feeding along the edges of structure or in the soft sediments adjacent to structure is also a foraging tactic identified for reef-associated fishes (Posey & Ambrose 1994, Langlois et al. 2005). The presence of polychaetes in reef-caught fish stomachs could again suggest habitat connectivity; fishes caught on the oyster reefs may be foraging for polychaetes in adjacent or nearby soft-sediments.

Alternatively, sciaenids may be foraging on polychaetes in abundance on oyster reefs (Karp 2016). Restored oyster reefs in the LRS are known to support polychaetes worms (particularly large-bodied, errant polychaetes, like the clamworm *Alitta succinea*) at densities equal to or greater than those in surrounding soft-sediments (Lawless & Seitz 2014, Karp 2016, Seitz & Karp *unpublished data*). This study did not specifically identify polychaete prey to species level, due to the challenges associated with identification of partially digested, soft-bodied worms. Qualitative observations suggest the polychaetes found in the stomachs of some fish from reef habitat (especially silver perch and croaker) tended to be large-bodied worms. Future work could shed light on the accessibility of reef-associated polychaetes to mobile fishes, how that accessibility changes as a function of predator size, prey density, and structural complexity, and the relative profitability of feeding on polychaetes from oyster reefs compared to unstructured bottom. Combining traditional stomach content analysis with DNA-based approaches may also assist with fine-scale resolution of soft-bodied prey (Carreon Martinez et al. 2011, Pompanon et al. 2012). Given the frequency of polychaete consumption by reef-caught fishes and the abundance of polychaetes on oyster reefs, it is reasonable to conclude that some portion of the identified polychaetes in the stomachs of croaker and silver perch originated from oyster reef habitat. This would increase the percent contribution of reef-derived prey estimated here (the estimates treated polychaetes as prey available in both reef and unstructured habitats) and suggests reefs are more important than shown in this study.

Spot in both habitat types frequently consumed benthic meiofauna (copepods, nematodes, nemerteans, etc.), though these prey types contributed little to overall diet by weight, mainly due to their small size and the impacts of digestion. Benthic meiofauna occur in high abundance in shallow, soft-sediment habitats and are known prey for spot, especially juveniles (Coull 1990, Feller et al. 1990, Akin & Winemiller 2012). There is little published research regarding the distribution patterns of benthic meiofauna on oyster reefs, and at present it is unclear whether the presence of copepods as prey in reef-caught fish reflect habitat connectivity (movement between habitats), reef-edge foraging, or the presence of available benthic meiofauna on oyster reefs.

Relative Abundance & Habitat Use Patterns

Contrary to initial expectations, large restored reefs supporting high densities of oysters did not harbor an increased relative abundance of mobile fishes, but seasonal patterns were observed. Previous studies have shown similar patterns and suggested landscape position and habitat redundancy as mechanisms explaining equivalent or reduced fish catches in restored reef habitat (Grabowski et al. 2005; Gregalis et al. 2009; Geraldi et al. 2009; Gain et al. 2017). Other natural and anthropogenic habitats known to harbor both juvenile and adult fishes (including fringing salt marsh, tidal creeks, and cage-aquaculture operations) occur throughout the LRS near the study sites; these habitats may provide alternative locations for shelter and foraging (Minello et al. 2003; Ruiz et al. 2003; Sheaves et al. 2005; Powers et al. 2007). Additionally, estimates of relative abundance in this study were based on a monthly survey that occurred only during daytime hours. Many fish are more active at dusk, night, and dawn than in the daytime, and thus may be less vulnerable to a daytime survey (Rountree & Able 1992, Clark et al. 2003). Gill nets are also highly size selective, and even with multi-panel nets, many fish may have remained untargeted (Hamley 1975).

Beyond habitat type, water temperature emerged as an important and positive predictor of relative abundance. Temperature is a primary determinant of fish habitat quality and drives seasonality by playing play key roles in recruitment (timing and success) and movement (Houde 2008, Hayes et al. 2009). Fish abundance in Chesapeake Bay increases in spring and summer as temperatures warm, estuarine-dependent and coastal species move inshore and to shallow waters, and new recruits arrive in the estuary (Murdy et al. 1997, Jung & Houde 2003). Abundance declines again once water temperatures begin to cool and fish move to deeper or offshore waters. The summertime peak in relative abundance observed suggest the monthly survey captured the strong seasonality of the Chesapeake Bay fish assemblage.

For spot, there were some habitat patterns detected, possibly the result of foraging behavior. Lower numbers of spot were found restored oyster reef compared to unstructured bottom, and reef-caught spot exhibited lower levels of stomach fullness. Field and lab studies have suggested food has a strong effect on spot distribution in estuaries, even stronger than the effect of predators or predation risk (Miltner et al. 1995, Craig et al. 2007). Given the importance of infaunal organisms in spot diet and the availability of those prey in unstructured, soft-sediments, the combination of greater prey availability or increased foraging efficiency in control habitat may drive the observed pattern in the relative abundance of spot. These findings highlight the usefulness of combining abundance data with stomach fullness and diet composition data to better understand patterns of habitat use in the field.

There were some differences in habitat use by fish size, as large croaker were caught more frequently in restored oyster habitat, while small croaker were caught more frequently in unstructured bottom. In the Piakatank River, a sub-estuary of the Chesapeake Bay, larger Atlantic croaker were also captured over oyster reef bottom, compared to unstructured bottom (Harding & Mann 2001b). Increased prey availability and the availability of larger-sized prey on restored oyster reefs may drive observed size-dependent habitat use by croaker (Scharf et al. 2000, Costa 2009). Limited sample size prevented an in-depth examination of croaker diet by size and habitat type, and future studies comparing prey size structure on reefs and unstructured bottom with croaker diet and habitat use could help better understand the observed pattern.

Conclusions

Overall, this study indicates sanctuary restored oyster reefs constructed within the past decade in Chesapeake Bay are utilized by both juvenile and adult stages of estuarine-dependent, mobile fishes, and restored reefs may influence relative abundance, distribution, and foraging patterns. Species that select for reef-associated prey types (epibenthic crustaceans, resident fishes, large-bodied polychaetes) and are capable of foraging effectively in structured habitats may benefit from oyster reef restoration. Furthermore, diet analyses in this study and others indicate silver perch represent an important trophic link between primary consumers and pisciviores in estuarine food webs like Chesapeake Bay (Allen et al. 2001, Walter & Austin 2002, Latour et al. 2008, Sobocinski & Latour 2015). Model-based research suggests sustained increases in small forage fishes can enhance the biomass and productivity of commercial important fishery species (Buchheister et al. 2015). By positively influencing consumption rates and possibly increasing the growth of an ecologically important forage fish (e.g., silver perch), restored reef habitats may promote enhanced productivity of higher trophic levels in Chesapeake Bay. Finally, bioenergetics models linking restored habitats to fishes are necessary to develop quantitative predictions regarding the impacts of habitat restoration on fish productivity (NASEM 2017). Few studies have explicitly estimated required model parameters in the field, and none have done so for restored oyster reef habitat. By generating habitat-based estimates of consumption for silver perch, as well as estimating the percentage of oyster-reef-derived prey in the diet of three common sciaenid species, this study advances knowledge of foraging ecology and habitat importance and provides intriguing results for future work to enhance our understanding of the links between oyster reefs, fisheries production, and ecosystem services

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Table 1: Candidate models for generalized linear and generalized linear mixed model analysis of fish relative abundance. *k* indicates model degrees of freedom, and Z indicates random effect term included in two models. Water Temp = Water Temperature; Habitat*Month = Interaction term between Habitat Type and Month.

		Variables							
Model	***k***	Intercept	x_1 Habitat	x_2 Month	x_3 Tide	x_4 Water Temp.	x_5 Salinity	x_6 Habitat* Month	Z Site
g_1	2	β_0							
g_2	3	β_0	β_1						
g_3	7	β_0	β_1	β_2					
g_4	11	β_0	β_1	β_2				β_6	
g_5	5	β_0	β_1		β_3				
g_6	4	β_0	β_1			β_4			
g_7	4	β_0	β_1				β_5		
g_8	9	β_0	β_1	β_2	β_3				
g_9	5	β_0	β_1			β_4	β_5		
g_{10}	8	β_0	β_1	β_2					X
g_{11}	5	β_0	β_1			β_4			X

Table 2: Candidate models for generalized linear model analysis of fish stomach fullness for the a) monthly survey and b) 24-hour survey. *k* indicates model degrees of freedom.

A) Monthly Survey

		Variables		
Model	***k***	Intercept	x_1 Habitat	x_2 Month
g_1	2	β_0		
g_2	3	β_0	β_1	
g_3	8	β_0	β_1	β_2

B) 24-Hour Survey

		Variables			
Model	***k***	Intercept	x_1 Habitat	x_2 Month	x_3 Set Time
g_1	2	β_0			
g_2	3	β_0	β_1		
g_3	7	β_0			β_3
g_4	8	β_0	β_1		β_3
g_5	5	β_0	β_1	β_2	
g_6	9	β_0	β_1	β_2	β_3

Table 3: Prey types used for calculation of diet indices (% F & % W) and assigned habitat categories. 'Both' indicates prey type found in both habitats, or quantitative prey data unavailable and assumed to co-occur; 'Reef-enhanced' indicates prey types found in higher abundance or biomass on restored oyster reefs compared to control bottom (unstructured soft sediments); 'Control-enhanced' indicates prey type found in higher abundance or biomass in control bottom. 'Unknown' used for unidentified material with uncertain habitat origin.

Prey Type	Details	Habitat Category
Fish	Unidentified teleost fish	Both
Anchovy	*Anchoa* sp. (primarily *Anchoa mitchilli*)	Both
Goby	*Gobiosoma bosc*	Reef-enhanced
Clam	--	Control-enhanced
Crangon Shrimp	*Crangon* sp. (Sand shrimps)	Both
Snapping Shrimp	*Alpheus heterochaelis*	Reef-enhanced
Grass Shrimp	*Palaemonetes* sp.	Reef-enhanced
Shrimp Unidentified	--	Both
Mysid Shrimp	*Neomysis* sp.	Both
Crabs	Xanthid mud crabs and *Callinectes sapidus* (Blue crab)	Reef-enhanced
Amphipod or Isopod	--	Reef-enhanced
Crustacean	Unidentified crustacean	Reef-enhanced
Polychaete	--	Both
Tunicate	*Molgula* sp.	Reef-enhanced
Copepod	primarily benthic copepods (Harpacticoida)	Both
Non-Polychaete Worms	Nematodes, nemerteans, oligochaetes, etc.	Both
Unidentified Material	Prey material too degraded to adequately classify or detritus-like material	Unknown

Table 4: Biomass and abundance of potential prey types in restored oyster reef and unstructured bottom (control) habitats. Reef prey sampled in 2014 – 2015 with settlement trays (n = 18), and control prey collected in 2014 using a suction sampling apparatus (n = 8). Abundance data available only for restored oyster reef habitats. AFDW = Ash free dry weight. Reef data from Karp 2016 and control data from Seitz & Karp *unpublished data.*

Potential Prey Type	**Restored Reef**		**Control**
	Biomass (g AFDW m^{-2})	Density (# ind. m^{-2})	Biomass (g AFDW m^{-2})
Amphipods & Isopods	0.06	538.25	0.00
Barnacle	0.34	43.72	--
Grass Shrimp (*Palaemonetes* sp.)	1.43	123.41	--
Snapping Shrimp (*Alpheus heterochaelis)*	2.96	47.81	--
Crabs (Xanthid mud crabs & *C. sapidus*)	22.28	112.93	0.15
Clams	1.32	7.74	1.54
Naked Goby (*Gobiosoma bosc*)	4.39	225.41	--
Gastropod	0.65	386.61	0.03
Mussel	1.54	11.84	--
Polychaete	2.50	965.85	0.86
Tunicate (*Molgula* sp.)	5.49	919.40	--

Table 5: Energy (caloric) density of silver perch (*Bairdiella chrysoura*) prey types and source of values. Caloric density estimated in literature studies via bomb calorimetry.

