A Fish Eat Fish World: Trophic Structure of the Fish Communities on Artificial and Natural Reefs in Onslow Bay, NC

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Abstract

Artificial reefs are increasingly being used to compensate for habitat loss due to the degradation of important marine ecosystems from human activities. Artificial reefs are created by intentionally sinking human-made structures to provide hard substrate habitat for fish and other marine organisms. The North Carolina Division of Marine Fisheries (NCDMF) maintains 42 artificial reefs in NC to sustain healthy fish populations (Comer, 2016). However, the ability of artificial reefs to support fish communities similar in diversity and complexity as natural reefs is still debated within the scientific community. In this study, we compared the relative fish abundance, species richness, and quantitative trophic structure of two artificial and two natural reefs located in Onslow Bay, NC. Additionally, we analyzed how the fish community metrics changed throughout the day to better understand the differences in crepuscular activity on the two reef types. The term “crepuscular” refers to the twilight time period, which includes dawn and dusk for this study (Myers, 2016). Species richness, fish abundance, and trophic level were significantly higher on artificial reefs than natural reefs. During dawn and dusk on artificial reefs, there were increases in both fish abundance and average trophic level, suggesting that crepuscular activity is more pronounced on artificial reefs than natural reefs. This difference may be explained by the increased structural complexity or differences in benthic organisms present on artificial reefs. Lastly, we researched the species observed in this study to create a food web as a tool to visualize how the trophic structure varies between artificial and natural reefs. This is the first food web created for this habitat and we hope it can be used by fisherpeople, managers, and members of the public to enhance the understanding of this complex ecosystem and inspire future research.
Background

Located along the mid-Atlantic coastline, North Carolina’s temperate reefs provide habitat for diverse fish populations, including tropical, subtropical, and temperate species. These reefs provide many essential functions for the fish communities that inhabit them. They are federally-designated as Essential Fish Habitats (EFH) because they are important nursery grounds for juvenile fish and provide refugia and foraging grounds for juvenile and adult fishes (National Marine Fisheries Service, 2007). Temperate reefs are hypothesized to act as “stepping stones” for juvenile fish as they migrate from inshore nursery habitats to the offshore habitats during ontogeny (Caddy, 2007). “Stepping stones” are conceptualized as well-connected areas of hard substrate, such as a submerged rocky ledge, that are found along a migration corridor. Juvenile fishes will travel from “stone to stone” while migrating to offshore habitats, as they provide a place of refuge and increase the likelihood of reaching the offshore habitats (Caddy, 2007).

Temperate reefs are home to dense fish populations that are attracted to hard bottom structures in an otherwise sandy bottom dominated ocean ecosystem. Algae and other encrusting species are able to colonize the hard structures of temperate reefs and provide the base of the food web to support a fish community with a diverse trophic structure. Trophic structure is the organization of different trophic levels present in a particular habitat, typically visualized as a pyramid (Figure 1). The largest component of the trophic structure in terms of biomass is the primary producers, and as organisms increase in trophic level, moving up the pyramid, they decrease in abundance. On temperate reefs, fishes occupy trophic levels as primary consumers, mesopredators, and apex predators. The primary consumers are the lowest trophic level and include fishes, such as the bicolor damselfish (*Stegastes partitus*), which eats only algae and...
detritus. The mesopredators, or secondary consumers, are above the primary consumers in the trophic pyramid. An example of a secondary consumer is the white margate (*Haemulon album*), which is an invertivore and eats invertebrates. At the top of the trophic pyramid is the apex predator, which are the highest trophic level organisms in a system. On temperate reefs, the apex predators are large fish such as sand tiger sharks (*Carcharias taurus*), which are piscivorous and eat other fish.