Prey Type	Calories per g (wet weight)	Source
Fish Unidentified	1140.057	Steimle 1985 (Demersal fish)
Anchovy (*Anchoa* sp.)	1073.70	MccCawley 2003 (*Anchoa hepsetus)*
Naked Goby (*Gobiosoma bosc*)	1140.057	Steimle 1985 (Demersal fish)
Clam	368.069	Steimle 1985 (Bivalves)
Sand Shrimp (*Crangon* sp.)	1290.63	Steimle 1985 (Benthic malacostraca)
Snapping Shrimp (*Alpheus heterochaelis*)	1290.63	Steimle 1985 (Benthic malacostraca)
Shrimp Unidentified	1290.63	Steimle 1985 (Benthic malacostraca)
Grass Shrimp (*Palaemonetes* sp.).	1290.63	Steimle 1985 (Benthic malacostraca)
Mysid (*Neomysis* sp.)	714	Morris & Hopkins 1983
Crabs	1290.63	Steimle 1985 (Benthic malacostraca)
Amphipod or Isopod	684	Wissing et al. 1973
Crustacean Unidentified	817	Cummins & Wuycheck 1971
Polychaete	1094.646	Steimle 1985
Tunicate	537.7629	Steimle 1985
Copepod	663.9	Morris & Hopkins 1983
Non-Polychaete Worms	600	Chosen from low range of lit. values
Unidentified Material	600	Chosen from low range of lit. values

Table 6: Species collected in restored oyster reef and control habitats via gill net in the Lynnhaven River System during a monthly survey (April – October 2016).

	Number of Individuals	
***Scientific Name* (Common Name)**	Oyster Reef	Control
Leiostomus xanthurus (Spot)	308	453
Brevoortia tyrannus (Atlantic menhaden)	324	325
Bairdiella chrysoura (Silver perch)	73	34
Micropogonias undulatus (Atlantic croaker)	24	23
Opisthonema oglinum (Atlantic thread herring)	17	17
Mugil cephalus (Striped mullet)	8	15
Dorosoma cepedianum (Gizzard shad)	6	15
Pomatomus saltatrix (Bluefish)	6	5
Prionotus carolinus (Northern sea robin)	4	2
Cynoscion nebulosus (Speckled trout)	1	2
Brama brama (Atlantic pomfret)	0	2
Cynoscion regalis (Weakfish)	2	1
Lagodon rhomboides (Pinfish)	1	1
Eucinostomus argenteus (Spotfin mojarra)	0	1
Pogonias cromis (Black drum)	0	1
Menticirrhus saxatilis (Northern kingfish)	1	0
Total Individuals	775	897

Table 7: Parameter estimates from the best fit generalized linear models for a) total fish, b) spot (*Leiostomus xanthurus*), and c) silver perch (*Bairdiella chrysoura*) catch. Bolded values indicate statistically significant estimates ($\alpha = 0.1$ level). *k* = degrees of freedom. List of possible models given in Table 1, and AIC model rankings in Table A4.

A) Total Catch
Model: g_6
AIC = 599.66, *k* = 4

Variable	Estimate	Std. Error	Z-Statistic	P
(Intercept)	**-2.82**	0.67	-4.23	**<0.005**
Habitat: Reef	**-0.33**	0.18	-1.83	**0.07**
Water Temperature	**0.16**	0.02	6.27	**<0.005**

B) Spot Catch
Model g_6
AIC = 458.17, *k* = 4

Variable	Estimate	Std. Error	Z-Statistic	P
(Intercept)	**-7.32**	1.11	-6.59	**<0.005**
Habitat: Reef	**-0.49**	0.26	-1.86	**0.06**
Water Temperature	**0.29**	0.04	7.08	**<0.005**

C) Silver Perch Catch
Model: g_4
AIC = 205.11, *k* = 9

Variable	Estimate	Std. Error	Z-Statistic	P
(Intercept)	**-1.15**	0.50	-2.29	**0.02**
Habitat: Reef	-0.48	0.71	-0.68	0.50
Month: July	-1.15	0.85	-1.35	0.18
Month: August	**-1.60**	0.86	-1.86	**0.06**
Month: October	-0.43	0.74	-0.58	0.56
Habitat: Reef*Month: July	**2.67**	1.12	2.39	**0.02**
Habitat: Reef*Month: August	0.97	1.17	0.83	0.41
Habitat: Reef*Month: October	-0.69	1.14	-0.61	0.54

Table 8: Parameter estimates from the best fit generalized linear models for a) large (> 190 mm) and b) small (< 190 mm) Atlantic croaker (*Micropognias undulatus*) presence or absence. Bolded values indicate statistically significant estimates ($\alpha = 0.1$ level). List of possible models given in Table 1, and AIC model rankings in Table A5.

A) Large Croaker
Model: g_2
AIC = 75.02, k = 2

Variable	Estimate	Std. Error	Z-Statistic	P
(Intercept)	**-1.34**	0.46	-2.93	**<0.005**
Habitat: Reef	**1.21**	0.59	2.06	**0.04**

B) Small Croaker
Model: g_2
AIC = 50.91, k = 2

Variable	Estimate	Std. Error	Z-Statistic	P
(Intercept)	-0.26	0.42	-0.62	0.53
Habitat: Reef	**-1.68**	0.75	-2.25	**0.02**

Table 9: Sample size (number of gill net sets and number of individuals) and size range of fish examined for stomach contents by species and habitat type in the a) monthly survey and b) 24-hour survey. Lengths are total lengths. Total number of sets during monthly survey: Reef = 45, Control = 44. Total number of sets during 24-hour survey number: Reef = 13, Control = 12.

A) Monthly Survey

Species	Habitat	Sets with Fish	# of Fish Sampled	Mean Length (mm)	Range (mm)
Silver perch *(Bairdiella chrysoura)*	Control	14	28	124.9	109 - 152
	Reef	22	43	129.6	111 - 159
Spot (*Leiostomus xanthurus)*	Control	34	113	108.4	92 - 230
	Reef	33	114	109.0	93 - 234
Atlantic croaker *(Micropogonias undulatus)*	Control	15	22	188.6	106 - 330
	Reef	18	24	246.1	113 - 315

B) 24-hour Survey

Species	Habitat	Sets with Fish	# of Fish Sampled	Mean Length (mm)	Range (mm)
Silver perch *(Bairdiella chrysoura)*	Control	11	28	128.3	110 - 157
	Reef	12	42	126.4	106 - 148
Spot (*Leiostomus xanthurus*)	Control	11	66	113.9	96 - 234
	Reef	13	57	134.7	95 - 270
Atlantic croaker *(Micropogonias undulatus)*	Control	4	8	186.4	160 - 277
	Reef	8	27	255.3	189 - 288

Table 10: Parameter estimates from the best-fit generalized linear models for a) silver perch (*Bairdiella chrysoura*) and B) spot (*Leiostomus xanthurus*) stomach fullness during the monthly survey. Bolded values indicate statistically significant estimates ($\alpha = 0.1$ level). List of possible models given in Table 2a, and AIC model rankings in Table A8.

A) Silver Perch
Model**:** g_2
AIC = 91.9, *k* = 3

Variable	Estimate	Std. Error	t-Statistic	P
(Intercept)	**-8.58**	0.48	-17.93	**<0.005**
Habitat: Reef	**1.59**	0.63	2.53	**0.02**

B) Spot
Model: g_2
AIC = 190.02, *k* = 7

Variable	Estimate	Std. Error	t-Statistic	P
(Intercept)	**-6.61**	0.31	-21.15	**<0.005**
Habitat: Reef	-0.04	0.26	-0.14	0.89
Month: July	**-1.33**	0.42	-3.19	**<0.005**
Month: August	**-1.47**	0.37	-4.00	**<0.005**
Month: September	**-1.18**	0.43	-2.77	**0.01**
Month: October	**-0.98**	0.43	-2.30	**0.03**

Table 11: Parameter estimates from the best-fit generalized linear models for a) silver perch (*Bairdiella chrysoura*) and spot (*Leiostomus xanthurus*) stomach fullness during the 24-hour survey. Bolded values indicate statistically significant estimates ($\alpha = 0.1$ level). List of possible models given in Table 2b, and AIC model rankings in Table A9.

A) Silver Perch
Model: g_4
AIC = 80.0, k = 8

Variable	Estimate	Std. Error	t-Statistic	P
(Intercept)	**-8.07**	0.75	-10.81	**<0.005**
Habitat: Reef	**1.07**	0.54	1.96	**0.07**
Set Time: 13:00	0.89	0.96	0.93	0.37
Set Time: 17:00	0.27	0.96	0.28	0.78
Set Time: 21:00	0.69	0.96	0.72	0.48
Set Time: 01:00	**2.99**	1.04	2.87	**0.01**
Set Time: 05:00	**2.36**	0.96	2.45	**0.03**

B) Spot
Model: g_5
AIC = 53.14, k = 4

Variable	Estimate	Std. Error	t-Statistic	P
(Intercept)	**-6.72**	0.25	-27.24	**<0.005**
Habitat: Reef	**-0.61**	0.29	-2.11	**0.05**
Month: September	**-1.39**	0.29	-4.81	**<0.005**

Table 12: Results of SIMPER Analysis between habitats for a) silver perch (*Bairdiella chrysoura*) % F, b) silver perch % W, c) spot (*Leiostomus xanthurus*) % F, and d) spot % W. Av. % F = Average % F; Av. % W = Average % W. Diss/SD = Ratio of average dissimilarity to standard deviation; % Contrib. = Percent contribution of prey type to overall dissimilarity; Cum. % Contrib. = Cumulative percent contribution of prey type to overall dissimilarity.

A) **Silver Perch % F**. Average Dissimilarity: 90.72

Prey Group	Av. % F Control	Av. % F Reef	Diss/SD	% Contrib.	Cum. % Contrib.
Crustacean Unidentified	36.19	1.92	0.82	17.94	17.94
Mysid shrimp	33.33	8.97	1.08	15.47	33.41
Snapping Shrimp	0.00	23.33	0.64	11.90	45.31
Polychaete	24.29	6.15	1.15	10.87	56.18
Amphipod/Isopod	14.76	0.00	0.69	8.97	65.15

B) **Silver Perch % W.** Average Dissimilarity: 94.61

Prey Group	Av. % W Control	Av. % W Reef	Diss/SD	% Contrib.	Cum. % Contrib.
Snapping Shrimp	0.00	33.62	0.72	17.77	17.77
Mysid Shrimp	24.40	8.59	0.71	15.17	32.93
Polychaete	15.43	15.98	0.88	13.88	46.82
Amphipod/Isopod	18.96	0.00	0.64	10.02	56.84
Fish Unidentified	0.00	16.67	0.44	8.81	65.64

C) **Spot % F**. Average Dissimilarity: 57.87

Prey Group	Av. % F Control	Av. % F Reef	Diss/SD	% Contrib.	Cum. % Contrib.
Polychaete	63.85	47.18	1.31	27.19	27.19
Copepod	34.48	48.09	1.20	27.05	54.24
Unidentified Material	16.81	24.33	0.90	17.75	71.99

D) **Spot % W**. Average Dissimilarity: 47.02

Prey Group	Av. % W Control	Av. % W Reef	Diss/SD	% Contrib.	Cum. % Contrib.
Polychaete	79.78	60.13	1.18	42.79	42.79
Copepod	8.03	15.80	0.72	21.32	64.11
Unidentified Material	8.42	11.20	0.56	18.35	82.46

Table 13: Ivlev's Foraging Ratio (*FR*) and Electivity (*E*) indices for selected prey types of silver perch (*Bairdiella chrysoura*), spot (*Leiostomus xanthurus*), and Atlantic croaker (*Micropogonias undulatus*) collected from oyster reef habitat during the monthly survey. The symbol (+) suggests selection for a particular prey type, and (–) suggests avoidance. Biomass:Biomass indicates prey % W used as r_i and relative prey biomass in the environment used as p_i in index calculation. Biomass:Abundance indicates prey % W used as r_i and relative prey abundance in environment used as p_i in index calculation.

Species	**Prey Groups**	**Ivlev's *FR***		**Ivlev's *E***	
		Biomass: Biomass	Biomass: Abundance	Biomass: Biomass	Biomass: Abundance
Silver perch	Snapping Shrimp	3.25 (+)	15.6 (+)	0.53 (+)	0.88 (+)
	Polychaete	9.46 (+)	1.90 (+)	0.81 (+)	0.31 (+)
	Goby	0.28 (–)	0.42 (–)	-0.56 (–)	-0.40 (–)
	Crabs	0.11 (–)	1.64 (+)	-0.81 (–)	0.24 (+)
Spot	Polychaete	13.7 (+)	2.74 (+)	0.86 (+)	0.47 (+)
	Tunicate	0.60 (–)	0.28 (–)	-0.25 (–)	-0.56 (–)
Atlantic croaker	Polychaete	11.8 (+)	2.36 (+)	0.84 (+)	0.40 (+)
	Clam	3.19 (+)	41.94 (+)	0.52 (+)	0.95 (+)
	Goby	0.03 (–)	0.05 (–)	-0.93 (–)	-0.90 (–)
	Mussel	0.87 (–)	8.75 (+)	-0.07 (–)	0.79 (+)

Table 14: A) Estimates of silver perch (*Bairdiella chrysoura*) daily consumption (g prey consumed g predator^{-1} day^{-1}), daily consumption per individual (g prey consumed fish^{-1} day^{-1}), and total daily caloric intake (calories day^{-1}) by habitat type and month. B) Total daily caloric intake by habitat type, estimated using % W estimations from the monthly and 24-hour surveys and identical daily consumption rates (set at the July-Reef estimate of 0.020 g prey consumed g predator^{-1} day^{-1}).

A) Varying Consumption Rates & Diet Composition

Month	**Habitat**	**Consumption (S.E.)**	**Consumption per ind.**	**Calories day^{-1} (Monthly % W)**	**Calories day^{-1} (24-H % W)**
July	Reef	0.020 (0.007)	0.514	585.4	590.6
	Control	0.011 (0.006)	0.288	232.1	348.2
Sept	Reef	0.018 (0.005)	0.453	515.3	519.9
	Control	0.003 (0.001)	0.074	60.1	90.1

B) Identical Consumption Rates & Varying Diet Composition

Month	**Habitat**	**Consumption**	**Consumption per ind.**	**Calories day^{-1} (Monthly % W)**	**Calories day^{-1} (24-H % W)**
--	Reef	0.020	0.514	585.4	590.6
	Control	0.020	0.514	414.9	622.2

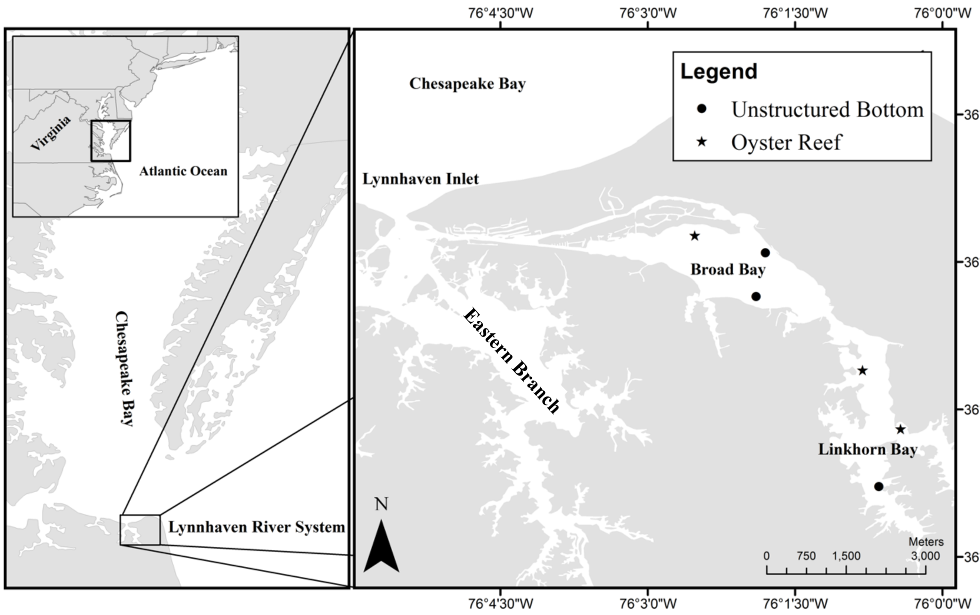

Figure 1: Map of study location and sample sites in the Lynnhaven River System, Virginia, USA. Stars denote restored oyster reefs sites and circles denote unstructured bottom control sites.

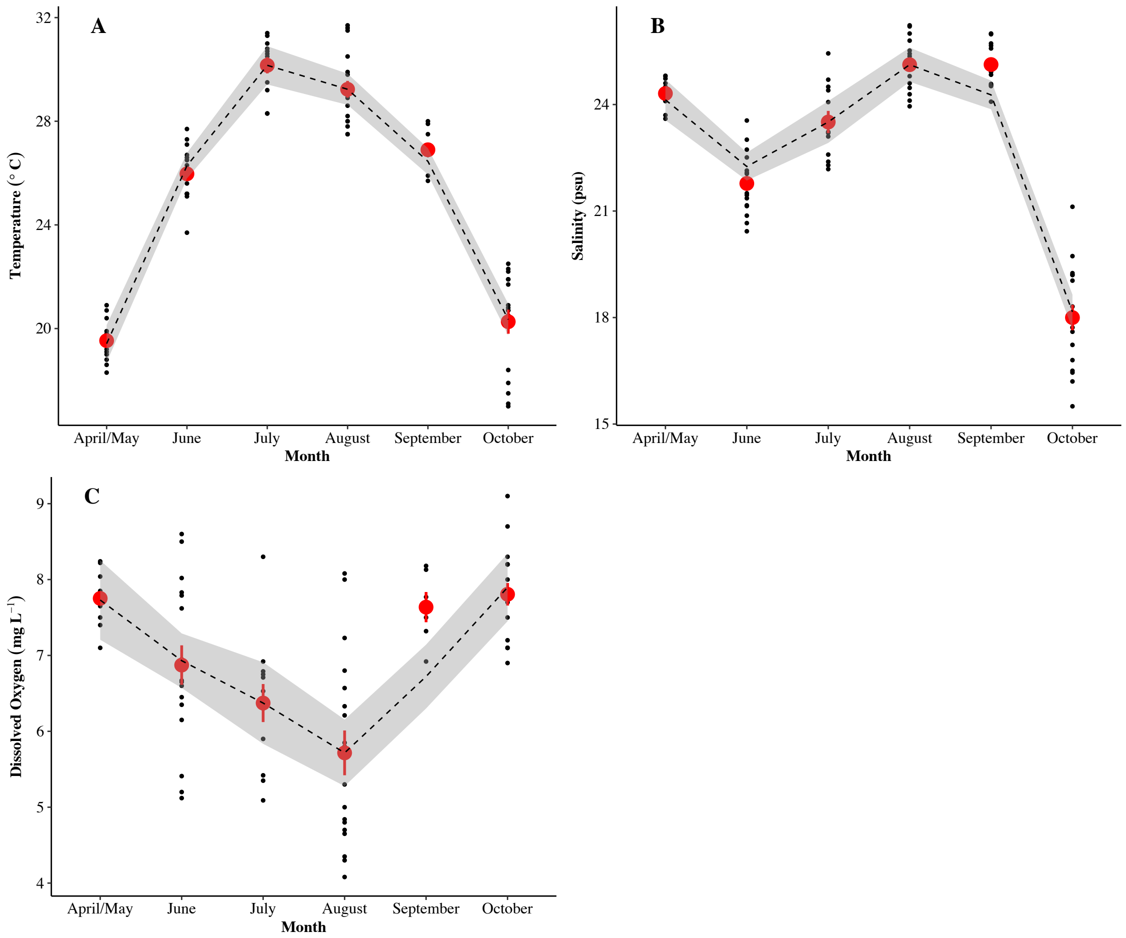

Figure 2: Mean a) Temperature, b) Salinity, and c) Dissolved oxygen recorded at all sites during the study period (April – October 2016). Black points represent individual observations and red points represent the monthly mean. Loess smoothing function (dotted line) and estimated 95 % confidence interval (grey shading) added to visualize seasonal trends. Note the change in y-axis scales among plots.