![Trophic structure modeled as a pyramid with the main categories of organisms shown. The trophic levels occupied by fish on temperate reefs are included inside the red rectangle.](image)

In North Carolina, temperate reefs are split into two main categories: natural and artificial. In the tropics, natural reefs are built with corals as the major foundation species; however, reef-building corals are not found in temperate waters. North Carolina’s natural reefs are made of rock formations that provide the structural complexity to support fish communities. They range in shape from low-lying rubble fields and flat pavement to ledges that can be several meters tall (Paxton, 2017). Natural reefs are protected under the Magnusson-Stevens Fishery Conservation and Management Act (2007) as EFH due to their important role in the life cycle of
commercially- and recreationally- relevant fish species, including the federally managed
grouper-snapper complex (South Atlantic Fishery Management Council, 1983).

Artificial reefs are created by intentionally sinking human-made structures, such as
cement pipes or derelict ships. Ships are structurally complex with high vertical relief, making
them ideal habitats for several pelagic fish species (Paxton, 2017). Artificial reefs may be an
effective management procedure to provide additional benthic habitats to fishes, especially as
human activities continue to disturb natural reef habitats. The extent to which artificial reefs are
able to mimic natural habitats is not well explored but is vital for understanding the benefits of
constructing artificial reefs to support large, diverse fish communities.

In this study, we examined differences in the fish communities present on artificial and
natural reefs. By assessing whether and how trophic structure differs between natural and
artificial reefs, we explored the ecological benefits of artificial reefs as a method for mitigating
habitat loss. Additionally, we aimed to understand how trophic structure varies over a diel cycle.
We asked: how does time of day (dawn, day, dusk, and night) impact the trophic structure of the
fish present on natural and artificial reefs? We hypothesized that trophic level would be higher
on artificial reefs than natural reefs due to increased structural complexity that may attract upper-
trophic level predators. We were also interested in how the fish communities changed during
crepuscular periods (the time between day and night), as studies have found increases in activity
during these “crossover” times (Myers, 2016). Our food web visualization will further aid in the
understanding of how different species use artificial reefs. This study will help guide future
management decisions regarding the intentional deployment of derelict ships to create artificial
reefs.
Methods

We selected four temperate reefs within Onslow Bay, NC (Figure 2). Of the four reefs included in the study, the Coast Guard Cutter Spar and the Aeolus are artificial reefs, and West Rock and 210 Rock are natural reefs. The Spar was sunk in 2004 in 34 meters of water. The Aeolus is in 35 meters of water and was sunk in 1988. Both artificial reefs are derelict ships that were intentionally sunk. The two natural reefs, West Rock and 210 Rock, are found in 26 and 32 meters of water respectively, and are both ledges with relatively high rugosity.

Unattended underwater video cameras were deployed on all four sites to capture videos of the reefs. The videos were recorded using GoPro (GoPro, USA) video cameras in GoTubes (Sexton Co., USA), a type of underwater housing that includes a large external battery attached.
to an LED light to illuminate the videos at night. An intervalometer was attached to the GoPro
turning the video camera on every 20 minutes for approximately two weeks, until it was
retrieved. Once the video camera turned on, it recorded a 20-second video, with the LED light
turned on for the last 10 seconds. All the GoPros were deployed by AAUS scientific divers.
Video footage from each reef was analyzed to determine the characteristics of the fish
community present on each reef. The video recordings from three deployments (November 2015,
January 2016 and April 2016) are included in this study. The data from the Aeolus and the CG
Spar were pooled together for the artificial reef data, and the West Rock and 210 Rock data were
pooled together for the natural reef data.

The data from each video were recorded and entered into a Microsoft Access database.
Data entered into the database from each video included the time of day of the video, the fish
species present, the number of each species, the behavior of each species, and the location of
each species in the water column. When counting fish, the number recorded was the maximum
number of each species seen in a single frame (maxN), in order to account for fish that may
swim in and out of view. Fish were identified to the lowest taxonomic level possible. To quantify
trophic structure, the trophic levels of each species of fish were loaded into the fish metadata
from the online reference FishBase (Froese, 2017). Fish that could not be positively identified to
species level were not included in the analysis, though we hope to eventually calculate a trophic
level for them using the average value of all fish of that family. For example, all fish categorized
as “unknown grunt” will be assigned the average value of all fish within the Haemulidae family.
This will allow for a more accurate portrayal of the trophic levels of unidentifiable fish in this
analysis.
Qualitative Methods