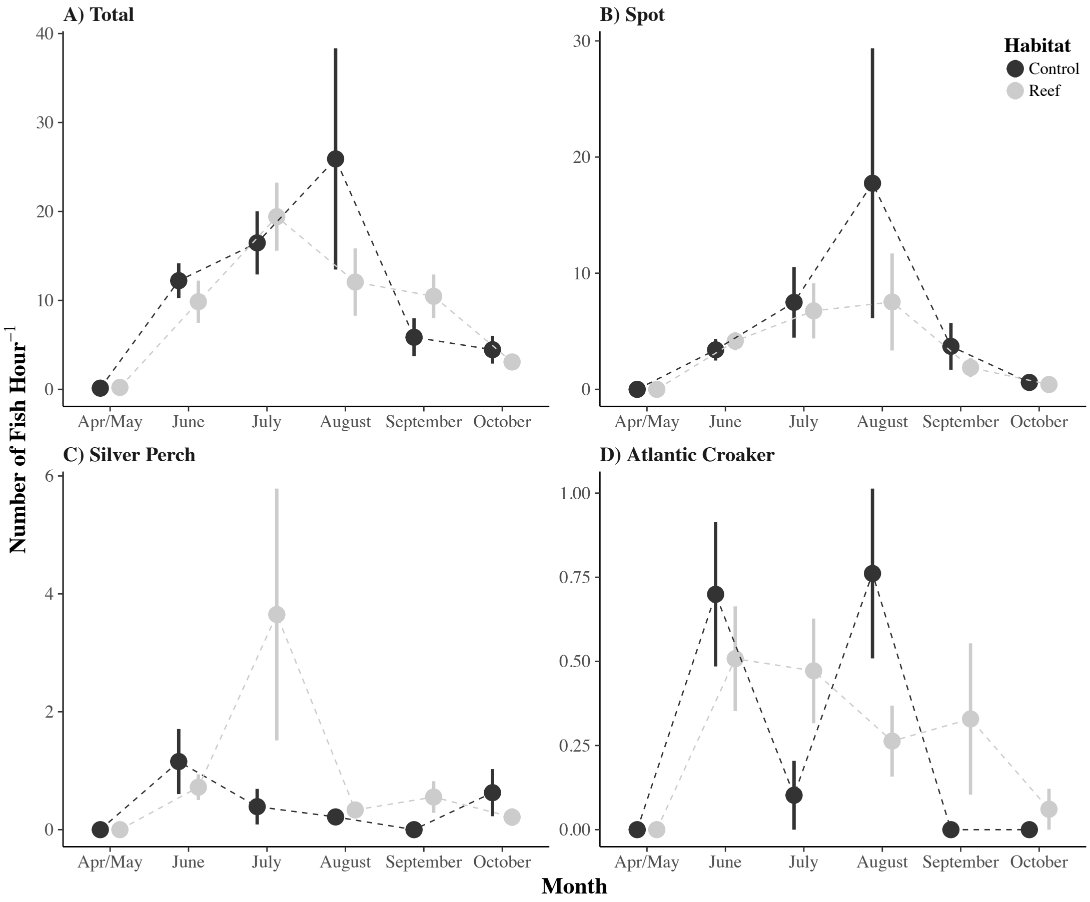

Figure 3: Mean (± 1 s.e.) relative abundance (gill net catch per unit effort [CPUE]; number of fish caught hour^{-1}) of fish by habitat type and month, April – October 2016. A) All fish collected; B) Spot (*Leiostomus xanthurus*); C) Silver perch (*Bairdiella chrysoura*); D) Atlantic croaker (*Micropogonias undulatus*). Note change in y-axis scales among plots.

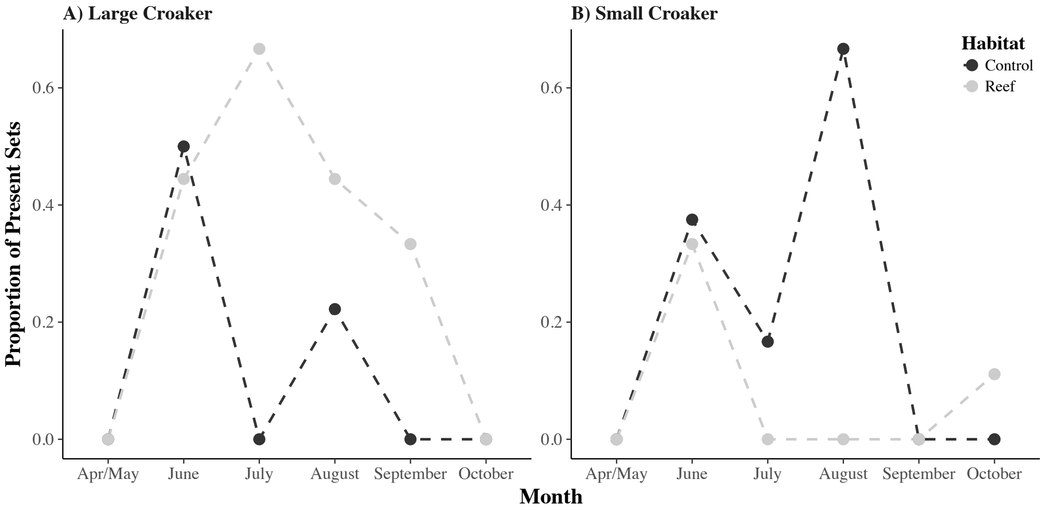

Figure 4: Proportion of gill net sets with at least one a) large (> 190 mm) and b) small (< 190 mm) Atlantic croaker (*Micropogonias undulatus*) by month and habitat type, April – October 2016.

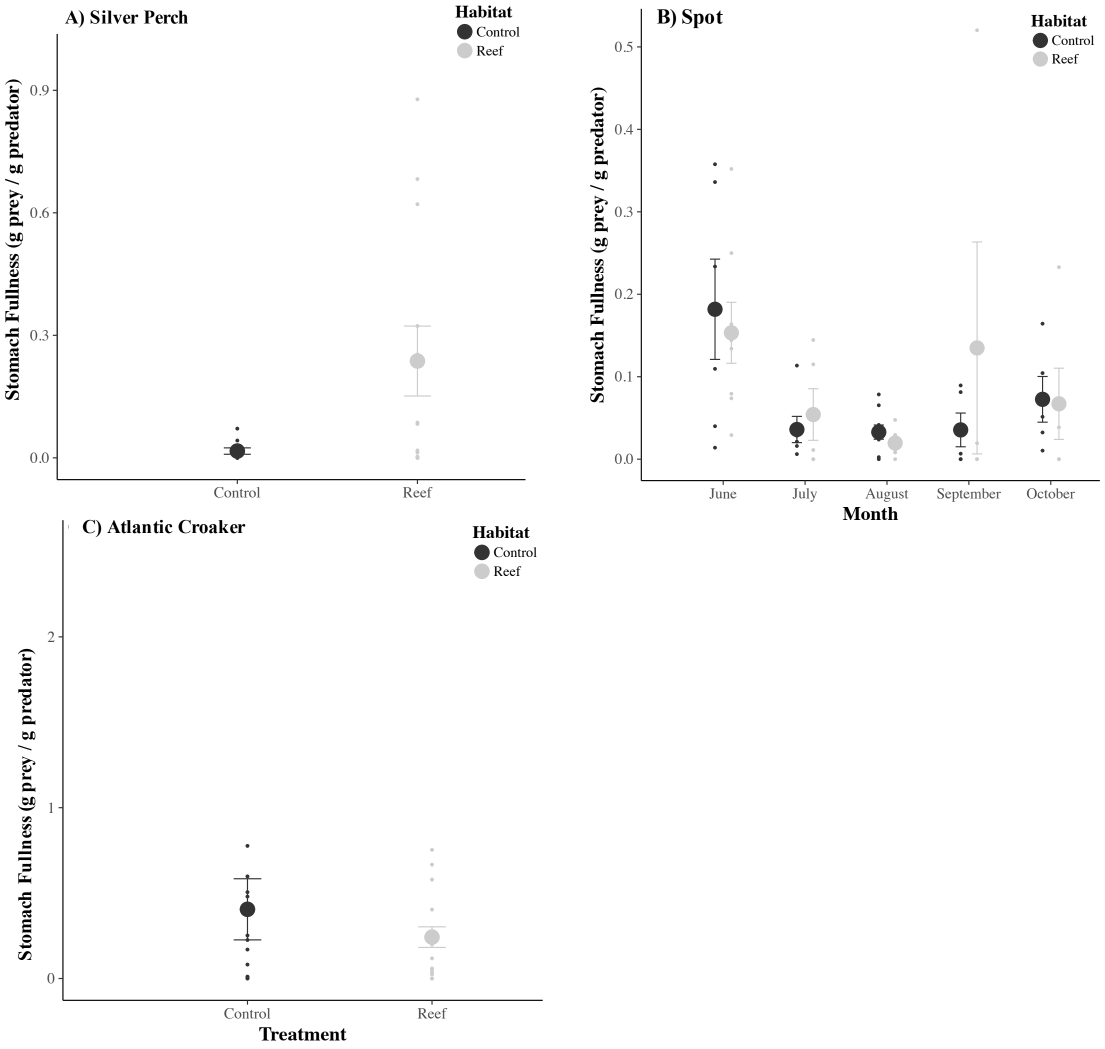

Figure 5: Mean (± 1 s.e.) stomach fullness (g prey g predator^{-1}) of a) silver perch (*Bairdiella chrysoura*) b) spot (*Leiostomus xanthurus*) and c) Atlantic croaker (*Micropogonias undulatus*) by habitat type (silver perch & croaker) and month (spot). Small points indicate individual observations (mean fullness per gill net set). Note change in y-axis scales among plots.

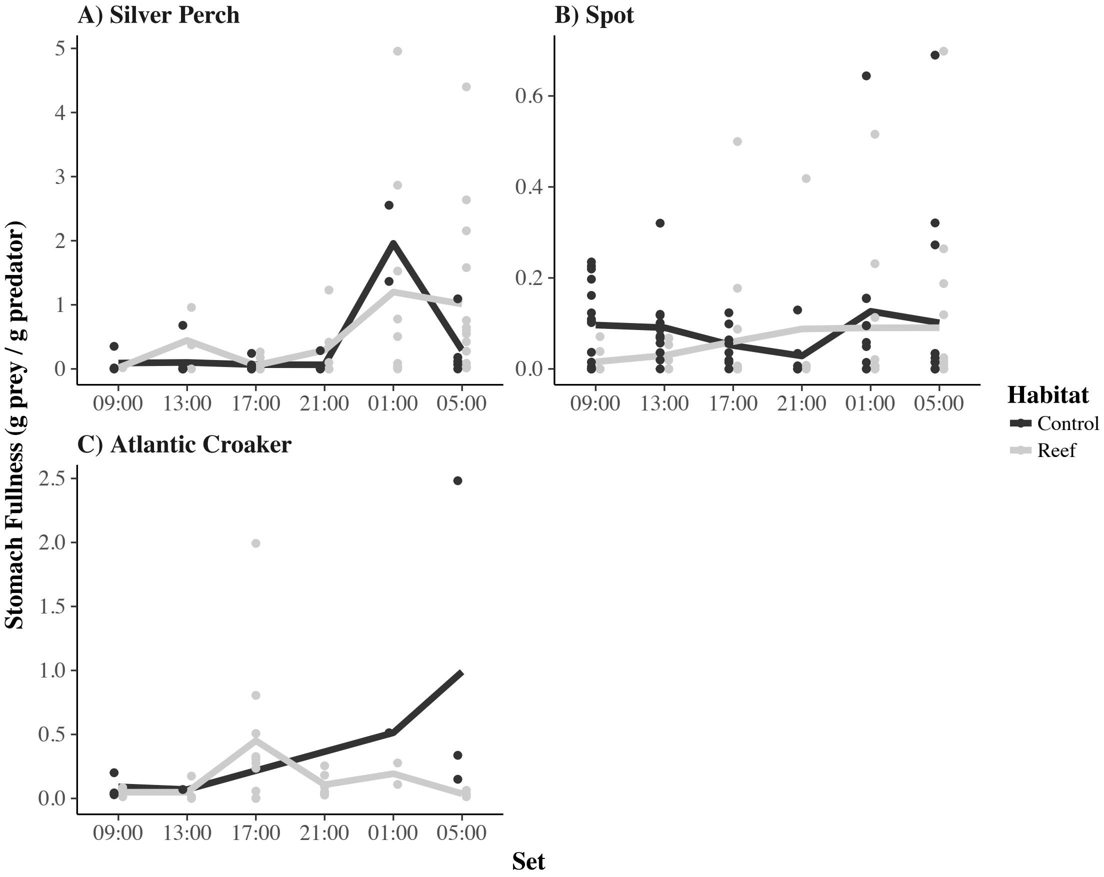

Figure 6: Mean (± 1 s.e.) stomach fullness (g prey g predator^{-1}) of a) silver perch (*Bairdiella chrysoura*), b) spot (*Leiostomus xanthurus*), and c) Atlantic croaker (*Micropogonias undulatus*) by habitat type and set time observed during the 24-hour survey in July and September 2016. Small points represent stomach fullness values of individual fish. Note change in y-axis scales among plots.

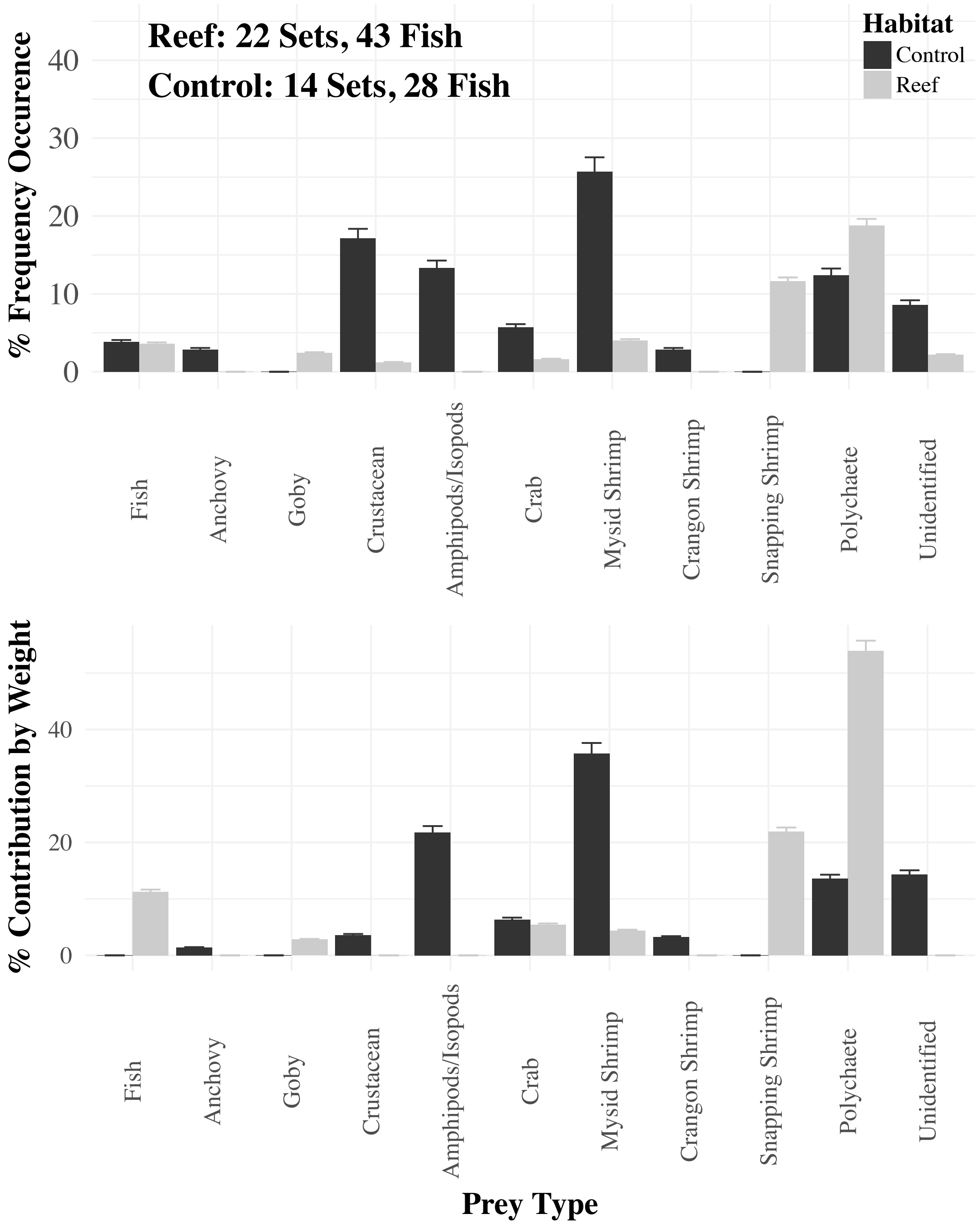

Figure 7: Mean (± 1 s.e.) frequency of occurrence (% F; upper panel) and percent by weight (% W; lower panel) of major prey types in the stomachs of silver perch (*Bairdiella chrysoura*) during the monthly survey, estimated by habitat type. Number of clusters (gill net sets) and number of fish sampled reported in upper panel. Prey types detailed in Table 3. Prey types plotted if they exceeded 3 % F.

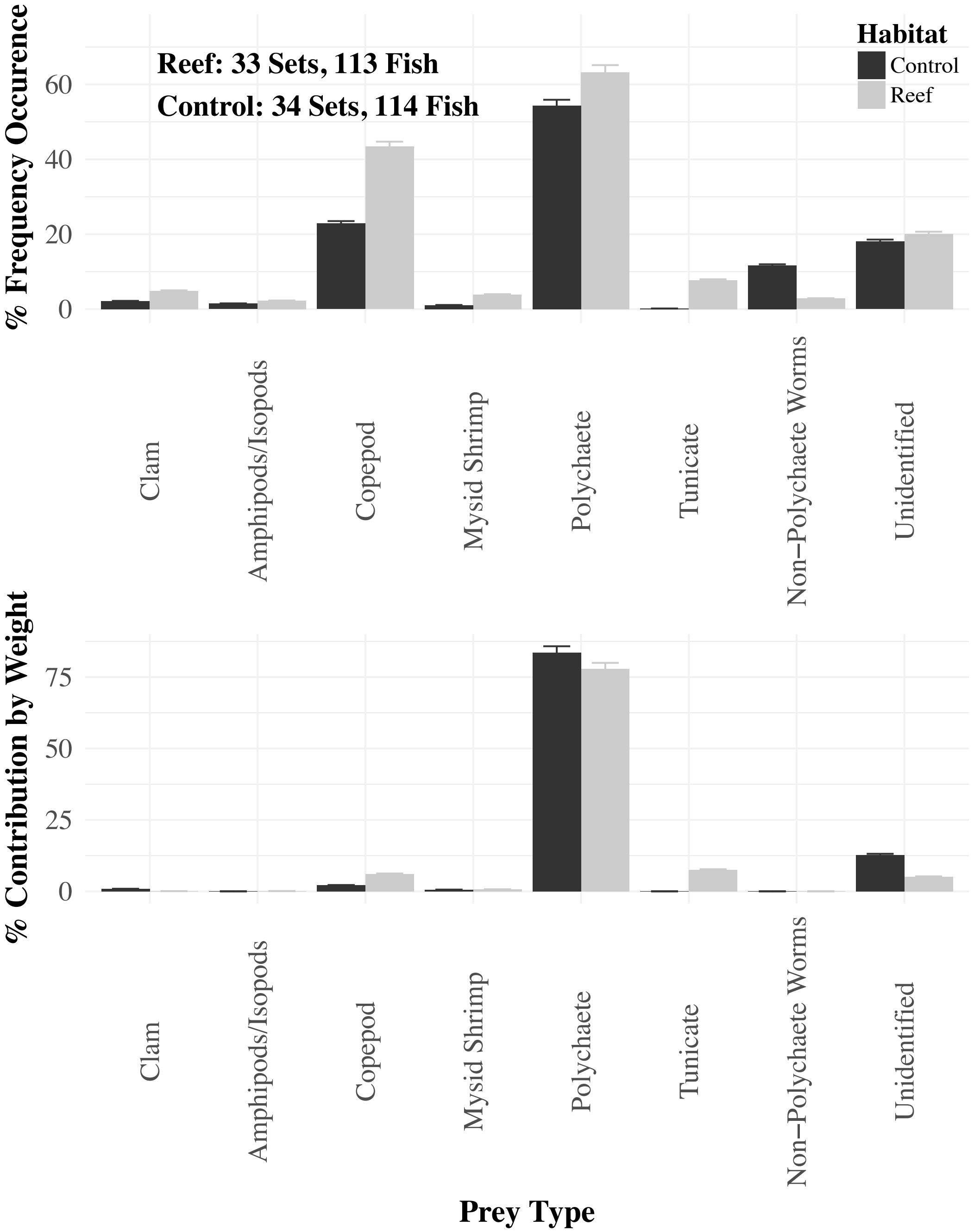

Figure 8: Mean (± 1 s.e.) % F (upper panel) and % W (lower panel) of major prey types in the stomachs of spot (*Leiostomus xanthurus*) during the monthly survey, estimated by habitat type. Number of clusters (gill net sets) and number of fish sampled reported in upper panel. Prey types detailed in Table 3.