A Microsoft Access database was created with each row as a single species of fish from a certain video, with a column for the number of that fish in the video. We developed an R script file to generate a table from the database where each row represents a single fish, and the columns include metadata for the video in which the fish was observed, including site, reef type, time of day, and season. The analysis of the trophic structure of the reef types was done on this table. This R script also creates a matrix with the fish abundance and species richness for each video. This matrix was used to generate plots to compare the two reef types and how the fish communities vary between the four temporal categories. We combined the data from the three deployments, allowing us to analyze how the trophic structure of fish communities varies as a function of reef type (artificial vs. natural) and time of day (dawn vs. day vs. dusk vs. night). To analyze the data, we used a univariate analysis of variance (ANOVA) to determine which factors impacted fish abundance, species richness, and trophic level with a significant p-value. A post-hoc Tukey HSD test was also used to determine which averages were most similar to each other by assigning letters to each value. Groups connected by the same letter are not statistically different from each other.

Quantitative Methods

To create the food web, first we had to determine the predator-prey relationships that were present on the reefs. Using a list of the 61 species that were positively-identified on the four study sites, I collected data from diet composition studies, FishBase.org, a NOAA diet study of North Atlantic fishes, and other scientific literature sources (Froese, 2017; Bowman, 2000; Randall, 1967). These data were put into a predator-prey matrix with the predatory fish as the row headers and the prey as the column header. I researched each fish individually to determine
both its predator and prey species. Additionally, I simplified the equation used by FishBase to recalculate the trophic levels of all of the fish species in my study using only the prey species present on the study sites. I found the unweighted average of the prey species for each fish and added one to determine a new, recalculated trophic level, then compared it to the literature value from FishBase (Froese, 2017).

To build the food web and make it publicly available, we chose to create a WordPress site to host the information. This website can be found at ncreefs.web.unc.edu. The food web was generated using a plug-in called Prospect, which is a program developed by the Digital Innovation Lab at the University of North Carolina at Chapel Hill. Prospect is a free data curation and visualization tool that is used to create open-source digital collections, particularly for the humanities and social sciences. This is the first known adaptation of this program for use in a STEM field. Prospect uses qualified relationships to connect different nodes, each with their own spatial location. A Matlab script was written to convert the predator-prey matrix to a CSV file, which allowed us to import the data into Prospect.

In this particular application, each node was a species of fish, as well as four nodes for lower level prey categories, including algae, detritus, zooplankton, and zoobenthos. The spatial locations were designed to align the fish into the trophic web, so the vertical distribution was determined by the recalculated trophic levels. The locations were artificially imposed onto a map for simplicity. The lower trophic level organisms were at the bottom (towards the South), and the upper trophic level organisms were at the top (towards the North). The horizontal distribution was randomized in order to spread out the nodes and make the web clearer and more legible. Once the predator-prey relationships were imported into Prospect, we put additional parameters into the species data to allow users to filter the trophic web by species present on natural and
artificial reefs. We also generated a “commonality” metric to filter out rare species. To determine whether a species was rare or common, we used a threshold of 20 individuals total from all the videos in each particular category. For example, if more than 20 individuals of a single species were identified in the study, they were considered to be common. If less than 20 individuals of a single species were identified in the videos from artificial reefs, the species was considered rare on artificial reefs. In order to allow the user to view commercially-relevant species, we also generated a filter than can select members of the snapper-grouper complex. Other filters that can be applied to the map view include the fish family and the functional groups.

Results- Quantitative

To visualize the differences between natural and artificial reefs, a boxplot was generated to compare relative fish abundance per video between the two reef types (Figure 3). Artificial reefs had an average relative fish abundance more than four times higher than on natural reefs.