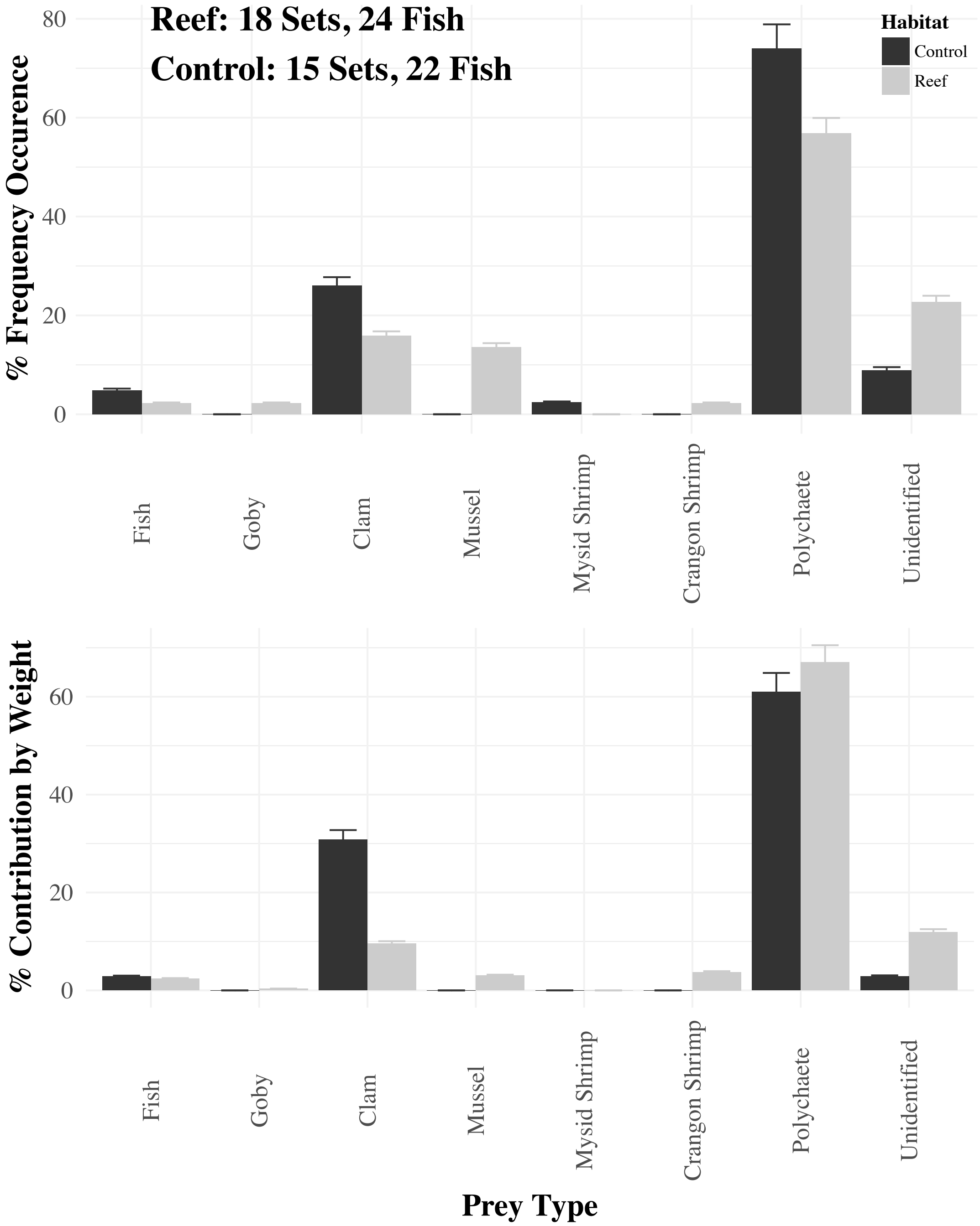

Figure 9: Mean (± 1 s.e.) % F (upper panel) and % W (lower panel) of major prey types in the stomachs of Atlantic croaker (*Micropogonias undulatus*) during the monthly survey, estimated by habitat type. Number of clusters (gill net sets) and number of fish sampled reported in upper panel. Prey types detailed in Table 3.

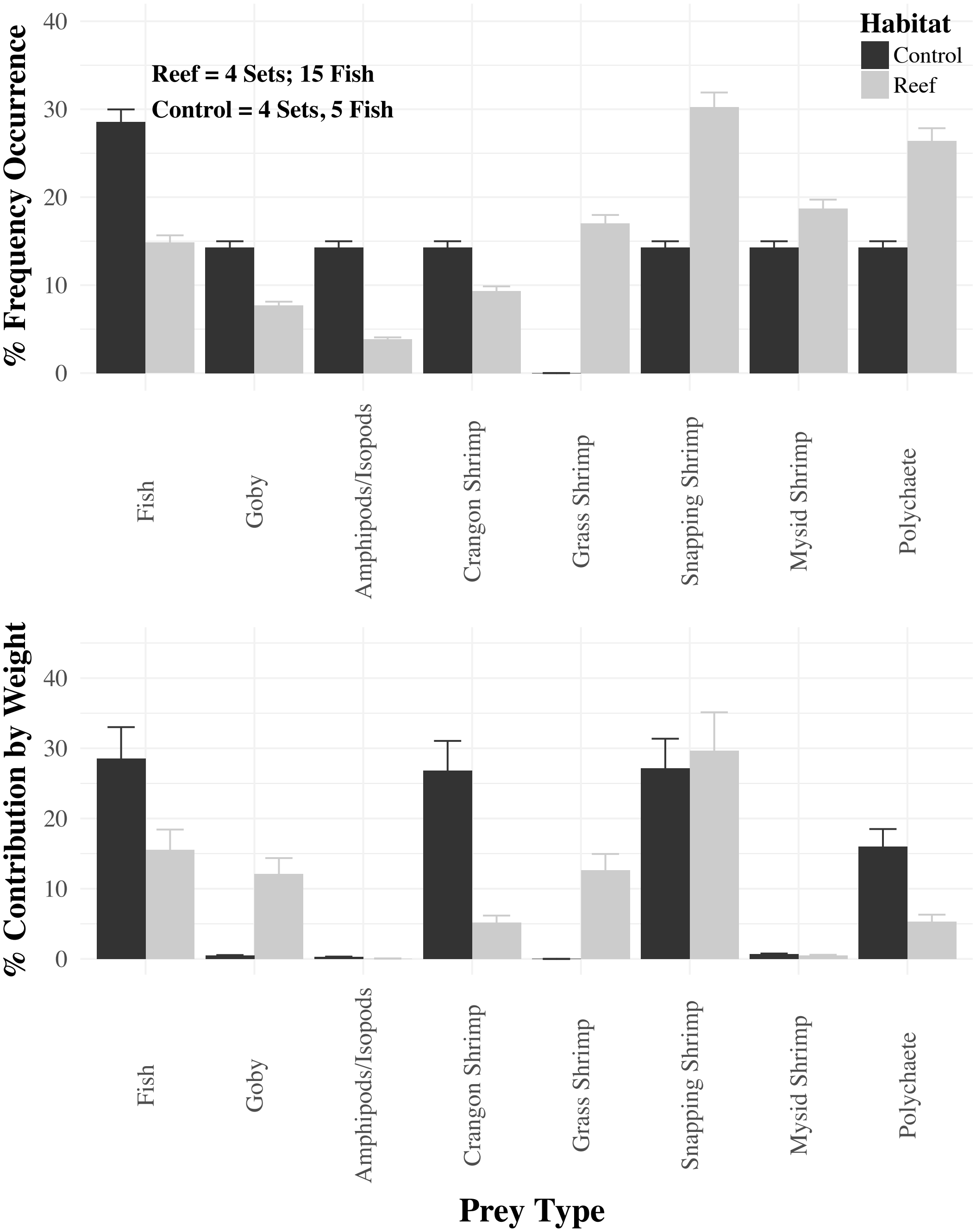

Figure 10: Mean (± 1 s.e.) % F (upper panel) and % W (lower panel) of major prey types in the stomachs of silver perch (*Bairdiella chrysoura*) during peak feeding hours (1 am – 9 am) of the 24-hour survey, estimated by habitat type. Number of clusters (gill net sets) and number of fish sampled reported in upper panel. Prey types detailed in Table 3.

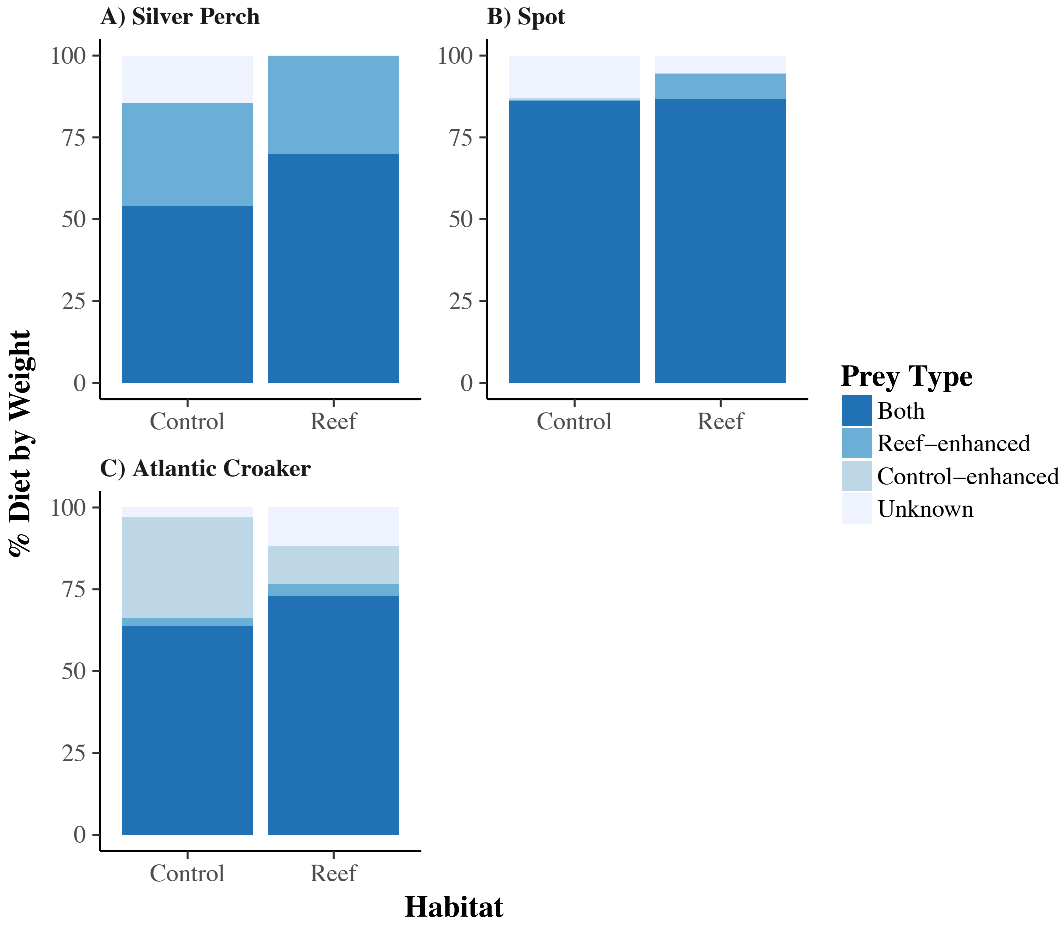

Figure 11: Percent contribution by weight of prey-habitat categories to the diets of a) silver perch (*Bairdiella chrysoura*), b) spot (*Leiostomus xanthurus*), and c) Atlantic croaker (*Micropogonias undulatus*) collected from restored oyster reef and control habitats during the monthly survey. 'Both' indicates prey types found in both habitats types; 'Reef-enhanced' indicates prey types found in higher abundance or biomass on oyster reefs compared to unstructured control bottom; 'Control-enhanced' indicates prey types found in higher abundance or biomass in unstructured control bottom. 'Unknown' used for unidentified material with uncertain habitat origin. Habitat designations (Table 3) based on prey abundance and biomass data (Table 4).