![Figure 3. Relative fish abundance per video by reef type. The average fish abundance for artificial reefs was 445 fish per video and the average for natural reefs was 98 fish. This is a statistically significant difference with a p-value of <0.0001.](image)
The relative fish abundance per video was further examined to analyze trends and differences between artificial and natural reefs by day category (Figure 4). In all day categories, except for night, artificial reefs had a significantly higher relative fish abundance per video. According to the Tukey test, the highest fish abundance was found on artificial reefs during dawn and dusk (Table 1). These two values are not significantly different from each other and are larger than the rest of the time of day categories for artificial and natural reefs. The relative fish abundance per video was lowest at night for both reef types. Note that the average fish abundance during the dawn and dusk on artificial reefs is almost an entire order of magnitude greater than that at night.

Figure 4. Relative fish abundance per video by reef type and day category. The interaction of these two factors resulted in a p-value of <0.0001.
Table 1. Tukey test results for the relative fish abundance per video by reef type and time of day. The values connected by the same group letter are not significantly different from each other.

<table>
<thead>
<tr>
<th>Reef Type</th>
<th>Time of Day</th>
<th>Average Fish Abundance (per video)</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artificial</td>
<td>Dawn</td>
<td>1080</td>
<td>a</td>
</tr>
<tr>
<td>Artificial</td>
<td>Dusk</td>
<td>910</td>
<td>a</td>
</tr>
<tr>
<td>Artificial</td>
<td>Day</td>
<td>600</td>
<td>b</td>
</tr>
<tr>
<td>Natural</td>
<td>Day</td>
<td>182</td>
<td>c</td>
</tr>
<tr>
<td>Natural</td>
<td>Dusk</td>
<td>166</td>
<td>cd</td>
</tr>
<tr>
<td>Natural</td>
<td>Dawn</td>
<td>156</td>
<td>cd</td>
</tr>
<tr>
<td>Artificial</td>
<td>Night</td>
<td>30</td>
<td>d</td>
</tr>
<tr>
<td>Natural</td>
<td>Night</td>
<td>14</td>
<td>d</td>
</tr>
</tbody>
</table>

Species richness was compared for the two reef types using a violin plot (Figure 5). The width of the plot corresponds to the relative frequency of each species richness occurrence. The species richness per video for artificial reefs is significantly higher than that for natural reefs with an average of 3.3 species per video compared to 2.8, with an ANOVA p-value of <0.0001.

Figure 5. Violin plot of species richness per video for the two reef types. The average species richness per video for the artificial reefs was 3.3, which is significantly higher than the average for the natural reefs, which was 2.8 fish species per video (p-value <0.0001).
Species richness per video was further analyzed for trends in time of day category and reef type (Figure 6). Species richness on artificial reefs ranked slightly above the species richness on natural reefs, but this difference is not significant according to the Tukey test (Table 2). Species richness seems to decrease at night for both reef types.

![Species richness per video for the two types of reefs and each time of day category.](image)

*Figure 6. Species richness per video for the two types of reefs and each time of day category.*

*Table 2. Tukey Test results for species richness per video and time of day.*

<table>
<thead>
<tr>
<th>Reef Type</th>
<th>Time of Day</th>
<th>Average Species Richness (per video)</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artificial</td>
<td>Dusk</td>
<td>3.03</td>
<td>a</td>
</tr>
<tr>
<td>Artificial</td>
<td>Day</td>
<td>2.98</td>
<td>a</td>
</tr>
<tr>
<td>Artificial</td>
<td>Dawn</td>
<td>2.97</td>
<td>ab</td>
</tr>
<tr>
<td>Natural</td>
<td>Day</td>
<td>2.90</td>
<td>ab</td>
</tr>
<tr>
<td>Natural</td>
<td>Dusk</td>
<td>2.44</td>
<td>abc</td>
</tr>
<tr>
<td>Natural</td>
<td>Dawn</td>
<td>2.35</td>
<td>bc</td>
</tr>
<tr>
<td>Artificial</td>
<td>Night</td>
<td>2.20</td>
<td>c</td>
</tr>
<tr>
<td>Natural</td>
<td>Night</td>
<td>1.77</td>
<td>d</td>
</tr>
</tbody>
</table>
The trophic levels on the artificial and natural reefs were visualized using a boxplot (Figure 7). Though visually there does not appear to be a significant trend, an ANOVA found a significant difference in the trophic levels of the two types of reefs ($p$-value <0.0001). The average trophic level of the artificial reefs was 4.31 and the average trophic level of the natural reefs was 4.26. However, the data was concentrated at a trophic level of 4.4, so the data were expressed by time of day category to further examine this trend.