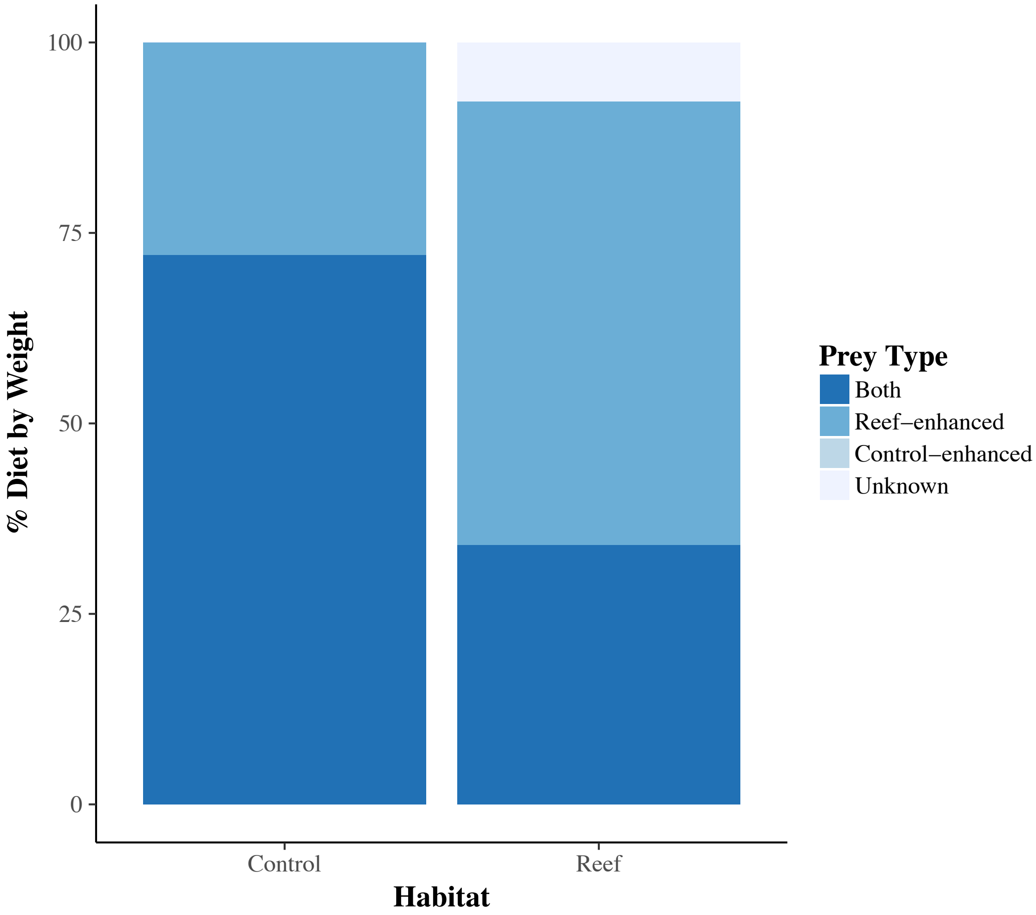

Figure 12: Percent contribution by weight of prey-habitat categories to the diet of silver perch (*Bairdiella chrysoura*), estimated from stomach content data taken during peak feeding hours (1 am – 9 am; 240-hour survey). ‘Both’ indicates prey types found in both habitats types; ‘Reef-enhanced’ indicates prey types found in higher abundance or biomass on oyster reefs compared to unstructured control bottom; ‘Control-enhanced’ indicates prey types found in higher abundance or biomass in unstructured control bottom. ‘Unknown’ used for unidentified material with uncertain habitat origin. Habitat designations (Table 3) based on prey abundance and biomass data (Table 4).

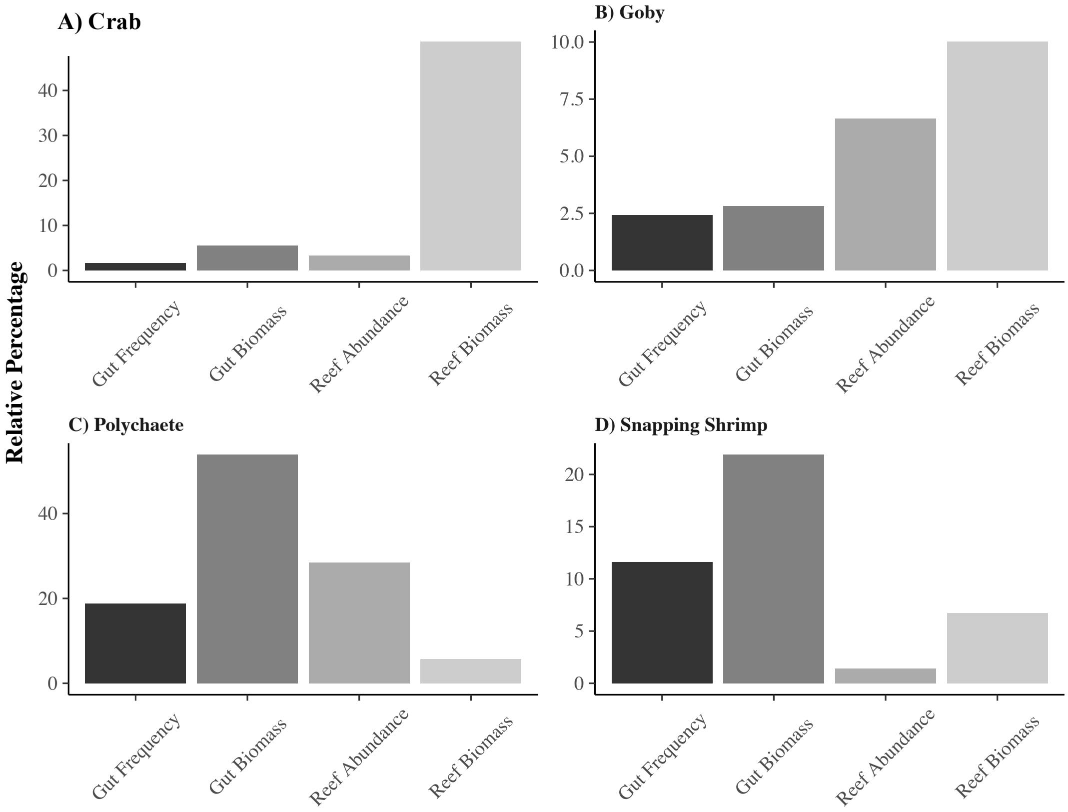

Figure 13: Mean % F (Gut Frequency), % W (Gut Biomass), relative abundance (Reef Abundance), and relative biomass (Reef Biomass) of selected prey types in the stomachs of silver perch (*Bairdiella chrysoura*) and on restored oyster reefs. A) Crabs (Xanthid mud crabs & *Callinectes sapidus*), B) Naked gobies (*Gobiosoma bosc*), C) Polychaete worms, D) Snapping shrimp (*Alpheus heterochaelis*).

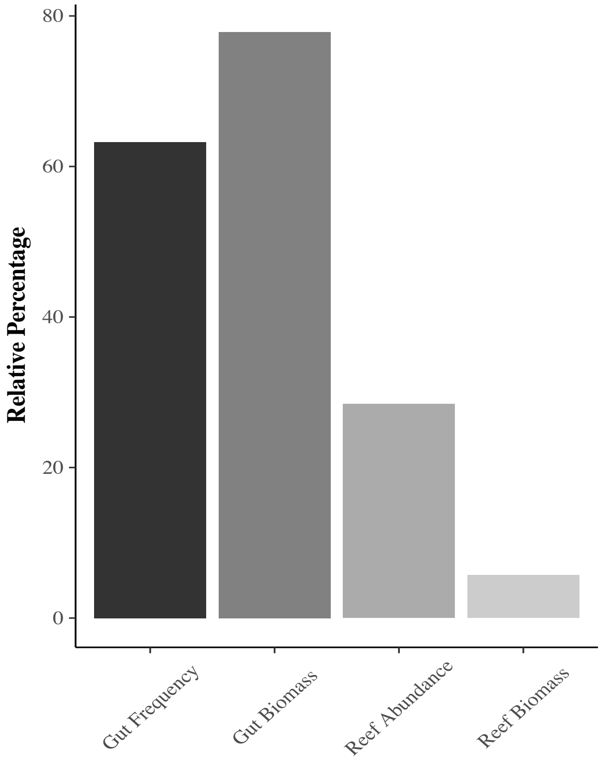

Figure 14: Mean % F (Gut Frequency), % W (Gut Biomass), relative abundance (Reef Abundance), and relative biomass (Reef Biomass) of polychaete worms in the stomachs of spot *(Leiostomus xanthurus*) and on restored oyster reefs.

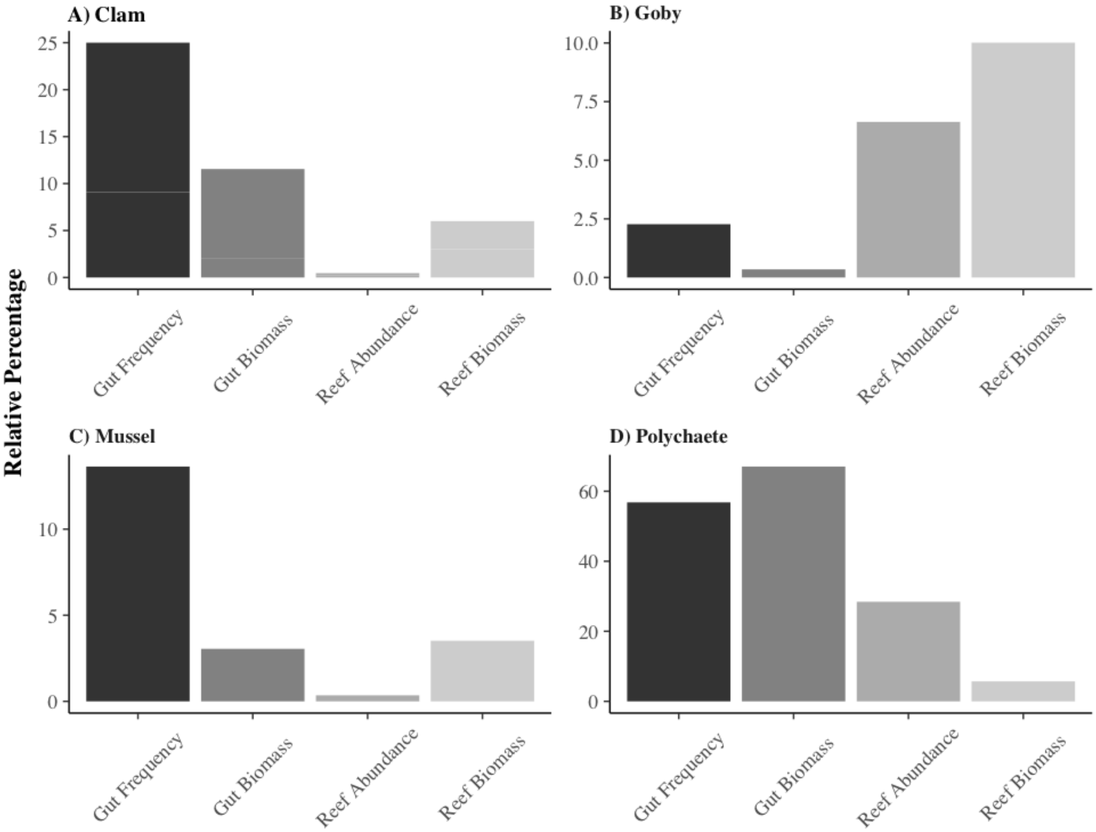

Figure 15: Mean % F (Gut Frequency), % W (Gut Biomass), relative abundance (Reef Abundance), and relative biomass (Reef Biomass) of selected prey types in the stomachs of Atlantic croaker (*Micropogonias undulatus*) and on restored oyster reefs. A) Clams, B) Naked gobies (*Gobiosoma bosc*), C) Mussels, and D) Polychaete worms.

APPENDIX

Table A1: Restored oyster reef site characteristics. Bold values exceed the target metrics established by Chesapeake Bay Program for oyster restoration. Data from Lipcius et al. 2015.