![Boxplot of trophic structure for artificial and natural reefs.](image)

**Figure 7. Boxplot of trophic structure for artificial and natural reefs.**

When the trophic level for artificial and natural reefs is further divided into time of day categories, there is still a strong bias towards a trophic level of 4.4, though there are still significant differences in the data (Figure 8). The night category for both artificial and natural reefs does not seem to be as influenced by the 4.4 trophic level organisms present during the other day categories. The highest trophic level was seen on artificial reefs at dusk, and the lowest trophic levels were seen at night on both reef types (Table 3).
Upon further inspection, the source of the bias was an overwhelmingly high number of tomtates (*Haemulon aurolineatum*, trophic level of 4.4), a species of schooling fish that is found in high abundance in North Carolina. The presence of rare and cryptic species found in much lower abundances were overshadowed by the sheer number of tomtates as there were hundreds,
even thousands, in certain videos. This hid any underlying patterns in the data, and therefore, tomtates were excluded from the remainder of the analysis. Approximately 30% of fish included in the initial analysis were tomtates. Without the tomtates, the artificial reef has a noticeably higher trophic level than the natural reef (Figure 9). This is a significant difference, with a $p$-value of $<0.0001$.

Finally, the trophic levels, excluding tomtates, for each reef type and time of day category were analyzed (Figure 10). Dawn on the artificial reefs had the highest average trophic level, with an average of 4.21 (Table 4). The second highest average trophic level was dusk on artificial reefs (average of 4.15). The lowest trophic levels were seen on the natural reefs during day and dawn. An ANOVA resulted in a $p$-value of $<0.0001$ for the interaction of time of day category and reef type at predicting trophic levels. The artificial reefs had a higher trophic level than the natural reefs in all day categories except night, which were not significantly different from each other.

Figure 9. Trophic structure by reef type, excluding the tomtates. Artificial reef average trophic level was 4.0, and the natural reef average trophic level was 3.6. This is a significant difference ($p<0.0001$).
Figure 9. Trophic structure without tomatates for both reef types divided by time of day categories. The interaction between day category and reef type produced a p-value of <0.0001 (ANOVA).

Table 4. Tukey test results for the trophic level of each reef type and time of day category.

<table>
<thead>
<tr>
<th>Reef Type</th>
<th>Time of Day</th>
<th>Average Trophic Level</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artificial</td>
<td>Dawn</td>
<td>4.212</td>
<td>a</td>
</tr>
<tr>
<td>Artificial</td>
<td>Day</td>
<td>4.148</td>
<td>b</td>
</tr>
<tr>
<td>Artificial</td>
<td>Dusk</td>
<td>4.078</td>
<td>c</td>
</tr>
<tr>
<td>Natural</td>
<td>Night</td>
<td>3.909</td>
<td>d</td>
</tr>
<tr>
<td>Artificial</td>
<td>Night</td>
<td>3.885</td>
<td>d</td>
</tr>
<tr>
<td>Natural</td>
<td>Dusk</td>
<td>3.876</td>
<td>d</td>
</tr>
<tr>
<td>Natural</td>
<td>Day</td>
<td>3.701</td>
<td>e</td>
</tr>
<tr>
<td>Natural</td>
<td>Dawn</td>
<td>3.532</td>
<td>f</td>
</tr>
</tbody>
</table>
Results - Qualitative

Initially, a map was generated that contained the 61 species of fish that were positively identified in this study (Figure 11). Each node represents a species of fish, and the colors represent their quantitative trophic level. Warmer colors are upper trophic level organisms, and cooler colors are lower trophic level organisms, as shown in the legend. Note that the trophic levels used to generate these webs are the new trophic levels that were calculated from this study rather than the literature values of the trophic levels found on FishBase.

Once the relationships were added to the map, the trophic web became incredibly complex (Figure 12). There were over 400 predator-prey relationships found between the fish species present on these reefs. The many filters, including commonality, reef type, and snapper-grouper complex, were added to simplify the trophic web and allow users to distinguish changes in the trophic structure under the different conditions.
Figure 12. Trophic web including all 61 species of fish found on the four study sites. Note that the species names cannot be displayed on the trophic web due to constraints from using Prospect. The species are in the same positions as in Figure 11.

After applying the commonality filter, 38 species of fish that were considered common remained in the food web (Figure 13). Using this simplification, predator-prey relationships can be observed in more detail.

Figure 13. Trophic web showing only the common species on the four study sites.
Of the 38 species of fish that were common in this study, 33 of them were commonly found on natural reefs (Figure 14).

![Figure 14. The trophic web for the species commonly found on natural reefs.](image)

24 of the 38 common fish species in this study were considered common on artificial reefs (Figure 15).

![Figure 15. Trophic web for the 24 common species on artificial reefs.](image)
Another capability of the food web filter is to examine where the fish in the snapper-grouper complex are found in the trophic web. This can be applied in tandem with the previous map filters and is shown below for the fish species commonly found in natural reefs (Figure 16).

*Figure 16. Trophic web including fish commonly found on natural reefs showing the members of the snapper-grouper complex.*

The green circles are for snapper-grouper complex fish, and the blue are for other fish not in the snapper-grouper complex.

Discussion

The ability of temperate reefs to support high abundances of fish is incredibly important for the fishing industry which depends on the production of commercially- and recreationally-relevant fish species. Understanding the ability of artificial reefs to provide habitat for large numbers of fish allows managers to make informed decisions regarding the protection of artificial reefs as essential fish habitat. The data presented above suggest that artificial reefs are able to support significantly higher fish abundance than natural reefs, as the average number of fish per video on artificial reefs was nearly 450% higher than on natural reefs. This pattern was also observed in the temperate reefs of Scotland, where complex artificial reefs were found to
host fish communities that were equal, if not greater, in fish abundance than natural reefs (Hunter, 2009). In southeast Florida, artificial reefs in the form of sunken vessels had a significantly higher mean fish abundance per count than natural coral reefs (Arena, 2007).

On the temperate reefs of North Carolina included in this study, fish abundance increased significantly on artificial reefs during dawn and dusk. Fish abundance was not significantly different on natural reefs during dawn, day, and dusk. At night, fish abundance seemed to decrease on both reef types, but not significantly less than during the dawn and dusk on natural reefs. The nighttime values for fish abundance are likely artificially low due to hindered visibility at night, which would have restricted the depth of the video footage. With that taken into consideration, it is still likely that fish abundance is lower at night than during the other times of day. This follows a similar pattern observed on the temperate reefs of Western Australia, where fish abundance was found to be higher during the day than at night using similar unattended underwater videos (Myers, 2016).

In order to evaluate the ability of artificial reefs to support diverse fish communities that are comparable to those on natural reefs, we compared the species richness per video between the two reef types. This comparison shows a higher species richness on artificial reefs than on natural reefs, which suggests that artificial reefs are able to support more biodiverse communities than natural reefs. The species richness is concentrated between three and five species per video, which makes differences more difficult to perceive between the two reef types. Of the 80 fish species identified in this study, 75 were present in the 1396 natural reef videos (0.054 unique species per video) and 57 species were present in the 775 artificial reef videos (0.074 unique species per video). This statistic is slightly deceiving, because there were more videos processed from the natural reefs than the artificial reefs, but on average, the artificial reefs had slightly
higher numbers of unique species per video when standardized by number of videos. It is difficult to make conclusions regarding the variances in species richness over the different time of day categories, as they are only marginally different from each other. In a similar study, ten artificial reefs and sixteen natural reefs were surveyed to compare the species richness of the two reef types. The data from that study showed significantly higher species richness on artificial reefs, with an average of 18.7 compared to 14.2 on natural reefs (Ambrose, 1999). In contrast, another study comparing natural and artificial reefs along the French-Catalan coast found higher fish density on artificial reefs, as well as nearly twice as many species encountered on artificial reefs than natural reefs (Koeck, 2014).