Site	Oyster Density (m^{-2})	Oyster Biomass ($g\ m^{-2}$)	Total Reef Area (ha)
Broad Bay Reef 3	**55.4**	31.1	4.86
Linkhorn Bay Reef 1	49.3	42.0	3.24
Linkhorn Bay Reef 2	**74.8**	**117.5**	5.67

Table A2: Species collected via otter trawl from restored oyster reef and unstructured (control) bottom in the Lynnhaven River System, April – July 2016.

***Scientific Name* (Common Name)**	**Number of Individuals** Oyster Reef	 Control
Leiostomus xanthurus (Spot)	231	344
Anchoa mitchilli (Bay anchovy)	182	293
Micropogonias undulatus (Atlantic croaker)	23	19
Bairdiella chrysoura (Silver perch)	15	2
Anchoa hepsetus (Striped anchovy)	12	5
Lagodon rhomboides (Pinfish)	6	2
Opsanus tau (Oyster toadfish)	6	2
Paralichthys dentatus (Summer flounder)	3	4
Trinectes maculatus (Hogchoker)	2	4
Brevoortia tyrannus (Atlantic menhaden)	1	0
Hippocampus erectus (Lined seahorse)	1	0
Orthopristis chrysoptera (Pigfish)	1	0
Urophycis regia (Spotted hake)	1	0
Chaetodipterus faber (Atlantic spadefish)	0	2
Gobiosoma bosc (Naked goby)	0	1
Menidia menidia (Atlantic silverside)	0	1
Prionotus carolinus (Northern sea robin)	0	1
Symphurus plagiusa (Black-cheek tonguefish)	0	1
Callinectes sapidus (Blue crab)	61	52
Total Individuals	545	733

Table A3: Species collected via gill net from one restored oyster reef and one unstructured (control) bottom in the Lynnhaven River System during two 24-hour sampling events in July and September 2016.

	Number of Individuals	
***Scientific Name* (Common Name)**	Oyster Reef	Control
Leiostomus xanthurus (Spot)	77	231
Bairdiella chrysoura (Silver perch)	52	28
Micropogonias undulatus (Atlantic croaker)	27	8
Pomatomus saltatrix (Bluefish)	5	2
Cynoscion regalis (Weakfish)	3	0
Trinectes maculatus (Hogchoker)	3	0
Cynoscion nebulosus (Speckled trout)	2	0
Lagodon rhomboides (Pinfish)	1	0
Pogonias cromis (Black drum)	1	1
Prionotus carolinus (Northern sea robin)	1	2
Scomberomorus maculatus (Spanish mackerel)	1	0
Lutjanus griseus (Gray snapper)	0	1
Mentichirrus americanus (Southern kingfish)	0	3
Total Individuals	173	276

Table A4: AIC results for generalized linear model analysis of fish abundance. A) Total fish, b) spot (*Leiostomus xanthurus*), c) silver perch (*Bairdiella chrysoura*) and d) silver perch (without outlier) catch. The five models with the lowest AIC values are listed for each response, and ranked in order of increasing AIC value. ΔAIC = difference in AIC from top model, k = model degrees of freedom, and w_i = Akaike weights. Bold indicates best-fit model. See Table 1 for model descriptions.

A) Total Catch

Model	k	AIC	ΔAIC	w_i
g_6	**4**	**599.66**	**0.00**	**0.49**
g_9	5	601.01	1.35	0.25
g_{11}	5	601.66	2.00	0.18
g_8	9	603.91	4.26	0.06
g_3	7	606.99	7.34	0.01

B) Spot Catch

Model	k	AIC	ΔAIC	w_i
g_6	**4**	**458.17**	**0.00**	**0.37**
g_{11}	5	459.98	1.81	0.15
g_8	9	460.02	1.85	0.15
g_9	5	460.12	1.95	0.14
g_{10}	8	460.43	2.25	0.12

C) Silver Perch Catch

Model	k	AIC	ΔAIC	w_i
g_4	**9**	**205.11**	**0.00**	**0.41**
g_3	6	206.80	1.68	0.18
g_1	2	207.21	2.10	0.14
g_2	3	208.33	3.22	0.08
g_6	4	209.21	4.10	0.05

D) Silver Perch Catch (outlier removed)

Model	k	AIC	ΔAIC	w_i
g_1	**2**	**187.17**	**0.00**	**0.48**
g_2	3	189.16	1.99	0.18
g_3	6	190.98	3.81	0.07
g_7	4	191.16	3.98	0.07
g_6	4	191.16	3.99	0.07

Table A5: AIC results for generalized linear model analysis of Atlantic croaker (*Micropogonias undulatus*) presence or absence. A) Large (> 190 mm) and B) Small (< 190 mm) Atlantic croaker. The five models with the lowest AIC values are listed for each response, and ranked in order of increasing AIC value. ΔAIC = difference in AIC from top model, k = model degrees of freedom, and w_i = Akaike weights. Bold indicates best-fit model. See Table 1 for model descriptions.

A) Large Croaker

Model	**k**	**AIC**	**ΔAIC**	**w_i**
g_2	**2**	**75.02**	**0.00**	**0.26**
g_6	3	76.01	0.98	0.16
g_7	3	76.35	1.33	0.13
g_4	8	76.63	1.61	0.12
g_1	1	77.56	2.54	0.07

B) Small Croaker

Model	**k**	**AIC**	**ΔAIC**	**w_i**
g_4	6	50.91	0.00	0.4
g_8	6	53.40	2.50	0.11
g_3	4	53.45	2.54	0.11
g_2	**2**	**53.58**	**2.67**	**0.10**
g_5	4	54.40	3.50	0.07

Table A6: % F, sample size (number of gill net sets, number of fish examined), and size range (total length, mm) of all individuals examined during monthly survey diet analysis. Prey types defined in Table 3.

Scientific Name	Habitat	# of Sets/ Fish	Size Range	Anchovy	Clam	Crab	Crangon	Fishes	Mysid	Paneid Shrmip	Polychaete	Tunicate
Cynoscion nebulosus	Control	2,2	125 – 290	--	--	--	--	50.0	--	--	--	--
	Reef	1,1	335	--	--	--	--	100.0	--	--	--	--
Cynoscion regalis	Control	1,1	183	100.0	--	--	--	--	--	--	--	--
	Reef	2,2	190 - 306	--	--	--	--	--	--	--	50.0	--
Eucinostomus argenteus	Control	1,1	126	--	--	--	--	--	--	--	100.0	--
Lagodon rhomboides	Control	1,1	158	--	--	--	--	--	--	--	100.0	100.0
	Reef	1,1	149	--	100.0	--	100.0	--	--	--	--	--
Menticirrhus saxatilis	Reef	1,1	310	--	--	--	--	--	--	100.0	--	--
Pogonias cromis	Control	1,1	213	--	100.0	--	--	--	--	--	100.0	--
Pomatomus saltatrix	Control	4,1	126 – 485	20.0	--	--	20.0	60.0	--	--	--	--
	Reef	4,1	140 – 410	33.3	--	--	--	50.0	--	--	--	--
Prionotus carolinus	Control	2,1	116 – 140	--	--	75.0	--	--	--	--	50.0	--
	Reef	2,1	124 – 149	--	--	--	--	--	75.0	--	--	25.0

Table A7: % W of all individuals examined during monthly survey diet analysis. Sample size given in Table A6. Prey types defined in Table 3.

Scientific Name	**Habitat**	Anchovy	Clam	Crab	Crangon	Fishes	Mysid	Paneid Shrimp	Polychaete	Tunicate
Cynoscion nebulosus	Control	--	--	--	--	100.0	--	--	--	--
	Reef	--	--	--	--	100.0	--	--	--	--
Cynoscion regalis	Control	100.0	--	--	--	--	--	--	--	--
	Reef	--	--	--	--	--	--	--	100.0	--
Eucinostomus argenteus	Control	--	--	--	--	--	--	--	100.0	--
Lagodon rhomboides	Control	--	--	--	--	--	--	--	64.8	35.2
	Reef	--	78.4	--	21.6	--	--	--	--	--
Menticirrhus saxatilis	Reef	--	--	--	--	--	--	100.0	--	--
Pogonias cromis	Control	--	22.6	--	--	--	--	--	77.4	--
Pomatomus saltatrix	Control	25.0	--	--	12.8	62.2	--	--	--	--
	Reef	44.8	--	--	--	55.2	--	--	--	--
Prionotus carolinus	Control	--	--	77.3	--	--	--	--	7.6	--
	Reef	--	--	--	--	--	64.5	--	--	35.5

Table A8: AIC results for generalized linear model analysis of a) silver perch (*Bairdiella chrysoura*), b) spot (*Leiostomus xanthurus*) and c) Atlantic croaker (*Micropogonias undulatus*) stomach fullness during the monthly survey. Models ranked in order of increasing AIC value. ΔAIC = difference in AIC from top model, k = model degrees of freedom, and w_i = Akaike weights. Bold indicates best-fit model. See Table 2a for model descriptions.

A) Silver Perch

Model	**k**	**AIC**	**ΔAIC**	**w_i**
g_2	**3**	**91.91**	**0.00**	**0.78**
g_3	5	95.78	3.88	0.11
g_1	2	96.05	4.14	0.10

B) Spot

Model	**k**	**AIC**	**ΔAIC**	**w_i**
g_3	**7**	**190.02**	**0.00**	**0.97**
g_1	2	197.55	7.53	0.02
g_2	3	199.53	9.52	0.01

C) Atlantic Croaker

Model	**k**	**AIC**	**ΔAIC**	**w_i**
g_1	2	115.49	0.00	0.73
g_2	3	117.48	1.99	0.27

Table A9: AIC results for generalized linear model analysis of a) silver perch (*Bairdiella chrysoura*), b) spot (*Leiostomus xanthurus*) and c) Atlantic croaker (*Micropogonias undulatus*) stomach fullness during the 24-hour survey. Models ranked in order of increasing AIC value. ΔAIC = difference in AIC from top model, k = model degrees of freedom, and w_i = Akaike weights. Bold indicates best-fit model. See Table 2b for model descriptions.

A) Silver Perch

Model	**k**	**AIC**	**ΔAIC**	**w_i**
g_4	**8**	**80.00**	**0.00**	**0.58**
g_6	9	81.99	1.99	0.22
g_3	7	83.03	3.03	0.12
g_2	3	85.27	5.26	0.04
g_5	4	87.24	7.24	0.02
g_1	2	87.43	7.43	0.01

B) Spot

Model	**k**	**AIC**	**ΔAIC**	**w_i**
g_5	**4**	**53.14**	**0.00**	**0.97**
g_6	9	60.51	7.38	0.02
g_2	3	68.83	15.69	0.00
g_1	2	69.55	16.42	0.00
g_4	8	76.97	23.83	0.00
g_3	7	78.24	25.10	0.00

C) Atlantic Croaker

Model	**k**	**AIC**	**ΔAIC**	**w_i**
g_1	2	35.37	0.00	0.73
g_2	7	37.62	2.25	0.27

VITA

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Born in Norfolk, Virginia, July 19, 1991. Graduated from Nile C. Kinnick High School in Yokosuka, Japan in 2009. Earned a B.S. in Biology from The College of William & Mary in 2013. Entered the M.S. program at the Virginia Institute of Marine Science / College of William and Mary School of Marine Science in 2014.