Visualizing patterns in trophic structure between the fish communities on natural and artificial reefs proved to be more difficult than previously thought due to certain hyper-abundant species, but a univariate ANOVA found a significant difference between the two reef types. This suggests that artificial reef characteristics are preferred by higher trophic level organisms. The higher fish abundance found on artificial reefs may attract larger predators to these habitats and subsequently increase the average trophic level. For example, sand tiger sharks (Carcharias taurus) were over 100 times more abundant on artificial reefs (1,974 sharks in 775 videos) than natural reefs (18 sharks in 1396 videos). This difference may be attributed to larger schools of baitfish present on artificial reefs or the higher vertical relief that may be preferable to sand tiger sharks. Fish density and size have been correlated to the quantity and size of recesses in the structure of reefs (Hixon, 1989). There is some evidence that piscivores prefer artificial reefs, specifically sunken ships, due to the associated larger recesses and crevices that can be used as refuge space (Simon, 2013). It is also possible that fish may be moving to artificial reefs from natural reefs, causing a decrease in abundance and trophic level on natural reefs. Understanding
whether production or attraction is the dominant force affecting the fish communities on artificial reefs is essential for making informed management decisions. This knowledge gap demonstrates that it is imperative to study this area more robustly.

The increase in fish abundance, species richness, and trophic level during dawn and dusk time periods on artificial reefs suggests that crepuscular activity is more pronounced on artificial reefs than natural reefs. This period is known for being the “crossover” between day and night and is characterized by the presence of both nocturnal and diurnal fish species. Predatory fish are likely active during crepuscular periods because there is enough light to see their prey, and the prey fish will be emerging from the crevices where they seek refuge during their inactive time periods, such as during the day for nocturnal species. Studies have suggested that fish activity increases during crepuscular time periods, as fish have been shown to swim longer and faster at twilight than during the day or night (Lokkeborg, 2000).

These data suggest that upper-trophic level organisms (i.e. predatory fish) are more active during crepuscular periods on artificial reefs than on natural reefs. Though there seems to be a higher abundance of upper-trophic level organisms on artificial reefs, the trophic level was still the highest during dawn on artificial reefs when compared to other times of day. On natural reefs, the increased pattern of crepuscular activity was not observed. There is likely a combination of abiotic and biotic factors that are causing this key difference in crepuscular activity between reef types, such as the higher structural complexity or differences in the benthic community found on artificial reefs. Koeck et al (2014) suggest that higher habitat complexity and lower fishing pressure on artificial reefs may be affiliated with functionally different fish communities than natural reefs. More research is needed to hone in on the factors influencing crepuscular behavior on artificial reefs that may not be present on natural reefs.
The qualitative food web also suggests that artificial and natural reefs support different fish assemblages and that management approaches should address these differences. By comparing the trophic webs for the artificial and natural reefs (shown in Figures 14 and 15), managers can tailor their strategies to the species found on these sites. These figures suggest that artificial reefs have more upper level predator species, whereas natural reefs have more mid-level mesopredator species present on the reefs. More research is needed to understand the characteristics of natural and artificial reefs that may cause these differences. The visualization of the trophic web under different filters can be applied to fisheries management to help promote the understanding of the interconnectedness of the fish populations at each of these sites, particularly with commercially relevant fish species such as the snapper-grouper complex.

Conclusions

The data presented in this study suggest that artificial and natural reefs in Onslow Bay, NC support different fish communities. Managers must take this into account when attempting to conserve these vital ecosystems, as different management regimes are likely warranted for the two reef types. Additionally, when deploying new artificial structures to enhance EFH, the preference of certain fish species for reefs with different characteristics may affect reef effectiveness for the target fish species. More research is needed to explain the mechanisms responsible for differences in the fish community between artificial and natural reefs. The novel trophic web presented in this study may assist managers in making decisions to sustain temperate reefs of NC and their associated fish populations.
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